CENTRO AGRONOMICO TROPICAL DE INVESTIGACION Y ENSEÑANZA

CATIE

PROYECTO MEJORAMIENTO GENETICO FORESTAL

COMPENDIO DE PUBLICACIONES 1984-1996

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PRESENTACION

En este documento, se pretende reunir, de manera accesible y conveniente, los artículos científicos y técnicos producidos por el Proyecto Mejoramiento Genético Forestal del CATIE en las últimas dos décadas. Se incluyen artículos clasificados en cinco categorías. Los artículos en la sección 1 constituyen uno de los principales productos del Proyecto: información genética sobre especies maderables plantadas en América Central. La sección 2 contiene artículos sobre la propagación vegetativa, herramienta básica del mejoramiento genético forestal, y una área en la cual el CATIE, mediante el Proyecto, ha asumido un papel pionero en América Central. Los artículos en la sección 3 se dirigen a aspectos más generales del mejoramiento y cubren una gama de temas de interés regional y general. En la sección 4, se presentan una serie de resúmenes de las características de algunas de las especies trabajadas por el Proyecto, elaboradas durante 1992 como respuesta a múltiples peticiones por parte de los usuarios del Proyecto, pero no diseminados o dados a conocer hasta ahora. Finalmente, en la sección 5 se presentan artículos misceláneos.

El trabajo del Proyecto Mejoramiento Genético Forestal del CATIE durante el período señalado y cubierto por los artículos fue posibilitado por el apoyo financiero de los gobiernos británico, estadounidense, noruego y suizo, así como la dedicación de todo el personal actual y pasado del mismo.

The objective of this volume is to bring together, in a convenient and accessible format, the scientific and technical articles produced by the personnel of CATIE's Tree Improvement Project in the last two decades. Five categories of article are included. Those in section 1 constitute one of the main products of the Project: genetic information on timber species planted in Central America. Section 2 is made up of articles on vegetative propagation, a basic tool of tree improvement, and one in which CATIE, through the Project, has assumed a pioneering role in Central America. The articles in section 3 cover more general aspects of tree improvement, including subjects of both regional and wider interest. Section 4 is comprised of a series of short monographs on characteristics of some of the species with which the project has worked. Prepared during 1992 in response to demands from the Project's users, these short articles are being distributed generally here for the first time. Finally, in section 5, a number of articles on miscellaneous forestry themes are included.

The Tree Improvement Project's work during the period covered by these articles was made possible by the financial support of the governments of Norway, Switzerland, the United Kingdom, and the United States of America, as well as by the dedication of all the personnel, past and present, of the Project.

Jonathan Cornelius
Líder del Proyecto 1993-96
Project Leader 1993-1996

Cómo citar los artículos

Los documentos deben citarse según como aparecen en tabla de contenido. Para citar el compendio en si, la forma correcta es: Proyecto Mejoramiento Genético Forestal (CATIE). 1996. Compendio de publicaciones, 1984-1996. CATIE; Turrialba, Costa Rica.

How to cite the articles

The correct citation form for each article included is as given in the detailed contents pages. To cite the compendium as a whole, the correct form is: Proyecto Mejoramiento Genético Forestal (CATIE). 1996. Compendio de publicaciones, 1984-1996. CATIE; Turrialba, Costa Rica.

1. VARIACION GENETICA DE ESPECIES FORESTALES MADERABLES PLANTADAS EN AMERICA CENTRAL

ANALISIS DE PROCEDENCIAS DE *ACACIA MANGIUM* EN COSTA RICA

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RESUMEN

Se estudia la altura total, Dap, supervivencia y porcentaje de árboles bifurcados en fase juvenil de diversas procedencias de *Acacia mangium* en dos sitios de ensayo de Costa Rica: Santa Clara (14 procedencias a los 4 años de edad) y Puriscal (6 procedencias a los 3 años de edad).

Se observaron diferencias significativas (test de Duncan) entre las procedencias ensayadas para los caracteres analizados. El crecimiento medio en altura y diámetro es muy similar en los dos sitios de ensayo, y las procedencias que muestran un mejor comportamiento en ambas parcelas son prácticamente las mismas.

PALABRAS CLAVE: Análisis de procedencias
Acacia mangium
Costa Rica

INTRODUCCION

Acacia mangium es una especie de uso múltiple de la familia Leguminosae, sub-familia Mimosoideae, originaria del noroeste de Australia, Papúa, Nueva Guinea y del este de Indonesia. El árbol puede alcanzar de 25 a 30 m de altura y el dap puede ser superior a los 25 cm; el fuste usualmente es recto con tendencia a bifurcarse a distintas alturas. La especie es cultivada tanto en plantaciones como en sistemas agroforestales y puede ser utilizada para madera y leña. La madera tiene un peso específico de 0,40 a 0,60 g/cm^3 y un poder calórico de 4.800-4.900 kcal/kg. Es una especie apta para las zonas húmedas con una estación seca definida y crece bien en suelos ácidos o ligeramente ácidos y pobres (2,5).

En América Central y el Caribe, la especie ha sido introducida recientemente y en la mayoria de los casos se cultiva a nivel experimental, con excepción de algunas plantaciones piloto establecidas en Panamá.

En Costa Rica se ha observado un incremento medio anual de 3,0 cm en dap y 3,3 m en altura total en parcelas de tres años. En República Dominicana el incremento medio anual observado a 3,6 años de edad es de 4,1 cm en dap y 3,5 m en altura total.

El buen comportamiento de la especie en la región ha despertado interés, pero todavía no han sido definidas las fuentes de semilla apropiadas. Para darle solución a este problema, en los últimos años se ha establecido una serie de pruebas de procedencias en América Central, las cuales apenas están en sus primeras etapas de análisis. Salazar, en un estudio con 16 procedencias a nivel de vivero en Turrialba, Costa Rica, encontró que existen diferencias considerables en el tamaño de las semillas y el crecimiento de las plántulas entre las fuentes de semillas estudiadas.

El presente estudio tiene como objetivo resumir los resultados de una prueba de procedencias de *A. mangium* establecida en 1984 en dos sitios en Costa Rica. La Tabla 1 muestra el origen de las fuentes de semillas estudiadas.

TABLA 1

IDENTIFICACION, UBICACION Y ALTITUD DE LAS PROCEDENCIAS DE *ACACIA MANGIUM* ESTUDIADAS EN COSTA RICA

Identification, situation and altitude of te Acacia mangium *provenances established in Costa Rica*

Procedencia	Código CSIRO *	Latitud (°S)	Longitud (°E)	Altitud (msnm)
Rex Range NR Nossman, Queensland (Old)	CSR12992	16°30	145°32	30
Cowley Beach Road, Old	CSR13232	17°41	146°05	5
Walsh's Pyramid, Old	CSR13233	17°06	145°48	20
Trinity Inlet, Old	CSR13234	17°02	145°48	20
Mourilyand Bay, Old	CSR13235	17°35	146°05	20
Tully Mission Beach Rd, Old	CSR13238	17°56	146°302	70
Syndicate Rd. Tully, Old	CSR13239	17°55	145°52	50
Ellerebeck Rd. Cardwell, Old	CSR13240	18°14	145°58	60
Broken Pole Creek, Old	CSR13241	18°21	146°03	50
Abergowrie, SF, Old	CSR13242	18°26	146°01	60
Claudie River, Old	CSR13229	12°44	143°13	60
W. of Morehead, Papúa Nueva Guinea	CSR13459	08°45	141°18	30
Oriomo River, Papúa Nueva Guinea	CSR13460	08°40	143°08	10
Piru Ceram, Indonesia	CSR13621	03°04	128°12	150
SE Mossman, N. Old	CSR13846	16°31	145°24	60

* Organizaciones de Investigación Científica e Industrial de la Mancomunidad

En los dos sitios donde se estableció la prueba se utilizó un diseño de bloques completos al azar con cinco repeticiones y parcelas de 36 árboles, a un distanciamiento de 3 × 2 m. En Santa Clara se plantaron 14 procedencias y 6 en Puriscal.

Sitio	Latitud	Longitud	Elevacion	Precipitacion	Temp.
Santa Clara	10° 21'	84° 32'	170	3400	25.7
Puriscal	9° 51'	84° 22'	960	2470	22.3

RESULTADOS

La Tabla 2 muestra los promedios de las variables analizadas a los cuatro anos en Santa Clara, donde el dap promedio alcanzó 11.4 cm y la altura 10.4 m. En dap se observó una diferencia de 30 p. 100 entre las procedencias extremas de Morehead de Papúa de Nueva Guinea como la mejor y Pyramid de Queensland como la de menor crecimiento. En altura total la diferencia fue de 41 p. 100 entre la mejor de Abergowrie de Queensland y nuevamente Pyramid como la de menor crecimiento. La incidencia de bifurcación varió en 38 p. 100, siendo Piru Ceram de Indonesia la que presentó el menor porcentaje de árboles bifurcados. El análisis de varianza encontró diferencias estadísticas significativas sólo para dap, y sobrevivencia; la prueba de Duncan sí encontró diferencias estadísticamente significativas para las cuatro variables.

TABLA 2

PROMEDIOS DE ALTURA TOTAL (M) Y DAP (M), Y PORCENTAJES DE SOBREVIVENCIA Y DE ARBOLES BIFURCADOS PARA 14 PROCEDENCIAS DE *ACACIA MANGIUM* A LOS 4 AÑOS DE EDAD EN SANTA CLARA, COSTA RICA

Average of Height (m), Dbh (cm) Survival (%) and Forked trees (%) of 14 provenances of Acacia mangium, *4 years old, at Santa Clara, Costa Rica*

Proced.	Altura total* (m)	Proced.	Dap* (cm)	Proced.	Sobrev.* (%)	Proced.	Incidencia de bifurcación* (%)
CSR13242	13,3	CSR13459	13,7	CSR13242	95	CSR13621	8
CSR13459	11,8	CSR13229	13,6	CSR13241	94	CSR13235	11
CSR13229	11,2	CSR13460	12,5	CSR12992	94	CSR13229	15
CSR13460	11,0	CSR13242	12,2	CSR13233	92	CSR13238	15
CSR13241	10,4	CSR13240	11,7	CSR13234	91	CSR13234	19
CSR13232	10,1	CSR13621	11,6	CSR13240	87	CSR13459	20
CSR13239	9,9	CSR13241	11,2	CSR13232	84	CSR13239	21
CSR13240	9,6	CSR13232	11,0	CSR13229	68	CSR13233	21
CSR13621	9,3	CSR13235	10,9	CSR13460	67	CSR13460	24
CSR12992	9,2	CSR13238	10,8	CSR13239	67	CSR13240	25
CSR13238	9,1	CSR13234	10,5	CSR13459	58	CSR12992	26
CSR13235	9,0	CSR13239	10,3	CSR13238	55	CSR13232	29
CSR13234	9,0	CSR12992	10,3	CSR13621	48	CSR13242	30
CSR13233	7,8	CSR13233	9,6	CSR13235	40	CSR13241	42

* Prueba de Duncan

La Tabla 3, resume los promedios de las variables analizadas a los tres anos en Puriscal Como se puede observar en las Tablas 2 y 3, son practicamente las mismas procedencias las que muestran mejor comportamiento en ambos sitios, aunque el numero de procedencias probadas en Puriscal fue menor.

Los resultados también muestran un crecimiento de la especie muy similar en ambos sitios, ya que se obtuvo un IMA en dap de 2,4 a 2,8 cm y un IMA en altura de 2,3 y 2,6 cm para Santa Clara y Puriscal respectivamente. Mesen menciona que uno de los factores limitantes para hacer uso de las mejores procedencias es la disponibilidad de semillas; además, indica que es importante identificar la causa de la muerte de los arboles en una repeticion de ensayo en Buenos Aires, C. R., antes de iniciar plantaciones a escala comercial.

TABLA 3

PROMEDIOS DE ALTURA TOTAL (M) Y DAP (CM), Y PORCENTAJE DE SOBREVIVENCIA Y DE ARBOLES BIFURCADOS PARA 6 PROCEDENCIAS DE *ACACIA MANGIUM* A LOS 3 AÑOS DE EDAD EN PURISCAL, COSTA RICA

Average of Height (m), Dbh (cm) Survival (%) and Forked trees (%) of 6 provenances of Acacia mangium, *3 years old, at Puriscal, Costa Rica*

Proced.	Altura total* (m)	Proced	Dap* (cm)	Proced.	Sobrev.* (%)	Proced.	Incidencia de bifurcación* (%)
CSR13229	6,1	CSR13229	8,2	CSR13242	95	CSR13846	14
CSR13242	6,1	CSR13459	7,7	CSR13459	85	CSR13621	38
CSR13459	6,0	CSR13242	7,5	CSR13229	84	CSR13233	39
CSR13233	5,8	CSR13233	7,5	CSR13621	73	CSR13459	45
CSR13846	5,5	CSR13621	5,4	CSR13846	50	CSR13229	63

* Prueba de Duncan

A nivel de esta etapa juvenil fue posible observar diferencias bastante claras entre las distintas fuentes de germoplasma.

Los estudios de rendimiento que se realizarán próximamente tanto en estas pruebas como en las establecidas en el resto de los paises de la región, serán básicos para identificar las fuentes de semillas más apropiadas para los distintos paises.

SUMMARY

Provenance tests of *Acacia mangium* in Costa Rica

Height, Dbh, survival, and percent of forked trees of several provenances of *Acacia mangium* were studied at two sites in Costa Rica: Santa Clara (14 provenances, 4 years old) and Puriscal (6 provenances, 3 years old).

Significant differences (Duncan's test) were detected between provenances. The average growth (in height and Dbh) were similar at the two sites, and the best provenances at the two provenance tests were at a guess rough the same.

KEY WORDS: Provenance test
Acacia mangium
Costa Rica

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Comportamiento en Costa Rica de procedencias de *Albizzia guachapele y Bombacopsis quinata*

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Puntos claves y recomendaciones prácticas

- Se presentan resultados de dos ensayos de procedencias/progenies de *Albizzia guachapele y Bombacopsis quinata*, ubicados en la parte baja de Guanacaste, Costa Rica.
- Hubo diferencias significativas en crecimiento entre las procedencias. Las procedencias de la Península de Nicoya (*Bombacopsis*: Hojancha y Nicoya hasta los 600m s.n.m.; *Albizzia*: Nandayure y Nicoya hasta los 200 m s.n.m.) fueron los de más rápido crecimiento.
- Las procedencias de Choluteca, Honduras (de ambas especies) crecieron más lentamente que las procedencias locales, resultado que constituye un ejemplo más de los peligros de utilizar semilla de zonas muy lejanas o distintas a la zona de plantación.
- La procedencia de *B. quinata* de Choluteca presentaba significativamente menos aguijones que las procedencias de Costa Rica.

INTRODUCCION

Es normal encontrar diferencias genéticas entre las poblaciones naturales de las especies forestales. En general, se supone que, por ser mejor adaptadas, las poblaciones locales son también más adecuadas del punto de vista comercial,. por lo cual normalmente se recomienda su uso a menos que se haya comprobado, a través de ensayos de campo, que otra procedencia sea mejor en la zona en cuestión.

En ediciones anteriores del boletín se han presentado resultados que demuestran las consecuencias adversas de usar procedencias inapropiadas. Sin embargo, en estos casos, se trata de movimientos de semilla sobre distancias grandes (Cornelius y Masís 1994, 1995) y/o entre zonas ambientales muy distintas. En el presente artículo se describe el comportamiento en el norte de Costa Rica de *Albizzia guachapele* (A. guachapele, guayaquil) y *Bombacopsis quinata* (cedro espino, B. quinata) de dos zonas climáticamente parecidas: las procedencias locales y de Choluteca (sur de Honduras), aproximadamente 300km al noroeste.

MATERIALES Y METODOS

Los sitios y tratamientos

Albizzia guachapele: el sitio se encuentra en Las Juntas de Abangares, Guanacaste, Costa Rican (60 m s.n.m., precipitación media anual (PMA) 2273±511mm con 5.0±1.0 meses secos (<80 mm), suelo franco-arcilloso de pH 5,7 (horizonte A). Los tratamientos son las descendencias (polinización abierta) de 41 familias de tres procedencias; Abangares, Nicoya (Guanacaste, Costa Rica) y Las Delicias, (Choluteca, Honduras). Se incluyeron dos lotes testigos comerciales de Abangares (de 20 árboles madres).

Bombacopsis quinata: El ensayo de B. quinata se encuentra en Pavones, Nandayure, Costa Rica (50m s.n.m, PMA 1780±523 mm con 5,2±1,0 meses secos. Los tratamientos son las descendencias (polinización abierta) de 66 familias de 4 procedencias: Cañas, Nicoya, Taboga (huerto semillero clonal) (Guanacaste, Costa Rica), Cedeño-Punta Ratón (Honduras). Además, se incluyó un lote comercial de Jicaral de Puntarenas, Costa Rica.

Tanto en el caso del *B. quinata* como *A. guachapele*, la semilla de las procedencias costarricenses proviene de árboles plus, seleccionados con base principalmente en su rectitud y proporción de fuste limpio de ramas. En las zonas de Las Delicias y Cedeño-Punta Ratón (Honduras), es muy difícil de ubicar verdaderos árboles plus, debido a la pobre calidad de los pocos árboles que quedan. Sin embargo, se seleccionaron los mejores árboles presentes.

Diseño experimental

En ambos ensayos se utilizó el diseño estándar de CAMCORE standard (Dvorak and Donahue, 1992): parcelas de familias de seis árboles en línea, con 9 bloques completos al azar, con la restricción que todas las familias de cada procedencia se plantan contiguamente en "parcelas grandes de procedencia".

Mediciones y análises

Se realizaron análisis de varianza de las diferencias entre procedencias para las siguientes variables:

Albizzia guachapele: altura total y hasta la primera bifurcación (40 meses); diametro a la altura del pecho (dap) (52 meses); presencia o ausencia de bifurcación (27 meses); rectitud del fuste (escala de 1 (peor) a 4 (mejor)).

Bombacopsis quinata: altura a los 29 meses; dap (antes y después de quitar los aguijones) a los 40 meses; cantidad de aguijones (escala de 1 (muchos) a 4 (casi sin aguijones) (53 meses); rectitud del fuste a los 53 meses (1-4, igual que *Albizzia*). Además, se derivó una medida cuantitativa de la cantidad de aguijones, con base en la diferencia entre dap sin y con aguijones.

Para ambas especies, se realizaron contrastes planificados entre las procedencias locales (combinadas) y exóticas utilizando el procedimiento GLM (CONTRAST) de SAS (SAS Institute, 1988; Stonecypher, 1994).

RESULTADOS

Albizzia guachapele

Las procedencias costarricenses crecieron significativamente más rápidamente que la procedencia hondureña. Además, fueron superior en cuanto a la altura de la primera bifurcación (cuadro 1). No hubo diferencias estádisticamente significativas en rectitud o la incidencia de bifurcación.

Entre las procedencias costarricenses (incluyendo el testigo) no se presentaban diferencias significativas.

Bombacopsis quinata

Las procedencias costarricenses fueron significativamente superiores a la de Choluteca en dap y altura. La procedencia hondureña presentaba significativamente menos aguijones que las costarricenses, tanto con la medida "sujetiva" como la "objetiva" (cuadro 2). No hubo diferencias significativas en rectitud.

La procedencia de Nicoya presentaba los promedios más altos para los rasgos de crecimiento, mientras el progenie del huerto semillero de Taboga fue el más lento en crecimiento de las procedencias costarricenses.

DISCUSION

Con base en estos ensayos, no es posible elucidar las razones por la inferioridad de la procedencias hondureñas. Podría ser que, en ambos casos, la procedencia incluida es una de las peores y que otras procedencias hondureñas hubieran comportado mejor. Sin embargo, los resultados sugieren que las consecuencias adversas de utilizar semilla de zonas muy lejos o diferentes de la zona de plantación no se limitan a los casos más extremos mencionados en la introducción. Aun cuando los zonas de origen son climáticamente parecidas, pueden existir diferencias genéticas de importancia en las poblaciones forestales. La procedencia hondureña de *B. quinata* exhibió dap sin aguijones 7,0% menor que el promedio de las fuentes locales, mientras que en *A. guachapele* la inferioridad de la procedencia hondureña es de un 9,0%. Estas diferencias relativamente pequeñas en dap pueden tener un impacto más apreciable sobre la productividad, debido a que volumen es función del dap cuadrado. Evidentemente, cuando sea posible, y a menos que se haya probado la superioridad de otra fuente, se debería preferir semilla local de estas especies. Para la bajura de Guanacaste, Costa Rica, tanto en el caso de *A. guachepele* como *B. quinata*, las procedenciaa de la Península de Nicoya (cantones de Nicoya y Nandayure, hasta los 200 m s.n.m., para Albizzia; cantones de

Nicoya a Hojancha, hasta los 600 m s.n.m., caso de B. quinata) parecieran ser las más prometedoras en cuanto a crecimiento y forma. Para Honduras y otros países y zonas, se deberían buscar fuentes locales; es probable que en Honduras la procedencias de Choluteca probadas aquí sean mejor que las de Costa Rica.

Los datos presentados aquí confirman que la cantidad de aguijones en *B. quinata* es una característica influida por factores genéticos. No se ha definido la importancia económica de esta característica, aunque se supone que los árboles y tocones con menos aguijones, o aguijones más pequeños, sean más baratos de procesar.

El comportamiento del progenie del huerto semillero de B. quinata es desalentador. Sin embargo, es importante destacar que los árboles plus no fueron seleccionados con base en crecimiento, mientras todavía a los 53 meses los árboles del ensayo estaban todavía relativamente pequeños como para permitir una evaluación completamente satisfactoria de forma. Es importante destacar también que, en el caso del progenie del huerto (no así el otro material), las plantas fueron producidos en un vivero local en condiciones no muy adecuados; es muy posible que su pobre crecimiento inicial está relacionado con este factor.

AGRADACIMIENTOS

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Cuadro 1 : Promedios y significancias de diferencias para 3 características de cuatro procedencias de *Albizzia guachapele* en un ensayo de procedencias/progenies ubicado en Las Juntas de Abangares, Guanacaste, Costa Rica.

PROCEDENCIA	CARACTERISTICA		
	altura promedio de la 1° bifurcación (m)	altura (m)	diametro a la altura de pecho (cm)
mes de medición	40	40	52
promedio general	1,30	3,53	6,0
significancia (global)	no significativa	≤0,001	≤0,001
significancia (CR v Honduras)	≤0,05	≤0,001	≤0,001
Testigo	1,55±0,13	3,73±0,16	6,6±0,3
Abangares	1,29±0,04	3,71±0,05	6,2±0,1
Nicoya	1,47±0,11	3,59±0,13	5,9±0,3
Las Delicias, Honduras	1,24±0,05	3,15±0,06	5,5±0,1

Cuadro 2 : Promedios y significancias de diferencias para 6 caracteristicas de cuatro procedencias de *Bombacopsis quinata*, en un ensayo de procedencias / progenies ubicado en Pavones, Nandayure, Costa Rica,

PROCEDENCIA	CARACTERISTICA				
	altura (m)	dap con aguijones (cm)	dap sin aguijones (cm)	cantidad de aguijones (cuantitativa)	cantidad de aguijones (cualitativa)
mes de medicion	29	40	40	40	53
Promedio de todos	2,45	6,1	5,6	0,08	1,9
signif (global)	≤0,001	≤0,001	≤0,001	≤0,001	≤0,001
Significancia (CR v for)	≤0,01	≤0,01	no sig.	≤0,001	≤0,001
Significancia (Nicoya v otros)	≤0,001	≤0,001	≤0,001		
Canas	2,50±0,07	5,8±0,3	5,3±0,2	0,07±0,02	2,0±0,06
Nicoya	2,73±0,07	7,1±0,3	6,5±0,3	0,08±0,02	1,8±0,06
Toboga	2,26±0,06	6,0±0,3	5,2±0,3	0,13±0,02	1,5±0,06
Cedeno Puerto Ralon, Honduras	2,37±0,06	5,6±0,2	5,3±0,2	0,05±0,01	2,3±0,05

LOS RIESGOS DE TRASLADO DE SEMILLA FORESTAL: EL CASO DE *Alnus acuminata*

Jonathan Cornelius[1,2] *y José Masis*[1]

PUNTOS CLAVES Y RECOMENDACIONES PRÁCTICAS

- En un ensayo de procedencias / progenies de *Alnus acuminata* en Costa Rica, la procedencia Palestina de los Altos, Guatemala, mostró crecimiento y forma muy inferior a las procedencias locales incluidas. Además fue fuertemente afectada por un ataque de *Scolytodes alni*. Las procedencias locales no fueron atacadas.
- Este caso representa un buen ejemplo del riesgo de no velar adecuadamente por el traslado seguro de semilla de especies nativas. El utilizar semilla proveniente de zonas distintas a la de plantación puede conducir incluso a la pérdida total de plantaciones costosas.
- Semilla mejorada de esta especie, proveniente de árboles élites (genéticamente comprobados), ya está disponible en Costa Rica

INTRODUCCIÓN

Como consecuencia de la selección natural, es de esperar que las poblaciones de árboles muestren adaptación a las zonas donde crecen naturalmente. Por este fenómeno, en muchos de los países donde se plantan especies nativas, particularmente en América del Norte y Europa, existen reglamentos o recomendaciones sobre "zonas semilleras", áreas geográficas o incluso bandas de altitud entre las cuales no se debe transportar semilla, con el fin de evitar el uso de semilla mal adaptada. En América Central, a pesar que se plantan cada vez más especies nativas, en general no existe conciencia sobre la importancia de ejercer prudencia en la distribución de semilla de estas especies. En el número anterior del Boletín, se presentó evidencia sobre como *Vochysia guatemalensis* de Izabal (Guatemala) y Atlántida (Honduras) crecen más lentamente que procedencias locales en sitios ácidos en la zona norte de Costa Rica. En el presente artículo, se presenta un ejemplo aún más llamativo de los riesgos de no velar adecuadamente por el traslado seguro de semilla de especies nativas. El artículo se basa en los resultados de un ensayo de procedencias / progenie de *Alnus acuminata*, los cuales se describen más detalladamente en Cornelius *et al.* (1995).

DESCRIPCIÓN DEL EXPERIMENTO

El experimento está ubicado a 2200 msnm en las faldas del Volcán Turrialba, Cordillera Central de Costa Rica. El diseño es de bloques completos aleatorios, con ocho bloques. Cada bloque contiene 6 árboles de cada uno de los 47 tratamientos (45 familias de polinización abierta y dos testigos). Las familias son derivadas de árboles plus seleccionados con base en la rectitud del fuste y corresponden a cuatro procedencias costarricenses (División, 1560-2700 msnm; Los Santos, 1850-2450 msnm; Pacayas 1680-2220 msnm y Prusia 2560-2840 msnm) y una procedencia de Guatemala (Palestina de los Altos, 2730-2840 msnm). Las selecciones costarricenses también tuvieron altura y diámetro superior al promedio del rodal. Todas las selecciones se realizaron en rodales naturales, excepto las de Prusia y dos familias de Los Santos. También se incluyeron dos testigos: División (2340-2610 msnm) y Prusia (2500 msnm, plantación). A los 34 meses, se midieron las siguientes características de cada árbol: altura (34 meses), rectitud del fuste (escala jerárquica de 1 a 4, 1 siendo mejor), presencia de torcedura basal, presencia de bifurcaciones basales y no basales, inclinación del fuste, ángulo de las ramas

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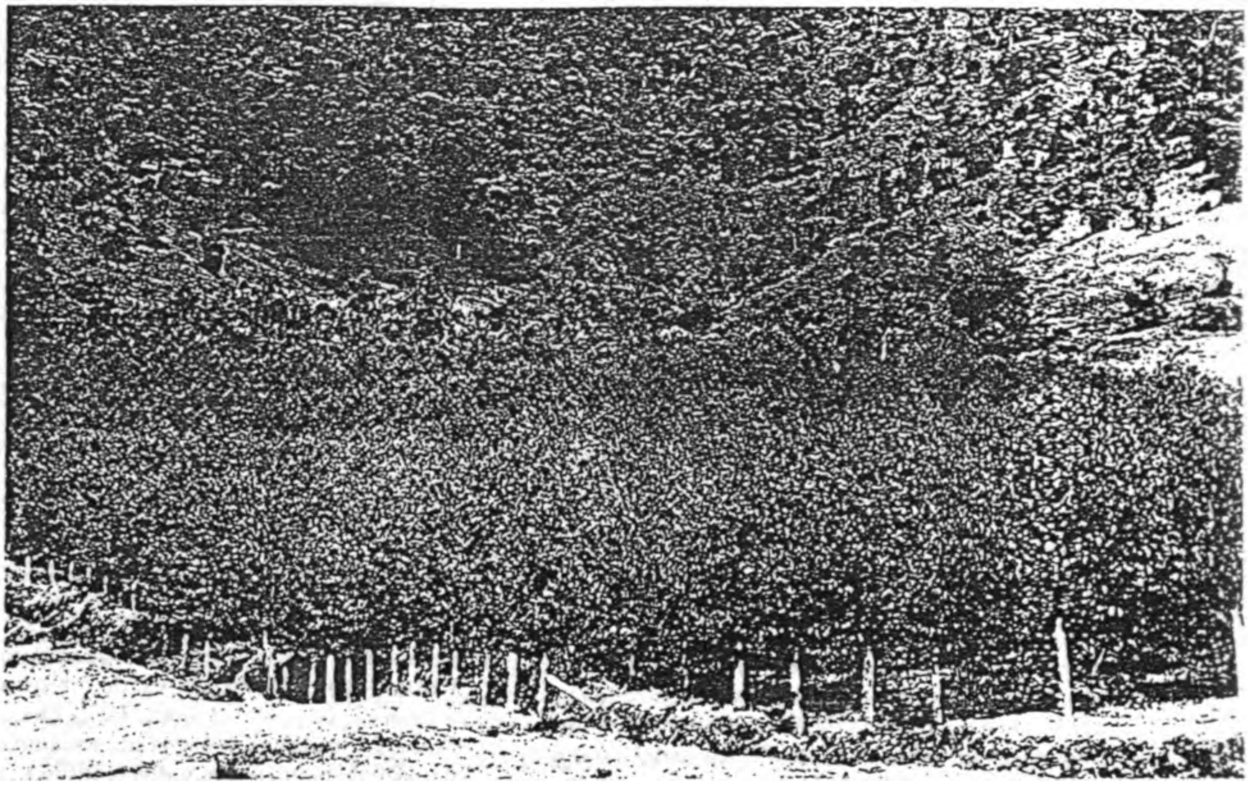
[1] Proyecto Mejoramiento Genético Forestal, CATIE

[2] Administración Británica para el Desarrollo en Ultramar



Ensayo de *Alnus acuminata* en Santa Cruz de Turrialba, Costa Rica, a los 21 meses de edad (Foto: Jonathan Cornelius)

(1 = horizontal, 2 = intermedio; 3 = 45° o mayor); grosor de las ramas (escala jerárquica de 1 (más delgado) a 3 (más grueso). También se evaluaron diámetro a 1,3 m (dap) a los 31 meses, altura (34 meses) e incrementos en altura (22 a 34 meses) y dap (22 a 31 meses).

Se realizaron análisis de covarianza, siendo la covariable una clasificación de 0 (buen drenaje) o 1 (drenaje impedido).

RESULTADOS

Hubo diferencias significativas entre las procedencias para todas las características excepto torcedura basal, ángulo de ramas e incremento en diámetro entre 22 y 31 meses (Cuadro [illegible]). En todos estos rasgos, la procedencia guatemalteca fue significativamente inferior. En cuanto a las procedencias costarricenses, la procedencia de División (testigo) fue la mejor o segunda mejor en todas los rasgos excepto en inclinación del fuste. La procedencia de Los Santos fue la peor procedencia costarricense para seis de las ocho características con diferencias significativas.

A partir de los 22 meses, se detectó en la plantación un ataque de la plaga *Scolytodes alni* (coleóptero) (abejón descortezador del jaúl). Este ataque, calificado como "drástico" por especialistas del Instituto Tecnológico de Costa Rica (Arguedas, 1993), se manifestó únicamente en árboles de la procedencia Palestina, los cuales prácticamente todos fueron atacados.

DISCUSIÓN Y CONCLUSIONES

Es evidente que la procedencia Palestina no se adapta bien a las condiciones de las faldas superiores de la Cordillera Central de Costa Rica. No se sabe si esta inferioridad se debe a algún factor específico de Palestina de los Altos o si en general *A. acuminata* de

Cuadro 1 Promedios y significancias de diferencias para ocho características de siete procedencias en un ensayo de procedencias/progenies de *Alnus acuminata*, ubicado en Santa Cruz, Turrialba, Costa Rica a los 34 meses.

	CARACTERISTICA							
	grosor de ramas[1]	dap[2] (cm)	altura (m)	incremento en altura 22-34 meses (m)	% árboles con bifurcación basal	% árboles con bifurcación no basales	% árboles con fuste inclinado	rectitud[3]
PROMEDIO	1,7	7,6	7,7	3,0	15,0	5,0	7,0	3,2
significancia (global)[4]	**	**	**	**	**	*	*	**
significancia[4,5] (CR vs Guat.)	**	**	**	**	**	*	**	**
	PROMEDIOS POR PROCEDENCIA							
PROCEDENCIA[6]								
División (testigo)	1,9	8,4	8,2	3,3	5,0	0,0	6,0	3,1
División	1,7	7,8	7,8	3,0	11,0	7,0	4,0	3,1
Los Santos	1,7	7,5	7,4	2,7	19,0	6,0	2,0	3,1
Pacayas	1,7	7,7	8,0	3,1	18,0	4,0	5,0	3,2
Palestina	1,5	6,4	6,4	2,3	28,0	8,0	11,0	3,5
Prusia	1,6	7,5	8,4	3,5	10,0	3,0	7,0	3,2
Prusia (testigo)	1,7	7,7	7,8	3,2	17,0	4,0	0,0	3,3

1/escala de 1 (delgado) a 3 (grueso). 2/a los 31 meses. 3/escala de 1(mejor) a 4 (peor); 4/probabilidad de un valor mas alto de F* = 0.05, ** = 0.01, probabilidad de un valor mas alto de F, comando 'CONTRAST' de SAS (Stonecypher, 1992). 6/todas de Costa Rica excepto Palestina, Guatemala

Guatemala no se adapta bien en Costa Rica. Sin embargo, aunque con base en los datos presentados no se puede identificar los factores causales en este caso particular, los riesgos de utilizar semilla de zonas muy distantes o muy distintas ecológicamente quedan claros. En casos extremos como el presente, el uso de semilla inapropiada puede resultar en la pérdida completa de plantaciones.

Para la reforestación en Costa Rica arriba de los 2000 msnm, ya se cuenta con semilla mejorada de jaúl, derivada de los árboles élites (árboles madres genéticamente superior en producción volumétrica hasta los 34 meses), identificados por el presente estudio. En caso que esta semilla no esté disponible, se recomienda como alternativa usar semilla recolectada en División entre los 2300 y 2600 msnm, la cual en el estudio presentó un comportamiento muy aceptable.

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Variation in Growth and Form of *Alnus acuminata* KUNTH. Grown in Costa Rica

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Summary

Results of a provenance/progeny test of *Alnus acuminata* in Costa Rica are presented. The treatments consisted of 45 open-pollinated families of one Guatemalan and 4 Costa Rican provenances. At 34 months, the Guatemalan provenance was significantly inferior in height and diameter growth rate, basal forking, stem lean and stem straightness. In addition, it was heavily attacked by the bark beetle *Scolytodes alni*, whilst the Costa Rican provenances were not attacked. There was little evidence for genetic differentiation between the Costa Rican provenances. There was no evidence of provenance related variation in the traits basal sweep and branch angle, nor in growth traits before age 34 months (except height increment between months 22 and 34). The family analysis, from which the Guatemalan families were omitted, revealed significant additive genetic variation in all the form and growth traits examined, except stem lean and non-basal forking. Estimates of heritability and additive genetic coefficient of variation for growth, stem straightness and branching traits were within the ranges typically found in forest trees. In spite of the presence of some adverse genetic correlations between height growth and form traits, in general the estimated values of the genetic parameters confirmed the potential for genetic improvement of *Alnus acuminata* in Costa Rica.

Key words: additive genetic variation, *Alnus acuminata*, Costa Rica, genetic correlations, heritability, insect attack, phenotypic selection, progeny testing, provenance variation, resistance, *Scolytodes alni*

FDC: 232.12, 232.11, 165.3, 165.62, 165.5, 176.1 *Alnus acuminata*, (728.6)

Introduction

Alnus acuminata, a fast-growing, nitrogen-fixing producer of light but versatile timber (LAMPRECHT, 1990), is one of the species most planted by smallholder farmers in the highlands of Costa Rica. One of the limitations both on the productivity of such plantations and their wider adoption by farmers has been the low genetic quality of the available seed (BOSHIER and MESÉN, 1986). For this reason, in 1989 CATIE, a regional organization dedicated to the improvement of smallholder forestry and agroforestry systems in Central America, initiated a programme of genetic improvement of the species.

The present article describes the results at ages up to 34 months of a provenance/progeny test of this species. The principal objectives of the test are to provide a basis for recommendations of appropriate seed sources for reforestation in the breeding zone in question, to identify elite trees for directed seed collections (WHITE, 1987) and, after conversion to seedling seed orchard, to produce improved seed.

Materials and Methods

The treatments

The treatments consisted of 45 open pollinated families of 5 provenances: Palestina de los Altos, Guatemala (15 families); Division, Costa Rica (5 families); Los Santos, Costa Rica (7 families); Pacayas, Costa Rica (11 families); Prusia, Costa Rica (6 families). The Guatemalan provenance was obtained

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[2] Overseas Development Administration, London, U.K.

through the CAMCORE (Central America and Mexico Coniferous Resources Cooperative) (Dvorak, 1990). Geographic and climatic information on the seed collection sites is presented in *table 1*. All the families included are derived from plus trees, selected primarily on the basis of stem straightness. In Costa Rica, all plus-trees also had diameter at breast height (dbh) and height superior to the stand mean (most stands are believed to be approximately even-aged). All the seed collections were made in natural stands, except for the Prusia provenance, which is a plantation established with seed of unknown origin, and 2 trees of the Los Santos provenance, which were planted with locally collected seed. Two controls consisting of commercially available seed, 1 from the Prusia provenance and 1 from the División provenance, were also included.

The experimental site

The experiment was planted in December 1990 in Santa Cruz de Turrialba, Costa Rica (latitude 9°58' north, longitude 83°47' west, elevation 2300 m a.s.l., mean annual precipitation 2912 mm, mean of 1.5 dry months (< 80 mm) per year). The soil is of sandy loam texture in horizons A and B, both of which have pH of 5.1. By agricultural standards the soil is slightly deficient in phosphorus and magnesium, and deficient in calcium and potassium (Bertsch, 1986). The topography is undulate and sloping, with some areas of poor drainage. Drainage canals were dug before planting, but these were only partially successful. Before planting the site was under pasture. The few trees remaining of the original forest cover were felled before planting. The trial was cleaned manually every 4 to 5 months during the first 2 years.

The experimental results are considered to be applicable principally to the upper slopes (above approximately 2000 m a.s.l.) of the Central Volcanic Range of Costa Rica, particularly sites of medium fertility in zones with annual rainfall above 2000 mm and with 0 to 2 dry months.

Experimental design

The experimental design followed the CAMCORE standard (Dvorak and Donahue, 1992) where possible; the provenances were randomized within block, and families and controls randomized as 6-tree row plots within their respective provenances.

There are 8 blocks. Two surround rows of material of unknown provenance, acquired from a commercial nursery, were planted. Spacing was 2.5 m x 2.5 m.

Measurements

Total tree height was measured at 12, 16, 22 and 34 months. Dbh was measured at 22 months and 34 months. Height increments (12 months to 16 months, 16 months to 24 months, 12 months to 24 months, 24 months to 34 months) and diameter increment were derived by subtraction. In addition, the following form traits were evaluated: stem straightness (scale of 1 to 4: 1 = straight or nearly so, 2 = straighter than average, 3 = less straight than average, 4 = crooked); basal sweep (present or absent), stem lean (present or absent), basal forking (present or absent), non-basal forking (present or absent), branch angle (scale of 1 to 4: 1 = horizontal or nearly so, 4 = 45° or nearly so, 2 = intermediate) and branch thickness (scale of 1 (thickest) to 4 (thinnest)).

As tree growth was markedly slower in the remaining areas of poor drainage than in the well drained areas, each tree's microsite was scored either 0 (free drainage) or 1 (impeded drainage). This score was used as a covariable (blocks were laid out based on slope rather than drainage patterns).

Hypotheses and statistical analysis

Null hypotheses, together with notes on their associated statistical analyses, are presented below. The underlying models are presented in *table 2*.

Null hypothesis (Ho) 1: there are no differences in the parametric mean values of the different provenances.

Ho 1 was tested using the F test derived from analysis of covariance on individual tree values. The following subsidiary hypotheses were also tested as part of the same analysis using single degree of freedom F tests (STONECYPHER, 1992): Ho 2 (there is no difference between the parametric mean of the 4 Costa Rica provenances as a group and that of the Palestina provenance); Ho 3 (there is no difference between the parametric mean of the División selected provenance and the División control), Ho 4 (there is no difference between the parametric mean of the selected treatments as a whole and the unselected treatments (controls)); Ho 5 (there is no difference between the parametric mean of the Prusia selected provenance and the Prusia control). Hypotheses 3 and 4 were tested only for those form characteristics which showed significant provenance variation under hypothesis 1. Hypothesis 5 was tested for all characteristics with significant provenance variation under hypothesis 1 (as the Prusia site is a plantation, gain would be expected in growth as well as form traits).

Ho 6: There is no additive genetic variation within the reference population sampled by the open-pollinated families.

Hypothesis 6 was tested using the 'F' test derived from analysis of covariance on family plot means. There is no provenance effect in the model (see *table 2*) because this is considered to be irrelevant to the ultimate application of the analysis, i.e. selection of superior families and individuals, independently of whether their superiority is due to provenance or family-within-provenance effects.

For those traits with significant (at p=0.05) family variation, variance components were derived from observed and expected mean squares and used to estimate family heritability. For the non-dichotomous variables, a separate analysis of covariance on individual-tree values was conducted and used to estimate the additive genetic variance, the additive genetic coefficient of variation (AGCV), heritabilities and genetic correlations (see *Table 3* for details). Phenotypic correlation coefficients based on plot means were also estimated.

Results

Provenance analysis

Results are presented in *tables 4* (significance tests) and 5 (provenance means). At age 22 months, none of the traits showed significant differences at the 5% probability level. However, at ages 31 and 34 months only basal sweep, branch angle and 22 to 31 month diameter increment were insignificant at the same level. Therefore, hypothesis 1 of no differences between the provenance parametric means for all the other traits at ages 31 months to 34 months may confidently be rejected

At 31 months and 34 months, the Guatemalan provenance was significantly inferior to the Costa Rican treatments as a group (*Table 4*), hypothesis 2 of no difference between the parametric means of the Guatemalan provenance and the Costa Rican provenances as a group may be confidently rejected for all these traits. In each case, the Guatemalan was the worst provenance. In addition, from age 31 months, an attack of the bark beetle *Scolytodes alni* (Coleoptera, Scolytidae) became evident. The attack was confined to trees of the Guatemalan provenance, all except a few of which were attacked

The evidence for genetic differentiation amongst the Costa Rican provenances was weak. However, the Division control provenance was best or second best in all traits except stem lean.

Family analysis

Family results (Costa Rican families only) are summarized in *tables 4* (significance tests), *6* (estimates of genetic parameters) and *7* (correlations). Because of their very poor performance, the Guatemalan families were omitted from the family analysis. To have included them would have given inflated estimates of heritability and genetic gain with no relevance to any likely or meaningful actual selection scenario.

There were significant differences (probability of 5% or less) between all traits except non-basal forking and stem lean. Individual-tree heritabilities ranged from 0.06 (22 month dbh) to 0.34 (height increment between 22 months and 34 months). Estimates of family heritabilities ranged from 0.11 (22 month height) to 0.62 for branch angle. Estimates of AGCV ranged from 7.5% (22 month height) to 13.2% (height increment between 22 months and 34 months) for the growth traits, and from 9.7% (stem straightness) through to 78.8% (basal forking) for form traits. In view of the assumption that the relationship within the open-pollinated families approximates that of half-sibs, these values would be overestimates insofar as the actual average coefficient of relationship is greater than 0.25 (SQUILLACE, 1974).

As, under the adopted evaluation scales, low values for some variables are favourable in terms of product characteristics, genetic correlations are most meaningfully described in terms of their being adverse or favourable, rather than simply their magnitude and direction. In this sense, the estimated values of the genetic correlations between height increment and branch thickness, height increment and stem straightness, height increment and basal sweep were strongly adverse. Other adverse correlations, including basal forking and branch thickness, basal forking and diameter increment, branch thickness and stem straightness, basal sweep and diameter increment, straightness and diameter increment, were moderate or low. The correlations between basal forking and basal sweep, basal sweep and stem straightness were strongly favourable. Other favourable correlations, including basal forking and stem straightness, branch thickness and diameter increment, had moderate or low values. Phenotypic correlations were generally weaker and sometimes of different sign to genetic correlations.

Discussion

The results conclusively demonstrate the inferiority of the Palestina provenance to the Costa Rican provenances; it grew relatively slowly and succumbed to the attack of a pest by which the local provenances were unaffected. Although the reason for the inferiority of the Palestina provenance cannot be elucidated from the evidence presented here, it is perhaps the result of poor adaptation to the local conditions. Whatever the causal factors involved, they may be present also in other Guatemalan seed sources of *A. acuminata* (e.g. macro-environmental variables such as day-length). As such, it would be prudent to avoid import to Costa Rica not only of *A. acuminata* seed from Palestina but *A. acuminata* seed from Guatemala in general.

The inferiority of the Palestina provenance is also a striking illustration of the danger in general of indiscriminate seed movements, even within relatively small regions such as Central America. It would be rash to assume that seed ciencies of a given species in one country or ecological zone n be made up with imports from another

The results suggest that any of the Costa Rican provenances, with the possible exception of Los Santos, are suitable for planting within the zone. The Prusia provenance is much used at present because of ease of seed collection and access (the plantations are located in a small country park close to urban centres). The results presented here do not suggest any reason for discouraging continued use of this convenient provenance in the case that improved seed from the best mother trees or from the test itself is unavailable.

Values of additive genetic variation and heritabilities within the Costa Rican provenances for growth, stem straightness and the branching traits are within the ranges typically found in forest trees (CORNELIUS, 1994). Other form traits showed moderate to high genetic variation. In general, considering that the families are derived from various provenances, higher levels of genetic variation might have been expected due to confounding of provenance and family effects. This feature of the results would appear to be a reflection of the low level of genetic differentiation between the Costa Rican provenances included.

The estimated values of heritability and genetic variation confirm the potential for improvement of *A. acuminata* in Costa Rica. Breeding programmes could be complicated by the existence of unfavourable genetic correlations, particularly between height and stem straightness and basal sweep. However, the correlations between dbh and these form characteristics are considerably weaker and would probably permit reasonable progress in selection for individual-tree volume without undue negative effects on mean straightness of final crop trees or the proportion of unmerchanteable trees.

Judging from the comparison between the División and Prusia provenances and their controls, the time-consuming phenotypic selection of the mother-trees for stem straightness appears to have been ineffective. However, in spite of the apparent ineffectiveness of phenotypic selection in the natural stands and the Prusia plantation, the heritability values for some of the form traits, particularly basal sweep, branch angle and basal forking, suggest that these should be retained as selection criteria in phenotypic selection. It is also worth stressing that the controls themselves, in accordance with commercial collection norms, were taken from phenotypically above average individuals. Although plus-tree progeny did not differ significantly from controls, this does not imply that form can be disregarded or, specifically, that collections can safely be made from poorly-formed individuals.

Conclusions

1. When planted in the upper slopes of the Costa Rican Central Volcanic Range, trees derived from the Palestina, Guatemala provenance are inferior in most traits of economic importance, including growth rate, most aspects of form and susceptibility to *Scolytodes alni* attack. This provenance should therefore not be planted in this area or in Costa Rica in general. Furthermore, it would in general be prudent to avoid Guatemalan and other seed sources from distant or environmentally very distinct zones of origin, until their potential has been examined through field testing.

2. There is enough additive genetic variation in growth and most of the form traits such as stem straightness to permit worthwhile genetic gains both from directed seed collection from the best mother trees and from converting the test to a seedling seed orchard

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Table 1 – Details of provenances included in a provenance/progeny trial of *Alnus acuminata* located in Santa Cruz de Turrialba, Costa Rica

Provenances[1]	Latitude [north]	Longitude [west]	Mean annual precipitation [mm]	Mean annual temperature [°C]	Elevation [m above sea level]	Mean number of dry months [<80 mm]
División	9°28'-9°32'	83°41'-83°43'	3910	12.7-19.0	1560-2700	2
División (control)	9°31'-9°32'	83°42'-83°43'	3910	17.0-19.0	2340-2610	2
Los Santos	9°38'-9°34'	83°55'-83°58'	2078	14.0-17.4	1850-2450	4
Pacayas	9°55'-9°58'	83°44'-83°51'	1845-3640	14.0-17.0	1680-2220	0-3
Palestina, Guatemala	14°53'	91°36'	unavailable	unavailable	2730-2840	unavailable
Prusia	9°57'	83°53'	1440	11.4-12.0	2560-2840	5
Prusia (control)	9°57'	83°53'	1440	12.0	2500	5

1)Costa Rica, unless stated

Table 2. – Linear models used in the analysis of covariance of a provenance/progeny trial of *Alnus acuminata* in Santa Cruz de Turrialba, Costa Rica

Hypotheses[1]	Model[2]	Random effects in model	Error term (F-test denominator)
1, 2, 3, 4, 5	$Y_{ijl}=\mu+\phi_i+\lambda_j+\beta(X_{ijl}-\bar{X})+\phi\lambda_{ij}+\epsilon_{ijl}$	λ_j	$\phi\lambda_{ij}$
6	$Y_{jk.}=\mu+\alpha_k+\lambda_j+\beta(X_{jk}-\bar{X})+\epsilon_{jk}$	λ_j	ϵ_{ij}

---

[1] see text; [2] Y_{ijl} = the observed value of the response variable 'Y' on the lth tree of the jth block of the ith performance, μ = the population mean, ϕ_i = the effect of the ith provenance, λ_j = the effect of the jth block, β = the regression coefficient of 'X' on 'Y', X_{ijl} = the value of the drainage covariable 'X' for the lth tree of the jth block of the ith provenance, $\bar{X}$ = the mean value of the drainage covariable 'X', $\phi\lambda_{ij}$ = the interaction of the effects of the ith provenance and the jth block, ϵ_{ijl} = the residual deviation of the lth tree of the ith provenance on the jth block, Y_{jk} = the observed mean value of the response variable 'Y' on the kth family in the jth block, α_k = the effect of the kth family, λ_j = the effect of the jth block, ϵ_{jk} = the residual deviation of the kth family in the jth block.

Table [illegible] Formulae for genetic parameter estimates in a provenance progeny trial of *[illegible]* in Santa Cruz de Turrialba, Costa Rica

parameter estimated[1]	formula for estimator	notes
additive genetic variance (σ^2_A)	$4\sigma^2_F$[2]	σ^2_F = variance component for half-sib families.
additive genetic coefficient of variation % (AGCV)	$100[\sigma_A / \bar{x}]$.	$\bar{x}$ = experimental mean
h^2 (narrow-sense individual-tree heritability)	$\sigma^2_A / [\sigma^2_E + \sigma^2_{FB} + \sigma^2_F]$	σ^2_E=error variance; σ^2_{FB} =block-family interaction varianc
h^2_F(plot mean heritability)	$\sigma^2_F / [\sigma^2_E/b + \sigma^2_F]$	b = number of blocks
$r_{a(x,y)}$ (genetic correlation between traits x and y)	$\sigma_{x,y} / \sqrt{[\sigma^2_x \sigma^2_y]}$	$\sigma_{x,y}$ = family covariance component between x and y[3]

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[1] all parameters include confounded effect of provenance.
[2] i.e. open-pollinated families are assumed to approximate to half-sibs.
[3] derived from variances of sums of traits (STONECYPHER, 1992)

Table 1. Analysis of covariance of a provenance progeny trial of [illegible] in Santa Cruz, Turrialba, Costa Rica at ages 12 to 34 months. F values and significance levels for provenance and family [illegible] provenance effects and planned comparisons.

Variable[2]	Provenance F[3]	Family[1] F[3]	Costa Rican families v. Guatemalan F[3]	División v. control F[3]	Prucia v. control F[3]	All Costa Rican families v. controls F[3]
basal sweep	1.2 NS	1.8**	-	-	-	-
branch angle	1.1 NS	3.5**	-	-	-	-
branch thickness	4.9**	2.5**	13.7**	2.2NS	1.6NS	3.8NS
dbh (22)	2.2 NS	1.6*	-	-	-	-
dbh (31)	6.2 **	1.8**	25.0**	.45NS	.08NS	.8NS
dbh inc. (22-31)	1.4 NS	2.7**	-	-	-	-
forking (basal)	8.9**	2.2**	38.3**	.74NS	1.26NS	.01NS
forking (non-basal)	2.5*	.83 NS	4.6*	2.2 NS	.8 NS	.09NS
height (12)	0.7 NS	-	-	-	-	-
height (16)	0.6 NS	-	-	-	-	-
height (22)	2.0 NS	1.8**	-	-	-	-
height (34)	13.7**	3.7**	65.6**	.3NS	1.23NS	.11NS
height inc. (12-16)	1.7 NS	-	-	-	-	-
height inc. (12-22)	1.8 NS	-	-	-	-	-
height inc. (16-22)	1.4 NS	-	-	-	-	-
height inc. 22-34)	7.4 **	4.0**	31.9**	.3NS	.4NS	0.0NS
number of stems	10.8 **	1.9**	63.5**	1.1 NS	1.22NS	0.0NS
stem lean	3.2*	1.4 NS	14.4**	.1 NS	1.49NS	.3 NS
stem straightness	7.5 **	2.0**	41.3**	0.0 NS	.36NS	0.2 NS

---

1) Analysis made on Costa Rica families only;
2) at 34 months unless stated;
3) * = significant at p = 0.05, ** = significant at p = 0.01, NS = not significant

[illegible] Least squared provenance means for 8 traits in a provenance progeny trial of *Alnus acuminata* at Santa Cruz de Turrialba, Costa Rica

Rank[1]	branch thickness[2]	dbh (31 months) (mm)	proportion with basal fork	proportion with non-basal fork	height, 34 months (m)	height inc. 22-34 months (m)	proportion with stem lean	stem straightness[3]
	TRAIT AND GRAND MEAN							
	1.71	7.6	.16	.06	7.7	3.0	.07	3.2
	PROVENANCE, MEAN (n)							
1	División control 1.66	División control 8.4 (.4)	División control .05 (.07)	División control 0.00 (.04)	Prusia 8.4 (.1)	Prusia 3.5 (.1)	Prusia control 0.0 (.04)	Los Santos 3.1 (.06) División 3.1 (.07) División control 3.1 (.14)
2	Pacayas 1.75 (.03)	División 7.8 (.2)	Prusia .1 (.03)	Prusia .03 (.04)	División control 8.2 (.2)	División control 3.3 (.1)	Los Santos .02 (.02)	
3	Prusia control 1.74 (.03)	Prusia control 7.7 (.4) Pacayas 7.7 (.1)	División .11 (.03)	Pacayas .04 (.01) Prusia control .04 (.04)	Pacayas 8.0 (.1)	Prusia control 3.2 (.1)	División .04 (.02)	
4	Los Santos 1.73 (.04)		Prusia control .17 (.06)		División 7.8 (.1) Prusia control 7.8 (.2)	Pacayas 3.1 (.1)	Pacayas .05 (.01)	Pacayas 3.2 (.04) Prusia 3.2 (.04)
5	División 1.72 (.05)	Prusia 7.5 (.1) Los Santos 7.5 (.2)	Pacayas .18 (.02)	Los Santos .06 (.02)		División 3.0 (.1)	División control .06 (.04)	
6	Prusia 1.56 (.03)		Los Santos .19 (.03)	División .07 (.02)	Los Santos 7.4 (.1)	Los Santos 2.7 (.1)	Prusia .07 (.02)	Prusia control 3.3 (.13)
7	Palestina 1.52 (.03)	Palestina 6.4 (.1)	Palestina .28 (.02)	Palestina .08 (.01)	Palestina 6.4 (.1)	Palestina 2.3 (.1)	Palestina .11 (.01)	Palestina 3.5 (.04)

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[1] (1 = best, 7 = worst in potential productivity and quality of sawtimber)

[2] (1 (thickest) to 3 (thinnest))

[3] (scale of 1 (staightest) to 4 (least straight))

Table 6 - Individual-tree heritabilities, family heritabilities and additive genetic coefficients of variation of 11 traits in a provenance/progeny test of *Alnus acuminata* located in Santa Cruz de Turrialba, Costa Rica (Costa Rican families only)

Variable (34 months unless stated)	Individual-tree heritability	Family heritability	Additive genetic coefficient of variation %
basal sweep	-	.56	20.6
branch angle	.28	.62	16.2
branch thickness	.16	.54	16.4
dbh (22 months)	.06	.15	9.8
dbh (31 months)	.08	.18	9.2
diameter increment (22-31 mths)	.19	.41	12.8
forking (basal)	-	.47	78.8
height (22 months)	.09	.11	7.5
height	.29	.45	9.6
height increment (22-34)	.34	.54	13.2
stem straightness	.12	.26	9.7

Table 7 - Additive genetic (above diagonal) and phenotypic (below diagonal) correlation coefficients between 5 traits in a provenance/progeny test of *Alnus acuminata* in Santa Cruz de Turrialba, Costa Rica[1].

VARIABLE (34 months)	height inc.[2]	basal forking	branch thickness	basal sweep	stem straightness	dbh inc.[3]
height inc.[2]		-.17	-.73	1.32	.64	.04
basal forking	.001 NS[4]		.21	.86	.21	.07
branch thickness	.06 NS	.03 NS		-.07	.32	.37
basal sweep	.11 NS	.16*	-.10		1.43	.21
stem straightness	-.03 NS	.24***	.07 NS	.48***		.14
dbh inc.[3]	.47***	-.09 NS	.33***	-.13*	-.18**	

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[1] Estimates based on confounded family and provenance effects.

[2] 22 to 34 months

[3] 22 to 31 months

[4] * = significant at p ≤ 0.05, ** = significant at p ≤ 0.01, *** = significant at p ≤ 0.001, NS = not significant

PROGRAMA DE CONSERVACION Y MEJORAMIENTO DE *Bombacopsis quinata* (JACQ.) DUGAND EN COSTA RICA

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Eugenio Corea[3*]

INTRODUCCION.-

Bombacopsis quinata (Jacq.) Dugand, conocido en Costa Rica como pochote, es una especie de gran valor comercial debido a su madera valiosa, la cual es utilizada principalmente en ebanistería, paneles interiores y confección de puertas y ventanas. Además, debido a la facilidad de propagación por estacones leñosos, se utiliza frecuentemente para el establecimiento de cercas vivas.

Durante muchos años, ***B. quinata*** ha sido sometido a una explotación severa en Costa Rica, a tal punto que actualmente se presenta únicamente como árboles aislados o rodales pequeños, con árboles generalmente de mala forma. Aparte de los problemas de erosión genética y extinción de muchas poblaciones, existe el problema de que los peores exponentes, que han sobrevivido debido a su poco valor maderable, son los que se utilizan para la recolección de semilla y el establecimiento de plantaciones. Aún más, debido a la dificultad de realizar colecciones en árboles adultos (por su poca producción de semilla y su fuste cubierto de espinas), se ha recurrido a la obtención de semilla a partir de árboles en cercas, los cuales se derivan de árboles de fenotipo desconocido y en muchos casos, pueden provenir de un solo individuo.

Esta situación, unida a una demanda creciente por semilla para el establecimiento de plantaciones comerciales, motivó el desarrollo de programas de conservación, mejoramiento genético y producción de semilla de calidad genética superior. El Centro Agrícola Cantonal de Hojancha (CACH) y la Dirección General Forestal (DGF) establecieron en 1983 y 1984, respectivamente, dos huertos semilleros clonales a partir de árboles seleccionados en la región del Pacífico Seco de Costa Rica. Estos huertos ya han iniciado su fase de producción. Posteriormente, en 1989, la Cooperativa de Recursos Forestales de Centro América y México (CAMCORE) y el Centro Agronómico Tropical de Investigación y Enseñanza (CATIE), con el aporte financiero de US/AID, iniciaron un programa de exploración, conservación y evaluación de descendencias de gran parte del rango de distribución natural de la especie, para el inicio de programas de selección y mejoramiento genético de *B. quinata* en Costa Rica.

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DISTRIBUCION NATURAL DE *Bombacopsis quinata* EN COSTA RICA

En Costa Rica, *B. quinata* ocurre en forma natural en la Vertiente Pacífica, desde la frontera con Nicaragua en el Pacífico Norte hasta el Cantón de Parrita en el Pacífico Central. Ingresa también al Valle Central por la cuenca del Río Grande de Tárcoles y del Río Virilla (Figura 1).

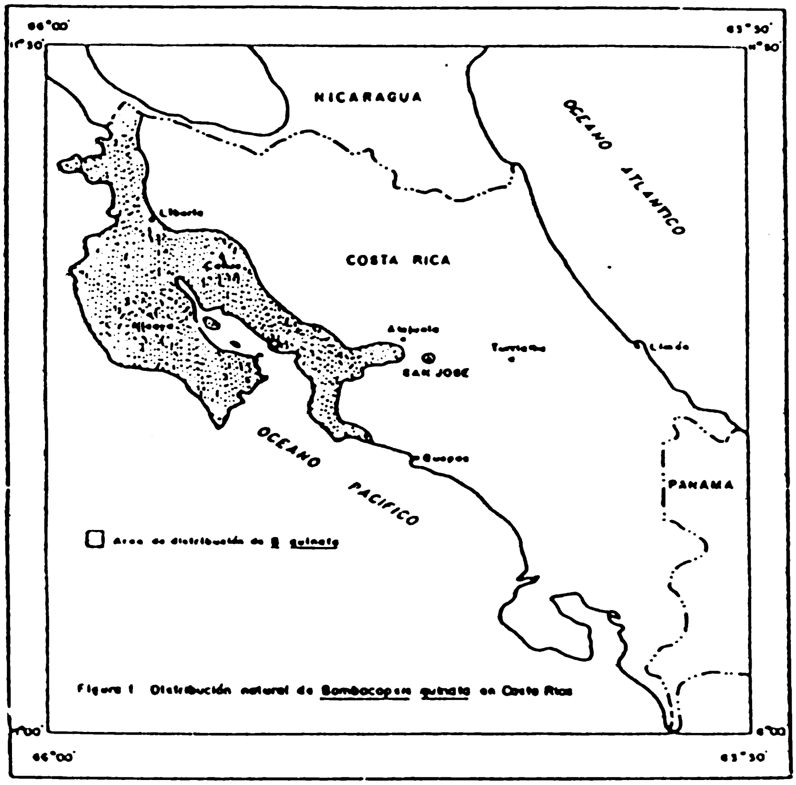

Figura 1. Distribución natural de ***Bombacopsis quinata*** en Costa Rica.

La especie se encuentra en sitios que van desde el nivel del mar hasta los 800 m de elevación, con temperaturas promedio anuales de 22,5 a 28 °C. La precipitación varia entre 1200 y 3000 mm anuales con una estación seca de 4 a 6 meses.

La distribución natural de *B. quinata* en Costa Rica está definida principalmente por la temperatura y la duración de la estación seca y no por la precipitación total Aparentemente el período seco debe ser de por lo menos cuatro meses. Existen áreas con poblaciones naturales en el extremo sur de la península de Nicoya (Reserva Biológica Cabo Blanco) y en el Pacífico Central (Esterillos) con 3000 mm de precipitación promedio anual, pero con una estación seca bien definida de cuatro meses. Es importante anotar que estos sitios representan el extremo más húmedo de todo el ámbito de distribución natural conocido de la especie Hasta ahora se había indicado 2500 mm como el límite superior de precipitación en su hábitat natural.

B. quinata crece en forma natural en una gran variedad de suelos. Se le encuentra principalmente en suelos bien drenados y profundos, aunque también se presenta en áreas con drenaje imperfecto o en lomas con suelos superficiales, rocosos y excesivamente drenados. Ocurre en inceptisoles, vertisoles, alfisoles y mollisoles. Existen algunas poblaciones naturales creciendo en arenas de playa en sitios tales como Playa Cabuya y Playa Tamarindo.

CONSERVACION Y MEJORAMIENTO

Selección de árboles fenotípicamente superiores

En 1983 el CACH seleccionó 35 árboles para establecer un huerto semillero. Los árboles fueron seleccionados en los cantones de Nicoya y Hojancha (Arguedas, 1985). Posteriormente, en 1984 la DGF seleccionó 40 árboles de 427 candidatos de los cantones de Liberia, Bagaces, Cañas, Abangares, Puntarenas y Santa Ana (Castillo y Bermúdez, 1986).

Las características que el CACH y la DGF tomaron en cuenta para la selección de árboles fueron principalmente volumen comercial (diámetro, y altura del fuste comercial), rectitud del fuste y estado fitosanitario.

Durante los años 1987, 1989 y 1990, personal del Proyecto Mejoramiento Genético Forestal (MGF) del CATIE recolectó semilla de 36 árboles seleccionados, de los 75 que están representados en los huertos. Se recolectó además de 13 árboles adicionales que no están incluidos en los huertos. Los árboles producen muy poca semilla, por lo que se tardó varios años para completar las cantidades necesarias para un ensayo. Muchos de los árboles seleccionados originalmente no pudieron ser localizados debido al falta de documentación y mapas adecuados. Además, ya en 1987 se pudo comprobar que por lo menos 8 árboles habían sido cortados.

Huertos semilleros clonales

De los árboles seleccionados (ver la sección anterior), 75 han sido incluidos en los huertos semilleros clonales establecidos por el CACH y la DGF en Hojancha, Guanacaste (1983) y Cañas, Guanacaste (1984-85) respectivamente. Ambos huertos fueron establecidos a partir de material adulto (estacones) y ya están entrando en la fase de producción. El huerto de la DGF cuenta con 57 clones en 3,0 ha, mientras que el del CACH tiene 24 clones en 0,32 ha.

Aunque los huertos presentan algunos problemas de diseño, la semilla producida es única en Costa Rica porque proviene de árboles madres y padres seleccionados fenotípicamente. El huerto de la DGF es suficientemente completo y grande para justificar una mayor intensidad de trabajo, incluyendo aclareos basados en ensayos de descendencias, los cuales permitirán la producción de semilla genéticamente mejorada. Recientemente, el Proyecto Mejoramiento Genético Forestal del CATIE elaboró un plan de manejo para el huerto que contempla estas acciones (Mesén *et al.*, 1991)

Aparte de su valor como fuentes de semilla, es importante destacar que, dado el alto riesgo de pérdida de los orets, ambos huertos revisten enorme importancia como bancos de conservación de alelos y genotipos.

Ensayos de descendencias

En colaboración con CAMCORE, el CATIE estableció en 1991 un ensayo de procedencias/descendencias (polinización abierta) en Nandayure, Guanacaste (50 msnm, 1780 mm p.m.a., cinco meses secos). El ensayo cuenta con 55 familias de Colombia, Costa Rica y Honduras, de las cuales 25 provienen de los genotipos incluidos en los huertos semilleros del CAHC y la DGF. El diseño es de bloques completos al azar con las familias anidadas dentro de las procedencias (las familias se agrupan por procedencia). La ubicación de las parcelas de procedencia y de las familias dentro de las procedencias es aleatoria. El ensayo cuenta con nueve bloques y la parcela de familia es de seis árboles en línea.

Estudios sobre enraizamiento de estacas

Las ventajas de la silvicultura clonal son en la actualidad ampliamente reconocidas (Leakey, 1987; Leakey y Mesén, 1990; Libby y Rauter, 1984). Desde 1987, el CATIE ha trabajado en el desarrollo de técnicas simples de enraizamiento de estacas juveniles para el establecimiento de plantaciones, mediante el uso de propagadores con sub-irrigación (Leakey *et al.*, 1990). Utilizando estos propagadores de bajo costo, se han realizado pruebas de enraizamiento con *B. quinata*, las cuales han mostrado la facilidad de propagación de esta especie a través de estacas uninodales de 5 cm de longitud, obtenidas de los 12-15 nudos superiores del brote, con sus hojas podadas para dejar 40-50 cm^2 de área foliar. Se han obtenido porcentajes de enraizamiento cercanos al 80% cuando se utilizó arena fina o aserrín como sustrato y concentraciones de 0,4 a 0,8% de ácido indol-3-butírico disuelto en metanol. Así mismo, la especie es apta para ser manejada fácilmente mediante setos vivos en jardines de multiplicación, produciendo cosechas abundantes de estacas aproximadamente cada tres meses. Los rebrotes utilizados se derivaron de estacas lignificadas de árboles de un huerto semillero; es posible que el enraizamiento sea aún mayor utilizando material juvenil.

TRABAJOS FUTUROS

Como una etapa siguiente, el Proyecto MGF ha iniciado la selección de árboles fenotípicamente superiores en la región de Jacó, Esterillos y en la región sur de la Península de Nicoya, abarcando la Reserva Biológica Cabo Blanco. Se han seleccionado 15 árboles y se espera completar 35-40 al final de 1991. Esto permitirá la evaluación de materiales costeros y material del extremo superior del ámbito de precipitación para la especie.

En cooperación con la Dirección General Forestal de Costa Rica, se establecerán pruebas de descendencias por polinización abierta a partir de los huertos semilleros clonales para evaluar el valor genético de los clones, así mismo, se establecerá un tercer huerto clonal probablemente en la región de Atenas, Costa Rica, con material procedente de los huertos existentes. El Proyecto MGF continuará con el programa de evaluaciones de la prueba de descendencias y eventualmente se prevee su conversión en un huerto semillero de plántulas.

También el Proyecto MGF dará énfasis a los estudios sobre enraizamiento de estacas juveniles y al establecimiento de plantaciones clonales experimentales. Los métodos de propagación se presentan como una alternativa excelente para el desarrollo de plantaciones de calidad superior, así como para reducir la dependencia del uso de semilla sexual, lo cual es una seria limitante en el caso de ***B. quinata***.

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Atlántico *vs.* Pacífico: distinción importante en la escogencia de fuentes de semilla forestal en América Central

Jonathan Cornelius[1]

Puntos claves y recomendaciones prácticas

- En América Central hay diferencias fundamentales en los climas de las vertientes pacífica y atlántica. La diferenciación genética es una consecuencia de las relativamente pocas especies forestales que crecen en ambas zonas. Como ilustración, se presenta información sobre procedencias de *Cedrela odorata y Cordia alliodora.*
- En ambas especies, el comportamiento de procedencias de zona seca plantadas en zona húmeda fueron inferiores a las locales. Las procedencias de laurel de zona húmeda, presentaron mejor comportamiento en la zona seca.
- En la zona húmeda, no debe utilizarse semilla de la zona seca.
- Es importante dar seguimiento a las plantaciones de laurel existentes, para monitorer el comportamiento a largo plazo de laurel de la zona húmeda plantado en climas secos.

Introducción:

En América Central hay diferencias fundamentales en los climas de las vertientes pacífica y atlántica. En general, la precipitación media anual de la zona pacífica es más baja y su estación seca es larga y bien definida, mientras en la zona atlántica la precipitación es mayor y su época seca es corta y menos marcada. Una consecuencia evidente de esta división son las floras arbóreas distintas de las dos zonas Otra consecuencia menos conocida es la diferenciación genética de las relativamente pocas especies forestales de ambas zonas. En la presente nota se ilustran, los casos de *Cedrela odorata* y *Cordia alliodora*.

Los experimentos

Cedrela odorata. En setiembre de 1994 se estableció un ensayo de procedencia y descendencias de esta especie en Muelle de San Carlos, provincia de Alajuela, Costa Rica El ensayo contó con tres procedencias de la zona

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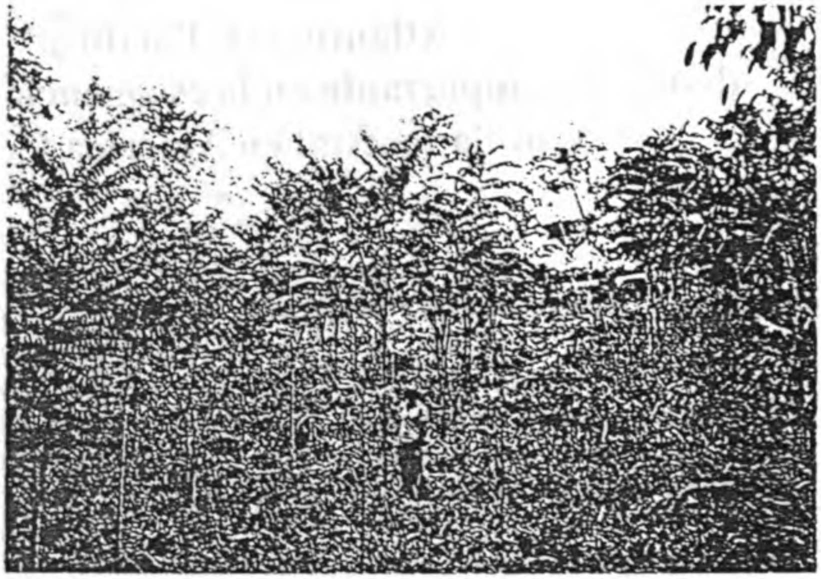
[1] Proyecto Mejoramiento Genético Forestal, CATIE

seca de Costa Rica (Cañas, Hojancha, Cóbano) y tres de la zona atlántica (San Carlos, Talamanca, Guápiles) Cada procedencia fue representada por cinco familias y cada familia por diez repeticiones de parcelas de tres árboles, para un total de 150 árboles por procedencia. A los 13 meses de midió la altura de cada árbol, y se realizó análisis de varianza, incluyendo una comparación planificada entre los dos grupos ("seca" *vs*. "húmeda").



Panorámica del ensayo de procedencias/progenie de *Cedrela odorata* en Florencia, Turrialba, donde se aprecian claramente las diferencias en crecimiento entre las familias de zona seca (derecha) y las provenientes de zona húmeda (izquierda). Foto: Jonathan Cornelius.

Cordia alliodora. Los ensayos internacionales coordinados por el Instituto Forestal de Oxford (Greaves y McCarter 1990) demostraron la superioridad de procedencias de zonas húmedas, tanto en las zonas secas como las mismas zonas húmedas. En 1993, se estableció en Guápiles (zona atlántica) y Garza de Nicoya (zona seca), Costa Rica, dos plantaciones para demostrar este fenómeno, en las cuales se incluyeron parcelas de la zonas atlántica y pacífica (18 y 24 árboles, respectivamente, en Garza; 24 y 18, respectivamente, en Guápiles). A los 14 meses (Guápiles) y 15 meses (Garza), se midió diámetro a 1,3m de cada árbol.

Resultados

A los 13 meses, la media de las tres procedencias de *Cedrela odorata* de la zona atlántica fue 27% mayor que la de la zona seca (F = 56,4, p = 0001). Con el laurel, el dap de las procedencias "húmedas" superó al dap de la procedencia "seca" en 127% y 55% en Guápiles y Nicoya, respectivamente. En este caso, no se pudo calcular la significancia, al no haber repetición dentro de sitio.

Implicaciones

El uso en la zona atlántica de semilla de laurel y cedro proveniente de la vertiente pacífica puede ocasionar pérdidas económicas importantes y debe evitarse. También, sería prudente evitar tales traslados en el caso de otras especies procedentes de ambas zonas (ej *Pinus caribaea* var *hondurensis*, *Swietenia macrophylla*)

El comportamiento del laurel en la zona seca es una interesante ilustración de un principio general el valor adaptativo, en el sentido estricto de "capacidad de sobrevivir y reproducir", no coincide necesariamente con el valor comercial. Independientemente de si se siembra en la zona seca o húmeda, el laurel de la zona seca germina más rápidamente y las plántulas, a diferencia de las de las procedencias húmedas, tienden a desarrollar una raiz pivotal profunda (Boshier 1984).

Al parecer, el laurel "seco" está genéticamente programado a dedicar más recursos al sistema radical que el laurel "húmedo". Tendencia que explica, en parte, el crecimiento aéreo inferior de las fuentes de la zona seca. Por lo tanto, podria ser posible ampliar la productividad de laurel en la zona seca con procedencias de la zona húmeda. Sin embargo, sería deseable conducir ensayos de largo plazo antes de hacer recomendaciones finales en este sentido.

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RESISTANCE TO THE MAHOGANY SHOOT BORER: RESULTS OF RESEARCH AT CATIE, 1990-1995

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Summary: The shoot borer *Hypsipyla* prevents successful plantation silviculture of mahogany and other commercially important Meliaceae. The present article describes the results to date of a programme of research on genetic variation in resistance to attack, initiated by CATIE and the Institute for Terrestrial Ecology, Scotland, in 1990. The three genetic tests described demonstrated the existence of provenance-level and family-level variation in resistance to attack. It is concluded that deployment of selectd germplasm has potential as one element of a pest management system for *Hypsipyla*.

Introduction

The attack of the shoot-borer *Hypsipyla* (Lepidoptera: Pyralidae) has long been recognized as a critically limiting factor in the successful plantation silviculture of mahogany (*Swietenia* spp). African mahogany (*Khaya* spp) and Spanish cedar (*Cedrela* spp.) (1,3,4). Although the insect has been closely studied (7), until recently, with the exception of work at the species level (2), there had been no efforts at approaching the problem through germplasm selection and breeding for resistance (5). For this reason, in 1990, CATIE, in collaboration with the Institute for Terrestrial Ecology, began a pilot programme of research into resistance breeding in *Cedrela* and *Swietenia*. In the present document we report results of three genetic field tests.

Materials and methods

In February 1991, provenance trials of *Cedrela odorata* and *Swietenia macrophylla* were established in Turrialba, Costa Rica. Each trial had five provenances. The mahogany provenances (Guajataca, Puerto Rico; Juan Diaz, Puerto Rico; Honduras; Trinidad; Haiti) were represented by bulked lots. Experimental design was randomized complete blocks, with 25-tree square plots and five blocks. Each of the *Cedrela* provenances (Cañas, Carmona, Hojancha, San Carlos (all Costa Rica), Trinidad) was represented by progeny of five trees. Experimental design was randomized complete blocks, with five-tree family line plots and nine blocks. The trials were assessed fortnightly for shoot borer attack and phenology from 22 April 1991 until early December 1992. Tree height was measured after 26, 56 and 88 weeks, and form evaluations (height to first branch and number of forks) made at 141 weeks (*Cedrela*) and 177 weeks (*Swietenia*). Analyses of variance of block and provenance effects was carried out. Further details on these two experiments are given elsewhere (6). In September 1994, a second *Cedrela* trial was established in San Carlos, Costa Rica. Six Costa Rican provenances were included (Cañas, Cóbano, Guápiles, Hojancha, San Carlos, Talamanca), each represented by five families. Design was randomized complete blocks, with three tree line plots and ten bloques. Tree height and presence of *Hypsipyla* attack was assessed in March, July, September and October 1995. In addition, in October 1995 the presence or absence of a dominant leader was assessed. Trees were also scored 1 (present) or 0 (absent) for tolerance, where a tolerant tree was defined as one that had been attacked at least once and had retained a dominant leading shoot, whereas an intolerant tree was defined as one that had been attacked and had no dominant leader. Trees that had never been attacked were considered to be missing values for tolerance. In addition, a score for degree of tolerance was derived; tolerance degree for those trees that scored 1 for tolerance was set equal to the total number of attacks. Tolerance degree of trees with zero tolerance was also zero. Analyses of variance of block, provenance and family effects were made for all variables.

Results

In all three trials, strong temporal trends were noted. The 1991 *Cedrela* trial evinced peaks in attack in May 1991 and, particularly, May-June 1992. The mahogany trial was virtually unattacked during the first year of growth, but experienced a sharp peak of attack from May to June 1992. The second Cedrela trial was unattacked at the time of the first evaluation in March 1994. By May, 14% of the trees were being attacked, rising to 56% in July, thereafter declining to 27% and 29% respectively in September and October. There is thus evidence that, at least in the Atlantic zone of Costa Rica, attacks tend to be concentrated in the May-July period, although the tail-off in attack has not been as marked in San Carlos as in the Turrialba trials.

Genetic variation in attack and tolerance

Swietenia macrophylla

At the time of peak attack, there were significant differences between the provenances in mean number of attacks per tree (p=.01), number of forks (p=.001), proportion attacked (p=.001) and height to the first fork (p=.01). The Juan Diaz (Puerto Rico) provenance was markedly superior in the first three characteristics, although its height at 68 weeks was 16.7% less than the best source.

Cedrela odorata

In the 1991 trial, at the time of the second peak there were significant differences in number of attacks per tree (p .001), number of forks (p .001), height to the first fork (p .001), and the proportion of trees attacked (p .001). The Costa Rican dry-zone provenances were attacked least (e.g. means of 0.94 and 2.3 attacks per tree in Hojancha and San Carlos respectively). However, the San Carlos provenance was much faster growing (3.1m (San Carlos) v 1.5m (Hojancha)) and had the best form.

In the 1994 trial, in October 1995 there was highly significant variation between the provenances in mean number of attacks per tree (p=.0001) (e.g. Hojancha 1.5±0.8, San Carlos 3.6±0.8), mean number of trees attacked (p=.0001) (e.g. Hojancha 0.6±0.2, San Carlos 0.9±0.05) and mean height (p=.0001) (e.g. Hojancha 0.8m±0.2m, San Carlos 1.3m±0.25m). The mean number of attacks per tree and mean number of trees attacked was significantly (p=.0001) lower for the dry zone provenances than the wet zone provenances. The mean height of the wet zone provenances was significantly (p=.0001) greater than that of the dry zone provenances. There were no significant differences in dominance between the provenances, and no significant differences in tolerance. However, degree of tolerance showed highly significant (p=.0001) provenance effects (e.g. Hojancha 1.3±0.5, San Carlos 2.9±0.7) and, in addition, the wet zone provenances showed significantly superior tolerance degree and tolerance (p=.0001, p=.07, respectively) to the dry zone provenances.

Because of the evidently strong zonal provenance effect, the dry-zone provenances were eliminated from the family-level analysis, in order to avoid undue confounding of family and provenance effects. The analysis therefore included five families from each of Guapiles, San Carlos and Talamanca, plus three families from Upala, which were excluded from the provenance analysis on grounds of inadequately representing the Upala source. The analysis of the October 1995 data revealed significant family effects on total height (p .0004) (e.g. best family 1.7±0.6m, worst 0.9m±0.4m) and total number of attacks (p .0007) (e.g. most severely attacked family 5.7±1.9 attacks per tree, least severely attacked family 2.1±0.7 attacks per tree). There were no significant family effects of proportion of trees attacked, tolerance, or tolerance degree.

Discussion and conclusions

The trials clearly demonstrate the existence of genetic variation in resistance to the attack of *Hypsipyla* both in the case of *Swietenia* and *Cedrela*. However, both for purposes of application of the results and design of future research directions, it is important to appreciate the scope of the research to date and the nature, particularly with regard to the structure, of the variation identified. The *Cedrela* trials provide very clear evidence for major genetic differences between the provenances from the seasonally-dry Pacific watershed and those from the Atlantic zone The magnitude of the growth differences are such that Pacific provenances would be unlikely to be selected for planting in the Atlantic zone, whilst their relative freedom from attack may in any case be a function of their size and consequent lower number of oviposition and feeding sites There are, however, clear indications in the data of more practically useful forms of genetic variation The continuing fast growth and good form of the San Carlos provenance and particularly the existence of genetic variation in attack severity within the broadly similar Atlantic zone provenances, are highly encouraging At the same time, the failure to detect variation in tolerance within the Atlantic zone material is disappointing Future research will concentrate on clonal testing of Atlantic-derived material and the development of an integrated pest management systemof which superior germplasm will be one element

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Genetic Variation in Apical Dominance of *Cedrela odorata* Seedlings in Response to Decapitation

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Summary

An assessment was made of genetic variation in apical dominance of *Cedrela odorata* L. using a decapitation test. Nineteen weeks after sowing, pot-grown seedlings belonging to 30 open-pollinated progenies from 5 provenances were decapitated by removal of the shoot apex, leaving shoots of a uniform height of 20 cm. Foliage was reduced to a single leaf with 2 pairs of leaflets on each plant. The length and number of lateral shoots subsequently formed were measured at 2 weeks, 4 weeks and 8 weeks after decapitation to determine the percentage bud activity and dominance ratio of the shoots. Percentage bud activity increased within the first 2 weeks to 4 weeks and declined thereafter as dominance was reimposed. Significant differences between provenances and progenies were recorded both in the timing and extent of peak bud activity ($P < 0.001$, ANOVA). Maximum bud activity ranged from 17.7% to 24.2% in the 5 provenances whereas mean values for the progenies differed by more than a factor of 2, ranging from 13.6% to 32.3%. Pronounced genetic variation in dominance ratio was also recorded; maximum values occurred 4 weeks after decapitation in all progenies. Dominance ratio was negatively correlated with percentage bud activity ($r = 0.65$, $P < 0.001$). These results indicate that significant potential exists for selection of *Cedrela odorata* genotypes with relatively high apical dominance, which may exhibit superior form and pest tolerance.

Key words: Apical dominance, correlative inhibition, genetic variation, branching, screening test, genetic improvement, *Cedrela odorata*.

FDC: 165.53; 161.4; 176.1 *Cedrela odorata*.

Introduction

Cedrela odorata L. ("Spanish Cedar"; Meliaceae) is a valuable timber tree native to Central and South America (LAMB, 1968; PENNINGTON, 1981), often grown in combination with coffee or cacao in agroforestry systems. However, attempts to establish the species in plantations in areas within its natural range have met with repeated failure, largely because of attacks by shoot boring moth larvae (*Hypsipyla* spp.) (NEWTON *et al.*, 1993a). Shoot borers destroy the terminal shoot, resulting in a highly branched or forked tree of little economic worth (GRIJPMA, 1976; NEWTON *et al.*, 1993a). Evidence from provenance and progeny tests of *C. odorata* indicate that some genotypes may display tolerance of the pest (GRIJPMA, 1976; NEWTON *et al.*, 1993b) by displaying strong apical growth of the leading shoot after attack (CHAPLIN, 1980; VEGA, 1976). Although such a characteristic is clearly of great potential value, the physiological and genetic basis of this pattern of response is not well understood.

Branch formation in trees is controlled by 2 processes: apical dominance (correlative inhibition), involving the regulation of axillary bud development by the terminal bud of a shoot, and apical control, the suppression of growth of existing branches imposed by more apical shoots (BROWN *et al.*, 1967; LEAKEY and LONGMAN, 1986). Although the mechanisms of these processes have not been clearly defined, apical dominance is thought to be controlled by auxins, perhaps in combination with other growth substances (FIELD and JACKSON, 1984). The dominance relationships of shoots have been shown to be particularly sensitive to gibberellin concentration. For example, injection of GA_3 into shoots of *Triplochiton scleroxylon* K. SCHUM. hastened the imposition of dominance by increasing vegetative growth of the dominant shoot (LEAKEY and LONGMAN, 1986). Both apical dominance and apical control are also known to be influenced by a range of environmental factors (LADIPO *et al.*, 1992; MCINTYRE, 1977).

Research into the processes of branch formation in *Triplochiton scleroxylon*, a West African hardwood, has identified pronounced genetic variation in apical dominance, primarily between clones (LEAKEY and LONGMAN, 1986; LEAKEY and LADIPO, 1987; LADIPO *et al.*, 1991b). This variation was identified by the development of a decapitation test, involving the removal of the apical part of the shoot of a young plant, and the subsequent release of axillary buds from correlative inhibition (LEAKEY and LONGMAN, 1986). The expression of apical dominance was found to be influenced by a range of environmental factors, including growth conditions, the height of the plant and the number of leaves (LADIPO *et al.*, 1991b, 1992; LEAKEY and LONGMAN, 1986). On the basis of these results, LADIPO *et al.* (1991b) suggested that decapitation tests could be used to screen genotypes for variation in apical dominance, and could thereby serve as an early selection technique for improved form and yield. This was supported by the strong correlation found between percentage bud activity following decapitation, and the branching frequency of clones at 4 years of age (LEAKEY, 1985).

The development of an early selection criterion for apical dominance would be of particular value in species such as *Cedrela odorata*, where the processes of branch formation appear to be strongly related to tolerance of pest attack. Consequently, this paper describes the first application of a decapitation test to this species. Unlike most previous investigations (LEAKEY and LONGMAN, 1986; LADIPO *et al.*, 1991b), this study was undertaken under operational conditions in the nursery, and involved screening of large numbers of seedlings rather than clones. The main objectives were: (i) to assess whether the decapitation test could be successfully applied to *Cedrela odorata*; (ii) to assess whether the responses of this species to decapitation differed to those observed previously; and (iii) to assess the extent of genetic variation in apical dominance observed using this technique.

Materials, Methods and Experimental Details

The experiment was carried out in the nursery of the Centro Agronómico de Investigación y Enseñanza (CATIE) in Turrial

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ba, Costa Rica (9° 54' N Lat., 83° 40' W Long.), which lies at an altitude of 600 m a s l, with a mean annual precipitation of approx. 2600 mm and a mean annual temperature of 22 °C. Seed was collected from open-pollinated trees selected from a range of localities in Costa Rica, and sown directly into black polythene bags (2.2 l capacity) containing a 1:1:1 mixture of forest soil, sand and organic compost. After 10 weeks, the plants were repotted into larger polythene bags (5.6 l capacity) filled with the same potting mixture. Plants were grown under full sunlight and received natural rainfall, supplemented by additional watering to field capacity when there was no rain for 2 consecutive days. The pots were hand-weeded at regular intervals.

The experiment included 30 families belonging to 5 provenances (see *Table 1*), with 6 trees per family per block arranged in a line, and 9 blocks in total, giving a total of 54 seedlings per family. The whole experiment was surrounded by a single-row border of a checklot, and the plants were arranged at a constant spacing of 25 cm x 25 cm. The seedlings were decapitated on 1 October 1990, 19 weeks after sowing, by which time they were 30 cm to 40 cm tall. LEAKEY and LADIPO (1987) recommended that decapitation tests should be carried out under uniformly high irradiance with plants of a uniform age, leaf area and size prior to decapitation. Consequently all plants were cut to a constant height of 20 cm, by removing the apical part of the shoot. All seedlings were partly defoliated, leaving a single leaf which was trimmed to 2 pairs of leaflets in each case. Any lateral shoots that were present at the time of decapitation were removed.

Table 1. – Origins of the *Cedrela odorata* seedlots used in this investigation. All the collection sites were in Costa Rica.

Provenance	Latitude N	Longitude W	Altitude (m)	Precipitation (mm)
Cañas	10° 25'	85° 6'	70-120	1829-2274
Carmona	9° 60'	85° 15'	60-70	1780
Hojancha	10° 04'	85° 25'	100-350	2232
San Carlos	10° 22'	84° 28'	80-260	2866-3609
Turrialba	9° 54'	83° 40'	600-620	2464-2605

Measurements were made of the proportion of buds that subsequently broke from correlative inhibition and the length of each branch produced after 2 weeks, 4 weeks and 8 weeks. Shoots were considered to be actively growing if they grew by more than 2 mm week^{-1}. Dominance ratio was calculated as the ratio of the length of the longest shoot: mean length of the remaining shoots (following LEAKEY and LONGMAN, 1986). Results were analyzed by ANOVA using SAS (SAS, 1980). Percentages were arcsin transformed prior to analysis, following SNEDECOR and COCHRAN (1980). Correlations were carried out using SigmaPlot v. 5.0 (Jandel Scientific GmbH, Erkrath, Germany).

Results

At the time of decapitation, the number of nodes per seedling varied between 2 to 18, with an overall mean of 9.2. The proportion of buds that were actively growing increased rapidly within the first few weeks after decapitation, reaching a peak at weeks 2 to 4, then declining thereafter. This overall pattern of response was exhibited by all seedlings, although variation was recorded between provenances and progenies in the timing and maximum value of peak bud activity. For example, peak bud activity in the San Carlos and Turrialba provenances was recorded at week 2, whereas in the other 3 provenances, maximum values were recorded at week 4 (*Fig. 1*).

Overall, significant differences in maximum bud activity were recorded between provenances ($P < 0.001$; ANOVA) at weeks 2 and 4. The maximum bud activities recorded in the 5 provenances ranged from 17.7% (Hojancha) to 24.2% (Turrialba) (*Fig. 1*). The maximum bud activity of the different progenies within each provenance was generally recorded at the same week, although in the case of San Carlos, peak values were recorded in 3 progenies at week 2, and in the other 4 at week 4. Pronounced differences between progenies in percentage bud activity were recorded at both weeks 2 and 4 ($P < 0.001$; ANOVA). Maximum bud activity ranged between 13.6% (progeny 1920) and 32.3% (progeny 1932) at week 4 (*Fig. 2*). The most striking variation between progenies within a provenance was observed in the Turrialba provenance, where progeny mean values ranged from 14.9% (progeny 1935) to 32.3% (progeny 1932).

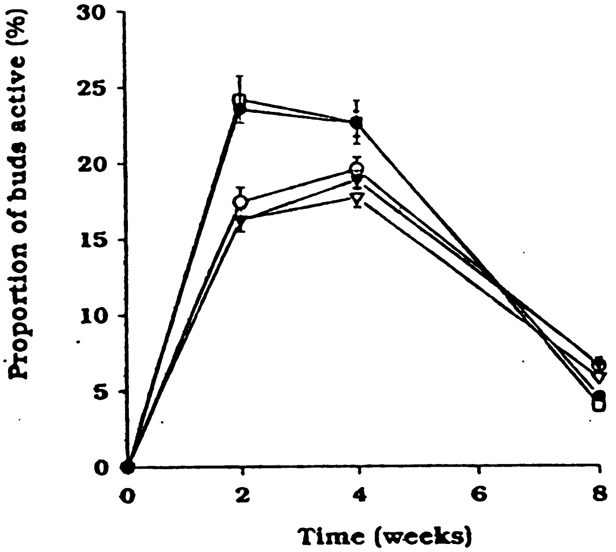

Figure 1. – The percentage bud activity of *Cedrela odorata* seedlings following decapitation in a nursery trial at CATIE, Costa Rica. Values presented are provenance means ($n > 216$); vertical bars represent s.e.m. Symbols: hollow circles, Cañas; filled circles, San Carlos; hollow triangles, Hojancha; filled triangles, Carmona; empty squares, Turrialba.

Dominance ratio increased rapidly in the first 4 weeks after decapitation, declining gradually thereafter (*Fig. 3*). The same trends were observed in all provenances, with maximum values recorded in all provenances at week 4. At this time, differences between provenances were not statistically significant ($P > 0.05$; ANOVA), values ranging from 31.7 (San Carlos) to 41.6 (Carmona). However, differences between progenies were highly significant at week 4 ($P < 0.001$; ANOVA); values ranging from 17.8 (progeny 1939) to 69.9 (progeny 1935). Again, pronounced variation between progenies within provenances was recorded, particularly in the case of the Turrialba provenance where values ranged from to 19.1 (progeny 1932) to 69.9 (progeny 1935) (*Fig. 4*). When examined by correlation, dominance ratio was found to be negatively correlated with percentage bud activity at week 4 ($r = 0.65$, $P < 0.001$)

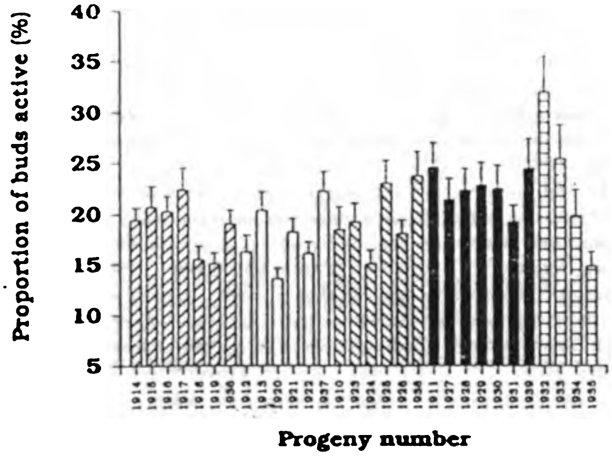

Figure 2. – Variation in percentage bud activity of *Cedrela odorata* seedlings 4 weeks after decapitation in a nursery trial sited at CATIE, Costa Rica. Values presented are progeny means ($n = 54$); vertical bars represent s.e.m. The progenies are arranged by provenance: right hatching, Carmona; hollow bars, Hojancha; left hatching, Cañas; solid bars, San Carlos; horizontal hatching, Turrialba.

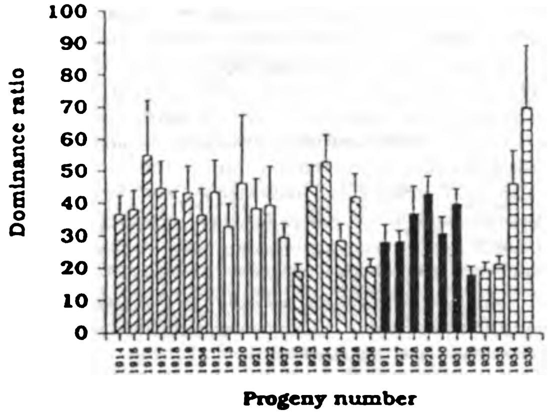

Figure 4. – Variation in dominance ratio of *Cedrela odorata* seedlings 4 weeks after decapitation in a nursery trial sited at CATIE, Costa Rica. Dominance ratio was calculated as the length of the dominant shoot: the mean length of the sub-dominant shoots (see text). Values presented are progeny means ($n = 54$); vertical bars represent s.e.m. The progenies are arranged by provenance: right hatching, Carmona; hollow bars, Hojancha; left hatching, Cañas; solid bars, San Carlos; horizontal hatching, Turrialba.

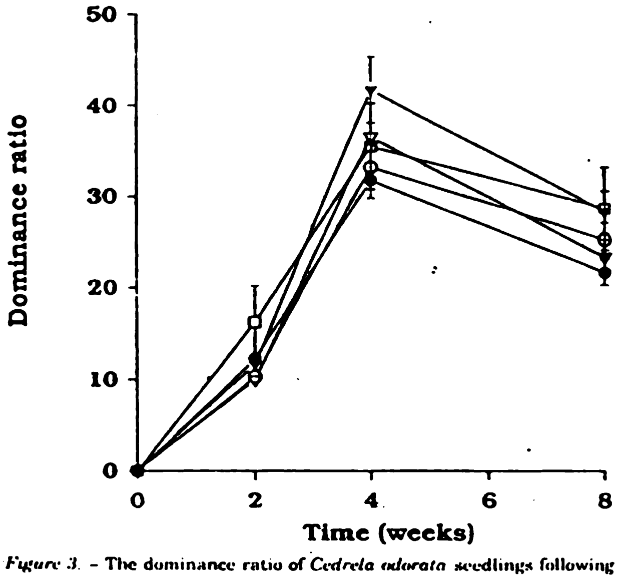

Figure 3. – The dominance ratio of *Cedrela odorata* seedlings following decapitation in a nursery trial at CATIE, Costa Rica. Dominance ratio was calculated as the length of the dominant shoot: the mean length of the sub-dominant shoots (see text). Values presented are provenance means ($n > 216$); vertical bars represent s.e.m. Symbols: hollow circles, Cañas; filled circles, San Carlos; hollow triangles, Hojancha; filled triangles, Carmona; empty squares, Turrialba.

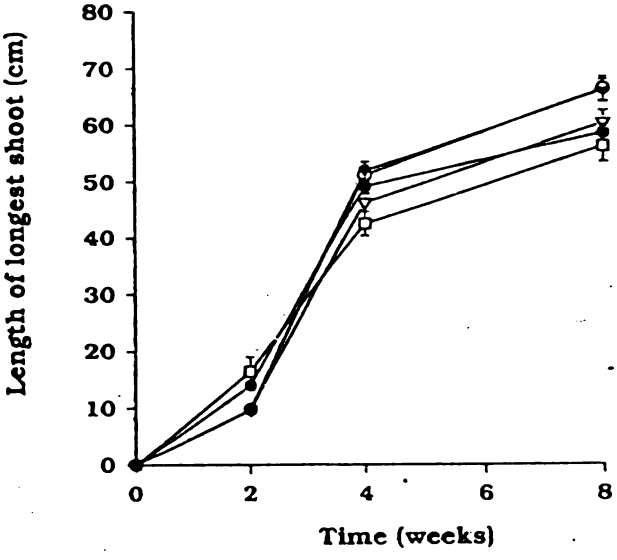

Figure 5. – The maximum shoot length of *Cedrela odorata* seedlings following decapitation in a nursery trial at CATIE, Costa Rica. Values presented are provenance means ($n > 216$); vertical bars represent s.e.m. Symbols: hollow circles, Cañas; filled circles, San Carlos; hollow triangles, Hojancha; filled triangles, Carmona; empty squares, Turrialba.

The length of the longest shoot increased continually throughout the period of assessment, with highest rates of increase recorded between weeks 2 and 4 (*Fig. 5*). A similar trend was recorded in all provenances. Differences between the provenances were highly significant ($P = 0.001$; ANOVA) at week 8, mean values ranging from 56.2 cm (Turrialba) to 66.4 cm (Cañas). Significant variation was also recorded between progenies ($P < 0.001$; ANOVA), mean values ranging from 43.9 cm (progeny 1920) to 94.6 cm (progeny 1938).

Discussion

Previous investigations of apical dominance in young plants have identified 2 phases of bud activity following decapitation: the "Sprouting Phase", in which buds are released from correlative inhibition, and the "Dominance Phase", in which the uppermost lateral shoots begin to suppress the growth of lower shoots (LEAKEY and LONGMAN, 1986). Lower bud activities are associated with relatively strong apical dominance (LADIPO *et* *al.*, 1991b). In *Triplochiton scleroxylon*, the Sprouting Phase generally lasts for the first 3 weeks to 4 weeks after decapitation, when peak values of bud activity are obtained (LADIPO *et al.*, 1991b; LEAKEY and LONGMAN, 1986). This pattern of response seems to be consistent in *T. scleroxylon*, whether the plants are grown under controlled environment conditions or in the nursery (LADIPO *et al.*, 1992). However, the reimposition of dominance in *T. scleroxylon*, indicated by the decline in bud activity after week 4, has not so far been recorded in nursery-grown plants, perhaps reflecting the relatively high nutrient availabilities in such conditions (LADIPO *et al.*, 1992).

The response of *Cedrela odorata* to decapitation was strikingly similar to that reported previously for *T. scleroxylon*, with peak bud activities recorded in weeks 2 to 4, and a subsequent decline in activity recorded at week 8. These results indicate that both the pattern and timing of the response to decapitation are common to more than one species; further investigations are clearly required to define how general these responses are in tropical trees. In comparison with results from *T. scleroxylon*, the values of percentage bud activity recorded here were relatively low, reaching a maximum of 32.3% as a progeny mean. Bud activity values in many of the experiments reported by LEAKEY and LONGMAN (1986) were in a similar range to those recorded here, but those reported by LADIPO *et al.* (1991b, 1992) were generally far higher, reaching maxima of over 80% in some cases. To a large extent this must reflect the conditions under which the plants were grown, as maximum bud activity is sensitive to a range of environmental factors, such as photoperiod (LEAKEY and LONGMAN, 1986), irradiance and humidity (LADIPO *et al.*, 1992). Bud activity is particularly sensitive to nutrient availability: when decapitated plants of *Triplochiton scleroxylon* were treated with 4% or 0,04% nutrient solutions, maximum bud activity in the high nutrient treatment was found to be almost double that in the lower treatment (LADIPO *et al.*, 1991b). In the current investigation, the fact that the seedlings were grown in standard nursery soil with no additional fertilizer may account for the relatively low percentage bud activities recorded. In a preliminary experiment carried out under glasshouse conditions in the UK, with high rates of nutrient addition, a maximum percentage bud activity of over 90% was recorded in *Cedrela odorata* (A. C. NEWTON, unpublished data). Despite the sensitivity of bud activity to environmental conditions, the results of decapitation tests in both controlled environments and nursery conditions appear to be consistent (LADIPO *et al.*, 1992); even though maximum bud activity may vary under different treatments, the ranking of genotypes is maintained (LADIPO *et al.*, 1991a).

The pattern of increase in dominance ratio was also similar to that recorded previously for *Triplochiton scleroxylon* (LEAKEY and LONGMAN, 1986), with a rapid increase during the first 4 weeks after decapitation. However, the subsequent decline in dominance ratio recorded in all provenances at week 8 was at variance with previous results; this may be attributed to the general decline in the rate of shoot growth recorded at the same time, perhaps reflecting the decline in nutrient reserves in the pots. In general, values of dominance ratio were far higher than in *T. scleroxylon*, where a maximum value of 9.6 was recorded previously (LEAKEY and LONGMAN, 1986). Mechanisms of dominance relationships between shoots are not well understood, but appear to be related to rates of shoot growth, which are influenced by gibberellin concentration (PHILLIPS, 1969). LEAKEY and LONGMAN (1986) observed that in *T. scleroxylon*, dominance ratio was increased by application of gibberellin (GA_3), at least within the first 4 weeks after decapitation.

The genetic variation in apical dominance recorded in this investigation highlights the scope for selection of this characteristic in *Cedrela odorata*. Although differences in bud activity between provenances were relatively slight, with the highest value recorded being 36% greater than the lowest, differences between progenies were more pronounced, the highest value being 138% greater than the lowest. This does not take account of the additional variation that exists at the level of individual genotypes: for example, percentage bud activity in 26 clones of *Triplochiton scleroxylon* from a variety of geographical origins varied between 16% to 75% (LEAKEY and LADIPO, 1987). The results presented here suggest that a similar degree of variation may exist within *Cedrela odorata*, particularly if growth conditions were used enabling a wider range of bud activities to be expressed. The differences between provenances recorded here are of particular interest; peak bud activities in the Turrialba and San Carlos provenances were significantly higher than in the other 3. These differences in response correlate with the geographic location of these provenances: while San Carlos and Turrialba are located on the humid Atlantic region of Costa Rica, the other 3 provenances are located in the drier Pacific zone. The apparently higher apical dominance in the Pacific provenances is surprising, given that the mature trees in this area generally appear to be inferior in form to those growing in the Atlantic region (A. C. NEWTON, personal observation).

The value of apical dominance as a selection criterion depends on its relationship to tree form. LEAKEY and LADIPO (1987) found a strong correlation ($r = 0.76$; $P = 0.001$) between percentage bud activity and the total number of branches formed by clones of *T. scleroxylon* after 4 years growth in a clonal plantation. This indicates that decapitation tests could be used as an early predictive test for branching frequency (LEAKEY, 1985; LEAKEY and LADIPO, 1987). Although percentage bud activity has received greatest attention in this context, the potential use of dominance ratio is supported by the significant correlation between these 2 variables recorded in the present investigation. LEAKEY and LADIPO (1987) proposed that decapitation tests could be used to screen a large number of seedlings, which could then be selected and vegetatively propagated for establishment in clonal tests. Following this suggestion, a large-scale screening of *Triplochiton scleroxylon* seedlings has recently been completed in Cameroon (LADIPO *et al.*, 1994). The advantage of screening seedlings in a progeny test design, as in the current investigation, is that genetic values may be estimated for the individual progenies, which may then form the basis of selection.

Decapitation tests may be of particular value in selection for the genetic improvement of *Cedrela odorata* as the removal of the apical portion of the shoot effectively simulates shoot borer attack. The problems with this pest are probably the main constraint to establishment of *Cedrela odorata* in plantations within its natural distribution (NEWTON *et al.*, 1993a). Further information is clearly required on the relationship between decapitation test results and the eventual field performance of *Cedrela odorata* genotypes, particularly with respect to response to shoot borer attack. If genotypes with the ability to recover from attack by strong apical growth could be identified at an early stage, this would greatly accelerate the genetic improvement process. Experiments to relate decapitation test results to eventual field performance of *Cedrela odorata* are currently being planned at CATIE in Costa Rica.

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THE INTERNATIONAL PROVENANCE TRIAL OF CORDIA ALLIODORA (R & P) OKEN IN COSTA RICA

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ABSTRACT

As part of the international provenance trials of Cordia alliodora coordinated by the Commonwealth Forestry Institute (CFI), Oxford, results are presented for a provenance trial on two sites in Costa Rica at four years. Traits evaluated at the nursery stage were height, diameter at soil level, number of days to first germination, root length and shoot/root length ratio. Germination rate appeared to be under strong genetic control with dry zone provenances germinating and growing initially more quickly than wet zone provenances. There was no apparent correlation between nursery growth and growth in the field.

Traits evaluated at the field stage were survival, height, diameter at breast height, stem form, forking, incidence of canker, flowering, bark type and thickness. Few significant differences were present between provenances due to large residual components of variation. The Limon (Costa Rica) provenance was highly susceptible to attack by the canker Puccinia cordiae. Two bark types were distinguished; the "smooth" type characterised by a thinner bark than the "rough" type. The "smooth" tended to be associated with wet zone provenances and the "rough" with dry zone provenances.

Recommendations are made with regard to the applicability of results to provenance selection of C. alliodora within Costa Rica and traits to be studied in more intensive assessments of the international trials.

INTRODUCTION - TRIAL BACKGROUND AND FORMULATION

Cordia alliodora Cham. is a well known tree in tropical and subtropical zones of Latin America and parts of the Caribbean, its timber being used for a wide variety of purposes. In Central America natural regeneration is generally profuse and is often maintained by farmers in combination with various perennial crops. It has been planted in trials in many countries. Reported growth has been excellent in some countries and led to the establishment of plantations, e.g. in Vanuatu (Bennett, 1980). In other countries growth has been variable to poor sometimes with disappointing final yields (Stead, 1980; Anon., 1983).

The FAO Panel of Experts on Forest Genetic Resources categorised C. alliodora as a very important species for wood production and in urgent need of botanical and genecological exploration, collecting and testing (FAO, 1977). The Commonwealth Forestry Institute (CFI), Oxford, initiated a programme of international provenance trials of C. alliodora in 1977, collecting seed from the natural range, mainly in Central America (Stead, 1979; 1980).

This paper reports the results of a provenance trial on two sites in Costa Rica at four years established with the CFI collections by CATIE (Tropical Agriculture Centre for Research and Training) in 1979. The paper also reports on data taken at the nursery stage, both for the sites established in 1979 and for new sites established in 1982-83. The trials on these latter sites include collections of other provenances within Costa Rica by CATIE.

Provenance Source Details

Details of the provenances in the trials and sources of information are given in Table 1. Other sources of information were used where the data was thought to be more representative of site conditions than those on the CFI site description sheets.

For the CFI seed collections, sites were selected to cover the range of observed altitudinal and habitat preference with particular attention to wet Atlantic and dry Pacific provenances. Collections were made in an area of about one square kilometre, combining equal quantities of seed from at least 25 trees (Stead, 1980). The 1977/78 Costa Rican collections included in the CFI trials were made from four to ten trees with no information given on distance between sampled trees or the proportion of seed from each sampled tree to give the bulk collection.

The 1981-83 CATIE collections in Costa Rica were made with equal quantities of seed from ten to 20 trees with 50-2000 metres between sampled trees.

Trial Site Descriptions

Details for the two sites are given in Table 2. The climatic conditions for the nursery where the plants were raised are the same as for Florencia Sur. Florencia Sur is situated on a south facing 35-45% slope previously occupied by Toona ciliata and Pinus caribaea var. hondurensis. Ground cover consists mainly of Panicum maximum, a tall bunch grass. La Suiza is situated on a south facing 50% slope previously occupied by an abandoned coffee plantation. Ground cover consists mainly of the stoloniferous grass Melinis minutiflora.

Trial Design - Nursery Stage

There was no formal experimental design for the 1978 or 1982-83 sowings in the nursery. Each seed lot was germinated in a separate compartment in the same nursery bed. Sowing in 1978 was at an approximate density of 12,000 seeds per m^2 whereas in 1982-83 it was 2-2,500 seeds per m^2 of nursery bed. Density was much higher where percentage germination of a lot was known to be low.

Spacing in the beds at pricking out was 17 x 17 cm in 1978, 15 x 15 cm in 1982 and 22.5 x 22.5 cm in 1983. Each provenance was pricked out into a number of different nursery beds, so although there was no formal replication each bed contained a number of provenances. It is therefore probable that in comparing growth of the provenances in the nursery the individual bed effect is small.

Trial Design - Field Stage

The field design was based on that suggested by the CFI to collaborators. Details are given in Table 3. At La Suiza smaller plots were used for lack of planting stock. At each site the outer row of trees in each plot is considered as border and so the inner 25 and 9 trees are measured at sites Florencia Sur and La Suiza respectively. One and three rows of external surround trees are planted at Florencia Sur and La Suiza respectively.

Trial Management - Nursery Stage

In 1979 the seed was sown in beds composed of a mixture of the original nursery soil (a clay loam), dried lake mud and sand in the approximate proportion of 6:3:1. The seed was covered with a thin layer of soil sufficient to prevent removal of the seed by wind. The beds were shaded by plastic netting of +50 percent density. For the 1983 sowings, seed was sown in wooden boxes (40 x 30 x 10 cm) filled with a 2:1 mixture of dried lake mud and sand. The boxes were maintained in the nursery greenhouse which gives approximately 50 percent density shade.

The seedlings were pricked out into unshaded beds of the same soil composition when the first true leaves appeared.

Trial Management - Field Stage

The trees previously occupying Florencia Sur, were felled and the remaining vegetation slashed back to ground level. Immediately prior to planting glyphosate (6.7 l/ha) was applied to the main area and paraquat (1.0 l/ha) to a smaller part. La Suiza was cleared manually by slashing back existing vegetation to ground level.

The plants were prepared for planting as stumps by cutting back the shoot to 25-30 cm and the root to 15-20 cm, but leaving some root hairs. Stem diameters at soil level were 1-3 cm. The stumps were planted manually and a one metre circle around each plant was cleared by spade at the same time.

Weeding has been generally manual whenever the surrounding vegetation reached tree height or to facilitate measurements. Frequency was four times per year in the first three years at Florencia Sur. La Suiza was cleared twice in the first year and three times in the second and third.

As the trees were stump planted it was necessary to select the best resprout and this was done at twelve months. Not all trees had more than one principal resprout and very few had three. On a good site it is probably better to do the selection earlier (about eight months) as some of the shoots removed were more than four metres tall. Further resprouting occurred on some trees and it was necessary to do another selection at two years of age.

No pruning has been carried out nor is it envisaged for the trial. C. alliodora in its natural state is moderately self pruning and in plantations there is therefore little need for pruning. No fertilizer was applied nor have any thinnings been made so far.

ASSESSMENTS AND RESULTS

Traits assessed - at nursery stage

For the seed sown in 1978 the following traits were assessed.

1. Number of days to first germination.
2. Total height at nine months of age - measured on approximately 18 plants per provenance.

For the seed sown in 1982-83 the following traits were assessed.

1. Number of days to first germination.
2. Total height - measured bi-weekly from four-seven months of age on 25 randomly selected plants per provenance per bed.
3. Diameter at soil level - measured bi-weekly as for total height.
4. Root length - measured at eight months of age on 20 plants per provenance.
5. Shoot/root length ratio - measured at eight months on the same plants as for root length.

Traits assessed - at field stage

The following assessments have been made so far:

Florencia Sur

1. Total height at 14 months of age in field.
2. Diameter at breast height (DBH) and total height at 25 months.
3. DBH, total height and stem form at 37 months.
4. Number of trees flowering/seeding at 32, 43 and 52 months.
5. Bark type at 52 months.
6. Occurrence of canker - Puccinia cordiae (P.Henn) Antheus, at 52 months.
7. Bark thickness - taken only for five trees in four selected provenances, at 45 months and 48 months.

La Suiza

1. DBH and total height at 25 months.
2. DBH, total height and stem form at 37 months.

The stem form assessment was an ocular estimation in three classes: 1) straight 2) sinuous 3) very sinuous. Assessment at both sites was carried out by the same person.

The bark type assessment was in two classes 1) rough - bark rough and strongly fissured 2) smooth - bark smooth without fissuring.

The rust P. cordiae causes large stem cankers which reduce stem quality and hence marketable timber (Briton-Jones, 1930; Marshall, 1930). The same or a similar disease is endemic to Costa Rica. The occurrence of canker at Florencia Sur was evaluated due to its high incidence in a nearby stand of older naturally regenerated trees standing over coffee.

Summary of latest results

Nursery stage

Table 4 shows the number of days to first germination for each provenance in the various sowings.

Table 5 presents mean values for total height from two different plantings in the nursery and for diameter at soil level for one planting. Figures 1 and 2 show the mean height growth of provenances over a period of 130-215 days after sowing. The provenances have been split into two groups to aid clarity and interpretation of the graphs. Figure 3 shows the mean diameter growth of the provenances over the same period. All provenances have been included in Figure 3 because of the apparent similarity of growth patterns.

Table 6 gives mean values for root length and shoot/root length ratio based on 20 measured trees per provenance.

Field stage

Tables 7, 8 and 9 show the analyses of variance and Tukey multiple range tests for the various traits assessed on the two sites. The growth and form of C. gerascanthus with many multiple stems was noticeably poorer than the provenances of C. alliodora. Due to the large differences between this and the provenances of C. alliodora it was omitted from the analyses so any significant differences found were due to provenance and not to species differences. Table 10 presents combined analyses of variance for the five C. alliodora provenances common to both sites.

The data were analysed using the program ANOVAR which also carries out Bartlett's test to look for heterogeneity of variance and the Tukey multiple range test. The arcsine transformation was used on survival percentage data when Bartlett's test showed heterogeneity of variance in the original data. For survival at Florencia Sur the arcsine transformation eliminated the heterogeneity but failed to do so for the combined site analysis.

Table 11 shows the mean percentage of trees flowering over three flowering seasons at Florencia Sur. No tests were made on the viability of the seed produced over the period. Results for the assessment of the incidence of canker and bark type are given in Table 12. Neither sets of data were analysed further than provenance means. In the case of canker incidence the high susceptibility of the Limon provenance compared to other provenances obviated the need for further analysis. The distribution of values for the bark type assessment was highly abnormal even with application of the arcsine transformation, thus invalidating any analysis of variance. It was felt that presentation of mean values and ranges would be as instructive as the results from any more complicated analysis.

The bark thickness measurements were made on only a small sample (five trees from each of four provenances, Tres Piedras, San Francisco, El Chilero and Limon) as part of a study on growth rhythms. A small sample 't' test was carried out to see if the apparent difference between means for the two bark types was significant. Calculation of the variance ratio indicated that the two samples could be compared by use of the small sample 't' test are shown in Table 13.

Discussion of Results

Nursery Stage

Examination of Table 4 suggests a separation into two groups of fast and slow germinators, with the climatic data in Table 1 indicating a correlation with the presence or absence of a pronounced dry season. This separation can also be seen to a certain extent in Figure 1 where the provenances Tres Piedras, Esteli and El Chilero showed a rapid initial growth in height followed by a decline in rate. In contrast San Francisco and all the Costa Rican provenances from uniform rainfall climates, showed a slow initial rate of height growth which increased with time (See Figures 1 and 2).

Seed fall of C. alliodora in Central America appears to coincide roughly with the end of any dry season and the onset of rains (see climatic records and dates of the CFI collections). Rapid germination and initial growth of provenances from areas with pronounced dry seasons would offer the best possibilities for good establishment of a plant before the next dry season begins. That the characteristic is apparent under the ideal conditions of a nursery would suggest that it is under strong genetic control.

Some provenances e.g. La Fortuna and La Pineda, although showing rapid germination, failed to show an initial rapid growth followed by a decline in rate. Neuva Guinea appears to show characteristics similar to the Costa Rican and San Francisco provenances with a slower germination and constant height growth rate.
Diameter growth (Figure 3) failed to show any differences in pattern between provenances. What was apparent was the general reduction in diameter increment after 175 days, although the plants were only approximately 1 cm in diameter. This would suggest that the 15 cm spacing was indeed too close to permit the quickest possible production of plants of a suitable size (1-2 cm diameter) for planting. C. alliodora planted in the nursery during 1983 at 22.5 x 22.5 cm produced adequate sized plants after seven months with an apparent reduction in the number of suppressed and unusable plants. The 22.5 cm square spacing would appear to be more suitable for C. alliodora in nursery beds.

Of interest is the poor nursery growth, both in 1979 and 1982, of the San Francisco provenance which in the field has so far shown the best growth. In contrast two of the provenances, Tres Piedras and Esteli, which show good initial nursery growth are the poorest performers in the field.

The data for root length also appear to separate the dry and wet zone provenances, the former generally showing a longer primary root presumably in adaptation to the lower water availability. The shoot/root length ratio data fails however to show any distinct trends or groupings, dry and wet area provenances being distributed fairly evenly through the range of values. These root data should be interpreted with great caution as only one sample was taken per provenance and in many cases the samples came from different nursery beds.

A replicated nursery experiment is now being carried out to confirm or change these initial findings.

Field stage

Looking first at Tables 7 and 8 it is noticeable that there are few significant differences due to between-provenance effects. At Florencia Sur the two large sources of variation were the replications and the residual. The differences between replicates appear to be a result of within site changes and suggested that good growth of C. alliodora is very site specific. The lack of between-provenance differences at Florencia Sur could be due to either a large provenance x replicate interaction due to the large variation between replicates or the existence of a greater within than between-provenance variation. Analysis of variance carried out on individual tree data showed there to be generally a large provenance x replicate interaction which even considering heterogeneity of residual variance, is likely to be real and to obscure any possible between-provenance differences.

La Suiza was apparently more uniform with little difference between replicates. There was still a large residual component of variation, but that due to provenances was greater at Florencia Sur and approached significance in most cases. The plots at La Suize with nine measured trees, may not be sufficient to give a good estimate of the mean and could partially explain the large residual component of variation.

It would appear that three years of age is too early for significant differences to occur between provenances on these two sites. Other results from Colombia suggest that about three years are needed before significant differences occur between provenances of C. alliodora. Venegas (1981) for a CFI trial in the Tumaco region of Colombia (altitude 20 metres, mean annual precipitation approx. 3000 mm, no dry season) reported differences between provenances significant at 99 percent probability for height, DBH, form, forking and survival at three years of age. In the Choco region of Colombia (similar climate to the Tumaco region) at two different sites, (alluvial terrace and hillside) significant differences were found between provenances for height, DBH and survival at three years and older. Little or no difference was found on the hillside site at 14 months whilst no measurements are reported before 3.5 years of age on the alluvial terrace (Anon, 1983).

Despite the lack of significant differences in Tables 7 and 8 certain trends were noticeable in provenance performance. San Francisco showed a mean height one metre greater than any of the other provenances at three years of age. The excellent performance of this provenance is also reported for two of the three Colombian sites mentioned above, though it performed poorly on the hillside site. Two provenances that have performed well on other sites, La Pineda and La Fortuna showed good growth at Florencia Sur though the latter has not performed so well at La Suiza.

Two of the provenances from particularly dry areas, Esteli and Tres Piedras have shown the poorest growth on both Costa Rican sites and on two of the three Colombian sites, suggesting that they are not suitable for sites with a climate of uniform rainfall.

The performance of the two provenances El Chilero and Limon was of interest. At both sites which are close to the altitudinal limit of C. alliodora in Costa Rica, El Chilero (a high altitude provenance from Guatemala) had mean height and diameter about the same as Limon from sea level in Costa Rica. In contrast, in the Colombian trials which are situated at low altitudes, Limon consistently out performs El Chilero by a wide margin. The only other existing data on provenances of C. alliodora in Turrialba (see Table 14) not surprisingly suggest that Limon is the least promising Costa Rican provenance on sites around 600 metres.

The poorer growth at La Suiza compared to Florencia Sur may be a result of poorer soil and/or the presence of Melinis minutiflora as part of the ground cover. The soil at La Suiza has a high percentage content of clay, high levels of aluminium and manganese and low levels of phosphorous, potassium and calcium whereas Florencia Sur has a much lower clay content, and higher levels of aluminium and manganese and low levels of phosphorous, potassium and calcium (see Annex 1). Of these soil factors the most likely to reduce growth are the high clay content, low phosphorous and the possible toxic effect of high manganese levels. M. minutiflora has been identified as having an allelopathic effect on nursery size plants of C. alliodora (Marinero, 1964) and it may be that its presence at La Suiza affected growth in the first three years.

The combined site analyses (Table 10) showed significant differences between provenances and for replicates in sites but failed to show any significant provenance x site interaction. Although soil conditions differ for the two sites, climatic conditions are almost identical. It will probably be necessary to look at more varied sites, such as low and high elevations or monsoonal versus aseasoral climates, to find such interactions in C. alliodora.

The analyses of stem form (Table 9) showed no differences between provenances. The small number of stem form classes used probably made consistent scoring easier but made between provenance differences less likely. Stem form appears to be worse at La Suiza than Florencia Sur, suggesting an environmental influence on this trait. The high percentage of forking shown by the provenances Esteli and El Chilero was consistent with the results report by Venegas (1981) from Colombia, as are the low percentage of forking shown by Limon.

The flowering at an early age of Esteli is apparent from Table 11, though no clear pattern emerges from the other provenances. The high susceptibility of the Limon provenance to canker attack at an early age was clear and it would seem to exclude the use of this provenance from any areas where P. cordiae is endemic. It will be of interest to see in future years if more trees are attacked and if other provenances show susceptibility or resistance.

The ocular classification into the two bark types "smooth" and "rough" appeared to be of use. The 't' test (Table 13) showed "smooth" barked trees to have a thinner bark than "rough" barked ones. Table 12 would suggest that rough bark and consequently thicker bark is a characteristic associated with provenances from the drier zones. The wide variation between minimum and maximum values for dry zone provenances and the small variation found in the wet zone provenances may be due to genotype-environment interaction. Under the uniform rainfall conditions at Florencia Sur the percentage of smooth barked trees may thus be increased.

IMPLICATIONS FOR THE FUTURE STRATEGY

It is obvious that sound recommendations on provenance selection for plantations in Costa Rica cannot be based on the results up to three years of age. As the sites reported on in this paper include only one Costa Rican provenance (a lowland one on upland sites) it would be unwise to recommend a particular exotic provenance for Costa Rica until other native provenances have been adequately tested. To this end a wider range of sites within Costa Rica were planted in 1982-83 including a greater range of Costa Rican provenances. Due to bad collection technique and treatment of the seed supplied from Costa Rica to the CFI the Costa Rican provenances had a low percentage germination and are often poorly represented in the CFI trials in other countries (CATIE, 1980). For any country with a serious interest in planting C. alliodora it would be worthwhile to test more Costa Rican provenances. (CATIE usually has seed available from at least three Costa Rican provenances).

The nursery stage results reported here suggest that it will not be possible with C. alliodora to correlate provenance nursery performance with later growth in the field. It will be of use for breeding strategy to evaluate if this lack of correlation applies also to individual trees within provenances.

The field results make it apparent that a number of traits and site characteristics will have to be considered before provenance selection can be made. For example, susceptibility/resistance to P. cordiae will be highly important where the disease is prevalent or likely to occur, but of reduced importance in other zones. Similarly susceptibility/resistance to misteltoe attack will be of importance in some zones of Costa Rica where it is fatal in extreme cases (Johnson and Morales, 1972).

It was noticeable that certain provenances flower at an earlier age than others. It will be of interest to try and correlate flowering with growth of individual trees within provenances and see if the expression of this trait varies from site to site. Time of leaf fall and flushing, though not evaluated here, appears to be another trait of importance. Blake et al. (1976) suggested that moisture stress is limiting in shoot formation and hence in crown size, indirectly affecting diameter growth. They suggested that stand production might be improved by the selection of late flushing trees which deveop when moisture stress is least. The CFI trials offer an ideal opportunity to test this theory, the effect of climate on the trait and as to whether there are differences between provenances or between trees within provenances.

The bark type classification appears to offer potential for use in selection, obviating the need for the more time consuming use of a bark gauge, provided the correlation for type and bark thickness holds for other climates. These two traits should be assessed in the CFI trials to see how climate affects bark type and thickness for provenances.

From the results presented here and from Colombia (Venegas, 1981; Anon, 1983) it appears that provenance differences take at least three years to appear. Bearing this in mind, five to six years of age is probably the most appropriate age for more intensive assessments of the CFI trials to be made. After five to six years thinning will become necessary and there will be a consequent loss of possible information from the trials.

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Table 1 Details of the provenances of *Cordia alliodora* [illegible]

Sources of information: CFI - [illegible]
[illegible]
[illegible]
[illegible]

Provenance	No. CFI	No. [illegible]	Source of information	Latitude	Longitude	Altitude metres above sea level	Mean annual precipitation mm	No. of dry months (< 100 mm)	Mean daily temp °C	No. of Repetitions in sites of Costa Rica: Flor. Sur	La Suiza
Finca El Chilero, Guatemala	41451077	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	5	5
Finca Rincón Alegre, Guatemala	41663078	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]		
Tres Piedras, Honduras	41440977	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	5	5
Finca La Fortuna, Honduras	41511977	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	5	5
San Francisco, Honduras	41532077	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	5	-
Estelí, Nicaragua	41461477	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	5	5
Finca La Pineda, Nicaragua	41521877	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	5	
Nueva Guinea, Nicaragua	41673378	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	-	
Turrialba, Costa Rica	5178	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]		-
Turrialba, Costa Rica	-	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]		
Turrialba, Costa Rica	3277	-	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]		
Limón, Costa Rica	3377	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	5	5
Limón, Costa Rica	5278	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]		
San Carlos, Costa Rica	5378	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]		-
San Carlos, Costa Rica	-	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	-	-
San Carlos, Costa Rica	3477	-	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	-	-
Guápiles, Costa Rica	-	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]		-
Esparza, Costa Rica	-	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]		
C. gerascanthus, Estelí, Nicaragua	41471677	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	5	5

TABLE 2 - TRIAL SITE DESCRIPTIONS

Site	Latitude	Longitude	Altitude (metres)	Mean Annual Precipitation mm	Mean daily temp. °C
1. Florencia Sur, CATIE	09°53'N	83°40'W	620	2674	22.2
2. Finca, Colegio Agropecuario de La Suiza, Turrialba	09°51'N	83°37'	680	2674	22.2

For soil classifications and analyses see Annex 1

TABLE 3 - DETAILS OF THE FIELD DESIGN OF SITES 1 AND 2

Site	Date of planting	Design	No. of Repetitions	No. of trees per plot	No. of provenances	Spacing in metres
1. Florencia Sur	01/08/79	RCB	5	49 (7 x 7)	8	2.5 x 2.5
2. La Suiza	17/10/79	RCB	5	25 (5 x 5)	6	2.5 x 2.5

RCB - randomized complete block

TABLE 4. NUMBER OF DAYS TO FIRST GERMINATION

[illegible]

Provenance	Number	Date of sowing 4/8/78	5/3/82	2/3/83	29/6/83	24/11/83
Finca El Chilero, Guatemala	41451077	12	12	11	9	13
Finca Rincón Alegre, Guatemala	41663078	-	12	-	10	14
Tres Piedras, Honduras	41440977	12	12		10	12
Finca La Fortuna, Honduras	41511977	12	14		12	16
San Francisco, Honduras	41532077	12	16	13	14	18
Estelí, Nicaragua	41461477	9-11*	13	11	10	15
Finca La Pineda, Nicaragua	41521877	9-11*	14	11	11	15
Nueva Guinea, Nicaragua	41673378		18		-	-
Turrialba, Costa Rica	5178	-	18	-	-	-
Turrialba, Costa Rica	BLSF1165	-	19		13	
Turrialba, Costa Rica	3277	19	-	-	-	-
Limón, Costa Rica	3377	16	19	-	-	-
Limón, Costa Rica	5278		17	-	-	
San Carlos, Costa Rica	5378	-	17		-	-
San Carlos, Costa Rica	BLSF1164	-	17	15	18	20
San Carlos, Costa Rica	3477	14				
Guápiles, Costa Rica	BLSF1166		17	15	15	25
Esparza, Costa Rica	BLSF1537	-	-		19	17
C. gerascanthus, Nicaragua	41471677	8				

TABLE 5. GROWTH IN THE NURSERY FOR TWO PLANTINGS

		213-216 days after sowing (measured 4-7/10/82)				264 days after sowing (measured 25/4/79)	
Provenance	Number	mean height in cm	S.E.	mean diameter at soil level in mm	S.E.	mean height in cm	S.D
Turrialba, Costa Rica	BLSF1165	96	11	12	1.4	-	-
Finca Rincón Alegre, Guatemala	K1663078	87	18	11	[illegible]	-	-
Limón, Costa Rica	5278	87	10	10	[illegible]	-	-
Nueva Guinea, Nicaragua	K1673378	84	16	11	2.3	-	-
Finca El Chilero, Guatemala	K1451077	79	19	9	[illegible]	89	15
Finca La Pineda, Nicaragua	K1521877	78	20	9	2.4	96	19
Tres Piedras, Honduras	K1440977	77	22	10	2.5	70	20
San Carlos, Costa Rica	5378	71	12	9	1.2	-	-
San Carlos, Costa Rica	BLSF1164	70	22	10	3.4	-	-
Turrialba, Costa Rica	5178	64	15	9	2.3	-	-
Estelí, Nicaragua	K1461477	58	19	9	2.4	83	16
Limón, Costa Rica	3377	57	17	9	2.4	58	15
San Francisco, Honduras	K1532077	49	17	9	2.5	51	17
Guápiles, Costa Rica	BLSF1166	47	10	7	1.6	-	-
Finca La Fortuna, Honduras	K1511977	45	11	7	1.8	69	17
Turrialba, Costa Rica	3277	-	-	-	-	39	11
San Carlos, Costa Rica	3477	-	-	-	-	38	16
C. gerascanthus, Nicaragua	K1471677	-	-	-	-	47	14

Values rounded off to nearest whole number except standard error for mean diameter

Provenances ordered in decreasing mean height for 4-7/10/82   S.E. - Standard Error   S.D - Standard Deviation

TABLE 6. ANALYSIS OF VARIANCE AND TUKEY MULTIPLE RANGE TEST FOR ROOT LENGTH AND SHOOT/ROOT LENGTH RATIO IN THE NURSERY 8 MONTHS AFTER SOWING

	Degrees of Freedom	Root length F. ratio	Root length SIG	Root length CV	Shoot/Root Ratio F. ratio	Shoot/Root Ratio SIG	Shoot/Root Ratio CV
Provenances	13	16.2	***	43.2	26.1	***	55.6
Residual	266			56.8			44.4

*** - significant at p - 0.001

CV - % component of variance

Provenance	Number	Mean Root Length cm	Provenance	Number	Mean Shoot/Root length ratio
Tres Piedras	K1440977	46	Nueva Guinea	K1673378	4.6
Finca Rincón Alegre	K1663078	42	San Carlos	BLSF1164	4.4
Finca El Chilero	K1451077	41	Turrialba	BLSF1165	3.7
Estelí	K1461477	39	Finca La Pineda	K1521877	3.6
Finca La Pineda	K1521877	36	Limón	3377	3.4
Nueva Guinea	K1673378	35	San Carlos	5378	3.3
Limón	3377	34	Estelí	K1461477	3.2
Turrialba	5178	34	Turrialba	5178	3.0
Turrialba	BLSF1165	32	Finca Rincón Alegre	K1663078	2.9
San Carlos	BLSF1164	32	Finca El Chilero	K1451077	2.8
Finca La Fortuna	K1511977	29	Tres Piedras	K1440977	2.4
San Carlos	5378	27	Guápiles	BLSF1166	2.0
San Francisco	K1532077	26	Finca La Fortuna	K1511977	1.6
Guápiles	BLSF1166	25	San Francisco	K1532077	1.4

Tukey multiple range test: means joined by a line are not significantly different at p - 0.05

TABLE 7. ANALYSES OF VARIANCE FOR HEIGHT AT SITES 1 AND 2

Site 1 - Florencia Sur

		Height at 16 months			Height at 25 months			Height at 37 months		
	D.F.	F	SIG	CV	F	SIG	CV	F	SIG	CV
Replicates	4	11.06	***	52.4	9.10	***	50.2	8.33	***	46.8
Provenances	6	2.52	*	11.1	1.74	n.s.	6.4	1.99	n.s.	8.8
Residual	24			36.5			43.4			44.3

Site 2 - La Suiza

D.F.	Height at 25 months F	SIG	CV	Height at 37 months F	SIG	CV
4	3.75	*	28.4	2.26	n.s.	24.5
4	2.95	n.s.	20.1	3.43	*	18.0
16			51.5			57.5

		Height 16 months in cm	Height 25 months in cm	Height 37 months in cm
San Francisco	61532077	27 │	43 │	65 │
Finca La Pimada	61521677	25 │	36 │	53 │
Finca La Fortuna	61511977	23 │	37 │	54 │
Finca El Chilloro	61651077	22 │	35 │	51 │
Linda	3377	21 │	36 │	50 │
Esteli	61461477	17 │	31 │	44 │
Tres Piedras	61440977	17 │	26 │	39 │
C. all. provenance	61471677	16	15	20

		Height 25 months in cm	Height 37 months in cm
Finca El Chilloro	61651077	26 │	35 │
Linda	3377	24 │ │	32 │ │
Finca La Fortuna	61511977	24 │ │	31 │ │
Esteli	61461677	21 │ │	27 │ │
Tres Piedras	61440977	13 │	22 │
		9	13

Tukey multiple range test - means joined together by the same line are not significantly different at p = 0.05

*** - significant at p = 0.001 Provenance means are given to the nearest whole number

** - significant at p = 0.01

* - significant at p = 0.05

ns - not significant at p = 0.05

CV - % component of variance

TABLE 8. ANALYSES OF VARIANCE OF DBH AND SURVIVAL AT SITES 1 AND 2

Site 1 - Florencia Sur

		DBH at 25 months			DBH at 37 months			Survival at 37 months (Arcsine transformation)		
	D.F.	F	SIG	CV	F	SIG	CV	F	SIG	CV
Replicates	4	7.64	***	45.8	6.60	**	41.6	3.14	*	19.0
Provenances	6	1.02	n.s.	6.9	1.61	n.s.	6.6	2.50	*	18.7
Residual	24			48.2			52.0			62.3

Site 2 - La Suiza

	DBH at 25 months			DBH at 37 months			Survival at 37 months		
D.F.	F	SIG	CV	F	SIG	CV	F	SIG	CV
4	2.08	n.s.	14.3	1.03	n.s.	0.5	2.38	n.s.	21.1
4	2.50	n.s.	19.7	2.71	n.s.	25.6	1.18	n.s.	2.7
16			66.0			73.9			76.2

		DBH 25 months in mm	DBH 37 months in mm	Survival 37 months %
San Francisco	61532077	42 │	69 │	93 │
Finca La Pimada	61521677	35 │	60 │	90 │ │
Finca La Fortuna	61511977	38 │	61 │	86 │ │
Finca El Chilloro	61651077	31 │	56 │	83 │ │
Linda	3377	32 │	55 │	82 │ │
Tres Piedras	61440977	23 │	40 │	82 │ │
Esteli	61461477	26 │	49 │	76 │
C. all. provenance	61471677	5	9	53

		DBH 25 months in mm	DBH 37 months in mm	Survival 37 months %
Finca El Chilloro	61651077	25 │	45 │	78 │
Linda	3377	24 │	45 │	76 │
Finca La Fortuna	61511977	21 │	36 │	84 │
Esteli	61461477	15 │	34 │	72 │
Tres Piedras	61440977	9 │	22 │	67 │
		4	5	27

Tukey multiple range test - means joined together by the same line are not significantly different at p = 0.05.

*** - significant at p = 0.001 Provenance means are given to the nearest whole number

** - significant at p = 0.01

* - significant at p = 0.05

ns - not significant at p = 0.05

CV - % component of variance

TABLE 9. ANALYSES OF VARIANCE FOR STEM FORM AND FORKING AT SITES 1 AND 2

Site 1 - Florencia Sur

		Stem Form at 37 months			Forked Trees at 37 months		
	D.F.	F	SIG	CV	F	SIG	CV
Replicates	4	3.33	*	26.9	8.41	***	45.8
Provenances	6	1.66	n.s.	4.3	2.19	n.s.	11.1
Residual	24			68.9			43.1

Site 2 - La Suiza

	Stem Form at 37 months			Forked Trees at 37 months		
D.F.	F	SIG	CV	F	SIG	CV
4	3.34	*	29.6	1.05	n.s.	0.8
4	1.57	n.s.	7.3	1.1?	n.s.	10.8
16			63.1			88.4

		Stem Form Score	Forked Trees 37 months %
Linda	3377	[illegible] │	45 │
Finca La Fortuna	61511977	[illegible] │	37 │ │
Finca La Pimada	61521677	[illegible] │	37 │ │
Tres Piedras	61440977	[illegible] │	33 │ │
San Francisco	61532077	[illegible] │	33 │ │
Esteli	61461477	[illegible] │	26 │ │
Finca El Chilloro	61651077	[illegible] │	31 │

		Stem Form Score		Forked Trees 37 months %
Finca La Fortuna	61511977	[illegible]	Linda	[illegible]
Finca El Chilloro	61651077	[illegible]	Finca El Chilloro	79
Tres Piedras	61440977	[illegible]	Finca La Fortuna	50
Esteli	61461477	[illegible]	Tres Piedras	10
Linda	3377	[illegible]	Esteli	41

Tukey multiple range test - means joined together by the same line are not significantly different at p = 0.05

*** significant at p = 0.001

** significant at p = 0.01

TABLE 10. COMBINED ANALYSIS OF VARIANCE FOR SITES 1 & 2 FOR HEIGHT, DBH AND SURVIVAL

		df	Test against no.	Height at 25 months[1/] F	SIG	CV	Height at 37 months[1/] F	SIG	CV	DBH at 25 months F	SIG	CV	DBH at 37 months[1/] F	SIG	CV	Survival at 37 months[1/] (transformation Arcsine) F	SIG	CV
1	Sites	1	2	5.34	*	31.0	8.46	*	42.4	2.61	n.s	12.5	4.12	n.s	19.9	0.10	n.s.	0.0
2	Reps in Sites	8	5	5.60	***	29.4	4.90	***	22.4	4.30	**	23.4	3.31	**	22.3	3.55	**	31.9
3.	Provenances	6	4	3.66	*	7.7	3.25	*	5.9	3.43	*	10.7	3.15	*	9.7	1.16	n.s.	1.3
4.	Prov × Sites	6	5	0.36	n.s.	0.0	0.21	n.s.	0.0	0.34	n.s.	0.0	0.41	n.s	0.0	1.34	n.s.	4.5
5	Residual	32				31.9			29.0			47.4			48.2			63.3

1/ Bartlett's test shows heterogeneity of variance

*** - significant at p = 0.001
** significant at p = 0.01
* - significant at p = 0.05
ns - not significant at p = 0.05
cv - % component of variance

TABLE 11. MEAN PERCENTAGE OF TREES FLOWERING AT SITE 1 - FLORENCIA SUR

Provenance	Number	1981-82 (2 1/2 years old)	1982-83 (3 1/2 years old)	1983-84 (4 1/2 years old)
Estelí, Nicaragua	K1461477	11.5	22.0	36.2
El Chilero, Guatemala	K1451077	3.1	6.3	15.8
La Pineda, Nicaragua	K1521877	0.9	1.0	10.5
San Francisco, Honduras	K1532077	0.9	1.7	10.1
Tres Piedras, Honduras	K1440977	2.1	4.3	9.8
Limón, Costa Rica	3377	0.0	1.0	1.3
La Fortuna, Honduras	K1511977	0.0	0.0	1.0

TABLE 12. MEAN PERCENTAGE OF TREES WITH A) CANKER - *P. cordiae* B) 'SMOOTH' BARK-ASSESSED 13/12/83

Provenance	Number	% trees with canker	% trees with smooth bark mean	min	max
Limón, Costa Rica	3377	40	96	90	100
La Pineda, Nicaragua	K1521877	4	74	63	82
El Chilero, Guatemala	K1451077	3	51	29	92
Estelí, Nicaragua	K1461477	3	66	38	95
La Fortuna, Honduras	K1511977	2	98	95	100
Tres Piedras, Honduras	K1440977	1	62	36	83
San Francisco, Honduras	K1532077	1	94	78	100

TABLE 13. MEAN BARK THICKNESS OF TWO BARK TYPES - 'SMOOTH' AND 'ROUGH' IN *C. alliodora* AT 4 YEARS OF AGE

Bark Type	mean bark thickness (mm) Age 45 months	Age 48 months
Smooth	6.8	7.7
Rough	8.7	10.3
	6.55 1/***	6.13 1/***

1/ Calculated value of 't' for small sample 't' test

*** - significant at p = 0.001

TABLE 14. GROWTH OF FIVE PROVENANCES OF C. alliodora FROM COSTA RICA AT TURRIALBA (CATIE - ODA EXPT 11? PROGENIES OF C. alliodora. CALCULATED MEANS BASED ON PROVENANCE PERFORMANCE) TRIAL PLANTED 2/7/76.

Provenance	Variable		Age at measurement 33 months mean	 S.D.	 72 months mean	 S.D.
San Carlos	Height	dm	58	15	108	31
	DBH	mm	73	26	146	38
Turrialba	Height	dm	50	18	101	21
	DBH	mm	54	21	121	37
Guápiles	Height	dm	46	17	96	33
	DBH	mm	53	28	121	44
Siquirres	Height	dm	45	16	82	29
	DBH	mm	48	25	102	43
Limón	Height	dm	41	16	69	17
	DBH	mm	49	29	88	43

Values given to nearest whole number

ANNEX 1 SOIL CLASSIFICATIONS AND ANALYSES

1. Florencia Sur: - Inceptisol - Typic Dystropept. (Aguirre 1971)

Horizon	Texture	Depth	Distribution of Particles % sand	 silt	 clay	pH H_2O	Organic matter %	C/N	Cation exchange capacity	Ca	Mg	K	Mn	Na	Available P ppm
									←		meq/100g of soil			→	
A_{11}	clay loam	0-12 cm	28.2	36.9	34.9	4.4	3.0	8.1	38.9	0.3	0.6	0.8	0.11	0.1	13.1
A_{12}	clay	12-35	17.0	31.0	52.0	5.0	1.0	3.7	39.8	2.C	1.0	0.6	0.02	0.2	2.4
AC	clay	35-60	24.6	27.2	48.2	5.7	0.1	1.2	30.7	1.3	1.7	0.2	0.03	0.1	1.2
C_1	clay	60-90	25.2	25.4	49.4	5.3	Trace		45.9	2.0	1.7	0.2	0.01	0.2	1.3
C_2	clay	90-120	31.4	25.3	43.3	5.5	Trace		48.3	1.4	2.7	0.1	0.01	0.2	1.2

2 La Selva Inceptisol · Andic Humitropept [illegible]

Horizon	Texture	Depth	Distribution of Particles % sand	 silt	 clay	pH H_2O	Organic matter %	Cation exchange capacity	Ca	Mg	K	Mn	Al meq/100g of soil	Available P mg/l
								←	meq/100g of soil		→	mg/l		
[illegible]	clay	0-19 cm	17	15	68	4.3	3.3	28.6	1.2	0.5	0.1	70	3.6	8
[illegible]	clay	19-38	13	16	71	4.7	6.1	24.8	1.4	0.4	0.1	21	1.5	5
[illegible]	clay	38-61	7	17	76	4.6	0.5	21.5	0.8	0.4	0.7	90	1.4	2
[illegible]	clay	61-120	14	16	70	4.6	0.5	[illegible]	0.8	0.4	0.7	18	1.3	1

Figure 1 Total height of provenances of *C alliodora* in the nursery 4-7 months after sowing

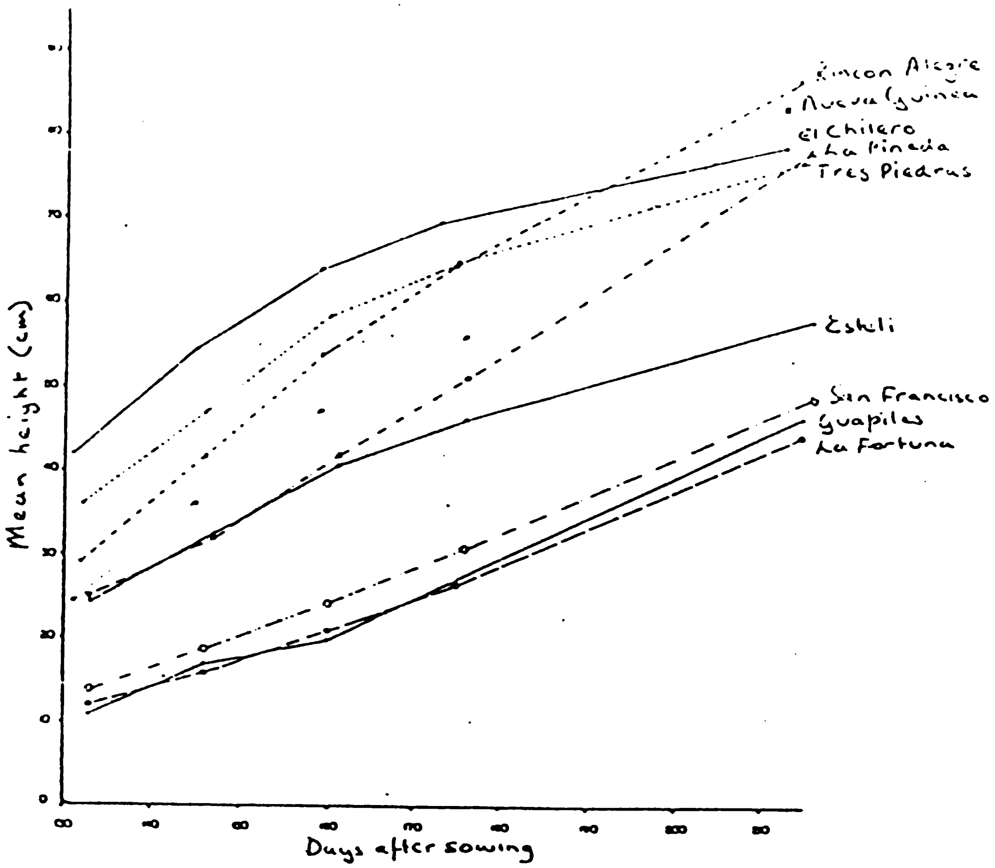


Figure 2 Total height of 6 collections of 3 provenances of *C alliodora* in the nursery 4-7 months after sowing

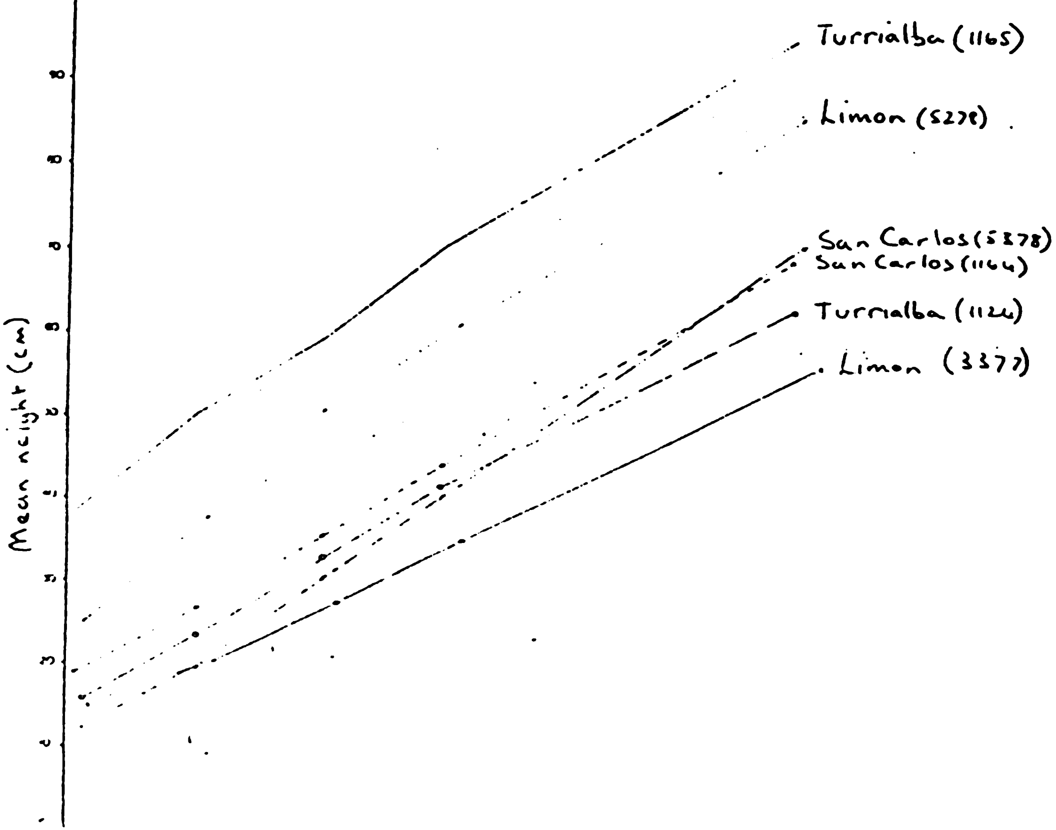
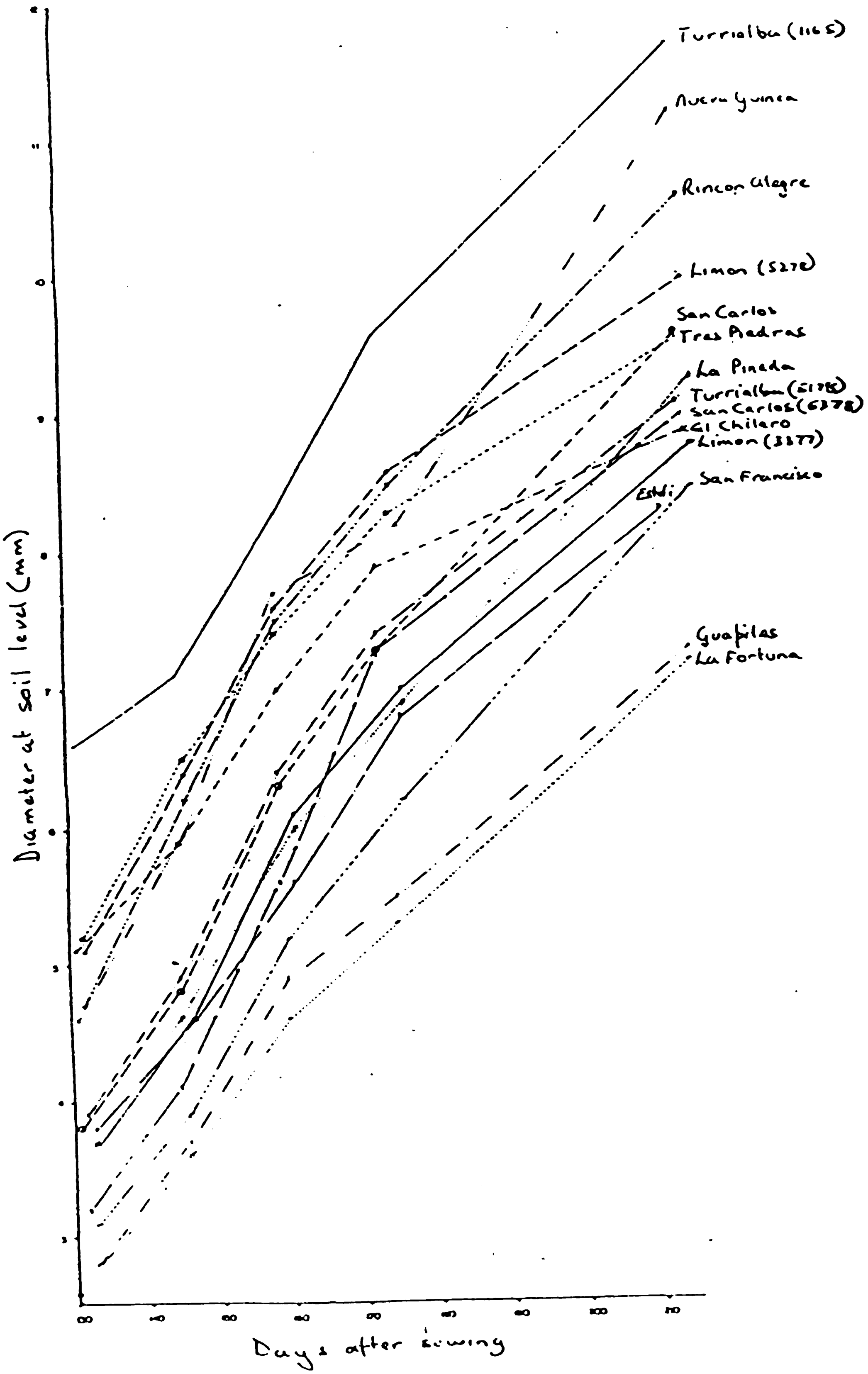


Figure 3 Diameter at soil level of provenances of *C. alliodora* in the nursery 4 - 7 months after sowing



DISPONIBILIDAD DE SEMILLA DE CORDIA ALLIODORA (R et P) PARA PRUEBA DE PROGENIES 1/

por

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RESUMEN

Se seleccionaron 58 árboles 'plus' de Cordia alliodora dentro de rodales naturales en 5 zonas de proveniencia en la región Atlántica de Costa Rica. Se indican detalles sobre los métodos de selección, sobre los árboles seleccionados y sobre las condiciones climáticas de las procedencias. Se da una información sobre la disponibilidad de semillas.

INTRODUCCION

La Cordia alliodora es un árbol maderable bien conocido en las zonas tropicales de América Latina y en partes del Caribe. En América Central la regeneración natural es por lo general abundante y a menudo los campesinos la mantienen combinándolas con varios cultivos perennes. Ha sido plantada experimentalmente en muchos países. En algunos países el crecimiento registrado ha sido excelente llevando al establecimiento de plantaciones, p.e. en Vanuatu (Hudson, 1984). En otros países el crecimiento ha resultado variable a pobre, a veces con rendimientos finales desanimantes (Stead, 1980; Anon, 1983).

El Cuadro de Expertos de FAO sobre Recursos Genéticos Forestales ha clasificado C. alliodora como especie muy importante para la producción de madera, requiriendo urgentemente su exploración botánica y genecológica, recolección y ensayos (FAO, 1977 y 1985). El Instituto Forestal de Oxford (OEFI, anteriormente CFI) ha encarado un programa internacional de ensayos de procedencias de C. alliodora en 1977 recogiendo semillas de áreas naturales, principalmente en América Central (Stead, 1979; 1980). Se ha informado ya sobre los resultados en una cierta cantidad de estos ensayos de procedencias (Venegas, 1981; Anon., 1983; Boshier, 1984; Neil, 1984). Estos ensayos han sido ahora sometidos también a la evaluación de la OEFI para obtener información detallada sobre el comportamiento por procedencia sobre una amplia gama de sitios; y sobre los esquemas de variación genética hallada dentro de la especie.

C. alliodora se halla en ambas regiones de Costa Rica, la Atlántica (0-800 m.s.n.m.) y Pacífica (0-1.200 m.s.m.n.), pero es más común en la región atlántica (bosque tropical húmedo) donde se encuentran los árboles más altos y mejor formados. En la región Seca del Pacífico los árboles son por lo general pequeños (10-15 m de altura) y de forma pobre. Es una especie que semilla prolíficamente y se regenera con facilidad; y se halla con frecuencia en rodales puros con variables grados de densidad. Los rodales naturales ofrecen gran variación fenotípica especialmente en las características de su forma (ver Figura 1 a 4). En muchos casos la tala selectiva parece estar degradando el fondo de genes.

1/ Manuscrito recibido en junio 1986.

SELECCION DE ARBOLES PLUS

En 1983 el proyecto de mejoramiento de árboles en CATIE (Centro Agronómico Tropical de Investigación y Enseñanza) inició un programa de selección de árboles 'plus' para *C. alliodora* dentro de rodales naturales en la región atlántica de Costa Rica. La selección de árboles-plus dentro de rodales naturales es difícil por la imposibilidad de comparar características de rendimiento con árboles vecinos de edades desconocidas. Los grados medios a elevados de heredabilidad a menudo encontrados para las características de forma en otras especies (Zobel y Talbert, 1984) y la gran variabilidad demostrada por los rodales naturales sugiere, sin embargo, que es posible obtener beneficios significativos por medio de la selección dentro de tales rodales. La selección seguida se concentró sobre la forma más que sobre la característica de producción, y se basó sobre una adaptación derivada de Brown y Goddard (1961) y Strauss (1976). En las Figuras 2 a 4 se indican ejemplos de algunos de los árboles selectos.

Si bien se visitó la mayoría de los lugares de la región del Atlántico, los árboles de suficiente calidad se hallaron solamente en cinco regiones de procedencia. Dos de ellas (Turrialba y San Carlos) corresponden a las procedencias establecidas en las pruebas OEFI, mientras que la procedencia de Limon no proporcionó ningun árbol adecuado. Los otros tres (Guápiles, Talamanca y Upala) no habían proporcionado muestras anteriormente. La Figura 5 muestra el área cubierta para la búsqueda de árboles y la ubicación de las proveniencias donde se seleccionaron las plantas. El Cuadro 1 ofrece detalles sobre los árboles selectos, mientras que el Cuadro 2 indica los datos climáticos para las diferentes áreas. En el curso de 1986-87 las selecciones se harán en rodales de la región seca del Pacífico de Costa Rica.

RECOLECCION DE SEMILLA

Durante 1984-86 la semilla de polinización abierta se recolectó trepándose sobre los árboles y se cortaron las inflorescencias maduras. Se secó luego la semilla a la sombra, hasta una humedad relativa inferior al 10% y conservada en almacenaje frío a 5ºC. El proyecto de mejoramiento de árboles de CATIE estaba plantando durante 1986 ensayos de progenie de medio-hermanos empleando este material, en tres sitios (Turrialba, San Carlos y Talamanca). Se está instalando un banco de clones incorporando árboles selectos, empleando material injertado sobre plantas de vivero siguiendo la técnica de la incisión lateral ("side veneer technique").

DISPONIBILIDAD DE SEMILLA

La semilla de estas colecciones se pondrá a disposición de los países interesados en ensayar progenies sobre una gama de sitios. Los interesados en recibir colecciones de semillas para establecer pruebas de progenie deberán dirigirse a: BLSF, CATIE, Turrialba, Costa Rica. Los pedidos de semillas con todos los permisos de importación necesarios deberán llegar al Banco Latinoamericano de Semillas Forestales (BLSF, CATIE) por lo menos tres meses antes de tener que plantar la semilla. La semilla será remitida con un certificado fitosanitario. Instrucciones especiales sobre tratamientos obligatorios con pesticidas y permisos de importación deberán acompañar todo pedido.

En el momento oportuno se invitará a los destinatarios de la semilla de informar sobre los ensayos por ellos encarados. Se incluirán con la semilla recomendaciones sobre un diseño experimental standard en la esperanza de que sea posible evaluar los ensayos sobre un rango de ambientes. El costo de una colección de semillas será de US $ 50, principalmente para cubrir el costo de la documentación, despacho y manipuleo. Se tendrán en cuenta también los ofrecimientos de intercambios de semilla.

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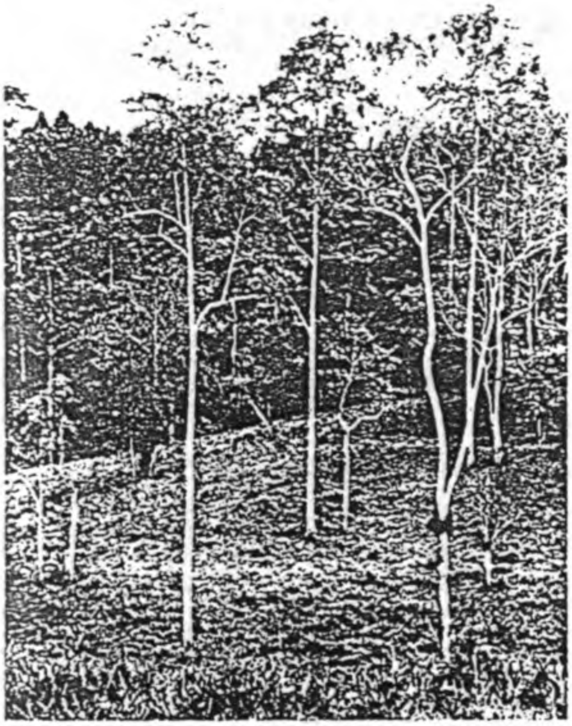

Fig. 1 Regeneración natural de *C. alliodora* Fig. 2 Arbol "plus" No. 5

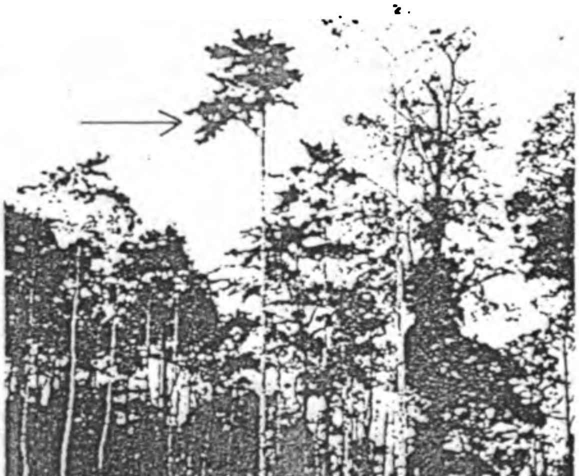

Fig. 5 Mapa indicando la localización de las proveniencias dentro de las cuales se seleccionaron los árboles "plus". Se indica la curva de nivel de 800 m para marcar la distribución aproximada de C. alliodora en la costa del Caribe de Costa Rica.

CUADRO 1. DETALLES SOBRE ARBOLES PLUS DE C. alliodora SELECCIONADOS EN COSTA RICA

Arbol No.	Localización	Proveniencia	Latitud °N	Longitud °O	Elevación msnm	Altura metros	D.A.P. cm	Puntos 1/
1	Celulosa	Turrialba	9°56'	83°37'	640	30.9	38.9	9
2	Celulosa	Turrialba	9°56'	83°37'	660	34.6	41.5	7
3	Celulosa	Turrialba	9°56'	83°54'	580	33.3	31.7	8
4	Celulosa	Turrialba	9°56'	83°56'	620	28.0	44.0	7
5	La Suiza	Turrialba	9°51'	83°37'	640	28.0	32.5	9
6	Bonilla	Turrialba	10°00'	83°37'	570	34.5	34.5	9
7	Noche Buena	Turrialba	9°53'	83°41'	760	32.2	37.0	8
8	Guácimo	Guápiles	10°15'	83°40'	60	29.0	55.5	7
9	Guácimo	Guápiles	10°15'	83°40'	60	24.3	40.2	6
10	Cariari	Guápiles	10°21'	83°44'	50	25.2	43.2	8
11	Cariari	Guápiles	10°22'	83°44'	50	30.0	37.4	10
12	Cariari	Guápiles	10°23'	83°45'	50	29.0	34.1	8
13	I.T.C.R.	San Carlos	10°21'	84°32'	170	27.0	38.0	8
14	Santa Clara	San Carlos	10°21'	84°31'	170	27.0	36.2	8
15	Valle Azul	San Carlos	10°20'	84°34'	220	31.1	37.8	7
16	Quebrada Azul	San Carlos	10°24'	83°27'	130	28.6	34.5	9
17	Pital	San Carlos	10°25'	84°20'	240	30.0	46.0	9
18	CATIE	Turrialba	9°54'	83°40'	600	33.3	37.0	6
19	La Suiza	Turrialba	9°51'	83°37'	680	24.7	30.8	8
20	La Suiza	Turrialba	9°51'	83°37'	620	28.6	45.8	9
21	La Suiza	Turrialba	9°51'	83°37'	660	29.7	48.7	9
22	Iroquois	Guápiles	10°10'	83°38'	160	25.6	34.0	8
23	Pascua	Turrialba	10°00'	83°37'	410	26.6	34.0	8
24	Tres Equis	Turrialba	9°57'	83°34'	630	27.5	47.9	7
25	Pascua	Turrialba	10°02'	83°37'	270	22.2	43.5	7
26	Pascua	Turrialba	10°02'	83°37'	280	20.0	33.7	7
27	Uatsi	Talamanca	9°38'	82°52'	50	19.7	36.4	5
28	Paraíso	Talamanca	9°35'	82°43'	25	35.8	46.1	[illegible]
29	Florencia	San Carlos	10°22'	84°28'	240	26.5	35.7	8
30	Florencia	San Carlos	10°22'	84°28'	240	23.0	32.7	8
31	Florencia	San Carlos	10°22'	84°28'	240	21.4	28.2	5
32	Florencia	San Carlos	10°22'	84°28'	240	23.0	31.1	5
33	Florencia	San Carlos	10°22'	84°28'	240	23.0	29.5	[illegible]
34	Florencia	San Carlos	10°22'	84°28'	240	22.2	32.5	9
35	Upala	Upala	10°52'	85°02'	65	26.5	42.9	9
36	Canalete	Upala	10°51'	85°02'	70	42.9	52.0	10
37	Paraíso	Talamanca	9°35'	82°43'	25	33.8	55.0	8
38	Uatsi	Talamanca	9°38'	82°53'	60	30.8	41.0	6
39	Suretka	Talamanca	9°35'	82°57'	50	28.6	34.2	7
40	Suretka	Talamanca	9°35'	82°57'	50	34.6	44.0	8
41	Bratsi	Talamanca	9°33'	82°54'	70	29.6	34.7	[illegible]
42	Suretka	Talamanca	9°34'	82°55'	90	29.7	36.3	9
43	Suretka	Talamanca	9°36'	82°56'	70	24.7	38.2	7
44	Suretka	Talamanca	9°36'	82°56'	70	19.5	30.0	4
45	Suretka	Talamanca	9°36'	82°57'	50	26.5	31.8	9
46	Suretka	Talamanca	9°35'	82°57'	50	32.0	38.1	10
47	Suretka	Talamanca	9°35'	82°57'	50	33.0	42.3	7
48	Schiroles	Talamanca	9°36'	82°57'	50	33.3	32.3	5
49	Suretka	Talamanca	9°34'	82°56'	40	28.5	28.3	10
50	Uatsi	Talamanca	9°37'	82°55'	160	41.2	43.3	8
51	Canalete	Upala	10°51'	85°03'	80	37.6	56.1	9
52	Canalete	Upala	10°51'	85°02'	70	32.0	37.0	9
53	Guacalito	Upala	10°52'	85°05'	70	30.8	39.7	[illegible]
54	Unión de Canalete	Upala	10°50'	85°02'	80	24.7	33.0	[illegible]
55	Unión de Canalete	Upala	10°50'	85°02'	30	27.5	30.1	[illegible]
56	Unión de Canalete	Upala	10°52'	85°02'	60	29.7	35.0	[illegible]
57	Unión de Canalete	Upala	10°52'	85°02'	50	28.6	27.7	[illegible]
58	Berbina	Upala	10°53'	85°01'	60	24.7	31.5	[illegible]

1/ Carácter del árbol "plus" con respecto a dominancia, ramificación, forma, etc., o sea, calidad. A más puntos mejor calidad.

Cuadro 2

Datos climáticos para los árboles "plus" de C. alliodora seleccionados en Costa Rica

Arboles plus: 5-7, 18-21 Estación meteorológica: CATIE, Turrialba
Latitud 9°53'N Longitud 83°38'O Altitud 602 m

Precipitación media mensual en mm y Temperatura media mensual en °C

	E	F	M	A	M	J	J	A	S	O	N	D	Total	Media	Años/Datos
mm	180	135	72	129	219	291	284	244	254	248	280	339	2675		34
°C	20.9	21.0	21.8	22.4	22.8	23.2	22.8	22.8	23.0	22.7	22.2	21.3		22.2	20

Arboles plus: 1-4, 24 Estación meteorológica: Celulosa, Pavones
Latitud 9°56'N Longitud 83°37'O Altitud 710 m

Precipitación media mensual en mm y Temperatura media mensual en °C

	E	F	M	A	M	J	J	A	S	O	N	D	Total	Media	Años/Datos
mm	236	206	176	169	301	294	326	377	309	332	336	305	3364		7
°C	20.3	20.4	21.2	21.8	22.2	22.6	22.2	22.2	22.4	22.1	21.6	20.7		21.6	20

Arboles plus: 8-12, 22 Estación meteorológica: Guácimo
Latitud 10°13'N Longitud 83°40'O Altitud 90 m

Precipitación media mensual en mm y Temperatura media mensual en °C

	E	F	M	A	M	J	J	A	S	O	N	D	Total	Media	Años/Datos
mm	257	158	159	180	287	291	386	252	220	262	332	340	3124		9
°C	24.5	25.0	26.1	26.7	26.1	25.0	25.6	25.0	24.5	24.5	23.9	23.9		25.1	9

Arboles plus: 6, 23, 25, 26 Estación meteorológica: Peralta
Latitud 9°58'N Longitud 83°37'O Altitud 368 m
Precipitación media mensual en mm y Temperatura media mensual en °C

	E	F	M	A	M	J	J	A	S	O	N	D	Total	Media	Años/Datos
mm	255	186	168	254	501	406	488	414	239	382	391	436	4119		18
°C	22.3	22.4	23.2	23.8	24.2	24.6	24.2	24.2	24.2	24.1	23.6	22.7		23.6	20

Arboles plus: 13-17, 29-34 Estación meteorológica: Los Llanos, San Carlos
Latitud 10°28'N Longitud 84°21'O Altitud 106 m

Precipitación media mensual en mm y Temperatura media mensual en °C

	E	F	M	A	M	J	J	A	S	O	N	D	Total	Media	Años/Datos
mm	189	146	110	120	262	410	384	349	284	329	337	355	3275		13
°C	20.3	20.1	20.7	20.5	21.1	21.4	21.2	20.9	21.2	21.0	20.6	20.3		20.8	
	31.6	32.9	33.6	34.5	35.0	34.4	33.6	34.5	35.3	34.8	32.6	33.7		33.7	

Arboles plus: 27, 28, 37-50 Estación meteorológica: Chase
Latitud 9°37'N Longitud 82°52'O Altitud 40 m

Precipitación media mensual en mm y Temperatura media mensual en °C

	E	F	M	A	M	J	J	A	S	O	N	D	Total	Media	Años/Datos
mm	189	144	145	136	204	177	247	156	77	134	244	257	2110		20
°C	24.4	24.9	25.9	26.4	25.9	24.9	25.4	24.9	24.4	24.4	23.9	23.9		24.9	20

Arboles plus: 35, 36, 51-58 Estación meteorológica: Upala
Latitud 10°54'N Longitud 85°01'O Altitud 50 m

Precipitación media mensual en mm y Temperatura media mensual en °C

	E	F	M	A	M	J	J	A	S	O	N	D	Total	Media	Años/Datos
mm	179	63	57	57	191	298	322	322	326	297	275	203	2590		13
°C	24.3	24.8	25.8	26.3	25.8	24.8	25.3	24.8	24.3	24.3	23.8	23.8		24.9	13

BREEDING POPULATION OF *CORDIA ALLIODORA* IN COSTA RICA

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Cordia alliodora is found in both the Atlantic (0-800 m.a.s.l.) and Pacific (0-1,200 m.a.s.l.) regions of Costa Rica, but is most common in the Atlantic region (wet tropical forest) where the tallest and best-formed trees are found. In the dry Pacific region, the trees are generally small (10-15m in height) and of poor form. Evaluation of the OFI international provenance trials of the species has shown this differentiation between Pacific and Atlantic provenances to be widespread throughout the Central American distribution of the species and suggests their distinction as ecotypes. On all sites evaluated worldwide, the Atlantic provenances have proved superior and although differences between provenances within the Atlantic ecotype have been small or non-significant, the Costa Rican and San Francisco, Honduras provenances have consistently shown good growth, (McCarter, 1988a; 1988b).

The great variability shown by the natural stands was observed also in the provenance trials, where selection of the best (largest diameter) 20% of trees per plot gives a volume increase in excess of 200% of the mean, (McCarter, 1988b). It would appear that significant gains will be made by use of simple selection methods. From 1983 to 1987 tree improvement staff at CATIE selected trees in the natural stands of the Atlantic region of Costa Rica and San Francisco, Honduras. Given the often poor form of the species and the difficulty of selecting for yield in open natural stands, selection was principally for stem quality (Boshier and Mesén, 1987). Only trees of a height (approx 18m) sufficient to show clearly their form characteristics were considered. In selecting trees within the Atlantic zone of Costa Rica no discrimination between provenance was made bearing in mind that within provenance variation will probably be more important than between provenance variation. Seventy one trees were selected within the following provenances.

	No. of trees
Guapiles, Costa Rica	6
San Carlos Costa Rica	11
Talamanca, Costa Rica	16
Turrialba, Costa Rica	15
Upala, Costa Rica	10
San Francisco, Honduras	13

Open-pollinated seed was collected from the plus trees and used to establish progeny trials on two sites in Costa Rica. Early rogueing of the trials to leave the best trees within the best families, without regard to provenance, will allow establishment of seedling seed orchards. Variation between provenances in flowering time has been observed in the natural stands and will be studied in the progeny trials. This will be taken into account in rogueing, to ensure optimal cross pollination between the trees. Seed production starts at roughly two years of age and collectable improved seed should be available at four to five years (1991-92). New selected trees from natural stands, plantations and provenance trials will be incorporated periodically into the breeding population.

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Analysis of provenance and progeny trials of *Cordia alliodora* (R. and P.) Oken in Costa Rica.

by

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A thesis submitted for the degree of
Master of Science at the University of Oxford

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Abstract

Cordia alliodora (R and P) Oken is an economically important neo-tropical timber tree, which is widely planted within and outside of its natural range. In 1978 the FAO Panel of Experts On Forest Genetic Resources targeted *Cordia alliodora* for botanical and genecological exploration, collecting and testing (FAO, 1977). In 1978 the then Commonwealth Forestry Institute initiated a series of international provenance trials of *Cordia alliodoara*, five of which were established in Costa Rica. A further five provenance/progeny trials of *Cordia alliodora* were established by the CATIE Tree Improvement Programme.

This study analysed the data from eight of these trials assessed over the last fifteen years. New assessments of wood density were made using a Pilodyn in two of the provenance/progeny trials. The analysis was performed using the GLM and REML procedures in Genstat 5 release 3. In a multiple site analysis significant ($p<0.01$) provenance differences were recorded for the traits diameter at breast height and height. Family differences in diameter were found not to be significant ($p>0.10$) in a multiple site provenance/progeny analysis. This is thought to be owing to a highly significant family×site interaction term obscuring the family differences.

The Pilodyn was found to be a very effective instrument for assessing relative wood density. Highly significant ($p<0.001$) provenance and family differences were found for relative wood density. Mean provenance wood density was found to be negatively correlated ($r = -0.78$) with provenance precipitation.

[illegible]

Provenance and Family Variation in Height and Diameter Growth of *Cupressus Lusitanica* MILL. at 28 Months in Costa Rica

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Summary

Results of a provenance / progeny trial of *Cupressus lusitanica* in Costa Rica are described. At age 28 months, progeny of plus-trees selected primarily for stem straightness and cylindricity had grown significantly faster than three commercial controls and a seedlot produced from a Colombian clonal seed orchard. The estimated values of additive genetic coefficients of variation (10.2% to 15.9%) and heritabilities (0.12 to 0.21) were within the ranges typically found in forest trees. There was no evidence for important differences between the Costa Rican, derived provenances.

Key words: additive genetic variation, heritability, progeny testing, provenance variation.

FDC: 232.11; 232.12; 165.5; 174.7 *Cupressus lusitanica;* (728.6).

Introduction

Cupressus lusitanica, a native of Mexico, El Salvador, Guatemala and Honduras (STYLES and HUGHES, 1983), was first introduced to Costa Rica at least 100 years ago (HOLDRIDGE, 1953). The species produces durable, easily-worked and attractive timber (LAMPRECHT, 1990) and has become one of the timber trees most planted by smallholder farmers in the highlands of Costa Rica, both in block plantations and in windbreaks (CHAVES and FONSECA, 1990). There is some evidence to suggest that the base population is of at least acceptable genetic quality: in a Costa Rican provenance trial reported by SOARES (1973), 2 local derived provenances grew faster than 7 other sources from Mexico, Kenya and New Zealand, whilst in a Colombian provenance trial reported by VELEZ (1984), the progeny of 3 trees selected in Costa Rica were taller than the other 16 seedlots (families from Kenya and Colombia, commercial bulked lots from Italy, Mexico and Portugal). Nevertheless, the amount of phenotypic variation between individual trees suggests that there is room for genetic improvement in traits of commercial interest, as has proved to be the case in Colombian (LADRACH, 1979; LADRACH and GUTIERREZ, 1979) and East African (DYSON and RAUNIO, 1977) populations of the species. For this reason, in 1989, CATIE, a regional organization dedicated to the improvement of smallholder forestry and agroforestry systems, initiated a programme of genetic improvement of the species.

The present document describes the results at 28 months of a provenance/progeny test located in the Cordillera Central of Costa Rica. The principal objectives of the test are to provide a base for recommendations of appropriate seed sources for reforestation in the breeding zone in question and, after conversion to a seedling seed orchard, to produce improved seed.

Materials and Methods

Treatments

The treatments consist of 45 open-pollinated families of 8 Costa Rican derived provenances: Cipresal, Birrí, Heredia (11 plus-tree progenies and 1 progeny from an 'average tree'); Monte de la Cruz, Heredia (7 plus-tree progenies and 1 progeny from an 'average tree'); Finca La Lucha, León Castro

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Cortés, San José (10 plus-tree progenies and 1 progeny from an 'average tree'); Bosque de la Hoja, Heredia (8 plus-tree progenies); Fraijanes, Poas, Alajuela (2 plus-tree families); El Roble, Heredia (1 plus-tree family); Paso Llano, Heredia (2 plus-tree families); Calle Lobos, Los Angeles, Heredia (1 plus-tree family). The mother trees of the plus-tree families were selected as having straight and cylindrical stems and a diameter at breast height (dbh) at least equal to that of the stand mean. In addition to the family seedlots, 4 bulk lots were included: 1 from a Colombian clonal seed orchard (La Arcadia, Popayán) belonging to Smurfit Carton of Colombia, and 3 local commercial controls supplied by the Latin American Forest Tree Seed Bank, CATIE, Costa Rica (Santa María de Dota; Las Chorreras, San Rafael de Heredia; Prusia, Cartago). All 3 commercial controls represent additional Costa Rican derived provenances, and are composed of the bulked seed of 8 to 20 healthy trees of at least average size and acceptable stem form, selected in commercial plantations.

Experimental site and planting details

The experiment was planted in May 1992 at a high elevation site located in Santa Cruz de Turrialba, Costa Rica (latitude latitude 9°58' north, longitude 83°47' west, elevation 2100 m a.s.l., mean annual precipitation 2912 mm, mean annual temperature 13.9°C, mean of 1.5 dry months (< 80 mm) per year). Before planting, the site was under pasture, with a few trees remaining of the original forest cover.

The progeny of the 3 unselected trees and the Colombian material were nursery sown 41 and 78 days respectively after the rest of the material, which was in the nursery for a total of 178 days.

Experimental design, measurements and statistical analysis

A randomized complete block design was used. The families and the 4 bulk lots were planted in 3-tree line plots, with 24 blocks. Two or more surround rows, composed of a mixture of the families, were planted around the entire experiment. Total tree height and diameter at 1.3 m (dbh) were measured at 28 months from outplanting, except in the case of the unselected families and the Colombian seedlot which, in order to reflect their later nursery sowing date (see above), were measured at 28 months plus 41 days and 78 days respectively. Trees of less than 1.3 m height were booked as having zero dbh. Survival percentages were derived from the data.

The experiment was designed to test the following null hypotheses (Ho) for the traits in question: Ho1 (there are no differences in the parametric mean values of the different provenances); Ho2 (there is no difference between the parametric mean of the Heredia provenances as a group and that of La Lucha); Ho3 (there is no difference between the parametric mean of the 'selected' provenances as a group and that of the commercial controls taken as a group; Ho4 (there is no difference between the parametric mean of the Costa Rican provenances as a group and that of the Colombian lot; Ho5 (there are no differences between the parametric means of the 49 treatments; Ho6 (there is no additive genetic variation in the Costa Rican base population).

Provenance analysis

Analysis of variance was carried out on height and diameter (see *Table 1* for linear model). Null hypothesis 1 was tested using an 'F' test with the provenance mean square as numerator and the error mean square as denominator. Null hypotheses 2, 3 and 4 were tested using single degree of freedom 'F' tests with the SAS© 'Contrast' statement, as described by STONECYPHER (1989). For provenance analysis purposes, the families of each provenance are considered to constitute non-contiguous provenance plots.

COTTERILL (1990) considers that a minimum of 5 families are necessary for a representative sample of provenances. For this reason, those provenances represented by less than 5 families (Fraijanes, El Roble, Paso Llano, Calle Lobos) were excluded from the provenance analysis. The progeny of the 'average trees' were also omitted.

Family analysis

Mixed model analysis of variance of height and diameter was carried out. No provenance effect was included in the model (*Table 1*) because this is considered to be irrelevant to the main application of the mixed model analysis, i.e. to identify which are the best treatments, independently of whether their superiority is due to provenance or family-within-provenance effects. Null hypothesis 5 was tested using an 'F'-test with family mean square as the numerator and the error as the denominator. Null hypothesis 6 was tested with using a random model analysis of variance. Individual-tree genetic parameters were estimated from the using the formulae detailed in *table 2*.

Results

General

The mean plantation height and dbh at 28 months were 2.70 m and 2.1 cm respectively. The overall survival was 92.3%.

Provenance results

Least squared means for height and diameter are included in *table 3*. Provenance mean height ranged from 2.20 m (Colombian seed orchard, Santa María de Dota control) to 2.80 m (Cipresal, Heredia). Provenance mean dbh ranged from 1.3 cm (Colombian seed orchard) to 2.2 cm (Monte de la Cruz, Heredia). The analysis of variance (*Table 3*) revealed highly significant differences in height growth and diameter amongst the 7 provenances included. The results of the planned comparisons (*Table 3*) indicated that the group of 'selected' provenances (grand mean height 2.73 m, grand mean dbh 2.1 cm) was highly significantly superior to the commercial controls (grand mean height 2.49 m, grand mean dbh 1.8 cm) and to the Colombian seed orchard material. The grand mean height of the Heredia selected provenances (2.75 m) was significantly superior to that of the La Lucha provenance (2.7 m), but the difference is of little practical importance. The 2 groups did not differ significantly in dbh.

Provenance least squared mean survival percentages ranged from 81.9% (Colombian seed orchard) to 95.8% (Prusia commercial control). Due to the generally acceptable survival, no further analysis of this trait was made.

Family results

Family least squares height and dbh means (*Table 3*) varied from 2.2 m and 1.5 cm (family 7) to 3.1 m and 2.6 cm (family 30). The grand least square height and diameter means of the best 10 families (2.90 m, 2.4 cm) was 7.4% and 14.3% respectively above the grand mean and 16.5% and 33.3% respectively above the mean of the 3 commercial controls. The analysis of variance revealed highly significant differences between treatments (*Table 3*). Only 7 families had survival percentages below 90%.

Genetic parameter estimates are included in *table 3*. Height had higher heritability than dbh but lower AGCV. There was highly significant additive genetic variance for both height and diameter (*Table 3*).

Discussion

At 28 months after planting, there is strong evidence for important differences in provenance and family parametric means. Although there appears to be little difference between the three provenances from the north of Heredia and the La Lucha provenance, the as a group they clearly have superior juvenile height growth to the 3 commercial controls, particularly with respect to the Santa María Dota source. The reasons for this superiority are not clear and cannot be elucidated from the data presented here. Possibly the superior height growth results from direct or indirect responses to selection for form and diameter. Alternatively or additionally, there may be genetic differences unrelated to the selection applied.

The Colombian seedlot is clearly inferior in the trial. This treatment was measured at the same total age as the other treatments. Nevertheless, it is possible that its inferior growth over the 28 month period might result from its smaller size at planting. Alternatively, it may be that, due to genotype-environment interaction, the genetic superiority (i.e. in Colombia) of the Colombian seed orchard seed is not maintained in the zone of the trial, or that the Colombian base population is inferior to the Costa Rican base population, as suggested by the reports mentioned above. In any case, until the reason for the inferiority of the Colombian seed orchard material is clarified, it would be imprudent to use this seed source for reforestation in Costa Rica.

The values of heritability and AGCV are within the ranges typically found for these traits in progeny tests of forest trees (CORNELIUS, 1994), and confirm the potential for improvement of the local base population.

The results do not permit firm conclusions to be drawn on possible variation in growth rate at later stages. However, unless age-to-age correlations are negative, then the selection of seed sources based on juvenile growth should produce a reduction in rotation length concomitant with the increased early growth. If, as LAMBETH's (1980) results suggest, age-to-age correlations tend to be positive, then this effect will be further enhanced by more rapid growth at later stages. However, it should be stressed that early growth rate is in itself a trait of key economic importance, as improvements in early growth rate can reduce early cleaning costs and their associated high interest charges.

Conclusions

1. The Cipresal, Bosque de la Hoja, Monte de la Cruz (all north of Heredia) and La Lucha provenance – all represented by plus-trees selected for form and girth – have faster juvenile growth rate than the 3 commercial controls included. It is recommended that commercial seed collections be made from well-formed trees of better than average diameter in these stands. Seed collections from the Santa María Dota source should be avoided, as should use of seed from the La Arcadia clonal seed orchard.

2. The estimated values of the genetic parameters suggest that worthwhile gains in growth traits may be made.

3. These conclusions apply principally to the breeding zone in question, i.e. the Cordillera Central of Costa Rica, at altitudes between 1900 m and 2300 m a.s.l..

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Table 1. – Linear models used in the analysis of variance of a progeny trial of *Cupressus lusitanica* in Santa Cruz de Turrialba, Costa Rica.

Hypotheses[1]	Model[2]	Random effects in model	Error term (F-test denominator)
1, 2, 3, 4	$Y_{ikl}=\mu+\phi_i+\beta_k+\varepsilon_{ikl}$	β_{ik}	ε_{ikl}
5	$Y_{jk}=\mu+\alpha_j+\beta_k+\varepsilon_{jk}$	β_k	ε_{jk}
6	$Y_{jkl}=\mu+\alpha_j+\beta_k+\alpha\beta_{jk}+\varepsilon_{jkl}$	all	$\alpha\beta_{jk}$

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[1] see text

[2] Y_{ikl} = the observed mean value of the response variable 'Y' on the lth tree of the ith provenance in the kth block; μ = the population mean; ϕ_i = the effect of the ith provenance; β_k = the effect of the jth block; ε_{ikl} = the residual variation of the lth tree of the ith provenance in the kth block; Y_{jk} = the observed mean value of the response variable 'Y' on the jth family in the kth block; α_j = the effect of the jth family; ε_{jk} = the residual variation of the jth family in the kth block; Y_{jkl} = the value of the response variable 'Y' on the lth tree of the jth family in the kth block; $\alpha\beta_{jk}$ = the interaction of the jth family and the kth block; ε_{jkl} = the residual variation of the lth tree of the jth family in the kth block.

Table 2. – Formulae for genetic parameter estimates in a progeny trial of *Cupressus lusitanica* in Santa Cruz de Turrialba, Costa Rica.

parameter estimated[1]	formula for estimator	notes
additive genetic variance (σ^2_A)	$4\sigma^2_F$	σ^2_F = variance component for half-sib families;
additive genetic coefficient of variation % (AGCV)	$100(\sigma_A / \bar{x}]$.	$\bar{x}$ = experimental mean
h^2 (narrow-sense individual-tree heritability)	$\sigma^2_A / [\sigma^2_E + \sigma^2_{FB} + \sigma^2_F]$	σ^2_E=error variance; σ^2_{FB} =block-family interaction variance

Table 3. Proportionally ranked provenance and family least squared means, results of significance tests, and genetic parameter estimates for height and diameter at 28 months in a progeny test of *Cupressus lusitanica* in Santa Cruz de Turrialba, Costa Rica

CHARACTERISTIC			
dbh (cm)[1]		height (m)[1]	
best family (#30) (2.6)		best family (#30) (3.1)	
best 10 familes (2.4)		best 10 families (2.9)	
		Cipresal (2.8)	
Monte de la Cruz (2.2)		overall mean, M.C[2]. (2.7)	B.H.[3], La Lucha
Cipresal (2.1)	overall mean	control Chorreras (2.6)	
Bosque de la Hoja (2.0)	La Lucha	control Prusia (2.5)	
control Chorreras (1.9)	Prusia control		
		control Santa Maria Dota (2.3)	
		Colombian seed orchard (2.2)	worst family (#7)
worst family (#7) (1.5)	control Sta. Ma. Dota		
Colombian seed orchard (1.3)			
'F' values, significance[4]			
global (provenances): F=11.42, p=.0001		F=8.35, p=.0001	
global (all treatments): F=3.3 p=.0001		F=5.2 p=.0001	
global (families): F=3.03, p=.01		F=2.47, p=.01	
controls v. families, F=15.1 p=.0001		F=28.8 p=.0001	
familles v. seed orchard F=31.9 p=.0001		F=32.0 p=.0001	
genetic parameters			
heritability[5]	AGCV[6]	heritability[5]	AGCV[6]
.12	15.9	.21	10.2

[1] Means are ranked proportionally along the vertical lines. Treatments with the same mean are positioned at the same horizontal point on the vertical lines.

[2] Monte de la Cruz

[3] Bosque de la Hoja

[4] probability of a higher value of 'F'

[5] narrow-sense heritability, based on individual trees

[6] additive genetic coefficient of variation

Familias superiores de *Cupressus lusitanica* en Costa Rica

Jonathan Cornelius[1] y Oldemar Baeza

Puntos claves y recomendaciones prácticas

- En un ensayo de descendencias de ciprés en Costa Rica, las descendencias de árboles plus exhibieron superioridad relativa a testigos comerciales de 8% y 11% en altura y dap a los 28 meses. Las 10 familias mejores mostraron una superioridad de 19% y 33% en relación a los testigos
- Un lote de semilla de un huerto semillero clonal de Popayán, Colombia presentó el crecimiento más lento de todos los tratamientos en el ensayo.
- No se debe utilizar para la reforestación en Costa Rica semilla de ciprés proveniente de Popayán, Colombia, ni de los testigos comerciales incluidos.
- **La semilla de los árboles élites identificados por el ensayo está disponible a reforestadores pequeños y medianos a través del Proyecto MGF del CATIE.**

Introducción

Desde su primera introducción a Costa Rica hace más de 100 años (Holdridge, 1953), el ciprés (*Cupressus lusitanica*) se ha convertido en una de las especies más plantadas en las zonas altas, tanto en plantaciones en bloque como en cortinas rompevientos (Chaves y Fonseca, 1990). Sin embargo, hasta la fecha, sólo se ha contado con información muy parcial sobre las características genéticas de la población base en Costa Rica (Soares, 1973; Vélez, 1984). Con el fin de contribuir a llenar este vacío de información, se presentan aquí los primeros resultados de un ensayo de progenies de ciprés establecido en Santa Cruz de Turrialba, Costa Rica en 1992.

Descripción del experimento

El experimento está ubicado en un potrero abandonado a 2100 msnm en las faldas superiores del volcán Turrialba (precipitación media

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1/ Proyecto Mejoramiento Genético Forestal, CATIE;
2/ Administración Británica para el Desarrollo en Ultramar (ODA)

anual 2912 mm, temperatura media anual 13,2°C, promedio de 1,5 meses secos (<80mm) por año). Los tratamientos son 45 familias de polinización abierta, derivadas de árboles plus seleccionados con base principalmente en rectitud y cilindrez del fuste, ubicados al norte de las ciudades de Heredia y Alajuela y en la Finca La Lucha, León Castro Cortés, San José. Además, se incluyeron un lote de un huerto semillero (La Arcadia, Popayán) de Smurfit Cartón de Colombia S.A. y tres testigos comerciales costarricenses suministrados por el Banco Latinoamericano de Semillas Forestales del CATIE: Santa María Dota; Las Chorreras, San Rafael de Heredia; Parque Prusia, Cartago.

El diseño experimental es de 24 bloques completos al azar, con parcelas de tres árboles en línea y dos líneas de borde compuestas de una mezcla de las diferentes familias.

Evaluaciones y análisis

A los 28 meses después de la plantación, se midió diámetro a 1,3m (dap) y altura de todos los árboles. Se analizaron los datos utilizando análisis de varianza. Se efectuaron comparaciones planificadas entre las familias seleccionadas y los testigos comerciales, utilizando el comando CONTRAST de SAS (Stonecypher, 1992). Se calcularon estimaciones de los parámetros genéticos heredabilidad y coeficiente de variación aditivo genético, con base en análisis de componentes de varianza (Buijtenen, 1992; Stonecypher, 1992).

Resultados y discusión

A los 28 meses, la plantación presentaba un desarrollo aceptable, con altura y dap promedio de 2,7m y 2,1cm respectivamente y una sobrevivencia de 92,3%. Sin embargo, se encontró variación significativa en crecimiento de los diferentes tratamientos (Cuadro 1). El dap y altura promedio de la mejor familia (#30) sobrepasaban los de la peor familia (#7) en 73% y 41% respectivamente. Además, los tres testigos Santa María de Dota, Las Chorreras y Prusia, tenían promedios para altura y dap 14% y 28%, 3% y 9%, 8% y 10%, respectivamente, por debajo de los promedios generales. Los promedios combinados de los tres testigos para altura y dap (2,47m y 1,8cm respectivamente) fueron significativamente (p=,0001) inferior (en 8% y 11%) a los promedios de las descendencias seleccionadas (2,67m y 2,0cm). Las 10 mejores familias promedios combinados de 2,94m y 2,4cm (altura y dap, respectivamente), una superioridad de 19% y 33%, respectivamente, con relación a los tres testigos.

El lote colombiano fue el más lento en crecimiento en altura, junto con la familia 7 (2,22m), y fue el más lento en crecimiento diamétrico (1,3cm). En ambos casos, fue significativamente (p=0,0001) inferior al material costarricense.

Es difícil explicar la evidente superioridad de las descendencias seleccionadas sobre los testigos, puesto que en la selección de árboles plus se enfatizó la forma más que el tamaño de los árboles. Sin embargo, es posible que los árboles más rectos también produzcan descendencias de más rápido crecimiento. También podría ser que los tres testigos son inferiores independiente de la selección aplicada.

Obviamente, el ensayo es todavía joven. Sin embargo, la implicación práctica de los resultados es la misma: sería prudente evitar el uso de semilla recolectada de árboles regulares en las procedencias Prusia, Las Chorreras y, particularmente, Santa María de Dota. Además, sería aconsejable evitar el uso de semilla importada del huerto semillero de Cartón de Colombia, la cual no se adapta bien en Costa Rica, por lo menos arriba de los 2000 msnm.

Los valores estimados de heredabilidad y coeficiente de variación aditiva genética (Cuadro 1) fueron dentro de los rangos típicos en los árboles forestales y confirman el potencial para mejoramiento de la población base de ciprés, en Costa Rica.

Cuadro 1. Promedios, pruebas de significancia y estimaciones de parámetros genéticos en un ensayo de descendencias de *Cupressus lusitanica*, en Santa Cruz de Turrialba, Costa Rica.

CARACTERISTICA dap (cm)		altura (m)	
mejor familia (#30) (2,6)		mejor familia (#30) (3,1)	
mejores 10 familias (2,4)		mejores 10 familias (2,9)	
		Cipresal (2,8)	
Monte de la Cruz (2,2)		promedio general, M.C[1] (2,7)	B.H.[2], La Lucha
Cipresal (2,1)	promedio general	testigo Chorreras (2,6)	
Bosque de la Hoja (2,0)	La Lucha	testigo Prusia (2,5)	
testigo Chorreras (1,9)	testigo Prusia		
		testigo Santa María Dota (2,3)	
		huerto semillero Carton (2,2) de Colombia	peor familia (#7)
peor familia (#7) (1,5)	testigo Sta. Ma. Dota		
huerto semillero Cartón (1,3) de Colombia			
comparación, valores de 'F' y significancia[3]			
global, F=3,3 p=,0001		F=5,2 p=,0001	
testigos vs familias, F=15,1 p=,0001		F=28,8 p=,0001	
familias vs huerto F=31,9 p=,0001		F=32,0 p=,0001	
parámetros genéticos			
heredabilidad[4]	CVGA[5]	heredabilidad[4]	CVGA[5]
,12	15,9	,21	10,2

[1] Monte de la Cruz; [2] Bosque de la Hoja; [3] probabilidad de un valor más alto de 'F'; [4] heredabilidad en el sentido estricto, basado en árboles individuales; [5] coeficiente de variación aditivo genético

Conclusiones

Las procedencias del norte de la ciudad de Heredia y de La Lucha - todas representadas por árboles plus seleccionados por rectitud y diámetro - exhibieron un crecimiento juvenil más rápido que los tres testigos comerciales. Ya está disponible la semilla de árboles élites (genéticamente comprobados) de estos rodales. Se debería evitar la realización de recolecciones de la procedencia Santa María de Dota y Parque Prusia, así como el uso de semilla importada del huerto semillero de Popayán, Colombia.

Agradecimientos

Se agradecen las contribuciones del personal actual y pasado del Proyecto Mejoramiento Ge-

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Avances en el mejoramiento genético de *Eucalyptus deglupta*

Jonathan Cornelius, Eugenio Corea, Marvin Hernandez[1]

Puntos claves y recomendaciones prácticas

- El Proyecto Mejoramiento Genético Forestal (PMGF) del CATIE ha desarrollado semilla mejorada de *Eucalyptus deglupta* Dicho material tiene una superioridad estimada en productividad juvenil mayor al 60%.
- Se recomienda el uso de semilla mejorada de *Eucalyptus deglupta* descrita aquí para la reforestación en sitios aptos para la especie en Costa Rica, así como en zonas vecinas de Panamá (Bocas del Toro) y Nicaragua (Río San Juan). La semilla mejorada está disponible a reforestadores interesados, a través del Proyecto Mejoramiento Genético Forestal del CATIE. Se puede adquirir el material en tres formas: como semilla, plantitas listas para repicar (con anticipación de 6 semanas) o plantas embolsadas (con anticipación de 5 meses) (por precios, ver texto).
- Se recomienda la eliminación de arbolitos con hojas fuertemente moradas en el vivero, debido a que estos tienden a ser genéticamente inferiores en cuanto a crecimiento. Normalmente, la coloración puede detectarse 4-6 semanas después del repique.
- Antes de comprar plántulas de *E. deglupta* en viveros comerciales, es aconsejable revisar que se han eliminado las plántulas moradas.

1. Introducción

El Proyecto Mejoramiento Genético Forestal del CATIE está trabajando con *Eucalyptus deglupta* desde 1990. Recientemente, el Proyecto ha logrado avances significativos tales como el desarrollo de semilla mejorada y la producción de información sobre el control genético y relación entre el crecimiento y el color de las hojas. Aquí se describen estos logros y, en forma resumida, como se fundamentó la investigación. (Cornelius *et al.* 1994).

2. Metodología

2.1. Selección de árboles plus y establecimiento de ensayos

En 1990 se recolectó semilla de 48 árboles plus seleccionados con base en la rectitud y cilindricidad de sus fustes y por tener un diámetro igual o mayor del promedio del rodal donde se seleccionó. Se mantuvo separada la semilla de cada árbol. En 1992 se plantaron los 48 lotes (familias -uno por cada árbol plus), más 4 lotes de árboles regulares y tres testigos comerciales, en tres ensayos de descendencias estadísticamente diseñados y ubicados en tres fincas en sitios con diferentes condiciones climáticas y edáficas en los cantones de Turrialba y Upala (cuadro 1). Los tres sitios muestran una amplia gama de condiciones ambientales. Para asegurar su representatividad, en el mantenimiento y manejo de los sitios se siguieron las prácticas normales para las plantaciones de *E. deglupta* en Costa Rica.

Cuadro 1. Ubicación y condiciones ambientales de tres ensayos de descendencias de *Eucalyptus deglupta* en Costa Rica.

Sitio	Zona de vida	Altitud (m s.n.m.)	Precipitación promedio anual	Número meses secos (≤50 mm por mes)	Suelo
Canalete de Upala	bosque muy húmedo tropical premontano, faja basal	80	1320	2.5	arcilloso pH 5.5
San José de Upala	bosque húmedo tropical	80*	1320*	2.5*	arcilloso, muy pesado y compactado pH 5
Tuis de Turrialba	bosque muy húmedo tropical premontano	770	2464**	1.5**	arcilloso, pH 4.9

* Estación Canalete ** Estación La Suiza

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[1] Proyecto Mejoramiento Genético Forestal, CATIE

2.2. *Evaluaciones y análisis*

Varios autores han notado la existencia de 'variedades' o 'procedencias' de *E. deglupta* con hojas moradas y verdes en Costa Rica, e incluso se ha sugerido que los árboles de hojas de color intermedio son los de más rápido crecimiento (Combe y Gewald, 1979; FAO, 1979). Por lo tanto, se efectuó también una evaluación del color de las hojas a los 14 y 16 meses en Tuis y a los 16 meses en Canalete, usando una escala sencilla con tres categorías: 1 (hojas verdes o más verdes que moradas); 2 (hojas de color intermedio); 3 (moradas o más moradas que verdes).

Los datos se evaluaron estadísticamente usando análisis de varianza, para comparar los valores promedio de los diferentes lotes, así como para comparar la tasa de crecimiento de árboles de hojas moradas y hojas verdes. Los resultados se refieren principalmente a la medición de 16 meses, dado que existen datos para los tres sitios a esta edad.

3. Resultados

3.1. *Variación genética en la tasa de crecimiento en altura de Eucalyptus deglupta en Costa Rica*

La altura promedio a los 16 meses fue de 2,7m, 1,4m y 2,4m en Canalete, San José y Tuis, respectivamente, mientras la sobrevivencia fue de 80%, 70% y 92%.

Hubo diferencias importantes en la altura promedio de los diferentes lotes. En Canalete, el promedio de la mejor familia (la descendencia del árbol 16, con promedio de 3,6m), fue del 73% superior al promedio de la peor familia (la descendencia del árbol 37, promedio 2,1m) y 33% por encima del promedio del ensayo (2,7m). A través del análisis estadístico, se pudo comprobar que gran parte de la variación entre familias es de origen genético.

3.2. *Semilla mejorada*

Se encontró que las mismas familias son las mejores en todos los sitios. Con base en estos resultados, el CATIE ha desarrollado semilla mejorada de *E. deglupta*. Esta semilla está constituida por una mezcla de cinco de las mejores familias. Cada una de las familias está derivada del cruce, por polinización abierta, del árbol madre con varios polinizadores, y por lo tanto, la mezcla cuenta con una amplia base genética. La altura promedio de las cinco familias a los 16 meses supera en 25% al promedio global general. Además, las mediciones de dap a los 22 meses en Tuis han revelado que las cinco familias tienen una superioridad en área basal de alrededor de 57%, lo cual, en conjunto con el mejoramiento en altura, implica una ganancia en productividad volumétrica por arriba de esta cifra

Esta semilla mejorada está disponible a reforestadores interesados, a través del Proyecto Mejoramiento Genético Forestal del CATIE. Se puede adquirir el material en tres formas diferentes: como semilla ($7.00 para semilla suficiente para producir 1600 plantas), como plantitas listas para ser repicadas ($20.00 por 1600 plántulas listas para el repique, 6 semanas de anticipación) o, como plantas enbolsadas listas para plantar (US$0.16 por planta con cinco meses de anticipación). Pequeños y medianos reforestadores o viveristas interesados pueden comunicarse con el Proyecto MGF, CATIE, Turrialba, Costa Rica (teléfono 556-6431 ext. 379, fax 556-1533).

3.3. *Variación genética en color de las hojas y su relación con el crecimiento*

Se observaron grandes diferencias entre el color de las hojas de las diferentes familias. Por ejemplo, en Tuis, el color promedio a los 14 meses fue 2.0 (es decir exactamente intermedio), mientras que la familia 16 tuvo un promedio de 1.1 (casi puro verde) y la familia 20 un promedio de 2.8 (casi puro morado). Se encontró que las familias de hojas verdes crecen más rápidamente que las familias de hojas moradas. Por ejemplo, en Tuis a los 14 meses, las familias con color promedio ≤1.5 fueron 17% más altas que las familias con color promedio de ≥2.5. Similarmente, las cinco mejores familias en Tuis y Canalete (con base en datos combinados de los dos sitios) tenían una altura promedio de 3.1m y un color promedio de 1.6, mientras las cinco peores familias, con altura promedio de 2.0m, tenían un color promedio de 2.3. Aunque existen familias moradas de crecimiento rápido y familias verdes de crecimiento lento, *los resultados demuestran que, en general, las familias de hojas moradas e intermedias tienden a exhibir un crecimiento juvenil mucho más lento que las familias de hojas verdes.*

Es importante destacar que las diferencias en pigmentación son fácilmente reconocibles en el vivero, permitiendo así su eliminación antes de plantar en el campo. Dichas medidas serán necesarias incluso en el caso de la semilla mejorada, debido a que aparentemente existen genes para coloración morada, aun dentro de las familias predominantemente verdes.

Ninguno de los tres lotes comerciales logró figurar entre los 15 mejores con base en los datos combinados.

4. Conclusiones

1. El Proyecto Mejoramiento Genético Forestal del CATIE ha desarrollado semilla mejorada de *Eucalyptus deglupta*. Dicho material tiene una superioridad estimada en más de 60% de productividad juvenil.

2. Se recomienda el uso de semilla mejorada de *Eucalyptus deglupta* descrita aquí para la reforestación en sitios aptos para la especie en Costa Rica

3. El material no ha sido ensayado fuera de Costa Rica. Sin embargo, debido a la similitud de las condiciones ambientales, se recomienda su uso en zonas vecinas de Panamá y Nicaragua (Provincia de Bocas del Toro y Departamento de Río San Juan).

4. El material no ha sido seleccionado bajo las condiciones ambientales de otras partes de América Central aptas para el cultivo de *E. deglupta* (por ej., la costa norte de Honduras, etc.). Por lo tanto, no se sabe si el material mantiene su superioridad en tales zonas, y se recomienda su uso únicamente si no se cuenta con fuentes locales de calidad aceptable.

6. En la población base de *Eucalyptus deglupta* en Costa Rica, existe variación genética en color de las hojas de plántulas y árboles jóvenes. Dicha variación está fuertemente relacionada con la tasa de crecimiento juvenil: los árboles con hojas moradas tienden a ser genotípicamente inferiores en cuanto a crecimiento.

7. Se recomienda la eliminación de arbolitos con hojas moradas en el vivero. Normalmente, la coloración puede detectarse 4-6 semanas después del repique.

8. Antes de comprar plántulas de *E. deglupta* en viveros comerciales, es aconsejable revisar que se hayan eliminado las plántulas moradas.

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METODOS PARA ACELERAR Y UNIFORMIZAR LA GERMINACION DE ESPECIES FORESTALES.

Emperatriz C. de Mayorga[1]

Con el propósito de avanzar en el conocimiento y manejo de semillas de especies forestales, se llevaron a término, diferentes experimentos tendientes a determinar las condiciones más apropiadas para inducir la velocidad y porcentaje de germinación de las semillas de cuatro especies forestales.

Como metodología general se empleó un diseño de bloques al azar con 3 repeticiones de 100 semillas cada una, para un total de 8 tratamientos. Los principales resultados se pueden resumir de la siguiente manera:

Especie	Tratamiento utilizado Germinación	(%)
Tectona grandis (Teca)	Colocados durante 3 horas en una solución soda cáustica al 4%	87
	Escarificación mecánica mediante desvastado de la testa con tijera	83
	Testigo	66
Andira inermis (Almendro de río)	Escarificación mecánica con tijera de podar	92
	Testigo	78
Swietenia humilis	Sumergir la semilla en agua dentro de un empaque por 1 día antes de la siembra a temperatura ambiente	85
	Testigo	63
Juglans nigra	Inmersión de la semilla en agua ambiente durante 3 días con cambio diario de agua	53
	Testigo	24
Myroxylon balsanum var *pereirae* Balsamo	Escarificación mecánica con tijera de podar (Escarificación directa al fruto)	37
	Testigo	29

Los ensayos se efectuaron en el Centro de Desarrollo Forestal San Andrés, perteneciente al Servicio Forestal y de Fauna del Ministerio de Agricultura de El Salvador.

Como se puede apreciar, todos los tratamientos aplicados a la semilla estimularon en un mayor o menor grado la germinación.

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A MORPHOLOGICAL GENETIC MARKER FOR EARLY GROWTH IN *Eucalyptus deglupta* BLUME

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Summary: In two progeny trials of *Eucalyptus deglupta*, purple leaves and green leaves were respectively genetically associated with slower early growth and faster early growth. As leaf colour is manifested early in the nursery production phase, leaf colour, particularly on a family mean basis, can be used a marker for elimination of slower growing genotypes. It is suggested that the phenomomen is possibly due to a provenance-mixing effect, consequently, the association and therefore the utility of the marker will be transient, tending to disappear as the purple strain of the species is gradually purged from the local base population

Introduction

Time is a major constraint on the genetic improvement of forest trees (3), both for reproductive reasons and because many economic traits are not expressed for several years (8). For these reasons, tree breeders have long been interested in the possibilities for marker-aided selection (8), under which traits are improved not through direct selection but by selection on another correlated trait. Such indirect selection is effective when $r_{X.Y}h_Y > h_X$ (where $r_{X.Y}$ = the genetic correlation between the trait (X) to be improved and the trait (Y) selected , h_Y = the square root of the heritability of trait Y) (6). Attention has been directed principally at early selection on the basis of juvenile expression of the trait to be improved (e.g. 10, 11). Morphological markers not based on age-to-age correlations are rare (9). Here we present an example of such a marker in *Eucalyptus deglupta*, a timber tree commonly planted in Central America.

Materials and methods

We collected open-pollinated seed from 48 plus-trees in the Atlantic zone of Costa Rica and established in two progeny tests in distinct climatic and soil conditions in Upala, Alajuela province and Turrialba, Cartago Province, Costa Rica. A randomized complete blocks design (11 blocks in Turrialba, 12 in Upala with three-tree line plots) was used. In the nursery and early field stages, pronounced variation in leaf colour was noted, corroborating both earlier subjective impressions and some references in the literature (3, 7). Because of this, at age sixteen months, both the total height (cm) and the leaf colour (1=green or more green than purple, 2=intermediate, 3=purple, or more purple than green) of each tree were evaluated. Data were analyzed using a mixed model analysis of variance with the GLM procedure of SAS (12). Significance of differences in height growth between families with high (> 2.5) and low (<1.5) leaf colour scores was tested using the SAS CONTRAST statement (12,13). A more detailed account of the analysis procedure, the treatments and sites, as well as the other aspects of the work not reported here, is given elsewhere (4)

Results

Phenotypic correlations between leaf colour and height growth were positive at Tuis and negative at Canalete, and in both cases close to zero. By contrast, genetic correlations were strongly negative (-0.4 at Tuis, -0.43 at Canalete). Across the two sites, the mean height of the 'green' group (2.6 m) was significantly greater (F=9.2, p=0.002) than that of the purple group (2.4 m). Six of the 15 tallest treatments were amongst the 15 greenest whilst six of the 15 shortest were drawn from the 15 most purple families. Only one of the 15 shortest families was drawn from the group of 15 most green, and only two of the 15 tallest were amongst the 15 most purple. Both family effects and block effects on leaf colour were significant but the contribution of block effects to total variance was much smaller than the contribution of family effects

Discussion and conclusions

The strongly negative genetic correlations and the significant superiority of the 'green' families indicates that families with fast initial growth genotypes tend also to be of green leaf-colour genotype. Purple-leaved families are easily evident soon after transplanting in the nursery (i.e. before outplanting), whereas the prediction of early field growth from nursery performance tends to be problematic. Leaf colour therefore has potential for use as a marker for early growth. However, the estimates of the phenotypic correlation and the presence of block effects indicate that the relationship may not be fully reliable on an individual-tree basis, except in extreme cases (see below). This problem can be overcome in the nursery by sowing by family and eliminating purple families. Alternatively, when this is not possible, all strongly purple trees could be culled, thus relying on the 'average effect' of the relationship, whilst accepting some loss of non-inferior genotypes.

The existence of a few slow growing green families and fast-growing purple families possibly gives a clue to the origin of the observed correlation. There are known to be provenance-related differences in leaf colour in *Eucalyptus deglupta* (5), whilst the Costa Rican base population of the species is also known to originate from widely separated parts of the species range (1). When two (or more) provenances with different leaf colours and growth rates are mixed, then both growth rate and leaf colour of an individual tree may reflect the contribution of the two provenances to its allelic composition, without this necessarily implying that the same genes which influence leaf colour also influence growth rate. In this case, the genetic correlation between leaf colour and growth rate, although important for practical purposes, may be spurious; it may be that within each provenance there is little or no additive genetic variation in leaf colour and/or no genetic correlation with growth rate. Fast-growing 'purple' families and slow-growing 'green' families are then explained respectively as fast- and slow-growing families within their respective provenances. Some weight is lent to this hypothesis by the appearance of trees representing 'extreme' examples of the purple phenomenon; these have flattened leaves, alate and cross-sectionally squarish stems, shallow, flat-topped crowns, and appear to be far more divergent from the green-leaved form than would be normal were the differences based solely on within-population variation. If correct, the provenance mixing hypothesis would also imply that, as the purple strain is progressively eliminated from the Costa Rican base population, the correlation will disappear.

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Forest Ecology and Management

Genetic variation in height growth and leaf colour of *Eucalyptus deglupta* Blume at ages up to 16 months in Costa Rica

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Abstract

Results of three progeny tests of *Eucalyptus deglupta* in Costa Rica are described and discussed. High levels of additive genetic variation were found in height growth up to 16 months. Heritabilities were within the range typically found in forest trees. High levels of additive genetic variation and family heritabilities in leaf colour were also found. Purple leaves were associated with slow growth, and green leaves with fast growth. The best families showed a high degree of stability across the three sites. Predicted genetic gain from directed seed collections of the best mother-trees ranged from 12.4 to 15.8%.

Keywords: *Eucalyptus deglupta*; Genetic correlation; Genotype–environment interaction; Heritability

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1. Introduction

Since its introduction from Papua New Guinea in the mid-1960s (CATIE, 1994), *Eucalyptus deglupta* has become one of the tree species most frequently planted by smallholder farmers in Costa Rica. It is favoured because of its rapid growth, tolerance of a wide range of altitudes and the relatively high quality of its timber, which is suitable for higher-value products such as transmission poles and furniture.

In spite of its generally satisfactory performance, there exists some evidence that the Costa Rican *E. deglupta* is genetically diverse and that, therefore, its growth and form could be improved. First, seed imports have been made from widely separated parts of the natural range, including Sulawesi (Indonesia), Mindanao (Philippines), and New Guinea mainland and New Britain (both Papua New Guinea); it is known that there are important genetic differences between these sources (Eldridge et al., 1993). Second, in Costa Rica, trees exhibit marked variation in leaf colour. This variation is most noticeable in saplings or in the nursery; colour ranges from bright green to intense purple. Informal observations in the CATIE (Centre for Research and Teaching in Tropical Agronomy) tree improvement nursery suggest that seedlings with purplish leaves grow more slowly and that particular trees tend to produce purple-leaved seedlings, thus suggesting that the observed variation has a genetic explanation.

Owing to its apparently high genetic variability and its increasing importance in smallholder forestry and agroforestry in Central America, in 1990 CATIE initiated a programme of genetic improvement of the species. Because of the high expenses of early cleaning costs, one of the key breeding objectives is the improvement of juvenile growth rate. The present paper

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describes the findings from evaluations up to age 16 months of height and leaf colour in three progeny trials. The objectives of the tests are the estimation of genetic parameters of height growth and leaf colour, the identification of elite trees for directed collections of improved seed (White, 1987) and, after conversion to seedling seed orchards, the production of improved seed.

2. Materials and methods

2.1. The treatments

The treatments consist of open-pollinated progeny of 52 mother-trees located in Costa Rican plantations. Forty-eight were plus-trees selected on the basis of stem straightness and cylindricity, with breast height diameter greater than or equal to the stand mean, and the remaining four were trees of average quality. The plantations were derived from seed imported by CATIE from New Guinea, New Britain, Indonesia, and the Philippines during the 1960s and early 1970s. The provenance of most of the individual plantations is unknown; however, there is some evidence that most are of Papua New Guinea (mainland and New Britain) provenances. Three commercial control lots collected in Costa Rica by CATIE were also included. In addition, Family 106, derived from a seed orchard in Papua New Guinea, was included. It is not known whether this family is open- or control-pollinated.

2.2. The experimental sites

The trials were planted at three sites in Costa Rica between May and July 1992. All sites have clay soils in Horizons A and B, with pH in the two horizons of 5.5 and 5.2, 5.2 and 4.8, and 4.9 and 4.6 in Canalete, San José and Tuis, respectively. Other site and geographical details are included in Table 1. Canalete is a site well suited to agricultural production, with no obvious limiting factors to growth, whereas San José is an exposed site with highly compacted soil. Canalete and San José were selected as representative of the extremes of the site conditions where the species might be planted in Costa Rica. By contrast, the Tuis site is fairly typical of the type of areas currently being reforested by smallholders with *E. deglupta* and other species. The principal limitations on growth were seen to be the competition from the sugar-cane and grass, the low nutrient content of the soil, and impeded drainage in the flat areas. The sites span the altitudinal range of successful plantations of the species in Costa Rica.

At San José, about half of the trees were destroyed by vandals 3 months after planting. The missing trees were replanted immediately.

2.3. Experimental design and measurements

A randomized complete block design with line plots of three trees was used. There are 12 blocks at Canalete, 19 blocks at San José and 11 blocks at Tuis. Two surround rows were planted, using a mixture of material from the families. All treatments are represented in all the sites, except for Families 43 (present only at San José) and 106 (absent at San José).

Total tree height was measured at 16 months and (Tuis only) 11 months. At Tuis, 11–16 month increments were derived from the data by subtraction. The leaf colour of each tree was assessed at 14 and 16 months (Tuis) and at 16 months (Canalete) using a three-point scale: one (green or tending more towards

Table 1
Geographical and environmental details of the planting sites of a progeny experiment of *Eucalyptus deglupta* in Costa Rica

Site	Altitude (m above sea-level)	Latitude (N)	Longitude (W)	Mean annual precipitation (mm) (σ)	Mean annual temperature (°C)	Mean no. of dry months ($\leq$ 50 mm of rain) (σ)
Canalete de Upala	80	10°50′	85°01′	1320 (199)[a]	27.5	2.5 (0.75)[a]
San José de Upala	80	10°56′	85°08′	1320 (199)[a]	27.5	2.5 (0.75)[a]
Tuis de Turrialba	770	9°50′	83°35′	2464 (500)[b]	21.5	1.5 (1.0)[b]

[a] Canalete meteorological station.
[b] La Suiza meteorological station.

Table 2
Underlying models used for the analysis of variance (ANOVA) and analysis of covariance (ANCOVA) of a *Eucalyptus deglupta* progeny experiment planted at three sites in Costa Rica

Hypothesis	Model[a]	Model type	Random effects in model	Denominator of *F* ratio
1 (height only)	$Yjkl = \mu + \alpha j + \lambda k + \epsilon jkl$	Random ANOVA on individual trees	All	ϵijk
1.2	$Yjk = \mu + \alpha j + \lambda k + \delta jk$	Random ANOVA on plot means	All	δjk
1 (height at San José)	$Yjkl = \mu + \alpha j + \lambda k + \beta(Xjkl - X) + \epsilon jkl$	Random ANCOVA on individual trees	All	ϵijk
3.4.5.6.7	$Yjk = \mu + \alpha j + \lambda k + \delta jk$	Mixed ANOVA on plot means	Blocks	δjk
3.4.5.6.7	$Yjk = \mu + \alpha j + \lambda k + \beta(Xjk - X) + \delta jk$	Mixed ANCOVA on plot means	Blocks	δjk
8.9.10	$Yijk(i) = \mu + \theta i + \alpha j + \lambda k(i) + \delta ijk(i)$	Mixed ANOVA on plot means	Blocks within sites	$\delta ijk(i)$
8.9.10	$Yijk(i) = \mu + \theta i + \alpha j + \lambda k(i) + \beta[Xijk(i) - X] + \sigma ijk(i)$	Mixed ANCOVA on plot means	Blocks within sites	$\delta ijk(i)$
11	$Yijk(i)l = \mu + \theta i + \alpha j + \lambda k(i) + \beta(Xijk(i)l - X) + \phi ij + \delta ijk(i)l$	Mixed ANCOVA on individual trees	Treatments, blocks within sites, Treatment by site interaction	$\delta ijk(i)l$

[a] Meaning of symbols: *Yjkl*, phenotypic value of *l*th tree of *j*th treatment in *k*th block; μ, population mean; αj, effect of *j*th treatment; λk, effect of *k*th block; ϵjkl, residual attached to *Yjkl* (pooled with treatment by block interaction); *Yjk*, plot mean of *j*th family in *k*th block; δjk, residual error attached to *Yjk*; β, the regression coefficient of *X* on *Y*; *Xijk(i)l*, the value of the age covariable *X* for the *l*th tree of the *j*th treatment of the *k*th block of the *i*th site; *X*, the mean value of the age variable *X*; *Xjk*, the mean value of the age covariable *X* for the *j*th treatment of the *k*th block; *Yijk(i)*, mean value of *j*th treatment in *k*th block of *i*th site; θi, effect of *i*th site; $\lambda k(i)$, effect of *k*th block within *i*th site; $\delta ijk(i)$, residual error attached to *Yijk(i)*; *Xijk(i)*, mean value of the age covariate for the *j*th treatment in the *k*th block in the *i*th site; ϕij, the interaction effect of the *j*th family and the *i*th site.

green than purple); two (intermediate); three (purple or tending more towards purple than green). The classifications were made by simple visual judgement on a whole-tree basis. Leaf colour was not assessed at San José.

2.4. Hypotheses and statistical analyses

Null hypotheses, together with additional notes on their associated statistical analyses, are presented below. For the individual-site analyses at Tuis and Canalete and the across-site analyses of these two sites only, all hypotheses were tested using *F* tests derived from analyses of variance. As half the trees at San José were replants, for that analysis and the combined analysis of all three sites, a covariate was introduced; for trees at San José this had values of zero (original trees) or one (replants). In the combined analysis, at Tuis and Canalete the covariate term in the model was set to zero by assigning to each tree a covariate value equal to the covariate mean at San José (Corea, 1989). The underlying models are presented in Table 2.

2.4.1. Hypothesis 1—there is no additive genetic variance for height and leaf colour in the Costa Rican base population of E. deglupta

Only the open-pollinated families were taken into account in the testing of this hypothesis. The following height growth parameters were estimated from analyses based on individual trees: the additive genetic variance, $\sigma_A^2 = 2.5\sigma_F^2$, where σ_F^2 is the variance component owing to open-pollinated families; the narrow-sense heritability on an individual-tree basis $h^2 = \sigma_A^2/(\sigma_E^2 + \sigma_F^2)$, where σ_E^2 is the residual variance; the additive genetic coefficient of variation $\mathrm{AGCV} = 100(\sigma_A/x)$, where x is the population mean. The multiplier of 2.5 assumes a coefficient of relationship between open-pollinated sibs of 0.4, based on an average outcrossing rate of 70% for *Eucalyptus* (Moran and Bell, 1983; Griffin and Cotterill, 1988). Block variance was omitted from the denominator of the heritability, as the practical application of the latter will be within-trial selection on block-adjusted values (Cotterill, 1987).

The following parameters (all traits, unless stated) were estimated from plot mean analyses: σ_A^2 (leaf colour only); heritability of family means, $h_F^2 = \sigma_F^2 / [(\sigma_E^2 / b) + \sigma_F^2]$, where b is the number of blocks; additive genetic correlation between height and leaf colour, $r_{a(h,c)} = \sigma_{h,c} / (\sigma_h^2 \sigma_c^2)^{1/2}$, where $\sigma_{h,c}$ is the additive genetic covariance between height and leaf colour, and $\sigma_{h,c} = (\sigma_{h+c}^2 - \sigma_h^2 - \sigma_c^2)/2$, σ_h^2 is the family variance component for height, σ_c^2 is the family variance component for leaf colour, and σ_{h+c}^2 is the family variance component of the sum of height and leaf colour (Stonecypher, 1992).

2.4.2. *Hypothesis 2—there are no within-site environmental effects on leaf colour*

Significant additive genetic variance in leaf colour would not imply that the trait is uninfluenced by environmental effects. For this reason, the significance of the block effect for leaf colour was tested. The block effect is considered to estimate within-site 'patchy' environmental effects in the reference population. A block variance component was also estimated, to compare the importance of the block effect relative to that of family and residual variance.

2.4.3. *Hypothesis 3—at each site individually, there are no differences between the parametric treatment means for height and leaf colour*

All treatments were included in this mixed model analysis. A number of subsidiary hypotheses involving planned comparisons were tested as part of the same analyses, using single degree of freedom *F*-tests (Stonecypher, 1992): at each site individually, there are no differences between the parametric treatment height means of the selected families and that of the three controls taken as a group (Hypothesis 4); there are no differences between the parametric treatment height means of the Costa Rican plus-tree families and the Papua New Guinea seedlot (Tuis only) (Hypothesis 5); at Tuis at 11 months and Canalete at 16 months, there is no difference between the parametric treatment height means of those treatments with mean leaf colour (at 14 months at Tuis and 16 months at Canalete) greater than or equal to 2.5 and those with mean leaf colour less than or equal to 1.5 (Hypothesis 6); at Tuis at 16 months there is no difference between the parametric treatment height means of those families with mean leaf colour greater than or equal to 2.0 and those with mean leaf colour less than or equal to 1.5 (Hypothesis 7). The selection of the leaf colour groups mentioned in Hypotheses 6 and 7 was made on the basis of the distribution of leaf colour treatment means at the two measurements in question, to ensure at least five treatments in each group.

2.4.4. *Hypothesis 8—over the three sites there are no differences between the parametric treatment means for height*

Rejection of this hypothesis would indicate that there are some treatments that are superior to others over all three sites, irrespective of any interaction that might exist (there is no interaction term in the model (Table 2)). The following subsidiary hypotheses were tested, as for Hypothesis 3: Hypothesis 9—over the three sites, there are no differences between the parametric treatment height means of the selected families and the three controls as a group; Hypothesis 10—over Tuis and Canalete, there are no differences between the parametric treatment 16 month height means of those treatments with mean 16 month leaf colour greater than or equal to 2.5 and those with mean 16 month leaf colour less than or equal to 1.5.

2.4.5. *Hypothesis 11—there is no family–site interaction for height growth over the three sites*

3. Results and discussion

The mean heights at the different sites (Table 3) were consistent with the perceived quality of the three sites, San José having a much lower mean (1.4 m) than Canalete (2.7 m) and Tuis (2.4 m), respectively (Table 3).

3.1. *Additive genetic variation and heritabilities of* E. deglupta *at the three sites*

At all sites and measurement ages, there were highly significant ($P = 0.0001$) family effects on height ble 3

sults of random and mixed model analyses of variance and covariance, with expected mean squares and estimates of genetic parameters in three progeny trials of calyptus deglupta in Costa Rica (for mixed model, only degrees of freedom, F and associated probability, and mean included (in braces, where different from ndom model))

ait	Effect	Degrees of freedom	Mean square	F	$P > F$	Expected mean squares	Variance component (VC%)	Mean (CV%)[a]	Genetic parameters
analete									
eight, 16 months[b]	Blocks	11	175489.5	16.41 {9.93}	0.0001	Var(Error) + 120.39 Var(BLQ)	1354		$\sigma^2_A = 1934$ AGCV = 16.2%
	Treatments	51 {54}	34258.8	3.65 {2.23}	0.0001	Var(Error) + 28.164 Var(Fam)	773.7	271 {36} {273}	$h^2 = 0.15$ $h^2_f = 0.61$
	Error	1448 {532}	12468.5			MS error	12468.5		
olour, 16 months	Blocks	11	0.52	1.88 {1.79}	0.04 {0.05}	Var(Error) + 45.545 Var(BLQ)	0.005 {0.7}	1.8 {29}	$\sigma^2_A = 0.575$ AGCV = 42.1%
	Treatments	51 {54}	2.74	9.84 {9.28}	0.0001	Var(Error) + 10.608 Var(Fam)	0.23 {36.0}		$h^2_f = 1.01$
	Error	490 {521}	0.28			MS error	0.40		
an José									
leight, 16 months[b]	Blocks	18	33714.9	15.03 {12.14}	0.0001	Var(Error) + 105.14 Var(BLQ)	299.3	146 {32} {143}	$\sigma^2_A = 452.0$ AGCV = 14.6%
	Treatments	50 {54}	9405.5	4.19 {3.13}	0.0001	Var(Error) + 39.605 Var(Fam)	180.8		$h^2 = 0.19$ $h^2_f = 0.73$
	Covariable	1	421026.6	187.53 {65.62}	0.0001				
	Error	1960 (875)	2245.1			MS error	2245.1		
Tuis									
Height, 11 months[b]	Blocks	10	157550	73.49 {47.69}	0.0001	Var(Error) + 141.06 Var(BLQ)	1102	118 {39}	$\sigma^2_A = 527.5$ AGCV = 19.4%
	Treatments	50 {54}	8588	4.01 {2.21}	0.0001	Var(Error) + 30.509 Var(Fam)	211		$h^2 = 0.22$ $h^2_f = 0.57$
	Error	1496 {511}	2143.8			MS error	2143.8		
Height, 16 months[b]	Blocks	10	10108	134.4 {86.88}	0.0001	Var(Error) + 140.19 Var(BLQ)	71.6	243 {36}	$\sigma^2_A = 22.5$ AGCV = 19.5%
	Treatments	50 {54}	347.0	4.61 {2.53}	0.0001	Var(Error) + 30.33 Var(Fam)	9		$h^2 = 0.27$ $h^2_f = 0.63$
	Error	1487 {511}	75.2			MS error	75.2		
Colour, 14 month	Blocks	10	1.65	6.86 {7.58}	0.0001	Var(Error) + 48.2 Var(BLQ)	0.03 {5.1}	2.0 (25)	$\sigma^2_A = 0.375$ AGCV = 30.9%
	Treatments	50 {54}	1.78	7.41 {6.98}	0.0001	Var(Error) + 10.4 Var(Fam)	0.15 {25.9}		$h^2_f = 0.91$
	Error	472 {511}	0.24			MS error	0.40		
Colour, 16 months	Blocks	10	3.11	15.33 {16.6}	0.0001	Var(Error) + 49.7 Var(BLQ)	0.05 {8.9}	2.4 {19} {2.3}	$\sigma^2_A = 0.275$ AGCV = 22.3%
	Treatments	50 {54}	1.62	8 {7.75}	0.0001	Var(Error) + 10.74 Var(Fam)	0.11 {19.6}		$h^2_f = 0.77$
	Error	487 {511}	0.4			MS error	0.40		
Increment[b]	Blocks	10	346548.1	108.8 {91.6}	0.0001	Var(Error) + 128.95 Var(BLQ)	2661.4	129 {44} {123}	$\sigma^2_A = 805$ AGCV = 21.9%
	Treatments	50 {54}	12403.9	3.9 {2.5}	0.0001	Var(Error) + 28.05 Var(Fam)	322		$h^2 = 0.23$ $h^2_f = 0.66$
	Error	1430 {511}	3185.7			MS error		3185.7	

[a] Height in centimetres, colour scored using index of one (green), two (intermediate) or three (purple).

[b] Family heritabilities based on plot mean analyses analogous to those on leaf colour.

Table 4
Estimates of additive genetic (above diagonal) and phenotypic (below diagonal) correlations between five variables in three progeny trials of *Eucalyptus deglupta* located in Costa Rica (1. Canalete trial; 2. Tuis trial)

	Height, 11 months	Height, 16 months	Increment	Colour, 14 months	Colour, 16 months
Height, 14 months		2. 0.91	2. 0.73	2. −1.16	2. −1.0
Height, 16 months	2. 0.91		2. 0.95	2. −0.40	1. −4.43 2. −0.40
Increment	2. 0.76	2. 0.95		2. −0.02	2. −0.36
Colour, 14 months	2. −0.3	2. −0.3	2. −0.28		1. 0.95
Colour, 16 months	2. 0.04	1. −0.17 2. 0.05	2. 0.05	2. 0.47	

growth (Table 3). Therefore, Null Hypothesis 1 can be confidently rejected for all ages: there is strong evidence for existence of additive genetic variance in juvenile height growth in the base population. AGCV for height varies from 14.6% at Canalete to 21.9% for the 14–16 month increment at Tuis. In forest trees, estimates of AGCV for height typically range from 5 to 15% (Cornelius, 1994). The estimates reported here, therefore, suggest rather high levels of additive genetic variation. Heritability estimates for height growth (Table 3) range from 0.15 at Canalete to 0.27 for 16 month height at Tuis. All are within the range typically found in forest trees for this trait (Cornelius, 1994). Family mean heritability ranged from 0.57 (Canalete) to 0.73 (San José).

At all sites and measurement ages, there were also significant ($P = 0.0001$) family effects on leaf colour (Table 3); the null hypothesis can therefore be confidently rejected, and it can be concluded that there is additive genetic variation in leaf colour in the base population. AGCV for leaf colour was high, varying from 22.3% (Tuis, 16 months) to 42.1% (Canalete). Estimates of family mean heritabilities for leaf colour were also high, ranging from 0.77 (Tuis, 16 months) to 1.01 (Canalete), and indicating that the greater part of the phenotypic variation between family means is of additive genetic origin. Although the analysis of block effects indicated that Null Hypothesis 2 can be confidently rejected and that there appear to be environmental effects on leaf colour, the contribution to total variance of block effects was much smaller than that of family effects: 0.70% against 36% at Canalete, 5.1% against 25.9% at 14 months at Tuis, and 8.9% against 19.6% at 16 months at Tuis.

It may be that the genetic variation in leaf colour reflects the diversity of provenances from which the base population was formed. Eldridge et al. (1993) mentioned the existence of provenance-related variation in leaf colour, provenances from New Britain having bright green leaves, in contrast to the whitish bloom observed on leaves of trees of Mindanao provenance.

3.2. *Relationship between leaf colour and growth rate*

Phenotypic correlations between height traits and leaf colour (Table 4) were close to zero and both negative and positive. Genetic correlations were moderately to strongly negative. In two cases the estimates were less than −1.0, and therefore outside the range of possible values of the parametric correlation. Estimates of genetic correlations tend to be imprecise (Falconer, 1989). Those reported here should not be considered as anything more than a guide to the sign and strength of the parametric association between the two variables. Together, the estimates of phenotypic and genetic correlations suggest that those alleles conducive to production of green leaves are also conducive to faster growth, but that this genetic relationship may not be apparent when comparing the phenotypes of individual trees or small groups (e.g. three-tree family plots) of trees.

Comparisons between height means of the different leaf colour groups are included in Table 5. At Canalete, the treatments with mean leaf colour less than or equal to 1.5 had mean height of 2.9 m, compared with 2.6 m for those treatments with mean leaf colour of 2.5 or greater ($F = 3.67$, $P = 0.06$). At Tuis, the respective heights of the two groups were 1.25 m and 1.07 m at 11 months ($F = 12.8$, $P = 0.0004$) and 2.5 m and 2.3 m at 16 months ($F = 14.5$, $P = 0.0002$). Between 11 and 16 months, the average increment of the green group was 1.3 m, against 1.09 m for the purple group

($F = 19.4$, $P = 0.0001$). Therefore, at Tuis, Null Hypotheses 6 and 7 of no difference in height growth between the two leaf colour groups can be confidently rejected. They may also be rejected, although with less confidence, at Canalete.

Across Tuis and Canalete, mean height of the green group was 2.6 m, against 2.4 m for the purple group ($F = 9.2$, $P = 0.002$); Null Hypothesis 10 can be confidently rejected. Across the two sites, six of the tallest treatments are among the 15 with lowest (greenest) leaf colour means, whereas six of the shortest families are among those with highest (most purple) leaf colour scores (Table 6). Although Families 14 and 15, both among the most purple, are also among the fastest growing, whereas Family 49, among the most green, is one of the slowest growing families, in general the association of purple leaves with slow growth, as evinced by the genetic correlations, is directly confirmed by the comparisons of the growth rates of the purple and green groups.

Table 6
Performance for height and leaf colour of those treatments among the best and worst 15 for height and/or leaf colour in a progeny test of *Eucalyptus deglupta* located at two sites in Costa Rica

	15 tallest	15 shortest
15 greenest	7,8,16,27,34,39	49
15 purplest	14,15	43,37,102,6,10,25

The existence of provenance effects for leaf colour, as suggested above, provides a plausible explanation for the occurrence of fast-growing purple families and slow-growing green families, which otherwise would suggest breakdown of the pleiotropic effects generally responsible for additive genetic correlation (Falconer, 1989). When two (or more) provenances with different leaf colours and growth rates are mixed, then both growth rate and leaf colour of an individual tree may reflect the contribution of the two provenances to its allelic composition, without this necessarily implying

Table 5
Results of planned comparisons between treatment groups in three progeny trials of *Eucalyptus deglupta* in Costa Rica

Comparison Group 1	Mean (cm) Group 1	Comparison Group 2	Mean (cm) Group 2	F	$P > F$
Canalete, 16 month height					
All plus-tree families	277	The three commercial controls	250	3.67	0.06
Treatments with mean leaf colour ≤ 1.5	289	Treatments with mean leaf colour ≥ 2.5	258	3.51	0.06
Tuis, 11 month height					
All plus-tree families	116	The three commercial controls	119	0.26	0.61
All plus-tree families	116	Papua New Guinea	113	0.11	0.74
Treatments with mean leaf colour ≤ 1.5	125	Treatments with mean leaf colour ≥ 2.5	107	12.8	0.0004
Tuis, 11–16 month increment					
All plus-tree families	121	The three commercial controls	135	3.52	0.06
All plus-tree families	121	Papua New Guinea	162	10.28	0.001
Treatments with mean leaf-colour ≤ 1.5	132	Treatments with mean leaf colour ≥ 2.5	109	12.77	0.0004
Treatments with mean leaf colour ≤ 2.0	131	Treatments with mean leaf colour ≥ 2.5	115	19.4	0.0001
Tuis, height at 16 months					
All plus-tree families	237	The three commercial controls	253	1.81	0.17
All plus-tree families	237	Papua New Guinea	246	0.18	0.67
Treatments with mean leaf colour ≤ 2.0	252	Treatments with mean leaf colour ≥ 2.5	228	14.47	0.0002
All three sites, 16 month height					
All plus-tree families	220	The three commercial controls	212	1.91	0.17
All plus-tree families	220	Papua New Guinea	208	0.99	0.32
Tuis and Canalete only, 16 month height					
All plus-tree families	256	The three commercial controls	251	8.7	0.003
Treatments with mean leaf colour ≤ 1.5	264	Treatments with mean leaf colour ≥ 2.5	241	9.2	0.002

that the same genes which influence leaf colour also influence growth rate. In this case, the genetic correlation between leaf colour and growth rate, although important for practical purposes, may be spurious; it may be that within each provenance there is little or no additive genetic variation in leaf colour and/or little or no genetic correlation with growth rate, leaf colour merely acting a marker of the faster growing provenance(s) when provenances are mixed. Fast-growing purple families and slow-growing green families are then explicable respectively as fast and slow-growing families within their respective provenances.

Published reports mentioning the existence in Costa Rica of two provenances (red and green) and the superiority of an intermediate provenance hybrid (e.g. Food and Agriculture Organization, 1979) seem to be based on a questionable interpretation of an unreplicated trial described by Combe and Gewald (1979), and do not appear to be fully reliable.

3.3. Performance of families at individual sites

The results of the mixed model analyses of variance, in which all treatments, rather than just the open-pollinated families as in the random analyses, were included, are presented in Table 3. Probability values for the calculated *F* values are the same as in the random model. Null Hypothesis 3, that there are no differences between parametric treatment means, can be confidently rejected.

Least-squared means for height growth traits are listed in Table 7. Family means at 16 months at Canalete ranged from 2.1 to 3.6 m, at San José from 1.1 to 1.8 m and at Tuis from 1.8 to 3.0 m. At Canalete, San José and Tuis, the best five families have pooled least-squared 16 month height means 25.9%, 17.4% and 19.7%, respectively, above the grand mean of the site in question.

3.4. Across site performance and genotype–environment interaction

Over the three sites, family–site interaction was a highly significant source of variation in height growth (Table 8); Null Hypothesis 11 may be confidently rejected. However, genotype–environment interaction variance may result not only from interactions of practical interest, i.e. cases when the best families at one or more sites are not the best at one or more other sites, but also from changes in rank among the worst or between the worst and the mediocre families, as well as changes in relative position without rank changes. It is, therefore, worthwhile to examine not only the significance of the genotype–environment interaction, but also to consider the behaviour of the best families across the different sites.

In spite of the significant interaction, across-site treatment effects were still highly significant when the interaction term is pooled with the error (Table 8). The least-squared mean 16 month heights of the best and worst 15 treatments across the three sites are included in Table 7. Overall means range from 1.7 to 2.7 m. Comparison with the individual site details (Table 7) reveals that seven of the 15 best families are among the 15 best at all the three sites individually, and 13 of them are among the best at two or three of the sites. Similarly, relatively few of the families among the best 15 at two of the sites are absent from the best 15 at the remaining site (Family 8 at Tuis, Families 101 and 39 at Canalete, Families 27, 14 and 41 at San José) (Table 7). Furthermore, even these are reasonably good performers at the site where they are not among the best 15: Family 8 ranked eighteenth at Tuis, Families 101 and 39 ranked twentieth and eighteenth, respectively, at Canalete, and Families 27, 14 and 41 ranked twenty-third, nineteenth and seventeenth, respectively, at San José. Given the overall slower growth at San José, it is also worth pointing out that the Tuis 11 month and 11–16 month increment results indicate that Families 27 and 41 are slow starters. It would be unwise to rule out the possibility that, with time, Families 27 and 41 may figure among the best families at San José as well. Four families were outstanding at one site only: at Canalete, Families 4 and 28, and at San José, Families 17 and 40. At Canalete, both Families 4 and 28 had values below the mean, whereas at Tuis they occupied Positions 20 and 23, respectively. Family 40 occupied Position 16 at Tuis and Position 17 at Canalete, and Family 17 occupied Position 22 at Tuis and had a value higher than the mean at Canalete. Therefore, the only families which demonstrated important rank changes between sites were Families 4 and 28 between Canalete and San José. In general, the best families show a high degree of stability across the three sites; the significant interaction would appear to be of little practical interest.

Table 7
Least-squared height means of best 15 and worst 15 treatments in three progeny trials of *Eucalyptus deglupta* in Costa Rica

Rank	All three sites				Tuis		Canalete		San José	
	16 month height (cm)		11–16 month height increment (cm)		16 month height (cm)		16 month height (cm)		16 month height (cm)	
	Treatment	Mean	Treatment	Mean	Treatment	Mean	Treatment	Mean	Treatment	Mean
1	26	271	27	165	16	302	26	364	34	178
2	16	269	106	162	26	300	16	355	17	175
3	34	253	41	156	27	292	8	340	101	171
4	7	253	109	152	109	282	22	324	26	169
5	8	248	26	152	7	278	7	323	16	164
6	27	247	39	149	41	277	14	321	7	164
7	101	247	16	149	101	276	27	320	109	161
8	48	244	107	146	15	272	48	318	42	159
9	22	243	7	144	39	270	34	314	8	158
10	14	242	40	143	34	268	42	311	39	158
11	41	242	101	141	31	267	41	306	48	157
12	39	239	48	139	14	264	4	302	40	157
13	17	237	31	136	22	263	13	299	13	156
14	40	236	111	135	48	261	28	298	31	153
15	13	236	15	135	111	259	15	296	22	152
41	33	201	33	108	37	211	33	247	2	133
42	38	200	44	106	51	211	6	242	25	131
43	21	200	3	105	5	209	38	239	47	129
44	102	194	42	105	25	208	25	238	37	129
45	25	194	5	105	20	207	107	236	49	126
46	50	191	20	100	45	206	19	239	111	124
47	19	189	37	99	38	202	21	235	102	124
48	110	189	6	98	50	197	110	231	50	123
49	12	188	38	96	49	194	12	228	10	123
50	37	186	21	95	29	194	10	227	5	120
51	6	184	102	94	108	185	43	222	106	119
52	49	184	12	92	102	184	49	221	19	117
53	10	181	49	89	6	183	45	211	110	115
54	45	177	108	89	12	182	108	210	108	112
55	108	171	10	84	10	181	37	210	45	111

3.5. Planned comparisons

The results of the planned comparisons (Hypotheses 4–7) are presented in Table 5. At Tuis, the grand least-squared mean of the three commercial controls was higher than that of the plus-tree families. However, the lowest probability value for the F values for the three traits was $P = 0.06$ (11–16 month increment). At Canalete, the 16 month height of the plus-tree families was greater than that of the three controls; probability of the calculated F value was again 0.06. Neither at Canalete or Tuis can Null Hypothesis 4 of no difference between the two groups be rejected with any confidence. For the combined site analysis over all three sites and only Tui and Canalete, the plus-tree families had a higher 1 month height mean than the three commercial controls Over all three sites, the associated probability of thi having occurred by chance alone was high ($P = 0.17$) Therefore, there do not exist sufficient grounds fo rejecting Hypothesis 9. There was no strong evidenc for differences in height growth between the control as a group and the plus-tree families. This is to b expected, as very little selection pressure was place on growth traits.

Null Hypothesis 5 of no difference between the par ametric means of the Papua New Guinea family an

Table 8
Results of combined site random and mixed model analyses of covariance of height at 16 months of a *Eucalyptus deglupta* progeny experiment located at three sites in Costa Rica

Effect	Degrees of freedom[a]	F	$P>F$	
Random model				
Sites	2 [1]	1333.9 [123.4]	0.0001 [0.0001]	
Block (site)	39 [21]	56.5 [70.2]	0.0001 [0.0001]	
Treatments	54 [55]	10.1 [6.4]	0.0001 [0.0001]	
Treatments × sites	107 [53]	1.75 [1.2]	0.0001 [0.13]	
Covariable	1 [n.a.]	77.1 [n.a.]	0.0001 [n.a.]	
Error	5186 [2979]			
Mixed model				**Mean (cm) [CV%]**
Sites	2	948.1	0.0001	206 [29.7]
Block (site)	39	34.5	0.0001	
Treatments	54	6.0	0.0001	
Covariable	1	28.3	0.0001	
Error	2050			

[a] In the case of the random model, values in square brackets refer to the analysis over Tuis and Canalete only.
n.a., not applicable.

the plus-tree families was tested only at Tuis. At 11 months, the seed orchard family was 3 cm shorter than the grand mean of the plus-trees. The calculated F value had 0.74 probability of occurring by chance alone. There are no grounds for rejecting the null hypothesis. The 16 month height was higher for the Papua family than for the plus-tree families, but again the observed F value had a high probability ($P=0.67$) of having occurred by chance alone. Between 11 and 16 months, the plus-tree families averaged 1.2 m increment, compared with 1.6 m for the Papua source, which was the second fastest grower in increment, with a behaviour similar to that of Families 27 and 41 (see above). The calculated F value had 0.001 probability of occurring by chance alone. Null Hypothesis 5 can be confidently rejected for 11–16 month height increment at Tuis. Although at the last measurement, the mean height of the Papua New Guinea family was not significantly different from the mean of the plus-trees, the significantly higher increment suggests that it is a relatively slow starter, which, after about 1 year of growth, will tend to grow faster than the mean of the plus-trees. This apparent superiority may be the result of prior selection and breeding, or may simply be a sampling effect (i.e. the family may be the best of a group of Papua seed orchard families that, on average, may be no better than the plus-tree families). It should not be concluded from this study that material improved elsewhere would necessarily be superior in Costa Rica.

3.6. Practical implications

The estimated values of the genetic parameters imply that there is considerable potential for genetic improvement in juvenile height growth. In the short term, this potential will be used through follow-up collections of seed from the five best plus-trees. For seed collection from the mother-trees of the best five families at each site (with planting within the environmental conditions represented by the site in question), predicted gains are $R\% = S \times h_F^2$, where S is percentage superiority over the mean of the five best families, and are therefore $19.7\% \times 0.63 = 12.4\%$ for Tuis, $25.9\% \times 0.61 = 15.8\%$ for Canalete, and $17.4\% \times 0.73 = 12.7\%$ for San José. Alternatively, the use of the five best families overall would yield predicted gains of $15.6\% \times 0.63 = 9.8\%$ on the site types similar to Tuis, $25\% \times 0.61 = 15.3\%$ on sites similar to Canalete, and $14.4\% \times 0.73 = 10.5\%$ on sites similar to San José. The lower gain at Tuis and San José represents the expected effect of ignoring rank changes between sites in the selection of trees for directed seed collection.

In the longer term, the trials will be converted to seedling seed orchards. Phenotypic selection for 16 month height growth at Tuis, assuming proportion selected of 10%, would yield gain of $R\% = iAGCV(h^2)^{1/2} = 1.755 \times 19.5\% \times 0.52 = 17.8\%$.

The results discussed here do not permit firm conclusions to be drawn on possible improvement in growth rate at later stages, or in other possibly correlated traits. However, unless age-to-age correlations are negative, then there should be a reduction in rotation length concomitant with the increased early growth. If, as Lambeth's (1980) results suggest, age-to-age correlations tend to be positive, then this effect will be further enhanced by more rapid growth at later stages. However, it should be stressed that the most important positive effect of increased early growth is likely to be a reduction in early cleaning costs and their associated high interest charges. Early growth rate is in itself a trait of key economic importance.

The high degree of genetic control of leaf colour, coupled with the association of purple leaves with slow growth, has direct practical implications in nursery management. Ideally, seed should be sown by mother-tree. Purple families could then be eliminated and repeat collections from the same tree could be avoided. Alternatively, all strongly purple seedlings could be culled.

4. Conclusions

(1) There are high levels of additive genetic variation for juvenile height growth rate and leaf colour in the Costa Rican base population of *E. deglupta*.

(2) Leaf colour and growth rate appear to have high additive genetic correlations, fast growth being associated with green leaves and slow growth with purple leaves. Although this correlation may be the result of provenance bulking rather than pleiotropic gene effects, it is of practical importance. It can be used in the nursery to cull out individual plants of slow growth potential.

(3) Estimates of heritability for height growth were within the ranges typical for forest trees and, together with the high levels of additive genetic variation, suggest that appreciable genetic gain can be achieved, both through directed seed collections from superior mother-trees and through conversion of tests to seedling seed orchards.

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VALERIO, J. 1986. Evaluación de nueve procedencias de *Gmelina arborea* Roxb. en Turrialba, Costa Rica. Tesis Mag.Sc. Turrialba, Costa Rica, UCR/CATIE. 92 p.

Palabras clave: *Gmelina arborea*, ensayos de procedencias, raleo en ensayos de procedencias, Costa Rica.

RESUMEN

Gmelina arborea es una especie de rápido crecimiento utilizada en reforestación para la producción de pulpa y madera para aserrío. En 1982 se estableció un ensayo en Pavones de Turrialba, Costa Rica, con el fin de obtener información sobre el comportamiento de nueve procedencias de esta especie, como parte de una serie internacional de ensayos coordinados por DANIDA Forest Seed Centre, entidad que suministró las semillas. Los objetivos de este trabajo fueron: 1) evaluar a edad temprana el grado de variación fenotípica entre las procedencias incluidas en dicho ensayo, con respecto a sobrevivencia, crecimiento y forma de los árboles, densidad de la madera y largo de fibra; 2) determinar el mejor criterio de selección de árboles para raleo el ensayo.

El trabajo se planteó sobre la hipótesis de que las condiciones ambientales particulares de las regiones en las que evolucionaron las procedencias han originado diferencias en sus frecuencias génicas.

En el ensayo se probaron dos procedencias derivadas, una de Manila, Siquirres, Costa Rica (BLSF1018) y otra de São Miguel, Pará, Brasil (DAN.4040) y siete procedencias nativas. Tres de ellas provienen del estado de Andhra Pradesh, India: Meredumilli (DAN.4058), Lambasingi (DAN.4065) y DAN.4066 cuya ubicación exacta se desconoce; una de Bengala Occidental, India: Sankosh-1 (DAN.4045); dos de Sri Lanka, de ubicación desconocida (DAN.4067 y DAN.4068); y una procedencia de Tailandia, de Kao Yai, Saraburi (D 1003/80).

Las variables de respuesta fueron: sobrevivencia, diámetro a la altura del pecho, altura total, dominancia del eje principal, altura de ramificación o bifurcación, rectitud, densidad básica de la madera y largo de fibras, y área basal por parcela como variable derivada. El análisis de varianza detectó diferencias entre procedencias

(P < 0,01) para las variables evaluadas, excepto para sobrevivencia y altura de ramificación o bifurcación. Aparentemente el sitio de estudio reúne las condiciones necesarias para el crecimiento de todas las procedencias probadas. La altura de ramificación o bifurcación la determinan principalmente factores ambientales como la incidencia de luz lateral.

El orden de las procedencias según las medias de las variables de crecimiento fue similar al orden según las medias de las variables de forma. No hubo una relación clara entre el comportamiento de las procedencias con respecto a las variables de crecimiento y las de densidad de madera y largo de fibra, ni entre estas últimas. Se determinó que la presencia de reiteraciones en el modelo arquitectural de la especie y su variación por procedencia determina la pérdida de dominancia del eje principal e influye en la pérdida de rectitud.

La procedencia local (BLSF1018) junto con la de São Miguel (DAN.4040) y una de Sri Lanka (DAN.4067) presentaron el mejor comportamiento, por lo que se recomienda partir de las plantaciones establecidas con semilla recolectada en Manila, para iniciar un programa de mejoramiento genético. En una primera etapa se deben considerar las variables de forma y crecimiento, dejando para una segunda etapa la selección por características como densidad de la madera y largo de fibra.

Debido a la evidente competencia entre los árboles en el ensayo y de acuerdo con la literatura consultada se propuso efectuar un raleo del 50 por ciento. Para recomendar el mejor criterio de selección de árboles se evaluaron cuatro alternativas: i) no ralear, ii) raleo sistemático, iii) raleo por diámetro y iv) raleo selectivo silvicultural. Se compararon las características de los posibles vuelos remanentes con respecto al promedio de las variables evaluadas, varianza, coeficientes de variación y posible efecto diferencial del raleo sobre alguna de las procedencias. Se determinó que el raleo selectivo silvicultural permite asegurar una adecuada distribución de los árboles en el ensayo, retiene los mejores individuos, mantiene la variabilidad dentro de las parcelas y no afecta en forma diferente a ninguna procedencia, lo que permite que el ensayo mantenga su validez para evaluaciones futuras.

Valerio, J. 1986 Evaluation of nine provenances of Gmelina arborea Roxb. in Turrialba, Costa Rica. Thesis Mag.Sc. Turrialba, Costa Rica, UCR/CATIE. 92 p.

Keywords: Gmelina arborea, provenances trials, thinings in provenances trials, Costa Rica.

SUMMARY

Gmelina arborea ia a species of rapid growth used in reforestation to produce pulp and sawn timber. In 1982 a trial was established in Pavones, Turrialba, Costa Rica, to obtain information on the performance of nine provenances of G. arborea as part of an international network of trials coordinated by the DANIDA Forest Seed Centre, who supplied the seeds. The objectives of this study were to: 1) Evaluate at an early age the phenotypic variation between the provenances in the trial with respect to survival, growth and form of trees, wood density and fibre length, 2) Determine the best tree selection criteria to thin the provenance trial.

The study was based on the hypothesis that environmental conditions specific to the provenances region of origin have produced differences in their respective gene frequencies.

The trial tested two derived provenances, one from Manila, Siquirres, Costa Rica, (BLSF1018) and the other from São Miguel, Pará, Brazil (DAN.4040). Seven native provenances were tested; three from Andhara Pradesh, India -Meredumilli (DAN.4058, Lambasingi (DAN.4065) and DAN.4066, whose exact location is unknown; one from West Bengal, India: Sankosh-1 (DAN.4045); two from Sri Lanka, location unknown (DAN.4067 and DAN.4068); and a provenance from Thailand, Kao Yai, Saraburi (D1003/80).

The traits evaluated were: survival, diameter at breast height, total height, main shoot dominance, branching height, straightness, basic wood density and fibre length. As a derived variable, basal area per plot was also evaluated. The analysis of variance detected differences between provenances ($P < 0,01$) for all variables, but sur-

vival and branching height. The trial site shows conditions suitable for the growth of all provenances tested. Branching height is determined principally by environmental factors, such as the incidence of lateral light.

The order of provenances by means for growth variables was similar to the rankings for form variables. There was no clear relationship between the performance of provenances with respect to growth variables, wood density and fibre length or between the latter two. It was found that the presence of reiterations in the architectural model of the species and its variation between provenances determine the loss of dominance in main shoot and influence loss of straightness.

The local provenance (BLSF1018) along with shat from São Miguel (DAN.4040) and one from Sri Lanka (DAN.4067) presented the best performance and as such the use of existing plantations in the country is recommended to start a genetic improvement programme. In the first stage of such a programme form and growth variables should be considered, leaving the selection of wood density and fibre length to a second stage.

Due to the evident tree competition and in agreement with literature for the species a 50 percent thinning was proposed. To allow recommendation of a criteria for tree selection four alternatives were evaluated: i) no thinning, ii) systematic thinning, iii) diameter thinning, and iv) selective silvicultural thinning. Characteristics of the remnan stands were compared considering the mean of evaluated variables, variance, coefficient of variation and possible differential effect of the thinning. It was concluded that the selective silvicultural thinning allows and adequate distribution of trees in the trial, retains the best individuals, maintains variability within plots and does no affect diferentially any of the provenances and assuring the validity of the trial for future evaluations.

BREEDING POPULATION OF *GMELINA ARBOREA* IN COSTA RICA

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Under the DANIDA Forest Seed Centre international programme, Valerio (1986) evaluated a provenance trial of *G. arborea* (seven indigenous provenances and two derived - Manila, Siquirres, Costa Rica and Sao Miguel, Para, Brazil) in Turrialba, Costa Rica. Survival, volume production, tree form, wood density and fibre length were assessed. Valerio concluded that the local Costa Rican derived provenance (Manila), along with that from Brazil and one of the native provenances from Sri Lanka presented the best performance. It was recommended that an improvement programme be initiated in Costa Rica, based on the plantations in Manila and other plantations derived from Manila seed.

The exact genetic makeup of the Manila plantations is not recorded. Approximately 400 hectares remain of the 600 established in 1966-67 by National Bulk Carriers, Inc. (New York) using seed principally from a number of derived West African provenances. Field notes from the time of planting suggest that provenances from the following countries were involved, with those from Nigeria predominant (Lega, 1988; J.R. Palmer, pers. comm.): Belize (Melinda), the Gambia, Nigeria, (Bende, Ikregon, Mamu, Onitsha), Malawi, Sierra Leone, and Zambia. Exact locations of individual provenance in Manila are unknown, but it is probable that they were planted in provenance blocks. This is corroborated by morphological differences between some compartments evident from casual field observation.

In conjunction with both government and private organizations, CATIE's tree improvement staff carried out plus tree selection in plantations of *G. arborea* in Costa Rica. High volume production and good stem form, expressed in nine traits, were considered the most important properties for selection, bearing in mind the actual and probable future uses for *G. arborea* wood in Costa Rica, (commercial plantations and small farmers' woodlots for pulp, sawn, roundwood and firewood).

Characters assessed were:

Measured
- Tree height
- Diameter at breast height
- Level of forking
- Level of branching

Scored
- Stem straightness
- Stem dominance
- Self-healing ability
- Invagination of the stem
- Crown

A minimum age of five years was set for selection, on the basis of trees having reached a height (approx 12 metres) at which the traits of interest would be clearly expressed. Five areas in Costa Rica were identified as having plantations of a suitable age and in systematic searching, 64 plus trees were selected. Selection intensity varied greatly between compartments in Manila and a number yielded no plus trees.

	Total area searched (hectares)	Approx. intensity of selection	Plus tree (no.)
1. Florencia Norte, Turrialba	1.5	1: 3,300	1
2. Manila, Siquirres	181.9	1:10,000	2-21
3. Nicoya peninsula	31.6	1: 2,300	22-36
4. Sardinal, San Carlos	46.7	1: 7,400	37-43
5. Pavones, Turrialba	75.0	1: 4,000	44-64
Total	336.7		

Open-pollinated seed collected from the plus trees will form the basis of progeny trials to be established in 1989. A variety of sites in Costa Rica will be used to determine the presence and degree of genotype-environment interaction particularly between dry and wet zones and therefore the desirability of developing separate breeding populations. Seed from selected Jari material is also being obtained to widen the genetic base for long term breeding. Wood property traits will be included in the second generation of selection, because of their importance in determining end use and their proven potencial for inprovement in *G. arborea.* Branch cuttings were set out for rooting under mist in a greenhouse at CATIE, and will be used to establish a seed orchard on the CATIE estate and provide material for the establishment of other seed orchards by collaborators in the project.

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VARIACIÓN GENÉTICA EN CRECIMIENTO Y RECTITUD DEL FUSTE EN *Gmelina arborea* EN COSTA RICA

Jonathan Cornelius[1,2] y Marvin Hernández[1]

PUNTOS CLAVES Y RECOMENDACIONES PRÁCTICAS

- **Se presentan los resultados en cuanto a la rectitud del fuste y el incremento mensual en diámetro (IMdap) de cuatro ensayos de descendencias de *Gmelina arborea* establecidos en los cantones de Hojancha, Nicoya, Santa Cruz y Upala en 1991 y 1992.**
- **En general, los valores de heredabilidad y coeficientes de variación genotípica aditiva indican que es posible obtener ganancias genéticas importantes.**
- **Las comparaciones entre las descendencias seleccionadas y los testigos indicaron que la selección fenotípica de árboles plus había producido ganancias genéticas en rectitud.**
- **La interacción genotipo-sitio fue significativa pero de poca importancia práctica.**
- **Los huertos semilleros establecidos por el Proyecto MGF entrarán en producción en 1995. Mientras tanto, se recomienda el uso en la zona de la Semilla Autorizada Tipo B y C, producida en algunos rodales semilleros de Hojancha.**
- **Debido a su crecimiento relativamente lento en los ensayos, no se recomienda utilizar semilla recolectada en Manila de Siquirres, Costa Rica, para establecer plantaciones en Guanacaste y en la zona de Canalete, Upala.**

INTRODUCCIÓN Y OBJETIVOS

Entre 1991 y 1993, el Proyecto MGF del CATIE estableció ocho ensayos de descendencias de melina (*Gmelina arborea*) en Guanacaste y la Zona Norte de Costa Rica. Los objetivos incluyeron, entre otros, la estimación de la magnitud e importancia de la variación genética en la población base y la examinación de la efectividad de la selección de árboles plus. En este artículo, se presentan algunos resultados de cuatro de estos ensayos. Esta información se fundamenta en un informe más detallado presentado por Cornelius (1994).

MÉTODOS

Los tratamientos son las descendencias (polinización abierta) de 44 árboles plus seleccionados en los cantones de Hojancha, Sarapiqui (Sardinal), Siquirres (Manila) y Turrialba (CATIE y Celulosa), en 1987. Se incluyeron cinco lotes testigos (semilla recolectada del piso, en los mismos rodales donde se encuentran los árboles plus) y un lote de Tailandia.

Los árboles plus se seleccionaron con base en nueve características escogidas por su relación con el volumen y forma del fuste.

Los cuatro ensayos descritos aquí, fueron establecidos en los cantones de Hojancha, Nicoya, Santa Cruz (Guanacaste) y Upala (Alajuela), en 1991 y 1992. Los sitios muestran un rango amplio de condiciones ambientales. No se incluyeron todos los tratamientos en todos los sitios (hay entre 33 y 49 tratamientos por sitio).

Se utilizó un diseño de bloques completos aleatorios con parcelas de tres árboles en línea. Los ensayos tienen entre 9 y 15 bloques. A los 32 (Nicoya), 31 (Hojancha), 29 (Santa Cruz) y 19 (Upala) meses se midieron el diámetro a la altura de pecho (dap) y la rectitud (escala jerárquica de 1 a 4, siendo 4 el mejor) de cada árbol. Con base en los valores de dap y la edad, se derivaron valores del IMdap (incremento mensual en dap). Se realizaron análisis de varianza de los datos.

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[1] Proyecto Mejoramiento Genético Forestal, CATIE

[2] Administración Británica para el Desarrollo en Ultramar

RESULTADOS Y DISCUSION

¿Fue efectiva la selección de árboles plus?

La efectividad de la selección de árboles plus se puede examinar calculando la ganancia genética realizada, definida como la diferencia entre los promedios de las descendencias seleccionadas y el promedio del testigo o testigos. En el Cuadro 1 se detallan las comparaciones en cuestión.

Con excepción de la procedencia de Celulosa, las descedencias seleccionadas siempre tienen valores mayores que los testigos. En el caso del IMdap, las diferencias no fueron significativas ni de mucha importancia práctica, excepto en el caso de Manila. En contraste, en el caso de rectitud, la ganancia genética fue significativa y de magnitud considerable. Este resultado es normal, considerando que en la selección de los árboles plus se puso mayor énfasis en la rectitud del fuste que en el diámetro.

¿Existe variación genética importante y utilizable en la población base de melina en Costa Rica?

Hubo variación genética significativa (p=.05 o menor) entre familias en todos los sitios, excepto en el caso de la rectitud en Santa Cruz. Sin embargo, es importante considerar no solamente la significancia de la variación, sino también su magnitud. En el Cuadro 2 se presentan los valores del coeficiente de variación genética aditiva (CVGA) y la heredabilidad correspondientes a los cuatro sitios y las dos variables. El CVGA expresa la magnitud de la varianza genética aditiva relativa al promedio, mientras la heredabilidad expresa, en una escala de 0 a 1, la importancia de efectos genéticos aditivos en el fenotipo relativa a los efectos ambientales y efectos genéticos no aditivos.

Los valores del CVGA variaron entre 8,3% y 20,8% para IMdap y entre 9,3% y 19,1% en el caso de la rectitud del fuste. Todos los valores están dentro de

Cuadro 1. Ganancia genética realizada (debida a la selección de árboles plus) en incremento mensual en diámetro (IMdap) y rectitud del fuste globalmente y por procedencia, con base en 4 ensayos de descendencias de *Gmelina arborea* en Costa Rica.

Procedencia	Ganancia[1] (%) en IMdap, y probabilidad[2]	Ganancia[1] (%) en rectitud, y probabilidad[2]
Manila	5,4 (p=,07)	12,5 (p=,08)
Hojancha	2,6 (,42)	8,3 (,01)
Celulosa	0	0
total	2,6 (,41)	8,3 (,006)

1/ diferencia entre promedios de descendencias seleccionadas y testigos 2/ probabilidad de un valor más alto de 'F', comando CONTRAST de SAS (Stonecypher, 1992)

Cuadro 2. Valores estimados de heredabilidad y coeficiente de variación genotípico aditivo (CVGA), para rectitud del fuste e incremento mensual en diámetro a la altura del pecho (IMdap), de *Gmelina arborea* en cuatro sitios en Costa Rica.

Sitio	Característica			
	IMdap		Rectitud	
	heredabilidad	CVGA	heredabilidad	CVGA
Nicoya	0,19	8,3	0,23	19,1
Hojancha	0,31	20,8	0,08	13,3
Santa Cruz	0,28	11,3	0,07	9,3
Canalete	0,21	10,6	0,29	16,0

los rangos encontrados típicamente para especies forestales (Cornelius, 1994), con la excepción del IMdap en Hojancha, el cual presentó un valor de CVGA notablemente alto. Las heredabilidades variaron entre 0,07 y 0,29 para rectitud. Los valores de 0,07 y 0,08 en Santa Cruz y Hojancha, respectivamente, son más bajos que lo normal para especies forestales. Las heredabilidades del IMdap variaron entre 0,19 y 0,31. Todos los valores están dentro de los rangos encontrados típicamente para especies forestales.

Los resultados confirman la existencia de variación genética importante y utilizable en la población base de *Gmelina arborea* en Costa Rica e indican que hay buenas posibilidades de obtener ganancias genéticas importantes a través de la selección. Por ejemplo, en el caso del ensayo de Hojancha, la ganancia genética estimada en IMdap, de la selección fenotípica de los mejores 10% de los árboles sería:

$G = i * CVGA * h^2$ (Falconer, 1992).

(donde: G=ganancia genética estimada; i=intensidad de selección; h^2=heredabilidad)

$= 1,755 * 20,8 * 0,31 = 20,3\%$

Similarmente, en el caso de Nicoya, se esperarían ganancias en rectitud de:

$G = 1,755 * 19,1 * 0,23 = 16,1\%$

COMPORTAMIENTO RELATIVO DE SEGUNDA Y TERCERA GENERACIONES

Las plantaciones de Manila representan la introducción original de melina a Costa Rica, es decir, la primera generación de la población local; mientras las plantaciones en Hojancha, Sarapiquí y Turrialba fueron derivadas de ellas, es decir, son de segunda generación. Por lo tanto, es posible hacer una comparación entre la segunda y tercera generación de la población local, representadas por descendencias de las plantaciones de Manila y las demás plantaciones, respectivamente.

En el caso del IMdap, el material seleccionado de tercera generación (promedio 4,0mm) fue significativamente superior (p=.03) al material seleccionado de la segunda generación (promedio 3,9 mm), sugiriendo que, a través de la selección natural, se está formando una raza local de melina, independientemente de cualquier selección humana que haya ocurrido. En el caso de rectitud, no hubo diferencias significativas (p=.91) entre las dos generaciones.

Ensayo de *Gmelina arborea* en Nicoya, Guanacaste, Costa Rica. En primer plano, se aprecian tres árboles (una parcela) de la familia 47, una de las mejores en incremento diamétrico, sobre los cuatro sitios probados.

Es interesante destacar también la diferencia entre el testigo de Manila (promedio 3,7mm IMdap) y las descendencias seleccionadas de tercera generación (promedio 4,0mm IMdap), las cuales representan respectivamente, las fuentes menos y más adaptadas y/o seleccionadas del material ensayado aquí (con la excepción de la procedencia tailandesa). El material derivado de árboles plus seleccionados en las plantaciones de segunda generación ya tiene una superioridad en crecimiento juvenil de casi un 10%, la cual puede traducirse a diferencias mucho más grandes en volumen.

INTERACCIÓN FAMILIA-SITIO Y GANANCIA GENÉTICA

A veces, en experimentos de este tipo, el comportamiento de las familias en los diferentes sitios no es relativamente el mismo, fenómeno denominado interacción genotipo-ambiente. Cornelius (1994) exploró con más detalle este aspecto del presente estudio. Se encontró que había interacción significativa entre tratamiento y sitio para IMdap, pero no para rectitud. Sin embargo, en ambos casos, la interacción contribuyó menos de 2% de la variación total, mientras los tratamientos contribuyeron con 6,0% y 8,2%, respectivamente, en el caso de rectitud e IMdap. Un análisis detallado de los promedios (Cornelius, 1994) confirmó que la interacción, aunque significativa, no tenía mucha importancia práctica pues para ambas características, las mejores familias en los cuatro sitios,también eran notablemente superiores en cada sitio individual, con excepción de la rectitud en el sitio de Hojancha.

Actualmente, el Proyecto MGF está en proceso de convertir los cuatro ensayos en huertos semilleros de plántulas. En cada caso, la estrategia adoptada dependerá de las estimaciones de los parámetros genéticos y promedios familiares en cada sitio. En el caso del sitio de Hojancha, el cual será raleado durante el verano de 1995, no es improbable que la selección se realice con base en rectitud, debido a los valores bajos de los parámetros genéticos, particularmente la heredabilidad. Por lo tanto, la interacción en rectitud en este sitio no tendría mayor importancia.

CONCLUSIONES

Existe variación genotípica aditiva de magnitud importante en rectitud del fuste y tasa de crecimiento en la población base de melina en Costa Rica. Dada esta variación, los valores estimados de heredabilidad indican que la selección puede producir ganancias genéticas importantes, expectativa confirmada aquí por la buena respuesta a la selección para rectitud, evidenciada por la diferencia entre los promedios de descendencias seleccionadas y árboles plus. La falta de interacción genotipo-ambiente de importancia, sugiere que tales ganancias pueden ser realizadas no sólo en el sitio de selección, sino también en otros ambientes diferentes. Sin embargo, siempre es deseable comprobar selecciones en varios sitios.

Los huertos semilleros establecidos por el Proyecto MGF entrarán en producción en 1995. Se proyecta que la semilla producida por los huertos exhibirá un grado de mejoramiento de alrededor de 20% en crecimiento diamétrico y de 16% en rectitud del fuste. En el interín, se recomienda el uso de la Semilla Autorizada Tipo[3] B y C producida en algunos rodales semilleros de Hojancha (Guevara y Mesén, 1994). Se debería evitar el uso en Guanacaste y Upala de semilla recolectada del sitio Manila, debido a su crecimiento relativamente lento en los 4 ensayos.

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[3] Reglamento técnico para la producción y comercialización de semillas y material de vivero certificado de especies forestales

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VARIATION IN VOLUME OVERBARK, STEM STRAIGHTNESS AND LONGEST INTERNODE LENGTH AT FIVE YEARS OF AGE BETWEEN TEN PROVENANCES OF PINUS CARIBAEA MORELET AND TWO PROVENANCES OF PINUS OOCARPA SCHIEDE IN COSTA RICA

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SUMMARY

This paper details the variation in volume overbark, stem straightness and longest internode length, observed after five years growth, between ten provenances of Pinus caribaea Morelet and two provenances of P. oocarpa Schiede in a provenance trial replicated over four sites in Costa Rica, Central America.

The variable survival and the lack of adequate protection against cattle and fire damage has placed considerable constraints on the interpretation of the data.

A test was made to assess the consistency of the measurements taken in the field. This was not found to be a statistically significant source of error.

The two provenances of P. oocarpa exhibited superior volume growth compared to both varieties of P. caribaea and in addition the Yucul origin of P. oocarpa showed excellent stability in its branching habit.

A combined analysis of variance failed to show a significant provenance x environment interaction for any of the three traits examined.

The Yucul provenance, which may belong to a new taxon, P. patula subsp. tecunumanii (Schwerdft.) Styles, would appear to have considerable potential as plantation material on those sites where growth was assessed.

INTRODUCTION

The absence of any fast growing indigenous conifers in Costa Rica has prompted the Centro Agronomico Tropical de Investigación y Ensenanza (CATIE) to carry out species trials with a wide variety of exotic conifers.

Pinus caribaea Morelet, since its introduction around 1960, has shown an ability to grow well in several parts of the country and this has generated interest in examining further the potential of this highly variable species, through the establishment of a series of provenance trials.

This paper describes the variation in three traits, namely volume overbark, stem straightness and longest internode length at five years between ten provenances of P. caribaea and two provenances of P. oocarpa Schiede (see Table 1), in a provenance trial replicated over four sites (Table 2), established with seed provided by the Commonwealth Forestry Institute, Oxford.

EXPERIMENTAL METHODS

Randomized complete block designs, with five replicates at sites one, two and four and four replicates at site three using seven tree line plots without surrounds were planted. At sites three and four no external surrounds were present either, although at sites one and two guard rows were planted and have variable survival.

Site 1 was the only site unaffected since plantation by external influences. Fire damage has occurred at sites three and four, more severely at the latter resulting in the complete loss of block two. Survival at site two was affected by cattle damage during the early years of the trial, particularly in block five which was therefore excluded from the statistical analyses. One additional factor complicating the interpretation of the results was the presence of other tree species within the experiment at sites two and four.

DATA COLLECTION AND ANALYSES

The field assessment procedure developed by Barnes and Gibson (1984) specifically for P. caribaea and P. oocarpa provenance trials was followed. On becoming familiar with the procedure the number of trees assessed rose to approximately sixty per day.

One possible source of error in assessment is observer inconsistency. To examine the magnitude of this source of error, two plots, selected at random, were re-measured at each of the four sites. The t-test for paired comparisons was used to evaluate the consistency of measurements.

At all sites the results obtained for the three traits were analysed by analysis of variance (ANOVA). However, as within-plot survival was variable, an approximate method was used, namely the unweighted analysis of cell means, where the analysis is carried out paying no attention to the number of trees per plot (Scheffé, 1959).

The Newman-Keuls method was then used to examine the difference between provenance means whenever the initial F-test was found to be significant at the 5% probability level, providing a conservative estimate of the minimum significant difference between ranked provenance means.

To assess the importance of the provenance x environment interaction a combined analysis was carried out. Due to the unequal replication and variable survival over the four sites it was decided to utilize an experimental approach employing the BMDP 3V program (Jennrich and Sampson, 1982), using a maximum likelihoods approach; testing the significance of each effect in the model sequentially.

Site 3 was excluded from the combined analyses of volume overbark and stem straightness, as this site had been planted six months after the other three. However, it was included in the analysis of the longest internode length as it was felt that the difference in age had affected the expression of this trait to a far lesser degree.

RESULTS AND DISCUSSION

Introduction

At all four sites the performance of P. caribaea var. caribaea in terms of volume growth was appreciably poorer than both P. caribaea var. hondurensis and P. oocarpa. Therefore it was decided to exclude this variety from analysis on the grounds that its inclusion might mask differences in performance between provenances of P. caribaea var. hondurensis.

The analyses of variance for each site were done twice, firstly including the two provenances of P. oocarpa, then only on the nine provenances of P. caribaea var. hondurensis.

Consistency checks

The following results, all based upon 48 degrees of freedom, were obtained:

Tree height	$t = -0.214$ NS
Diameter breast height	$t = -0.460$ NS
Stem straightness	$t = 0.506$ NS
Longest internode length	$t = -0.467$ NS

None of these results approaches the 5% probability level, which for 50 degrees of freedom is 2.009, thus no evidence exists to suggest that inconsistency of measurement was an appreciable source of error.

This exercise was of paramount importance and the short time spent on re-measurement and the ease of the analysis should allow consistency checks to become an integral part of field assessment.

Individual traits

The results of the within site analyses of variance are given in Table 3 and the results of the Newman-Keuls test in Table 4. Table 5 presents the results of the combined analyses.

Volume overbark

The same trend was observed at all four sites. No significant block effects were obtained at any site, whilst the significant provenance effects were almost entirely attributable to the superior growth of the two provenances of P. oocarpa. Their removal from the analyses generally led to the provenance effect becoming non-significant.

There was no evidence of a significant site x provenance interaction, but highly significant site effects were apparent.

Unfortunately the considerable intra-provenance variation in tree volume may have masked differences in performance between the provenances of P. caribaea var. hondurensis. This suggests that plot size was too small for provenance trials, particularly if maintenance is sub-optimal.

Stem straightness

No significant differences between blocks were detected at any site and significant provenance effects were present at site 4.

Whilst site uniformity may partially explain the lack of significant differences between blocks, the large standard errors (especially at site 2), reflecting the large amount of variation between individual trees within provenances, is thought to have been a major factor in obscuring differences between provenances.

Superior stem form was a characteristic of Alamicamba, previously found to be the straightest provenance of P. caribaea var. hondurensis over many sites (Gibson, 1982).

The site x provenance interaction was non-significant in the combined analysis. Likewise the site effect was non-significant which, as first noted by Barnes, Gibson and Bardey (1980) suggests that stem straightness is under strong genetic control.

Longest internode length

Significant differences between blocks were a feature at site 1 only, the only site with variable topography, suggesting that microsite conditions influence this trait. Significant provenance differences were found at all sites except site 2. At both this site and site 3 growth was slow and few foxtails recorded, although the slightly smaller standard error at site 3 resulted in significant differences between means. At sites 1 and 4, where growth was better, foxtails were more prevalent.

At all four sites Brus Lagoon produced the largest foxtails and Alamicamba was always in the top three. This result is consistent with published work (Greaves, 1980; Gibson, 1982). The only other provenance that retained the same ranking across all four sites was the Yucul provenance of P. oocarpa which consistently occupied the lowest ranking.

The site x provenance interaction term was found to be non-significant.

CONCLUSIONS

The results obtained from any assessment must be evaluated in the light of the present condition of the experiment under investigation.

Two aspects of the original experimental design warrant criticism, namely the plot size and the absence of surround rows within the experiment. With regard to the former, the small plot size, confounded by the variable survival, is thought to have led to poor estimates of the provenance mean values, with the occasional exceptional individual inflating some means, leading to a high standard error for the trait in question. For this type of provenance trial Gibson (1982) recommended the use of 36 tree plots with the assessment of the central 4 x 4 trees.

In addition to these two weaknesses, the standard of maintenance of this experiment has been low. The failure to replace early losses, the retention of other tree species within two of the sites and the lack of adequate protection are factors which make subsequent evaluations of provenance performance less precise.

However, one of the most important findings was the superior growth rate of the two provenances of P. oocarpa, Yucul and Mountain Pine Ridge, compared to both varieties of P. caribaea. Although this concerns growth over only the first five years this result does question the long held assumption that P. caribaea var. hondurensis would be the most important pine species for lowland tropical sites (Lamb, 1973).

In addition the stability of the Yucul origin of P. oocarpa in producing regular branch whorls under conditions of rapid growth is noteworthy, as the combination of these two characteristics is clearly desirable.

The failure to detect a significant provenance x environment interaction, suggests that the rankings obtained for the provenances represented in this trial will not be dramatically altered on other sites suitable for these two species of pine throughout Costa Rica.

Finally, mention should be made of recent taxonomic studies (Barnes and Styles, 1983) which indicated that part of the Central American population of P. oocarpa, including the Yucul provenance, may in fact be P. patula subsp. tecunumanii (Schwerdft.) Styles. As Barnes and Styles report "this new taxon may provide some excellent plantation material for very extensive areas in the tropics and sub-tropics".

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Table 1. Provenance Source Information (from Greaves, 1978)

CATIE Trial No.	Seed Sources		Latitude (°N)	Longitude (°W)	Elevation (m)
	Country	Provenance			
1	Nicaragua	Alamicamba	13°34'	84°17'	20- 30
2	Nicaragua	Rio Coco	14°45'	83°55'	50-100
3	Honduras	Guanaja	16°27'	85°54'	50-100
4	Guatemala	Poptun	16°21'	89°25'	500
5	Honduras	Culmi	15°06'	85°37'	500-600
6	Honduras	Brus Lagoon	15°45'	84°40'	10
7	Honduras	Los Limones	14°03'	86°42'	700
8	Belize	Mountain Pine Ridge	17°00'	88°55'	400
9	Belize	Melinda	17°01'	88°20'	10- 15
10	Cuba	Pinar del Rio/1	22°49'	82°57'	-
11	Nicaragua	Yucul/2	12°55'	85°47'	900
12	Belize	Mountain Pine Ridge/2	17°00'	88°55'	700

/1 *P. caribaea* var. *caribaea*
/2 *P. oocarpa*

Table 2. Site Information Summary

	Site	Lat. (°W)	Long. (°N)	Alt. (m)	Mean Precip. (mm)	Soil Type/1	Previous Land Use	Ecological Life Zone/2
1	Celulosa	83°37'	9°56'	720	3665	Andic Humitropept	Cut-over Secondary Forest	Tropical Wet Forest, Premontane Belt Transition
2	Florencia Norte	83°41'	9°53'	650	2639	Andic Humitropept	Mixed Forest Plantation	Tropical Moist Forest, Premontane Belt Transition
3	Volcan	83°28'	9°12'	420	3666	Ustic Tropohumult	Open Pasture	Tropical Moist Forest
4	San Isidro	83°41'	9°21'	670	3054	Orthoxic Palehumult	Coffee Plantation	Tropical Moist Forest, Premontane Belt Transition

/1 US soil classification system
/2 Holdridge Life Zone system

Table 3. ANOVA: Significance of the F test

Volume Overbark

Site	1 Celulosa		2 Florencia		3 Volcan		4 San Isidro	
No. of Prov.	11	9	11	9	11	9	11	9
Block effect	NS	NS	NS	NS	NS	NS	NS	NS
Prov. effect	**	NS	*	NS	***	*	NS	NS

Stem straightness

Site	1 Celulosa		2 Florencia		3 Volcan		4 San Isidro	
No. of Prov.	11	9	11	9	11	9	11	9
Block effect	NS	NS	NS	NS	NS	NS	NS	NS
Prov. effect	NS	NS	NS	NS	NS	NS	***	**

Longest internode

Site	1 Celulosa		2 Florencia		3 Volcan		4 San Isidro	
No. of Prov.	11	9	11	9	11	9	11	9
Block effect	NS	*	NS	NS	NS	NS	NS	NS
Prov. effect	***	**	NS	NS	**	**	***	**

$P > 0.05$: NS
$0.05 > P > 0.01$: *
$0.01 > P > 0.001$: **
$P < 0.001$: ***

Table 4. Combined Analysis: Significance of the Likelihood ratio test

	Trait		
	Volume Overbark	Stem Straightness	Longest Internode
No. of Prov.	11	11	11
No. of Sites	3	3	4
Site x Block effect	*	NS	NS
Block x Provenance effect	NS	NS	NS
Site x Provenance effect	NS	NS	NS
Block effect	NS	NS	NS
Site effect	***	NS	***
Provenance effect	***	*	***

Table 5. Newman-Keuls test excluding Provenance 10.

Volume Overbark (m^3)

1: Celulosa		2: Florencia		3: Volcan		4: San Isidro	
Prov.	Value	Prov.	Value	Prov.	Value	Prov.	Value
12	0.16	12	0.12	12	0.10	11	0.14
11	0.14	5	0.07	11	0.10	12	0.13
5	0.14	8	0.06	7	0.06	1	0.13
6	0.13	4	0.06	4	0.06	5	0.13
4	0.13	1	0.06	1	0.06	4	0.12
2	0.12	7	0.05	8	0.06	9	0.11
9	0.12	11	0.05	5	0.06	8	0.11
8	0.11	2	0.05	9	0.05	6	0.10
1	0.10	6	0.05	6	0.05	2	0.10
3	0.10	9	0.04	3	0.04	3	0.09
7	0.08	3	0.04	2	0.04	7	0.09

Longest Internode (m)

1: Celulosa		2: Florencia		3: Volcan		4: San Isidro	
Prov.	Value	Prov.	Value	Prov.	Value	Prov.	Value
6	3.5	6	1.5	6	1.7	6	3.5
1	3.3	5	1.4	4	1.5	8	3.5
2	2.8	1	1.2	1	1.4	1	2.2
9	2.4	2	1.2	9	1.4	2	2.0
8	2.3	12	1.2	12	1.2	4	1.5
4	1.8	3	0.9	7	1.0	9	1.5
5	1.7	4	0.8	8	0.9	3	1.4
12	1.4	7	0.8	2	0.8	5	1.4
7	1.3	8	0.8	5	0.8	7	1.2
3	1.3	9	0.6	11	0.6	12	0.9
11	0.7	11	0.5	3	0.6	11	0.8

Stem straightness (rating)

1: Celulosa		2: Florencia		3: Volcan		4: San Isidro	
Prov.	Value	Prov.	Value	Prov.	Value	Prov.	Value
3	98.3	8	112.1	1	68.0	1	104.9
1	96.6	12	97.3	7	60.7	11	79.2
8	94.4	9	89.8	4	60.5	6	69.5
6	87.0	4	87.1	2	52.0	3	62.2
12	79.4	2	86.4	6	51.3	2	53.3
9	75.4	11	86.3	8	47.9	9	51.0
2	71.0	1	71.0	11	45.6	7	42.8
5	68.1	7	60.9	9	44.9	8	41.1
11	67.1	6	48.6	12	37.2	5	36.8
4	54.3	5	44.1	5	33.6	12	35.0
7	54.1	3	42.5	3	22.8	4	31.3

COREA, E. 1989. Evaluación de un ensayo de procedencias de Pinus oocarpa - Pinus patula ssp. tecunumanii en cuatro sitios de Costa Rica. Tesis Mag.Sc. Turrialba, Costa Rica. UCR/CATIE. 179 p.

Palabras Clave: Pinus oocarpa, Pinus caribaea, Pinus patula ssp. tecunumanii, Pinus tecunumanii, procedencias, interacción genotipo-ambiente, adaptación, correlación juvenil-maduro, Costa Rica.

RESUMEN

El ensayo evaluado en este estudio es parte del Proyecto Internacional de Investigaciones de Procedencias de Pinos Centroamericanos coordinado por el OFI y del Proyecto de Mejoramiento Genético Forestal del CATIE. El experimento fue plantado en cuatro sitios húmedos de Costa Rica, ubicados entre 680 y 1160 msnm, consta de 13 procedencias de P. oocarpa, 2 de P. patula ssp. tecunumanii y 1 de P. caribaea var. hondurensis La edad promedio de evaluación fue de 6 años y 7 meses

Los objetivos de este trabajo fueron: 1) estimar las medias poblacionales de las procedencias y las diferencias entre ellas, 2) estimar el porcentaje de la variación fenotípica observada dentro de los sitios que es atribuible a procedencias, 3) determinar la existencia de interacciones procedencia-sitio y su importancia y 4) estimar el grado de correlación entre el comportamiento inicial de las procedencias y su comportamiento a la edad de la evaluación, para las variables de crecimiento (correlación juvenil-maduro).

Las variables de respuesta fueron: supervivencia, diámetro, altura total, área basal, volumen con corteza, volumen sin corteza, porcentaje de corteza, longitud del internodio mayor, número de verticilos, número de ramas por verticilo, número de ramas, porcentaje de árboles bifurcados, número de bifurcaciones, índice de bifurcación y rectitud del fuste.

El análisis de varianza detectó diferencias altamente significativas (P<0,001) entre procedencias para todas las variables de respuesta indicando un fuerte control genético. El porcentaje de la variacion fenotípica total observada dentro de sitios atribuible a diferencias genéticas entre procedencias fue alto (36-63%) en todas las variables de respuesta, con excepción de la altura total (24%) y la supervivencia (20%), con valores medios, y las variables relacionadas con el hábito de bifurcar que obtuvieron valores bajos (10-13%).

Las procedencias mostraron una estabilidad alta en su comportamiento relativo al cambiar el ambiente. La interacción procedencia-sitio solo fue significativa (P<0,05) para la altura total y el número de verticilos. El análisis bajo el modelo de Eberhart y Russell mostró que la significancia de la interacción en esas dos variables obedece principalmente al comportamiento inestable de unas pocas procedencias de _P. oocarpa_ de baja productividad.

El análisis de correlación "juvenil-maduro" para las variables de crecimiento indicó que, bajo las condiciones de estudío, las posibles diferencias genéticas entre procedencias se manifiestan a temprana edad (3-4 años) lo que permite una selección preliminar con un alto nivel de confianza.

Las procedencias más productivas fueron Yucul (Nicaragua), Mountain Pine Ridge (MPTB)(Belice), ambas de _P. patula_ ssp. _tecunumanii_, Mountain Pine Ridge (MPCHB) (Belice) de _P. caribaea_ var. _hondurensis_ y Dipilto (Nicaragua) de _P. oocarpa_, en ese mismo orden. Yucul calificó primera en todos los sitios y fue significativamente superior (alfa = 0,05) a 14 de las 15 procedencias restantes, produciendo 112% más volumen sin corteza que el promedio de las procedencias de _P. oocarpa_ y 36% más que la procedencia MCHB de _P. caribaea_. Las dos procedencias de _P. patula_ ssp. _tecunumanii_ fueron también las que presentaron los porcentajes de corteza menores y calificaron entre las tres procedencias con el número de bifurcaciones por árbol y el porcentaje de árboles bifurcados más bajos.

Las procedencias de mayor crecimiento presentaron algunas características indeseables en sus hábitos de ramificación. Yucul, MPTB y Dipilto fueron las que produjeron mayor cantidad de ramas por verticilo. Particularmente, Yucul fue la que presentó mayor cantidad de ramas por unidad de longitud del fuste. Por otra parte, las dos procedencias de Belice (MPTB y MCHB) fueron las únicas que mostraron inestabilidad en la longitud de los internodios que producen, siendo que la procedencia de _P. caribaea_ (MCHB) produjo crecimientos tipo "cola de zorro" con mayor frecuencia y longitud que la procedencia de _P. patula_ ssp. _tecunumanii_ (MPTB).

Entre las procedencias más productivas se presentaron también diferencias importantes en la rectitud del fuste. Yucul y Dipilto calificaron entre las cinco mejores procedencias para esta característica mientras que, las procedencias de Belice (MPTB y MCHB) calificaron entre las de peor forma.

COREA, E. 1989. Evaluation of a provenance trial of Pinus oocarpa and Pinus patula ssp. tecunumanii in four sites of Costa Rica. Thesis Mag.Sc. Turrialba, Costa Rica. UCR/CATIE. 179 p.

Keywords: Pinus oocarpa, Pinus caribaea, Pinus patula ssp. tecunumanii, Pinus tecunumanii, provenances, genotype-environment interaction, adaptation, juvenile-mature correlation, Costa Rica.

SUMMARY

The trial evaluated in this study is part of the OFI-coordinated international series of provenance trials of Central American pines and of the Forest Tree Improvement Project at CATIE. The experiment was planted on four humid sites in Costa Rica, located between 680 and 1160 m.a.s.l. It involves 13 provenances of P. oocarpa, 2 of P. patula ssp. tecunumanii and 1 of P. caribaea var. hondurensis. Average evaluation age was 6 years and 7 months.

The objectives of this work were to: 1) Estimate the population means of the provenances and the differences between them, 2) Estimate the percentage of the phenotypic variation within sites due to provenances, 3) Determine the existence of provenance-site interactions and their importance and 4) Estimate the correlation between the initial performance of the provenances and their performance at evaluation age for growth traits (juvenile-mature correlation).

The traits evaluated were: survival, diameter at breast height, total height, basal area, volume over bark, volume under bark, bark percentage, longest internode length, number of whorls, number of branches, number of branches per whorl, percentage of forked trees, number of forks per tree, forking index and stem straightness.

The analysis of variance detected highly significant differences (P < 0.001) between provenances for all variables, indicating a very strong genetic control. The percentage of phenotypic variation within sites due to genetic differences between provenances was high (34-63%) in all variables, except for total height (24%) and survival (20%), with medium values, and forking variables with low values (10-13%).

Relative performance of provenances was highly stable over the four locations; provenance-site interaction being significant ($P < 0.05$) only for total height and number of whorls. Analysis based on Eberhart and Russell's model showed that significant interaction for both variables was due basically to the unstable performance of a few, low productive provenances of P. oocarpa. These interactions are not of practical or economic importance.

Juvenile-mature correlation analysis for growth traits indicated that, under the study conditions, possible genetic differences between provenances become evident at early age (3-4 years). Thus, a preliminary selection of provenances may be made with a high level of confidence.

The most productive provenances were Yucul (Nicaragua), Mountain Pine Ridge (MPTB) (Belize), both P. patula ssp. tecunumanii, Mountain Pine Ridge (MCHB) of P. caribaea var. hondurensis and Dipilto (Nicaragua) of P. oocarpa, in that order. Yucul ranked first at all sites and was significantly better (alfa=0.05) than 14 of the 15 remaining provenances, producing 112% more volume under bark than the mean of the P. oocarpa provenances and 36% more than MCHB of P. caribaea. Yucul and MPTB showed the lowest bark percentage and ranked among the three provenances with the smallest values for the number of forks per tree and the percentage of forked trees.

The best growing provenances presented some undesirable branching characteristics. Yucul, MPTB, and Dipilto produce the most branches per whorl, with Yucul also producing the largest number of branches per unit length of stem. In addition, the two Belizean provenances (MPTB and MCHB) were the only ones to show high within tree variability of internode length, with MCHB of P. caribaea producing more and longer "foxtails" than MPTB of P. patula ssp. tecunumanii.

There were also important differences in stem straightness within the most productive provenances. Yucul and Dipilto ranked within the 5 straightest-stemmed provenances, whilst the Belizean provenances were among those of poorest stem form.

PINUS TECUNUMANII, UNA ALTERNATIVA PARA LA REFORESTACION EN SUELOS TROPICALES DEGRADADOS [1]

Eugenio Corea[2]
Jonathan Cornelius[2]
Francisco Mesén[3]

1. Introducción

Los pinos nativos de América Central, principalmente *P. caribaea* var. *hondurensis* y *P. oocarpa*, han sido utilizados ampliamente en programas de reforestación en muchos países del trópico, debido a la gran diversidad de usos de sus maderas, a su crecimiento rápido y a su adaptación a suelos erosionados, compactados, ácidos y poco fértiles (Lamb, 1973). Su utilización en sitios degradados generalmente ha dado mejores resultados que el uso de especies latifoliadas y de otras coníferas más exigentes. Debido a que estos pinos están adaptados y pueden crecer exitosamente en esos suelos, se ha creído que ellos causan erosión o acidez. En realidad, estas especies tienen un efecto positivo sobre el suelo cuando crecen en sitios degradados (Cartón de Colombia, 1989).

Debido a la importancia de estos pinos, en los años sesenta se inició el Proyecto Internacional sobre Procedencias de Pinos Centroamericanos, coordinado por el Instituto Forestal de Oxford. Como parte de este proyecto se recolectó semilla de 70 procedencias de *P. oocarpa* (Greaves, 1979), 36 de *P. caribaea* (Greaves, 1978) y 4 de *P. tecunumanii* (McCarter y Birks, 1985). El Proyecto Mejoramiento Genético Forestal (MGF) del CATIE ha participado en este esfuerzo y ha establecido 13 ensayos de procedencias de estas especies en Costa Rica.

2. Comportamiento de *P. tecunumanii* en Costa Rica

2.1 Ensayos de procedencias

Los resultados de los ensayos establecidos en una gran diversidad de climas y suelos en Costa Rica, han demostrado que las procedencias Yucul, Nicaragua y Mountain Pine Ridge (MPR), Belice, de *Pinus tecunumanii* son superiores a las trece procedencias de *P. oocarpa* y a diez procedencias de *P. caribaea* que han sido probadas y entre las que se encuentran la mayoría de las de mayor crecimiento de estas especies (Corea, 1989, Mesén, 1990). La mejor procedencia ha sido Yucul (*P. tecunumanii*), la cual supera en 112% en volúmen sin corteza al promedio de las procedencias de *P. oocarpa* y en 46% al promedio de las procedencias de *P. caribaea*. Yucul también supera en un 44% a la mejor procedencia de *P. oocarpa* (Dipilto, Nicaragua), y entre 27% a 36% a las mejores procedencias de *P. caribaea* (M.P.R y Culmí). Estas diferencias son bastante grandes e indican claramente que la selección de la procedencia puede significar la diferencia entre el éxito o el fracaso de un proyecto de reforestación.

Los resultados obtenidos en Costa Rica han sido muy similares a los que se han presentado en varios cientos de ensayos establecidos en más de 50 países tropicales en todo el mundo (Birks y Barnes, 1990), en donde las cuatro procedencias de *P. tecunumanii* evaluadas (Yucul, Las Camelias y San Rafael de Nicaragua Y MPR de Belice) han sido superiores, en casi todos los sitios, a las procedencias de *P. caribaea* y *P. oocarpa*. (Greaves, 1980; 1984; Birks y Barnes, 1990; Crockford, et al., 1990).

En Costa Rica, la única excepción se ha presentado en Santa Cruz, Guanacaste, donde las procedencias Guanaja de Honduras, Mountain Pine Ridge de Belice y Poptún de Guatemala de *P. caribaea* tienen un mejor comportamiento (Mesén, 1990). Este resultado sugiere que las procedencias probadas de *P. tecunumanii* no se adaptan bien a zonas bajas, calientes y con estación seca marcada. Sin embargo, hace falta más investigación para aclarar este hecho.

2.2 Plantaciones piloto

Considerando los excelentes resultados de *P. tecunumanii* y tomando en cuenta la necesidad de la región de contar con especies aptas para la reforestación de sitios degradados, el proyecto MGF estableció nueve plantaciones

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[1] Resumen de "Pinus tecunumanii y su papel en la reforestación". Sometido a la Revista Forestal Centroamericana

[2] Proyecto Mejoramiento Genético Forestal, CATIE

[3] Proyecto Semillas Forestales, CATIE

piloto (1-2 ha c/u) en Costa Rica (Cuadro 1). Las plantaciones fueron establecidas en suelos con pendiente fuerte, compactados por sobrepastoreo, erosionados y poco fértiles, ubicados entre 550 y 1700 msnm, en áreas con una estación seca marcada de 4 a 5 meses. En estos sitios, las especies tradicionalmente plantadas en la región, como melina, pochote, ciprés, y varios eucaliptos, entre otras, no han dado buenos resultados.

La sobrevivencia en las plantaciones piloto durante el primer año fue de 80% a 90%. La mortalidad ocurrió principalmente durante la primera estación seca. Después del primer año, la mortalidad se redujo a casi cero. En la plantación piloto de Orosi, la sobrevivencia fue de sólo un 25%, debido a las condiciones de mal drenaje que presenta el sitio. Se esima que, en general los porcentajes de sobrevivencia inicial pueden mejorarse produciendo los árboles en la misma región donde van a ser plantados, reduciéndoles el riego un mes antes de plantarlos para endurecer (lignificar) los tallos.

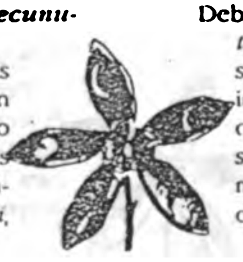
Tomando en cuenta las malas condiciones del sitio, el comportamiento de *P. tecunumanii* en las plantaciones piloto ha sido excelente. El incremento medio diamétrico es superior a los 2 cm/año y el crecimiento medio en altura es superior a 1,5 m/año, en plantaciones de 4 a 6 años de edad, (Cuadro 2). El crecimiento fue lento durante los primeros dos años. Sin embargo, posteriormente, el crecimiento corriente anual aumentó a más 3,5 cm/año en diámetro y 2,0 m/año en altura, lo que da una mejor idea del crecimiento actual y futuro en estas parcelas, y del potencial de la especie en sitios degradados.

Cuadro 1. Información general sobre los sitios de las plantaciones piloto de *P. tecunumanii*

Sitio	Lat. (N)	Long. (O)	Altitud (msnm)	Temp. media anual (°C)	Precipitación media anual (mm)	Meses secos (<80 mm)
Sabanillas, Acosta	09°44'	84°15'	1100	20,7	2784	4
Jericó, Aserrí	09°50'	84°04'	1650	17,7	1712	4
Barbacoas, Puriscal	09°51'	84°22'	1000	21,4	2541	4
Orosi, Cartago	09°45'	83°52'	1700	17,5	3218	0
Tres Ríos, Cartago	09°57'	83°57'	1700	17,5	1538	5
El Guarco, Cartago	09°50'	83°58'	1500	18,5	1456	5
Monte Romo, Hojancha	10°00'	85°24'	800	22,3	1978	5
Pita Rayada, Hojancha	10°02'	85°23'	650	23,2	1978	5
Huacas, Hojancha	10°00'	85°22'	550	23,7	1978	5

3. Caracterización silvicultural de *P. tecunumanii*

De acuerdo a los resultados de evaluaciones intensivas de los ensayos de procedencias en Costa Rica (Corea, 1989) y el resto del mundo (Greaves, 1980; Birks y Bames, 1990), algunas características silviculturales de las procedencias hasta ahora estudiadas de *P. tecunumanii*, en comparación con las de *P. caribaea* y *P. oocarpa* son las siguientes:



3.1 Variables de producción

Las procedencias de *P. tecunumanii* presentan una mayor tasa de crecimiento que las de *P. oocarpa* y *P. caribaea*, tanto a elevaciones bajas y medias (0-1800 msnm) en áreas tropicales húmedas como a alturas medias (400-1800 msnm) en áreas con estación seca marcada. En zonas bajas (<400 msnm), con altas temperaturas (>25°C) y con estación seca de cuatro meses o más, algunas procedencias de *P. caribaea* var. *hondurensis*, principalmente Guanaja, parecen estar mejor adaptadas. Las procedencias de *P. tecunumanii* presentan un porcentaje de corteza menor que las *P. caribaea* y las de *P. oocarpa*.

3.2 Variables de forma y ramificación

Las procedencias de *P. tecunumanii*, especialmente la de Nicaragua, generalmente presentan mejor forma del fuste, ramas más delgadas y en mayor número y copas más densas que las procedencias de mayor crecimiento de *P. caribaea* var. *hondurensis* y *P. oocarpa*. Por otra parte, a diferencia de muchas de las procedencias de *P. caribaea*, casi nunca presentan árboles con crecimientos tipo "cola de zorro".

Debido a las características de la copa de *P. tecunumanii* y a la mayor tasa de crecimiento, se reducen los costos y período de control inicial de malezas. Sin embargo, es necesario que los raleos se efectúen más temprano, no sólo para favorecer el crecimiento de los mejores árboles, sino también para permitir el crecimiento de un sotobosque adecuado para la protección del sitio.

3.3 Madera

La madera de *P. tecunumanii* es liviana y fácil de trabajar. Presenta una densidad básica promedio muy similar a la de *P. caribaea* y *P. oocarpa* (0,40-0,41 g/cm³). Se puede usar en carpintería, ebanistería, tableros, vigas, madera de aserrío, pulpa para papel, etc.

Cuadro 2. Diámetro (DAP), altura (ALT) e incremento medio anual en diámetro (IMD) y altura (IMA) de nueve plantaciones piloto de *P. tecunumanii* establecidas en sitios marginales en Costa Rica.

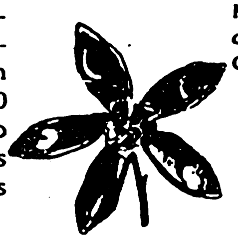
SITIO	PROCEDENCIA	EDAD (años)	DENSIDAD (arb./ha)	DAP (cm)	IMD (cm/año)	ALT (m)	IMA (m/año)
Sabanillas, Acosta	Yucul, Nic.	5.5	740	13,2	2,4	9,0	1,6
El Guarco, Cartago	Yucul, Nic.	6.7	1706	15,5	2,3	13,9	2,1
Monte Romo, Hojancha	Yucul, Nic.	4.8	800	12,7	2,6	7,7	1,6
Jericó, Aserrí	San Rafael, Nic.	5.4	855	11,2	2,1	6,8	1,3
Pita Rayada, Hojancha	San Rafael, Nic.	4.7	733	12,2	2,6	8,9	1,9
Orosí, Cartago	San Rafael, Nic.	4.5	277	14,5	3,2	9,0	2,0
Barbacoas, Puriscal	M.P.R. Belice	6.5	922	15,2	2,3	13,0	2,0
Tres Ríos, Cartago	M.P.R. Belice	3.2	633	4,1	1,3	3.7	1,2
Huacas, Hojancha	M.P.R. Belice	4.7	778	8,6	1,8	7,1	1,5

3.4 Resistencia a vientos

Las procedencias de *P. tecunumanii* y *P. oocarpa* son más susceptibles que las de *P. caribaea* a daños causados por vientos fuertes, por lo que no se recomienda plantarlas en sitios expuestos, tales como los pasos entre montañas o en áreas que pueden ser afectadas por huracanes. Con un adecuado manejo de la densidad, efectuando los raleos a tiempo, se puede reducir el riesgo a daños causados por vientos.

4. Conclusiones

Los pinos tropicales nativos de América Central han demostrado que son una excelente alternativa para la reforestación de sitios degradados por el sobreuso, donde otras especies, principalmente latifoliadas, no han dado buenos resultados. De estos pinos, *P. tecunumanii*, especialmente la procedencia Yucul de Nicaragua, es el más adecuado para regiones húmedas entre 0-1800 msnm y para zonas con estación seca entre 400-1800 msnm, en sitios donde no ocurra mal drenaje o vientos muy fuertes o huracanados. En zonas con estación seca marcada a elevaciones bajas (0-400 msnm), la procedencia Guanaja de Honduras es la que se ha comportado mejor, aunque hace falta establecer más ensayos en esta región para confirmar este resultado. ■



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ACTIVIDADES DE INVESTIGACION

NUEVA INFORMACIÓN SOBRE PROCEDENCIAS DE *Pinus tecunumanii*[1]

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Proyecto Mejoramiento Genético Forestal CATIE

PUNTOS CLAVES Y RECOMENDACIONES PRACTICAS

-Recientemente se ha recomendado el uso de la procedencia Yucul de *Pinus tecunumanii* para la reforestación en América Central (Corea *et al.*, 1993), debido a su mejor comportamiento con respecto a *Pinus caribaea* var. *hondurensis* y *Pinus oocarpa*.

-En el presente artículo se describen los resultados de un ensayo de procedencias, en el cual se comparó Yucul no sólo con *Pinus oocarpa*, sino también con otras fuentes de *Pinus tecunumanii*, provenientes de Honduras.

- Los resultados sugieren que la procedencia Yucul, junto con otra procedencia nicaragüense (San Rafael del Norte), es superior en crecimiento hasta los 4,5 años, a las cuatro procedencias hondureñas incluidas y también a la procedencia beliceña Mountain Pine Ridge, por los menos en sitios húmedos de altura. Los resultados, por lo tanto, respaldan las recomendaciones mencionadas y resaltan la importancia de los esfuerzos en conservación *in situ* que actualmente realizan las autoridades nicaragüenses (Ravensbeck, 1994).

INTRODUCCION

La superioridad de *Pinus tecunumanii*[1] sobre *Pinus caribaea* var. *hondurensis* (en sitios de bajura) y *Pinus oocarpa* (en sitios de altura), ha sido ampliamente demostrada, tanto a nivel centroamericano como mundial (Birks y Barnes, 1990; Corea y otros 1993). Sin embargo, hasta el momento esta conclusión se ha fundamentado principalmente en el comportamiento de cuatro procedencias: Mountain Pine Ridge (MPR), de Belice y Las Camelias, San Rafael del Norte y Yucul de Nicaragua. Las tres procedencias nicaragüenses han exhibido un comportamiento similar y superior a la de MPR. Existe poca información sobre el comportamiento de otras procedencias. El presente artículo describe en forma resumida los resultados a los 4,5 años de un experimento de procedencias/descendencias, en el cual se incluyó material de MPR, Yucul y San Rafael junto con cuatro procedencias hondureñas. La información presentada se fundamenta en el artículo de Cornelius *et al.*, (1994).

EL EXPERIMENTO

El experimento está ubicado en Orosi, Cartago, Costa Rica, a una altitud de 1640 msnm, en un sitio de fertilidad baja a mediana, sin una época seca marcada, muy representativo del sitio donde se ha plantado *Pinus oocarpa* en Costa Rica.

El diseño es de nueve bloques completos aleatorios, con parcelas de 6 árboles por familia. Cada bloque contiene 49 familias de polinización abierta de las siguientes procedencias hondureñas: Jocón, Yoro (16 familias); San Esteban, Olancho (10 familias); San Francisco de la Paz, Olancho (11 familias) Villa Santa, El Paraíso (12 familias). Los testigos (MPR, San Rafael y Yucul de *Pinus tecunumanii* y Dipilto (Nicaragua) de *Pinus oocarpa*), fueron representados por una parcela de seis árboles en cada bloque. Se escogió Dipilto como testigo con base en su buen comportamiento en otros ensayos centroamericanos (Corea, 1989; Cornelius y Ponce, 1990).

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[1] Styles (1985) aclaró que el nombre científico correcto de esta taxa es *Pinus patula* ssp *tecunumanii*. Sin embargo, para evitar confusión a nivel operacional con *Pinus patula* ssp *patula*, el Proyecto MGF del CATIE, utiliza el nombre *Pinus tecunumanii* en sus publicaciones no científicas.

OBJETIVOS Y EVALUACIONES

En el presente contexto, el objetivo principal del ensayo es la identificación de la mejor procedencia y la comparación de las 'nuevas' procedencias hondureñas, con las mejores conocidas de Nicaragua y Belice. A nivel de familia, el experimento tiene otros objetivos adicionales, los cuales se describen en el artículo mencionado anteriormente (Cornelius *et al.* 1994).

A los 55 meses, se midieron las siguientes características de cada árbol: altura total, diámetro a 1,3 m de altura (dap), rectitud del fuste (escala jerárquica de 1 (peor) a 3 (mejor)), grosor de las ramas (1(delgado) a 3 (grueso)) y presencia o ausencia de bifurcaciones. Se realizó un análisis de varianza con base en los valores de los árboles individuales.

RESULTADOS Y DISCUSION

Se presentó variación significativa (p= 0.01 o menor) entre las procedencias en los rasgos de crecimiento, pero no en los rasgos de forma. Los promedios para los rasgos de crecimiento se presentan en el Cuadro 1, junto con los valores de significancia. El área basal promedio de las dos procedencias nicaragüenses superó el de la mejor procedencia hondureña (Villa Santa), en 52% (San Rafael) y 23% (Yucul). Para dap y área basal, ambas procedencias son significativamente superiores a las de Honduras, tomadas como un grupo (Cuadro 1). Aunque la misma comparación para altura no fue estadísticamente significativa, es evidente la

Cuadro 1. Promedios para tres características de siete procedencias de *Pinus tecunumanii* y una de *Pinus oocarpa* a los 55 meses de edad en un ensayo ubicado en Orosi, Cartago, Costa Rica.

	Promedios [% superioridad o inferioridad[1]]		
	altura [m]	dap [cm]	área basal [cm^2] por árbol
Promedio experimental:	6.7	8.7	72.3
Valor de 'F' y [nivel de probabilidad]:	8.0 [0.0001]	5.7 [0.0001]	3.6 [0.003]
Procedencia **[Pinus tecunumanii]**			
Jocón, Honduras	6.0 [-11.0%]	7.6 [-13.3%]	58.7 [-18.8%]
San Esteban, Honduras	6.9 [3.0%]	9.0 [3.6%]	75.7 [4.7%]
San Francisco de la Paz, Honduras	6.9 [3.4%]	9.1 [4.0%]	74.9 [3.7%]
Villa Santa, Honduras	7.0 [4.8%]	9.1 [4.4%]	77.0 [6.6%]
Yucul, Nicaragua	7.2 [7.6%]	10.3 [17.9%]	94.7 [31.0%]
MPR, Belice	6.4 [-4.8%]	8.7 [-0.3%]	74.9 [3.7%]
San Rafael, Nicaragua	7.1 [6.4%]	11.1 [27.4%]	117.1 [62.0%]
[Pinus oocarpa]			
Dipilto, Nicaragua	6.4 [-4.9%]	8.0 [-8.7%]	60.6 [-16.1%]

Comparaciones[3]	Valor de 'F' probabilidad	Valor de 'F' probabilidad	Valor de 'F' probabilidad
Yucul vs procedencias hondureñas	F=2.54, p=0.11	F=6.3, p=0.01	F=6.16, p=0.01
San Rafael vs procedencias hondureñas	F=1.57, p=0.21	F=12.65, p=0.0004	F=20.92, p=0.0001
Mountain Pine Ridge vs procs hondureñas	F=0.98, p=0.32	F=0.0, p=0.99	F=0.12, p=0.73
Dipilto vs procedencias hondureñas	F=0.94, p=0.33	F=1.13, p=0.29	F=1.19, p=0.27

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[1] Con respecto del promedio del experimento

[2] Calculado como [dap² π/4]

[3] Comparaciones planificadas a priori

5

superioridad de las procedencias nicaragüenses en cuanto a productividad, por lo menos en las condiciones representadas por el ensayo.

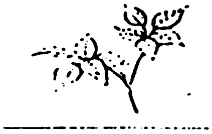
Por otra parte, la procedencia de MPR presenta un crecimiento parecido o inferior a tres de las cuatro procedencias hondureñas. Birks y Barnes (1990), sugirieron que esta procedencia muestra índices de haber hibridizado naturalmente con *Pinus caribaea*, lo cual podría explicar su comportamiento relativamente malo en este sitio de altura.

Entre las procedencias hondureñas, Villa Santa parece ser la mejor y Jocón parece claramente inferior en crecimiento. Las mismas procedencias fueron incluidas en otros ocho ensayos reportados por Dvorak y Donahue (1992), con resultados muy parecidos. Dada la magnitud de las diferencias en la productividad de Villa Santa y las procedencias de Nicaragua, no parece representar una alternativa aceptable a estas últimas.

Como grupo, las procedencias de *P. tecunumanii* no fueron significativamente superiores a la procedencia Dipilto de *Pinus oocarpa*; incluso la productividad de Dipilto fue muy parecida a la de Jocón. Sin embargo, la superioridad de las mejores procedencias de *Pinus tecunumanii* sobre Dipilto es evidente.

CONCLUSIONES

1. Se debe seguir la recomendación de Corea *et al.* (1993), de utilizar la procedencia de Yucul de *Pinus tecunumanii* para la reforestación en sitios del tipo normalmente plantado con *P. caribaea* o *P. oocarpa*. Por lo menos en sitios húmedos de altura, la procedencia de San Rafael del Norte también puede ser recomendada. Se debe evitar el uso de la procedencia MPR y las procedencias hondureñas incluidas en sitios altos.
2. Los resultados resaltan la importancia de las actividades actuales de conservación *in situ* de la procedencia Yucul (Ravensbeck, 1994). Si fuera posible, dichas actividades se deben extender para abarcar también la población de San Rafael de Norte.



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Domestication of mahoganies

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ABSTRACT

Despite the economic importance of mahoganies, few attempts have been made at genetic improvement, partly because of the high incidence of pest attack when mahoganies are grown in areas where they are native. A suggested domestication strategy for mahoganies is outlined, centred on the selection for pest resistance as part of a genetic improvement programme, the capture of selected genotypes using vegetative propagation techniques, and the deployment of selected material in appropriate silvicultural systems which optimise pest control. Current progress in developing such a strategy is described, including the assessment of genetic variation using field tests and molecular methods and the development of vegetative propagation techniques with in vitro approaches. The importance of conserving genetic resources of mahogany species is highlighted, and the prospects for the future development of a domestication strategy are discussed. It is suggested that the development and implementation of such a strategy should be given high priority, if a sustainable resource of mahogany is to be guaranteed in the future.

INTRODUCTION

Mahoganies are among the most economically important tropical timber species, accounting for a significant proportion of world trade in tropical hardwood. Despite this fact, the mahoganies remain largely undomesticated: very little is known about the extent of genetic variation in wild populations, and very few attempts have been made at genetic improvement (see Palmer, pp16–24).

In the strict sense, the term 'mahogany' applies to members of the genus *Swietenia* (Meliaceae), which comprises three species, all native to the neotropics (see Styles 1981, for a detailed review). The natural distribution of *S. humilis* is the Pacific coast region of Central America, whereas *S. mahagoni* is found on a number of Caribbean islands and mainland USA (southern Florida). *S. macrophylla*, now the principal mahogany of commerce, occurs over a large geographical area, from Mexico to the southern Amazon in Bolivia and Brazil (see Styles 1981).

In this paper, mahogany is also taken to include the closely related genus *Khaya* (African mahogany), which bears a number of morphological and ecological similarities to *Swietenia*. A number of points are illustrated by reference to other economically important genera in the same family, such as *Cedrela* and *Lovoa*. About seven species of *Khaya* are recognised by Styles (1981), including *K. anthotheca*, *K. grandifoliola*, *K. ivorensis*, *K. madagascariensis*, *K. nyasica* and *K. senegalensis*. Most of the species are native to tropical Africa; *K. ivorensis* is native to coastal rainforests of West Africa, whereas *K. senegalensis* occurs in the drier northern parts of the same region.

The most important product obtained from mahogany is timber, which is principally used for furniture and veneers; it is easily worked and strong for its weight (Lamb 1966). Often, mahogany species are also favoured for use in agroforestry systems (eg in Central America and parts of Indonesia), where they may provide shade for crops and fuelwood. Other products derived from Meliaceae [illegible] the seed of *Carapa* spp. (see France, pp7–15) and biological insecticides (such as neem, obtained from *Azadirachta indica*). Medicinal products, such as treatments for whooping cough, rheumatism and lumbago, are derived from *Khaya* spp. (Abbiw 1990). Products such as these could potentially be derived from other meliaceous species by appropriate selection programmes.

The main factor which has limited the cultivation of mahoganies is attack by shoot-boring moths (*Hypsipyla* spp.), which are widespread throughout the tropics. The moth larvae destroy the terminal bud of the young tree, which then frequently branches or forks, reducing the economic value of the timber considerably. This pest has resulted in the failure of many attempts at reforestation with mahoganies in countries where they are native, including Puerto Rico, Guatemala, Peru and Cuba in the case of neotropical species (see Newton *et al.* 1993 for details). Similarly, planting of *Khaya* spp. has been almost completely abandoned in both Ghana and Nigeria because of shoot-borer attacks (Wagner, Atuahene & Cobbinah 1991). For this reason, selection for pest-resistant genotypes may form a critical part of the domestication strategy for mahoganies.

As few successful examples exist of mahogany cultivation in plantations, most timber continues to be derived from the exploitation of natural forests. This work is largely undertaken in a non-sustainable way. Domestication of mahogany is crucial for the development of an alternative resource, to guarantee the supply of high-quality timber into the future. In this paper, we consider three stages in the domestication process:

i. the assessment and selection of genetic variation;

ii. the capture of selected genotypes by the use of propagation techniques; and

iii. the deployment of genetically improved material in silvicultural or agroforestry systems to realise the full genetic potential.

THE ASSESSMENT AND SELECTION OF GENETIC VARIATION

Assessments of genetic variation have traditionally been made by comparing the growth of material from different geographical origins in provenance and progeny tests. However, recently developed molecular techniques enable the extent of genetic differentiation between genera, species and populations to be quantified directly. Preliminary results from both these approaches are described below, together with a consideration of selection for pest resistance and genetic conservation.

Provenance and progeny tests

Very few genetic tests have been established with either New or Old World mahoganies (see Palmer, pp16–24). For example, the National Research Council (1991) reported that there are no active tree improvement activities with *Swietenia* species. The most extensive provenance tests of *Swietenia* which have been established to date are those of the Institute of Tropical Forestry in Puerto Rico (Geary, Barres & Ybarra-Coronado 1973, see also Bocne & Chudnoff 1970), although no data have apparently been published describing the variation observed (but see Glogiewicz 1986). However, the broad ecological and geographical ranges of *Swietenia* species, coupled with their ability to hybridise, suggest that a high degree of genetic diversity may exist within the genus (Newton, Leakey & Mesén 1993; see also Liu 1970).

Even less is known about the extent of genetic variation in *Khaya* spp. than in their neotropical relatives. A number of workers have outlined the early stages of genetic improvement programmes with *Khaya* spp. Betancourt, Marquetti and Garcia (1972) described the possibility of hybridisation between *K. nyasica* and *K. senegalensis*, and noted that a programme for selection of resistance to stem cankers was initiated in Cuba. A preliminary programme of plus-tree selection was undertaken in Ghana, including six trees of *K. anthotheca* and four of *K. ivorensis* (Britwum 1970). However, there are apparently no published data describing results from progeny or provenance tests of *Khaya* spp. in any area, although Chapuis (1990) gave brief details of the breeding programme with both *Khaya* and *Swietenia* spp. in Cuba.

The only species of the Meliaceae which has been investigated in any detail with respect to genetic variation is *Cedrela odorata* (Spanish cedar). A series of international provenance trials were co-ordinated by the Oxford Forestry Institute, UK, in the 1960s and 1970s (Chaplin 1980; see also Burley & Lamb 1971). In 1967, seedlots of 14 provenances were distributed to 21 collaborating countries throughout the tropics, for use in trials. Provenance differences in mean height growth by up to a factor of six were subsequently recorded (see papers in Burley & Nikles 1973, Nikles, Burley & Barnes 1978). In general, the most promising provenances in terms of height growth were those from Costa Rica and Belize (Chaplin 1980). These results indicate the extent of genetic variation which could potentially be recorded in other species of Meliaceae, were they to be investigated (Newton, Leakey & Mesén 1993). The pattern of genetic variation within the genus *Cedrela* is obscured, however, because some of the species (such as *C. angustifolia*) are poorly defined taxonomically (see Styles 1981) and susceptible to hybridisation

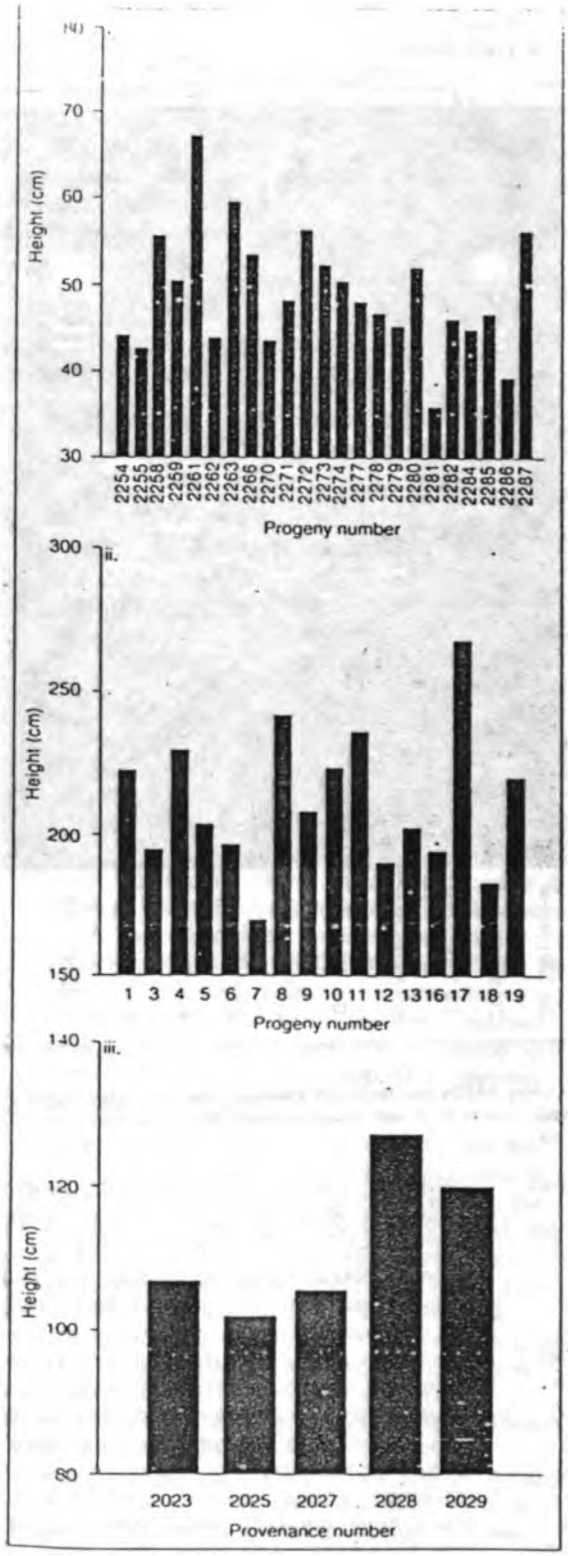

Figure 1 Preliminary results from field trials of *Swietenia macrophylla*, illustrating the extent of genetic variation in height growth

i progeny test, including 23 half-sib progenies from a range of sites in Costa Rica, Honduras and Trinidad, after 15 months' growth at Bajo Chino, CATIE, Costa Rica

ii progeny test, including 16 half-sib progenies from a range of sites in Trinidad after 17 months' growth at Moruga, Trinidad

iii provenance test, including five provenances from the Central American/Caribbean region after 14 months' growth at Florencia Sur, CATIE, Costa Rica

A number of [illegible] trials of neotropical mahogany species have recently been established in Central America and the Caribbean, in an attempt to initiate a programme of genetic selection and conservation. For example, two progeny tests and a provenance test of *Swietenia macrophylla* have been established in Costa Rica and Trinidad as part of a collaborative link between the Institute of Terrestrial Ecology (ITE), the Centro Agronomico Tropical de Investigacion y Enseñanza (CATIE) and the International Institute of Biological Control (Newton 1990; Newton, Mesén & Leakey 1992; Newton, Leakey & Mesén 1993). In addition, the conservation and genetic improvement of Honduras forest resources (CONSEFORH) project (see Mesén, Boshier & Cornelius, pp249–255) has established two progeny tests of *S. humilis*, which are probably the first for this species. No results of these trials have been published so far.

Preliminary results from the *S. macrophylla* trials in Costa Rica and Trinidad indicate a significant degree of genetic variation in rate of height growth. In a progeny test at CATIE, Costa Rica, half-sib progenies differed by a factor of two in mean height after 15 months' growth (Figure 1i). A similar degree of variation (by a factor of 1.5) was recorded in a progeny test in Trinidad after 17 months (Figure 1ii), but five provenances tested at CATIE were less markedly different (Figure 1iii).

Molecular techniques

Traditionally, genetic resources have been characterised on the basis of morphological and agronomic traits. The effectiveness of this approach for estimating genetic diversity however, has been questioned by several authors (Gottlieb 1977; Brown 1979). The subsequent development of isozyme and other biochemical markers represented a significant improvement. However, the effectiveness of such biochemical markers is limited by the number of polymorphic loci detected.

With the advent of molecular techniques, DNA-based procedures for detecting genetic variation have been proposed. They include restriction fragment length polymorphisms (RFLPs) which have the potential to detect almost unlimited amounts of variation. Although chloroplast DNA (Palmer *et al.* 1988) and nuclear RFLPs (Debener, Salamini & Gebhardt 1990) have been used for taxonomic studies, the

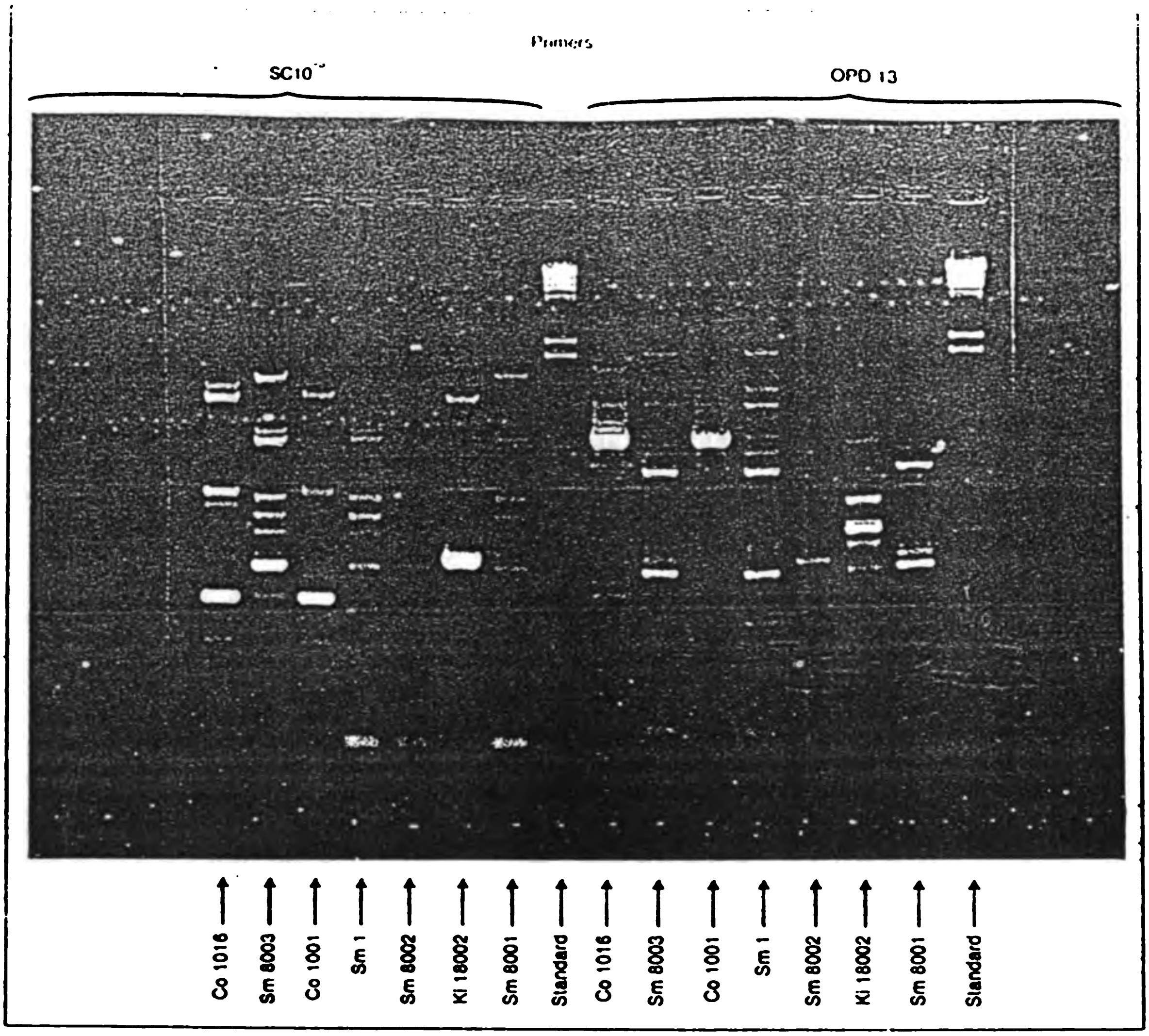

Figure 2 Genetic variation in mahogany species, detected using RAPDs (for details of methods, see text) The Figure presents amplification products of *Swietenia macrophylla* (Sm), *Cedrela odorata* (Co) and *Khaya ivorensis* (Ki) on an ethidium bromide-stained gel, using two primers, SC10^{-3} and OPD 13

usefulness of these markers is limited by the fact that they are costly, time-consuming and technically demanding

Recently, a new procedure based on the polymerase chain reaction, termed randomly amplified polymorphic DNA (RAPDs), has been developed for detecting polymorphisms in plants (Williams *et al* 1990, Welsh & McClelland 1990, Waugh & Powell 1992) This technique is based on the polymerase chain reaction (PCR) amplification of unknown DNA sequences using short (10-mer) synthetic oligonucleotide primers Polymorphisms can simply be identified as the presence or absence of an amplification product on an ethidium bromide-stained gel. The RAPD method overcomes many of the limitations of RFLP and has been used for clone identification in cocoa and banana (Wilde, Waugh & Powell 1992), population differentiation in *Gliricidia* spp (Chalmers *et al.* 1992), and genetic mapping (Carlson *et al.* 1991; Roy *et al* 1992).

Recently, RAPDs were applied for the first time to mahoganies in a preliminary investigation to test the applicability of the techniques to these species. A number of different genera were compared, including *Khaya*, *Swietenia* and *Cedrela* spp., and pronounced polymorphisms were detected at the genus level (Figure 2) These encouraging results suggest that DNA extraction of these species is not difficult, and that a more detailed investigation using RAPDs may be profitable to assess the extent of genetic variation within and between mahogany populations, and to resolve some of the taxonomic difficulties with mahogany species and hybrids (W Powell *et al.*, unpublished).

Selection for pest resistance

As attack by shoot-borers (*Hypsipyla* spp) is the main factor restricting the cultivation of mahoganies in plantations, selection for pest resistance could be considered to be a key aim of a domestication strategy. Pest resistance may arise through three main mechanisms (Grijpma 1976):

i. *non-preference*, when the insect is not attracted to or is actively repelled from ovipositing or feeding on the tree;

ii. *antibiosis*, in which the insect is killed, injured or prevented from completing its life cycle after feeding on the tree; and

iii. *tolerance*, in which the tree recovers from attack to an acceptable level.

There is evidence for all three mechanisms within the Meliaceae family as a whole. With respect to non-preference, some mahogany species are clearly less susceptible to attack than others, such as *S. mahagoni* compared with *S. macrophylla* (Whitmore & Hinojosa 1977). Such differences in susceptibility may reflect variation in the production of chemical attractants, although differences in growth rate may also be influential (Grijpma 1976). Antibiosis is demonstrated by species such as *Toona ciliata*, a native of SE Asia and Australasia, which produces water-soluble compounds toxic to *Hypsipyla grandella*, the native shoot-borer of the Americas (Grijpma & Roberts 1975). Some mahoganies produce resins, which may also hinder shoot-borer attack (Wilkins 1972; Lamb 1968; Whitmore 1978). The ability of individual trees to tolerate attack by strong apical growth has also been observed in both *Cedrela* spp. (Chaplin 1980; Grijpma 1976; Vega 1976) and *Swietenia* spp. (A C Newton, personal observation).

However, little information is available on the intraspecific variation in these mechanisms of pest resistance. To investigate this aspect, the genetic tests established by the ITE/CATIE link and CONSEFORH project (see above) have been intensively assessed for the incidence of pest attack. Preliminary results, from combined provenance/progeny tests of *C. odorata* in Costa Rica, have indicated intraspecific variation in different forms of resistance. Apart from pronounced differences in growth rate, different families displayed three-fold variation in susceptibility to attack (Newton, Leakey & Mesén 1993). In addition, some individuals were able to tolerate attack by vigorous growth of a new dominant lateral shoot, although the genetic basis of this characteristic has not yet been examined in detail. These preliminary results suggest that selection for pest resistance may be an achievable objective in mahoganies, although further research on this aspect is clearly required

Genetic conservation

Concern has recently been voiced about the conservation status of neotropical mahoganies (Newton, Leakey & Mesén 1993; Rodan, Newton & Verissimo 1992), as reflected in the listing of two species (*S. humilis* and *S. mahagoni*) on Appendix II of the Convention on International Trade in Endangered Species (CITES). A proposal to include *S. macrophylla* on this listing was made in 1992 by the governments of the USA and Costa Rica, but was eventually withdrawn prior to consideration by the committee (Rodan *et al.* 1992). It is possible that this proposal will be renewed in the future. *S macrophylla* is considered by some to be endangered or vulnerable in a number of countries (US CITES proposal 1992), although others have suggested that large stocks still exist (Anon 1992). In fact, little detailed information exists on the extent of remaining populations.

Many of the Old World mahogany species are perhaps in an even more precarious state, and are considered to be vulnerable or endangered in many parts of their range (World Conservation Monitoring Centre, Cambridge, UK, unpublished information). Germplasm collection and exploration of *Khaya* spp. have been accorded high priority by the Food and Agriculture Organisation (1989), and there have been suggestions that this genus should also be listed on Appendix II of CITES (Flora and Fauna Preservation Society, UK, personal communication)

The concerns about genetic conservation arise from the fact that the vast majority of mahogany timber is harvested from natural stands. Selective logging, involving removal of the most economically desirable phenotypes, may result in the genetic depletion of the forest stand and a reduction in its future economic value. *Swietenia mahagoni*, which has been logged intensively over the past 400 years, is perhaps the most striking example of genetic erosion in tropical forestry: most individuals which remain are highly branched or forked (Styles 1981). The same processes are undoubtedly acting on *S macrophylla* and other mahogany species currently being harvested, although the extent of any genetic erosion which may be occurring is difficult to assess quantitatively.

CAPTURE OF GENETIC VARIATION

Selected genotypes may be captured for use in cultivation by seed and vegetative propagation techniques. The requirements for the storage of mahogany seed are described elsewhere (Tompsett, pp61-71) and are therefore not discussed further in this paper. Instead, the progress made in developing practical protocols for the vegetative propagation of mahoganies is described, including both propagation by leafy cuttings and *in vitro* techniques

Vegetative propagation by rooting of leafy cuttings

A number of Meliaceae species, including most mahoganies, have now been successfully propagated by rooting leafy cuttings (Leakey, Last & Longman 1982; Newton, Leakey & Mesén 1993). Successful results have been obtained with a number of different propagation systems, including traditional mist propagators (Howard, Verkade & DeFilippis 1988; Tchoundjeu 1989), and also low-technology non-mist propagators (Leakey *et al.* 1990; see also Leakey, Newton & Dick, pp72–83; Mesén *et al.*, pp249–255). However, if mahoganies are to be propagated on a commercial scale, detailed information is required on the appropriate treatments which should be applied to both the stockplants and the cuttings to obtain consistently high rooting success. Such information is gained primarily through specific experimental programmes with individual species.

The most extensive propagation studies to date have been with *Khaya ivorensis* under mist (Tchoundjeu 1989) and with *Lovoa trichilioides* (African walnut) in non-mist propagators (Tchoundjeu 1989). These examples are consequently described here in some detail. Initial experiments were designed to determine the optimal conditions for rooting single-node, leafy cuttings from hedged juvenile stockplants. It was hypothesised that, for a species for which little is known about the conditions for rooting, the most important factors to test and optimise were auxin concentration, leaf area, cutting length and node position (Tchoundjeu & Leakey 1993). The basic methods and mist propagation system used were as previously described by Leakey *et al.* (1982) for the West African hardwood *Triplochiton scleroxylon*.

By comparison with *T. scleroxylon*, the highest rooting percentages of *K. ivorensis* were obtained with a considerably higher applied auxin concentration (200 µg IBA per cutting) but a smaller leaf area (10 cm^2). Subsequently, Asanga (1989) determined that the optimal leaf area under the conditions tested was about 30 cm^2. As with many other species, long cuttings (39 mm) rooted better than short ones (19 mm), especially if associated with a supra-optimal leaf area. Unlike *T. scleroxylon* and some other light-demanding species, the cuttings from basal nodes rooted better than those from apical nodes. These basal node cuttings had higher N, P, K, soluble carbohydrate and starch contents than those from apical nodes. One other observation from this study was that cuttings developed a one-sided root system if the cutting base was made by an oblique cut as opposed to a square cut (Tchoundjeu 1989).

Like many other members of the Meliaceae, plants of *K. ivorensis* grow by recurrent flushing; there are therefore alternating periods of terminal bud activity and dormancy. Higher rooting percentages were obtained when cuttings were taken from dormant shoots than from flushing shoots, although the latter had higher concentrations of soluble carbohydrates throughout the period of propagation.

In a more detailed study of the rooting of *K. ivorensis* cuttings, an attempt was made to investigate the relationships between rooting and the carbohydrate dynamics of the cuttings (Tchoundjeu 1989). This study included an examination of the effects of stockplant irradiance and nutrient applications on the dynamics of reducing sugar and starch contents of both the leaf and stem portions of cuttings in the propagator. Results showed that rooting never seemed to be limited by the stored carbohydrate reserves of the cuttings. Leakey *et al.* (pp72–83) present evidence derived mostly from light-demanding, pioneer species that rooting generally tends to be carbohydrate-driven. It, therefore, appears that, for *K. ivorensis*, and perhaps other relatively shade-tolerant species, rooting ability may not be limited by either carbohydrate reserves or the production of current assimilates. This conclusion was clearly demonstrated in a further study of the effects of stockplant nutrition on rooting. In this case, there was no effect of nutrient application on stockplant growth or rooting, although there were very considerable effects on the conversion of stored starch to sugars. Cutting mortalities were, however, greatest in cuttings from stockplants receiving the highest rate of nitrogen application (Tchoundjeu 1989).

Additional experiments were undertaken in Cameroon, investigating the factors which influence the rooting of *Lovoa trichilioides*, using a non-mist propagator as described by Leakey *et al.* (1990). In the early experiments, the propagators were not as air-tight as in later experiments, and the rooting percentages were frequently less than 50%. Nevertheless, by comparison with *K. ivorensis*, the auxin requirements of *L. trichilioides* cuttings were relatively low (Tchoundjeu 1989), with an optimum concentration in one experiment of 50 µg per cutting, while, in another, untreated controls rooted as well as treated cuttings. The highest rooting percentages were achieved with leaf lamina areas of 200 cm^2, about ten times that of *K. ivorensis*. These large-leaved cuttings also produced the most roots and had the lowest cutting mortalities. In a number of experiments it was found that, as in *T. scleroxylon* but in contrast to *K. ivorensis*, a higher proportion of cuttings rooted from apical nodes of the top shoot, while those from basal nodes had the greatest mortality rates (Tchoundjeu 1989). Higher rooting percentages were obtained with cuttings from basal shoots, these having the greatest leaf and stem nitrogen concentrations, and high foliar carbohydrate contents.

In an attempt to examine the effect of cutting size (stem length and diameter), cuttings of three size categories were collected from similar positions within shoots. In this case, higher rooting percentages were obtained with long thin cuttings (38 mm x 4 mm) than long thick cuttings (45 mm x 8 mm); short thin cuttings (15 mm x 4 mm) were intermediate. To examine the effects of cutting origin on rooting, cuttings were collected from hedged stockplants producing one, two, three or four shoots per plant. In this instance, the mean percentage rooting of all cuttings harvested per plant was similar in all four treatments (Tchoundjeu 1989). However, the relative rooting percentage of cuttings from the different shoots was strongly influenced by the number of shoots per plant and their position on the plant.

As in *K. ivorensis*, the effects of stockplant management treatments, such as nutrient application and shading (irradiance and light quality), were not conclusive. It seems that, unlike light-demanding species such as *T. scleroxylon* and *Eucalyptus grandis* (Leakey & Storeton-West 1992; Hoad & Leakey 1992), rooting in relatively shade-tolerant hardwoods is not predetermined by the stockplant's light environment and the interactions of light with nutrients. Further studies are, therefore, required to examine the differences between these two groups of trees and determine the reasons for these differences in rooting physiology. However, despite this lack of conformity with other well-studied tropical hardwoods, it is clear that both these species of the Meliaceae are relatively easy to root as stem cuttings under either mist or non-mist propagation systems.

Few detailed vegetative propagation experiments have been undertaken with the neotropical species of the Meliaceae. In a preliminary investigation using non-mist propagators, the percentage rooting of *Swietenia macrophylla* cuttings was found to be higher when a rooting medium with a high proportion of sand was used; maximum rooting of over 60% was achieved with 75:25 sand/gravel (Mesén, Leakey & Newton 1992; Newton, Leakey & Mesén 1993). The concentration of IBA applied to the base of the cuttings was found to have only a slight effect on rooting. In these experiments, the cuttings were relatively slow to root (11 weeks), indicating that further research is needed if propagation protocols are to be improved. In general, *Cedrela odorata* appears relatively easy to root, displaying higher rooting percentages in sand than gravel, and with relatively low (0.2–0.4%) concentrations of applied IBA (Maldonado, Salazar & Mesén 1992).

In vitro micropropagation

A number of mahogany species have now been successfully micropropagated using *in vitro* techniques, including *Cedrela odorata* and *Swietenia macrophylla* (Lee & Rao 1988, Maruyama *et al.* 1989). One of the few species which has been investigated in any detail, however, is *Khaya ivorensis* (Mathias 1988), and is described here.

By comparison with another W African hardwood species, *Nauclea diderrichii*, explants of *K. ivorensis* were easy to sterilise with commercial sterilant (5%, 10% and 20% for 10, 20 or 30 minutes) (Mathias, Alderson & Leakey 1989). Those explants treated with 5–10% sterilant were free from tissue browning and were viable. The medium used in this study was that of Murashige and Skoog, with a carbon source of 20 g l^{-1} galactose (Mathias 1988). The stockplants were grown under tropical glasshouse conditions in Britain and explants cultured at 25°C at a photon flux of 50–60 μmol m^{-2} s^{-1} for 16 h each day. The experimental programme examined the effects of pre-severance stockplant treatments on culture initiation and the conditions required for shoot proliferation, and is described in full by Mathias (1988).

The environmental factors investigated in order to improve the success of culture initiation were the photon flux of photosynthetically active radiation (PAR), light quality (red/far-red ratio), daylength, day/night temperatures and stockplant nutrition. In addition, because *K. ivorensis* grows by recurrent flushing, experiments tested the effects of collecting explants at different times during the flushing cycles, as well as at different times after removal of the terminal bud.

Explants collected from dormant shoots had the highest bud activity in culture and the lowest mean callus score. When dormant shoots were decapitated prior to collecting explants, greater bud activities were found in explants collected either two to three or eight to nine days after decapitation than in those collected at other times. The application of fertilizers to stockplants had some effects on shoot growth prior to the collection of the explants, but little effect on culture initiation. In contrast, the stockplant light environment did influence bud activity in culture, with the greatest activity occurring in explants from plants grown at 60 μmol m^{-2} s^{-1} at R/FR of 0.3, especially in the absence of applied nutrients (Mathias 1988). Analysis over a number of different treatments, however, showed that the greatest increases in explant activity were achieved by increases in the red light/photosynthetic photon flux ratio (ie the proportion of red light [660 nm] in the whole band of photosynthetically active radiation [400–700 nm])

Regarding the [illegible] of shoot production [illegible] *K. ivorensis*, the cytokinins benzylaminopurine (BAP) and zeatin at 2. 5 and 10 mg l^{-1} increased the mean number of axillary shoots formed per explant. Subsequently, a study of the effects of auxin (naphthalene acetic acid [NAA])/cytokinin (BAP) ratio on bud activity showed that the optimal combination was around 1:100–1:200 in the first subculture, but that in the second subculture even greater bud activities occurred, with an optimum NAA/BAP ratio of 1 25 (Mathias 1988). In another experiment, the transfer of cultures which had previously proliferated and had their shoots harvested, to media containing gibberellic acid (GA_3), stimulated further proliferation/elongation of shoots. However, in all these studies there was evidence that growth regulatory substances accumulated in the tissues, and consequently that they could reach inhibitory concentrations, if applied repeatedly through several subcultures.

In conclusion, it is clear that *K. ivorensis* (African mahogany) is amenable to micropropagation, and that practical protocols could be developed with further study. The major problem encountered in micropropagation was the initiation of a proliferating culture, owing to variability in the explants.

DEVELOPMENT OF APPROPRIATE SILVICULTURAL SYSTEMS

In order to realise the full genetic gains obtained through selection, the trees should be established in appropriate silvicultural systems. The choice of an appropriate system is determined partly by the physiological responses of the individual species (see Fasehun & Grace, pp148–157). The photosynthetic responses of *Swietenia macrophylla*, *Cedrela odorata* and *Khaya ivorensis* have now been analysed in some detail under controlled conditions (Kwesiga & Grace 1986; Kwesiga, Grace & Sandford 1986; Ramos & Grace 1990). In general, *Swietenia* and *Cedrela* spp. are highly light-demanding, and this fact should be taken into account in cultivation. Many of the failures in mahogany cultivation in silvicultural systems, such as line enrichment, can be attributed to inadequate intervention leading to excessive shading (cf Palmer 1988).

A wide range of different silvicultural approaches has been applied to the production of mahoganies with the aim of controlling shoot-borer attack. Most have resulted in failure, but there are examples of trials where shoot-borer damage has been at least partly controlled by cultural methods (Newton *et al* 1993). For example, in Puerto Rico, line enrichment plantings resulted in as few as 11% of the trees being attacked (Weaver 1987; Weaver & Bauer 1986). Similarly Vega (1976) described a series of trials in Surinam, involving establishment of *Cedrela* spp in natural regeneration, line enrichment and open plantation systems. After two years, the proportion of plants attacked was higher in plantations established in the open (10–60%) than in enrichment plantings (4–40% attacked). In other enrichment trials, the proportion attacked was less than 10% after 22 months. In trials established in Brazil, Yared and Carpanezzi (1981) reported that shoot-borer damage of *Swietenia macrophylla* was virtually absent in the line enrichment system employed.

The reasons for the success of these examples have not been investigated in detail, but may involve a variety of processes, such as the effects of shading on the growth rate of the trees and the production of terminal shoots (Newton *et al.* 1993). In particular, it has been suggested that the presence of other tree species may hinder location of meliaceous trees by the adult moth (Grijpma 1976; Morgan & Suratmo 1976). Very little precise information is available to indicate whether this process actually occurs, but it is conceivable that low densities of susceptible trees may prevent the build-up of moth populations (Weaver & Bauer 1986). In addition, populations of natural predators of *Hypsipyla* could be maintained in systems such as line enrichment, where much of the original vegetation is left intact (see Gibson & Jones 1977).

It should be noted that the planting of mahoganies in mixtures with crops or non-susceptible tree species does not guarantee successful shoot-borer control. For example, when a number of different silvicultural and agroforestry systems were tested in Colombia, no consistently successful method of shoot-borer control was identified (Vega 1987; Neyra & Martinez 1985). These results emphasise the importance of viewing the silvicultural system as one aspect of an integrated domestication strategy. Such a system might involve incorporation of pest-resistant genotypes into a silvicultural system optimising natural biological control, such as a line enrichment system, thereby providing an integrated system of pest management (Newton *et al.* 1993).

Mahoganies have been established successfully in monocultures in a number of countries where they are not native, such as *Swietenia macrophylla* in Indonesia and the S Pacific (Evans 1982). In such situations, mahoganies are often (but not always) resistant to the native shoot-borers, and can be grown successfully at high density, offering the prospect of rapid genetic gains in improvement programmes. Plantation establishment of exotic mahoganies is likely to increase in the future (Newton 1993), perhaps including the introduction of *Khaya* spp into the neotropics (Betancourt *et al.* 1972), an approach which has so far not been tested on a large scale despite its obvious potential

CONCLUSIONS

The development of a domestication strategy for mahoganies offers the prospect of overcoming the problems which have limited mahogany cultivation so far. Such a strategy should involve selection for pest resistance as one component of a genetic improvement programme, and should also involve the deployment of selected genotypes in appropriate silvicultural systems to optimise pest control as well as growth. Techniques for capturing selected genotypes, including *in vitro* techniques and propagation by leafy cuttings, have been successfully developed for a number of mahogany species, although further research is required to refine the precise treatments required for sustained successful rooting. Application of these propagation techniques to genetic improvement should enable rapid progress to be made in generating superior clonal populations for use in reforestation.

Apart from increasing efforts at genetic improvement of mahoganies, attention should also be directed towards genetic conservation, both of populations *in situ* and of selected genotypes *ex situ*. Increased exploration and testing of genetic resources of mahogany species are urgently required, particularly of the African species, which have hardly been investigated in this regard. High rates of deforestation in both palaeotropical and neotropical regions continue to deplete these genetic resources, and could limit the potential for sustainable production of mahogany in the future.

It is to be hoped that the prospects of developing a successful domestication strategy for mahoganies will stimulate interest within the timber industry, and encourage attempts to regenerate a resource. The economic incentives for such an initiative certainly exist: the demand and value of the timber are likely to remain high for the foreseeable future (Palmer, pp16–24).

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Genetic variation in mahoganies: its importance, capture and utilization

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Mahoganies (*Swietenia* spp.; Meliaceae) are amongst the most economically important tropical hardwoods, and yet little information exists concerning their patterns of genetic variation. The characterization of this variation is essential for defining more accurately the conservation status of mahogany populations, and for their economic utilization. The loss of genetic variation through deforestation may be critical for these species, which are highly susceptible to pest attacks when grown in plantations. This paper assesses the current state of knowledge concerning the extent of genetic variation in mahoganies, and highlights its potential importance. It is suggested that any conservation strategy developed for mahoganies should include a genetic selection and improvement programme as well as the protection of natural stands *in situ*. Techniques by which particular genotypes may be captured for *ex situ* conservation are briefly described.

Keywords: mahogany; genetic conservation; propagation

Introduction

Although mahoganies (*Swietenia* spp.; Meliaceae) are amongst the most commercially important hardwoods in the neotropics (Lamb, 1966), little attention has been paid to the extent of genetic variation that exists within the natural distribution of these species. Characterizing this variation is of importance for defining both the *in situ* and *ex situ* conservation status of particular populations, and for the development of afforestation and tree improvement programmes. The conservation status of mahogany species in the neotropics has recently been the subject of increasing concern, as natural populations are currently being severely depleted by deforestation (Read, 1990). As an illustration of this, the United States and Costa Rican governments recently proposed the genus *Swietenia* for listing in Appendix II of the Convention on International Trade in Endangered Species (CITES) (US CITES proposal, 1992).

The aim of this review is to survey the known extent of genetic variation that exists in neotropical mahoganies, particularly with respect to the results of genetic tests which have been performed to date. The importance of this variation for the conservation and

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economic utilization of these species is discussed, and the techniques that enable certain genotypes to be conserved *ex situ* are briefly described. Although concerned primarily with the neotropical mahoganies in the strict sense (*Swietenia* spp.), a number of points will be illustrated by reference to closely related species within the Meliaceae, from both the Americas and other geographical regions.

The extent of genetic variation in wild populations

Taxonomic definition of species

The taxonomy of *Swietenia* has been described in detail in two recent monographs (Pennington and Styles, 1975; B.T. Styles in Pennington, 1981). The genus is represented in the neotropics by three species, *S. macrophylla* King, *S. humilis* Zuccarini and *S. mahagoni* (Linnaeus) Jacquin. These species are interfertile, which hinders the attribution of many individuals to a particular species in some areas of their natural distribution. For example, naturally occurring hybrids of *S. humilis* × *S. macrophylla* occur in N.-W. Costa Rica (Holdridge and Poveda, 1975; Whitmore, 1983); variation in characteristics such as leaf morphology and fruit size is continuous in this area (Eugenio Corea, personal communication). Similarly, the hybrid between *S. macrophylla* and *S. mahagoni* arose spontaneously after the introduction of *S. macrophylla* to a number of Caribbean islands (Whitmore and Hinojosa, 1977; B.T. Styles in Pennington, 1981). The putative hybrid *S. humilis* × *S. mahagoni* has also been recorded (Whitmore and Honojosa, 1977).

The ability to hybridise greatly influences the genetic composition of individual populations. For example, the *Swietenia* population present in Puerto Rico effectively constitutes a hybrid swarm, with hybrids and backcrosses between the two main species (see Whitmore and Hinojosa, 1977). The occurrence of such hybrids has important implications for genetic conservation strategies, as well as for tree improvement research. For example, the introgressive hybridization caused by the presence of *S. macrophylla* on Caribbean islands such as Puerto Rico represents a form of genetic erosion of *S. mahagoni*. It is conceivable that pure genetic stocks of both species could eventually disappear in such localities.

In terms of intraspecific genetic variation, chromosome races have been identified in *Swietenia* as well as other species of Meliaceae (Styles and Khosla, 1976). Both diploid ($2n = 54$) and tetraploid ($2n = 108$) races occur in *S. macrophylla*, and a polyploid series has been identified in *S. mahagoni* in plantations in Fiji (Styles and Khosla, 1976). The evolution and geographical distribution of these genetic races is imperfectly understood.

Variation in growth and form

The extent of genetic variation in a wild population may be assessed by carrying out a genetic test of the chosen material. This involves the growth of material of different origins in trials either within or outwith the natural range, to compare growth attributes. Traditionally, this has primarily involved provenance and progeny tests (Zobel and Talbert, 1984). In the former, seeds collected from a number of different trees in a particular geographical region are bulked together, whereas in a progeny test, seedlings collected from individual mother trees are kept separate. Combined tests may incorporate progenies from a number of different provenances. Progeny tests allow the heritability of different attributes to be estimated which gives a quantitative indication of the degree genetic variation for the attribute concerned.

Very few provenance or progeny tests have been carried out with *Swietenia* species, although such tests are the basis of many of the genetic improvement programmes that have now been initiated with other tropical timber species (see papers in Gibson *et al.*, 1989). The lack of such tests partly reflects the difficulties in growing mahoganies in the presence of shoot boring moths (*Hypsipyla* spp). Although the growth of *Swietenia* spp. in Puerto Rico has been investigated in detail (Weaver, 1987; Weaver and Bauer, 1986), and provenance tests have been established (Geary *et al.*, 1973; see also Boone and Chudnoff, 1970), there are apparently no published data describing provenance variation (but see Glogiewicz, 1986). Similarly, the National Resources Council (1991) reported that there are no active tree improvement activities with *Swietenia* species. The broad ecological and geographical ranges of *Swietenia* species, coupled with their ability to hybridize, would suggest that a high degree of genetic diversity may exist in mahoganies.

In contrast to the situation with *Swietenia*, the genetic variation in *Cedrela odorata* L. (Spanish Cedar) has been investigated in some detail. The results of trials of *C. odorata*, which is closely related to *Swietenia* spp., illustrate the kind of variation which might exist in *Swietenia*. The main studies undertaken to date with *C. odorata* are the international provenance trials coordinated by the Oxford Forestry Institute, UK. The results of these trials were summarized by Chaplin (1980) (see also Burley and Lamb, 1971). In 1967, seedlots of 14 provenances were distributed to 21 collaborating countries throughout the tropics, for use in trials. In the neotropics few trials were successfully established, and problems with shoot borer attack and site incompatibility were encountered (Whitmore, 1978). The same seedlots were also tested in a number of localities in Africa, where pronounced differences in growth and form were observed between provenances, partly because of the low incidence of shoot borer attack. Provenance differences in mean height growth by up to a factor of six were recorded in these trials (see papers in Burley and Nikles, 1973; Nikles *et al.*, 1978). In general, the most promising provenances in terms of growth were those from Costa Rica and Belize (Chaplin, 1980).

As noted above, few published data of a similar nature exist for *Swietenia* spp. at present. However, a number of initial small-scale trials are currently in progress. As part of a collaborative link between the Institute of Terrestrial Ecology (ITE), the Centro Agronomico Tropical de Investigacion y Enseñanza (CATIE) and the International Institute of Biological Control (IIBC), a number of provenance tests and combined progeny/provenance tests have recently been established in both Costa Rica and Trinidad (Newton, 1990; Newton *et al.*, 1991, 1992). Although some origins of *S. humilis* and *S. mahagoni* are being tested on a small scale, the principal species in this programme are *C. odorata* and *S. macrophylla*. In addition, a tree improvement group based at ESNACIFOR (Siguatepeque) in Honduras is currently establishing provenance/progeny tests of *S. humilis*. No results of these trials have been published to date.

Variation in pest resistance

As noted above, mahogany species are susceptible to attack by shoot borers (*Hypsipyla* spp.), perhaps the best known insect pest of any tropical forest tree (see Grijpma, 1973; Whitmore, 1976a,b). The larvae of the moth bore into the apical part of the stem, destroying the terminal shoot and bud, and resulting in forking or deformation of the trunk. Attacks by shoot borers virtually prevent establishment of *Swietenia* in plantations in many parts of the neotropics. Although considerable research effort has been devoted to the development of control methods for this insect pest (Grijpma, 1974; Whitmore, 1976a,b), few practical control measures have been developed.

If mahoganies are to be established in plantations to offset losses through degradation of natural stands, it is essential that the shoot borer problem is overcome. This might be achieved by a combination of silvicultural, biological and perhaps chemical control methods (Newton *et al.*, 1992). However, it has repeatedly been suggested that the most effective way to combat this pest would be to produce resistant plants, through selection in a breeding programme (Grijpma, 1976; Newton, 1990; Newton *et al.*, 1992).

Resistance may arise through three main mechanisms (Grijpma, 1976):

(i) non-preference, when the insect is not attracted to or is actively repelled from ovipositing or feeding on the tree;
(ii) antibiosis, in which the insect is killed, injured or prevented from completing its lifecycle after feeding on the tree;
(iii) tolerance, in which the tree recovers from attack to an acceptable level.

Evidence for each of these mechanisms of resistance has been documented for different species of Meliaceae, but very little information is available concerning the intraspecific variation in these attributes.

The fact that some mahogany species are less susceptible to attack than others is well established. In Puerto Rico, *S. mahagoni* is less attacked than *S. macrophylla*, and the hybrid *S. mahagoni* × *S. macrophylla* is intermediate (Whitmore and Honojosa, 1977). Similarly, *Cedrela* species are generally thought to be attacked more readily than *Swietenia* spp. (Dourojeanni, 1963; Grijpma, 1970). These differences in susceptibility may reflect variation in the production of chemical attractants or toxins, although differences in growth rate and form may also be influential (Grijpma, 1976). As noted by Grijpma (1976), there is a strong possiblity that non-preferred mahoganies may exist, which could be exploited in a selection programme. However, few studies have been made of intraspecific variation in susceptibility to attack (see Whitmore, 1978).

Examples of antibiosis are provided by species exotic to the Americas, such as *Toona ciliata* M. Roem. This species produces water-soluble compounds which are toxic to *Hypsipyla grandella* (Zeller), by retarding growth and interfering with pupal development (Grijpma and Roberts, 1975). These chemical compounds are translocated to *C. odorata* when the latter is grafted onto *Toona* rootstocks, conferring resistance (Grijpma and Roberts, 1975). Furthermore, some mahoganies produce resins, which may hinder shoot borer attack (Lamb, 1968; Whitmore, 1978; Wilkins, 1972), but again, no information is available on the intraspecific variation in the production of these compounds.

The ability of certain *Cedrela* trees to recover following attack by strong apical growth has been repeatedly observed (Chaplin, 1980; Grijpma, 1976; Vega, 1976). This kind of tolerance is at least partially under genetic control (Chaplin, 1980) and therefore could also form the basis of a selection programme (Grijpma, 1976). Although not widely recorded for *Swietenia* species, *S. macrophylla* clearly can display this pattern of response (Newton, personal observation). Pronounced genetic variation in apical dominance, the physiological process determining the relative strength of apical and lateral meristems, has been recorded for other tropical hardwood species by Leakey and Longman (1986) and Leakey and Ladipo (1987). A simple nursery test to predict the genotypic variation in apical dominance (and branchiness) of individual trees has also been developed (Ladipo *et* *al.*, 1991a,b). This is currently being applied to *Cedrela odorata* (Newton, Mesén an Leakey, 1991).

Preliminary results from combined provenance/progeny tests of *C. odorata* in Cost Rica, undertaken as part of the ITE/CATIE link project (Newton *et al.*, 1991, 1992 Newton, 1990), have indicated intraspecific variation in different forms of resistance Apart from pronounced differences in growth rate, different families (or progeny sharing common parent) displayed three-fold variation in susceptibility to attack (Fig. 1). Thi variation was highly significant ($p < 0.001$, ANOVA). In addition, some of those individuals which were attacked were subsequently able to recover well by vigorous growth of a new dominant lateral shoot. Further investigations are required to test whether intraspecific variation in susceptibility is caused by variation in the production of chemical attractants or toxins, and the extent to which these different forms of resistance are under genetic control.

If variation in resistance occurs at the level of individual genotypes, as well as at the family level, then this can be captured by vegetative propagation (see later).

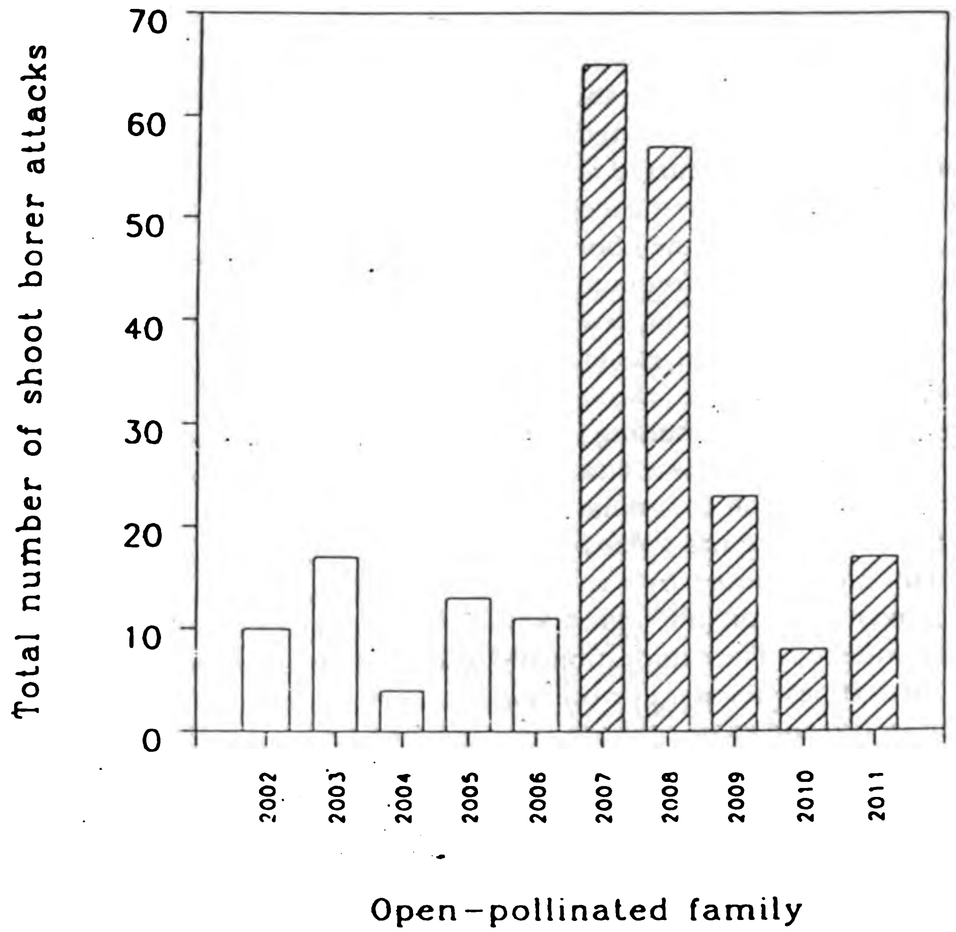


Fig. 1. The variation in susceptibility of shoot borer attack displayed by 10 open-pollinated half sib progenies from two provenances of *Cedrela odorata* in a field trial in Turrialba, Costa Rica. Th two provenances were San Carlos, Costa Rica (open bars) and Cañas, Costa Rica (hatched bars) Assessments of attack were made every two weeks over the first 24 weeks after establishmen Presence of fresh frass was taken to indicate a single attack locus. A more detailed set of analyse of the whole trial (25 families) are presented in Newton *et al.* (1992).

The case for genetic conservation

The conservation status of mahoganies has recently been the subject of some attention, as a result of the proposal by the United States and Costa Rican governments to list the genus *Swietenia* on Appendix II of the Convention on International Trade in Endangered Species (CITES). *Swietenia humilis* was listed on CITES Appendix II in 1973, following a proposal from Mexico. *Swietenia mahagoni* was listed as a result of a meeting by the Convention in 1992, but the proposal to list *S. macrophylla* was withdrawn prior to voting. Although concern about the status of *S. macrophylla* is growing (Read, 1990), little detailed information exists about the extent of native populations (US CITES proposal, 1992). The species is considered as vulnerable in many parts of its natural range because of over-exploitation (National Research Council, 1991; Palmberg, 1987), and has been listed as a high priority species for genetic conservation by the Food and Agriculture Organization (FAO, 1989; see also Palmberg, 1987) and the International Board for Plant Genetic Resources (IBPGR). The current conservation status of neotropical mahoganies is discussed in more detail by Rodan *et al.* (1992).

Selective logging acts as a source of dysgenic selection, whereby the best genotypes (in terms of growth or form) are selectively removed during the course of forestry operations. This results in a population depleted in its most favoured genotypes (genetic erosion). *Swietenia mahagoni* is perhaps the most striking example of genetic erosion in tropical forestry. This species is now most commonly seen as a highly branched shrub or small tree, whereas it was formerly abundant as a large tree of good form throughout its natural range (B.T. Styles in Pennington, 1981). Genetic erosion of other *Swietenia* and *Cedrela* species has already occurred in Central and South America, where trees of good form are now rarely encountered except in isolated areas (Styles and Khosla, 1976). In all these species it is likely that the poorly formed trees left by loggers are those with little resistance to *Hypsipyla*, since frequent attack affects tree form.

As noted in the previous section, few analyses have been made of the extent of genetic variation within mahogany species, in terms of the differences between provenances, families or individuals, or the existence of particular races. The reduction in this intraspecific genetic diversity resulting from logging remains unquantified. The potential loss of genotypes resistant to pest attack is perhaps one of the strongest arguments in favour of greater protection for remaining stands of mahogany. As described above, selection for pest resistance has great potential as a method of reducing the damage to commercial plantations caused by the mahogany shoot borer. Similarly, the possible existence of provenances or individuals with enhanced growth rates or wood quality remains largely untested. The exploration and testing of *Swietenia* genotypes is therefore an urgent priority. If pest resistant or otherwise superior genotypes and populations are identified, their *in situ* and *ex situ* conservation and utilization should become immediate objectives, on economic as well as biological grounds. The techniques by which such valuable or endangered genotypes might be conserved *ex situ* are described below.

The capture of genetic variation

Selected genotypes may be 'captured' (i.e. conserved *ex situ*) through the techniques of vegative propagation, either through rooting leafy cuttings (macropropagation) or by meristem proliferation *in vitro* (micropropagation). These techniques enable selected genotypes to be multiplied asexually, or cloned. The domestication of mahoganies by selection for pest resistance, tree form and growth rates, and by breeding between resistant parents in clonal seed orchards, could enable progress to be made in the creation of a commercial resource of profitable mahogany plantations to take the pressures off threatened natural stands. Cloning techniques are also useful for the characterization and quantification of genetic variation, and for *ex situ* conservation of endangered genotypes. Looking further to the future, micropropagation techniques may contribute to genetic engineering for pest resistance and other attributes.

Macropropagation

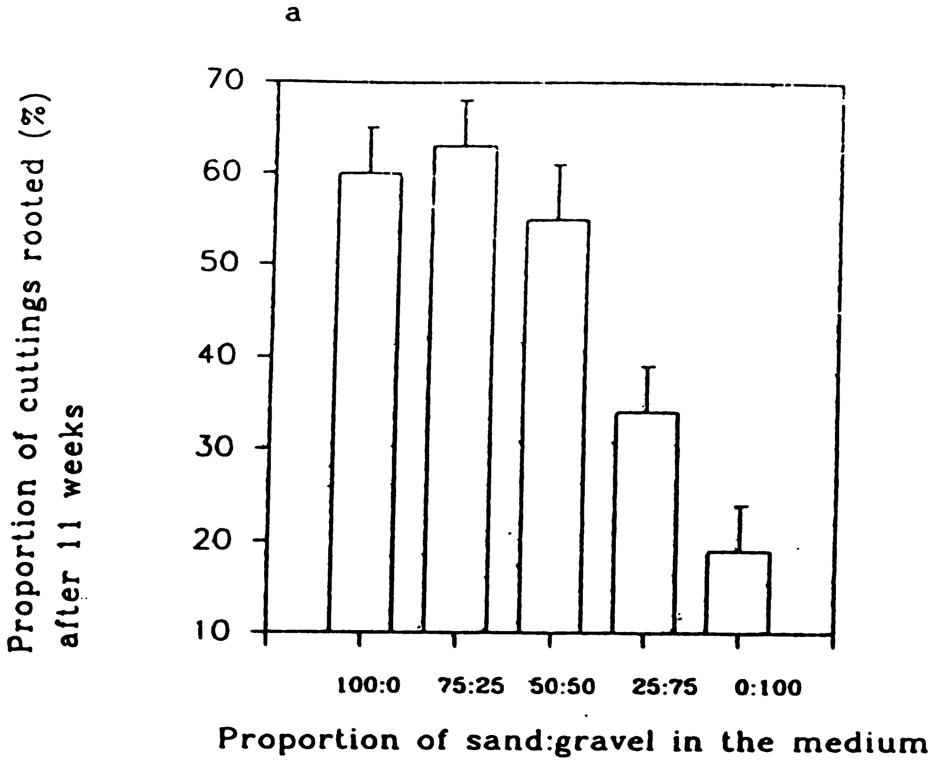
To date, more work has been done to develop techniques of rooting stem cuttings in African Mahogany (*Khaya ivorensis*) and African Walnut (*Lovoa trichilioides*) (Tchoundjeu, 1989; Z. Tchoundjeu and R.R.B. Leakey, in preparation) than in the neotropical members of the Meliaceae, although a number of different species of both the wet and dry tropics have been successfully propagated vegetatively (Table 1). From these reports from West Africa and elsewhere, it is clear that existing techniques are applicable to *Swietenia* spp. and to *Cedrela odorata* (see Leakey *et al.*, 1982; Newton *et al.*, 1991; Mesén *et al.*, 1992; Howard *et al.*, 1988).

Much is now known about the physiology of rooting and how to manage juvenile stockplants to maximize and sustain good rooting ability, in the relatively fast growing, light demanding tropical hardwoods such as *Triplochiton scleroxylon* (Leakey, 1983;

Table 1. Species of the Meliaceae which have been propagated vegetatively (by macropropagation)

Azadirachta indica	Leakey *et al.* (1982)
Carapa procera	Dick *et al.* (1992)
Cedrela odorata	Addei (1977)[a]
	Britwum (1970)[a]
	Howland and Bowen (1977)
	Leakey *et al.* (1982)
Entandrophragma angolense	Dick *et al.* (1992)
Khaya anthotheca	Dick *et al.* (1992)
Khaya ivorensis	Tchoundjeu (1989)
	Asanga (1989)
Khaya senegalensis	Dick *et al.* (1992)
Lovoa trichilioides	Tchoundjeu (1989)
Melia azedarach	K. Milimo (unpublished)
Melia volkensii	Dick *et al.* (1992)
Swietenia humilis	J.F. Mesén (unpublished)
Swietenia macrophylla	Mesén *et al.* (1992)
	Howard *et al.* (1988)
Swietenia mahagoni	Leakey *et al.* (1982)
Toona ciliata	Leakey *et al.* (1982)

[a] Propagation by leafy cuttings by air layering. Hybrid material of *Swietenia* has also been propagated successfully (Howard *et al.*, unpublished data; J.F. Mesén, 1988).



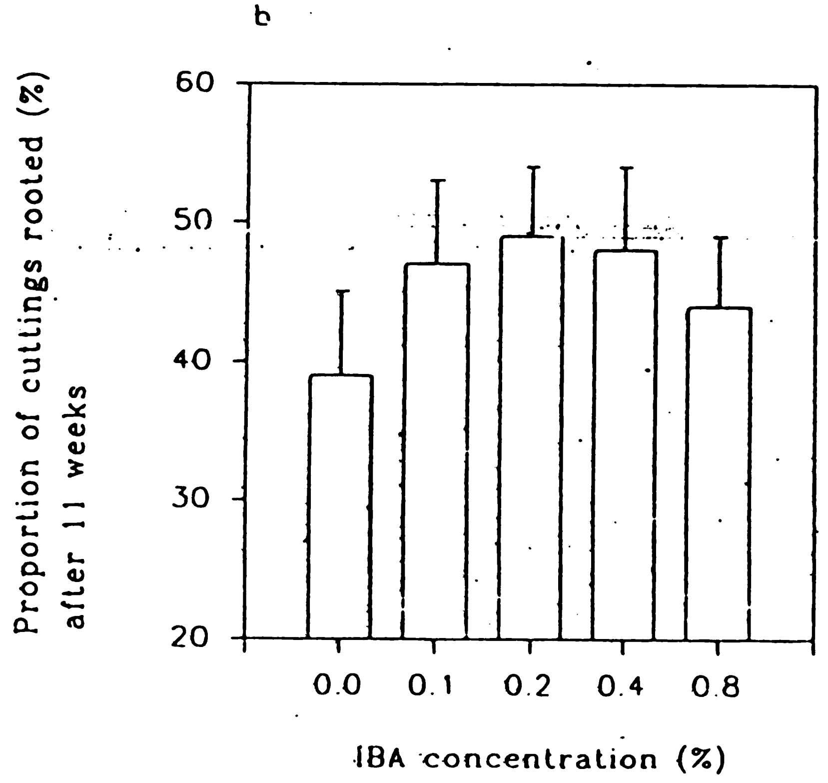


Fig. 2. The effect of variation in (a) the composition of the rooting medium and (b) IBA concentration on the rooting of *Swietenia macrophylla* leafy cuttings, in a non-mist propagator in Turrialba, Costa Rica. Data represent the final assessment 11 weeks after insertion. Vertical bars represent SEM. Data reproduced from Mesén *et al.* (1992).

increasing the availability of commercially acceptable planting stock, which preferably would display some degree of pest resistance. This same material would then be ideal for a future breeding programme aimed at improving pest resistance, and perhaps incorporating several forms of resistance into new progenies. A breeding programme should take into account the fact that the *Swietenioideae* are monoecious and little is known about their incompatibility systems (Styles and Khosla, 1976), although at least under experimental conditions, self-pollination can apparently occur (Yang, 1965; see Styles and Khosla, 1976). In a breeding programme it would be necessary to include growth parameters so that, for example, pest resistant lines could be screened for growth rate/yield and other attributes such as wood quality. Throughout such a programme it would be very important to establish a germplasm bank, incorporating as much of the genetic variation as possible (see Leakey, 1991 for a strategy for clonal approaches to tree improvement). Use should be made of the potentail to hybridize between species, as this can increase the genetic variation within the population. It is important to remember, however, that hybrids can be infertile or may not breed true, so that a complex programme of back-crossing may be necessary to maintain genetic improvements and diversity.

Conclusion

It is clear from this review of genetic variation that any conservation strategy for the mahoganies should include a well coordinated tree improvement/breeding programme as well as the protection of natural stands *in situ*. This programme should incorporate both new cloning techniques and traditional tree breeding, with an intensive programme of genetic exploration, inventory and testing, and would require a permanent and secure location with reliable long term funding. Such a programme would enable *ex situ* conservation of desirable or endangered genotypes in germplasm banks, and should increase the availability of commercially acceptable planting stock with enhanced resistance to shoot borer attack. We believe that a genetic conservation strategy following these guidelines is urgently required, if mahogany is to be maintained as a commercial resource into the next century.

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The mahogany shoot borer: prospects for control

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ABSTRACT

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The mahogany shoot borers (*Hypsipyla* spp.) are among the most economically important insect pests in tropical forestry, virtually preventing the cultivation of mahoganies (*Swietenia* spp., *Khaya* spp. etc.) in their native areas. Attack results in destruction of the apical shoot, causing deformation or branching of the tree, and significantly reducing the economic value of the timber. Although mahogany shoot borers have been intensively investigated from an entomological standpoint, no consistently effective control methods currently exist. This review describes those aspects of previous research relevant to the development of control methods, firstly by providing background information on the behaviour of both the hosts and the pests. Three main control methods are then considered: silvicultural, chemical and biological. Examples of investigations where some degree of control has been achieved are highlighted, and the prospects for selecting for resistance are discussed. On the basis of previous experience, it is suggested that an integrated method of pest management might be achieved by the incorporation of pest resistant planting stock in silvicultural systems which encourage natural biological control.

INTRODUCTION

Attack by mahogany shoot borers (*Hypsipyla* spp.; Lepidoptera: Pyralidae) is the overriding factor restricting the establishment and cultivation of many tropical members of the Meliaceae (Entwhistle, 1967; Food and Agriculture Organization (FAO), 1958, Whitmore, 1983). Some of the most highly

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valued tropical timber species are included in this family, including *Swietenia* spp. (mahogany), *Cedrela odorata* L. (Spanish cedar), and *Khaya* spp. (African mahogany). All of these species are attacked by shoot borers, along with members of other economically important genera such as *Toona*, *Entandrophragma* and *Lovoa* (Grijpma, 1976). The problem is endemic throughout the tropics, particularly where these species are planted in homogeneous stands.

The current high value and high demand for mahoganies (Read, 1990), together with the continuing rapid depletion of natural stands (Collins, 1990), increases the need for effective pest control measures. A number of previous attempts have been made to apply various biological, chemical and silvicultural control methods (Grijpma, 1973a, b, 1974; Whitmore, 1976a, b), but these have largely failed to reduce shoot borer damage to economically acceptable levels.

Rather than present a comprehensive account of the problem of shoot borers in the silviculture of tropical mahoganies, the aim of this review is to describe previous research relevant to the development of practical control methods. The review first provides background information on the behaviour of both the hosts and the pests; and then considers three main control methods: silvicultural, chemical and biological. From previous experience of these three approaches, suggestions are made as to how an integrated method of control might be achieved.

CHARACTERISTICS OF THE MELIACEAE

Meliaceous trees are found throughout the tropics, and include a range of economically important genera (such as *Cedrela*, *Swietenia*, *Khaya*, *Lovoa*, *Toona*, *Guarea*, *Carapa*, *Entandrophragma*, *Chukrasia*). The taxonomy of the family is described in two recent monographs (Pennington and Styles, 1975; Pennington, 1981). Most species in this family have a high degree of internal variability, as they are often members of either closely related pairs or groups of species, which in some cases are interfertile (Styles in Pennington, 1981). For example, naturally occurring hybrids of *S. humilis* Zuccarini × *S. macrophylla* King occur in NW Costa Rica (Holdridge and Poveda, 1975; Whitmore, 1983), and the hybrid between *S. macrophylla* and *S. mahagoni* (Linnaeus) Jacquin has arisen spontaneously on a number of Caribbean islands (Whitmore and Hinojosa, 1977; Styles in Pennington, 1981). Chromosome races have been identified in *Swietenia* as well as other genera of Meliaceae (Styles and Vosa, 1971; Styles and Khosla, 1976).

Although a large number of species in the family have economic potential as timber trees, only a few are used extensively for timber production; for example, principally *Cedrela* spp. and *Swietenia* spp. are used in the neotropics. Many of the desired Meliaceae can reach diameters up to 2.0 m and heights of over 40 m in favourable conditions (Pennington and Styles, 1975). The wood is principally used for furniture and veneers; it is easily worked and strong for its weight (Lamb, 1966). Rotation cycles of around 40 years are thought appropriate for production of commercial timber, if the site is of good quality and shoot borer attacks can be controlled (Vega, 1976; Bascope et al., 1957). In natural forest, mahoganies of harvestable size usually occur at the relatively low densities of one to six trees ha^{-1} (Lamb, 1966). Extensive pure mahogany plantations thus represent an unnatural situation (Grijpma, 1976). Species differ in their silvicultural characteristics; for example, *Cedrela odorata* Linnaeus is a fast-growing pioneer species (Pennington and Styles, 1975), whilst *Swietenia macropyhlla* is considered to be somewhat more shade tolerant (Marshall, 1939; Lamb, 1966). Meliaceous trees are found in a variety of different situations, from predominantly dry forest (e.g. *Swietenia humilis*, *Khaya senegalensis* (Desr.) A. Juss) through to seasonally dry or moist forest types (*Swietenia macrophylla*, *Khaya ivorensis* A. Chev.; Pennington and Styles, 1975).

In many genera (e.g. *Cedrela*, *Swietenia*, *Khaya*) the trees are deciduous, generally producing new flushes of leaves once a year. Individuals vary in the timing of leaf fall, fruiting and flushing (Grijpma, 1974).

Populations of mahoganies have been severely depleted in recent years by selective extraction and general deforestation (Lamb, 1966; Betancourt, 1987; Collins, 1990; Foster, 1990). In many species, large trees of good form are now rarely found. For example, *Swietenia mahagoni*, which was once the most commercially favoured species of mahogany, is now most commonly seen as a short, highly branched tree or bush (Pennington and Styles, 1975; Styles in Pennington, 1981). This is perhaps one of the most striking examples of genetic erosion of a tropical forest tree species. The conservation of remaining mahogany populations is now considered to be a high priority (Lamb, 1966; Whitmore, 1981; Knees and Gardner, 1983a, b; Oldfield, 1988; Read, 1990; Newton et al., 1992).

CHARACTERISTICS OF *HYPSIPYLA*

Taxonomy and distribution

The taxonomy of American *Hypsipyla* spp. is relatively well known (Heinrich, 1956; Becker, 1971, 1973); the species from other tropical regions are less well defined (Entwistle, 1967; Bradley, 1968). The two most important species with respect to activity as shoot borers are *Hypsipyla grandella* (Zeller) and *Hypsipyla robusta* (Moore). *H. grandella* is found throughout Central and South America (except Chile), and also occurs on many Caribbean islands and the southern tip of Florida (Entwistle, 1967). *Hypsipyla ferrealis* (Hampson) is less widely distributed in tropical America, where it exclusively attacks the fruit of *Carapa guianensis* Aublet. The closely related *H. robusta* (Moore) is widely distributed throughout West and East Africa, India, Indonesia, Australia and South East Asia (Entwistle, 1967). Bibliographies on *Hypsipyla* have been compiled by Tillmans (1964) and Grijpma and Styles (1973) (see also Whitmore, 1976a, b).

H. grandella and *H. robusta* are associated exclusively with the Meliaceae. Although it has been stated that *H. grandella* will attack any member of the family (Browne, 1968), most authors consider that attacks by both species are limited primarily if not completely to members of the subfamily Swietenioideae (Grijpma, 1976). The observations that *H. grandella* attacks *Guarea trichilioides* L. (Huguet and Marie, 1951) and *Trichilia* spp. (Huguet and Verduzco, 1952) (both members of the Melioideae) may represent misidentifications, although Ramirez Sanchez (1964) established that *H. grandella* collected from *Cedrela* shoots will continue to feed normally on shoots of *G. trichilioides*. Species of commercial importance that both *H. grandella* and *H. robusta* are known to attack include *Carapa guianensis*, *Cedrela odorata*, *Khaya senegalensis*, *K. ivorensis*, *S. macrophylla*, *S. mahagoni* and *Toona ciliata* M. Roem. (Beeson, 1941; Martorell, 1943; Tillmans, 1964; Entwistle, 1967; Browne, 1968).

Life cycle characteristics

The biology of *H. grandella* is known in some detail (Ramirez Sanchez, 1964; Roovers, 1971); less information is available concerning the life history of *H. robusta* (Roberts, 1968, Wagner et al., 1991) although the two species appear to behave similarly. The total life cycle of both species usually lasts between 1 and 2 months, depending on climate and food availability (Beeson, 1941; Roovers, 1971; Morgan and Suratmo, 1976). In *H. grandella*, oviposition occurs during evening or early morning, and egg eclosion occurs at night (Wilkins, 1972; Holsten, 1977). An individual female lays one to seven eggs at a time on one or more plants, and may repeat oviposition over a period of about 6 days, laying 200–300 eggs in all (Grijpma, 1971; Samaniego and Sterringa, 1976). Eggs are laid singly, or occasionally in clusters of three to four, on or near leaf axils, scars or veins (Ramirez Sanchez, 1964; Grijpma, 1971; Roovers, 1971). Usually only one to three eggs are laid on each tree (Grijpma, 1974).

The eggs hatch after around 3 days. The newly hatched larvae are small and highly mobile; they move towards new shoots and burrow into the stem or leaf midrib, often at the leaf axil. After 2–4 days those larvae that have invaded leaves or small side shoots, reemerge and migrate to the terminal shoot of the stem or main branch (Ramirez Sanchez, 1964; Roovers, 1971; Sliwa, 1973). About 3 days after penetration, the larvae cover their entrance holes with a protective web which is covered with plant particles and frass (Grijpma, 1974). The remainder of the larval stage is spent boring into the primary stem or branches of the tree, feeding on the pith. The combined duration of the five or six larval stages is around 30 days (Ramirez Sanchez, 1964; Roovers, 1971). Around 10% of this time is spent on the surface of the plant, in web building and moulting activities (Sliwa, 1973). The larvae can adapt to a lack of green shoots by feeding on subcortical tissue, sometimes boring into thick bark. They have also been observed feeding on young leaves brought together in webs (Ramirez Sanchez, 1964; Lamb, 1966; Wilkins, 1972).

The larvae usually pupate in the galleries bored into the tree stem, but may also do so in the soil beneath attacked trees (Sliwa, 1973). Later instar larvae spin a cocoon at the upper end of the tunnel where they pupate. Most adults emerge during sunset, after pupating for 8–10 days; a 1:1 sex ratio is common (Roovers, 1971; Sterringa, 1973; Sliwa and Becker, 1973). The duration of the adult stage in captivity is about 8 days for females and 6 days for males (Roovers, 1971). Courtship activities are minimal; males are attracted to the females, which adopt a calling position (with the abdomen bent upwards between the wings) lasting on average 1.6 h. Mating lasts between 1.5–3 h, and is followed by oviposition (Grijpma, 1971; Samaniego and Sterringa, 1973).

The adult moth is nocturnal. Peak flight activity occurs between 24:00 and 05:00 h; flight activity ceases when temperatures fall below 15°C and during high precipitation (Gara et al., 1973). Although the adult insects are able to fly many kilometers (Fasoranti et al., 1982), the moths apparently do not disperse readily from areas of active infestation (Grijpma and Gara, 1970a). *H. grandella* appears to orientate itself to its host plant by means of chemoreception (Grijpma and Gara, 1970b; Gara et al., 1973). Although the nature of the attractants emitted by the plant is unknown, preliminary results suggest that sesquiterpenes may be involved (Carruyo, 1973, 1976). The preferred host and phenological state of the plant are probably selected by virgin females (Gara et al., 1973; Holsten and Gara, 1977). Males are subsequently attracted to the females by a sex pheromone (Holsten and Gara, 1974). The composition of this pheromone is not known, but that of *H. robusta* consists of a mixture of tetradecenyl acetates (Bosson and Gallois, 1982).

Females are particularly attracted to new foliage for oviposition (Grijpma and Gara, 1970a) and also exhibit definite preferences for certain Meliaceous species. For example, Grijpma and Gara (1970a) demonstrated that field-collected *H. grandella* prefer *C. odorata* to *S. macrophylla* as host plants; in addition, females were not attracted to *Toona ciliata*. Preferences for certain species are also exhibited by the feeding larvae (Roovers, 1970, 1971; Grijpma and Gara, 1970b; Morgen and Suratmo, 1976).

The number of generations a year varies with variations in climatic conditions and availability of new shoots. In areas which are wet all year round, the insects are able to attack continuously, as the young trees repeatedly resprout. In areas with a pronounced dry season, attacks switch from shoots to fruits during the dry period when no unlignified shoots are available (Grijpma, 1974). Attacks are more numerous in the rainy season, when new shoots are produced (Beard, 1942; Burgos, 1954; Ramirez Sanchez, 1964; Morgan and Suratmo, 1976). Grijpma and Gara (1970a) recorded an increase in *Hypsipyla* flight activity 3–4 days after rain, corresponding with the production of new shoots. In Florida, larval populations coincide with the spring flush of mahogany foliage (Howard, 1991).

Characteristics of damage

Damage to the tree is caused by the larval stage hollowing out the softer shoots, often causing shoot mortality. As a consequence of the death of the leading shoot, overall growth is reduced and branching may occur, producing a forked or poorly formed tree. Although attacks do not normally cause death, repeated attacks can kill the tree (Whitmore, 1976c; Dourojeanni, 1963; Chable, 1967; Browne, 1968). Trees may be attacked whilst still in the nursery, and may continue to be attacked until maturity (Grijpma, 1974). Young trees are particularly affected by shoot borer damage because of the dependence of growth on the apical meristem; attacks up to pole stage are most critical from a silvicultural point of view (Kalshoven, 1926; Lamb, 1966; Grijpma, 1974).

Even though shoot borer attack rarely kills the plant, the economic losses can be considerable. As a result of *Hypsipyla* attack, attempts to use *Cedrela* for reforestation in Puerto Rico were abandoned, as between 1935 and 1943 835 000 *Swietenia* and 1 000 000 *Cedrela* trees were effectively destroyed by shoot borers (Strong, 1940; Martorell, 1943). *Hypsipyla* is considered to be a major limitation to planting *Swietenia* throughout the Caribbean (Martorell, 1943; Ramirez Sanchez, 1964; Bauer, 1987). In the Peten district of Guatemala, 250 ha of *Swietenia* and *Cedrela* were decimated within 2 years of planting (Grijpma, 1974; Holsten, 1977). In Tingo Maria, Peru, 10% of *Swietenia* and 60% of *Cedrela* were attacked within 4 months of planting (Dourojeanni, 1963). Of 1 800 000 *Cedrela* seedlings provided by nurseries in Cuba to private farmers, an estimated 90% died, at least partly as a result of shoot borer damage (Fors, 1941, 1944; Roig, 1945, 1946). In India, large scale reforestation with *Toona* was abandoned following attacks by *H. robusta* (Rao and Bennett, 1969). In Ghana, when *Khaya ivorensis* is planted, up to 100% of the stand is commonly affected by shoot borer damage (Atuahene, 1972). As a result, planting of mahogany has been almost completely abandoned in both Ghana and Nigeria (Wagner et al., 1991).

SILVICULTURAL CONTROL

A wide range of different silvicultural approaches have been applied to the production of the meliaceous tree species which are susceptible to shoot borers. Most have resulted in failure, as noted earlier. However, there are examples of trials where shoot borer damage has been at least partially controlled by cultural methods. Most of these trials involve establishment of meliaceous trees with other trees or crops, either in mixed plantations with non-susceptible tree species, agroforestry systems such as taungya, or enrichment planting. Some of these successful examples are described here, along with an analysis of the possible reasons for their success. In addition, the prospects for selection of species or races which are resistant to attack are also discussed.

Experience with mixed and enrichment planting

In the Luquillo mountains of Puerto Rico, about 1275 ha of *Swietenia* was planted up until 1981, as the result of a programme organised by the US Forest Service. These trials were described in detail by Weaver (1987) and Weaver and Bauer (1986) following their evaluation in the early 1980s. In the earlier plantings, seeds were planted at 3 m × 3 m spacing under the canopy of a secondary forest which was gradually poisoned. Later plantings were established as lines; trees were spaced 2 m apart within rows, and 11 m apart between rows. The mean annual height increases were in the range 0.7–1.0 m, dependent on topography, with growth rates being lower on ridges. The basal area around individual trees also influenced height growth and diameter in the 1974 plantings (Weaver and Bauer, 1986).

Shoot borer damage was found on 58%, 11% and 18% of the trees planted in 1974, 1979 and 1980, respectively. No significant relationships between the incidence of shoot borer damage and surrounding crown class or basal areas were apparent. The 1974 planting displayed less damage on ridges than on other topographic features; this was attributed to the possible effect of wind on moth dispersal (Weaver and Bauer, 1986). Although shoot borer atacks were not eliminated completely, damage was reduced to acceptable levels in most of the plantings. As a result, Weaver and Bauer (1986) suggested that spacing mahogany at 11 m × 15 m and interplanting with other commercial species could yield about 60 trees ha^{-1} and might alleviate the shoot borer problem considerably; overall, line planting was adjudged to be the ideal method for mahogany establishment.

Vega (1976) described in detail the results of a series of trials in Surinam, involving establishment of *Cedrela* spp. in natural regeneration, line enrichment and open plantation systems. The enrichment trials were intensively managed during the first four years after establishment, by opening the canopy above the planted trees, clearing lianes and weeds, utilising lateral shade, and pruning the lateral branches of the planted trees. The proportion of plants attacked by shoot borers was found to vary with plant height, with highest proportions generally recorded when the plants were between 1 and 2 m tall. After 2 years, the proportion of plants attacked was higher in plantations established in the open (10–60% attacked, depending on size class), than in enrichment plantings (4–40% attacked). In other enrichment trials, the proportion attacked was less than 10% after 22 months. Eventual yields of 150–270 m^3 ha^{-1} were estimated in a 35-year commercial rotation, based on the growth during the first 7 years.

In trials established in Brazil, Yared and Carpenezzi (1981) reported that shoot borer damage was virtually absent in the line enrichment system employed ('recru'). *Swietenia macropyhlla* was established in a 25 year-old secondary forest, from which the undesirable trees were removed. Mean annual increment in height over the first 4 years was between 1.4 and 1.9 m, comparing favourably with plantations established in the open. The absence of shoot borer damage was attributed to a combination of low initial planting density (less than 100 trees ha^{-1}), the presence of lateral shade, and the maintenance of some of the ecological conditions of the original forest (such as floristic diversity and microclimate). It has been suggested previously that these latter factors are of importance (Catinot, 1965; Dubois, 1971), although as stated by Yared and Carpenezzi (1981), the scientific reasons for this are unclear.

Hypsipyla was also successfully controlled in the Columbia River Forest Reserve of Belize, between 1955 and 1964. *S. macrophylla* was direct sown with maize in a taungya system, at a spacing of 9 m × 9 m. The remaining 200 ha of the original 700 ha were inventoried by Wilson in 1981 (cited by Palmer, 1988). The contribution of *Swietenia* varied from 8 to 26% by volume, and from 52 to 188 trees ha^{-1}. The success achieved in these trials was attributed to good species–site matching and early maintenance, including weed control (Palmer, 1988).

In a trial plantation in Costa Rica, lines of *Cedrela tonduzii* have been planted between three lines of *Cordia alliodora*. After 10 years, the proportion of *Cedrela* trees damaged by shoot borer attack was less than 10% (Hilje et al., 1991). Similar designs have been tested on a larger scale in Guatemala, with *Swietenia macrophylla* and *Cedrela odorata* interplanted between rows of *Cybistax donnell-smithii* and *Tabebuia microphylla*. Again, after 7 years growth, the proportion of trees attacked was less than 10% (Hilje et al., 1991).

The Forestry Department of Nigeria have also employed mixtures as an attempt to control shoot borers silviculturally. When the nurse crop (usually *Nuclea diderichii* de Wild and Th. Dur. or *Gmelina arborea* Roxb.) and the mahogany were planted in pure lines, there was little evidence of control, but when shade trees and Meliaceae were planted in the same line some degree of control was obtained (Roberts, 1968). Entwhistle (1967) also recommended the taungya systems used in Nigeria, which involved planting with a cover crop in a ratio of 1:5, giving a mixture of species in each row.

The examples described above share certain features in common: growing the mahoganies in mixtures with other species seems to have afforded some degree of protection. The reasons for this are unclear; there are very few data concerning the impact of different silvicultural systems on shoot borer populations or patterns of attack. Despite this lack of information, successful silvicultural control has been attributed to three main processes: the effects of (1) shading; (2) low density of susceptible species; (3) growth rate.

The effects of shade

Although this aspect has received a great deal of attention, the situation is confused. For example, Entwistle (1967) concluded from a wide-ranging survey that the presence of overhead shade minimises attack. Beeson (1941) indicated that mahogany can be raised with a minimum of damage using a shade tree crop and planting the mahogany in dense lines. Similarly, Campbell (1966) stated that about 50% shade is needed to reduce borer infestations, so as to permit acceptable growth of *Toona ciliata* var *australis*. A number of other authors have stated that shoot borer attack is reduced when the trees are grown under partially shaded conditions (Kalshoven, 1926; Holdridge and Marrero, 1940; Lamb, 1966).

In contrast, Whitmore (1976c) observed that shaded seedlings are in fact attacked by shoot borers. This viewpoint is supported by a range of evidence. For example, Chable (1967) stated that in Honduras, *Hypsipyla* damage is widespread regardless of whether mahogany trees are grown in the open or in heavy shade. Similarly, Roberts (1966) and Tillmans (1964) both found that shade or cover did not reduce attack by *Hypsipyla*, and Combe and Gewald (1979) described a high incidence of *Hypsipyla* attack under heavily shaded conditions, in trial plots of *Swietenia* planted under *Gmelina arborea* and *Cassia siamea* Lam. in Costa Rica.

These apparently conflicting reports may be explained by the contrasting effects of overhead and lateral shade. Young trees of *Swictenia* and *Cedrela* are highly intolerant of overhead shade (Noltée et al., 1926; Lamb, 1960, 1966, 1968; Fors, 1941), and plants grown in such conditions are presumably less able to recover after attack. It has been suggested that lateral shade reduces the growth and production of branches and promotes growth of the leader (Aubreville, 1953; Yared and Carpenezzi, 1981), thereby also reducing the number of sites available for attack (Entwistle, 1967; Grijpma, 1976).

The effects of planting density

In some cases, the effects of growing meliaceous species in mixtures cannot simply be attributed to the effects of shade. Dourojeanni (1963) described plantations of *Cedrela* in Peru which were initially heavily attacked by shoot borers, but recovered after weed control was abandoned. The trees subsequently developed into straight saplings. Similar results have been obtained in Costa Rica (Grijpma, 1974), although the form of the trees in this case was poor. Holdridge (1943) favoured the establishment of *C. odorata* without shade, and hoped to avoid shoot borer attack by employing wide spacing.

He recommended that no more than ten *C. odorata* trees ha^{-1} should be brought to maturity. This system was based on the supposition that by planting at densities similar to those in natural forests, where meliaceous trees are able to grow successfully, the seedlings may largely escape attack.

Such results have led to the suggestion that low planting densities may contribute to shoot borer control (Beard, 1942; Holdridge, 1943; Cater, 1945). This may operate in a number of ways. For example, it has repeatedly been suggested that the presence of other tree species may hinder location of meliaceous trees by the adult moth (Grijpma, 1976; Morgan and Suratmo, 1976). Very little precise information is available to indicate whether this process actually occurs (c.f. Gibson and Jones, 1977; Kareiva, 1983). As noted earlier, the pattern of dispersal of the adult moths is poorly understood. The evidence suggesting that host selection is primarily by olfaction, and that the moths tend not to disperse away from sites of infestation (Grijpma and Gara, 1970a) is clearly of relevance in this context. Low densities of susceptible trees may therefore prevent build-up of moth populations (Weaver and Bauer, 1986; see also Watt, 1992). Further research is needed to establish whether these processes actually operate, both in natural forest, and in different planting mixtures and densities (Grijpma, 1976). In Colombia, when *C. odorata* was planted in different mixtures with *Tabebuia rosea* Bertola and *Cordia alliodora* (Ruiz and Pav.) Oken, shoot borer attack was found to occur at the same intensity in each case (Neyra and Martinez, 1985).

The importance of growth rate

The relationship between growth rate of the tree and shoot borer attack is another aspect which has been subject to conflicting viewpoints. Lamb (1968) suggested that slower growing trees are more susceptible to attack, as they are less able to inhibit shoot borer activity through production of resins. In contrast, in a provenance trial of *C. odorata*, Whitmore (1978) found a direct relationship between height growth and borer attack; faster growing trees were attacked more often. Similar correlations have been recorded by Ramnarine (1992a). This may be attributed to the fact that the insects select newly produced shoots for oviposition (Gara et al., 1973); faster growing trees would produce more susceptible sites.

The production of resins as a defence mechanism has been noted by a number of authors (Wilkins, 1972; Styles in Pennington, 1981). However, little information is available concerning its effectiveness in countering shoot borer attacks. If resin flow is greater in more vigorous trees (Lamb, 1968), then this may enable them to better withstand attack, as noted by Whitmore (1978). Trees which display higher vigour are also better able to recover after attack, by producing strong apical growth (Grijpma, 1976).

As site quality is a prime determinant of growth rate, a relationship between site quality and susceptibility to attack is expected. *Swietenia* spp. are more susceptible to attack planted on poor soils and unfavourable sites (Holdridge and Marrero 1940; Marie, 1949; Huguet and Marie, 1951). Entwhistle (1967) suggested that site quality may also influence the quantity and quality of available shoots. Site interactions are particularly evident in the case of *C. odorata*: for example, Cater (1945) noted that numerous attempts to grow *Cedrela* in Caribbean countries has ended in failure as a result of site effects. The main problem appears to be that *Cedrela* spp. are intolerant of poor drainage and compacted soils, and perform best on freely draining soils or ridgetops (Marshall, 1939; Holdridge, 1943; Entwistle, 1967). The importance of good species/site matching for successful cultivation of Meliaceae has been stressed repeatedly (Whitmore, 1978; Palmer, 1988).

The relative importance of the three factors described above is difficult to ascertain, as to some extent their effects are interactive. For example, growth rate of the trees will be influenced by planting density and the degree of shade. In addition, planting in mixtures or in enrichment plantings may reduce the incidence of attack in other ways. Yared and Carpenezzi (1981) suggested that maintenance of the microclimate and florisitic diversity of the original forest may be beneficial, although the reasons for this are unclear. Maintenance of soil fertility or populations of natural predators (Gibson and Jones, 1977; Watt, 1992) may be contributory factors. We are aware of no information concerning the behaviour of *Hypsipyla* populations in natural forest.

It should be emphasized that the planting of mahoganies in mixtures with crops or non-susceptible species does not guarantee successful shoot borer control. Detailed research in Colombia, utilizing a range of silvicultural and agroforestry systems, has failed to identify an appropriate system for effective control (Neyra and Martinez, 1985; Vega, 1987). These results emphasize the need to view silvicultural control as one component of a system of integrated pest management.

Selecting for resistance

Another silvicultural approach which offers promise as a means of controlling *Hypsipyla* is to select for resistance: this may involve the inclusion of resistant species in planting programmes, or the selection for resistant strains within a susceptible species. Of these two approaches, the first has received most attention. The second option constitutes one aspect of a genetic improvement programme; as few attempts at genetic improvement of mahoganies have been made, we describe here the prospects for this approach.

An understanding of the mechanisms of resistance is important if resistant trees are to be developed or utilised successfully in silviculture. In discussing resistance, it is helpful to define the terminology, as these terms have had a number of different uses in the past. Resistance is here defined as the ability of trees (either species or individuals) to grow and develop normally even when attacked by pests (Zobel and Talbert, 1984). Resistance may arise as a result of three factors (Painter, 1951; Gerhold, 1962; Van Emden, 1987): (1) antixenosis (= non-preference), in which plant is avoided or less colonized by pests; (2) antibiosis, in which the plant possesses some property which affects the performance of the pest in terms of growth, survival etc.; (3) tolerance, in which the tree recovers from insect attack to an acceptable level.

Susceptibility is a measure of how much the tree is attacked by the insect (Henson et al., 1970). Escape is when a tree avoids attack altogether, by chance; such a tree may falsely appear to be resistant.

Resistant species

Resistant species of Meliaceae certainly exist; for example, as stated earlier, most members of the Melioideae are not attacked by shoot borers. This group includes some desirable timber species, such as *Guarea* spp. and *Melia* spp. It has repeatedly been suggested that greater attention should be paid to these species in the future, as potential plantation trees (Grijpma, 1976; Styles in Pennington, 1981; Weaver, 1987; Palmer, 1988). The basis of the resistance of these species presumably lies in their antixenosis.

Within the Swietenioideae, exotic Meliaceae have often been found to be less susceptible than indigenous species to attacks of native *Hypsipyla* spp. (Chable, 1967; Lamb, 1968; Grijpma and Ramalho, 1969). This has enabled a number of mahogany species to be grown successfully in areas where they are not native, such as SE Asia and the south Pacific in the case of *Swietenia macrophylla* (Evans, 1982; Whitmore, 1992). In the neotropics, particular attention has been paid to *Toona ciliata* var *australis* (F. v. Muell.) C.DC., an Asian and African species closely related to *Cedrela*. Although heavily attacked by *H. robusta* when grown in its native habitat, this species is not attacked by *H. grandella* when planted in Central America (see Whitmore, 1976c). *H. grandella* larvae die when they are fed stems of *Toona*, or when exposed to volatiles emanating from it (Gripjma and Gara, 1970b). This suggests that there may be a biochemical basis to the resistance of *Toona* to *H. grandella*, an example of antibiosis. A similar mechanism may account for the apparent resistance of *C. odorata* to *H. robusta*, although observations suggest that this may be a case of antixenosis ('non-preference') (Roberts, 1966).

Grijpma and Roberts (1975) showed that the chemical compounds responsible for resistance of *Toona* can be translocated to *C. odorata* shoots grafted onto *Toona* rootstocks; the *Cedrela* then becomes toxic to larvae. Aqueous extracts of dried *Toona* leaves have been demonstrated to deter feeding and retard growth of *H. grandella* in laboratory tests (Grijpma and Roberts, 1975). Grijpma (1976) suggested that the toxic water-soluble extracts of *Toona* may be alkaloids, which have been extracted from *Toona* and *Cedrela* (Smolenski et al., 1972, 1974). Both *Cedrela* and *Toona* also contain limonoids, many of which are powerful insecticides and feeding deterrents (Kubo and Klocke, 1986). These chemicals are non-volatile, water insoluble, and derived from triterpenes. Cedrelone, a limonoid isolated from *Toona*, was the second-most powerful insect growth inhibitor of the 18 limonoids tested by Kubo and Klocke (1986). Such a substance may also account for the interference of *Toona* extracts on moults and pupal wing development observed by Grijpma and Roberts (1975). The existence of these toxic compounds suggests that there may be scope for breeding resistant Meliaceae in the future, although the relationship between these different chemicals and *Hypsipyla* attack is still obscure (Grijpma, 1976).

In some areas, introduction of exotics such as *Toona* may not be desirable, or indeed possible. For example, a number of trials of *Toona ciliata* were established at CATIE in Costa Rica during the 1960s and 1970s, as this species was thought to be resistant to *H. grandella*. Despite showing excellent early growth, the trees began to display dieback after 2–3 years, and subsequently the trials failed completely (Otárola et al., 1976; Sanchez et al., 1976). This may reflect some incompatability with either soil or climatic factors, and serves to illustrate that exotic species may behave unpredictably when introduced to new areas.

In such circumstances, indigenous species may be preferred. Within the Swietenioideae, species which are indigenous to a region exhibit differences in susceptibility to shoot borer attack. In Puerto Rico, *S. mahagoni* is less susceptible to attack than *S. macrophylla*; the hybrid between these two species is intermediate (Whitmore and Hinojosa, 1977). Grijpma (1970) reported that *H. grandella* shows a preference for *C. odorata* over *S. macrophylla*, *S. humilis* and *S. macrophylla* × *S. mahagoni*. Other authors have also reported that *Cedrela* spp. are attacked more often than *Swietenia* spp. (Dourojeanni, 1963; Food and Agriculture Organization, 1958). In Nigeria, Roberts (1966) indicated that *Khaya* spp., particularly *K. ivorensis*, are more susceptible to attacks of *H. robusta*, than species of *Entandrophragma* and *Lovoa*. Interestingly, larvae of *H. robusta* were found to prefer *Swietenia macrophylla* to *Khaya anthotheca* and *Toona sureni*, despite the former species being exotic to this insect (Morgan and Suratmo, 1976). These contrasting susceptibilities may reflect variation in the production of chemical attractants, although differences in growth rate and form may also be influential (Grijpma, 1976).

Resistant strains or races

It has been suggested that resistant individuals or races may exist within wild populations, and that there may be scope for breeding or selecting for resistant Meliaceae (Lamb, 1966; Roberts 1966; Grijpma, 1976). However, few attempts have been made to screen for genetic variation in susceptibility to attack. The main example is provided by the international provenance trials of *C. odorata*, which were coordinated by the Oxford Forestry Institute, UK. The results of these trials are summarised by Chaplin (1980).

In 1967, seedlots of 14 provenances were distributed to 21 collaborating countries for use in preliminary trials (Burley and Lamb, 1971). In the neotropics few trials were successfully established, and problems were experienced with site incompatibility and shoot borer attack (e.g. see Weaver and Francis, 1988). Whitmore (1978) reported no difference between the provenances tested in Puerto Rico in the incidence of attack. Trials in Africa were more successful; results were reported by a range of authors in two sets of conference proceedings (Burley and Nikles, 1973; Nikles et al., 1978). Clear differences in growth were observed between provenances; in general, the most promising provenances originated from Costa Rica and Belize.

Few results have been published from the second phase of trials, which were initiated in 1978 (Chaplin, 1980). In Trinidad, two provenance trials were established; survival was again poor and *Hypsipyla* attacks were severe (McCarter, 1986; Ramnarine, 1992 a, b). However, a provenance from NW Colombia (Apartado — 25/80) grew more vigorously than the other provenances tested, and was able to recover after shoot borer attack. This same provenance also displayed superior growth rate and form in trials in Ecuador and West Africa (McCarter, 1986, 1988). Some other provenances, such as one from Costa Rica (75/79 San Carlos), have also showed potential (McCarter, 1986).

The apparent resistance to shoot borer attack displayed in some of these provenance trials was dependent on the vigorous growth of the young plant, and the reestablishment of a a new leading shoot with strong apical growth after attack (Chaplin, 1980; McCarter, 1986). This is an example of tolerance, as defined earlier. Whilst characteristics such as vigour are influenced by environmental conditions, the fact that the re-imposition of a vigorous dominant leader is under some degree of genetic control (as indicated by results from provenance tests) suggests that there may be scope for selecting strains on the basis of their tolerance (Grijpma, 1976; Styles and Khosla, 1976).

Further evidence of tolerance has been provided by trials with *C. angustifolia* Moc. and Sesse ex DC. This is a species of uncertain taxonomic status (Styles in Pennington, 1981), certainly closely related to *C. odorata* and possibly conspecific with it. This 'species' has repeatedly been found to display a greater ability to recover after shoot borer attack than *C. odorata* (Melchior and Quijada, 1972; Vega, 1976; Sanchez et al., 1976). Again, the basis of tolerance is pronounced vigour and the ability to produce a single strong leader after attack.

Evidence is therefore available for all three mechanisms of resistance in the Meliaceae — antixenosis, antibioisis and tolerance. There may be scope for breeding for resistance based on antixenosis or antibiosis, as noted by Grijpma

(1976). To date, no evidence has been presented for resistant strains within susceptible species based on either of these characteristics (but see Melchior and Quijada, 1972; Newton et al., 1992). Progress in selection may be made more rapidly by selection for tolerance (Chaplin, 1980). This may be made through selections at the provenance, family or individual level. What is required is information on the genetic basis to the variation in tolerance observed.

CHEMICAL CONTROL

Attempts to control *Hypsipyla* by spraying insecticides have repeatedly failed as a result of high rainfall and the fact that the larvae are inaccessible (Gripma, 1974; Allan et al., 1976; Wagner et al., 1991). For example, in Peru, trials with lead arsenate, DDT and Parathion applied at 2 weekly intervals were abandoned as a result of a low success rate and high costs (Dourojeanni, 1963). In Venezuela, Ramirez Sanchez (1966) investigated control of *Hypsipyla* in small plantations of *C. odorata*, by spraying with DDT, metasystox, endrin, aldrin, parathion and combinations of these insecticides. DDT was found to be most effective, but repeated applications at every oviposition period (every 6 weeks) were required for control. This level of application is clearly impractical on economic and ecological grounds (Wilkins et al., 1976).

The effectiveness of controlled release systemic insecticides was investigated in detail by Wilkins et al. (1976). Of a total of 28 different insecticides that were screened, five were found to be particularly effective in terms of pest control and lack of phytotoxicity. These five were tested in a series of field trials at CATIE, Costa Rica. The insecticides were applied in pellet form (consisting of polyamide resin) at planting. Carbofuran was found to be the most effective, giving complete control for 340 days at one of the sites tested. This was accompanied by lower mortality and higher growth rates of the treated trees (Wilkins et al., 1976). However, when a polymer preparation of carbofuran was tested in Trinidad, application of the insecticide was found to be completely ineffective in controlling shoot borer attack (Ramnarine, 1992b).

Controlled release insecticides may provide economical and ecological advantages when compared with conventional spraying (Allan et al., 1976). However, further research is required on the effects of soil and climatic conditions on the effectiveness of the treatments (Wilkins et al., 1976). The uptake and translocation of insecticide during dry periods may be ineffective (Grijpma, 1974). The impact of systemic insecticide/polymer combinations on other insects, parasites and predators also needs investigation (Grijpma, 1974). The main use of systemic insecticides may be as an interim measure, for protecting plants in the nursery, or perhaps as part of an overall programme of integrated pest management (Wilkins et al., 1976).

BIOLOGICAL CONTROL

H. robusta has been studied in the most detail; Rao (1969) and Rao and Bennett (1969) list more than 50 species of parasitoid and predator, including 17 braconids, nine chalcids, one elasmid, one eulophid, one eurytomid, 13 ichneumonids, two trichogrammids, two tachinids, one nematode and two coleopterans. Nearly all of these were found in India from Uttar Pradesh, Punjab, West Bengal and Himachal Pradesh, and they are mostly larval and pupal parasitoids. Most were found in very low numbers, i.e. infestation rates of < 1%. A few were more common, including *Apanteles leptanus*, *Flavopimpla latiannulata* and *Tetrastichus spirabilis*.

Fewer natural enemies have been recorded for *H. grandella* in the New World; Rao and Bennett (1969) could list only 12, including five braconids, two ichneumonids, two trichogrammids, two tachinids and a mermethid. Since then a few more have been found (De Santis, 1972; Grijpma, 1972, 1973a; Nagarkatti, 1973), but there are still considerably fewer than for *H. robusta* though the reason may simply be that less effort has been made to look for them.

It is clear that both in the New and Old World natural enemies do not control *Hypsipyla* populations sufficiently for reafforestation purposes. Thus what are the prospects for biological control of this pest?

Classical biocontrol

This method involves releasing new species of natural enemy to a region in the hope that they will proliferate and control the pest without further human intervention. Over the last century this technique has successfully controlled many pests, though there have also been many failures. In the case of *Hypsipyla*, a serious attempt was made in the 1960s and 1970s to introduce parasitoids from India to Trinidad and other parts of the Caribbean to control this pest (Cock, 1985). It was reasoned that as there were so few natural enemies in Trinidad, one or more exotic species might exert an extra level of control. At first sight this might seem strange, as apparently *H. robusta* is not under adequate control in India. However, it is quite possible that a biocontrol agent, stripped of its own natural enemies (hyperparasitoids, predators and pathogens) could perform better than in its native environment. It is also common for the natural host of the parasitoid to have evolved some immunity to attack, for example by a physiological response to the presence of a foreign egg in its haemocoel; there is a continuing debate amongst biocontrol workers about whether new host–parasitoid associations might be more effective than old ones (Hokkanen and Pimentel, 1989).

In the case of Trinidad at least six species were imported from India, though appreciable numbers of only four species were released: *Tetrastichus spirabilis*

Waterston (Eulophidae) (155 releases of a total of 103 050 over 10 years in eight localities), *Trichogrammatoidea robusta* Nagaraja (118 releases, totalling 35 000 over 8 years in nine places), *Phanerotoma* sp. (Braconidae) (142 releases of 42 540 over 8 years), *Anthrocephalus renalis* Waterston (Chalcididae) (26 releases of 3340). Appreciable numbers of these parasitoids were also released in Belize, Dominica, Grenada, St. Kitts, St. Lucia and St. Vincent (Cock, 1985).

Only one, the egg parasitoid *T. robusta*, has been recovered consistently from the field in Trinidad and can therefore be said to have become established. Infestation rates of this parasitoid vary between 5 and 9%, but there is no evidence that it is having a significant effect. There are many possible reasons for the failure of this project, some of them related to costs and logistics. For instance, analysis of previous classical control projects suggests that the greater the number of a parasitoid species released, the greater the chance of successful establishment (Bierne, 1975). Although the above release figures appear large, they were spread over many years and sites so that individual releases were small, no more then a few hundred at a time; considering the great volume of a mahogany canopy and relative rareness of its host, the parasitoid could have great difficulty finding mates and oviposition sites. Cock (1985) implies that any future *Hypsipyla* project should involve substantial breeding programmes to bulk up the numbers to be released.

Other reasons for failure to establish could be physiological, behavioural or semiochemical differences of the target host. Over the last few years it has become clear that the plant–host–parasitoid relationship is often very complex. Hérard et al. (1988) found that when a parasitoid emerges from its host it may become imprinted on specific chemicals (synomones) in the nearby frass of its host species and thence use that odour to locate a host in which to oviposit. From an unpublished report of introductions in the Caribbean for the years 1966–1975 (Yaseen and Bennett, 1975), it is apparent that *Hypsipyla* host material was often scarce and that alternative host species were used to culture the insects before release. It would seem possible therefore that the emerging insects could have been inadvertently conditioned to look for the wrong host. It may not be coincidental that the only natural enemy to become established was an egg parasitoid that presumably would not become imprinted on frass synomones.

There are still many parasitoids that could be introduced, but the cost to culture *Hypsipyla* on mahogany seedlings to supply the necessary host material to release large amounts of natural enemies could be high. A possible strategy to circumvent this difficulty would be to combine such work with a large scale nursery trial of tolerant clones (see the section on Silvicultural control) which would then produce large numbers of *Hypsipyla* attacks, which could then be available to culture parasitoids. In this way the extra cost of a biocontrol project could be greatly reduced.

Augmentative biocontrol

If classical biocontrol does not achieve the desired result then some form of augmentative release of agents can be considered. This tends to happen in cases where there is a certain level of control exerted by a parasitoid but not sufficient to drive pest levels below the economic threshold; a common example is the massive release of *Trichogramma* spp. which appears to work well under certain cirumstances in the Cauca valley in Colombia (Holl et al., 1990) for the control of pests of coffee.

In the case of *Hypsipyla* and mahogany there is a requirement for a very low insect attack rate. The economic threshold for this insect has never been calculated but it must be extremely small, perhaps in the order of ten attacks per hectare per year for outplanted saplings. In fact it is difficult to imagine a crop that has more stringent requirements, because the threshold must remain at that low level for about 5 years; i.e. until the trunk has achieved such a height that subsequent damage will not significantly affect the market value. It is hard to envisage that natural enemies could maintain such low levels constantly without augmentation. In the present case, however, production facilities for massive releases have yet to be developed, and it would be difficult to justify such an approach given the large and inaccessible areas over which such a scheme would have to operate.

Microbial control

Myers (1935) reported a *Cordyceps* sp. fungus from *H. grandella* in Trinidad. Rao (1969) recorded disease levels of 4–16% of *H. robusta* larvae sampled, but no identifications were made. There have also been various reports of susceptibility of *H. grandella* to pathogens; in the laboratory, larvae have been killed with *Bacillus thuringiensis* (Hidalgo-Salvatierra and Palm, 1972), *Beauvaria bassiana* and *B. tenella* (Berrios and Hidalgo-Salvatierra, 1971) and *Metarhizum anisopliae* (Hidalgo-Salvatierra and Berrios, 1972).

The general lack of reports of *Hypsipyla* disease in the field lead one to suspect that it is fairly uncommon; this is not surprising given the probable low population density compared with many insects and the protection conferred on the larva by its concealment inside the mahogany stem or seed. It is hard to imagine a practical control strategy in plantations based on pathogen applications. The only possible use for pathogens that can be envisaged would be prophylactic sprays on nursery material.

In conclusion, there seems at present to be little prospect for biocontrol alone to solve the *Hypsipyla* problem. It is very difficult to assess the effect that the natural enemy complex already exerts on *Hypsipyla* populations, and because of this it is easy to forget about them altogether. However, the sensible approach to control this pest is to work on the assumption that no single method will be adequate; thus an approach that can maintain or enhance biocontrol is to be preferred over dependence on a single procedure. For example, it is quite possible that inappropriate chemical control could destroy the natural enemy complex; knowledge about natural enemies could help minimize such problems and form the basis of integrated pest management, the subject of the following section.

CONCLUSIONS AND PROSPECTS FOR INTEGRATED PEST MANAGEMENT

The shoot borer of the Meliaceae is perhaps one of the most economically important insect pests in tropical forestry. The problem has attracted a great deal of attention from foresters, ecologists, entomologists and plant chemists, as is evident in the size of the literature devoted to the subject. The most obvious solution is to avoid the problem altogether, by planting alternative species which are resistant (Grijpma, 1976). However, susceptible species are likely to continue to be favoured in the countries where they are indigenous, where they have traditionally been used, and where they are of economic importance. In such situations it is clear that practical methods of overcoming the problem are urgently required.

It is probably impossible, in any given situation, to totally eliminate losses to *Hypsipyla*. The objective is rather to reduce damage to a tolerable level. Some success in this regard has been obtained with a number of different approaches, as noted in this review. The mahogany shoot borer may therefore be an example of a pest where some form of integrated approach is likely to be most successful. The potential benefits of integrated pest management have been highlighted previously (Grijpma, 1974; Morgan and Suratmo, 1976). However, we know of no conscious attempt to control *Hypsipyla* in this way.

As described earlier, there may be scope for selecting races or strains of meliaceous species which display resistance. This approach has a number of advantages. Firstly, it avoids the problem of insects adapting to artificial chemical control methods. Secondly, as the main problem of shoot borer damage is the effect on tree form, any selections based on superior apical growth or recuperative ability should also lead to improvements in tree form as well as tolerance to attack. A project investigating this approach has recently been initiated as a cooperative venture between the Institute of Terrestrial Ecology (ITE, Edinburgh, UK), the Centro Agronomico Tropical de Investigacion y Enseñanza (CATIE, Costa Rica) and the International Institute of Biological Control (IIBC, Trinidad), funded by the UK Overseas Development Administration (ODA) (Newton, 1990; Newton et al., 1991). This involves screening of seedling populations in genetic tests, and multiplication of resistant genotypes by vegetative propagation (Newton et al., 1991). Genetic screening and conservation of many meliaceous species is now a matter of urgency, as a result of the continuing high rate of depletion of natural stands, especially as pest resistant genotypes may exist (Newton et al., 1992). In the future there may also be scope for the genetic engineering of pest resistance in mahoganies, for example by inserting toxin genes of *Bacillus thuringiensis* (Strauss et al., 1991).

However, gains from the use of genetically improved trees can only be fully realised if appropriate silvicultural management systems are employed. This might involve the use of enrichment planting or mixed species plantations, as suggested earlier. Correct species/site matching and careful tending would necessarily be components of such an approach (Palmer, 1988). However, as noted earlier, there is still a dearth of information about the behaviour of the insect in different silvicultural systems. Such information is a pre-requisite for defining more precisely the silvicultural conditions needed for effective control (c.f. Watt, 1992).

Chemical control methods could also contribute to a system of integrated pest management, perhaps by incorporating slow-release pesticides (Wilkins et al., 1976). These methods may be particularly applicable to control in the nursery, prior to outplanting. However, there are adverse environmental consequences of pesticide application; populations of natural predators which control *Hypsipyla* could be adversely affected. The maintenance of predator populations by the adoption of appropriate silvicultural systems may enhance biological control (Gibson and Jones, 1977). However, information on this aspect is scant. As noted by Pimentel (1991), the combined use of natural enemies with increased pest resistance of the host plants, increases the overall effectiveness of biological control.

On the basis of experience decribed in this review, it would seem that effective control of the mahogany shoot borer is indeed possible (Grijpma, 1976; Vega, 1976). We believe that the incorporation of pest resistant genotypes into an appropriate silvicultural system, which enhances natural biological control, offers greatest potential. It is hoped that this review will encourage developments in this direction.

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RESISTANCE TO THE MAHOGANY SHOOT BORER: RESULTS OF RESEARCH AT CATIE, 1990-1995

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Summary: The shoot borer *Hypsipyla* prevents successful plantation silviculture of mahogany and other commercially important Meliaceae. The present article describes the results to date of a programme of research on genetic variation in resistance to attack, initiated by CATIE and the Institute for Terrestrial Ecology, Scotland, in 1990. The three genetic tests described demonstrated the existence of provenance-level and family-level variation in resistance to attack. It is concluded that deployment of selectd germplasm has potential as one element of a pest management system for *Hypsipyla*.

Introduction

The attack of the shoot-borer *Hypsipyla* (Lepidoptera: Pyralidae) has long been recognized as a critically limiting factor in the successful plantation silviculture of mahogany (*Swietenia* spp), African mahogany (*Khaya* spp) and Spanish cedar (*Cedrela* spp.) (1,3,4). Although the insect has been closely studied (7), until recently, with the exception of work at the species level (2), there had been no efforts at approaching the problem through germplasm selection and breeding for resistance (5). For this reason, in 1990, CATIE, in collaboration with the Institute for Terrestrial Ecology, began a pilot programme of research into resistance breeding in *Cedrela* and *Swietenia*. In the present document we report results of three genetic field tests.

Materials and methods

In February 1991, provenance trials of *Cedrela odorata* and *Swietenia macrophylla* were established in Turrialba, Costa Rica. Each trial had five provenances. The mahogany provenances (Guajataca, Puerto Rico; Juan Díaz, Puerto Rico; Honduras; Trinidad; Haiti) were represented by bulked lots. Experimental design was randomized complete blocks, with 25-tree square plots and five blocks. Each of the *Cedrela* provenances (Cañas, Carmona, Hojancha, San Carlos (all Costa Rica); Trinidad) was represented by progeny of five trees. Experimental design was randomized complete blocks, with five-tree family line plots and nine blocks. The trials were assessed fortnightly for shoot borer attack and phenology from 22 April 1991 until early December 1992. Tree height was measured after 26, 56 and 88 weeks, and form evaluations (height to first branch and number of forks) made at 141 weeks (*Cedrela*) and 177 weeks (*Swietenia*). Analyses of variance of block and provenance effects was carried out. Further details on these two experiments are given elsewhere (6). In September 1994, a second *Cedrela* trial was established in San Carlos, Costa Rica. Six Costa Rican provenances were included (Cañas, Cóbano, Guápiles, Hojancha, San Carlos, Talamanca), each represented by five families. Design was randomized complete blocks, with three tree line plots and ten bloques. Tree height and presence of *Hypsipyla* attack was assessed in March, July, September and October 1995. In addition, in October 1995 the presence or absence of a dominant leader was assessed. Trees were also scored 1 (present) or 0 (absent) for tolerance, where a tolerant tree was defined as one that had been attacked at least once and had retained a dominant leading shoot, whereas an intolerant tree was defined as one that had been attacked and had no dominant leader. Trees that had never been attacked were considered to be missing values for tolerance. In addition, a score for degree of tolerance was derived; tolerance degree for those trees that scored 1 for tolerance was set equal to the total number of attacks. Tolerance degree of trees with zero tolerance was also zero. Analyses of variance of block, provenance and family effects were made for all variables

Results

In all three trials. strong temporal trends were noted. The 1991 *Cedrela* trial evinced peaks in attack in May 1991 and. particularly. May-June 1992. The mahogany trial was virtually unattacked during the first year of growth, but experienced a sharp peak of attack from May to June 1992. The second Cedrela trial was unattacked at the time of the first evaluation in March 1994. By May. 14% of the trees were being attacked. rising to 56% in July, thereafter declining to 27% and 29% respectively in September and October There is thus evidence that, at least in the Atlantic zone of Costa Rica. attacks tend to be concentrated in the May-July period. although the tail-off in attack has not been as marked in San Carlos as in the Turrialba trials.

Genetic variation in attack and tolerance

Swietenia macrophylla.

At the time of peak attack, there were significant differences between the provenances in mean number of attacks per tree (p=.01). number of forks (p=.001), proportion attacked (p=.001) and height to the first fork (p=.01). The Juan Díaz (Puerto Rico) provenance was markedly superior in the first three characteristics. although its height at 68 weeks was 16.7% less than the best source.

Cedrela odorata.

In the 1991 trial. at the time of the second peak there were significant differences in number of attacks per tree (p=.001), number of forks (p=.001). height to the first fork (p=.001). and the proportion of trees attacked (p=.001). The Costa Rican dry-zone provenances were attacked least (e.g. means of 0.94 and 2.3 attacks per tree in Hojancha and San Carlos respectively). However. the San Carlos provenance was much faster growing (3.1m (San Carlos) v. 1.5m (Hojancha)) and had the best form.

In the 1994 trial. in October 1995 there was highly significant variation between the provenances in mean number of attacks per tree (p=.0001) (e.g. Hojancha 1.5±0.8. San Carlos 3.6±0.8). mean number of trees attacked (p=.0001) (e.g. Hojancha 0.6±0.2. San Carlos 0.9±0.05) and mean height (p=.0001) (e.g. Hojancha 0.8m±0.2m. San Carlos 1.3m±0.25m). The mean number of attacks per tree and mean number of trees attacked was significantly (p=.0001) lower for the dry zone provenances than the wet zone provenances. The mean height of the wet zone provenances was significantly (p=.0001) greater than that of the dry zone provenances. There were no significant differences in dominance between the provenances. and no significant differences in tolerance. However. degree of tolerance showed highly significant (p=.0001) provenance effects (e.g. Hojancha 1.3±0.5. San Carlos 2.9±0.7) and. in addition. the wet zone provenances showed significantly superior tolerance degree and tolerance (p=.0001. p=.07. respectively) to the dry zone provenances.

Because of the evidently strong zonal provenance effect. the dry-zone provenances were eliminated from the family-level analysis. in order to avoid undue confounding of family and provenance effects. The analysis therefore included five families from each of Guápiles. San Carlos and Talamanca. plus three families from Upala. which were excluded from the provenance analysis on grounds of inadequately representing the Upala source. The analysis of the October 1995 data revealed significant family effects on total height (p=.0004) (e.g. best family 1.7±0.6m. worst 0.9m±0.4m) and total number of attacks (p=.0007) (e.g. most severely attacked family 5.7±1.9 attacks per tree. least severely attacked family 2.1±0.7 attacks per tree) There were no significant family effects of proportion of trees attacked. tolerance. or tolerance degree

Discussion and conclusions

The trials clearly demonstrate the existence of genetic variation in resistance to the attack of *Hypsipyla*. both in the case of *Swietenia* and *Cedrela* However. both for purposes of application of the results and design of future research directions. it is important to appreciate the scope of the research to date and the nature. particularly with regard to genetic structure. of the variation identified The *Cedrela* trials provide very clear evidence for major genetic differences between the provenances from the seasonally-dry Pacific watershed and those from the Atlantic zone. The magnitude of the growth differences are such that Pacific provenances would be unlikely to be selected for planting in the Atlantic zone, whilst their relative freedom from attack may in any case be a function of their size and consequent lower number of oviposition and feeding sites. There are, however, clear indications in the data of more practically useful forms of genetic variation. The continuing fast growth and good form of the San Carlos provenance and particularly the existence of genetic variation in attack severity within the broadly similar Atlantic zone provenances, are highly encouraging. At the same time, the failure to detect variation in tolerance within the Atlantic zone material is disappointing. Future research will concentrate on clonal testing of Atlantic-derived material and the development of an integrated pest management systemof which superior germplasm will be one element.

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Genetic variation in host susceptibility to attack by the mahogany shoot borer, *Hypsipyla grandella* (Zeller).

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Summary

Attack by shoot borers (*Hypsipyla grandella* Zeller) is the main factor limiting the cultivation of *Cedrela odorata* and *Swietenia macrophylla*, two economically important members of the mahogany family. No viable methods of pest control are currently available. To assess for genetic variation in susceptibility to pest attack, a combined progeny /provenance test of *C. odorata* and a provenance test of *S. macrophylla* were established at CATIE, Costa Rica and assessed intensively over an 84 week period. Variation in height growth between provenances was highly significant in both species ($P < 0.001$, ANOVA), provenance means varying by a factor of 2.7 and 1.2 in *C. odorata* and *S. macrophylla* respectively. *C. odorata* also displayed provenance variation in foliar phenology, with 94.7% of the trees from a 'wet zone' provenance remaining foliated, whereas > 35% of trees from three 'dry zone' provenances abscised their leaves during the dry season. Both species displayed significant genetic variation in susceptibility to shoot borer attack. At the peak of attack during the second year of growth, the effect of provenance was highly significant in both species ($P < 0.001$ and $P = 0.014$, ANOVA, in *C. odorata* and *S. macrophylla* respectively), the mean number of attacks per tree varying between 0.84 - 2.38 and 0.58 - 1.25 in the two species respectively, depending on provenance. These results indicate that there may be scope for selecting for pest resistance in both species. In particular, a provenance of *C. odorata* from San Carlos, Costa Rica displayed consistently lower susceptibility to pest attack, being subjected to fewer attacks during the first year and demonstrating a higher mean height to first damage locus. The ability of some trees of this provenance to tolerate attack by vigorous apical growth has particular potential for incorporation into future selection programmes.

Introduction

The mahogany shoot borer (*Hypsipyla grandella* (Zeller); Lepidoptera, Pyralidae) is a serious pest of the mahogany family (Meliaceae) in the neotropics, severely restricting the cultivation of *Cedrela odorata* L. (Spanish Cedar) and *Swietenia macrophylla* King (American mahogany), both of which produce highly valuable timber. *H. grandella* larvae destroy the terminal shoots of the host plant by boring the pith, resulting in a highly branched tree of little economic value (Newton et al. 1993a). Young trees are particularly susceptible to attack, because of their greater dependence on a single leading shoot for growth (Vega 1987). Despite a considerable research effort (Grijpma 1974; Whitmore 1976a,b), no viable methods of controlling this pest are currently available (Newton et al. 1993a). The development of pest resistant planting stock would therefore be of great value for reforestation efforts with these species.

Previous research on the occurrence of pest resistance in the Meliaceae has largely centred on *Toona ciliata* (F.v. Muell.) C.DC., an Asian and African species closely related to *Cedrela* spp. which is not attacked by *H. grandella* when planted in Central America (Whitmore 1976c). Water-soluble extracts of *Toona* foliage, which may be alkaloids, have been shown to be toxic to *H. grandella* larvae (Grijpma 1976). Both *Cedrela* and *Toona* are known to contain limonoids, many of which are known to be potent insecticides or feeding deterrents (Kubo and Klocke 1986). Such observations suggest that it may be possible to select pest resistant individuals within species of Meliaceae for multiplication in a breeding programme

(Grijpma 1976). However, little information is currently available on infraspecific variation in these characteristics.

Pest resistance may arise as a result of three processes (Painter 1951; Van Emden 1987): (i) *antixenosis* (= *non-preference*), in which the plant is avoided or colonized by the pest to a lesser extent; (ii) *antibiosis*, in which the plant reduces the performance of the growth or survival of the pest, usually by possession of chemical defenses; and (iii) *tolerance*, where the tree recovers from insect attack to an economically acceptable level. This investigation was designed to assess the occurrence of genetic variation in these different forms of resistance within both *C. odorata* and *S. macrophylla*, by the use of screening trials. The trials were designed as genetic tests, incorporating a range of different provenances and/or half-sib progenies.

Materials and Methods

The investigation was carried out at the Centro Agronómico de Investigación y Enseñanza (CATIE) in Turrialba, Costa Rica (9° 54' N Lat., 83° 40' W Long.) at 600 m.a.s.l. Mean annual precipitation and temperature of this site are approx. 2 600 mm and 22 °C respectively. Seed of *C. odorata* was collected from open-pollinated trees growing on farms, from four localities in Costa Rica, namely Carmona, Hojancha, Cañas, San Carlos, and one in Trinidad (see Table 1). Trees were selected on the basis of stem straightness and lack of forking (clear bole > 7 m). Seed of *S. macrophylla* was obtained from bulked collections from five provenances, namely Haiti, Trinidad, Honduras and two from Puerto Rico (Table 1). Seed was germinated in seed trays, then transferred to black polyethylene bags (2.2 litre capacity) containing a 1:1:1 mixture of forest soil, sand and organic compost. Seedlings were raised in full sunlight in the CATIE nursery, and received natural rainwater only.

Two field trials, screening *Cedrela odorata* and *Swietenia macrophylla* respectively, were established on adjacent sites at Florencia Sur, CATIE, during February 1991. The soil of this site is argillaceous, with a pH of 4.4, and is considered deficient in P and Ca (Bertsch 1986). The sites were prepared, and trials established, as described by Newton et al. (1996). The first experiment included twenty-five families of *C. odorata* divided equally between the five provenances. Trees were arranged by family in fully randomized 5-tree row plots, in nine replicate blocks, at a spacing of 2.5 x 2.5 m. The whole experiment was surrounded by a single-row border of the same family as the adjacent plot. In the second experiment, seedlings of *S. macrophylla* were arranged in fully randomized square plots of 25 trees in a 5 x 5 array, with five replicate blocks, at a spacing of 2.5 x 2.5 m. The trials were cleaned of weed growth by hand approximately every 3 months.

Each tree in both experiments was assessed for the incidence of shoot borer attack at 14 day intervals, starting on 22nd April 1991 and continuing for a total of 84 weeks. Assessments of attack were made by visually inspecting each plant, and counting the number of attack loci indicated by the presence of fresh frass. The trees were also assessed for the presence or absence of foliage. Tree height was measured after 26, 56 and 88 weeks. In addition, the two experiments were assessed after 141 and 177 weeks (*C. odorata* and *S. macrophylla* respectively) for height to first branching and for the number of damage loci, indicated by forking.

Data were analyzed by *t*-test or ANOVA, where appropriate, using SAS (SAS 1980). Proportions were arcsin transformed prior to analysis, following Snedecor and Cochran (1980). To assess the relative influence of different factors, the data were analysed using an individual tree model (Stonecypher 1992) with random main effects and full interactions. Family was nested within provenance. 'F'-tests were generated using the TEST option of the GLM RANDOM statement of SAS (SAS 1980). SAS uses Satterthwaite's (1946) approximations for appropriate degrees of freedom, when necessary. Variance components were estimated using the SAS VARCOMP procedure. Standard errors of variance components were calculated following Gordon et al. (1972).

Results

Genetic variation in height growth was recorded in both experiments at all three assessments, differences between both provenances and families tending to become more pronounced with time. In *C. odorata*, mean values ranged from 101-165 cm in family nos. 2011 and 2006 respectively, at the first assessment. The relative performance of the different families remained fairly constant throughout the experiment. At the third assessment, mean height varied by a factor of 2.4, maximum values being recorded in family 2006 (Figure 1a). At this time, variation between families and provenances was highly significant ($P < 0.001$ in both cases, when tested separately by ANOVA), provenance means ranging from 148 - 313 cm in Hojancha and San Carlos provenances respectively. The variance component analysis indicated that the family effect in *C. odorata* was largely attributable to variation between provenances (Table 2). In *S. macrophylla*, provenance means varied between 61.6 - 72.4 cm (in Juan Diaz, Puerto Rico and Honduras respectively) at the first assessment. At the third assessment, the effect of provenance was highly significant ($P = 0.002$, ANOVA), mean provenance values varying by a factor of 1.2 (Figure 1b). At the final assessment (week 141) in *C. odorata* mean height varied from 140 - 491 cm in families 2015 and 2006 respectively, provenance means ranging from 183-501 cm in Hojancha and San Carlos respectively. Differences between families and provenances were both highly significant at this time ($P < 0.001$, ANOVA). At the final assessment of *S. macrophylla* (week 177), provenance mean values ranged from 211-267 cm in Dirici and Guajataca respectively, the effect of provenance being highly significant overall ($P < 0.001$, ANOVA). A pronounced block effect, and an interaction between block and provenance, was also noted (Table 3).

Genetic variation in phenology was also observed, particularly with respect to leaf abscission during the dry season. For example, at week 48 when the proportion of trees with leaves was at its lowest (Newton et al. 1996), there was a pronounced difference between provenances ($P < 0.001$, ANOVA) in the proportion of trees which remained foliated. The mean proportion of trees with leaves was 94.7% and 70.5% in San Carlos and Trinidad respectively, with means of < 35% recorded in each of the other three provenances. Values for individual families ranged from 17%-97.6% in 2018 and 2006 respectively. As the majority of *S. macrophylla* trees possessed foliage throughout the experiment, no analysis of variation in phenology was carried out in this species.

Pronounced variation in leaf colour was also observed in *C. odorata*. Flushing foliage in the San Carlos provenance was noticeably redder than in the other provenances. When each tree was assessed after 88 weeks for red colouration, 73% of trees in the San Carlos provenance were found to possess this characteristic, whereas values for the other four provenances were < 1%. The maximum value (80%) was recorded in family 2006.

In *C. odorata*, pronounced peaks in attack were observed at weeks 12 and 68 after the initiation of assessments (Newton et al. 1996). At the first peak, significant variation in the mean number of attacks per tree was observed between both families (P = 0.017, ANOVA) and provenances (P = 0.01, ANOVA). Values ranged from 0.02-0.66 in families 2005 and 2000 respectively, whereas provenance means varied between 0.09 - 0.29 in San Carlos and Trinidad respectively (Figure 2a). At the second peak after 68 weeks, the effect of both provenance and family was again highly significant (P < 0.001 in both cases, when tested separately by ANOVA), family mean values ranging from 0.29 (2011) - 2.75 (2006), and provenance means varying between 0.84 (Cañas) - 2.38 (Trinidad). Variance component analysis indicated that the family effect was entirely attributable to provenance variation (Table 2). In *S. macrophylla*, the number of shoot borer attacks peaked at week 60, when 559 attacks was recorded in the trial as a whole (Newton et al. 1996). At this time, the number of attacks differed significantly (P = 0.014, ANOVA) between provenances, the mean number of attacks per tree ranging from 0.58-1.25 in Juan Diaz and Guajataca respectively (Figure 2b). An block x provenance interaction was again noted, as for height (Table 3). The proportion of *C. odorata* trees attacked also varied between provenances, with 5.1-17.4% in San Carlos and Trinidad respectively at the first peak (P = 0.02, ANOVA), and 28.0-58.9% in Cañas and Trinidad respectively at the second peak (P < 0.001, ANOVA). Family values ranged from 2.2-34.3% in 2005 and 2000 respectively at the first peak, and 12.1-66% in 2011 and 1999 respectively at the second peak. In *S. macrophylla*, percentage values varied between 28.5-52.1% in Juan Diaz and Guajataca respectively.

The number of damage loci in *C. odorata*, assessed after 141 weeks, was also significantly affected by both family and provenance (P < 0.001 in both cases, when tested separately by ANOVA). The mean number of damage loci per tree varied between 0.7-3.0 in families 2015 and 1998, provenance means ranged between 1.55-2.64 in Hojancha and Trinidad respectively (Figure 3a). In *S. macrophylla*, when the trial was assessed after 177 weeks, the effect of provenance was highly significant (P < 0.001, ANOVA), values ranging from 1.8-2.9 in Juan Diaz and Trinidad respectively (Figure 3b). Similarly, the height to first damage locus was significantly affected by both provenance and family in *C. odorata* (P < 0.001 in both cases, when tested separately by ANOVA), mean values ranging from 0.72-2.37 m in families 2015 and 2005, provenance means ranging from 0.92-1.98 m in Hojancha and San Carlos respectively (Figure 4a). As with height and incidence of attack, the family effect was largely attributable to provenance variation (Table 2). In *S. macrophylla*, provenance means ranged from 1.14-1.39 m in Dirici and Trinidad respectively (P = 0.005, ANOVA; Figure 4b). A large proportion of the variation was unexplained (Table 3), reflecting the relatively low number of provenances included in the experiment.

Discussion

The results from the *C. odorata* trial indicate that the San Carlos provenance, derived from the Atlantic zone of Costa Rica, is highly distinctive in terms of growth characteristics. The superiority of this provenance in terms of growth rate became progressively more apparent with time. The contrast in height growth between provenances was visually very striking, with both maximum and family mean values in the San Carlos provenance being more than double the values in Carmona and Hojancha provenances. Trees in the San Carlos provenance also appeared to be morphologically distinctive, tending to have larger leaves and more leaflets per leaf than the other provenances (A C Newton, personal observation), as well as distinctive foliar coloration.

The extent of genetic variation in growth rate within *C. odorata* is illustrated by results from an international series of provenance trials established in the 1960's and 1970's, co-ordinated by the Oxford Forestry Institute (OFI), U.K. (Burley and Lamb 1971). In 1967, seedlots of 14 provenances were distributed to 21 collaborating countries throughout the tropics for use in trials, the results of which were summarised by Chaplin (1980). In all of the provenance tests established in Africa, where no problems with shoot borer attack were encountered, pronounced intraspecific variation in growth rate and form was recorded (see papers by Egenti, Kaumi and Malimbwi in Nikles et al. 1978). For example, the mean height of different provenances tested in Côte d'Ivoire varied between 3-19 m after 7.5 years growth (Delaunay 1978). In general, the most promising provenances in terms of growth rate were those from Costa Rica and Belize (Chaplin 1980). In 1978, a second series of international provenance trials were planned (Chaplin 1980). Although seed was disseminated to a number of collaborating countries, few results from these trials have been published to date.

In the neotropics, few trials were successfully established in either of these programmes, as problems with shoot borer attack and site incompatibility were encountered (Chaplin 1980; McCarter 1986). Whitmore (1978) described results from provenances tests established on five sites in Puerto Rico as part of the original OFI programme. Highest growth rates were obtained in the Turrialba (Costa Rica) provenance, averaging 0.8 - 1.1 m annual height growth, with variation between provenances recorded by more than a factor of three. In Trinidad, highest growth rates were recorded in the Apartado provenance from Colombia. Material from San Carlos (Costa Rica) also grew relatively rapidly, with a mean height of 4.34 m after 3 yrs, provenance means varying by a factor of six (Ramnarine 1989). These values are comparable to those recorded in the present investigation, both in terms of height growth and the extent of difference between provenances.

Genetic variation in phenology of *C. odorata* has apparently not been recorded in any of the provenance tests established previously. The results presented here indicate a clear difference between provenances originating from low and high rainfall areas ('dry' and 'wet' zone), the former displaying a greater tendency to abscise foliage during the dry season. These results therefore suggest that leaf phenology is under a degree of genetic control. As the incidence of shoot borer attack is closely related to foliar phenology (Newton et al. 1996), this is a characteristic which could potentially be exploited in a breeding programme for pest resistance.

Similarly, few data are available concerning variation in susceptibility to shoot borer attack within *C. odorata*. Whitmore (1978), in provenance tests established in Puerto Rico, recorded mean numbers of shoot borer attacks per tree ranging from 0.66-0.77 after three years growth, lowest values being recorded in a Jamaican provenance which was also the slowest growing (Whitmore 1978). In this investigation, provenance variation in the incidence of shoot borer attack was also recorded. In particular, trees of the San Carlos provenance experienced relatively few attacks during the first year. In contrast, the proportion of trees of the Trinidadian provenance which were attacked remained high throughout the period of observation. Such variation may reflect preference of the insect for particular host genotypes, and may be attributable to variation in the production of chemical attractants (Grijpma 1976).

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The relationship between height growth and incidence of attack has previously been the subject of some controversy. Whereas Gara et al. (1973) indicated that shoot borers tend to select taller trees, an observation supported by Whitmore (1978) and Ramnarine (1989), Lamb (1968) observed that attacks tended to fail on more vigorous trees as a result of high rates of resin flow. The production of resin by *C. odorata* has been noted by a number of other authors (e.g see Wilkins 1972), although its effectiveness in countering shoot borer attacks has not been studied in detail. No assessments of resin production were made during the curent investigation, although this may be one mechanism which may account for the variation in damage observed. The current results confirm the tendency of larger trees to be attacked more often, as indicated by the higher number of attacks per tree recorded in the San Carlos and Trinidadian provenances in the second year. This relationship may be attributed simply to the larger number of suitable shoots available for attack on a larger tree (c.f. Sanchez et al. 1976).

The characteristic of greatest economic importance is height to first damage locus, as a clear bole of at least 3 m length is required for economic use as timber (Vega 1987). With respect to this characteristic, the San Carlos provenance was again superior, reflecting relatively high initial growth rates and lower initial susceptibility to attack. Trees from this provenance also displayed significantly fewer damage loci per unit stem length than the other provenances, partly reflecting the ability of individual trees of this provenance to recover from attack by vigorous growth of the leading shoot. The ability of some *Cedrela* trees to tolerate attack in this way has been observed previously. For example, Ramnarine (1989) noted that provenances from San Carlos, Costa Rica and Apartado, Colombia demonstrated a more pronounced ability to tolerate attack despite being attacked more often. Similarly, a provenance of *Cedrela angustifolia* Moc. and Sess ex DC. from south of Lake Maracaibo, Venezuela (Melchior and Quijada 1972) was found to display a relatively high degree of tolerance to shoot borer attack despite being attacked heavily, both in line enrichment trials in Surinam (Vega 1976) and in species trials in Costa Rica (Sanchez et al. 1976). The taxonomic position of *C. angustifolia* is uncertain (Chaplin 1980); although Smith (1960) recognised it as a distinct species, in a more recent revision of the genus Styles (in Pennington 1981) considered that it does not merit specific rank. The relatively rapid growth rates and the lower incidence of shoot borer damage recorded in the San Carlos provenance tested here, together with the red flushing foliage, suggests that this provenance may have some taxonomic affinity with the '*C. angustifolia*' originating from Venezuela.

In the case of *S. macrophylla*, very little information is available concerning genetic variation in either growth or susceptibility to shoot borer attack (Newton et al. 1993b). In progeny tests established in Costa Rica and Trinidad, Newton et al. (1996) recorded significant variation in height growth, family means varying by 132% and 192% respectively, within the first three years after establishment. Genetic variation in susceptibility to shoot borer attack was also recorded, the mean number of damage loci per tree varying between 2.2-4.7 and 2.7-4.4 in Costa Rica and Trinidad respectively. These results are consistent with those of the current investigation. However, none of the provenances of *S. macrophylla* tested was comparable to the San Carlos provenance of *C. odorata* in terms of lowered susceptibility to pest attack. Further screening, including a much larger number of provenances, would clearly be desirable to evaluate the occurrence of pest resistance characteristics more fully.

Conclusion

Results from this investigation clearly indicate that genetic variation in susceptibility to shoot borer attack exists within both *C. odorata* and *S. macrophylla*. However, the occurrence of different mechanisms of resistance (c.f. Grijpma 1976) is difficult to elucidate. Although tolerance was clearly observed in both species, reflected in the response of the trees to damage, both antibiosis and non-preference may have contributed to the variation in attack observed. For example, further observations are required to assess whether the relatively low initial attack on the San Carlos provenance of *C. odorata* was the result of a lack of chemical attractants produced by the trees, or failure of attack resulting from anitbiosis. While resin production constitutes a relatively obvious form of antibiosis, both *C. odorata* and *S. macrophylla* contain a variety of other compounds deleterious to feeding insects (Newton et al. 1993a), which may conceivably vary genetically.

These results suggest that there may be scope for breeding for pest resistance in both species, by the selection of superior genotypes. Both *C. odorata* and *S. macrophylla* are amenable to vegetative propagation techniques (Newton et al. 1993b, 1994), offering the possibility of clonal multiplication of genotypes displaying resistance. Genetic variation in apical dominance of *C. odorata* has been highlighted by decapitation tests of seedling material (Newton et al. 1995), which may enable genotypes displaying a degree of tolerance to be identified at an early age. To realize the full genetic potential of any improved germplasm developed, particular attention should be paid to the choice of planting site (Whitmore 1978) and silvicultural system. The potential exists for incorporating material with a degree of pest resistance in silvicultural systems which encourage pest control, leading to the development of an integrated system of pest management (Newton et al. 1993a).

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Figure captions

Figure 1. Variation in height growth of (a) *Cedrela odorata* and (b) *Swietenia macrophylla* in field trials at CATIE, Costa Rica after 88 weeks. Values presented are means (n = 45 and n = 125 for *C. odorata* and *S. macrophylla* respectively); vertical bars represent s.e.m. Right hatched bars, Trinidad; filled bars, San Carlos; cross-hatched bars, Cañas; empty bars, Carmona; left-hatched bars, Hojancha. For details of seed origins see Table 1.

Figure 2. Variation in mean number of shoot borer attacks per tree of (a) *Cedrela odorata* and (b) *Swietenia macrophylla* in field trials at CATIE, Costa Rica, after 68 and 60 weeks in the two species respectively, when the number of attacks reached a peak. Values presented are means (n = 45 and n = 125 for *C. odorata* and *S. macrophylla* respectively); vertical bars represent s.e.m. Right hatched bars, Trinidad; filled bars, San Carlos; cross-hatched bars, Cañas; empty bars, Carmona; left-hatched bars, Hojancha. For details of seed origins see Table 1.

Figure 3. Variation in mean number of shoot borer damage loci per tree of (a) *Cedrela odorata* and (b) *Swietenia macrophylla* in field trials at CATIE, Costa Rica, after 141 and 177 weeks respectively. Values presented are means (n = 45 and n = 125 for *C. odorata* and *S. macrophylla* respectively); vertical bars represent s.e.m. Right hatched bars, Trinidad; filled bars, San Carlos; cross-hatched bars, Cañas; empty bars, Carmona; left-hatched bars, Hojancha. For details of seed origins see Table 1.

Figure 4. Variation in the height to first shoot borer damage locus in (a) *Cedrela odorata* and (b) *Swietenia macrophylla* in field trials at CATIE, Costa Rica, after 141 and 177 weeks respectively. Values presented are means (n = 45 and n = 125 for *C. odorata* and *S. macrophylla* respectively); vertical bars represent s.e.m. Right hatched bars, Trinidad; filled bars, San Carlos; cross-hatched bars, Cañas; empty bars, Carmona; left-hatched bars, Hojancha. For details of seed origins see Table 1.

TABLE 1. Origins of the seedlots used in field trials to assess variation in susceptibility to shoot borer attack.

a. Cedrela odorata

Provenance	Latitude N	Longitude W	Altitude (m)	Precipitation (mm)
Cañas, Costa Rica	10° 25'	85° 6'	70-120	1829-2274
Carmona, Costa Rica	9° 60'	85° 15'	60-70	1780
Hojancha, Costa Rica	10° 04'	85° 25'	100-350	2232
San Carlos, Costa Rica	10° 22'	84° 28'	80-260	2866-3609
St. Andrew, Trinidad	10° 28'	61° 05'	10-100	2500

b. Swietenia macrophylla

Provenance	Latitude N	Longitude W	Altitude (m)	Precipitation (mm)
Guajataca, Puerto Rico	18° 22'	67° 00'	200	2000
Juan Diaz, Puerto Rico	18° 00'	66° 31'	10	900
Dirici, Haiti	19° 42'	72° 24'	40	1999
La Mosquitia, Honduras	15° 20'	84° 24'	11-170	2859
St. Andrew, Trinidad	10° 28'	61° 05'	10-100	2500

TABLE 2. Analysis of variance components for growth and susceptibility to pest attack in combined provenance / progeny test of *Cedrela odorata*

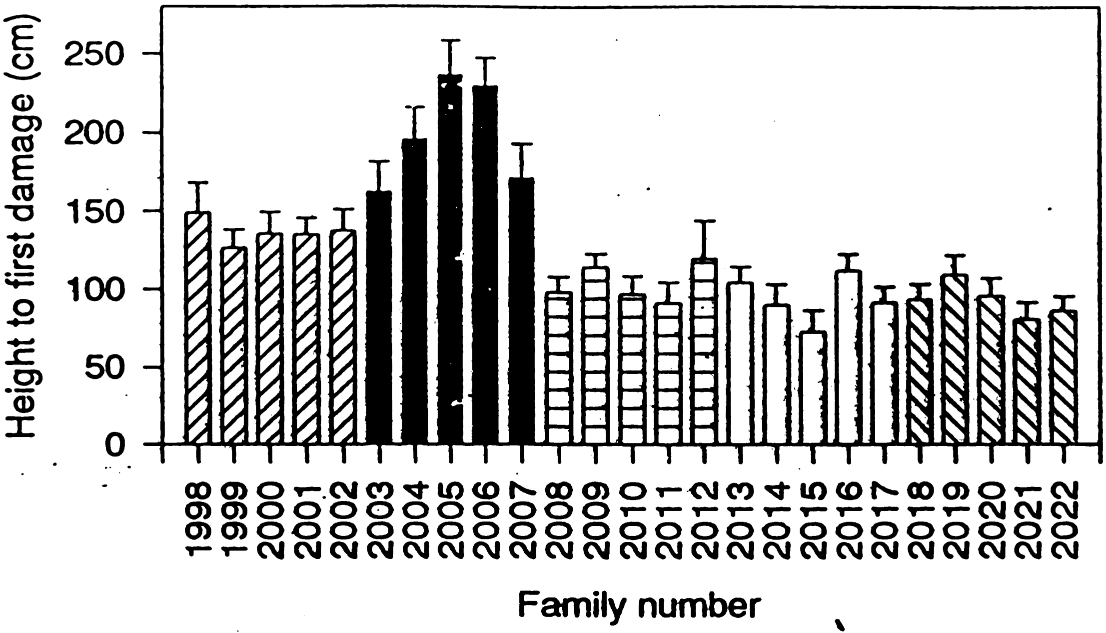
Trait	Effect	VC (%)	s.e. (%)
Height growth	block	1680 (12.6)	923 (6.9)
	prov	4948 (37.2)	3095 (23.3)
	fam (prov)	192 (1.4)	184 (1.4)
	block x prov	835 (6.3)	300 (2.2)
	block x fam (prov)	916 (35.6)	241 (1.7)
	error	4722 (35.6)	223 (1.7)
Number of attacks Peak 1	block	0.011261 (2.4)	0.00754 (1.6)
	prov	0.003253 (0.6)	0.00412 (0.9)
	fam (prov)	0.000053 (0.1)	0.00369 (0.8)
	block x prov	0.011292 (2.4)	0.00832 (1.8)
	block x fam (prov)	0.027153 (5.7)	0.01324 (2.8)
	error	0.418501 (88.8)	0.02051 (4.3)
Number of attacks Peak 2	block	0.24025 (5.3)	0.147 (3.2)
	prov	0.52458 (11.6)	0.3077 (6.8)
	fam (prov)	0 (0)	0.04115 (0.9)
	block x prov	0 (0)	0.06755 (1.5)
	block x fam (prov)	0.43249 (9.5)	0.1297 (2.9)
	error	3.33023 (73.6)	0.1629 (17.6)
Height to first damage locus	block	8.9 (8.6)	4.92 (4.8)
	prov	22.3 (21.6)	15.6 (15.1)
	fam (prov)	1.4 (1.4)	1.55 (1.5)
	block x prov	6.5 (6.3)	2.25 (2.2)
	block x fam (prov)	0.1 (0)	2.38 (2.3)
	error	63.9 (62.0)	3.46 (3.3)
Number of damage loci	block	0.11 (5.1)	0.063 (2.9)
	prov	0.158 (7.3)	0.114 (5.2)
	fam (prov)	0.054 (2.5)	0.043 (2.0)
	block x prov	0.052 (2.5)	0.038 (1.7)
	block x fam (prov)	0.111 (5.1)	0.073 (3.3)
	error	1.69 (77.7)	0.091 (4.2)

Abbreviations: VC, variance component; s.e., standard error; prov., provenance; fam., family.

TABLE 3. Analysis of variance components for growth and susceptibility to pest attack in a provenance test of *Swietenia macrophylla*

Trait	Effect	VC (%)	s.e. (%)
Height growth	block	0.08871 (10.6)	0.0632 (35.1)
	prov	0.01689 (2.0)	0.0268 (14.9)
	block x prov	0.10980 (13.1)	0.0500 (27.8)
	error	0.62326 (74.3)	0.0400 (22.2)
Height to first attack	block	0.05408 (9.7)	0.0105 (12.1)
	prov	0.01048 (1.89)	0.0341 (39.2)
	block x prov	0.02940 (5.3)	0.0159 (18.3)
	error	0.45986 (83.0)	0.0265 (30.5)
Number of attacks	block	0.05442 (2.3)	0.01216 (23.8)
	prov	0.02600 (1.1)	0.01031 (20.1)
	block x prov	0.11389 (4.8)	0.01312 (25.6)
	error	2.18027 (91.8)	0.1558 (30.4)
Number of damage loci	block	0.13678 (4.7)	0.0523 (18.3)
	prov	0.10286 (3.5)	0.0405 (14.2)
	block x prov	0.028291 (9.7)	0.0672 (23.5)
	error	2.38379 (82.0)	0.1256 (43.9)

Abbreviations: VC, variance component; s.e., standard error; prov., provenance.


Height to first damage (cm)
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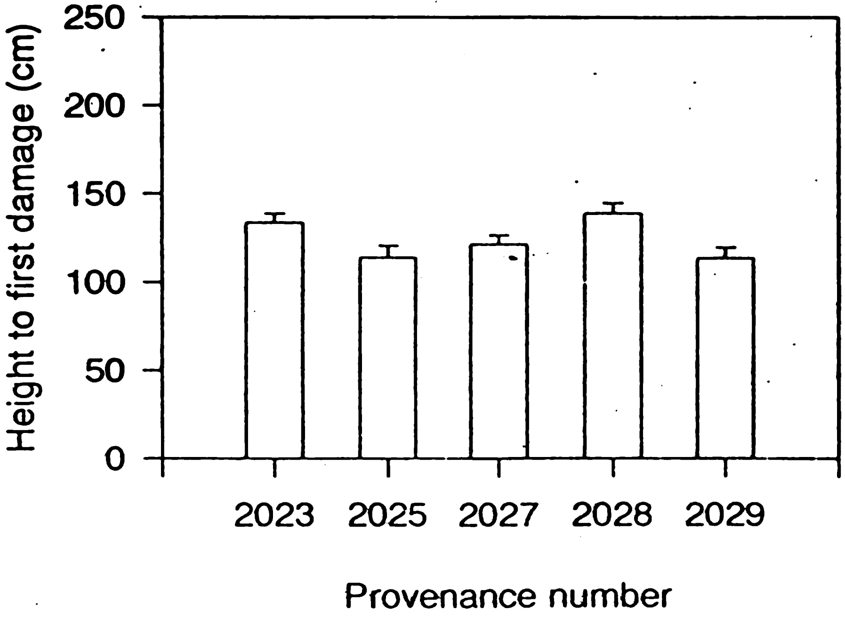
2021
2022
Family number


Height to first damage (cm)
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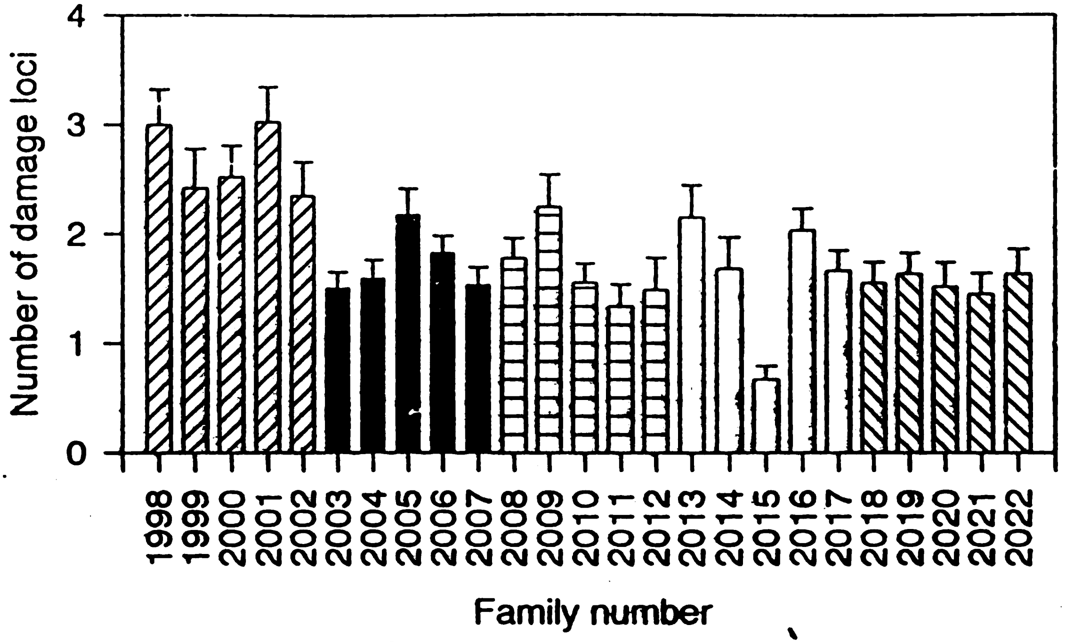
Provenance number


Number of damage loci
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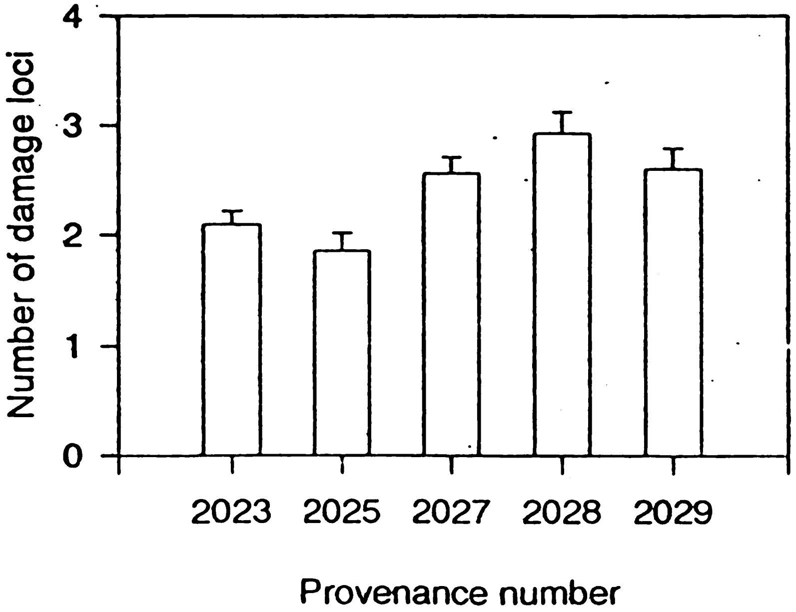
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2023
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Provenance number

Variation in attack by the mahogany shoot borer, *Hypsipyla grandella* (Zeller), in relation to host growth and phenology

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Summary

1. In order to evaluate the relationships between attacks by shoot borers (*Hypsipyla grandella* Zeller), host growth and phenology, field trials of *Cedrela odorata* and *Swietenia macrophylla* were assessed intensively over an 84 week period.

2. Height growth of *C. odorata* was approximately twice that of *S. macrophylla*, with mean growth rates of 2.0 and 1.3 cm week^{-1} respectively over the entire period of measurement.

3. *C. odorata* displayed pronounced temporal variation in leaf phenology, with a minimum of 51% trees with foliage during a relatively dry period. In contrast, the minimum proportion of foliated *S. macrophylla* trees was 87%.

4. No shoot borer attacks were recorded on *S. macrophylla* until week 50, whereas initial attacks of *C. odorata* were recorded at week 6. However, by week 84 after establishment, the proportion of trees attacked was 74% and 77% respectively. In both species, attacks tended to be concentrated in seasonal peaks, coinciding with the production of new shoots.

5. Pronounced spatial variation in attack was observed in both species. At week 12, the number of attacks per block in *C. odorata* was negatively correlated with available calcium concentration ($r = 0.85$, $P < 0.001$), whereas mean height growth of *C. odorata* was positively correlated with available phosphate concentration ($r = 0.84$; $P < 0.001$) throughout the experiment.

6. Significant variation in the height to first damaging attack was also observed in both species; by the end of the period of observations, a total of only 6% and 0.4% of *C. odorata* and *S. macrophylla* respectively remained undamaged until over 3 m in height, the economically acceptable minimum for production of timber.

7. It is suggested that control methods for the mahogany shoot borer should take account of temporal dynamics in attack, and relationship to host phenology. For example, if pesticides

are used, application should be concentrated in that part of the growing season when new shoots are being produced. Manipulation of the soil nutrient status may also form part of an integrated approach to pest management.

Key-words: Mahogany shoot borer, pest resistance, pest dynamics, *Cedrela odorata, Hypsipyla grandella, Swietenia macrophylla*

Introduction

The mahogany shoot borer (*Hypsipyla* spp., Lepidoptera, Pyralidae) is one of the most important pests in tropical forestry, largely preventing the cultivation of members of the mahogany family (Meliaceae) in areas where these trees are native. In the neotropics, both *Cedrela odorata* L. (Spanish cedar) and *Swietenia* spp. (American mahogany) are attacked by larvae of *Hypsipyla grandella* (Zeller), which destroy the terminal shoots of the tree by tunnelling the pith. As a result, the tree branches or forks, reducing the economic value considerably (Newton *et al.* 1993). Attacks may be rapid and intense, as illustrated by Dourojeanni's (1963) observations of trials in Peru, where 60% and 10% of *C. odorata* and *S. macrophylla* trees were attacked in the first four months. Major efforts at reforestation using these species, involving the establishment of thousands of trees, have been abandoned because of shoot borer attack (Newton *et al.* 1993). For example, between 1935 and 1943, 835,000 *Swietenia* and 1,000,000 *Cedrela* trees were effectively destroyed by shoot borers in Puerto Rico (Martorell 1943).

Although a considerable research effort has been devoted to the development of pest control techniques (Whitmore 1976a,b), no practical method of control currently exists (Newton *et* *al.* 1993). Trials with sprayed insecticides have repeatedly failed because of the effects of rainfall, and the fact that the larvae are inaccessible (Grijpma 1974). Some success has been obtained with systemic insecticides such as carbofuran (Wilkins *et al.* 1976), although the same insecticide was found to be ineffective in trials in Puerto Rico (Whitmore 1976c) and Trinidad (Ramnarine 1992b). A serious attempt to develop and apply biological control methods was made in Trinidad in the 1960s and 1970s, involving the introduction of four parasitoids from India. Only one of the four species (*Trichogrammatoidea robusta*) successfully established itself, and no significant effect on shoot borer infestation was recorded (Cock 1985; Newton *et al.* 1993).

The life-cycle and flight behaviour of the insect have been studied in some detail (Ramírez Sánchez 1964; Roovers 1971). The moths are nocturnal, oviposition occurring during early morning or evening (Holsten 1977; Wilkins 1972). Flight activity is reduced when temperatures fall below 15 °C, and during heavy rain (Gara *et al.* 1973). The larvae enter the shoot immediately after hatching, then cover their entrance holes with a protective web covered with frass (Grijpma 1974). The larvae pass through five or six stages while feeding on the pith, spending around 10% of their time in web building activities on the surface of the plant. The duration of the larval stages is around 30 days, with the total life cycle lasting between 1 and 2 months (Ramírez Sánchez 1964; Roovers 1971). The moth may therefore pass through several generations per year, depending on climatic conditions and the availability of shoots (Grijpma 1974).

Despite the detailed information available concerning the life-cycle of *H. grandella*, the relative importance of the factors influencing attack by shoot borers are not well known. An understanding of these factors is essential if practical control methods are to be developed. This investigation was designed to assess the extent of temporal and spatial variation in shoot borer attack, in relation to host growth and phenology. This was achieved by the use of screening trials of *Cedrela odorata* and *Swietenia macrophylla* King established in Costa Rica

Materials and methods

The investigation was carried out at the Centro Agronómico de Investigación y Enseñanza (CATIE) in Turrialba, Costa Rica (9° 54' N Lat., 83° 40' W Long.) at an altitude of 600 m a.s.l., with a mean annual precipitation of approximately 2600 mm and a mean annual temperature of 22 °C. In the case of *C. odorata*, seed was collected from open-pollinated trees growing either singly or in small groups on farms, from four localities in Costa Rica (namely Carmona, Hojancha, Cañas and San Carlos) and one location in Trinidad (St Andrew). Trees were selected on the basis of stem straightness and lack of forking (clear bole > 7 m). Seed of *S. macrophylla* was obtained from bulked collections from five provenances (Haiti, Trinidad, Honduras and two from Puerto Rico). Seed was germinated in seed trays, then transferred to black polyethylene bags (2.2 litre capacity) containing a 1:1:1 mixture of forest soil, sand and organic compost, positioned in full sun in the CATIE nursery.

Two field trials, screening *Cedrela odorata* and *Swietenia macrophylla* respectively, were established on adjacent sites at Florencia Sur, CATIE, during February 1991. The soil of this site is of argillaceous texture, with a mean pH of 4.4, and by agricultural standards is particularly deficient in P and Ca (Bertsch 1986). Prior to establishment, the sites were cleared of exisiting vegetation (*Calliandra* and *Acacia* plantations) by hand, supplemented by application of herbicide. As the topography of the site is gently undulating, slope was the main factor taken into account in the blocking.

Seedlings were transferred directly from the polyethylene bags to planting holes of approx. 20 cm depth, then watered in. After two months, the few seedlings which had died were replaced with others from the appropriate seedlot. The trees were arranged in fully randomized 5-tree row plots, in nine replicate blocks, at a spacing of 2.5 x 2.5 m. The whole experiment was surrounded by a single-row border. In the second experiment, seedlings of *S. macrophylla* were arranged in fully randomized square plots of 25 trees in a 5 x 5 array, with five replicate blocks, at a spacing of 2.5 x 2.5 m. The trials were cleaned of weed growth by hand approximately every 3 months.

Each tree in both experiments was assessed for the incidence of shoot borer attack at 14 day intervals, starting on 22nd April 1991 and continuing for a total of 84 weeks. Assessments of attack were made by visually inspecting each plant, and counting the number of attack loci indicated by the presence of fresh frass. The trees were also assessed for the presence or absence of foliage. Tree height was measured after 26, 56 and 88 weeks. In addition, the two experiments were assessed after 141 and 177 weeks (*C. odorata* and *S. macrophylla* respectively) for height to first branching and for the number of damage loci, indicated by forking.

Data were analyzed by *t*-test or ANOVA and *F*-test, where appropriate, using SAS (SAS 1980). Correlations were carried out using SigmaPlot v5.0 (Jandel Scientific GmbH, Erkrath, Germany).

Results

A total of 4018 mm of rain fell at CATIE during the experimental period, values from 14-day intervals ranging from 0 - 278 mm (Figure 1a). Despite pronounced fluctuations from week to week, the rainfall did not decline below 39 mm in any 2-week period for the first 36 weeks of the experiment. A total of 211 mm was recorded in the following 18 weeks, indicating the onset of the dry season (January - April). Thereafter, rainfall again increased, reaching a peak of 234 mm at weeks 75-6. No rain was recorded in the final month of assessment, reflecting the onset of the dry season at the start of December 1992.

Although both experiments were established at the same time, height growth of *C. odorata* was more than twice that of *S. macrophylla* by the time of the first assessment at 25 weeks (Figure 1b). Thereafter height of *S. macrophylla* increased at a fairly constant rate, such that the overall mean at week 87 was 166 cm. The increase in height growth of *C. odorata* between weeks 25 and 55 was relatively slight, coinciding with the period of lower rainfall. However, growth rates increased thereafter, such that a mean growth rate of 1.8 cm per week was recorded between weeks 55 and 87. At weeks 141 and 177, mean tree heights were found to be 287 and 245 cm for *C. odorata* and *S. macrophylla* respectively, representing growth rates of 2.0 and 1.3 cm per week respectively.

Throughout the experiment, the majority of the *S. macrophylla* trees continually possessed foliage, the proportion with foliage declining to a minimum value of 87% at week 78 (Figure 1c). In contrast, *C. odorata* displayed pronounced seasonal variation in foliar phenology. Although > 90% of trees possessed foliage between weeks 10-32, values declined rapidly thereafter, with a minimum of 51% trees foliated at week 48. The majority of trees subsequently produced new foliage, with values of > 95% trees foliated after week 60. The proportion of trees with foliage declined again towards the end of the experimental period, with a minimum value of 89% recorded at week 84.

No shoot borer attacks were recorded on any of the *S. macrophylla* trees until week 50 (Figure 1d). The number of attacks recorded increased rapidly thereafter, particularly between weeks 58 and 60, when a maximum of 559 attacks was recorded in the trial as a whole. Values declined for the following 7 assessments, reaching a minimum of zero at week 74. A second peak in attack was recorded at week 78, when a value of 257 was recorded. In contrast, initial attack in *C. odorata* was recorded at week 6, with a peak of 245 attacks recorded at week 12. Attacks continued at a relatively low level (< 100) for the following 20 weeks, with < 10 attacks recorded at each assessment during weeks 32-48. After this time the number of attacks increased sharply, reaching a maximum value of 1529 at week 68, declining to 13 by the next assessment. Although the number of attacks increased again to 240 at week 72, values subsequently declined, with a value of 56 recorded at the last assessment after 84 weeks.

The pronounced temporal variation in attack was reflected in the cumulative proportion of trees which were attacked (Figure 1e). After week 48, the proportion of *S. macrophylla* trees attacked increased rapidly from zero to 55% by week 62 The cumulative proportion of attacked trees continued to increase throughout the remainder of the period of observations, such that by week 84, 77% of trees of this species had been attacked. The pattern of attack in *C. odorata* was markedly different, with 16% of the trees attacked by week 12. Values continued to increase gradually until week 60, and more rapidly thereafter, such that 74% had been attacked by week 84.

Pronounced spatial variation in shoot borer attack was recorded in both experiments. At week 12, when the first peak in attack was recorded in the *C. odorata* experiment, significant differences in the mean number of attacks per tree were recorded between the nine blocks ($P < 0.001$, ANOVA), values ranging from 0-0.4 in blocks 9 and 1 respectively. However, during the second peak at week 68 the pattern was quite different, the mean number of attacks per tree varying from 0.5-2.2 in blocks 8 and 4 respectively. Similarly, in *S. macrophylla* significant variation between blocks was recorded at week 6 ($P < 0.001$, ANOVA), values ranging from 0.8-1.5 in blocks 5 and 1 respectively. Height growth also varied between blocks ($P < 0.001$, ANOVA), the differences evident at the first assessment persisting throughout the period of observation. In *C. odorata*, mean tree height in block 5 was double that in block 1, whereas in *S. macrophylla*, the mean tree height in block 1 was greater than that in block 5 by a factor of 1.5, at the end of the experiment.

The relationship between spatial variation in attack and soil characteristics was examined by correlation. The number of attacks per block at week 12 in *C. odorata* was negatively correlated with soil calcium ($r = 0.85$; $P < 0.001$; Figure 2a). Although this relationship was no longer significant at the second peak in attack at week 68, mean attack was negatively correlated with total base concentration at this time ($r = 0.70$; $P < 0.05$; Figure 2b). Mean height growth of *C. odorata* per block was positively correlated with phosphate availability throughout the experiment ($r = 0.84$; $P < 0.001$ at week 87) (Figure 2c). Soil analyses were not available for each block in the *S. macrophylla* experiment.

The pattern of attack also differed between trees, some being attacked far more severely than others. For example, at the peaks of attack at weeks 12 and 68 in *C. odorata*, the number of attacks per tree varied from 0-5 and 0-15 respectively, with mean number of attacks of 0.23 ± 0.02 and 1.48 ± 0.06. In the peak attack at week 60 in *S. macrophylla*, the number of attacks per tree varied from 0-10, with an overall mean of 1.00 ± 0.07. The frequency distribution of number of attacks per tree differed slightly between the two species, with a modal percentage of attacked trees experiencing 3 attacks in the case of *C. odorata* in 1992 and 1 attack in the case of *S. macrophylla* (Figure 3a,b).

The mean number of damaging attacks per tree at the final damage assessments were 1.9 ± 0.04 on *C. odorata* (after 33 months) and 2.4 ± 0.03 attacks on *S. macrophylla* (after 41 months), when the modal percentage of attacked trees of both species was 2 damaging attacks per tree (Figure 4). The final damage assessments also showed large variation between trees in the height at which trees experienced their first damaging attack (Figure 5). A total of only 6% *C. odorata* and 0.4% *S. macrophylla* trees remained undamaged until over 3 m.

Discussion

The fact that over 94% of the trees of both *Cedrela odorata* and *Swietenia macrophylla* were attacked by shoot borers during the first three years of growth emphasizes the seriousness of this pest for the cultivation of these species. Other investigations have recorded similar levels of infestation. For example, in Amazonian Peru, Yamazaki *et al.* (1992) recorded percentage attack of up to 98% and 49% in experimental plots of *C. odorata* and *S. macrophylla* respectively, within the first 16 months after planting. By comparison, values of 47% and 53% were recorded for these two species respectively during the first two years growth in

Trinidad (Ramnarine 1992b), whereas Grijpma (1970) found that 60-100% of *C. odorata* and 33% of *S. macrophylla* trees were attacked in the first 13 months in Costa Rica. The results of these various investigations illustrate the fact that *H. grandella* is a serious problem throughout the natural range of both *C. odorata* and *S. macrophylla* (Newton *et al.* 1993).

The fact that no attacks were recorded in *S. macrophylla* until week 50, whereas 25% of *C. odorata* had been attacked by this time, suggests that *H. grandella* displays a degree of preference for the latter species. This trend has been noted in a number of other studies. For example, Roovers (1971) found that *H. grandella* oviposits a greater number of eggs on *C. odorata* than *S. macrophylla*, and Grijpma & Gara (1970a) recorded fewer attacks on *S. macrophylla* when the two species were compared in the same experiment. In feeding tests, larvae of *H. grandella* were found to display a slight preference for *S. macrophylla* over *C. odorata*, although this difference was not pronounced (Grijpma & Gara 1970b). Similar results were obtained in Peru, where *C. odorata* was consistently found to be attacked more often than *S. macrophylla* (Yamazaki *et al.* 1992). In contrast, Ramnarine (1992b) found that both *S. macrophylla* and *C. odorata* were attacked with equal frequency in trials in Trinidad, and Sanchez *et al.* (1976) found that in Costa Rican trials *S. macrophylla* was more susceptible to shoot borer attack than *C. odorata* by a factor of more than three. Differences in susceptibility to attack may reflect variation in the production of chemical attractants detected by ovipositing females, although differences in shoot growth and morphology may also be influential (Grijpma 1976). The fact that the proportion of trees attacked did not differ significantly between the two species by the end of the experiment described here suggests that *S. macrophylla* becomes more susceptible to attack as it ages, perhaps because the species produces more vigorous or succulent shoots once it has become fully established.

A complete absence of attack in the first year of growth was also recorded in another trial of *S. macrophylla* at CATIE in Costa Rica (A. C. Newton *et al.*, unpublished data).

Pronounced temporal variation in attack has been recorded in a number of other studies. For example, Ramnarine (1992b) observed that in Trinidad, < 1% of *C. odorata* trees were attacked between October and January, with peak attacks occurring in July and August, whereas in a separate study, Ramnarine (1992a) noted peaks in shoot borer activity in late May - early June and mid July - August. When weekly assessments were made of *S. mahagoni* in Florida, Howard (1991) found that the percentage of shoots which were infested peaked at values > 30% in May of each year, coinciding with the Spring flush of new foliage. Larval populations of *H. grandella* infesting *C. odorata* and *S. macrophylla* in Barinitas, Venezuela displayed 4-5 peaks between April - November, with highest values recorded in May (Roovers 1971). Shoot borer infestation of *S. macrophylla* was also found to be consistently highest in May for three successive years in Puerto Rico (Bauer 1987), whereas in Colombia, Neyra & Higuera (1985) found that *C. odorata* was attacked most heavily between July - September. The previous most detailed investigation of seasonal dynamics of shoot borer attack is that of Yamazaki *et al.* (1992), who observed that in the Peruvian Amazon, seasonal variation in attack precisely coincided with variation in rainfall, when averaged monthly. Attacks increased at the beginning of the rainy season in September, peaked in October, then gradually decreased thereafter. This pattern was attributed to variation in shoot production coinciding with the onset of rains after the dry season. Both *C. odorata* and *S. macrophylla* behaved similarly in terms of seasonality of new shoot production.

The importance of the availability of young shoots for attracting ovipositing females (Grijpma

& Gara 1970a) and for the development of larval populations (Roovers 1971) is well established. The results presented here indicated that shoot borer attacks in C. *odorata* peaked approximately eight weeks after the onset of refoliation. The relationship between shoot phenology and rainfall was not, however, so clear. Although leaf abscission in C. *odorata* coincided clearly with the onset of a relatively dry period, refoliation commenced prior to any significant increase in rainfall, a response which is not uncommon in tropical trees (Longman & Jeník 1987). Although leaf abscission was far less pronounced in *S. macrophylla*, the peak in attack roughly coincided with that of C. *odorata* and the production of new shoots. These results contrast with those of Vega (1987), who found no clear relationship between rainfall and attack in Amazonian Colombia, despite pronounced seasonal variation in both. In general, attacks were higher in the dry season, although the relationship with new shoot production was not assessed. As noted by Yamazaki *et al.* (1992), the fact that the number of shoot borer attacks does not remain high throughout continuously rainy periods is surprising, considering that both C. *odorata* and *S. macrophylla* will flush continually in such conditions. The fact that flight activity is reduced by high precipitation (Gara *et al.* 1973) may be of relevance in this context.

Although the availability of young shoots undoubtedly had a major impact on the patterns of shoot damage observed in this study, other factors are also likely to have been influential. The initial rise in shoot borer attack is dependent upon both shoot availability and the abundance of adult moths. In both tree species in this study, the main peaks in shoot borer attack were preceded by smaller peaks in shoot borer attack. This may have been due to the presence of two more-or-less distinct shoot borer generations, the adults of the first smaller peak in shoot borer attack giving rise to the second larger peak in attack. Without information on seasonal variation in the abundance of adult moths it is impossible to quantify the relative importance of moth and tree phenology. Another factor which may have had an impact on seasonal variation on the abundance of shoot borers is the action of natural enemies. The decline of the mid-year peak in abundance was possibly accelerated by mortality caused by predators, parasites or pathogens, an aspect which requires further investigation.

The first two years of the growth of the tree appear to be critical with respect to shoot borer attack. In support of the results presented here, Vega (1987) found that attacks were more frequent when trees were between 1 and 2 m tall, which concords with the typical flight height of 1 - 2 m recorded by Grijpma & Gara (1970a) and Ikeda *et al.* (1992). The fact that the mean height of *S. macrophylla* trees was < 1 m may account for the lack of attack in the first year recorded in this investigation. The main impact of shoot borer attack damage is on the form of the tree, rather than growth rate. Howard & Meerow (1993) found that the effect of shoot borer attack on height growth of *S. mahagoni* was insignificant, as by the end of the growing season, growth of a new leader shoot had fully compensated for the loss of shoot growth resulting from attack. However, lateral branching was significantly increased. A clear trunk of 3 m is considered to be the economically acceptable minimum for production of timber of these species (Vega 1987), which may be achieved within the first 1-3 years of growth. In this experiment 6% *C. odorata* and 0.4% *S. macrophylla* trees remained undamaged until over 3 m. The increase in the number of attacks in both experiments in year two clearly reflects the increase in size of the trees, and the increase in the number of available shoots.

The frequency distribution of attack indicates clearly that trees vary in the number of attacks received, an aspect often ignored in previous studies. In 1992, the modal value of attacks to *C. odorata* (excluding non-attacked trees) was 3, as also recorded by Yamazaki *et al.* (1992), and the modal value of attacks to *S. macrophylla* in 1992 was 1. The maximum figure of 10 attacks in one tree recorded by Yamazaki *et al.* (1992) is also similar to the values recorded here (10 and 15 in *S. macrophylla* and *C. odorata* respectively). As usually only 1-3 eggs are laid on each tree (Grijpma 1974), these results suggest that several females may have oviposited on the same tree in such cases. However, larval migration between trees has also been observed (Roovers 1971). Differences between trees in the number of attacks received may reflect variation in production of chemical attractants (Grijpma 1976), or may simply reflect variation in the number of shoot tips available for attack.

Few other studies have assessed spatial variation in attack. The contrasting pattern of spatial variation between the two years in the *C. odorata* trial, even though relative height growth in the different blocks was the same from year to year, may simply be attributable to random clustering. Grijpma & Gara (1970a) indicated that shoot borer attacks tend to be concentrated spatially, as the insects apparently do not disperse readily from sites of active infestation. No evidence of a switch from *C. odorata* to *S. macrophylla* in the dry season, as recorded by Grijpma & Gara (1970a), was observed here. The relationship between soil characteristics and incidence of attack is also a novel result. Vega (1976) found no effect of soil type on the incidence of attack in *Cedrela angustifolia*, the size and vigour of the plant being more influential. Among other lepidopteran forest pests, *Operophtera brumata* has also been shown to be influenced by calcium availability, although in this case larval weight and abundance were found to be negatively related to foliar calcium content (Hunter, Watt & Docherty

1991).

The results presented here are of relevance to the pest management of *H. grandella* in several ways. Most importantly, the fact that attacks are concentrated both in space and time suggests that if pesticides are used, applications should be preferentially applied to specific areas at those times of year when attack is likely to be concentrated. In addition, the apparent relationships of attack with soil mineral status suggest that manipulation of soil conditions (for example by fertilization) might also form part of a pest control system. Furthermore, the overriding influence of shoot phenology suggests that silvicultural systems where this could be manipulated might also be of value.

Although this study has shown the influence of several temporal and spatial factors on the attack by *H. grandella* to *C. odorata* and *S. macrophylla*, the occurrence of such variation in attack makes the role of host-susceptibility and tolerance difficult to assess. For example, the fact that some trees either escaped attack or experienced fewer attacks than others might indicate the occurrence of resistance characteristics, or could simply be due to chance. The genetic basis to these characteristics is examined in a separate paper (Newton *et al., in prep*).

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Figure captions

Figure 1(a). The rainfall recorded at CATIE, Costa Rica, during the first 86 weeks after establishment of the field trials. Values presented are totals for each two-week period.

(b). Height growth of *Cedrela odorata* (open symbols) and *Swietenia macrophylla* (closed symbols) trees in field trials at CATIE, Costa Rica. Values presented are means (n = 1125 and 625 respectively); vertical bars represent s.e.m.

(c). The proportion of *Cedrela odorata* (open symbols) and *Swietenia macrophylla* (closed symbols) trees with foliage in field trials at CATIE, Costa Rica during the first 86 weeks after establishment.

(d). The total number of shoot borer attacks recorded on *Cedrela odorata* (open symbols) and *Swietenia macrophylla* (closed symbols) trees in field trials at CATIE, Costa Rica during the first 86 weeks after establishment.

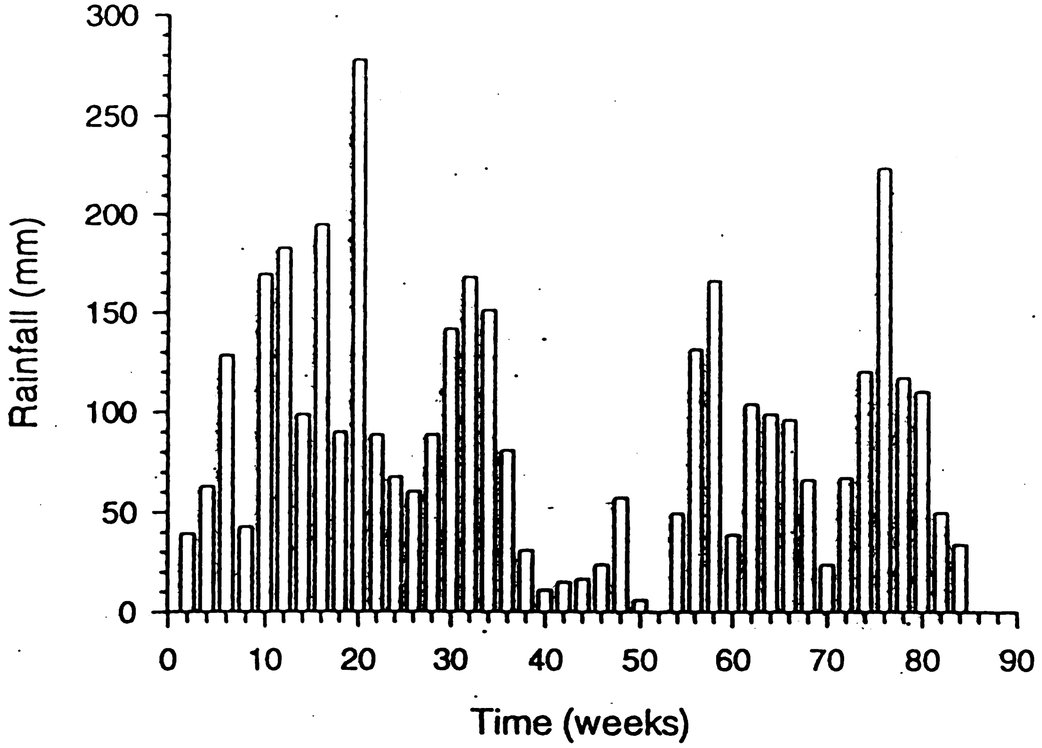
(e). The cumulative proportion of *Cedrela odorata* (open symbols) and *Swietenia macrophylla* (closed symbols) trees attacked by shoot borers in field trials at CATIE, Costa Rica during the first 86 weeks after establishment.

Figure 2. Correlations between (a) the mean number of shoot borer attacks per tree and the calcium concentration in the soil, at week 12 after establishment; (b) the mean number of shoot borer attacks per tree and the total base concentration in the soil at week 68 after establishment, and (c) mean tree height and phosphate concentration in the soil at week 87 after establishment, in a field trial of *Cedrela odorata* at CATIE, Costa Rica. For statistical analyses see text. Value presented are block means in each case.

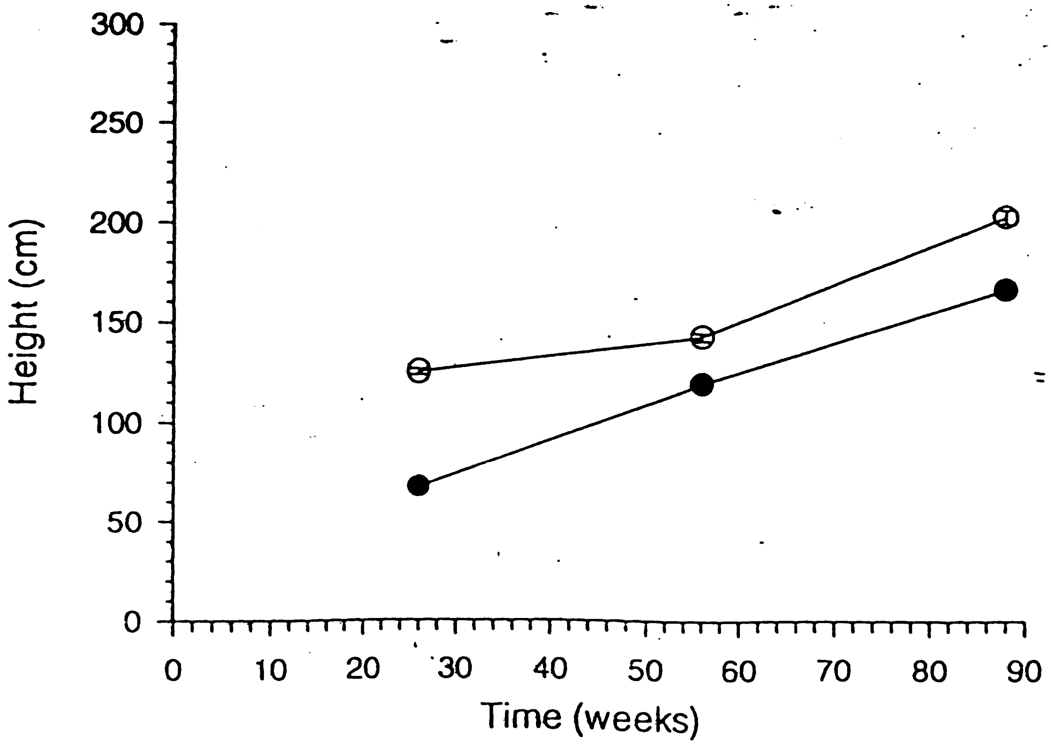
Figure 3. The frequency distribution of number of shoot borer attacks per tree in (a) *Cedrela odorata* at the peak in attack at week 68 after establishment, and (b) *Swietenia macrophylla* at the peak in attack at week 60 after establishment, in field trials at CATIE, Costa Rica.

Figure 4. The percentage frequency of the number of damaging attacks per tree in (a) *Cedrela odorata*, 33 months after establishment, and (b) *Swietenia macrophylla*, 41 months after establishment, in field trials at CATIE, Costa Rica.

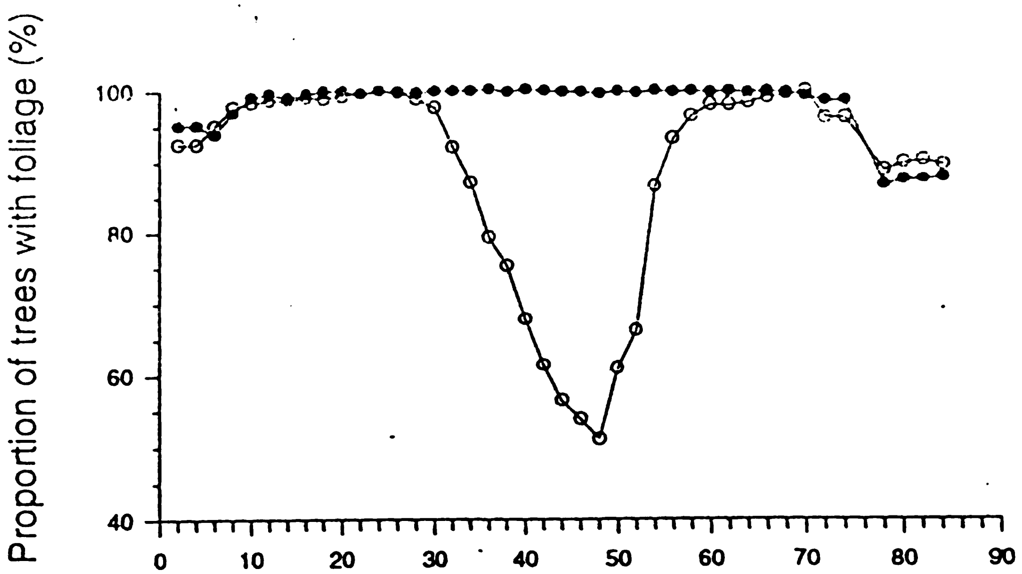
Figure 5. The percentage frequency of the height to first damaging attack in (a) *Cedrela odorata*, 33 months after establishment, and (b) *Swietenia macrophylla*, 41 months after establishment, in field trials at CATIE, Costa Rica.

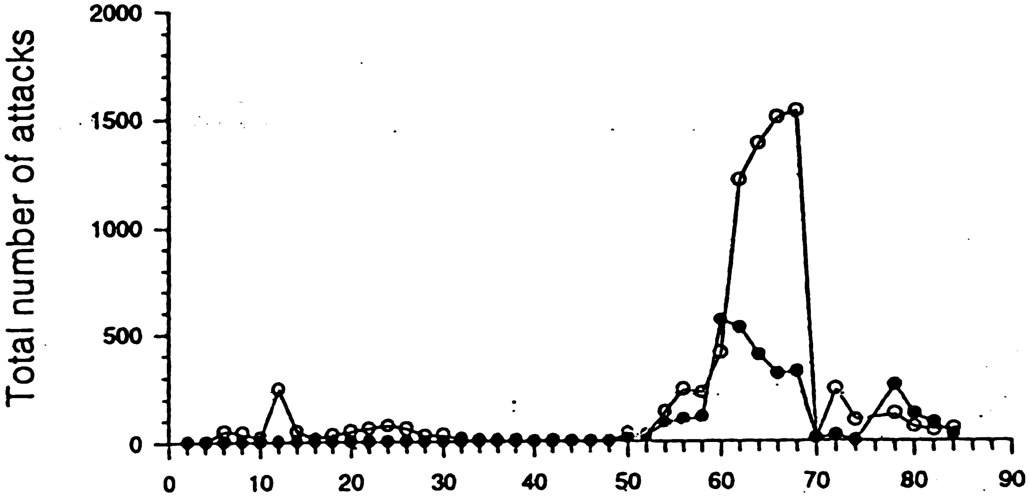


Rainfall (mm)
300
250
200
150
100
50
0
0
10
20
30
40
50
60
70
80
90
Time (weeks)



Height (cm)
300
250
200
150
100
50
0
0
10
20
30
40
50
60
70
80
90
Time (weeks)


Proportion of trees with foliage (%)
100
80
60
40
0
10
20
30
40
50
60
70
80
90


Total number of attacks
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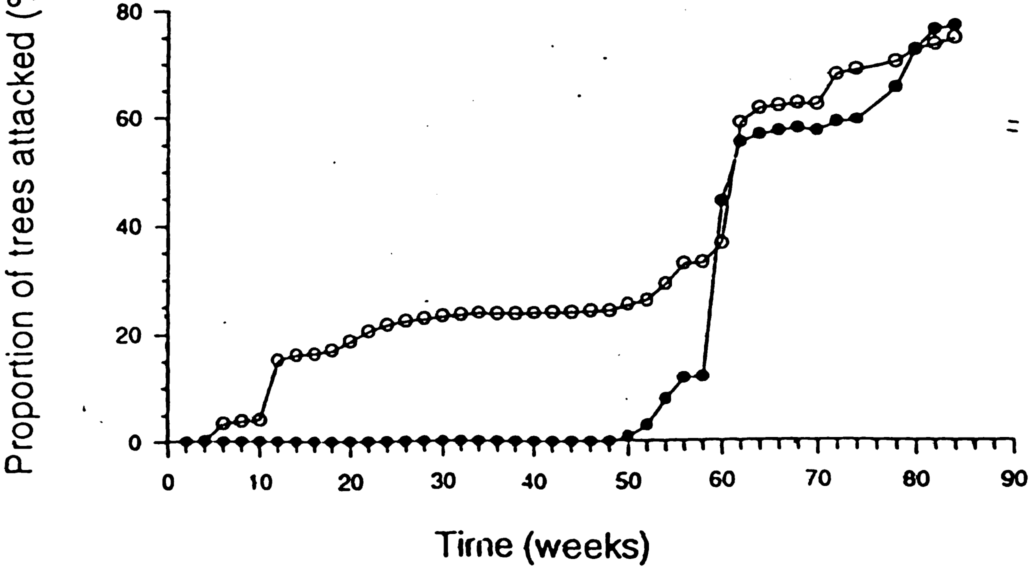
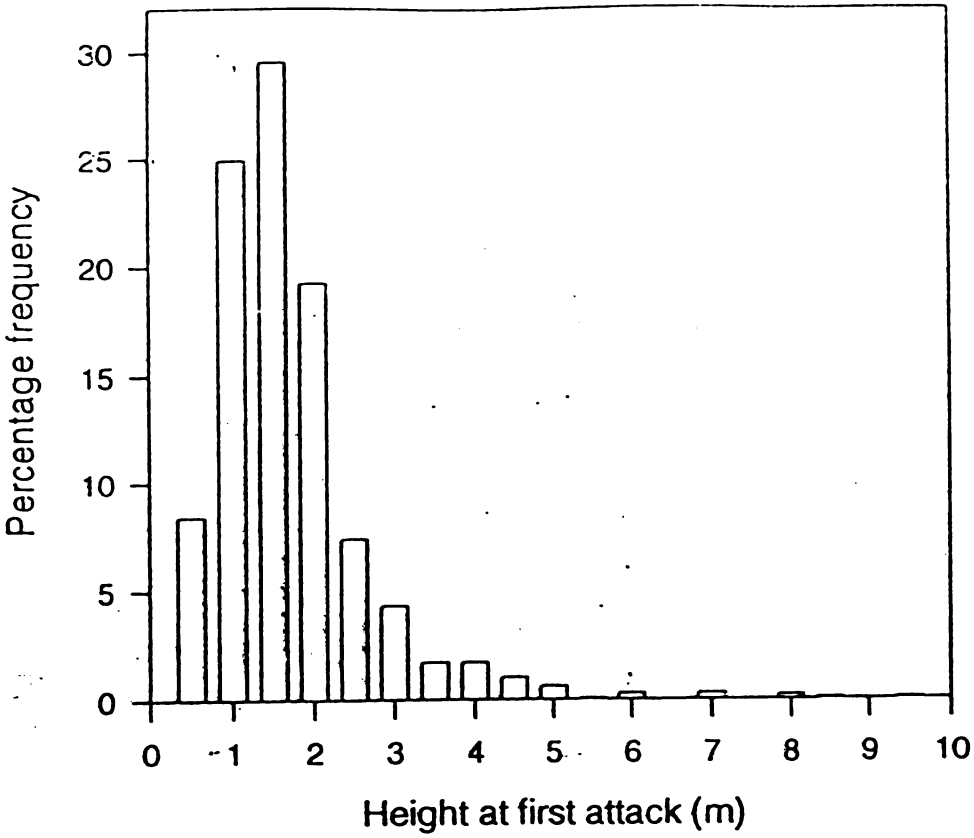
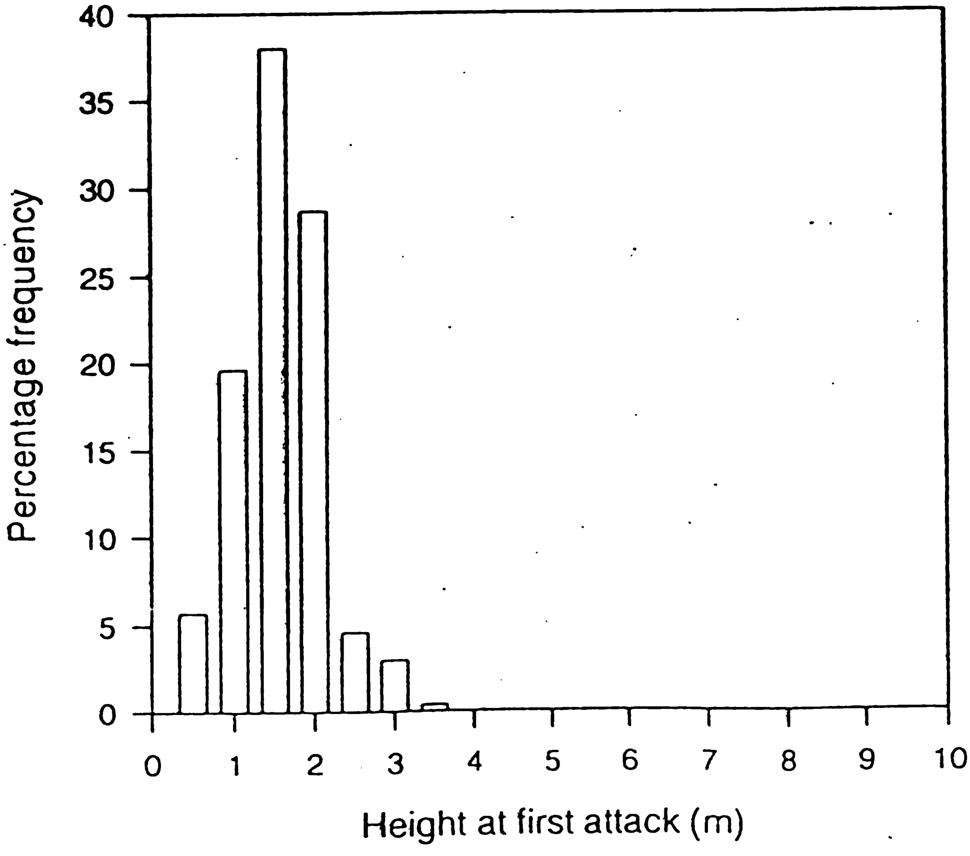
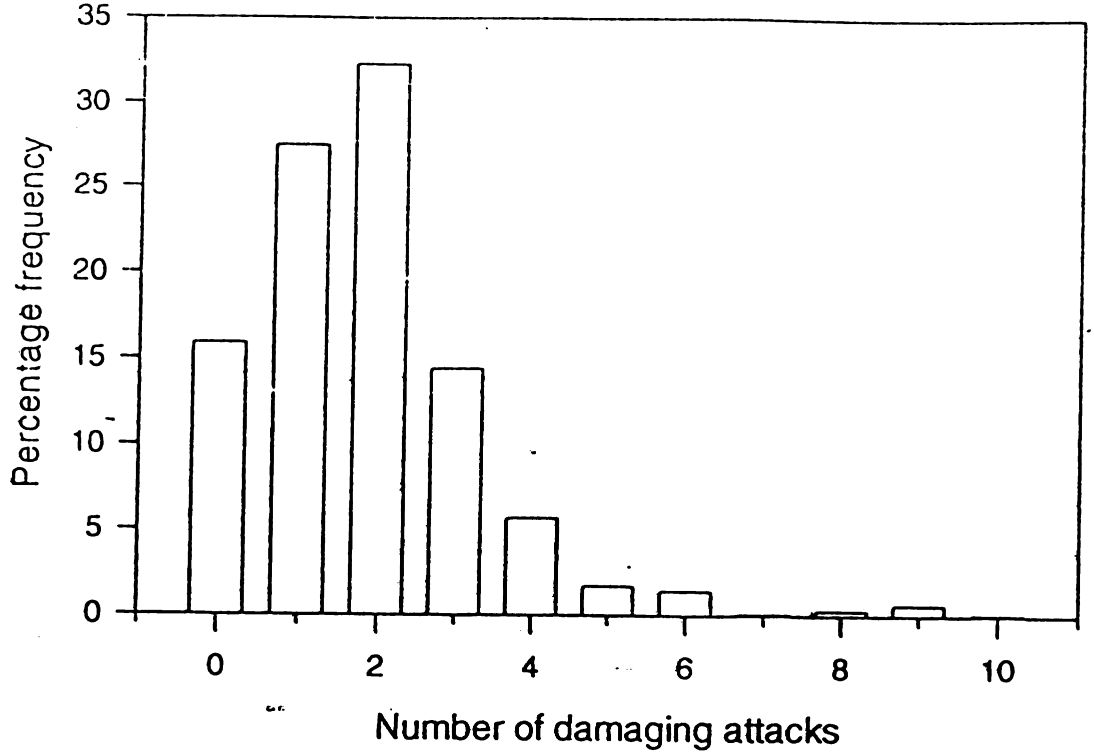
1500
1000
500
0
0
10
20
30
40
50
60
70
80
90

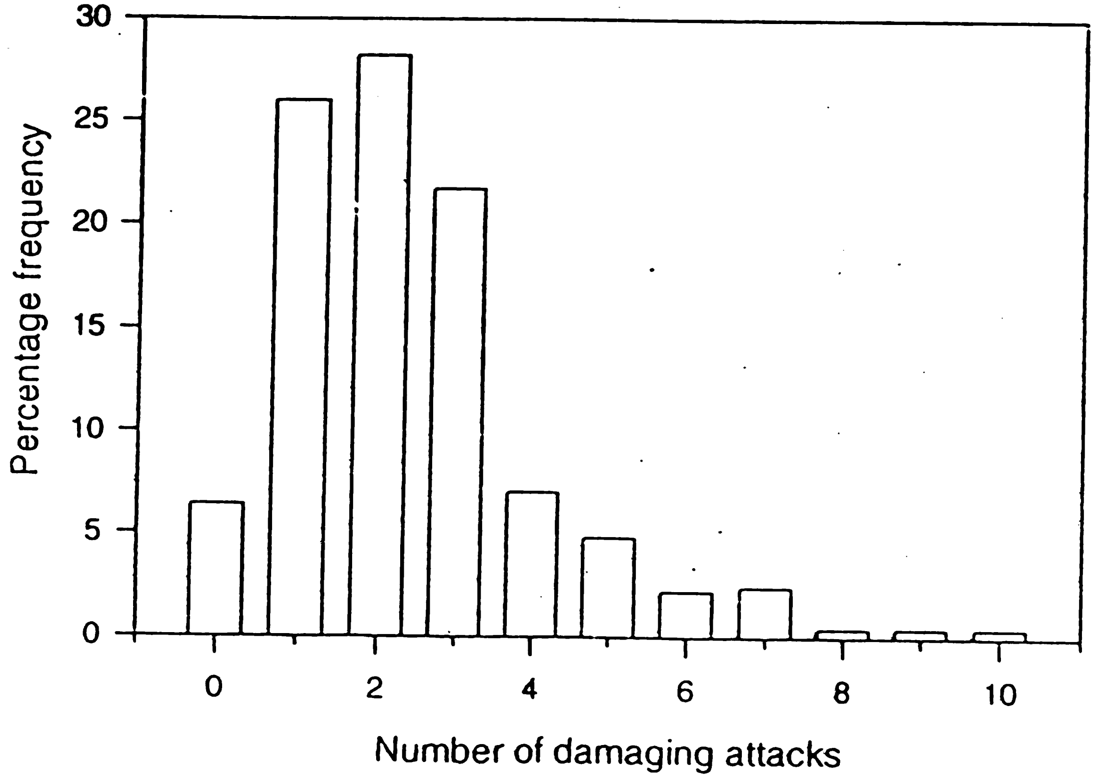

Proportion of trees attacked (%)
80
60
40
20
0
0
10
20
30
40
50
60
70
80
90
Time (weeks)


30
25
20
15
10
5
0
Percentage frequency
0
1
2
3
4
5
6
7
8
9
10
Height at first attack (m)

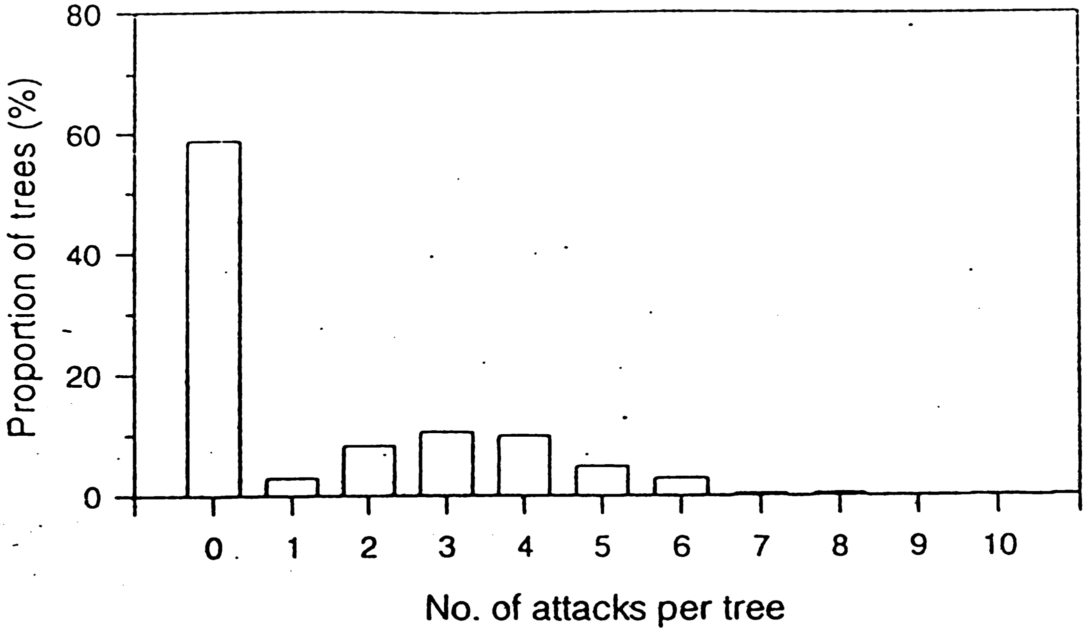

40
35
30
25
20
15
10
5
0
Percentage frequency
0
1
2
3
4
5
6
7
8
9
10
Height at first attack (m)

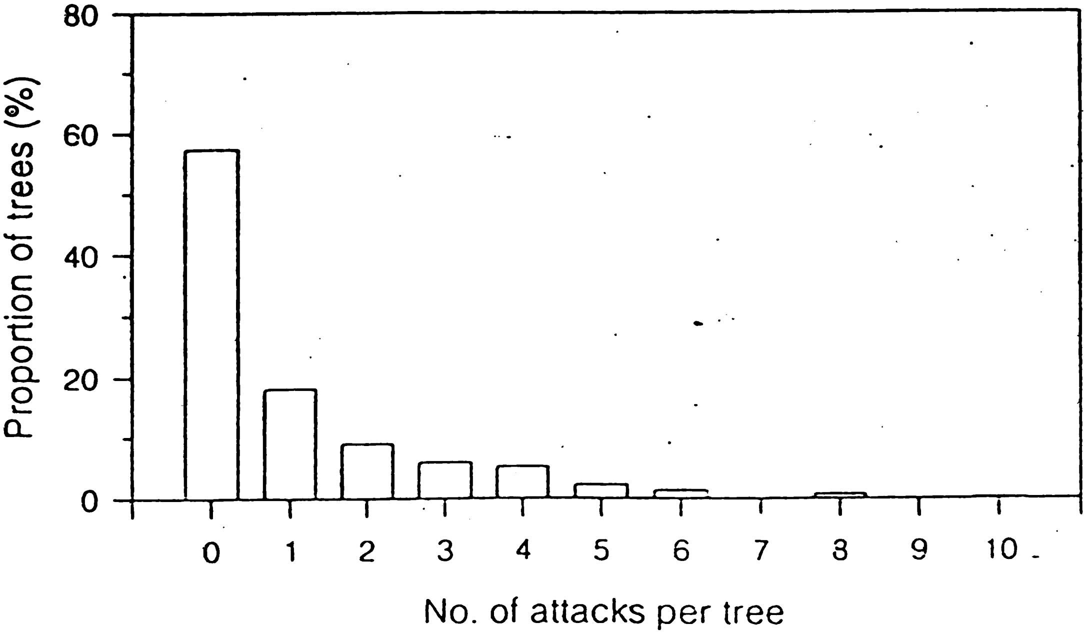


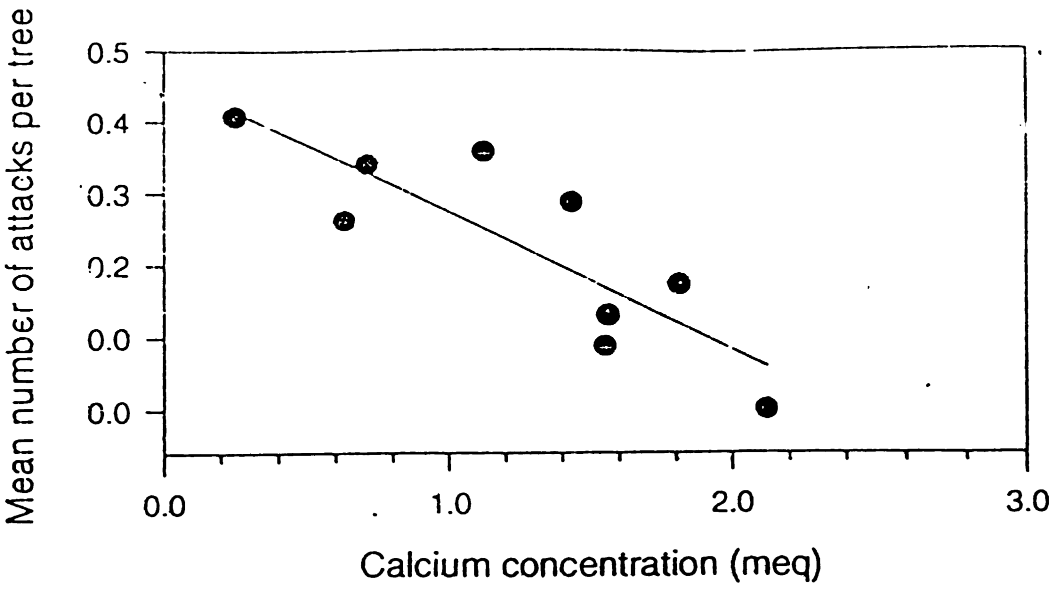
35
30
25
20
15
10
5
0
Percentage frequency
0
2
4
6
8
10
Number of damaging attacks



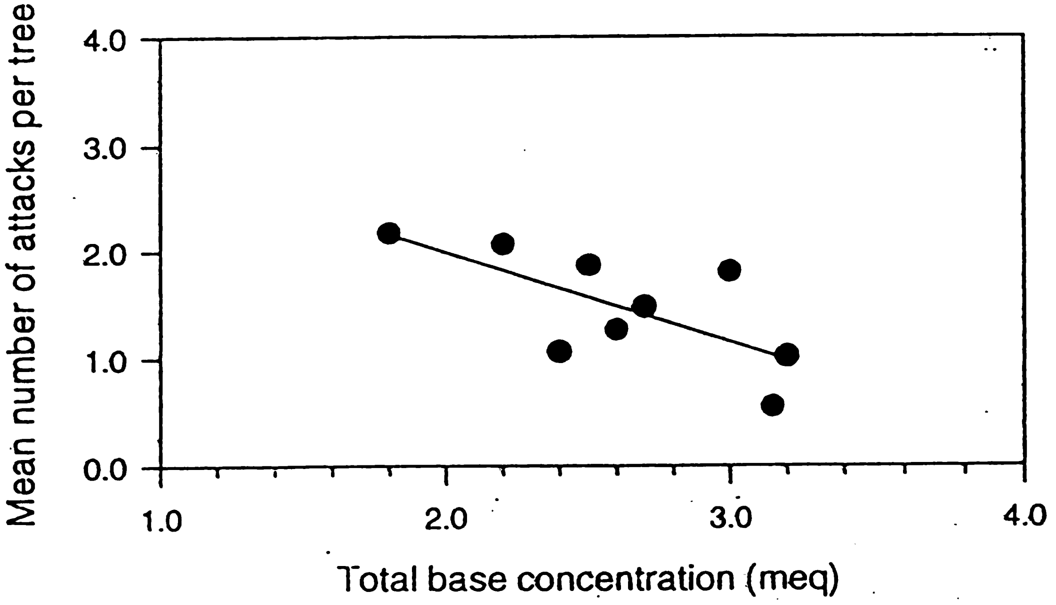
30
25
20
15
10
5
0
Percentage frequency
0
2
4
6
8
10
Number of damaging attacks


Proportion of trees (%)
80
60
40
20
0
0
1
2
3
4
5
6
7
8
9
10
No. of attacks per tree

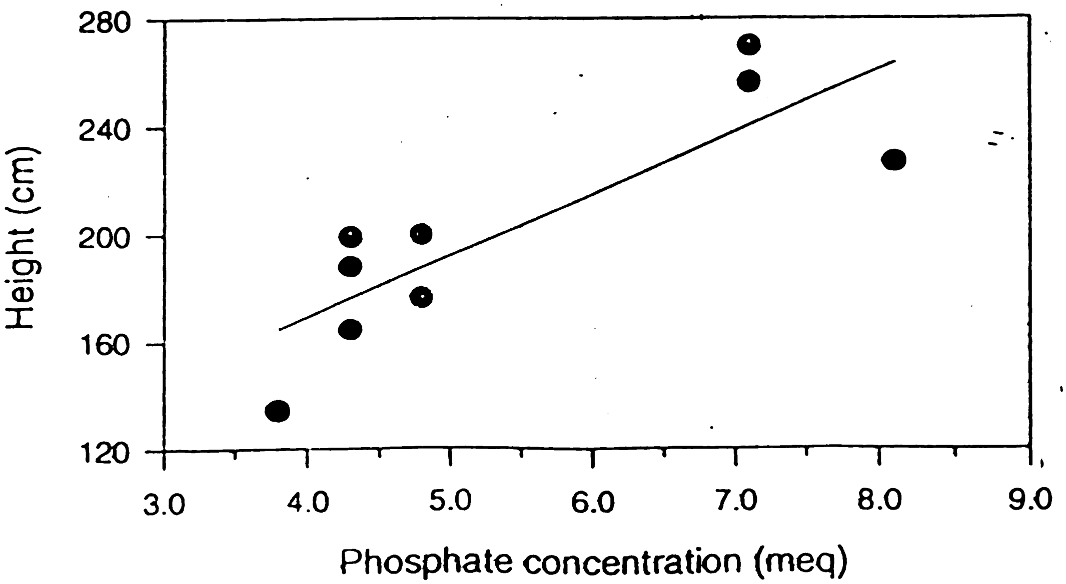

Proportion of trees (%)
80
60
40
20
0
0
1
2
3
4
5
6
7
8
9
10
No. of attacks per tree



Mean number of attacks per tree
0.5
0.4
0.3
0.2
0.0
0.0
0.0
1.0
2.0
3.0
Calcium concentration (meq)



Mean number of attacks per tree
4.0
3.0
2.0
1.0
0.0
1.0
2.0
3.0
4.0
Total base concentration (meq)



Height (cm)
280
240
200
160
120
3.0
4.0
5.0
6.0
7.0
8.0
9.0
Phosphate concentration (meq)

Mahogany as a genetic resource

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ABSTRACT

The development of a strategy for the sustainable management and conservation of mahogany is an urgent priority. Such a strategy should be based upon clear information about the extent of genetic differentiation within and between populations, and on an understanding of the processes maintaining this variation. At present, such information is very limited for mahogany. Preliminary data are presented from two genetic tests of *Swietenia macrophylla* King (Meliaceae), indicating significant differences between provenances and half-sib progenies in both growth and form characteristics. In addition, the use of molecular markers for the characterization of genetic resources of mahogany is discussed. On the basis of the results available, the impacts of deforestation and logging activities on genetic resources are evaluated. Although both deforestation and selective logging may deplete genetic resources, no quantitative information on the extent of such depletion in mahogany is currently available. Additional research is therefore required before clear guidelines can be provided for the sustainable management of mahogany.

KEY WORDS: *Swietenia* - genetic variation - conservation - sustainable management

CONTENTS

INTRODUCTION

The economic importance of mahogany is beyond question. The demand for mahogany timber remains high, particularly in the USA and the UK (Sullivan, 1993; Rodan, Newton & Verissimo, 1992), and finely finished mahogany products continue to fetch high prices (Palmer, 1994). Despite this, little attention has been given to how resources of mahogany may be sustainably managed and conserved. Consideration of mahogany from a genetic perspective is of fundamental importance in this context, because the genetic viability of any forest resource underpins both economic and environmental viability. From an environmental standpoint, sufficient genetic variation must exist to maintain natural populations as evolutionarily viable units able to adapt to changing conditions in the long term. For sustainable economic viability, the resource must be able to produce revenues indefinitely. Sustainable production is threatened if those genetic characteristics of value, such as wood quality or pest resistance, are lost. This is equally true whether the species is harvested from natural forests or cultivated in plantations.

Sustainable management of forest genetic resources may be considered to comprise three components: (i) characterization, (ii) conservation and (iii) sustainable use (Newton, Cornelius & Corea, 1994a; Cornelius, Corea & Mesén, 1994). This paper considers each of these aspects separately with respect to mahogany. However, for an effective management and conservation strategy to be developed, these three components need to be closely integrated (Newton *et al.*, 1994a). The paper focuses on *Swietenia macrophylla* King (Meliaceae), currently the main species of commercial interest, although reference to other *Swietenia* species is made where appropriate.

CHARACTERIZATION OF GENETIC RESOURCES

The main methods of characterizing genetic resources of forest trees involve the assessment of morphological variation (including growth characteristics), or the use of biochemical or molecular markers. Morphological variation in *Swietenia* is discussed elsewhere (see Helgason *et al.*, this volume) in the context of taxonomic classification. To test whether variation in any particular morphological or growth characteristic has a genetic basis, it is desirable to conduct a genetic test, such as a provenance or progeny trial (Zobel & Talbert, 1984). Preliminary results from such tests of *Swietenia macrophylla* are presented below. The use of molecular markers is also described in some detail, as these techniques are now being applied to the analysis of genetic variation in mahogany and are likely to play an increasingly important role in the future.

Results from genetic tests of Swietenia *spp.*

Very few data are available from genetic tests of mahogany, as few tests have been established (Newton, Leakey & Mesén, 1993b). As noted by Palmer (1994), the most thorough provenance collections of both *Swietenia macrophylla* and *S. humilis* were those made by the Institute of Tropical Forestry in Puerto Rico during 1964-5. The initial aim was to collect from 41 locations in the case of *Swietenia macrophylla* and 7 in the case of *S. humilis* (Barres, 1963), although in the event, the number of collections of *S. macrophylla* was reduced to 14 locations in Mexico and C. America (Boone & Chudnoff, 1970). The seed was established in seven contrasting locations in Puerto Rico. Chudnoff & Geary (1973) analysed wood density of 12 progenies of *S. macrophylla* at each of four of these locations, sampling one tree per progeny per site. Highly significant differences between progenies were recorded, mean values ranging from 0.48 to 0.57 g cm^{-3}. The same trials were assessed for both growth and form traits by Glogiewicz (1986), who again recorded different differences between provenances of *S. macrophylla*, although these were not consistent across the different sites.

More recently, two genetic tests of *S. macrophylla* were established in Costa Rica and Trinidad (in 1991 and 1990 respectively), as part of a collaborative project between the Centro Agronómico de Investigación y Enseñanza (CATIE), Costa Rica, the Institute of Terrestrial Ecology, Edinburgh, UK, the International Institute of Biological Control (IIBC), Trinidad, and the Trinidadian Forest Service. Details of the experimental designs and seed origins employed are given in Table 1. The trials were assessed for height growth and incidence of pest attack 30-33 months after establishment, depending on the trial. In the combined provenance/progeny test established at CATIE, mean height growth of different progenies ranged between 245 and 471 cm after 33 months (Fig. 1a). Similarly, in the progeny test in Trinidad, mean height growth of the different half-sib families varied between 357 and 470 cm after 30 months (Fig. 1b). In the former trial, the maximum family mean was

192% of the minimum value, giving an indication of the extent of genetic variation recorded The effect of genetic origin (either provenance or family) was statistically highly significant ($P < 0.001$; ANOVA, F test) in both of the trials. individual-tree narrow-sense heritabilities of height growth in the Costa Rican and Trinidadian trials were 0.38 ± 0.12 and 0.11 ± 0.06, respectively. Although these results are preliminary in nature, based on tests with only a limited range of material and after fewer than four years' growth, they indicate clearly that significant genetic variation exists both within and between different mahogany populations in terms of height growth.

One of the purposes of these trials was to screen for pest resistance, as attacks by shoot borers (*Hypsipyla* spp.; Lepidoptera: Pyralidae) are the main factor limiting cultivation of mahoganies, particularly in areas where they are native. The larvae of these moths live inside the stem, tunnelling the pith, and killing the apical parts of the shoot (Grijpma, 1976). Although attack rarely kills the tree, the stem branches or forks as a result, reducing the economic value of the tree significantly. This pest is very widespread and often extremely damaging, as no economically viable methods of control are currently available. The life cycle of the moth, and the previous experience with different control methods, were recently reviewed by Newton *et al.* (1993a).

The response of *Swietenia macrophylla* to shoot borer attack was assessed by scoring each tree in the genetic tests for the number of damage sites (branching or forking points). This gives an indication primarily of variation in susceptibility to attack, but may also be used to identify individuals that are able to tolerate attack by recovery of the leading shoot (cf. Grijpma, 1976). In the progeny tests established in Costa Rica and Trinidad, family mean number of attack sites varied between 2.2 - 4.7 and 2.7 - 4.4, respectively (Fig. 2a,b). The most pronounced genetic variation was recorded in the Bajo Chino trial at CATIE, where the maximum family mean was 217% of the minimum value. The effect of genetic origin (either provenance or family) was statistically significant in both of the trials ($P < 0.001$ in the Costa Rica trial and $P < 0.023$ in the Trinidadian trial; ANOVA, F test). Individual-tree narrow-sense heritabilities of number of forking points in the Costa Rican and Trinidadian trials were 0.56 ± 0.15 and 0.42 ± 0.12, respectively. The results from these trials indicate that significant genetic variation exists within *S. macrophylla* in terms of susceptibility to pest attack. This suggests that there may be scope for the development of pest-tolerant planting stock for use in reforestation, through a programme of genetic improvement (Newton *et al.*, 1993a,b; Grijpma, 1976). Long-term trials, testing a wider range of material, are required to develop this approach.

The preliminary results reported here, indicating variation in height growth between half-sib families by up to a factor of two, suggest that the extent of genetic variation in mahogany is comparable with that of other tropical tree species. For example, in a range of tests with a number of different tropical timber species, productivity of the most superior provenances was found to be 26-276% higher than the mean values of the respective trial (Newton *et al.*, 1994a). Similarly, the international provenance tests of *Cedrela odorata*, which is in the same family as *Swietenia macrophylla*, identified provenance variation in height growth by up to a factor of six (see papers in Burley & Nikles, 1973; Nikles, Burley & Barnes, 1978). Individual-tree narrow-sense heritabilities for growth and form traits of forest trees tend to fall within the range 0.1-0.4 (Cornelius, 1994), indicating that the heritabilities recorded here for *S. macrophylla* are comparable with those of a wide range of other species. Together, these figures indicate the gains that might be achieved in a genetic improvement programme of *S. macrophylla*, if a wide range of material were tested.

The use of molecular markers for estimation of genetic diversity

Molecular markers are increasingly being used for detection and analysis of genetic diversity within and between plant populations. This is because molecular markers are not subject to environmental selection pressure in the same way as morphological characters, and the differences they detect have a genetic basis. A number of different molecular markers are currently available, some of which are described below. The application of these techniques to the study of genetic variation in mahogany is at an early stage. Helgason *et al.* (this volume) describe the application of these techniques to resolving taxonomic problems within the genus *Swietenia*, with particular reference to chloroplast DNA. A number of other studies are currently in progress, as indicated below.

(i) *Isozymes*

Isozymes are the most frequently used markers for assessment of genetic variation within and between plant populations, enabling a large number of individuals to be screened rapidly at one time. In a recent review, Hamrick & Godt (1990) analysed the results of studies that used isozymes to examine the population genetic structure of more than 400 different plant species. They established that, on average, 50% of isozyme loci in plant species were polymorphic and mean genetic diversity at the species level, measured in terms of average expected heterozygosity over the loci examined, was 15%. Within a population, however, values were reduced, with 34% of loci polymorphic and genetic diversity estimated to be 11%. Hamrick & Godt (1990) also concluded that species with widespread geographic ranges tend to have relatively high degrees of genetic variation. On the basis of this, *S. macrophylla* would be expected to display a high degree of variation, as the species ranges from Mexico to Brazil (Styles in Pennington, 1981). Although no published data are currently available for mahogany, current studies at the Oxford Forestry Institute (Dr D. Boshier, personal communication) are employing isozymes to study gene flow and the genetic structure of populations of *Swietenia humilis* and *S. macrophylla* in Central America.

(ii) *Randomly Amplified Polymorphic DNA (RAPDs)*

Amplification of DNA samples via PCR with random primers results in the production of markers known as Randomly Amplified Polymorphic DNAs, or RAPDs. These banding patterns can be used to "fingerprint" individual taxa (Devos & Gale, 1992; Hadrys, Balick & Schierwater, 1992). They have also been used to elucidate species relationships (Halward *et al.*, 1992; Stiles *et al.*, 1993), as markers linked to particular quantitative traits (Hayley *et al.*, 1993) and to measure genetic diversity within and between plant populations (Chalmers *et al.*, 1992). The technique is relatively quick and simple, although in some studies results have been inconsistent. Chalmers *et al.* (1994) used RAPDs to differentiate between genera of the Meliaceae, and showed that this technique may be used to detect variation both within and between mahogany species. A collaborative EC-funded project between CATIE, ITE, INRA and the University of Edinburgh is currently in progress, aimed at quantifying the degree of genetic differentiation between populations of *S. macrophylla*, primarily using RAPDs.

(iii) *Microsatellites (Simple Sequence Repeats or SSRs)*

Microsatellites (also called simple sequence repeats, or SSRs) are composed of short tandem repeats of DNA and vary in terms of the number of repeats present at each particular locus in different individuals. A large number of loci are present throughout the entire genome, and the level of variation is relatively high. The technique has the advantage over RAPDs in that heterozygous individuals can be readily identified, although the development of primers can take a significant amount of time and effort. Primers for *Swietenia* spp. are currently being developed by the Oxford Forestry Institute in collaboration with the Scottish Crops Research Institute, Dundee.

Hopefully the research in progress will provide clear information, not only about the extent of genetic variation in mahogany, but also about the processes maintaining it and about the effects of human disturbance. As results become available, they should also be of value in according conservation priorities to different mahogany populations.

GENETIC CONSERVATION

In recent years, there has been increasing concern about the conservation of *Swietenia* species, as reflected in the listing of both *S. humilis* and *S. mahagoni* on Appendix II of CITES, and the 1994 proposal to include *S. macrophylla* (Rodan *et al.*, 1992; CITES proposal, 1994). Both the International Board for Plant Genetic Resources (IBPGR) and the Food and Agriculture Organization of the United Nations have accorded high priority to the conservation of *Swietenia macrophylla* (Rodan *et al.*, 1992). However, at present, no organization has attempted to develop or implement an overall strategy for the conservation of mahogany. Such a strategy is urgently required (Newton *et al.*, 1993b; Sullivan, 1993).

S. macrophylla is included in a number of national parks and forest reserves, such as the Biosphere Reserves Montes Azules in Chiapas (c. 331 000 ha) and Calakmul in Campeche

(c. 700 000 ha) in S. Mexico, and the Mayan Biosphere Reserve (1.5 million ha) in the northern Petén, Central America (CITES proposal, 1994). In addition, some 3.5 million ha of parks and reserves have been created within the mahogany zone of Brazil (CITES proposal, 1994). However, the enforcement of these protected areas is clearly problematic, and illegal logging is known to be widespread (see Watson, this volume). Without information about the pattern of genetic variation in the species, it is impossible to assess the number and distribution of populations needed to conserve a high proportion of genetic diversity, and therefore to judge whether current *in situ* initiatives are sufficient. In such a situation the safest conservation strategy requires conserving as much as possible, without according priorities (National Research Council, 1991). Apart from resource characterization, future research on mahogany should be aimed at defining the minimum viable population size and the associated area required for effective conservation (Primack, 1993).

In addition to *in situ* conservation, techniques are available for the conservation of selected genotypes *ex situ*. Significant progress has been made in defining the appropriate conditions for long-term storage of mahogany seed (see Tompsett, 1994; and this volume). Protocols for *in vitro* propagation of *Swietenia* species have been successfully developed in Singapore (Lee & Rao, 1988), and mahoganies may also be vegetatively propagated using low-technology approaches by taking leafy cuttings (Newton *et al.*, 1994b). However, additional research is required to define the optimum conditions for the multiplication of mahogany germplasm using these techniques.

Few living collections of mahogany have been established with the aim of genetic conservation in mind. The most important such collection is probably the provenance tests established in Puerto Rico (Chudnoff & Geary, 1973) which constitute a significant gene bank. Characterization of this resource is required, using the approaches described earlier, before its usefulness can be fully assessed. The extensive plantations in areas such as Indonesia, Fiji and Sri Lanka (see Evans, 1992) include economically important genotypes, although the ultimate origin of the material is often unknown, and again the extent of genetic variation needs to be analysed before their conservation value can be ascertained. Collections established for *ex situ* conservation could usefully form the basis of breeding populations for genetic improvement, as well as assisting in the conservation of particularly valuable genes or gene complexes (Zobel & Talbert, 1984).

Although the techniques for effective genetic conservation of mahogany are available, they are not currently being implemented in a co-ordinated fashion. What is required is an integrated strategy, involving both *in* and *ex situ* approaches, based on sound information about the nature of the resource. As the species has such a broad distribution, the implementation of such a strategy would require collaboration between a wide range of different organizations, and significant international co-ordination (Newton *et al.*, 1994a). Recommendations for the development of such a strategy for Brazil were presented by Barros *et al.* (1992).

SUSTAINABLE USE

As noted by Ledig (1988), there is no biological reason why conservation objectives cannot be combined with forest use, provided the management system employed is designed appropriately. As described elsewhere (see papers by Snook and Verissimo, this volume), the key to sustainable management of mahogany lies in an understanding of the effects of forest disturbance on regeneration processes and growth. The sustainability of forest management may also be considered from a genetic standpoint. In particular, populations of mahogany need to be maintained which can persist indefinitely as evolutionarily viable units. As populations of tree species decline in size, the degree of inbreeding tends to increase, reducing the amount of genetic variation. This may restrict the ability of the population to adapt to environmental change, leading to a further decline in population size and an increasing susceptibility to extinction (Gilpin & Soulé, 1986). The processes countering these effects, such as gene flow from neighbouring populations, are poorly understood for mahogany. Research on the effects of forest disturbance and fragmentation on the gene flow and genetic diversity in *Swietenia* species, such as the current programme at the Oxford Forestry Institute (Boshier, 1994), should contribute greatly to the development of silvicultural systems which will ensure the long-term survival of managed populations.

One aspect which has attracted particular debate is whether selective logging may contribute to the genetic erosion of mahogany stands. This process is thought to have degraded resources of two pine species in the USA (Ledig, 1986), and the poor form of a number of Mexican pine species is attributed to the same cause (Jasso, 1970). Similarly, in Roatán, Bay Islands, Honduras, populations of *Pinus caribaea* var *hondurensis* seem to have degenerated phenotypically. This forest was described in 1742 as possessing trees of a sufficient size for production of masts for merchant vessels; by the late 1980s, the forests were considered phenotypically of poor form, with no trees of acceptable form for this purpose (Cornelius *et al.*, 1994). The evidence that genetic erosion has occurred in mahogany is largely based on similar field observations. Styles in Pennington (1981) stated that *S. mahagoni* is a prime example of genetic erosion resulting from past exploitation of preferred genotypes, because those populations that remain are almost entirely composed of highly branched trees. Styles & Khosla (1976) suggested that genetic erosion has also occurred among other species of *Swietenia*, as trees of good form are now rare and only remain in inaccessible places

No quantitative information is currently available to assess whether or not genetic erosion has in fact occurred in apparently depleted populations. From a theoretical standpoint, it is conceivable that the selective removal of trees of superior form (long, straight trunks) could deplete a population of particular genetic combinations, if variation in form has a significant heritable component (Zobel & Talbert, 1984). In forest trees in general, mean heritabilities for traits such as stem straightness and branching are similar to values for height, diameter and volume growth, although rather lower than specific gravity (Cornelius, 1994). The results presented here confirm that both growth and form traits are under significant genetic control in mahogany. Loss of gene complexes associated with superior form is therefore likely to occur as a consequence of selective logging (Zobel & Talbert, 1984), even if the process is difficult to quantify. It is also worth noting that if pest resistant trees were present in a population, these genotypes would also tend to be removed by logging activities (Newton *et al.*, 1993b).

Whether or not logging will cause genetic erosion will largely depend on the genetic structure and age distribution of the population, as well as the silvicultural system used. Ledig (1992) highlighted the importance of harvesting intensity: impacts of logging on genetic variation are likely to be higher the greater the proportion of trees removed, particularly if only the poorest formed trees are left after logging. With mahogany, in the cases where very few trees are recorded in the smaller size classes (as described by Snook and Verissimo, this volume), removal of the largest trees could have a very severe effect on total genetic variation of a population. In such circumstances, it is conceivable that a single harvest could cause significant genetic erosion, particularly if individual populations tend to be genetically distinctive.

Logging may also increase the incidence of inbreeding, by reducing the density of reproductively mature individuals (Ledig, 1992). This could have implications for the evolutionary viability of an individual population. For example, in *Shorea congestifolia*, logged populations wre found to have a lower rate of outcrossing than populations in unlogged forests (Murawski, Dayanandan & Bawa, 1994). Similarly, Hall, Orrell & Bawa (1994) described the impact of logging on the mating system of *Carapa guianensis*, another member of the Meliaceae, using isozymes. In this case no effect of logging on outcrossing rate was recorded although, perhaps atypically, the logged populations had a higher density of trees than the unlogged populations. This kind of research approach is required with *Swietenia macrophylla*, to define how genetic variation is distributed within and between populations and to define the genetic effects of logging. The molecular techniques described above have particular value in this context. Such information would be relevant to defining appropriate selection intensities during logging operations, to ensure their long-term sustainability.

Another key aspect of sustainable management of genetic resources is the conservation of characteristics that are of current or potential economic value for breeding purposes (Newton *et al.*, 1994b; Zobel & Talbert, 1984). Although few programmes of genetic improvement have been initiated with mahogany, there is clearly great potential for genetic gains to be made in growth and yield, and this approach is likely to become more important as plantation forestry of mahogany develops in the future. Genes that confer pest resistance should obviously be accorded particularly high priority for conservation, although many other characteristics (such as wood density and growth rate) are of obvious economic importance. As has been repeatedly pointed out (Zobel & Talbert, 1984; Ledig, 1988), it is difficult to predict which characteristics will be required by tree breeders in the future, and therefore a wide range of genetic variability should be conserved. It is salutary to consider that economically valuable genes or gene complexes may already have been permanently lost through the effects of logging and deforestation.

CONCLUSIONS

Deforestation and selective logging certainly have the potential to deplete the genetic resources of tropical timber species, but as yet there is only qualitative evidence to support the occurrence of genetic erosion in mahogany. In the light of current high deforestation rates, and the continuing high demand for mahogany products, the development of an integrated conservation strategy is an urgent priority. This should encompass the characterization of genetic resources, the identification of conservation priorities, the delineation and enforcement of protected areas, the development and implementation of sustainable management systems, and the creation of *ex situ* gene banks of particularly valuable genotypes for use in breeding and plantation forestry. Such a programme would require secure long-term funding and international co-ordination (Newton *et al.*, 1993b, 1994a).

Although more research is certainly needed, particularly in resource characterization, many techniques are now available which could contribute to the sustainable genetic resource management of mahogany. These techniques need to be implemented in a co-ordinated fashion. Ideally, those involved in the timber trade should take the initiative, as they have a great deal to gain in the long term from managing the resource sustainably. There is no biological reason why conservation and timber production objectives cannot be combined; what is required is the financial and political will to make it happen.

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Figure captions

Figure 1. Variation in height growth of open-pollinated half-sib families of *Swietenia macrophylla* in: (a) a combined provenance / progeny test established at Bajo Chino, CATIE, Costa Rica and assessed at age 33 months. Hatched bars, Chapernal / Fila Mora, Costa Rica; open bars, Lancetilla, Honduras; (b) a progeny test established at St Andrew, Trinidad and assessed at age 30 months. Values are means (*n* = 36 and 54 respectively); vertical bars represent s.e.m. For details of seed origins see Table 1.

Figure 2. Variation in the number of shoot borer damage sites of open-pollinated half-sib families of *Swietenia macrophylla* in: (a) a combined provenance / progeny test established at Bajo Chino, CATIE, Costa Rica and assessed at age 33 months. Hatched bars, Chapernal / Fila Mora, Costa Rica; open bars, Lancetilla, Honduras; (b) a progeny test established at St Andrew, Trinidad and assessed at age 30 months. Values are means (*n* = 36 and 54 respectively); vertical bars represent s.e.m. For details of seed origins see Table 1.

Table 1. Details of genetic tests of *Swietenia macrophylla*

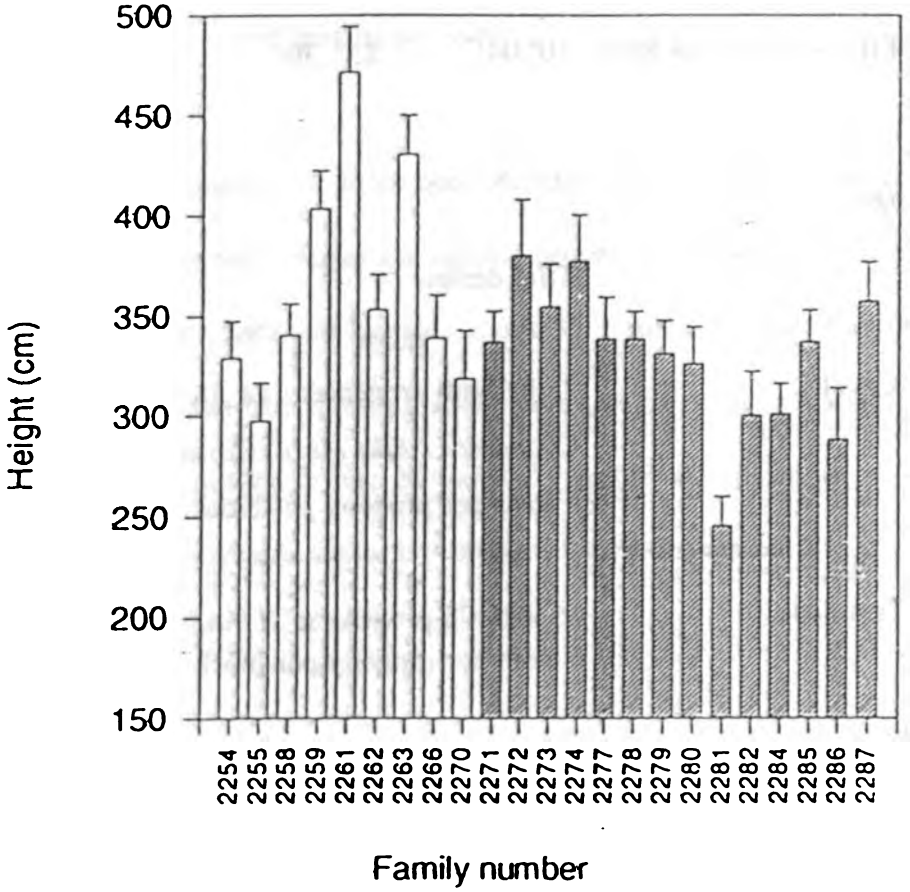
(a) Seed origin

Provenance	Latitude	Longitude	Altitude	Precipitation
	N	W	(m)	(mm)
La Mosquitia, Honduras	15° 30'	87° 24'	11-170	2859
St. Andrew, Trinidad	10° 28'	61° 05'	10-100	2500
Chapernal / Fila Mora, Costa Rica	10° 04'	85° 30'	100-350	2232

(b) Trial design

Site of trial	Trial design
Bajo Chino, CATIE, Costa Rica	23 half-sib progenies: *La Mosquitia, Honduras (9), Chapernal / Fila Mora, Costa Rica (14)* 6 trees per progeny per block; 6 blocks
St. Andrew, Trinidad	16 half-sib progenies: *St. Andrew, Trinidad* 6 trees per progeny per block; 9 blocks

Names in italics indicate the origin of the material employed


500
450
400
350
300
250
200
150
Height (cm)
2254
2255
2258
2259
2261
2262
2263
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2270
2271
2272
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2278
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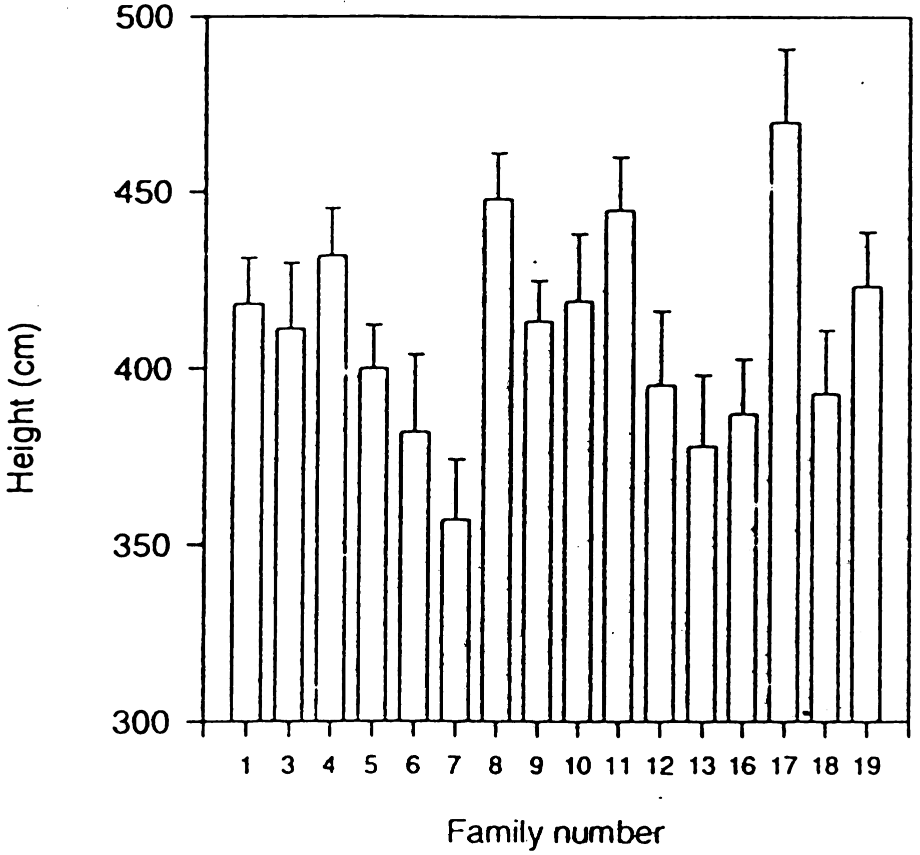
2284
2285
2286
2287
Family number


500
450
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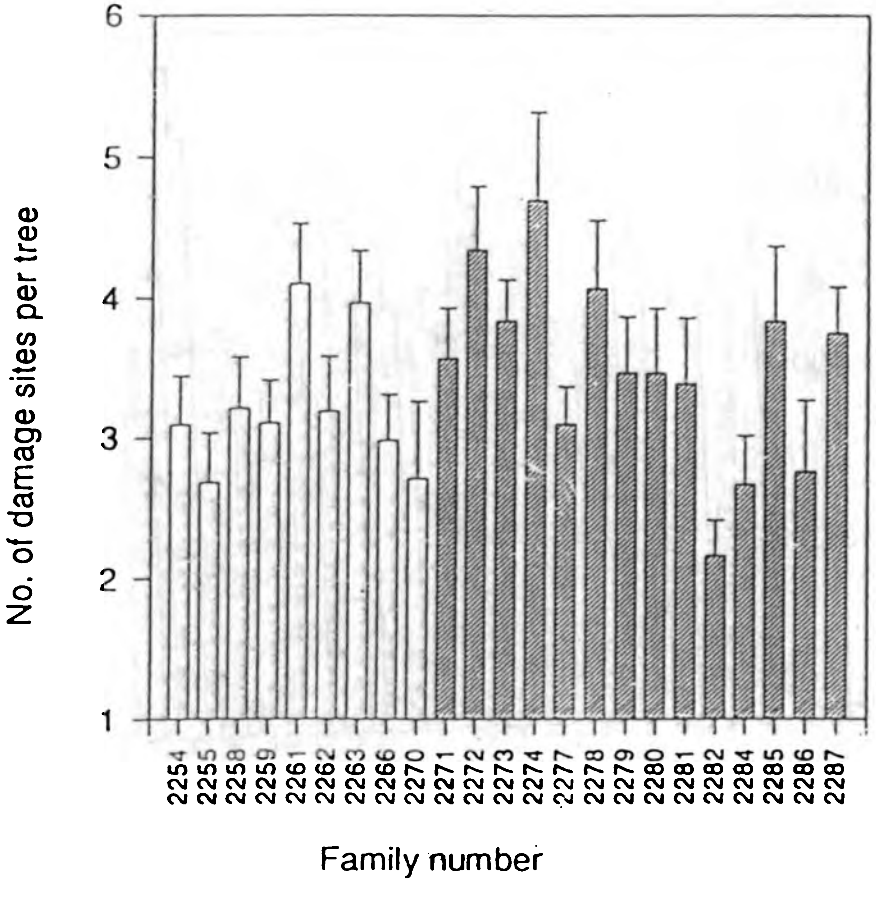
350
300
Height (cm)
1 3 4 5 6 7 8 9 10 11 12 13 16 17 18 19
Family number



No. of damage sites per tree
6
5
4
3
2
1
2254
2255
2258
2259
2261
2262
2263
2266
2270
2271
2272
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2281
2282
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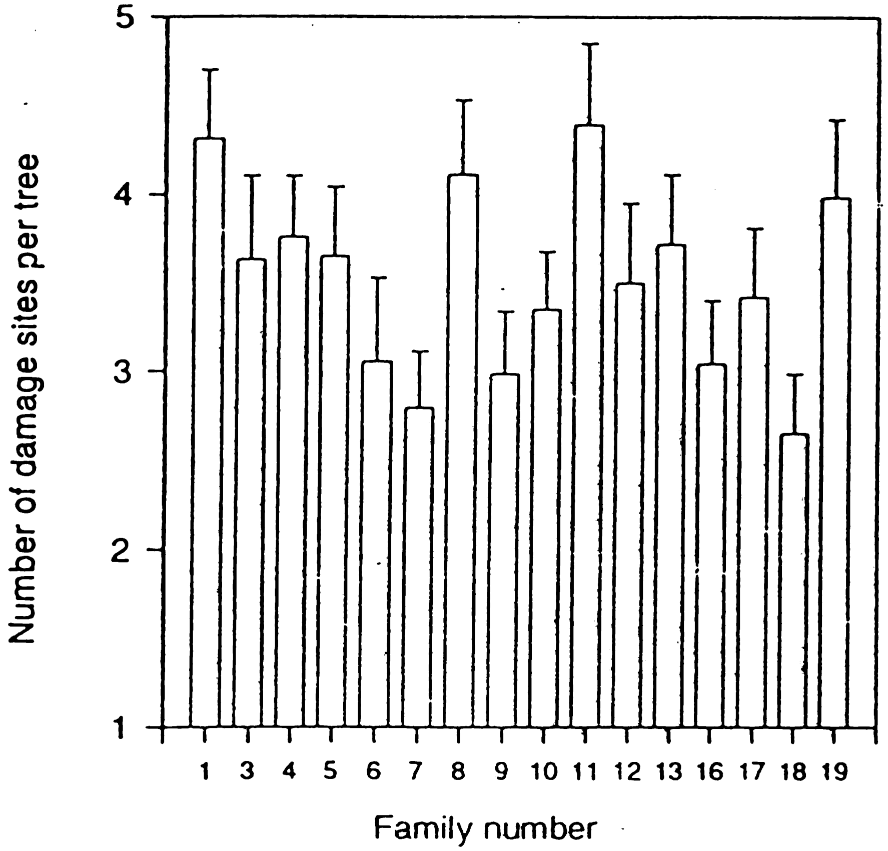
Family number


5
4
3
2
1
Number of damage sites per tree
1
3
4
5
6
7
8
9
10
11
12
13
16
17
18
19
Family number

AVANCES EN EL MEJORAMIENTO GENETICO DE *Vochysia guatemalensis*

[illegible] Cornelius y [illegible] Mesén
Proyecto Mejoramiento Genético Forestal [illegible]

PUNTOS CLAVES Y RECOMENDACIONES PRACTICAS

- Existe gran variación genética entre procedencias de *Vochysia guatemalensis* de diferentes partes de América Central.
- Al ser plantadas en sitios ácidos de la zona atlántica de Costa Rica, las procedencias de Izabal (Guatemala) y La Ceiba (Honduras), crecen más lentas que procedencias de la misma zona atlántica costarricense, aunque la procedencia Izabal exhibió superioridad en cuanto a rectitud del fuste. Las dos procedencias costarricenses incluidas (San Miguel de Sarapiquí y Guápiles), tuvieron un comportamiento muy similar.
- Existe gran variación genética en rectitud del fuste entre árboles dentro de cada procedencia.
- Existe gran variación genética en crecimiento entre árboles dentro de las procedencias de Costa Rica y Honduras, pero poca variación genética entre los árboles de Izabal, Guatemala.
- Para la reforestación, se debería utilizar semilla recolectada de árboles de buena forma ubicados en la misma región ambiental donde se plantará. En particular, se debe evitar el uso de semilla de Izabal (Guatemala) y La Ceiba (Honduras), en sitios ácidos en la zona atlántica de Costa Rica.
- En el caso de selección en plantaciones o rodales naturales coetáneos, es justificable también seleccionar árboles superiores en cuanto a dap y altura.

INTRODUCCION

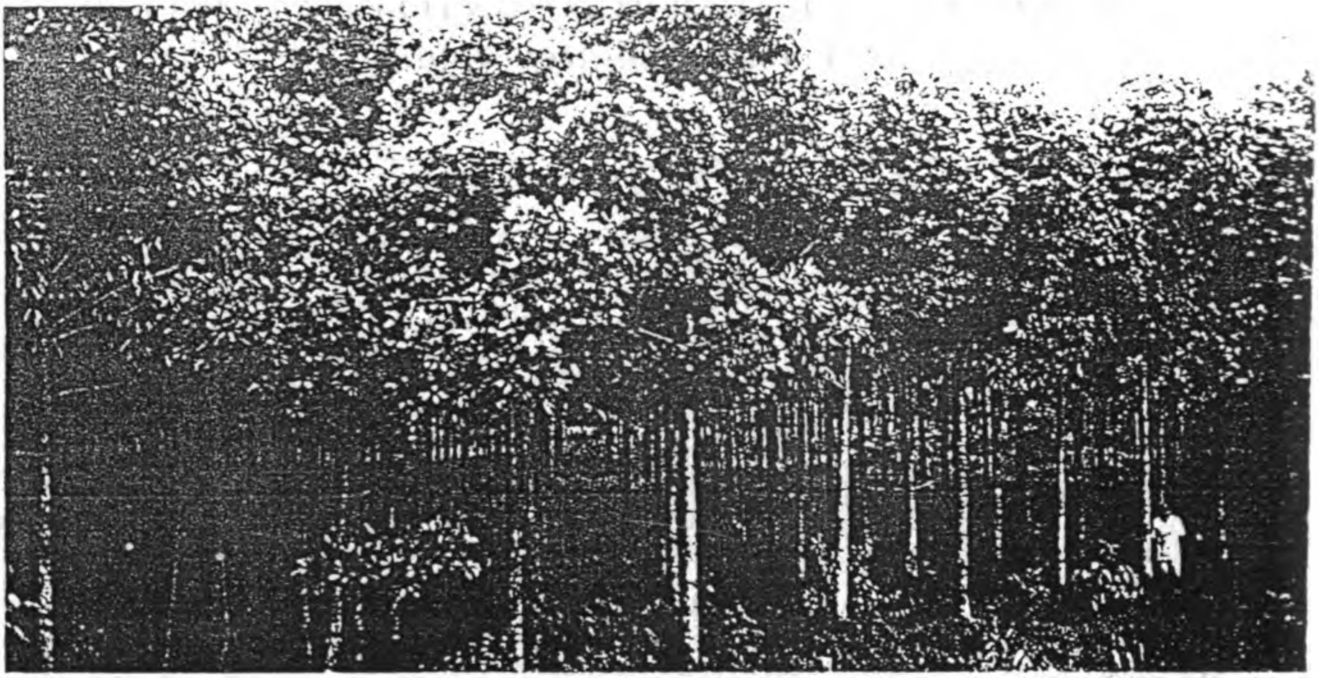
Vochysia guatemalensis (cebo, chancho, mayo, San Juan) es una especie de gran potencial para la reforestación en zonas húmedas de bajura en Centroamérica, debido a su buen comportamiento en sitios altamente ácidos, donde otras especies no pueden desarrollarse bien (Espinoza y Butterfield, 1989) y a la versatilidad y facilidad de trabajo de su madera (ACEN, 1994), la cual tiene buena aceptación en los mercados nacionales.

En años recientes, se ha generado una cantidad importante de información básica sobre la silvicultura de la especie (ACEN, 1994; Chavarria y Valerio, 1993). Sin embargo, hasta la fecha, la genética de la especie ha sido prácticamente desconocida. El presente artículo, pretende llenar este vacío a través de la presentación de los resultados más sobresalientes de un experimento de procedencias y descendencias establecido hace 4,5 años. La información presentada se fundamenta en el artículo de Cornelius *et al.*, 1994

EL EXPERIMENTO

El experimento está ubicado en Puerto Viejo de Sarapiquí, Provincia de Heredia, Costa Rica. El sitio es infértil, altamente ácido, está en una zona baja y húmeda y es bastante representativo del tipo de sitio considerado apto para la plantación de esta especie. Anteriormente, el sitio estuvo cubierto por bosque secundario joven ("tacotal").

El diseño es de ocho bloques completos alcatorios, con parcelas de seis árboles por familia. Cada bloque contiene 48 familias de polinización abierta, las cuales corresponden a cuatro procedencias costarricenses: Florencia de San Carlos (dos familias), Guápiles (5 familias), San Miguel de Sarapiquí (7 familias), Siquirres (3 familias), una procedencia guatemalteca (Izabal, 23 familias) y una procedencia hondureña (La Ceiba, Atlántida, con 8 familias)



Variación genética de *Vochysia guatemalensis* En un sitio altamente ácido en Sarapiquí de Costa Rica, la procedencia Izabal, Guatemala (en el centro), presentó un menor crecimiento pero una mejor forma que las procedencias costarricenses (extrema derecha). (Foto L Apedaile)

OBJETIVOS Y EVALUACIONES

Los objetivos del experimento fueron investigar si existe variación genética de importancia entre procedencias y familias de la especie y estimar valores de los parámetros genéticos, identificar procedencias y árboles madres superiores para la recolección de semilla y producir semilla mejorada.

A los 42 meses, se midieron las siguientes características de cada árbol: altura total, diámetro a 1,3 m de altura (dap), rectitud del fuste (escala jerárquica de 1 (mejor) a 4 (peor), número de bifurcaciones, presencia de copa quebrada y ataque de comején. Se realizó un análisis de varianza a dos niveles: de procedencias y de familias. Se excluyeron del análisis de procedencias las de menos de 5 familias, por no constituir muestras adecuadas de la procedencia (Cotterill, 1990)

RESULTADOS

¿Existe variación genética de importancia a nivel de procedencia?

Los resultados a nivel de procedencia se resumen en el Cuadro 1. En el caso de las cinco características (tres de crecimiento, dos de forma), incluidas en el cuadro, existen diferencias estadísticamente significativas (p=0,01 o menor) y de magnitud importante. Para los rasgos de crecimiento, las procedencias costarricenses fueron muy superiores (ej. la procedencia de San Miguel supera en un 43% el volumen por árbol a la procedencia Izabal). Las procedencias de Guápiles y San Miguel fueron también superiores en cuanto a la proporción de árboles con copa quebrada. Sin embargo, en el caso de la rectitud del fuste, las dos procedencias exóticas y particularmente la procedencia Izabal fueron mejores

En el caso de los otros rasgos (cantidad de bifurcaciones y ataque de comején), no hubo diferencias significativas entre las procedencias: no existe eviden

Cuadro 1 Promedios para cinco características de cuatro procedencias de *Vochysia guatemalensis* a los 42 meses de edad en un ensayo de procedencias/descendencias ubicado en Puerto Viejo de Sarapiquí, Costa Rica.

Procedencia	Promedios [% superioridad o inferioridad[1]]				
	altura (m)	dap (cm)	Indice de volumen[2] por árbol (m^3)	rectitud [1] (mejor)-4 (peor)	porcentaje de árboles con copa quebrada
Guápiles, Costa Rica	9,7 (5,7%)	14,8 (4,4%)	,091(15,2%)	2,7 (+3,8%)	9,4 (-16,9%)
Izabal, Guatemala	8,6 (-6,2%)	13,5 (-4,8%)	,065 (-17,7%)	2,2 (-15,4%)	16,9 (49,2%)
La Ceiba, Honduras	8,5 (-7,3%)	13,6 (-4,0%)	,067(-15,2%)	2,5 (-3,8%)	12,2 (7,7%)
San Miguel, Costa Rica	9,9 (7,9%)	14,8 (4,4%)	,093 (17,7%)	3,0 (15,4%)	6,8 (-39,9%)
Promedio	9.2	14.2	0.079	2.6	11.3
Significancia[3]	***	***	***	***	**

[1] Con respecto al promedio de las cuatro procedencias

[2] Calculado como $dap^2 \times \pi/4 \times altura \times 0,5$ No se pretende estimar el volumen real, sino estimar las diferencias relativas en volumen por arbol entre las procedencias

[3] ** Probabilidad de p=0 01. *** probabilidad de p= 0 001

Cuadro 2. Variación y heredabilidad para cinco características a los 42 meses de edad en un ensayo de procedencias/descendencias de *Vochysia guatemalensis* ubicado en Puerto Viejo de Sarapiquí, Costa Rica.

Procedencia		altura	dap	Indice de volumen[1] por árbol	rectitud	porcentaje de árboles con copa quebrada
Costa Rica	significancia[2]	**	**	**	**	**
	rango de promedios[3]	16,3%	23,6%	48,9%	35,8%	247%
	heredabilidad	0,20	0,17	0,16	0,35	
Izabal, Guatemala	significancia[2]	NS	NS	NS	***	***
	rango de promedios[3]	9,6%	10,7%	27,7%	52,7%	231,9%
	heredabilidad	0,08	0,07	0,04	0,32	
La Ceiba, Honduras	significancia[2]	NS	***	**	***	NS
	rango de promedios[3]	10,6%	15,4%	43,3%	45,2%	71,3%
	heredabilidad	0,18	0,32	0,25	0,48	

[1] /Calculado como $dap^2 \times \pi/4 \times altura \times 0,5$ No se pretende estimar el volumen real, sino expresar las diferencias relativas

[2] /** = Significativa con probabilidad de p= 01 *** = significativa con probabilidad de p=0 001 NS = no significativa

[3] /Rango de promedios = la diferencia entre la mejor y la peor familia, dividida entre el promedio de la procedencia

cia de diferencias genéticas a nivel de procedencia en estas características

¿Existe variación genética de importancia a nivel de familia?

Para evaluar la importancia de la variación a nivel de familia, se realizaron análisis de varianza separados de cada procedencia. Se calcularon los promedios de cada familia y se estimaron los valores de la heredabilidad[1]. Los resultados se resumen en la Cuadro 2. Para las procedencias costarricenses y hondureñas, se observó que, para los cinco rasgos con importante variación a nivel de procedencia, había también variación estadísticamente significativa (p=0,01 o menor), dentro de las procedencias. La mejor familia costarricense en cuanto a dap mostró una superioridad de 26% con respecto al promedio de las familias costarricenses, mientras los análisis de heredabilidad revelaron que una gran parte de la variación entre árboles individuales es de origen genético. La magnitud de las heredabilidades fue similar a la que se encontraba para estos rasgos en especies forestales (Cornelius, 1994).

El caso de la procedencia guatemalteca fue otro. Hubo muy poca variación entre las familias en cuanto a la tasa de crecimiento. Sin embargo, la procedencia Izabal sí manifestó una considerable variación y alta heredabilidad en cuanto a rectitud.

CONCLUSIONES

Selección de fuentes de semilla para reforestación en sitios altamente ácidos de la zona atlántica de Costa Rica

Aunque la rectitud y otros aspectos de la forma del material guatemalteco son superiores a las procedencias costarricenses, su uso en sitios ácidos en la zona no se considera recomendable, debido al mayor crecimiento que presentan las procedencias costarricenses. Se recomienda el uso de semilla de procedencias locales para la reforestación en la zona atlántica de Costa Rica.

¿Es aconsejable utilizar semilla de *Vochysia guatemalensis* recolectada en una zona para plantarla en otra zona diferente?

Los resultados sugieren que no es prudente utilizar semilla recolectada en una zona para establecer plantaciones en otra región de ambiente diferente. Es importante enfatizar que esta conclusión aplica tanto a movimientos dentro de un país como movimientos transnacionales. Por ejemplo, sería imprudente recolectar semilla en la zona atlántica de Costa Rica para establecer plantaciones en el Pacífico Sur o Upala, donde hay una época seca corta pero marcada. Dichas prácticas pueden conllevar a pérdidas en productividad.

¿Aplican los resultados en otras partes de Centroamérica?

El estudio fue diseñado para examinar el comportamiento de los diferentes genotipos en suelos degradados de la zona atlántica de Costa Rica. Sin comprobación adicional, no se pueden aplicar los resultados a otros sitios con condiciones ambientales muy distintas. En particular, es muy posible que, en sus lugares de origen, las procedencias de La Ceiba e Izabal muestren un comportamiento muy diferente.

¿De qué tipo de árbol hay que recolectar semilla?

Los resultados confirman la importancia de recolectar semilla de árboles rectos, dado que los valores relativamente altos de variación y heredabilidad indican que árboles de apariencia superior tienden a ser genéticamente superiores. Además, los árboles deben ser sanos. En el caso de plantaciones o rodales naturales coetáneos, es justificable también seleccionar árboles superiores en cuando a dap y altura. Aparentemente, no valdría la pena seleccionar para crecimiento en la procedencia Izabal, puesto que evidencia muy poca variación genética en los rasgos de crecimiento.

¿Cuándo habrá semilla mejorada?

El CATIE dispondrá de semilla mejorada a partir de setiembre de 1995, cuando se efectúen las primeras recolecciones de los árboles madres superiores. El ensayo en sí, ya se está convirtiendo en huerto semille-

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[1] La heredabilidad, la cual varía entre 0 y 100%, mide el grado de control genético de una característica.

to, pero no se espera producción de semilla hasta el año 1996

AGRADECIMIENTOS

Agradecemos a todas las personas e instituciones que han colaborado con los trabajos descritos (particularmente la Cooperativa de Recursos Coníferos de Centroamérica y México (CAMCORE), la Organización para Estudios Tropicales, y el personal del Proyecto MGF del CATIE), así como el apoyo financiero del Ministerio Noruego para Asuntos Exteriores, la ODA (Gran Bretaña) y USAID.

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RESULTADOS DE ANALISIS DE SEMILLAS DE ESPECIES FORESTALES DE GUATEMALA[1]

Mario Buch Texaj[2]

INTRODUCCION

La información generada en los análisis de semillas efectuados en el Laboratorio del Banco de Semillas de Guatemala (BANSEFOR), además del control de rutina de la calidad de los lotes, está dirigida a incrementar el conocimiento de las especies nativas y algunas exóticas. Se destacan los registros de germinación y la descripción de algunas de sus características.

El objetivo fundamental de este artículo es presentar el número de semillas de especies forestales obtenidas por kilogramo utilizadas en Guatemala y establecer algunos rangos en los tiempos de germinación.

METODOLOGIA

Los resultados presentados en el Cuadro No.1, se basan en la recopilación de información de los resultados obtenidos en los análisis de rutina, utilizando la metodología de la Asociación Internacional para Ensayos de Semillas (ISTA), efectuados en el laboratorio durante 8 años y la experimentación del proyecto específico de tesis.

Para los ensayos de germinación se establecieron 4 repeticiones de 100 semillas colocadas en cajas germinadoras de plástico transparente y se utilizó como sustrato arena de rio esterilizada (estufa a 200°C x 3 horas), con el método de siembra en arena (Cuadro No. 2).

La humedad del sustrato fue de 20 % con temperatura ambiente de 20°, con temperatura ambiente de 20°C - 25°C y periodos de luz natural. Para la valoración de semillas /kg y semillas capaces de germinar/kg, se tomaron los datos del análisis de determinación de peso y germinación. Estos datos deben ser interpretados con precaución, dado que son obtenidos en condiciones ideales de laboratorio y no aplican para el cálculo de semillas en vivero

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[1] Artículo editado por Enrique Trujillo y Mario Alvarez del BLSF/PROSEFOR-CATIE. El estudio se desarrolló en laboratorio bajo condiciones controladas como parte del trabajo de grado del autor para optar al título de Dasónomo

[2] Encargado Laboratorio de Análisis de Semillas de BANSEFOR-DIGEBOS, Guatemala

Genetic variation in growth rate, stem straightness and foliar mineral content in Vochysia guatemalensis

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Abstract

CORNELIUS, J.P.; and MESÉN, J.F. 1995. Genetic variation in growth rate, stem straightness and foliar mineral content in *Vochysia guatemalensis*

Vochysia guatemalensis Sm., J.D. is a fast-growing tropical rain forest tree, native from southern Mexico to Panama. It is being increasingly planted in Costa Rica, principally by smallholders for timber production. In 1990 a provenance/progeny trial was established in a wet lowland zone of Costa Rica. At 42 months, the two Costa Rican provenances included grew significantly faster than a Honduran and a Guatemalan source, whilst the Guatemalan source had the best stem form. The use of local genetic material is recommended in Costa Rica, as its stem straightness, although slightly inferior to that of Guatemala, is acceptable. At 58 months, there was significant provenance variation in foliar Ca content, which was inversely correlated with provenance growth rates. The provenances did not differ significantly in levels of other foliar minerals. Within-provenance additive genetic variation and heritabilities in growth traits were low, particularly in the case of the Guatemalan provenance. Additive genetic variation and heritability of stem straightness were moderate. The stem straightness of the plus-tree progenies was not superior to the control, indicating that plus-tree selection for stem straightness had been ineffective.

Key-words: *Vochysia guatemalensis*, provenance, heritability, additive genetic variation, aluminium accumulation, calcium, foliar analysis, allautogamy.

Introduction

Vochysia guatemalensis Sm., J.D. (chancho blanco, San Juan, white yemeri) is a long-lived intolerant tree species (Finegan, 1992), native from southern Mexico to Panama (Flores, 1993). It occurs principally below 1000 m a.s.l. in zones without a prolonged dry season, and reaches dimensions of 0.5-1.5m dbh and 30-55m height (Flores, 1993). The species appears to be oxyphylatous, and is well-adapted to growth on highly acid Oxisols and Ultisols with high Al-saturation (see below), as well as being found on less adverse soils within the humid tropics. Since the late 1980s, V. guatemalensis has been increasingly used in smallholder plantations in the north Atlantic and southern Pacific zones of Costa Rica, a trend due principally to the excellent performance shown by the species in trials and initial plantations on degraded, highly acidic sites (González and Fisher, 1994), as well as its locally well-known, attractive and versatile wood (Flores, 1993).

Like other members of the Vochysiaceae (Chenery, 1948), and in common with many other arborescent species of 'tropical rain forest families' (Foy et al., 1978; Webb, 1953), V. guatemalensis accumulates aluminium in its foliage (Montagnini and Sancho, 1991). This phenomenon is one of a number of aluminium tolerance strategies found in plants (Foy et al., 1978). Accumulation is made possible by detoxification (e.g. chelation) or storage in locations where the cytoplasm cannot be damaged (Cuenca et al., 1990), and may permit accumulating species to overcome the aluminium-caused difficulties in nutrient uptake and transport (Haridasan, 1982) common in soils of the humid tropics (Sánchez, 1976).

The present article reports on genetic variation in growth and form traits at provenance and family level, as manifested in a field trial located in the Atlantic zone of

Costa Rica. In addition, foliar levels of Al, Ca, P, K, Zn, Mg and Mn were assessed for the different provenances, principally with a view to examining whether intraspecific differences, if present, might be related to any provenance differences in growth rate.

Materials and methods

Treatments

The treatments consisted of 45 open-pollinated families of six provenances: Izabal, Guatemala (24 families); La Ceiba, Honduras (8 families); Florencia (2 families), Guápiles (7 families), San Miguel (8 families) and Siquirres (3 families) (all Costa Rica). The Guatemalan and Honduran families were obtained through the CAMCORE (Central America and Mexico Coniferous Resources) cooperative (Dvorak, 1990). Geographic and climatic information on the seed collection sites is presented in Table 1. All the families included were derived from plus-trees, selected primarily on the basis of stem straightness. In Costa Rica, all plus-trees also had diameter at breast height (dbh) and height superior to the stand mean (most stands are believed to be approximately even-aged). All the seed collections were made in natural stands. A control, consisting of plants derived from an 'operational' seed collection made by the Organization for Tropical Studies, Costa Rica, in San Miguel, Costa Rica, was also included.

The experimental site

The trial was planted on 3-4 July, 1990 near Puerto Viejo de Sarapiquí, Heredia province, on land belonging to the Organization for Tropical Studies. The site is located at 40 m a.s.l., and is within the natural range of the species. Life-zone (Holdridge, 1967) is tropical wet forest (Tropical Science Center, 1969). Mean annual rainfall is 3700± 825mm. A short dry spell frequently occurs at some time during the first four months of the year (mean number of dry months (< 80 mm) per year is 1.04±1.08) (MIRENEM, 1988). The site is flat. The strongly acid, clay soil is well drained but, by agricultural standards (Bertsch, 1986), deficient in phosphorus, calcium and magnesium (see Table 2 for soil details). Before planting, it was cleared of the vegetation that had grown since its abandonment as pastureland 10 years earlier. Subsequently, three to four manual cleanings were made in each of the first two years. No fertilizer was applied, and the site was not burned before planting.

Experimental design

The experimental design followed the CAMCORE standard (Dvorak and Donahue, 1992); the provenances were randomized within blocks, and families and controls randomized as six-tree row plots within their respective provenances. There were nine blocks and at least two surround rows around the experiment. The trees were planted at 3m x 3m spacing.

Measurements

Total tree height, diameter at breast height (dbh) and stem straightness (scale of one to four, where four is the straightest) were evaluated 42 months after planting. At 58 months, five months after a 20% thinning, one mature leaf was collected from the upper crown of the first tree in each family plot. Leaves were then bulked by block and provenance (insufficient resources were available for individual family analysis). Each sample was dried at 65°C, milled and passed through a 1mm sieve and digested in a nitro-perchloric solution (0.5 g sample:10 ml solution+sample). Mineral contents were determined by atomic absorbtion spectrography (Perkin Elmer Model 2380). In the case of Ca, K and Mg, readings were made on a diluted aliquot of the extract. In the case of Al, the aliquot was diluted with Cesium chloride under a nitrous oxide-acetylene flame. For P, the calorimetric method with Mb indicator was used.

Hypotheses and statistical analysis

Null hypotheses, together with notes on their associated statistical analyses, are presented below.

Null hypothesis (Ho) 1: there are no differences in the parametric mean values of the different provenances;

Ho 2: there is no genetic variation within provenances;

Ho 3: height and diameter are uncorrelated with foliar mineral *levels.*

Ho 4: there are no differences between the parametric stem straightness means of progeny of the San Miguel plus-trees and the San Miguel unselected trees (control)

In the case of height, diameter and form, hypotheses 1 and 2 were tested using ANOVA under the following model:

$$Y_{jkl[k]m} = \mu + \beta_j + \phi_k + \lambda_{l[k]} + \beta_j\phi_k + \varepsilon_{jkl[k]m},$$

where $Y_{jkl[k]m}$ = value of the response variable measured on the mth tree of the lth family of the kth provenance in the jth block; μ = the population mean; β_j = random effect of the jth block; ϕ_k = fixed effect of the kth provenance; $\lambda_{l[k]}$ = random effect of the lth family of the kth provenance; $\beta_j\phi_k$ = random effect of the interaction between the jth block and the kth provenance; $\varepsilon_{jkl[k]m}$ = residual variation affecting the mth tree of the lth family of the kth provenance in the jth block.

For the analysis of mineral content, hypothesis 1 was tested using ANOVA under the following model:

$$Y_{jk} = \mu + \beta_j + \phi_k + \varepsilon_{jk}$$

Y_{jk} = the mean value of the response variable of the kth provenance in the jth block; μ = the population mean; β_j = random effect of the jth block; ϕ_k = fixed effect of the kth provenance; ε_{jk} = residual variation affecting the kth provenance in the jth block. As the Costa Rican provenances were bulked for the mineral analysis, height and diameter were also reanalyzed under this model in order to permit valid comparisons with the mineral data.

Cotterill (1990) considers that a minimum of five families are necessary for a representative sample of provenances. For this reason, those provenances represented by less than five families (Florencia, Siquirres) were excluded from the analysis of provenance growth and form. This did not apply to the analysis of provenance effects on foliar minerals; as the Costa Rican material was considered to constitute one provenance, all Costa Rican families were sampled and bulked together.

Family variance components were estimated based on the nested family effect. In addition, for the Guatemalan families, an ANOVA under the following random model was carried out:

$$Y_{jlm} = \mu + \beta_j + \lambda_l + \beta\lambda_{jl} + \varepsilon_{jlm},$$

where Y_{jlm} = the value of the response variable on tree m of family l of San Miguel provenance in the jth block; μ = the population mean; β_j = random effect of the jth block; λ_l = the random effect of the lth family; $\beta\lambda_{jl}$ = interaction of the jth block and the lth family; ε_{jlm} = residual variation affecting the mth tree of the lth family of the jth block. Families not of the Izabal provenance were omitted from this analysis, i.e., in effect the

Guatemalan plots were analyzed as a separate progeny trial. Genetic parameters were not estimated individually for the other provenances because of the low number of families included. Standard errors of heritabilities were estimated following Swiger *et al.* (1964).

Flores (1993) presents evidence that *V. guatemalensis* is allautogamous, with autogamy predominating, possibly through cleistogamy. However, these conclusions are based on floral structure rather than mating system studies. In order to reflect the uncertainty over the mating system, we estimated genetic parameters using two sets of assumptions, corresponding to two extremes of 100% selfing and 20% selfing. For the latter, we arbitrarily assumed there to be 8 pollinators (excluding the mother tree), each contributing the same number of progeny. The average genetic correlations (r_o) between members of the open-pollinated families were then calculated using Squillace's (1974) methodology, as $r_o=1$ (selfs of inbred parents) and $r_o=.4597$ (20% selfing) and additive genetic variance (σ^2_A) was estimated as σ^2_F/r_o, where σ^2_F=variance component due to open-pollinated families. As genetic covariance between full-sibs is partially caused by correlation of dominance deviations (Falconer, 1989), Squillace's formulation assumes that dominance variance is negligible. Narrow-sense heritability on an individual-tree basis (h^2) was estimated by $\sigma^2_A/[\sigma^2_E+\sigma^2_F+\sigma^2_{BF}]$, where σ^2_E = residual variance and σ^2_{BF} = block-family interaction variance. The additive genetic coefficient of variation (AGCV) was estimated by $100[\sigma_A / x]$, where x = experimental mean (or Izabal provenance mean in the case of the Guatemalan analysis).

Correlations between mineral content and the growth variables were estimated using the plot mean values for each provenance separately. In addition, correlations between the provenance experimental means of the variables were estimated. The two types of correlation correspond respectively to purely environmental correlations and a genetic (provenance-level) correlation.

'F'-tests were generated using the TEST option of the GLM RANDOM statement of SAS (SAS Institute Inc. 1988). SAS uses Satterthwaite's (1946) approximations for appropriate degrees of freedom. when necessary. In the analysis of provenance effects on foliar mineral levels, the SAS WEIGHT statement was used in order to take into account the different number of trees contributing to the sample means of the three provenances.

No statistical test was made of hypothesis 4, as the two groups had the same mean (see results).

Results

At 42 months, mean height was 9.0 m, mean dbh was 14.0 cm and survival was above 90%. Foliar mineral levels are detailed in Table 3.

Provenance effects

There were highly significant provenance effects on growth traits (Table 3). The estimates of the true means of the two Costa Rican provenances were similar, but both were superior to the Guatemalan and Honduran provenances. Provenance effects on stem straightness were also significant. The Guatemalan provenance was the straightest, and the San Miguel, Costa Rica provenance the least straight. Other provenance differences, although not formally evaluated, were evident: the trees of Costa Rican provenance had thicker and larger leaves, coarser branches, and heavier crowns. Provenance plot boundaries could be determined easily based on these characteristics, without recourse to trial maps.

There were significant (p=.007) provenance effects on Ca content (Table 4). The Honduran provenance showed the highest concentration and the Costa Rican the lowest. Provenance effects on Al concentration were significant at p = 0.06. The Honduran provenance had the highest concentrations, the Guatemalan the lowest.

Provenance mean (genetic) correlations were generally strong, but non-significant at p=.05. Height was strongly negatively correlated with Mg (r=-1.0, p=.04). Calcium was strongly negatively correlated with potassium (r=-1.0, p=.05). Other correlations significant at p<0.2 were height with Ca (-.97) and K (.99) and dbh with Mg (-.96). The following environmental correlations (i.e. within provenance) had associated probabilities less than 0.2: height and Zn (-0.62, p=.07) (Costa Rica), height and Mn (.52, p=.15) (Guatemala), height and P (0.51, p=.16; 0.57, p=.1) (Guatemala and Honduras, respectively), height and Ca (-.5, p=.17, -.52, p=.14) (Guatemala and Honduras, respectively), dbh and Al (-.52, p=.15) (Guatemala), dbh and Mg (-.51, p=.15) (Honduras).

Family effects and genetic parameters

There were highly significant family-within-provenance effects on dbh (F=2.95; p=.0001; df=39, 346.69 (family, error); MS(error)=7.2), height (F=2.25; p=.0001; df=39, 340.92 (family, error); MS(error)=1.84) and stem straightness (F=4.49; p=.0001; df=39, 344.4 (family, error); MS(error)=0.83). Under the selfing assumption, heritabilities and AGCV of height, dbh and stem straightness were estimated as 0.03±0.03 and 2.6%, 0.05±0.04 and 4.1%, 0.08±0.07 and 10.5%, respectively. Under the 20% selfing assumption, they were estimated as 0.75±0.06 and 4.1%, 0.1±0.08 and 6.1%, and 0.18± 0.13 and 15.5%.

Within the Izabal provenance, family effects on growth were non-significant at 5% (height: F=1.49; p=.08; df=22, 186.69 (family, error); MS(error)=1.69) (dbh: F=1.51; p=.07; df=22, 189.94 (family, error); MS(error)=5.96), whilst family effects on stem straightness were highly significant (F=4.41; p=.0001; df=22, 190.70 (family, error); MS(error)=0.88). The Guatemalan families with the highest values for height, dbh and straightness were respectively 10%, 13.4% and 50% higher than the worst families. Under the selfing assumption, heritabilities and AGCV of height, dbh and stem straightness were estimated at 0.02±0.02 and 1.6%, 0.01±0.02 and 2.0%, 0.08±0.09 and 9.6%, respectively. Under the 20% selfing assumption, they were estimated as 0.03±0.04 and 2.3%, 0.03±0.04 and 2.9%, and 0.18±0.18 and 14.1%.

The least squared grand mean stem straightness for the San Miguel families was the same (2.0) as that of the control.

Discussion

General

Growth and survival was satisfactory and comparable with other published reports on plantation growth of V. guatemalensis. For example, on sites located close to the present one, Espinoza and Butterfield (1989) and González and Fisher (1994), reported mean height and diameter at three years of 8.0m and 10.1cm and 7.5m and 12.7cm respectively.

The experimental mean Ca and P contents are very similar to those reported by Montagnini and Sancho (1994) (.09%, 1.22%, respectively) for 4-year old V.

guatemalensis on a nearby, similar site. Mg and K levels were approximately half and four times those recorded by the latter authors, who did not report on the other minerals evaluated in the present study. As the trees showed no obvious deficiency symptoms, the values reported in the present study can be considered to correspond to the mineral status of healthy, five-year-old, plantation-grown trees of the species. In the case of P, Ca, Mg, K, Mn and Zn, the levels recorded were consistent with the 'intermediate' foliar mineral levels tabulated for 40 tropical and subtropical trees by Drechsel and Zech (1991). As expected, this was not true of Al; the highest aluminium concentration recorded by Drechsel and Zech (1991) for healthy trees was 0.002% (Acacia senegal), as against 2.43% here.

Provenance effects on growth and form

The results demonstrate conclusively the existence of important provenance differences in stem straightness and growth traits in Vochysia guatemalensis. The provenances examined fall into two groups: the faster growing, more coarsely-formed Costa Rican sources, and the straighter-stemmed, thinner-branched, but slower-growing northern Central American (La Ceiba and Izabal) material. In general, Costa Rican Vochysia guatemalensis is a well-formed tree. In spite of its inferior form relative to the other sources, pure, thinned plantations of Costa Rican material should yield as many straight or nearly straight final crop trees as the other sources. Therefore, in such plantations in Costa Rica, local provenances should be preferred. However, in very small plantations, and possibly in agroforestry situations, the Guatemalan provenance might be preferred because it is straighter and has a lighter crown. CATIE has recently established clonal trials of this species; it is possible that some clones of all three provenances will exhibit both fast growth and straight stems.

Provenance foliar mineral levels: general implications and relationship to provenance effects on growth traits

The relatively low probability values associated with two of the environmental correlations between Ca and height suggest that trees of a given provenance will tend to grow more slowly in soils with higher Ca than lower Ca concentrations. The significant provenance effect on Ca suggests that, when grown on a common site, the La Ceiba source takes up more Ca than the Costa Rican and, possibly, Izabal, sources, whilst both the Guatemalan and Honduran sources grew more slowly than those from Costa Rica. Both results are suggestive of a negative association between Ca uptake and height growth in V. guatemalensis. However, such a relationship is not axiomatic in species tolerant of low pH; further studies are needed to confirm or disprove its existence in V. guatemalensis.

The correlation of P with height growth is wholly environmental in origin, as the provenance P means were identical. The results are consistent with the positive and significant responses of the species to P-rich (10-30-10) fertilizer reported by Russo et al. (1994).

There is fairly strong evidence of provenance effects on Al accumulation. However, given that the Guatemalan provenance has the lowest Al content, but with growth no better than the Honduran source, there is no justification for suggesting that differing Al accumulation capabilities might explain growth rate differences. Similarly, data presented by Chenery (1955) for tea (Camellia sinensis), another aluminium accumulator, indicates that some high accumulating clones are high (leaf) producers, some low producers, and vice versa. Chenery also presents evidence of some beneficial effects of aluminium in tea. The present study provides no evidence that this might be the case for V. guatemalensis. Rather, although the species thrives in low pH, this appears to be a consequence of its evident capacity to tolerate Al, rather than any need for it.

The remaining provenance mean correlation between minerals and growth are of little interest, as there was no significant provenance effect on the levels of the minerals in question.

Family effects on growth and stem form

The relatively low associated probability values (including the Guatemalan provenance) suggest strongly that there is additive genetic variation within populations of the species. However, in the growth traits, it appears to be rather low, particularly in the case of the Guatemalan material. The relatively high variation of stem straightness, which is similar to values typically found in forest trees (Cornelius, 1994), suggests that the low genetic variation in growth is not a consequence of the mating system; were this true, all traits should show low variation. It should also be stressed that the effects of autogamy on genetic variation as detected in field trials are dependent on the distribution of mother-trees in relation to the spatial genetic structure. If individual selections sample different inbred lines, then high estimates of genetic variation could result. By contrast, if some inbred lines are sampled by more than one mother-tree (e.g. if two trees are selected in one stand derived from one or more trees of the same line), low estimates of genetic variation could result. In the present study, trees within provenances were separated by from 100m to several kilometers. It seems likely that they sample more than one inbred line within each provenance. However, as the spatial distribution of genetic variation is unknown, no firm conclusion can be drawn.

Heritabilities of both diameter and height were low. Selection for growth rate within the Guatemalan provenance would probably not be worthwhile. The heritability and AGCV estimates from the nested analysis are higher than the Guatemalan estimates, suggesting that selection for growth within the Honduran and Costa Rican provenances might be more effective. In all the provenances, there appears to be good potential for selection to improve stem form. The lack of response to selection in the San Miguel provenance is most probably the result of low heritabilities in natural, highly environmentally variable populations, and should not discourage selection for form in plantations.

Breeding strategies should not be finalized until definitive information on reproductive biology is available. If the species is tolerant of inbreeding and if dominance effects exist, inbreeding and hybridization could usefully complement or even replace selection.

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TABLE 1. Geographic and climatic information on provenances included in a provenance/progeny experiment of Vochysia guatemalensis in Sarapiquí, Heredia Province, Costa Rica.

Provenances[a]	Latitude (N)	Longitude (W)	m.a.p.[b] (mm)	a.a.s.l.[c] (m)	n.d.m.[d]
Florencia	10°22'	84°31'	3118	160	2
Guápiles	9°31'-9°32'	83°42'-83°43'	4494	250	0.4
San Miguel	10°19'	84°11'	4532	500	0.6
Siquirres	10°07	83°32'	3863	60	0.3
La Ceiba, Honduras	15°47'	86°50'	2857	8	2[e]
Izabal, Guatemala	15°38'	88°32'	40	1750[f]	unavailable

[a]Costa Rica, unless stated; [b]mean annual precipitation; [c]altitude above sea level; [d]mean number of dry (<80 mm precipitation) months per year; [e]Robbins and Hughes, 1983; [f]estimate (Dvorak and Donahue, 1993);

TABLE 2. Soil characteristics of a *Vochysia guatemalensis* provenance / progeny experiment planted Sarapiqui, Heredia province, Costa Rica

Horizon	pH (H_2O)	P[a]	Ca[b]	Mg[b]	K[b]
A	4.8	8.0	0.8	0.79	0.23
B	4.6	11.0	0.24	0.33	0.12

[a] ($\mu g\ ml^{-1}$); [b] ($cmol(+)\ l^{-1}$ soil)

TABLE 3. Provenance height, diameter and stem straightness means and significance of provenance differences in a provenance / progeny experiment of *Vochysia guatemalensis* in Sarapiquí, Costa Rica.

		trait	
provenance	height (m)	diameter at breast height (cm)	stem straightness[a]
		least squared means (standard error)	
Guápiles	9.8 (0.08)	14.9 (.17)	2.2 (0.06)
San Miguel	10.0 (1.8)[b]	14.7 (3.3)[b]	2.0 (0.8)[b]
Izabal	8.7 (.04)	13.6 (.08)	2.8 (0.03)
La Ceiba	8.5 (.07)	13.8 (.15)	2.5 (0.05)
F value for provenance	22.2 (p=0.0001)	8.7 (p=0.0002)	10.7 (p=0.0001)
df (provenance, error)	3, 35.42	3, 36.58	3, 44.58
MS (error)	8.73	23.19	4.50

[a] 4 (straightest) to 1 (least straight); [b] arithmetic means and standard deviations (least squared means for the San Miguel provenance were non-estimable)

TABLE 4. Site and provenance foliar mineral content means and significance of provenance differences in a provenance / progeny experiment of <u>Vochysia</u> <u>guatemalensis</u> in Sarapiquí, Costa Rica.

Provenance	height (m)	dbh (cm)	Al (%)	P (%)	Ca (%)	Mg (%)	K (%)	Zn (mg/l)	Mn mg/l)
					experimental means (standard errors)				
	9.1	14.1	2.43	.13	1.24	.29	.84	13	311
	(.1)	(.2)	(.03)	(.002)	(.07)	(.006)	(.03)	(.7)	(17)
					provenance means (standard errors)				
Costa Rica	10.0	15.0	2.43	.12	0.98	.28	.94	13.0	259
	(0.10)	(.10)	(.04)	(.002)	(0.03)	(.007)	(.04)	(.52)	(14)
Izabal,	8.7	13.5	2.33	.12	1.12	.30	.84	13.4	264
Guatemala	(0.10)	(.10)	(.03)	(.002)	(0.03)	(.006)	(.03)	(.46)	(13)
La Ceiba,	8.6	13.9	2.47	.12	1.18	.30	.81	14.0	305
Honduras	(0.16)	(.15)	(.05)	(004)	(.005)	(.01)	(.06)	(.78)	(22)
F value for	F=51.5	F=62.6	F=3.3	F=.93	F=7.0	F=2.7	F=2.4	F=.59	F=1.7
provenance	p=.0001	p=.0001	p=.06	p=0.41	p=0.007	p=.1	p=.12	p=.60	p=.21
df (provenance, error)	2, 16	2, 16	2, 16	2, 16	2, 16	2, 16	2, 16	2, 16	2, 16
MS error	9.12	8.02	2194.8	10.8	1868.7	76.9	2471.1	44.2	33828.4

Proyecto de mejoramiento genético de árboles del CATIE
Estado de avance y principales resultados

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Resumen

El proyecto de mejoramiento genético de árboles del CATIE ha trabajado en Costa Rica desde finales de 1977. Se dan detalles de los experimentos que se han establecido en varias partes del país. Principalmente se trata de ensayos de procedencias de *Pinus caribaea*, *P. oocarpa*, *Cordia alliodora*, *Gmelina arborea*, especies de *Eucalyptus* y más recientemente de ensayos de *Acacia mangium*. Se presentan los principales resultados para las especies de *Pinus*, *C. alliodora* y *G. arborea* y sus implicaciones para el futuro de la reforestación en Costa Rica. También se presenta en forma breve los planes futuros de trabajo para algunas de las principales especies.

Introducción

La alarmante tasa de deforestación en Costa Rica, entre 60 000 y 70 000 ha por año (Hartshorn *et al.*, 1982) y limitantes en conocimientos que dificultan la explotación racional de los bosques nativos han hecho necesario el establecimiento de plantaciones con especies de rápido crecimiento para satisfacer la demanda por productos forestales. Sin embargo hasta el momento el área reforestada ha sido muy poca, estimada en un total de 4000 ha hasta 1983 (Hartshorn *et al.*, 1982) y actualmente con una tasa inferior a las 1000 ha por año. Aún con los pocos intentos de reforestación los resultados no han sido muy satisfactorios. Generalmente las plantaciones presentan baja sobrevivencia y/o pobre crecimiento. Matamoros (1982), en una muestra de ocho proyectos de reforestación dentro del país encontró niveles de sobrevivencia entre 30-95 por ciento con un promedio ponderado de 60 por ciento.

Dentro de las empresas reforestadoras se habla de los problemas encontrados en la reforestación y se identifica como causa principal la falta de semilla de calidad adecuada. Sin embargo, las causas principales del fracaso de las plantaciones en el país son: i) la mala calidad de la plántula producida en los viveros y ii) atención inadecuada después de plantar. La calidad de la semilla disponible o utilizada, aunque es importante es solo la tercera causa. Es probable que el problema de la calidad de la semilla haya sido más destacado por ser el factor menos controlable por la industria.

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Proyecto de mejoramiento genético del CATIE

Reconociendo el efecto que la calidad genética de la semilla puede tener sobre el éxito de proyectos de reforestación, el CATIE inició un programa de mejoramiento genético de árboles de valor económico en Costa Rica a finales de 1977. Las especies incluidas en el programa fueron seleccionadas con base en los resultados de ensayos con muchas especies que fueron establecidos en el CATIE y en muchas otras partes del país (Combe y Gewald, 1979; Camacho, 1982). Unas de las especies han sido la base de la reforestación en el país y han sido promovidas por la DGF en su estímulo a la reforestación.

El proyecto de mejoramiento genético del CATIE ha trabajado principalmente en las zonas del país entre 0-1400 msnm con las siguientes especies (en orden alfabético) *Acacia mangium*, *Araucaria hunsteinii*, *Cordia alliodora*, *Eucalyptus grandis*, *E. urophylla*, *Gmelina arborea*, *Pinus caribaea*, *P. oocarpa* y *P. tecunumanii*. El Anexo 1 muestra detalles de los ensayos establecidos y la Figura 1 su ubicación dentro del país. Los ensayos han sido establecidos en una variedad de sitios en el país tratando de incluir las diferentes zonas ecológicas que se consideran aptas para reforestación con la especie en particular. También se pretende identificar los patrones de interacción genotipo ambiente que se presentan para cada especie y que afectarían las estrategias de mejoramiento genético a seguir en el país.

El proyecto empezó con el establecimiento de ensayos de procedencias de las especies mencionadas, como participante en una red internacional de ensayos coordinados por organizaciones como; IUFRO, FAO, CFI (Inglaterra); CSIRO (Australia) y DANIDA (Dinamarca). Esta estrategia se basó en el hecho de que la forma más económica y rápida de obtener mayores ganancias en productividad en plantaciones puede ser mediante el uso de la especie y la procedencia más apropiada (Zobel y Talbert, 1984). Las pérdidas asociadas con el uso de una fuente de semilla no apropiada pueden ser grandes y hasta desastrosas.

Después del establecimiento de ensayos de procedencias para identificar la mejor procedencia o procedencias para cada especie, la estrategia de mejoramiento a seguir depende de las necesidades de cada especie. Sin embargo, por lo general se ha procedido con la identificación de árboles "plus" (fenotípicamente superiores) dentro de la mejor o mejores procedencias, seguida por el establecimiento de ensayos de descendencias para comprobar las selecciones y de plantaciones para la producción de semilla mejorada.

A continuación se dan detalles de los logros, los planes futuros y sus implicaciones para la reforestación en Costa Rica para cinco de las especies principales con las cuales trabaja el proyecto.

Pinus caribaea, *P. oocarpa* y *P. tecunumanii*

El ensayo 112, procedencias de *P. caribaea*, fue establecido principalmente en 1977 (en cuatro sitios) y en dos sitios más en 1983 para extender el rango de sitios cubiertos. El ensayo (115 + 144) de *P. oocarpa* fue plantado en 1978-79 también en cuatro sitios. Como comparadores en el ensayo de *P. caribaea* se incluyeron dos procedencias de *P. oocarpa* (Yucul, Nicaragua y Mountain Pine Ridge, Belice) y en el ensayo de *P. oocarpa* una de *P. caribaea* (Mountain Pine Ridge, Belice) (ver Anexo 1 para detalles del diseño experimen-

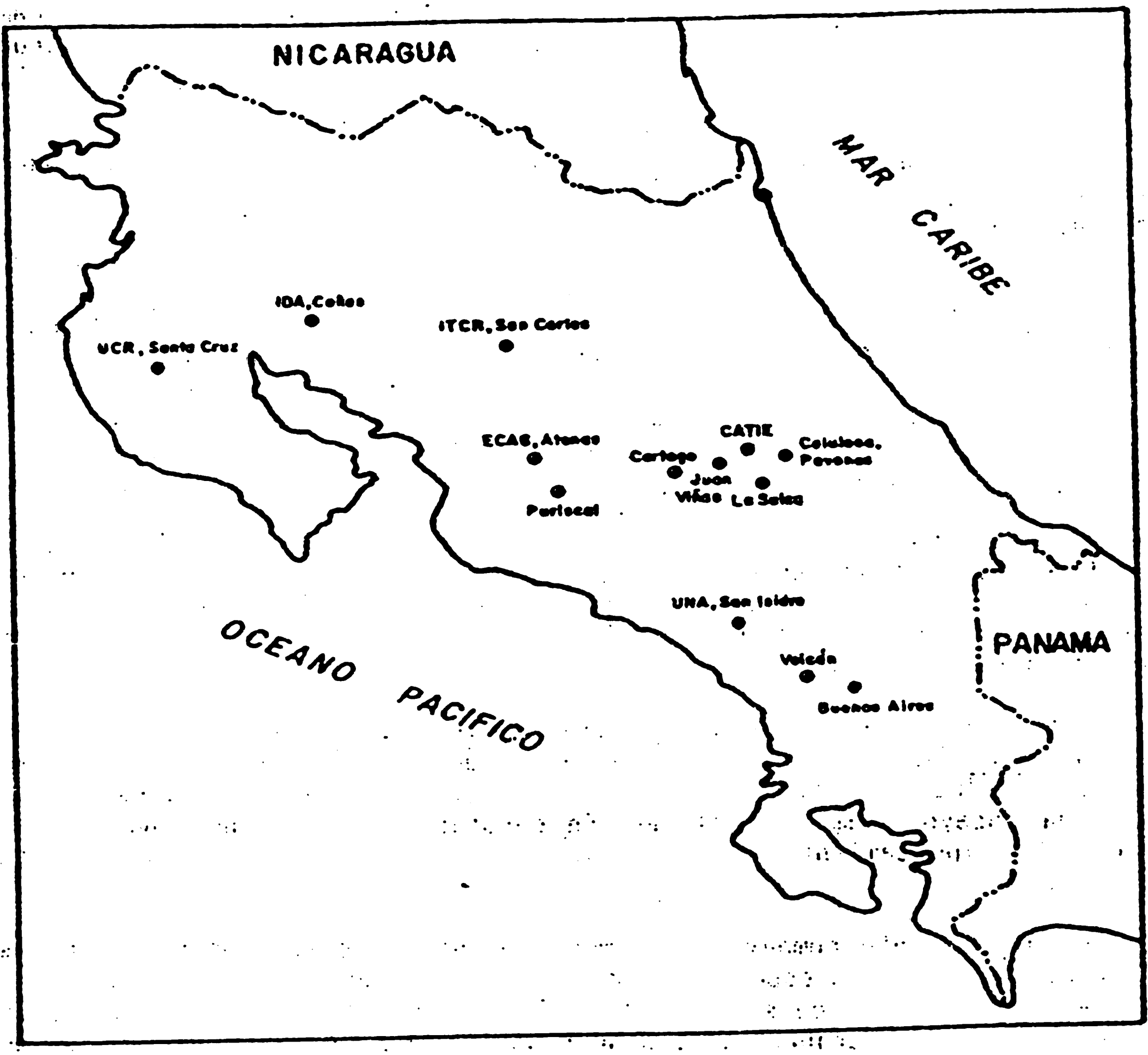


Figura 1. ubicación de los ensayos del Proyecto de Mejoramiento Genético de Arboles del CATIE dentro de Costa Rica

tal). Para P. caribaea los sitios han incluido altitudes desde 35-720 msnm, desde zonas de vida de bosque seco tropical, en Guanacaste hasta bosque muy húmedo premontano, en San Carlos. El P. oocarpa fue plantado en zonas desde 680-1100 msnm en climas húmedos con época seca definida como San Isidro del General y sin época seca definida como Turrialba.

Estudios taxonómicos en los últimos años han mostrado que las procedencias Yucul y Mountain Pine Ridge de P. oocarpa son diferentes taxonómicamente al P. oocarpa y se han reclasificado como P. patula subsp. tecunumanii (Eguiluz & Perry), Styles (Styles, 1985) o P. tecunumanii (Eguiluz & Perry) (Egüiluz y Perry, 1983).

Los resultados iniciales del ensayo de P. caribaea fueron publicados por Salazar (1981, 1982) y Bird (1983, 1984). Bird evaluó: i) volumen sobre corteza, ii) longitud del entrenudo más largo y iii) rectitud del fuste a los cinco años de edad y encontró diferencias entre procedencias para las variables i) y ii). Las procedencias de P. tecunumanii de Yucul y Mountain Pine Ridge fueron sobresalientes en su comportamiento. La variable iii) rectitud del fuste, no mostró diferencias significativas entre procedencias probablemente debido a deficiencias en el diseño experimental original. El análisis combinando los cuatro sitios no mostró una interacción significativa procedencia-ambiente para ninguna de las tres variables. En el Cuadro 1 se presentan los datos de volumen a los cuatro años de edad para P. caribaea y en los Cuadros 2 y 3 para altura y DAP a los siete años de edad. En los Cuadros 4 y 5 se presentan datos de altura y DAP para el ensayo de P. oocarpa a los cuatro años de edad. Las líneas muestran cambio de comportamiento de cada procedencia en los diferentes sitios. Los datos fueron sometidos al análisis de varianza que mostró diferencias significativas entre procedencias al nivel $P < 0.01$ para casi todos los sitios y variables evaluados.

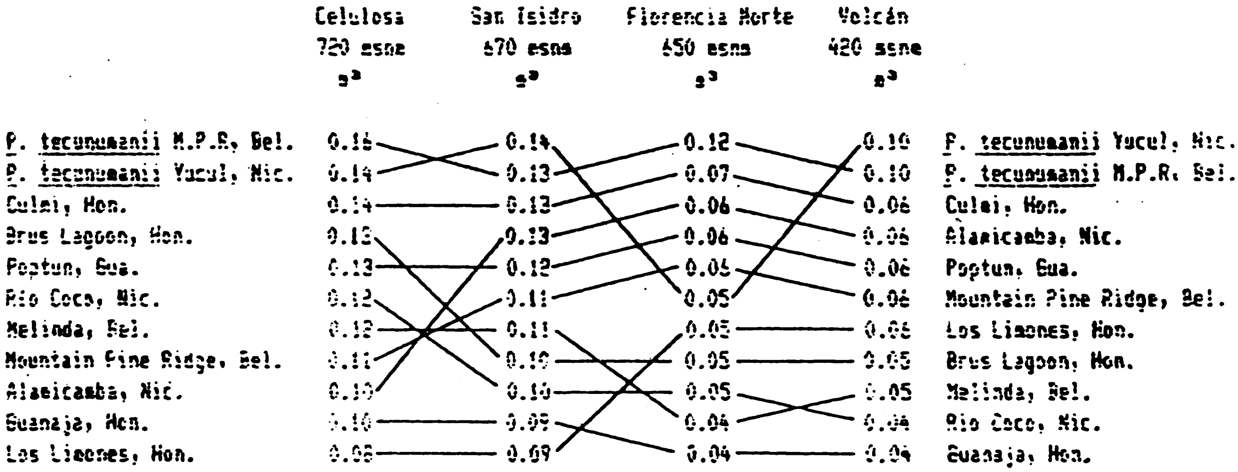
Como se puede ver el buen comportamiento de las dos procedencias de P. tecunumanii (Yucul y Mountain Pine Ridge) se ha mostrado en todos los sitios. Incluso el análisis de varianza para los cuatro sitios combinados para cada ensayo no mostró interacción genotipo-ambiente indicando la estabilidad del comportamiento de la mayoría de las procedencias en los sitios probados.

Es interesante comparar el comportamiento de estas dos procedencias con las de P. caribaea, la especie que más se ha plantado en Costa Rica y la recomendada para un rango de sitios entre 0-800 msnm. La mayoría de las primeras plantaciones de P. caribaea var. hondurensis en Costa Rica fueran establecidas con semilla procedente de Poptún, Guatemala, en parte Mountain Pine Ridge, Belice y últimamente Culmi, Honduras. Sin embargo, los resultados de los ensayos muestran que se pueden esperar mayores rendimientos con Yucul y Mountain Pine Ridge (P. tecunumanii) que con cualquier de las procedencias de P. caribaea.

Se han reportado resultados similares de los mismos ensayos internacionales en otros países (Greaves, 1980) con el comportamieno superior de estas dos procedencias Yucul y Mountain Pine Ridge, y otras dos Camelias y San Rafael, Nicaragua que no fueron probados en Costa Rica.

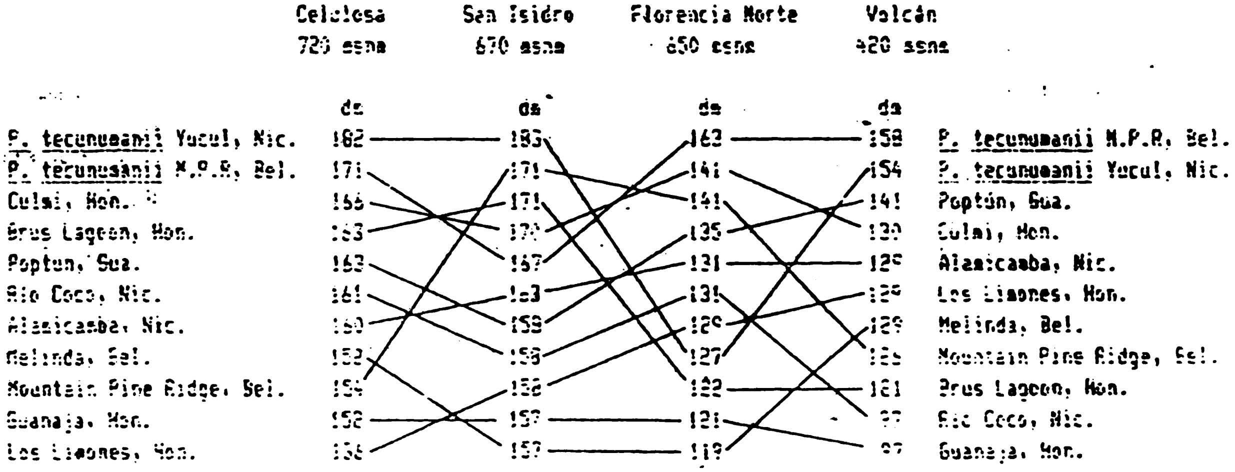
Con base en los resultados se recomienda la utilización de las procedencias bajas de P. tecunumanii y en particular Yucul (debido a su mejor forma)

Cuadro 1
Expto. 112 - Procedencias de *Pinus caribaea* volumen promedio a 5 años de edad en 4 sitios, plantado 1977 y 78 (Bird, 1984)



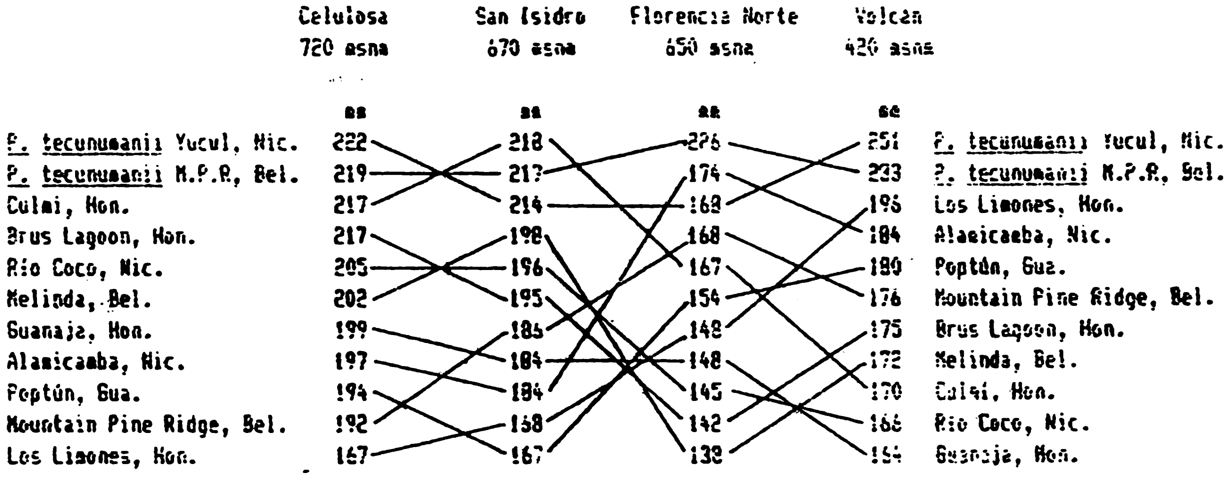
	Celulosa 720 msnm m³	San Isidro 670 msnm m³	Florencia Norte 650 msnm m³	Volcán 420 msnm m³	
P. tecunumanii M.P.R, Bel.	0.16	0.14	0.12	0.10	*P. tecunumanii* Yucul, Nic.
P. tecunumanii Yucul, Nic.	0.14	0.13	0.07	0.10	*P. tecunumanii* M.P.R. Bel.
Culmi, Hon.	0.14	0.13	0.06	0.06	Culmi, Hon.
Brus Lagoon, Hon.	0.13	0.13	0.06	0.06	Alamicamba, Nic.
Poptun, Gua.	0.13	0.12	0.05	0.06	Poptun, Gua.
Rio Coco, Nic.	0.12	0.11	0.05	0.06	Mountain Pine Ridge, Bel.
Melinda, Bel.	0.12	0.11	0.05	0.06	Los Limones, Hon.
Mountain Pine Ridge, Bel.	0.11	0.10	0.05	0.05	Brus Lagoon, Hon.
Alamicamba, Nic.	0.10	0.10	0.05	0.05	Melinda, Bel.
Guanaja, Hon.	0.10	0.09	0.04	0.04	Rio Coco, Nic.
Los Limones, Hon.	0.08	0.69	0.04	0.04	Guanaja, Hon.

Cuadro 2
Expto. 112 Procedencias de *Pinus caribaea*- altura promedio a los 8 años de edad en 4 sitios, plantado 1977 y 78.

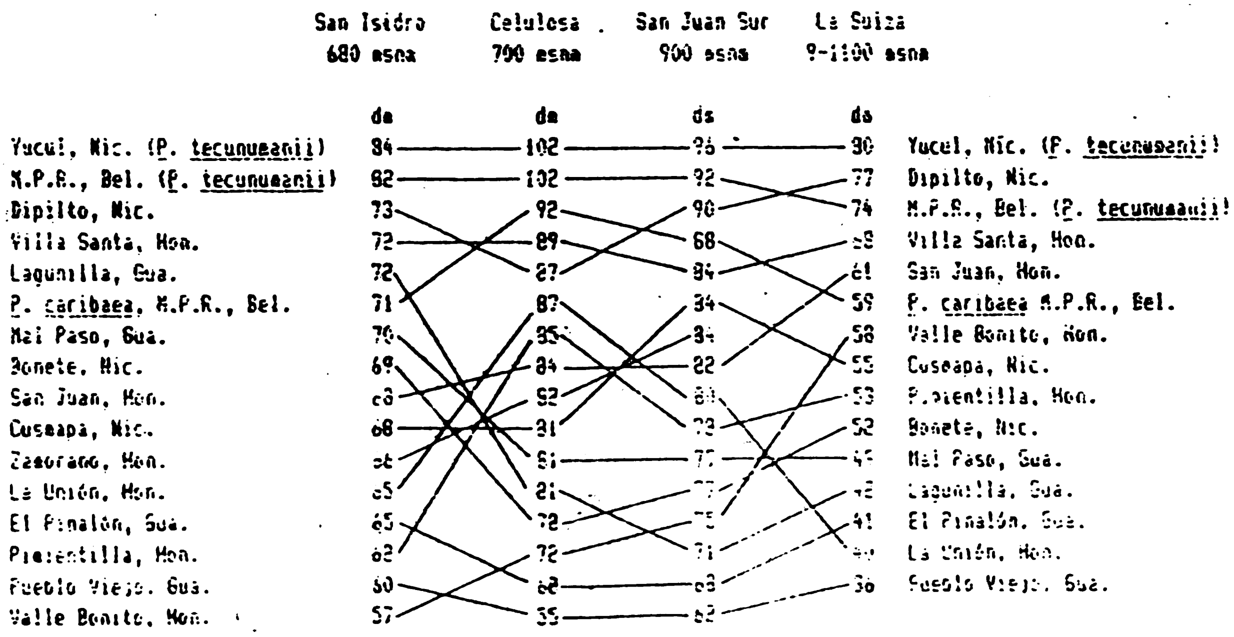


	Celulosa 720 msnm dm	San Isidro 670 msnm dm	Florencia Norte 650 msnm dm	Volcán 420 msnm dm	
P. tecunumanii Yucul, Nic.	182	183	163	158	*P. tecunumanii* M.P.R. Bel.
P. tecunumanii M.P.R, Bel.	171	171	141	154	*P. tecunumanii* Yucul, Nic.
Culmi, Hon.	166	171	141	141	Poptún, Gua.
Brus Lagoon, Hon.	163	170	135	130	Culmi, Hon.
Poptun, Gua.	163	167	131	129	Alamicamba, Nic.
Rio Coco, Nic.	161	163	131	129	Los Limones, Hon.
Alamicamba, Nic.	160	159	129	129	Melinda, Bel.
Melinda, Bel.	155	158	127	125	Mountain Pine Ridge, Bel.
Mountain Pine Ridge, Bel.	154	158	122	121	Brus Lagoon, Hon.
Guanaja, Hon.	152	157	121	97	Rio Coco, Nic.
Los Limones, Hon.	136	157	119	97	Guanaja, Hon.

Cuadro 3
Expto. 112 Procedencias de *Pinus caribaea* - DAP promedio a los 3 años de edad en 4 sitios.
plantado 1977 y 1978

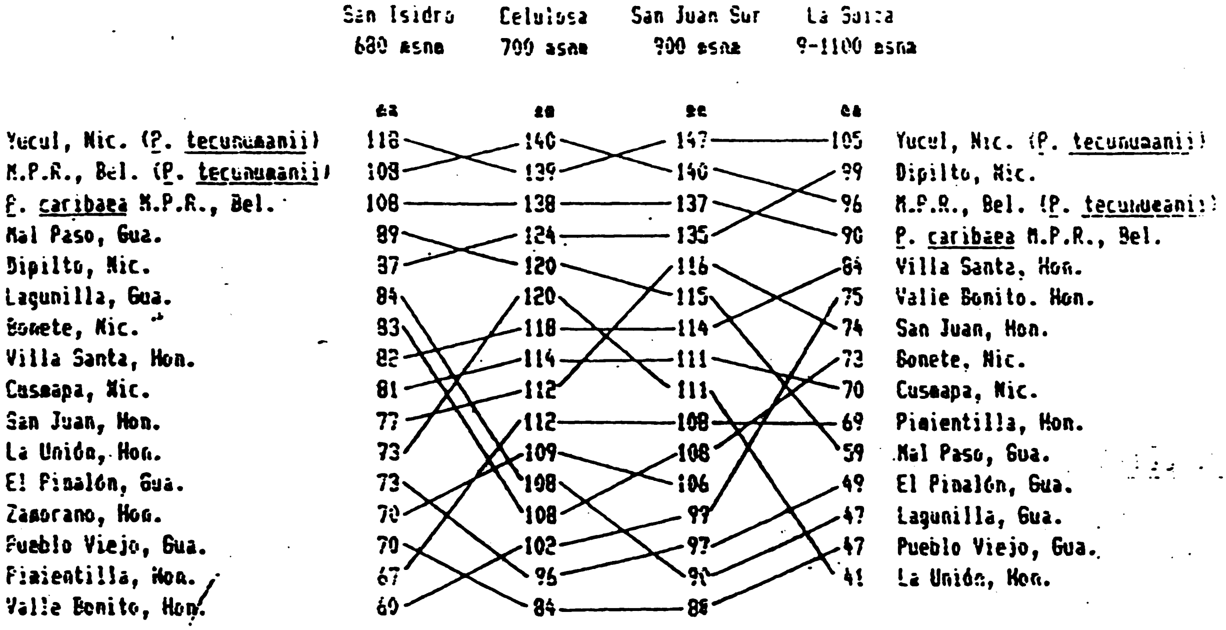


Cuadro 4
Expto. 115.- Procedencias de *Pinus oocarpa*- altura promedio a los 4 años de edad en 4 sitios,
plantado 1978 y 79.



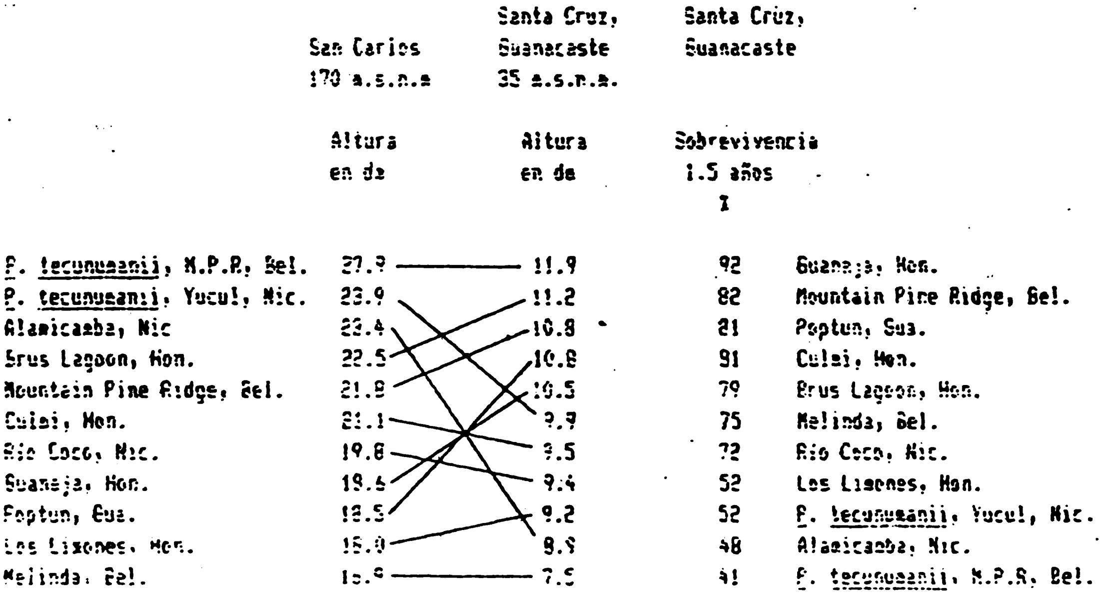
Cuadro 5

Expto 115. Procedencias de *Pinus oocarpa* -DAP promedio a los 4 años de edad en 4 sitios, plantado 1978-1979.



Cuadro 6

Expto. 112 Procedencias de *Pinus caribaea* promedios de altura total en los sitios 6 y 7, a 1'5 años, plantado 1983



Sin consideración de la discusión taxonómica se recomienda dentro del uso normal y medios de comunicación en Costa Rica usar el nombre P. *tecunumanii* y no P. *patula* subsp. *tecunumanii* para evitar confusiones con P. *patula* el cual tiene un comportamiento muy diferente.

Con base en los resultados presentados, el proyecto de mejoramiento ha procedido a una siguiente fase del programa para

para reforestación en la zona entre 400-1200 msnm en Costa Rica. Esta recomendación apoya la de Ford (1982) quien recomendó no utilizar *P. caribaea* en altitudes superiores a los 800 msnm debido al peligro de ataque de *Dothistroma pini* y la resistencia aparente de *P. oocarpa*. Para las zonas más bajas hasta el momento no es posible ser tan concluyente debido a que los sitios (en Guanacaste y San Carlos) están recién plantados. Sin embargo, los datos a un año y medio presentados en el Cuadro 6 indican que el *P. tecunumanii* no se adapta a las condiciones severas de Guanacaste y que las fuentes de *P. caribaea* que muestran mayor sobrevivencia serán las más importantes. En San Carlos no hubo diferencias significativas entre procedencias para sobrevivencia y pareciera que el *P. tecunumanii* tiene potencial para las zonas bajas húmedas del país. Se esperarán resultados futuros para confirmar o negar estas observaciones.

Sin consideración de la discusión taxonómica se recomienda dentro del uso normal y medios de comunicación en Costa Rica usar el nombre *P. tecunumanii* y no *P. patula* subsp. *tecunumanii* para evitar confusiones con *P. patula*, el cual tiene un comportamiento muy diferente.

Con base en los resultados presentados, el proyecto de mejoramiento ha procedido a una siguiente fase del programa para lograr en un futuro la producción de semilla mejorada de pino para uso local. Esta fase está siguiendo tres líneas.

i) la primera línea ha sido el establecimiento de ensayos de descendencias (exptos. 119 y 156) de nuevo como parte de una red internacional de ensayos. Aparte de proveer datos de parámetros genéticos para las especies y material apto para selección, se espera que los ensayos establecidos en Atenas y Guanacaste puedan ser raleados con fines de crear huertos semilleros que provean semilla mejorada.

ii) dentro de los árboles de Yucul y Mountain Pine Ridge en los ensayos de procedencias se han seleccionado los 11-12 mejores árboles por procedencia. Esto corresponde a una intensidad de selección de aproximadamente 1:45 que es mayor de lo normal para rodales semilleros pero menor que para árboles plus. Utilizando propagación vegetativa por injertos, los árboles seleccionados se han establecido en huertos semilleros de tipo experimental de media hectárea por procedencia. Yucul se estableció en El Guarco y Mountain Pine Ridge en Ochomogo, sitios con clima similar al de sus zonas de origen. Se espera que los huertos estén produciendo la primera cosecha de semilla en 1991-1992.

iii) se ha reconocido que la base genética de *P. tecunumanii* y la información sobre la especie dentro del país son muy reducidas. Por esta razón en 1987 se pretende establecer un ensayo de descendencias en una variedad de sitios entre 600-1800 msnm. Al mismo tiempo se establecerán pequeñas plantaciones de dos a tres hectáreas con semilla de Yucul, Mountain Pine Ridge y Camelias que proverán más material para selecciones y que además podrían servir como rodales semilleros en el futuro.

Cordia alliodora

C. alliodora (Laurel) es una de las especies más utilizadas en el país y cada día el diámetro mínimo de las tucas disminuye indicando un sobre apro-

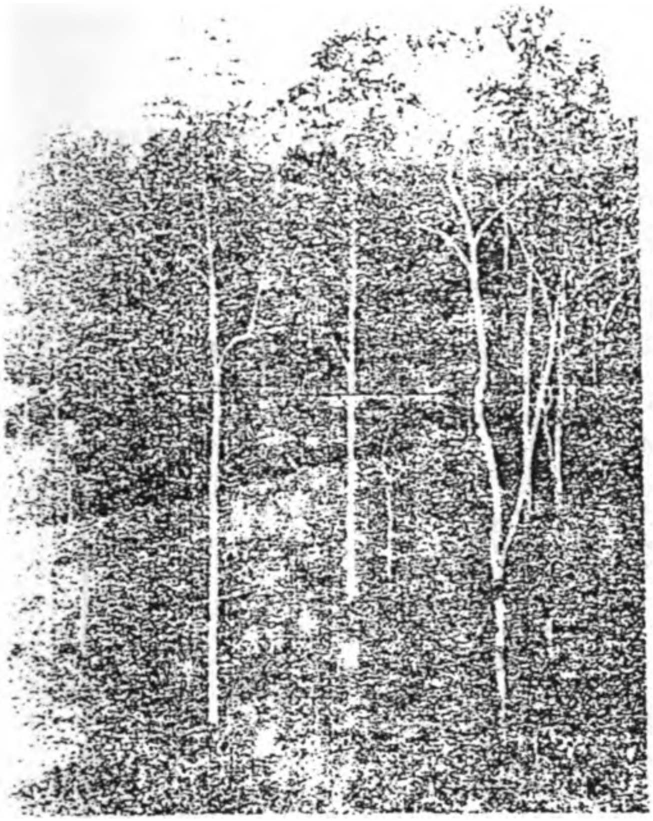


Fig. 2 Regeneración natural de *C. alliodora*

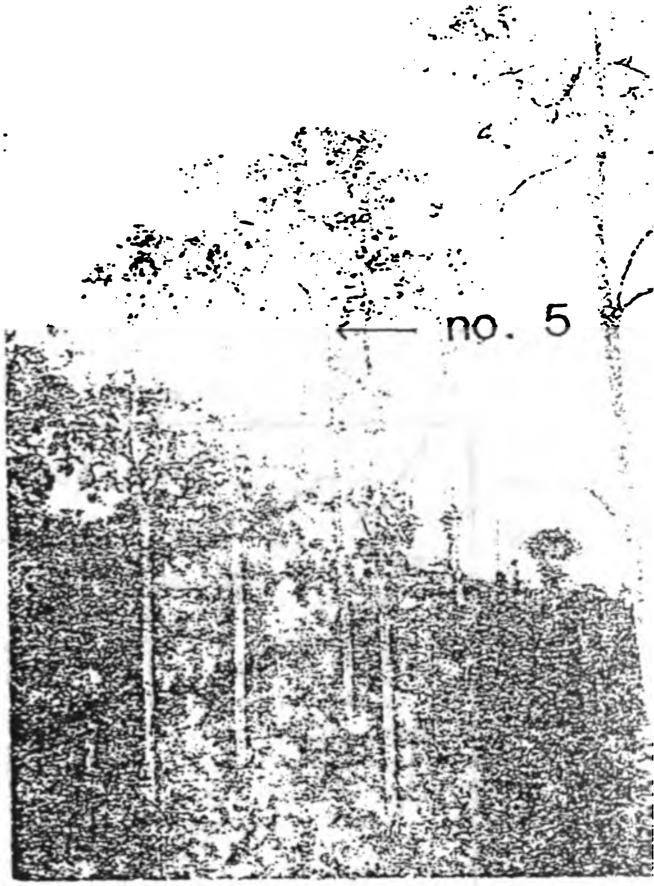


Fig. 3 Arbol plus no. 5

Fig. 4 Arbol plus no. 8

Fig. 5 Arbol plus no. 12

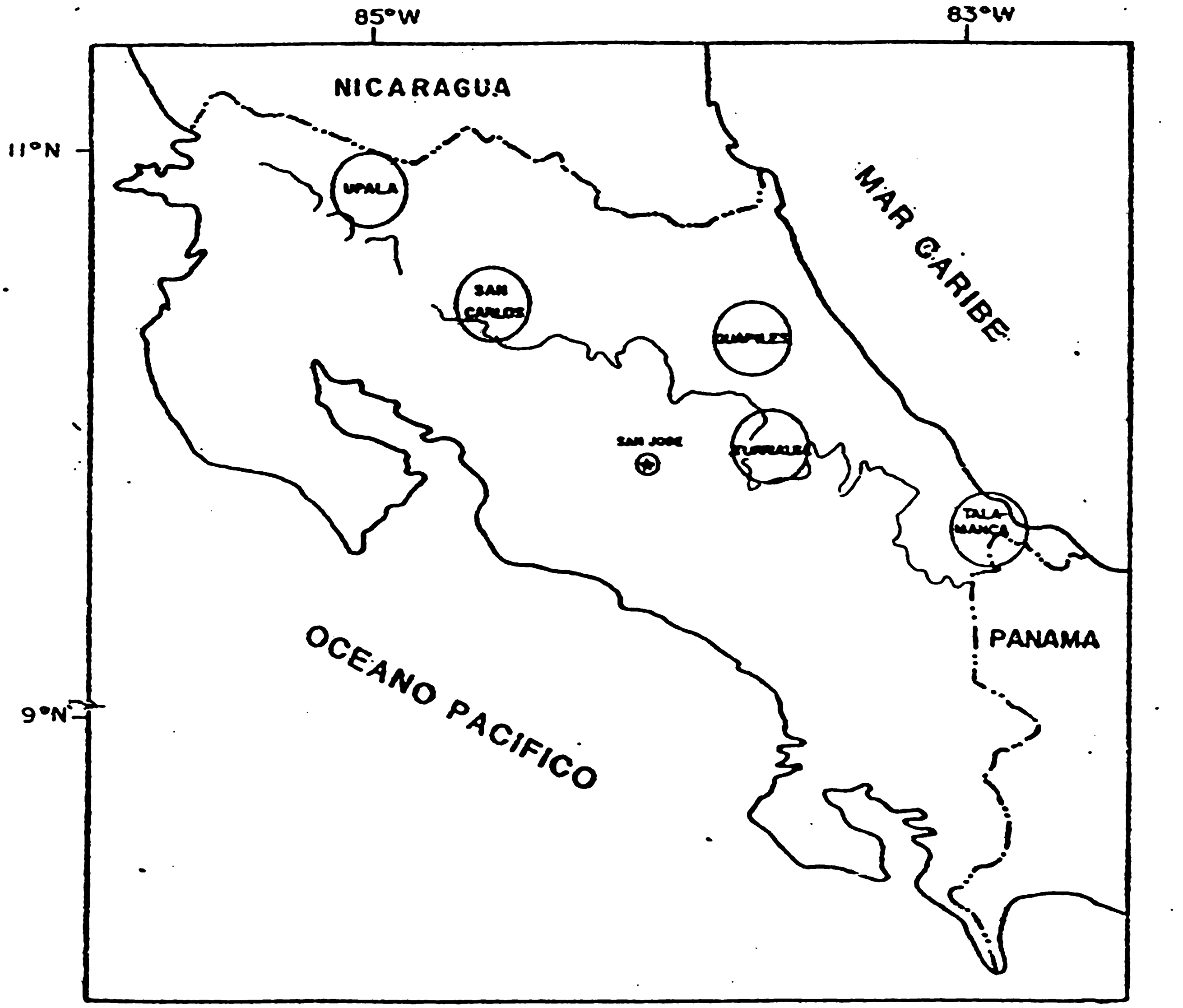


Figura 6. : ubicación de procedencias dentro de las cuales se seleccionaron árboles plus. Se muestra la curva de nivel de 800 metros para indicar la distribución aproximada de *C. alliodora* en la costa atlántica de Costa Rica.

vechamiento que llevará a una escasez y una degradación del recurso genético debido a la explotación disgénica. La forma de los árboles que se encuentran en los rodales naturales es muy variada (vea Figura 2) y muchas veces limita la cantidad de madera que se puede aprovechar de los árboles. Esto indica una gran variabilidad genética dentro de la especie y la posibilidad de ganancias significativas por medio de selección de árboles individuales.

Desde 1983 el proyecto de mejoramiento ha llevado a cabo un programa de selección de árboles "plus" dentro de los rodales de la zona altántica. Hasta la fecha se han seleccionado 60 árboles en cinco procedencias (vea Figura 3-6) y se ha recolectado semilla para el establecimiento de un ensayo de descendencias en 1986-87 en tres partes del país (Turrialba, Guápiles y Talamanca). Se está enviando semilla a otros países que tienen interés en C. alliodora para establecer el mismo ensayo. Dicho ensayo tendrá los siguientes objetivos: i) Comprobar las selecciones fenotípicas originales, ii) Proveer información sobre parámetros genéticos, hasta el momento desconocidos para la especie, iii) Proveer material apto para una segunda generación de selección y iv) Proveer semilla mejorada para su uso en plantaciones comerciales (Boshier y Mesén, 1986 en prensa). Los árboles seleccionados han sido injertados para fines de conservación en un banco clonal. Hasta que los ensayos produzcan semilla mejorada, semilla de los árboles seleccionados estará disponible en el BLSF (Banco Latinoamericana de Semillas Forestales) del CATIE a partir de abril 1987.

En 1979 y 1982 el proyecto estableció en cinco sitios un ensayo de procedencias de C. alliodora (ver Anexo 1). Los resultados iniciales de los sitios plantados en 1979 mostraron el buen comportamiento de la procedencia de San Francisco, Honduras (Boshier, 1984). Informes de otros países también han indicado el buen comportamiento de esta procedencia, por lo cual se aprovechó una visita a Honduras en 1986 para seleccionar y recolectar semillas de diez árboles en San Francisco que se adjuntarán a la población de mejoramiento. Sin embargo hasta el momento no ha sido posible comparar esta procedencia con las de Costa Rica dado que en los dos sitios plantados en 1979 la representación de las procedencias locales fue muy pobre. Los sitios plantados en 1982 en los cuales hay unas cuatro procedencias de Costa Rica son todavía demasiado jóvenes para hacer comparaciones concluyentes entre las procedencias de Costa Rica y la de San Francisco.

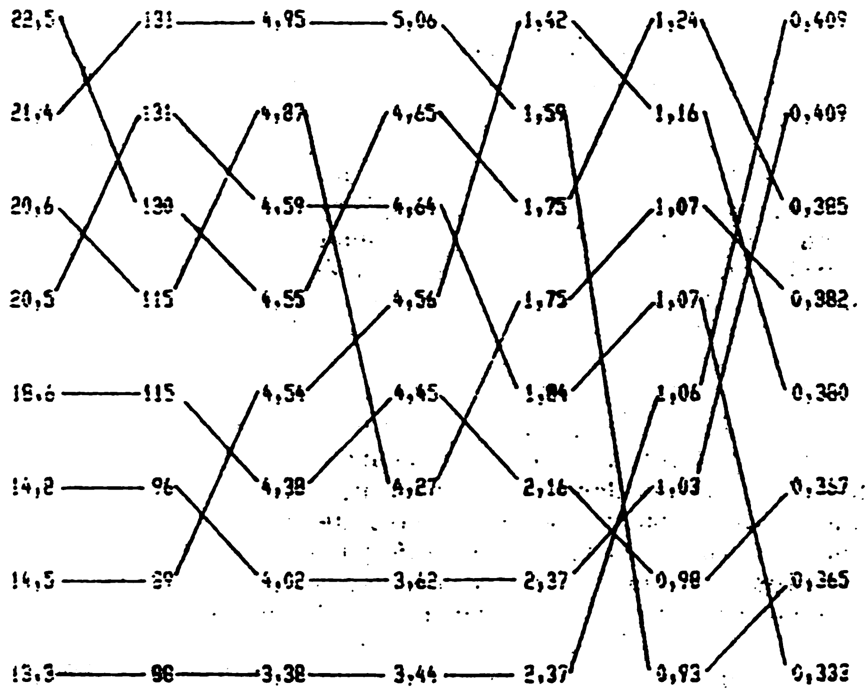
Gmelina arborea

La utilización de G. arborea (Melina) para la obtención de pulpa por parte de la Compañía Scott Paper y las plantaciones establecidas y propuestas para Guanacaste demuestran el interés por esta especie en el país. En 1982 el proyecto estableció un ensayo de procedencias de G. arborea en la finca de la Scott Paper en Pavones, Turrialba (ver Anexo 1).

La evaluación del ensayo para una serie de caracteristicas de producción, forma y calidad de la madera a los tres años de edad mostró diferencias significativas entre procedencias para la mayoría de las variables estudiadas (Valerio, 1986). Unos de los resultados resumidos en el Cuadro 7 muestran el buen comportamiento de la procedencia local derivada de las plantaciones en Manila, Siquirres.

Cuadro 7

Expto. 188 Procedencias de *Gmelina arborea* plantado en Pavones, Turrialba, 500-540 m.s.n.m.
Valores promedios a 3 años de edad (Fuente: Valerio, 1986)



Procedencia	Código	Area Basal m²/ha	Altura dm	Dominancia del eje	Rectitud del fuste principal	Frecuencia Bifurcación	Largo de fibra mm	Densidad básica
Sao Miguel, Jari, Para, Brasil	DAN.4040	22,5	131	4,95	5,06	1,42	1,24	0,409
Manila, Siquirres Costa Rica	BLSF 1018	21,4	131	4,87	4,65	1,59	1,16	0,409
Andhra Pradesh, India	DAN 4066	20,6	130	4,59	4,64	1,75	1,07	0,385
'A', Sri Lanka.	DAN 4067	20,5	115	4,55	4,56	1,75	1,07	0,382
Kao Yai, Saraburi, Tailandia	D1003/80	18,6	115	4,54	4,45	1,84	1,06	0,380
Maredumilli, Andhra Pradesh, India	DAN 4058	14,8	96	4,38	4,27	2,16	1,03	0,367
Sankosh-1, Bengala Occidental, India	DAN 4045	14,5	89	4,02	3,62	2,37	0,98	0,365
Lambasingi, Andhra Pradesh, India	DAN 4065	13,3	88	3,38	3,44	2,37	0,93	0,333

Dominancia del eje principal: -escala de 1 (pérdida total) hasta 7 (dominancia completa)
Rectitud del fuste: - escala de 1 (deformado) hasta 9 (recto)

Valerio concluye que por el momento se pueden obtener mayores rendimientos en plantaciones de G. arborea en la zona atlántica a través de semilla recolectada de las plantaciones en Siquirres. Sin embargo, dado la naturaleza heterogénea de las plantaciones (Zeazer, 1978) es aconsejable que se definan zonas de recolección dentro de los rodales y que haya un manejo selectivo para dejar los mejores árboles como árboles semilleros.

En la zona de Guanacaste es aconsejable utilizar semilla de los rodales semilleros que están en proceso de establecimiento por el Centro Agrícola Cantonal de Hojancha (Barquero, 1985). Aunque los rodales fueron establecidos con semilla de las mismas plantaciones de Siquirres, han pasado por un leve período de adaptación y selección para las condiciones más severas encontradas en Guanacaste.

Para mejoramiento a más largo plazo el proyecto, en conjunto con el ITCR y la Scott Paper, iniciará en 1987 la selección de árboles plus dentro de las plantaciones ya establecidas en el país. Con base en estas selecciones se estudiará en particular la interacción genotipo-ambiente. El grado de interacción indicará si es necesario trabajar con una o dos poblaciones mejoradas, una para la zona seca y otra para la zona húmeda.

Al mismo tiempo se estudiará la posibilidad de traer más material de la procedencia Sri Lanka 'A' lo cual mostró muy buen comportamiento y posiblemente tendrá mayor potencial para mejoramiento a largo plazo que la procedencia local.

Agradecimientos

Este trabajo ha sido financiado por la Administración para el Desarrollo en Ultramar (ODA) del Reino Unido y la Dirección de la Cooperación al Desarrollo de la Confederación Suiza (COSUDE).

Se agradece profundamente a todas las personas e instituciones que han permitido el establecimiento de ensayos en sus terrenos y han facilitado el estudio de las especies en tantas partes del país. Los señores P.Beita, W.Beita, V.Cartín, E.Sánchez, G.Thiele; Colegio Agropecuario de La Suiza, ECAG, Hacienda Juan Viñas, ICE, IDA, ITCR, PINDECO, Scott Paper, UCR, UNA.

Queremos agradecer también a todo el personal que ha colaborado a través de los años en el establecimiento, mantenimiento y medición de los ensayos del proyecto, señores C.Castro, M.Hernández, J.Masís, R.Nuñez, J.A.Quirós, A.Ramírez y L.Sánchez.

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Anexo 1. Lista de ensayos del Proyecto Mejoramiento de Arboles de Valor Económico, CATIE

Expto. Nº	Nombre	Rep. Nº	Sitio Nº	Lote Nº	Nombre del sitio	Fecha de plantación	Arboles por parcela	Nº de bloques	Nº de fuentes de semilla
48(68)	Variedades de *Pinus caribaea*	1	609	008	Florencia Sur, CATIE, Turrialba	10-6-83	110	1	4
		2	641	001	Hacienda Atirro, Atirro, Turrialba	06-7-68	110	1	4
		3	604	010	Bajo San Lucas, CATIE, Turrialba	21-8-68	100	1	4
		4	610	024	Florencia Norte, CATIE, Turrialba	28-10-68	100	1	4
8(73-1)	Procedencias de *P. caribaea*	1	614	007	Puente Cajón, CATIE Turrialba	03-1-73	49	1	10
		2	614	007	Puente Cajón, CATIE Turrialba	03-1-73	49	1	10
		3	610	026	Florencia Norte, CATIE, Turrialba	05-1-73	49	1	10
		4	615	001	San Juan Sur, CATIE Turrialba	06-1-73	49	1	10
		5	613	001	Noche Buena, CATIE Turrialba	10-1-73	49	1	10
112(77-1)	Procedencias de *P. caribaea*	1	642	002	Celulosa de Turrialba, Pavones, Turrialba	-9-77	7	5	12
		2	610	002	Florencia Norte, CATIE, Turrialba	-9-77	7	5	12
		3	703	003	ICE, La Garita, Alajuela	-10-77	7	5	12
		4	305	011	Finca W. Beita, Vol. Buenos Aires	31-3-78	7	4	12
		5	311	001	Univ. Nac. Aut., San Isidro del General	-9-77	7	5	12
		6	214	004	ITCR, Santa Clara, San Carlos	7/9-6-83	36	5	12
		7	454	001	Est. Exp. U.C.R. Sta.Cruz, Guanacaste	21/23-6-83	36	5	12

Expto. Nº	Nombre	Rep. Nº	Sitio Nº	Lote Nº	Nombre del sitio	Fecha de plantación	Arboles por parcela	Nº de bloques	Nº de fuentes de semilla
113(73-1)	Procedencias de _P_. _caribaea_	1	614	009	Puente Cajón, CATIE Turrialba	20/21-3-78	49	3	16
115(78-3)	Procedencias de _P_. _oocarpa_	1	642	002	Celulosa de Turrialba, Pavones, Turrialba	18-10-78	10	5	16
		2	615	003	San Juan Sur, CATIE Turrialba	1-12-78	10	5	16
		3	311	002	Univ. Nac. Aut. San Isidro del General	10-5-79	10	5	16
		* 4	410	017	Est. Exp. Jiménez Núñez, Cañas	30-5-79	10	5	16
117(77-2)	Descendencias de _Cordia_ _alliodora_	1	610	014	Florencia Norte, CATIE, Turrialba	2-7-76	1	15	25
113(78-5)	Procedencias de _C_. _alliodora_	1	609	014	Florencia Sur, CATIE, Turrialba	7-8-79	49	5	8
		2	627	001	Col Agrop. La Suiza, Turrialba	17-10-79	25	5	6
		* 3	311	005	Univ. Nac. Aut., San Isidro del General	14/19-10-82	36	5	13
		4	642	012	Celulosa de Turrialba, Pavones, Turrialba	16/20-8-83	36	5	12
		5	214	003	ITCR, Santa Clara, San Carlos	16/19-5-83	36	5	14
119(78-6)	Descendencias de _P_. _caribaea_	* 1	410	018	Est. Exp. Jiménez Núñez, Cañas	-6-79	6	5	41
		2	409	001	Vivero For. ITCO, El Pochote, Cañas	-9-79	6	5	32
136(79-3)	Especies y proc. de _Eucalyptus_	1	612	015	La Isla, CATIE, Turrialba	23/28-4-80	36	5	23
139(79-6)	Procedencias de _Araucaria_ _hunsteinii_ y _A_. _cunninghamii_	1	614	011	Puente Cajón, CATIE, Turrialba	7-7-81	49	2	4
142(79-9)	Procedencias de _Eucalyptus_ _grandis_	* 1	408	001	ITCO, Finca Llanos de Cortés, Bagaces	-8-80	36	5	12
		2	306	002	Finca W. Beita, Vol. Buenos Aires	22/26-6-81	36	5	10
		3	307	003	Finca P. Beita, Vol Buenos Aires	26/30-6-81	36	3	6

144(79-1)	Reforestación de pastizales degradados en La Suiza (procedencias de P. oocarpa)	1	635	001	Finca Sánchez, La Suiza, Turrialba	20-07-79	49	1	15
		2	636	002	Finca Thiele, La Suiza La Suiza, Turrialba	22-06-79	49	1	15
145(80-1)	Procedencias de E. tereticornis	* 1	408	002	ITCO, Finca Llanos de Cortés, Bagaces	-8-80	36	5	14
151(80-7)	Procedencias de E. urophylla	1	214	002	ITCR, Santa Clara San Carlos	19-8-81	36	5	14
		2	311	004	Univ. Nac. Aut., San Isidro del Gnl.	29-7-81	36	5	4
		3	609	006	Florencia Sur, CATIE, Turrialba	28/10 al 4-11-81	25	5	3
156(82-2)	Procedencias y Descendencias de P. caribaea y P. oocarpa	1 a y b	716	001	Esc. Centroamericana de Ganadería, Atenas	27-7 al 3-8-82	5	10	78
		2 a	646	003	Hda. Juan Viñas, Turrialba	26/31-7-84	5	10	41
		2 b	610	035	Florencia Norte, CATIE, Turrialba	15/30-10-84	5	10	42
188(82-1)	Procedencias de Gmelina arborea	1	642	012	Celulosa de Turrialba, Pavones, Turrialba	30-8 al 1-9-82	36	4	9
201	Procedencias de Acacia mangium	1	214	006	ITCR, Santa Clara San Carlos	4/6-12-84	36	5	14
		2	319	001	PINDECO, Buenos Aires	26-10 al 1-11-84	36	5	11
		* 3	482	001	Colorado, Abangares, Guanacaste	13-09-84	36	5	6
		4	513	001	Cortezal de Barbacoas, Puriscal	08-08-84	36	5	6
203	Propagación vegetativa de Araucaria hunsteinii	-	---	---	Vivero Forestal Turrialba	Desde 83	-	-	-
211	Rodales y huertos semilleros de Pinus tecunumanii	1	513	003	Cortezal de Barbacoas, Puriscal	03-07-85	394	1	1
		2	622	001	El Guarco, Cartago	08-86	1	14	12
		3	623	001	Vivero Anderson, Ochomogo, Cartago	08-86	1	19	11

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* Sitios abandonados debido a baja sobrevivencia.

PROYECTO DE MEJORAMIENTO GENETICO DE ARBOLES

David Boshier*
José F. Mesén*

Reconociendo el efecto que la calidad genética de la semilla puede tener sobre el éxito de proyectos de reforestación, el CATIE inició un programa de mejoramiento genético de árboles de valor económico en Costa Rica a finales de 1977. Las especies incluidas en el programa fueron seleccionadas con base en los resultados de ensayos con muchas especies, las cuales fueron establecidos en el CATIE y en otras partes del país. Algunas de las especies son la base de la reforestación en Costa Rica y han sido promovidas por la Dirección General Forestal (DGF) como estímulo a la reforestación.

El proyecto de mejoramiento genético del CATIE ha trabajado principalmente en zonas entre 0-1400 msnm con las siguientes especies: Acacia mangium, Araucaria hunsteinii, Cordia alliodora, Eucalyptus grandis, E. urophylla, Gmelina arborea, Pinus caribaea, P. ocarpa y P. tecunumanii. Los ensayos han sido establecidos en una variedad de sitios, tratando de incluir las diferentes zonas ecológicas que se consideran aptas para reforestación con la especie en particular (ver Anexo 1 para detalles de los ensayos establecidos). También se pretende identificar los patrones de interacción genotipo-ambiente que se presentan para cada especie y que afectarían las estrategias de mejoramiento genético a seguir en el país.

El proyecto empezó con el establecimiento de ensayos de procedencias de las especies mencionadas, como participante en los ensayos coordinados por organizaciones como IUFRO, FAO, OFI (Inglaterra) CSIRO (Australia) y DANIDA (Dinamarca).

Después del establecimiento de ensayos de procedencias para identificar las mejores para cada especie, la estrategia de mejoramiento a seguir depende de las necesidades de cada especie. Sin embargo, por lo general se ha procedido con la identificación de árboles "plus" (fenotípicamente superiores) dentro de la mejor o mejores procedencias, seguida por el establecimiento de ensayos de descendencias para comprobar las selecciones, y de plantaciones para la producción de semilla mejorada.

A continuación se dan detalles de los planes futuros para cuatro de las especies principales con las cuales trabaja el proyecto.

Pinus caribaea, P. oocarpa y P. tecunumanii

Los resultados de los ensayos de procedencias han mostrado el comportamiento superior de las procedencias de P. tecunumanii de Yucul y Mountain Pine Ridge en todos los sitios excepto en el Pacífico seco bajo, donde las procedencias Guanaja y Mountain Pine Ridge de P. caribaea parecen las más adaptadas (Bird, 1984; Boshier y Mesén, 1986). Con base en los resultados, el Proyecto

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ha procedido a una siguiente fase para lograr en un futuro la producción de semilla mejorada de pino para uso local. Esta fase sigue tres líneas.

i) Establecimiento de ensayos de descendencias (experimentos 119 y 156), de nuevo como parte de una red internacional de ensayos. Aparte de proveer datos de parámetros genéticos para las especies y material apto para selección, se espera que los ensayos establecidos en dos zonas del Pacífico seco de Costa Rica (Atenas y Guanacaste) puedan ser raleados con el fin de crear huertos semilleros.

ii) Entre los árboles de Yucul y Mountain Pine Ridge en los ensayos de procedencias se han seleccionado los 11-12 mejores árboles por procedencia. Esto corresponde a una intensidad de selección de aproximadamente 1:45, que es mayor de lo normal para rodales semilleros pero menor que para árboles plus. Utilizando propagación vegetativa por injertos, los árboles seleccionados se han establecido en huertos semilleros de tipo experimental de media hectárea por procedencia en sitios con clima similar al de sus zonas de origen.

iii) La base genética de P. tecunumanii y la información sobre la especie dentro del país son muy reducidas. Por esta razón en 1988 se pretende establecer un ensayo de descendencias en una variedad de sitios entre 600-1800 msnm. Al mismo tiempo se establecerán pequeñas plantaciones de dos a tres hectáreas con semilla de Yucul, Mountain Pine Ridge y Camelias que proveerán más material para selecciones y que además podrían servir como rodales semilleros en el futuro.

Cordia alliodora

C. alliodora (laurel) es una de las especies más utilizadas en el país. Actualmente existe un sobreaprovechamiento que llevará a una escasez y una degradación del recurso genético debido a la explotación disgénica. La gran variabilidad en forma de la especie sugiere la posibilidad de ganancias significativas por medio de selección de árboles individuales.

Desde 1983 el proyecto de mejoramiento ha llevado a cabo un programa de selección de árboles "plus" en los rodales naturales de la zona atlántica de Costa Rica. Hasta la fecha se han seleccionado 60 árboles de cinco procedencias y se ha recolectado semilla para el establecimiento de un ensayo de descendencias en tres sitios en el país. Se está enviando semilla a otros países que tienen interés en C. alliodora para establecer el mismo ensayo. Dicho ensayo tendrá los siguientes objetivos: i) comprobar las selecciones fenotípicas originales; ii) proveer información sobre parámetros genéticos, hasta el momento desconocidos para la especie; iii) proveer material apto para una segunda generación de selección y iv) proveer semilla mejorada para su uso en plantaciones comerciales. Los árboles seleccionados han sido injertados para fines de conservación en un banco clonal. Hasta que los ensayos produzcan semilla mejorada, semilla de los árboles seleccionados estará disponible en el BLSF del CATIE, a partir de abril 1987.

Informes de varios países han indicado el buen comportamiento de la procedencia de San Francisco, Honduras (Boshier, 1984), por lo cual se aprovechó una visita a Honduras en 1986 para seleccionar y recolectar semillas de 10 árboles en San Francisco que se adjuntarán a la población de mejoramiento.

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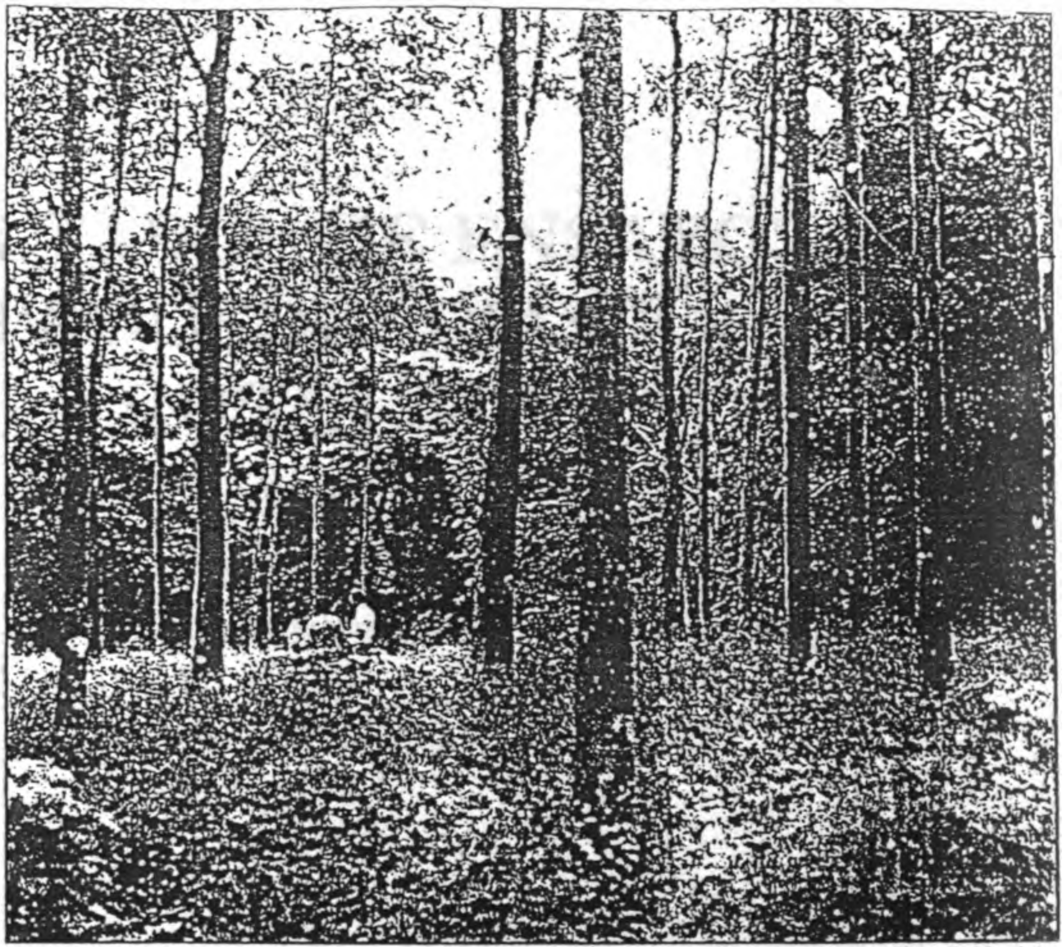
Ensayo N°	Nombre	Exp. N°	Finca N°	Lote N°	Nombre de finca	Fecha de plantación	N° de repeticiones	N° de tratamientos
46(68)	Variedades de *Pinus caribaea*	1	609	008	Florencia Sur, CATIE, Turrialba	10-6-68	1	4
		2	641	001	Hacienda Atirro, Atirro, Turrialba	06-[illegible]-68	1	4
		3	664	010	Bajo San Lucas, CATIE, Turrialba	21-8-68	1	4
		4	610	028	Florencia Norte, CATIE, Turrialba	28-10-68	1	4
8(73-1)	Procedencias de *P. caribaea*	1	614	007	Puente Cajón, CATIE Turrialba	03-1-73	1	10
		2	614	007	Puente Cajón, CATIE Turrialba	03-1-73	1	10
		• 3	610	026	Florencia Norte, CATIE, Turrialba	05-1-73	1	10
		4	615	001	San Juan Sur, CATIE Turrialba	06-1-73	1	10
		5	613	001	Noche Buena, CATIE Turrialba	10-1-73	1	10
112(77-1)	Procedencias de *P. caribaea*	1	642	002	Celulosa de Turrialba, Pavones, Turrialba	-9-77	5	12
		2	610	002	Florencia Norte, CATIE, Turrialba	-9-77	5	12
		• 3	703	003	ICE, La Garita, Alajuela	-10-77	5	12
		4	306	001	Finca W. Beita, Vol. Buenos Aires	31-3-78	4	10
		5	311	001	Univ. Nac. Aut., San Isidro del General	-9-77	5	12
		6	214	004	ITCR, Santa Clara, San Carlos	7/9-6-83	5	12
		7	454	001	Est. Exp. U.C.R. Sta.Cruz, Guanacaste	21/23-6-83	5	12
113(73-1)	Procedencias de *P. caribaea*	1	614	009	Puente Cajón, CATIE Turrialba	20/21-3-78	3	10
115(78-3)	Procedencias de *P. oocarpa*	1	642	002	Celulosa de Turrialba, Pavones, Turrialba	18-10-78	5	16
		2	615	003	San Juan Sur, CATIE Turrialba	1-12-78	5	16
		3	311	002	Univ. Nac. Aut. San Isidro del General	16-5-79	5	16
		• 4	410	017	Est. Exp. Jiménez Núñez, Cañas	30-5-79	5	16
117(77-2)	Descendencias de *Cordia alliodora*	1	610	014	Florencia Norte, CATIE, Turrialba	2-7-76	15	25
118(78-5)	Procedencias de *C. alliodora*	1	609	014	Florencia Sur, CATIE, Turrialba	7-8-79	5	8
		2	627	001	Col Agrop. La Suiza, Turrialba	17-10-79	5	6
		• 3	311	005	Univ. Nac. Aut., San Isidro del General	14/19-10-82	5	13
		4	642	012	Celulosa de Turrialba, Pavones, Turrialba	16/20-6-83	5	12
		5	214	003	ITCR, Santa Clara, San Carlos	16/19-5-83	5	14
119(78-6)	Descendencias de *P. caribaea*	• 1	410	016	Est. Exp. Jiménez Núñez, Cañas	-6-79	5	41
		2	409	001	Vivero For. ITCO, El Pochote, Cañas	-9-79	5	32
136(79-3)	Especies y proc. de *Eucalyptus*	1	612	015	La Isla, CATIE, Turrialba	23/28-4-80	5	23
139(79-6)	Procedencias de *Araucaria hunsteinii* y *A. cunninghamii*	1	614	011	Puente Cajón, CATIE, Turrialba	7-7-81	2	4
142(79-5)	Procedencias de *Eucalyptus grandis*	• 1	408	001	ITCO, Finca Llanos de Cortés, Bagaces	-8-80	5	12
		2	306	002	Finca W. Beita, Vol. Buenos Aires	22/26-6-81	5	10
		3	307	003	Finca P. Beita, Vol Buenos Aires	26/30-6-81	3	6
144(79-1)	Reforestación de pastizales degradados en La Suiza (procedencias de *P. oocarpa*)	1	635	001	Finca Sánchez, La Suiza, Turrialba	20-07-79	1	15
		2	636	002	Finca Thiele, La Suiza La Suiza, Turrialba	22-06-79	1	15
145(80-1)	Procedencias de *E. tereticornis*	• 1	408	002	ITCO, Finca Llanos de Cortés, Bagaces	-8-80	5	14
151(80-7)	Procedencias de *E. urophylla*	1	214	002	ITCR, Santa Clara San Carlos	19-8-81	5	14
		2	311	004	Univ. Nac. Aut., San Isidro del Gnl.	29-7-81	5	4
		3	609	006	Florencia Sur, CATIE, Turrialba	28/10 al 4-11-81	5	3
156(82-2)	Procedencias y descendencias de *P. caribaea* y *P. oocarpa*	1 a y b	716	001	Esc. Centroamericana de Ganadería, Atenas	27-7 al 3-8-82	10	78
		2 a	646	003	Hda. Juan Viñas, Turrialba	26/31-7-84	10	41
		2 b	610	035	Florencia Norte, CATIE, Turrialba	15/30-10-84	10	45
160(82-1)	Procedencias de *Gmelina arborea*	1	642	012	Celulosa de Turrialba, Pavones, Turrialba	30-8 al 1-9-82	4	9
201	Procedencias de *Acacia mangium*	1	214	006	ITCR, Santa Clara San Carlos	4/6-12-84	5	[illegible]
		2	319	001	PINDECO, Buenos Aires	26-10 al 1-11-84	5	11
		• 3	482	001	Colorado, Abangares, Guanacaste	13-09-84	5	6
		4	513	001	Cortezal de Barbacoas, Puriscal	08-08-84	5	[illegible]
203	Propagación vegetativa de *Araucaria hunsteinii*	...			Vivero Forestal, Turrialba	Desde 83		
211	Rodales y huertos semilleros de *Pinus tecunumanii*	1	513	003	Cortezal de Barbacoas, Puriscal	03-07-85		
		2	622	001	El Guarco, Cartago	08-86	14	
		3	623	001	Vivero Anderson, Ochomogo, Cartago	08-86	19	

Procuran avance genético forestal

JONATHAN CORNELIUS*
Genetista forestal



En Hojancha se han seleccionado plantaciones, para que funcionen como rodales semilleros. (Foto F. Mesén).

El número de proyectos de reforestación en Costa Rica ha aumentado notablemente en los últimos años. Sin embargo, no todas las plantaciones forestales han sido exitosas. Una de las razones importantes para tales fracasos, ha sido el uso de semilla de mala calidad genética.

En ese sentido, el Proyecto de Mejoramiento Genético Forestal, del Centro Agronómico Tropical de Investigación y Enseñanza (CATIE), en la actualidad financiado principalmente por el Ministerio noruego de Cooperación para el Desarrollo, realiza investigaciones, desde 1977, tendientes a solucionar este problema.

Uno de los objetivos del proyecto del CATIE es la identificación de procedencias superiores de las principales especies para reforestación en Costa Rica, por medio de la realización de las llamadas "pruebas de procedencia".

El proyecto ha establecido pruebas de procedencia para 11 especies, entre ellas el pino caribe o pino hondureño (Pinus caribaea var hondurensis), el pino oocarpa (Pinus oocarpa) y la melina (Gmelina arborea).

En el campo forestal el término "procedencia" se define como la fuente u origen de la semilla, y corresponde normalmente a una recolección de semillas de varios árboles en un área geográfica limitada.

Por lo general, en cada especie existen procedencias bien adaptadas a un sitio dado de plantación, y procedencias mal adaptadas, así como procedencias de crecimiento rápido y buena forma o de crecimiento lento y mala forma. En algunos casos se han obtenido incrementos en productividad de hasta el 400 por ciento, con sólo seleccionar las mejores procedencias.

Mejor pino

Para las especies de pino estudiadas, se ha probado un número bastante grande de procedencias, que cubren la mayor parte del rango de distribución de ellas.

Los ensayos se han establecido en sitios con altitudes que van desde 35 hasta 1.200 metros sobre el nivel del mar, en varias zonas del país.

En casi todos los sitios la procedencia **Yucul** (Nicaragua) mostró mejor comportamiento que cualquier otra procedencia de pino caribe o pino oocarpa. La única excepción se dio en Guanacaste donde la procedencia Guanaja (Honduras) de pino caribe fue superior.

La procedencia Yucul estaba clasificada originalmente como pino oocarpa, pero recientemente fue reclasificada como otra especie llamada **Pinus** tecunumanii.

Con base en los anteriores resultados, se recomienda el uso de pino tecunumanii, procedencia Yucul (Nicaragua), para la reforestación en áreas situadas entre el nivel del mar y 1.200 metros de altitud, en regiones húmedas de Costa Rica.

Semilla de esa procedencia se puede conseguir por medio del Banco Latinoamericano de Semillas Forestales del CATIE.

La melina

La melina es una especie asiática de muy rápido crecimiento que fue introducida a Costa Rica entre 1966 y 1970, en la zona de Manila, Siquirres. Actualmente hay varios proyectos de reforestación con esta especie en Guanacaste, el Pacífico Sur, y la zona norte del país.

La melina tiene una gran variedad de usos como leña, postes, construcción rural, muebles, pulpa para elaboración de papel, y otros. A diferencia de los pinos, la melina produce semillas en abundancia en Costa Rica.

En ensayos de procedencia establecidos por el CATIE, la fuente local derivada de las plantaciones de Siquirres demostró su superioridad, tanto en forma como en crecimiento.

Lo anterior quiere decir que ya todas las plantaciones del país se derivan de la fuente de Siquirres y que se pueden utilizar sus semillas sin necesidad de importar.

Sin embargo, se recomienda recolectar semillas de plantaciones que han sido raleadas, eliminando los peores árboles. Algunas plantaciones de la zona de Hojancha, Guanacaste, han sido raleadas para convertirlas en rodales semilleros, con la colaboración del CATIE, el Instituto Tecnológico de Costa Rica (ITCR) y el Centro Agrícola Cantonal de ese cantón del Pacífico Seco.

Semilla de esos rodales semilleros es apropiada para el establecimiento de plantaciones en el Pacífico Seco. Para plantaciones en las zonas húmedas se debería de recolectar semilla de plantaciones existentes en esa región, seleccionando siempre los mejores árboles como semilleros.

Semilla y éxito

Vale la pena destacar que una semilla de buena calidad genética no garantiza por sí misma una plantación exitosa. También es necesario producir plantas de buena calidad en el vivero, plantarlas en un sitio adecuado, y efectuar limpiezas regulares, hasta que los árboles tengan el tamaño para competir exitosamente con las malezas y efectuar las podas y raleos adecuados en el tiempo apropiado.

Otras actividades del proyecto de mejoramiento genético forestal son el establecimiento de huertos semilleros para producir material genéticamente superior, y el establecimiento de nuevos métodos de bajo costo y tecnología para la clonación de árboles superiores con el fin de instalar plantaciones comerciales.

Los trabajos se están realizando tanto con especies nativas, como el laurel y el pochote, como con especies exóticas.

Si desea mayor información comuníquese con el Proyecto Mejoramiento Genético Forestal, CATIE, Turrialba.

*** Técnico de administración para el desarrollo en ultramar del Gobierno de Gran Bretaña.**

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INFORME TECNICO No.156

RESULTADOS DE ENSAYOS DE PROCEDENCIAS EN COSTA RICA

Francisco Mesén

Publicación patrocinada por el
Proyecto Mejoramiento Genético Forestal (MGF)
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CENTRO AGRONOMICO TROPICAL DE INVESTIGACION Y ENSEÑANZA
Programa de Producción y Desarrollo Agropecuario Sostenido
Area de Producción Forestal y Agroforestal
Turrialba, Costa Rica, 1990

CONTENIDO

RESUMEN

El Proyecto de Mejoramiento Genético Forestal del CATIE, ha venido trabajando desde 1977 en el establecimiento de pruebas de procedencias de especies forestales con potencial para producción de madera en Costa Rica. Hasta 1989 se han establecido cerca de 40 ensayos de este tipo, en las zonas ecológicas con mayor potencial para reforestación en el país. Este documento presenta un resumen de progreso sobre los resultados de algunos de estos ensayos, y describe brevemente sus implicaciones en futuros programas de investigación y reforestación en Costa Rica.

INTRODUCCION

En Costa Rica, el número de proyectos de reforestación se ha incrementado notoriamente en los últimos años, pero al mismo tiempo, la experiencia acumulada confirma que el uso de procedencias inapropiadas de semilla es una de las causas principales del fracaso o de la baja productividad observada en muchas de estas plantaciones. Se sabe que el éxito en el establecimiento y productividad de plantaciones forestales está determinado en gran medida por la selección correcta no sólo de la especie, sino también de la procedencia dentro de la especie. Se ha considerado que la selección de procedencias es una de las decisiones más importantes en silvicultura, puesto que una mala selección puede llevar a más problemas a largo plazo que casi cualquier otro factor.

"Procedencia" o "fuente de semilla" son términos puramente forestales que no tienen lugar en la taxonomía formal, y se refieren solamente a una área geográfica limitada donde crecieron los árboles (Burley y Wood, 1979). Por ejemplo, la procedencia ***Pinus tecunumanii*** "Yucul" se refiere a aquella población de árboles que ocurren en esta área de Nicaragua, y que han desarrollado una composición genética particular como respuesta a las condiciones ecológicas que allí prevalecen. Los ensayos de procedencias adquieren mayor importancia en aquellas especies que presentan rangos de distribución geográficos y/o ecológicos amplios, ya que se espera que las condiciones ecológicas diferentes que prevalecen a lo largo del rango, hayan originado cambios en las frecuencias génicas de sus poblaciones. La descendencia de estas poblaciones podrán mostrar diferencias, que pueden ser desde pequeñas hasta dramáticas, cuando son plantadas juntas en un ambiente nuevo.

Reconociendo la importancia para Costa Rica de iniciar un programa de mejoramiento genético a partir de las mejores especies y procedencias, el CATIE inició en 1977 el Proyecto de Mejoramiento de Arboles de Valor Económico, actualmente denominado Proyecto de Mejoramiento Genético Forestal (MGF). Desde esta fecha, el Proyecto ha trabajado en las zonas desde 0 a 1700 msnm, con especies con potencial para producción de madera para aserrío. En el Anexo 1 se muestra la ubicación de los ensayos establecidos en Costa Rica, y en el Anexo 2 se presentan los detalles de los ensayos. Las especies incluidas fueron seleccionadas con base en los resultados de ensayos con más de cien especies, nativas y exóticas, que fueron establecidas en el CATIE y en otras partes del país (Camacho, 1982; Combe y Gewald, 1979).

El Proyecto empezó como participante de una red internacional de ensayos de procedencias, coordinados por la Unión Internacional de Organizaciones de Investigación Forestal (IUFRO), el Instituto Forestal de Oxford (OFI), la Unión de Organizaciones de Investigación Científica e Industrial de la Mancomunidad (CSIRO), la Organización de las Naciones Unidas para la Agricultura y la Alimentación (FAO) y el Centro de Semillas Forestales de Dinamarca/DANIDA. Los ensayos fueron establecidos en una amplia variedad de sitios, tratando de incluir las diferentes regiones que se consideran con potencial para reforestación. La selección de sitios se hizo tratando de identificar los patrones de interacción genotipo-ambiente, que afectarían las estrategias de mejoramiento genético a seguir con cada especie.

Algunos resultados preliminares de estos ensayos han sido publicados por Salazar, 1981, 1982; Bird, 1983, 1984; Boshier, 1984; Valerio, 1986; Boshier y Mesén, 1987 y Corea, 1989.

Este documento presenta un resumen de progreso de los ensayos más antiguos, los cuales dan una buena indicación del comportamiento de las procedencias. Los resultados finales de estos ensayos, así como de aquellos establecidos más recientemente, serán presentados en próximas publicaciones.

Se espera que estos resultados sean de utilidad para futuros programas de investigación y reforestación, así como para lograr una mejor comprensión por parte de los técnicos forestales y reforestadores acerca de la importancia de la selección de la procedencia en el éxito de las plantaciones forestales.

AGRADECIMIENTOS

El Proyecto en su primera fase fue coordinado por el Dr. William Dyson, de grata memoria, y el M.Sc. David Boshier, ambos Oficiales de Cooperación Técnica de la Administración para el Desarrollo de Ultramar (ODA) del Reino Unido. Para el establecimiento, mantenimiento y evaluación de los ensayos se ha requerido del trabajo de gran cantidad de personas a través de los años, en especial, los Sres. José Masís, Marvin Hernández, Carlos Castro, Luis Sánchez y José Angel Quirós, así como de colaboradores particulares e Instituciones quienes gentilmente han ofrecido sus terrenos para las investigaciones.

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La B.Sc. Julie Brown de López realizó gran parte de los análisis estadísticos de los ensayos; el Dr. Rodolfo Salazar y los M.Sc Jonathan Cornelius y Eugenio Corea, aportaron valiosas sugerencias y comentarios al borrador.

El autor deja constancia de su agradecimiento a todas estas personas e instituciones, y a aquellas otras quienes en una forma u otra colaboraron en la realización de las investigaciones y de este trabajo.

1. PRUEBAS DE PROCEDENCIAS DE *Pinus caribaea*, *P. oocarpa* Y *P. tecunumanii*.

Los ensayos de procedencias de *Pinus* spp. forman parte de los ensayos internacionales coordinados por el Instituto Forestal de Oxford (OFI), e incluye una procedencia de *P. caribaea* var. *caribaea*, nueve procedencias de *P. caribaea* var. *hondurensis*, 13 procedencias de *P. oocarpa* y dos procedencias de *P. tecunumanii*. El Cuadro 1 muestra la identificación, ubicación y algunos datos climáticos de las procedencias.

El ensayo de procedencias de *P. caribaea* fue establecido en siete sitios, y el de *P. oocarpa* en cuatro sitios en Costa Rica. Uno de los sitios con *P. caribaea*, La Garita de Alajuela, presentó una alta mortalidad y fue excluido de los análisis. El suelo en este sitio era muy superficial y de drenaje deficiente, inapropiado para la especie. La descripción de los sitios evaluados (1-6 para *P. caribaea* y 7-10 para *P. oocarpa*) se muestra en el Cuadro 2. Como comparadores en el ensayo de *P. caribaea* var. *hondurensis* se incluyeron dos procedencias de *P. tecunumanii* y una de *P. caribaea* var. *caribaea*; en el ensayo de *P. oocarpa* fueron incluidas las mismas procedencias de *P. tecunumanii* y una de *P. caribaea* var. *hondurensis*.

El diseño utilizado en cada sitio y la fecha de establecimiento se muestran en el Cuadro 3. El sitio La Suiza fue establecido como paarte de un proyecto agroforestal y con objetivos diferentes, de ahí que sólo cuente con dos repeticiones. Sin embargo, se consideró que podría dar información valiosa por encontrarse en uno de los extremos de altitud para los ensayos (960-1160 msnm). Asimismo, el error experimental en este sitio fue casi la mitad del encontrado en los otros sitios (Corea, 1989), lo que sugiere que el mayor tamaño de parcela en este sitio contribuyó a obtener un mejor estimado de la media.

Las parcelas pequeñas (7 a 10 árboles en línea) no son las más recomendables para ensayos de procedencias, debido a que las pérdidas por mortalidad pueden dejar muy pocos árboles remanentes para obtener un buen estimado de la media de la parcela y de las procedencias; además, la ausencia de líneas de borde entre parcelas puede llevar a estimados erróneos del comportamiento de las procedencias debido a los efectos de competencia desigual entre ellas. Las parcelas de 36 árboles, donde se miden únicamente los 16 árboles centrales, han probado ser los más recomendables para este tipo de ensayos (Gibson, 1982). Sin embargo, las variaciones en este diseño estándar estuvieron determinadas en la mayoría de los casos por la disponibilidad de material y de terreno para los ensayos.

Cuadro 1. Identificación, ubicación y algunos datos climáticos de las procedencias de coníferas estudiadas en Costa Rica.

Especie	Procedencia*	Abrev. en los cuadros	Código OFI**	Lat. (°N)	Long. (°O)	Elev. (msnm)	Temp. media anual (°C)	Prec. media anual (mm)
P. caribaea var. car.	Pinar d/ Rio, CUBA		(0976)	22°49'	82°57'	120	NI***	NI
P. caribaea var. hond.	Alamicamba, NIC	ALA	K106(0674)	13°34'	84°17'	20-30	NI	2610
P. caribaea var. hond.	Rio Coco, NIC	RIO	K022(2470)	14°45'	83°55'	50-100	NI	2863
P. caribaea var. hond.	Guanaja, HON	GUA	K024(2870)	16°27'	85°54'	50-100	NI	2308
P. caribaea var. hond.	Poptún, GUA	POP	K025(2970)	16°21'	89°25'	500	NI	1688
P. caribaea var. hond.	Culmi, HON	CUL	K057(3771)	15°06'	85°37'	500-600	NI	1325
P. caribaea var. hond.	Brus Laguna, HON	BRU	K058(3871)	15°45'	84°40'	7	NI	2840
P. caribaea var. hond.	Los Limones, HON	LIM	K124(2475)	14°03'	86°42'	700	NI	663
P. caribaea var. hond.	Melinda, BEL	MEL	K107(1574)	17°01'	88°20'	10-15	NI	2137
P. caribaea var. hond.	Mountain Pine Ridge, BEL	MPC	(3073)	17°00'	88°55'	400	NI	1558
P. oocarpa	La Unión, HON	UNI	K078(1272)	14°32'	86°38'	800	22,9	1272
P. oocarpa	Zamorano, HON	ZAM	K086(0373)	14°02'	87°03'	1100-1240	20,2	1117
P. oocarpa	Villa Santa, HON	VST	K085(0273)	14°12'	86°25'	900	22,4	1348
P. oocarpa	Valle Bonito, HON	VBO	K102(0374)	14°53'	87°31'	850-950	22,4	1134
P. oocarpa	San Juan, HON	SJU	K098(0474)	14°24'	88°23'	1250-1330	20,2	1261
P. oocarpa	Pimientilla, HON	PIM	K099(0574)	14°54'	87°30'	650-850	23,5	1134
P. oocarpa	Cerro Bonete, HON	CBO	K103(0774)	12°50'	86°18'	950	21,4	922
P. oocarpa	Pueblo Viejo, GUA	PVI	K111(0775)	15°22'	91°36'	1790-1900	16,5	1036
P. oocarpa	Mal Paso, GUA	MPA	K114(0475)	15°11'	89°21'	1000	22,4	1800
P. oocarpa	El Pinalón, GUA	PIN	K113(0575)	14°43'	89°46'	1300-1400	20,8	936
P. oocarpa	Dipilto, NIC	DIP	K116(0675)	13°43'	86°32'	1100-1200	21,3	1143
P. oocarpa	Cusmapa, NIC	CUS	K117(0775)	13°17'	86°37'	1250	20,5	1474
P. oocarpa	Lagunilla, GUA	LAG	K112(0875)	14°42'	89°57'	1600	19,5	936
P. tecunumanii	Yucul, NIC	YUC	K128(0276)	12°55'	85°47'	900	22,4	1394
P. tecunumanii	Mountain Pine Ridge, BEL	MPT	(1174)	17°00'	88°55'	400	23,9	1558

* BEL: Belice
GUA: Guatemala
HON: Honduras
NIC: Nicaragua

** Oxford Forestry Institute

*** No se suministró la información.

Cuadro 2. **Identificación, ubicación y algunos datos climáticos de los sitios donde fueron establecidos los los ensayos de *Pinus* spp. en Costa Rica**

Sitio	Latitud (°N)	Longitud (°O)	Altitud (msnm)	Temperatura media anual (°C)	Precipitación media anual (mm)
Pinus caribaea					
1. Pavones, Turrialba	09°56'	83°37'	720	20,9	3360
2. Florencia Norte, CATIE, Turrialba	09°53'	83°41'	660	21,6	2660
3. Volcán, Buenos Aires	09°12'	83°28'	420	27,5	3513
4. San Isidro de Pérez Zeledón	09°21'	83°41'	680	24,5	2955
5. Santa Clara, Ciudad Quesada	10°21'	84°32'	170	25,7	3400
6. Santa Cruz, Guanacaste	10°17'	85°36'	35	28,3	1800
Pinus oocarpa					
7. Pavones, Turrialba	09°56'	83°37'	720	20,9	3360
8. San Juan Sur, Turrialba	09°53'	83°42'	940	19,6	3000
9. San Isidro de Pérez Zeledón	09°21'	83°41'	680	24,5	2955
10. La Suiza, Turrialba	09°51'	83°36'	960-1160	19,0	3350

Cuadro 3. **Detalles del diseño experimental y fecha de establecimiento de los ensayos de procedencias de *Pinus* spp. en Costa Rica.**

Sitio	Fecha de establec.	Diseño	N° bloques	Arboles por parcela	Distanciamiento entre árboles
1. Pavones	1977	BCA*	5	7	2,5m
2. Florencia Norte	1977	BCA	5	7	2,5m
3. Volcán	1977	BCA	4	7	2,5m
4. San Isidro	1977	BCA	5	7	2,5m
5. Santa Clara	1983	BCA	5	36	3,0m
6. Santa Cruz	1983	BCA	5	36	3,0m
7. Pavones	1978	BCA	5	30	2,5m
8. San Juan Sur	1978	BCA	5	10	2,5m
9. San Isidro	1978	BCA	5	10	2,5m
10. La Suiza	1978	BCA	2	49	2,5m

*BCA: Bloques completos al azar

Análisis

Cada sitio fue analizado separadamente para la última medición de altura total, diámetro a la altura del pecho (dap), sobrevivencia y en algunos casos, forma del fuste y volumen, utilizando los datos de árboles individuales. La procedencia de *P. caribaea* var. *caribaea* se excluyó de los análisis formales, debido a que en los análisis preliminares evidenció un comportamiento claramente inferior.

Para cada sitio se realizaron dos análisis de varianza; uno incluyendo todas las procedencias, y otro excluyendo las procedencias de *P. tecunumanii*, con el fin de determinar claramente la naturaleza de las posibles diferencias.

Para observar diferencias globales entre especies, se realizaron pruebas de contrastes agrupando las procedencias de cada especie, y análisis combinados entre los ensayos de la misma edad para detectar posibles interacciones genotipo-ambiente.

Resultados

Los Cuadros 4 y 5 muestran los promedios de crecimiento en altura total y dap para *P. caribaea*, a los siete años de edad para los sitios 1 a 4, y a los tres años de edad para los sitios 5 y 6. La sobrevivencia varió entre 50 y 100% en los sitios 1 a 5, y estas diferencias no fueron estadísticamente significativas. En el sitio Santa Cruz, por otra parte, la sobrevivencia varió entre 22 y 83%, y mostró diferencias significativas entre procedencias. Los datos de sobrevivencia para este sitio se incluyen en el Cuadro 5. El Cuadro 6 muestra el análisis combinado de los sitios 1 a 4 de altura total y dap para *P. caribaea*. Los Cuadros 7 a 9 muestran los promedios de crecimiento en altura total y dap, y la producción en volumen sin corteza para *P. oocarpa* a los 6,5 años de edad, y el Cuadro 10 muestra el análisis combinado de los sitios 7 a 10 para estas tres variables.

Cuadro 4. Promedios de altura total (m) de nueve procedencias de *P. caribaea* var *hondurensis* y dos procedencias de *P. tecunumanii* a los siete años de edad en los sitios 1 a 4, y a los tres años de edad en los sitios 5 y 6.

1.Celulosa		2.Florencia		3.Volcán		4.San Isidro		5.Sta Clara		6.Sta Cruz	
Proc.	Alt.	Proc.	Alt.	Proc.	Alt.	Proc.	Alt.	Proc.	Alt.	Proc.	Alt
YUC	18,3 a*	MPT	16,1 a	MPT	15,8 a	YUC	18,3 a	MPT	8,0 a	MPT	3,5 a
MPT	17,5 ab	MPC	13,6 b	YUC	15,4 a	MPT	17,2 a	YUC	7,9 a	POP	3,3 a
POP	16,6 abc	ALA	13,4 b	POP	14,0 b	MPC	17,0 a	ALA	6,8 b	GUA	3,3 a
CUL	16,6 abc	CUL	13,3 b	LIM	13,2 bc	POP	16,9 a	BRU	6,5 bc	MPC	3,1 ab
BRU	16,4 bc	POP	12,8 b	CUL	13,1 bc	ALA	16,8 a	CUL	6,2 bc	BRU	3,0 abc
MEL	16,1 bc	RIO	12,5 b	MEL	12,9 bc	BRU	16,6 a	GUA	6,1 cd	ALA	3,0 abc
RIO	15,9 bc	YUC	12,5 b	ALA	12,8 bc	RIO	16,5 a	MPC	6,0 cd	CUL	2,9 abc
ALA	15,9 bc	GUA	12,4 b	MPC	12,7 bc	CUL	16,4 a	RIO	5,5 de	MEL	2,5 bcd
MPC	15,6 cd	BRU	12,1 b	BRU	12,1 c	LIM	16,3 a	LIM	5,3 de	RIO	2,5 bcd
GUA	15,2 cd	LIM	12,1 b	GUA	10,0 d	MEL	15,7 a	POP	5,3 e	YUC	2,3 cd
LIM	14,2 d	MEL	11,6 b	RIO	9,7 d	GUA	14,9 a	MEL	5,2 e	LIM	2,0 d

* Letras diferentes indican diferencias significativas al cinco por ciento (Prueba de Duncan)

Cuadro 5. Promedios de dap (cm) de nueve procedencias de *P. caribaea* y dos procedencias de *P. tecunumanii* a los siete años de edad en los sitios 1 a 4, y a los tres años de edad en los sitios 5 y 6; porcentaje de sobrevivencia (Sobrev) en el sitio 6, Santa Cruz

1.Celulosa		2.Florencia		3.Volcán		4.San Isidro		5.Sta Clara		6. Sta Cruz		
Proc.	dap	Proc.	dap	Proc.	dap	Proc.	dap	Proc.	dap	Proc.	dap	Sobrev.
MPT	22,4 a	MPT	22,3 a*	YUC	25,3 a	CUL	23,8 a	MPT	11,9 a	POP	6,0 a	73
YUC	22,3 a	ALA	17,4 b	MPT	23,7 a	YUC	22,4 a	YUC	11,4 ab	GUA	5,8 a	83
CUL	21,6 a	MPC	16,3 bc	LIM	19,2 b	MPT	21,4 a	CUL	11,0 abc	MPC	5,5 ab	78
BRU	21,6 a	YUC	16,3 bc	ALA	18,5 b	ALA	20,9 a	ALA	10,8 bcd	BRU	5,3 abc	73
MEL	20,8 a	CUL	15,9 bc	BRU	17,5 b	RIO	20,7 a	BRU	10,2 cde	MEL	5,2 abc	57
RIO	20,2 a	GUA	15,1 bc	POP	17,5 b	MEL	20,3 a	GUA	10,2 cde	ALA	5,0 abc	35
POP	19,9 a	POP	14,8 bc	MPC	17,5 b	BRU	19,9 a	MPC	10,2 cde	CUL	4,9 abc	65
GUA	19,9 a	BRU	14,2 bc	CUL	17,5 b	MPC	19,3 a	POP	9,7 de	MPT	4,6 abc	22
MPC	19,5 a	RIO	13,9 bc	MEL	17,1 b	POP	10,9 a	RIO	9,5 e	RIO	3,8 bcd	57
ALA	19,1 a	MEL	13,5 bc	GUA	16,9 b	GUA	18,8 a	LIM	9,4 e	LIM	3,7 cd	46
LIM	17,2 a	LIM	12,9 c	RIO	16,8 b	LIM	18,1 a	MEL	9,2 e	YUC	2,4 d	58

* Letras diferentes indican diferencias significativas al cinco por ciento (Prueba de Duncan)

Cuadro 6. **Análisis combinado de los sitios 1 a 4 para *P. caribaea* en altura total y dap a los 7 años de edad.**

Proc.	Altura total (m)	Proc.	dap (cm)
YUC	16,7 a*	MPT	21,0 a
MPT	16,6 a	YUC	20,7 a
POP	15,0 b	CUL	19,7 b
CUL	15,0 b	ALA	19,3 bc
ALA	15,0 b	BRU	19,1 bc
BRU	14,6 bc	MPC	18,8 bcd
MPC	14,5 bc	MEL	18,7 cd
MEL	14,2 bc	RIO	18,7 cd
LIM	13,9 cd	GUA	18,6 cd
RIO	13,7 cd	POP	18,6 cd
GUA	13,2 d	LIM	18,1 d

* Letras diferentes indican diferencias significativas al cinco por ciento (Prueba de Duncan)

Cuadro 7. Promedios de altura total en metros (Alt) de trece procedencias de *P. oocarpa*, dos procedencias de *P. tecunumanii* y una procedencia de *P. caribaea* var. *hondurensis* a los 6,5 años de edad en cuatro sitios de Costa Rica. (Fuente: Corea, 1989)

7.Celulosa		8.San Juan Sur		9.San Isidro		10.La Suiza	
Proc.	Alt.	Proc.	Alt	Proc.	Alt.	Proc.	Alt
YUC	16,3 a*	YUC	15,3 a	MPT	12,6 a**	DIP	14,7 a**
MPT	15,9 a	UNI	15,1 a	YUC	12,4 a	YUC	14,2 ab
UNI	15,2 ab	VST	14,7 a	MPC	11,7 ab	MPT	14,1 abc
DIP	14,6 ab	DIP	14,6 a	DIP	11,6 ab	VST	13,0 abc
MPC	14,6 ab	PIM	14,6 a	UNI	11,4 ab	SJU	12,9 abc
VST	14,5 ab	CBO	14,4 a	MPA	11,3 ab	MPC	12,5 abcd
PIM	14,3 ab	ZAM	14,4 a	CUS	11,2 ab	VBO	12,5 abcd
SJU	14,2 ab	MPT	14,4 a	VST	11,1 ab	CBO	11,4 abcd
MPA	13,9 ab	MPC	14,2 a	ZAM	11,1 ab	CUS	10,9 abcd
ZAM	13,9 ab	CUS	13,9 a	CBO	11,0 ab	PIM	10,8 abcd
CUS	13,8 ab	VBO	13,9 a	LAG	11,0 ab	PVI	9,6 bcd
CBO	13,6 ab	MPA	13,9 a	SJU	10,7 ab	MPA	9,5 cd
LAG	13,3 ab	SJU	13,8 a	PVI	10,5 ab	PIN	9,4 cd
PIN	13,0 abc	PIN	12,8 a	PIN	10,3 ab	UNI	9,4 d
VBO	12,6 bc	LAG	12,7 a	PIM	9,4 b	LAG	8,2 d
PVI	9,9 c	PVI	12,6 a	VBO	9,1 b		

*,** Letras diferentes indican diferencias significativas al cinco por ciento (*Prueba de Bonferroni; **Prueba de Tukey)

Cuadro 8. Promedios de dap (cm) de trece procedencias de *P. oocarpa*, dos procedencias de *P. tecunumanii* y una procedencia de *P. caribaea* var. *hondurensis* a los 6,5 años de edad en cuatro sitios de Costa Rica. (Fuente: Corea, 1989)

7.Celulosa		8.San Juan Sur		9.San Isidro		10.La Suiza	
Proc.	dap	Proc.	dap	Proc.	dap	Proc.	dap
YUC	18,5 a*	YUC	20,3 a**	YUC	16,5 a**	MPC	16,9 a**
MPC	17,9 ab	DIP	19,2 ab	MPT	15,5 ab	YUC	16,3 ab
MPT	17,6 abc	MPT	18,9 ab	MPC	15,3 ab	DIP	16,0 abc
MPA	16,9 abc	MPC	18,9 ab	MPA	13,1 abc	MPT	15,0 abcd
DIP	16,8 abc	MPA	18,6 ab	DIP	12,6 abc	VST	14,1 abcd
UNI	16,7 abc	UNI	17,6 ab	CBO	12,1 abcd	VBO	14,1 abcd
VST	16,5 abc	CBO	17,0 ab	CUS	12,1 abcd	CBO	13,9 abcd
CUS	16,3 abc	VST	17,0 ab	UNI	11,8 bcd	SJU	13,7 abcd
PIM	15,5 abc	SJU	16,9 ab	VST	11,6 bcd	CUS	13,0 abcd
ZAM	15,4 abc	PIM	16,8 ab	LAG	11,5 bcd	PIM	12,4 abcd
PIN	15,3 abc	VBO	16,3 ab	PIN	11.1 bcd	PVI	12,0 abcd
SJU	15,2 abc	ZAM	16,1 ab	SJU	10,7 cd	MPA	11,5 abcd
LAG	14,9 abc	PIN	15,8 ab	ZAM	10,5 d	PIN	10,8 bcd
CBO	14,4 abc	CUS	15,6 ab	PVI	10,5 d	UNI	10,3 cd
VBO	13,5 bc	LAG	14,4 b	VBO	8,9 d	LAG	9,9 d
PVI	13,5 c	PVI	14,4 b	PIM	8,8 d		

*, ** Letras diferentes indican diferencias significativas al cinco por ciento *Prueba de Bonferroni, **Prueba de Tukey)

Cuadro 9. Volumen sin corteza ($m3ha^{-1}$) de trece procedencias de *P. oocarpa*, dos procedencias de *P. tecunumanii* y una procedencia de *P. caribaea* var. *hondurensis* a los 6,5 años de edad en cuatro sitios en Costa Rica. (Fuente: Corea, 1989)

7.Celulosa		8.San Juan Sur		9.San Isidro		10.La Suiza	
Proc.	VSC	Proc.	VSC	Proc.	VSC	Proc.	VSC
YUC	180,9 a*	YUC	207,6 a**	YUC	134,7 a**	YUC	131,6 a**
MPT	173,8 a	MPT	191,2 ab	MPT	102,8 ab	MPT	123,7 ab
MPC	149,7 ab	DIP	172,0 abc	MPC	82,0 ab	DIP	113,7 abc
UNI	128,9 abc	MPC	152,4 abc	DIP	74,3 bc	MPC	106,5 abcd
VST	122,7 abc	VST	144,8 abc	MPA	72,1 bc	SJU	97,6 abcd
DIP	113,9 abc	SJU	138,5 abc	CUS	63,0 bc	VST	95,8 abcd
SJU	101,7 bc	UNI	130,9 abcd	CBO	58,4 bc	CBO	74,2 abcd
CUS	100,4 bcd	CBO	116,9 abcd	VST	56,7 bc	VBO	72,8 abcd
PIM	96,6 bcd	CUS	115,9 abcd	LAG	51,2 bc	CUS	71,9 abcd
LAG	90,8 bcd	MPA	107,5 bcd	UNI	48,3 bc	PIM	68,3 abcd
PIN	87,5 bcd	ZAM	104,4 bcd	SJU	43,4 c	MPA	49,1 bcd
MPA	87,3 bcd	PIM	104,1 bcd	PIN	40,3 c	PVI	43,6 cd
ZAM	85,2 bcd	VBO	98,1 bcd	ZAM	37,0 c	PIN	43,6 cd
CBO	82,9 bcd	PIN	82,1 cd	PVI	35,8 c	LAG	31,5 d
VBO	70,8 cd	LAG	81,0 cd	PIM	30,0 c	UNI	31,3 d
PVI	30,9 d	PVI	32,2 d	VBO	26,0 c		

*, ** Letras diferentes indican diferencias significativas al cinco por ciento (*Prueba de Bonferroni, ** Prueba de Tukey)

Cuadro 10. Análisis combinado de los sitios 7 a 10 de *Pinus oocarpa* para altura total (m), dap (cm) y volumen sin corteza (VSC, $m3ha^{-1}$) a los 6,5 años de edad (Fuente: Corea, 1989)

Proc.	Altura total	Proc.	dap	Proc.	VSC
YUC	14,7 a*	YUC	17,9 a	YUC	166,6 a
MPT	14,3 ab	MPC	17,1 ab	MPT	150,8 ab
UNI	13,8 abc	MPT	16,8 abc	MPC	122,8 bc
DIP	13,6 abcd	DIP	16,0 abcd	DIP	116,3 bc
MPC	13,5 abcd	MPA	15,4 abcde	VST	103,8 cd
VST	13,4 abcd	VST	14,7 bcdef	SJU	92,2 cd
ZAM	13,1 abcd	UNI	14,5 cdef	UNI	91,4 cd
MPA	13,0 abcd	CUS	14,2 def	CUS	87,7 cd
CBO	13,0 abcd	CBO	14,2 def	CBO	81,9 cd
CUS	13,0 abcd	SJU	14,0 def	MPA	81,5 cd
SJU	12,9 abcd	ZAM	13,6 def	PIM	72,9 d
PIM	12,8 bcd	PIN	13,4 ef	ZAM	70,2 de
LAG	12,3 cde	PIM	13,3 ef	LAG	66,6 de
PIN	12,0 de	LAG	13,0 ef	PIN	64,0 de
VBO	11,9 de	VBO	12,8 f	VBO	63,1 de
PVI	11,0 e	PVI	12,4 f	PVI	31,3 e

* Letras diferentes indican diferencias significativas al cinco por ciento (Prueba de Bonferroni)

Como se puede ver en los cuadros, es evidente el comportamiento superior de las dos procedencias de *P. tecunumanii* (Yucul de Nicaragua y Mountain Pine Ridge de Belice) en todos los sitios estudiados, excepto en el sitio más seco, Santa Cruz de Guanacaste. En crecimiento en altura total, la procedencia Mountain Pine Ridge ocupó uno de los tres primeros lugares en nueve de los diez sitios estudiados, mientras que la procedencia Yucul ocupó alguna de estas posiciones en ocho de los sitios. Para la variable dap, ambas procedencias ocuparon uno de los tres primeros lugares en ocho de los sitios. El comportamiento de la procedencia Yucul en Florencia de Turrialba puede interpretarse más bien como un efecto atípico debido a las deficiencias en el diseño apuntadas anteriormente.

En cuanto a forma del fuste, si bien la procedencia Yucul se ubicó entre las mejores procedencias para esta característica, la procedencia Mountain Pine Ridge fue una de las que mostró peor forma (Corea, 1989).

El comportamiento pobre de las dos procedencias de *P. tecunumanii* en Santa Cruz, parece confirmar el hecho de que estas procedencias requieren climas más húmedos, y que no se adaptan a las condiciones de estación seca prolongada y vientos fuertes como las encontradas en Guanacaste (Boshier y Mesén, 1987). Las procedencias de *P. caribaea* que presentaron mejor sobrevivencia (ej. Guanaja, Mountain Pine Ridge, Poptún) son las más importantes para estas condiciones de Guanacaste.

Con excepción del análisis de Santa Cruz, la exclusión de las procedencias de *P. tecunumanii* del análisis, generalmente resultó en la desaparición de diferencias significativas entre procedencias, o en una disminución de las mismas, indicando que las diferencias fueron debidas principalmente al comportamiento superior de las procedencias de *P. tecunumanii*. Incluso el análisis combinado de los sitios 1 a 4 y 7 a 10, no mostró interacciones genotipo-ambiente, indicando la alta estabilidad en la superioridad de *P. tecunumanni* con respecto las demás procedencias.

Por su parte, el comportamiento de las procedencias de *P. caribaea* fue altamente inestable, en algunos casos variando en dos sitios desde una tercera a una última posición, de manera que no se puede decir que alguna procedencia fuera mejor para todos los sitios. En el caso de las procedencias de *P. oocarpa*, las procedencias Dipilto de Nicaragua y Villa Santa de Honduras, fueron las más sobresalientes, además de que ocuparon los primeros lugares en cuanto a forma del fuste. Se ha sugerido que el buen comportamiento de estas dos procedencias pueda estar relacionado con algún nivel de mezcla con *P. tecunumanii*, ya sea por la presencia de individuos híbridos, o por la inclusión de genes de *P. tecunumanii* en estas poblaciones de *P. oocarpa*. Esta opinión se basa en el hecho de que algunos árboles de Dipilto y Villa Santa en los ensayos, presentan características similares a las de *P. tecunumanii* (Corea, 1989)

Los datos de volumen sin corteza (Cuadros 9 y 10), que representan la variable de producción más importante, muestran muy claramente la importancia de la selección correcta de procedencias para plantaciones forestales. La procedencia Yucul de Nicaragua superó en todos los sitios a las procedencias de *P. oocarpa*, y a la procedencia de *P. caribaea* var. *hondurensis*. La diferencia en producción de volumen entre Yucul y el promedio de las procedencias de *P. oocarpa* fue de 112%, mientras que la diferencia con respecto a la procedencia más pobre, Pueblo Viejo de Guatemala, fue del 432%. El porcentaje de corteza fue alto para todas las procedencias, y varió entre 31 y 42% (Corea, 1989), aunque de nuevo, las procedencias de *P. tecunumanii* presentaron los menores valores para esta variable (31% para Mountain Pine Ridge y 33% para Yucul).

Tradicionalmente, se ha utilizado *P. caribaea* var. *hondurensis*, en particular las procedencias Poptún de Guatemala, Culmí de Honduras y Mountain Pine Ridge de Belice (Boshier y Mesén, 1987) para las zonas húmedas hasta 800 msnm, y *P. oocarpa* para las zonas de mayor altitud de Costa Rica. Sin embargo, los resultados de estos ensayos muestran que se pueden obtener mayores rendimientos con las procedencias Yucul y Mountain Pine Ridge de *P. tecunumanii*, y en particular con Yucul debido a su mejor forma, que con cualquiera de las otras procedencias estudiadas, en regiones húmedas entre 120 y 1160 msnm.

Estos resultados coinciden plenamente con los resultados de ensayos similares establecidos en varios otros países del mundo tropical, donde las procedencias de *P. tecunumanii* invariablemente han mostrado el mejor comportamiento (Bridgen *et al*, 1984; Chagala y Gibson, 1984; Ferreira y Kageyama, 1977; Granhof, 1977; Greaves, 1980; Liegel, 1984a y 1984b; Mullin y Quaile, 1984; Wright, Gibson y Barnes, 1986)

Como una siguiente fase en las investigaciones con coníferas, el Proyecto MGF ha establecido pruebas de procedencias/descendencias y plantaciones piloto a altitudes mayores (Aserrí, 1650 msnm; Tres Ríos, 1700 msnm y Orosi, 1500 msnm), para determinar con mayor exactitud el rango de adaptación de la especie, y realizar selecciones de segunda generación. Asímismo se han incluido dos procedencias más de *P. tecunumanii*, Camelias y San Rafael de Nicaragua, las cuales han mostrado superioridad en otros países, pero aun no habían sido probadas en Costa Rica.

Las plantaciones piloto también darán información sobre las posibilidades de producción de semilla en Costa Rica, ya que las plantaciones establecidas hasta la fecha no han producido cantidades significativas de semilla, debido posiblemente a la ausencia de una estación seca definida en las zonas donde han sido plantadas. Hasta que no se logre la producción local de semilla, se deberá continuar con su importación de los Bancos de Semilla de la Región.

2. PRUEBA DE ESPECIES Y PROCEDENCIAS DE *Eucalyptus* spp.

Este ensayo forma parte de los ensayos internacionales coordinados por CSIRO, e incluye 20 procedencias nativas de 8 especies de *Eucalyptus*. Como comparadores en este ensayo se incluyeron tres procedencias derivadas de Costa Rica: una de *E. saligna* de Juan Viñas, una de *E. citridora* de Orosi y una de *E. deglupta* de Turrialba. El Cuadro 11 muestra algunas características de las procedencias estudiadas.

Cuadro 11. Identificación, ubicación y elevación (msnm) de las procedencias de *Eucalyptus* evaluadas en Turrialba, Costa Rica.

Especie	Procedencia	Abreviación en los cuadros	N°. CSIRO*	Elevación (msnm)
E. alba	S. Cooktown, N. Qld.	COO	11669	30
E. alba	Greenvale, Qld.	GRE	11957	610
E. alba	S. Maningrida, N.T.	MAN	11113	70
E. camaldulensis	Petford, N. Qld.	PET	12139	460
E. camaldulensis	Gibb River, W.A.	GIB	12346	430
E. camaldulensis	Katherine, N.T.	KAT	12181	110
E. citridora	Atherton, N. Qld.	ATN	12379	600
E. citridora	Dawson Range, Qld.	DAW	12012	180
E. citridora	Orosi, Costa Rica	ORO	1465**	1000
E. cloeziana	N. Paluma, N. Qld.	PAL	10270	270
E. cloeziana	N.E. Gympie, Qld.	GYE	10691	76
E. cloeziana	Cardwell, Qld.	CAR	9785	120
E. deglupta	Turrialba, Costa Rica	TUR	1466**	600
E. grandis	Gympie, Qld.	GYM	11761	400
E. grandis	Atherton, Qld.	ATH	12002	300
E. grandis	Crediton, Qld.	CRE	11891	760
E. saligna	S. Calliope, Qld.	CAL	12064	800
E. saligna	N. Raymond Terr., N.S.W.	RAY	11605	225
E. saligna	Gladfield, Qld.	GLA	11894	1020
E. saligna	Juan Viñas, Costa Rica	JVI	903**	1200
E. tereticornis	Mt. Poverty, N. Qld.	POV	11955	550
E. tereticornis	N. Mt. Malloy, N. Qld.	MAL	11952	610
E. tereticornis	S.W. Mt. Garnett, Qld.	GAR	12181	875

* Organizaciones de Investigación Científica e Industrial de la Mancomunidad

**Numero local

El ensayo fue establecido en 1980 en los terrenos del CATIE, Turrialba, Costa Rica, en el área conocida como La Isla. El sitio se ubica a 9°53' de latitud norte, 83°42' de longitud oeste y a una altitud de 600 msnm. La precipitación promedio anual en el sitio es de 2660 mm, y la temperatura media anual de 21,2°C.

Se utilizó un diseño de bloques completos al azar con cinco bloques, y parcelas de 36 árboles a un distanciamiento de 3 x 3m, en las cuales se evaluaron únicamente los 16 árboles centrales.

Análisis

El ensayo fue analizado para los datos de altura total, dap y sobrevivencia a los cinco años, utilizando los valores de árboles individuales. El análisis del porcentaje de sobrevivencia se llevó a cabo utilizando el modelo usual para evaluar diferencias entre bloques y procedencias. Los análisis de altura y dap se hicieron utilizando un modelo anidado para evaluar diferencias entre bloques, especies y procedencias dentro de las especies.

Resultados

El Cuadro 12 muestra los promedios de crecimiento en altura total y dap a los cinco años, agrupados por especie; el Cuadro 13 muestra los promedios de crecimiento en altura total y dap, y la sobrevivencia por procedencia.

Cuadro 12. **Promedios de altura total (m) y dap (cm) agrupados por especie, del ensayo de especies y procedencias de *Eucalyptus* a los 5 años de edad en Turrialba, Costa Rica.**

Especie	Altura total	Especie	dap
E. grandis	18,2 a*	E. grandis	14,3 a
E. saligna	14,7 ab	E. saligna	11,8 ab
E. citridora	14,1 ab	E. citridora	10,8 ab
E. deglupta	13,0 b	E. tereticornis	10,3 b
E. tereticornis	11,9 bc	E. deglupta	9,8 bc
E. camaldulensis	11,0 bc	E. camaldulensis	9,0 bc
E. cloeziana	10,9 bc	E. cloeziana	8,2 bc
E. alba	7,6 c	E. alba	6,3 c

* Letras diferentes indican diferencias significativas al cinco por ciento (Prueba de Duncan)

Cuadro 13. Promedios de altura total (m), dap (cm) y sobrevivencia (%) de 23 procedencias de *Eucalyptus* a los 5 años de edad en Turrialba, Costa Rica.

Especie	Proc.	Altura total (m)	Especie	Proc.	dap (cm)	Especie	Proc.	Sobrev. (%)
E. grandis	GYM	19,0 a*	E. grandis	CRE	16,5 a	E. teret.	MAL	82 a
E. grandis	CRE	19,0 a	E. saligna	JVI	14,3 a	E. grandis	GYM	80 a
E. saligna	JVI	18,2 ab	E. grandis	GYM	14,1 a	E. alba	MAN	79 a
E. grandis	ATH	16,1 abc	E. grandis	ATH	13,4 a	E. deglupta	TUR	69 ab
E. citrid.	DAW	14,8 abc	E. teret.	MAL	12,5 a	E. saligna	JVI	69 ab
E. citrid.	ATN	14,4 bcd	E. citrid.	ATN	11,7 a	E. teret.	CAR	65 abc
E. teret.	MAL	14,2 bcd	E. citrid.	DAW	10,9 a	E. teret.	POV	65 abc
E. saligna	RAY	13,5 bcd	E. saligna	RAY	10,8 a	E. cloez.	GYE	60 abc
E. saligna	CAL	13,1 cde	E. saligna	CAL	10,7 a	E. saligna	CAL	58 abcd
E. deglupta	TUR	13,0 cde	E. saligna	GLA	10,2 a	E. camald.	PET	51 abcd
E. camald.	PET	12,8 cde	E. teret.	GAR	9,9 a	E. saligna	GLA	49 abcd
E. citrid.	ORO	12,8 cdef	E. camald.	PET	9,9 a	E. camald.	KAT	47 abcd
E. saligna	GLA	12,6 cdefg	E. deglupta	TUR	9,8 a	E. camald.	GIB	46 abcd
E. teret.	CAR	12,5 cdefg	E. citrid.	ORO	9,4 a	E. alba	GRE	43 bcd
E. cloez.	PAL	12,0 cdefgh	E. cloez.	GYE	9,1 a	E. saligna	RAY	39 bcd
E. cloez.	GYE	11,8 cdefgh	E. camald.	KAT	8,6 a	E. grandis	ATH	38 bcd
E. camald.	KAT	10,1 cdefgh	E. cloez.	PAL	8,4 a	E. citrid.	DAW	38 bcd
E. camald.	GIB	10,0 cdefghi	E. camald.	GIB	8,3 a	E. alba	COO	33 bcd
E. teret.	POV	8,6 efghi	E. teret.	POV	8,1 a	E. citrid.	ATN	33 bcd
E. alba	MAN	8,4 fghi	E. alba	MAN	7,6 a	E. grandis	CRE	31 cd
E. cloez.	CAR	8,1 ghi	E. cloez.	CAR	5,9 a	E. cloez.	CAR	27 d
E. alba	GRE	7,6 hi	E. alba	GRE	5,4 a	E. cloez.	PAL	24 d
E. alba	COO	5,9 i	E. alba	COO	4,6 a	E. citrid.	ORO	23 d

* Letras diferentes indican diferencias significativas al cinco por ciento (Prueba de Duncan)

El análisis anidado por especie (Cuadro 12) muestra claramente el comportamiento superior de ***E. grandis***, el cual contrasta con el comportamiento pobre de ***E. alba***. La superioridad global de ***E. grandis*** con respecto a ***E. alba*** fue de 42% para altura total y de 44% para dap, lo que indica una vez más la importancia de las pruebas de especies antes de iniciar plantaciones a gran escala. Estos resultados son consistentes con la experiencia en otras regiones, tales como el sur de Africa, India y América del Sur, donde ***E. grandis*** representa una de las especies principales para producción de pulpa y madera (Turnbull y Pryor, 1978), con una forma excelente e incrementos anuales en volumen en algunos casos de hasta 55 m3ha^{-1} (Aracruz Celulose, 1989). Por su parte, ***E. alba*** ha mostrado un crecimiento pobre en la mayoría de los sitios donde ha sido introducido, con árboles pequeños y fuertemente bifurcados, con poco o ningún potencial para reforestación comercial (Poynton, 1979).

En los análisis por procedencia (Cuadro 13), las tres procedencias de ***E. grandis*** (Gympie, Crediton y Atherton) se ubicaron en las cuatro primeras posiciones en cuanto a altura total y dap, y de ellas, la procedencia Gympie presentó la mejor combinación de altura total, dap y sobrevivencia. Las procedencias Crediton y Atherton presentaron porcentajes de sobrevivencia muy bajos (31 y 38%), lo que limitaría su utilización en

Por su parte, es interesante el comportamiento de la procedencia derivada de *E. saligna* de Juan Viñas, la cual se ubicó en una tercera posición en cuanto a altura total, y en una segunda posición en cuanto a dap. Asímismo, ocupó una quinta posición para la variable sobrevivencia. Esta tendencia de las procedencias derivadas de comportarse mejor que muchas procedencias nativas, ha sido bien documentado para muchas otras especies (Burley y Wood, 1979; Owino, 1977; Valerio, 1986; Zobel y Talbert, 1984), y sugiere el desarrollo de razas locales, o poblaciones de individuos que por selección natural se han adaptado al ambiente específico donde han sido plantadas, incluso después de una sola generación (Zobel y Talbert, 1984). El uso de razas locales es una de las formas más rápidas y económicas de obtener ganancias genéticas cuando se trabaja con exóticas, puesto que la descendencia de estas poblaciones usualmente mostrará un comportamiento superior a la descendencia del rodal nativo original.

El Cuadro 13 muestra claramente que dentro de una misma especie, el comportamiento de sus procedencias puede variar grandemente, y que tendría poco sentido generalizar sobre el comportamiento de una especie basándose en las experiencias con una única fuente de semilla. En *E. saligna*, por ejemplo, las diferencias en altura total y dap entre la mejor y la peor procedencia fueron del 44% y el 40% respectivamente, de magnitud similar a la diferencia global entre dos especie (*E. grandis* y *E. alba*) mencionadas al inicio de esta sección.

Basado en los resultados de este ensayo, el Proyecto MGF estableció dos ensayos de descendencias con la especie *E. grandis* en Tucurrique y Atirro, Turrialba, para evaluar el comportamiento de familias dentro de procedencias, y de árboles individuales dentro de familias. Esto permitirá el establecimiento eventual de huertos semilleros, con ganancias genéticas a tres niveles: procedencia, familia y árbol individual. La procedencia derivada de *E. saligna*, por su parte, está siendo utilizada por el Banco de Semillas Forestales (BLSF) del CATIE en sus recolecciones comerciales.

3. PRUEBA DE PROCEDENCIAS DE *Eucalyptus urophylla*

Aunque *E. urophylla* no estuvo representado en el ensayo de especies discutic anteriormente, ha sido identificado como una de los eucaliptos con mayor potencial par zonas tropicales húmedas (Pryor, 1975). Asimismo, por poseer un rango amplio d distribución altitudinal (300 a 3000 msnm), ofrece un potencial grande para ser utilizada e zonas de altitud y latitud bajas en los trópicos. El ensayo de procedencias de *E. urophyll* forma parte de los ensayos internacionales coordinados por CSIRO, e incluye 1 procedencias nativas. El Cuadro 14 muestra la identificación, ubicación y algunos dato climáticos de las procedencias.

El ensayo fue establecido en 1981 en tres sitios de Costa Rica: Turrialba, San Isidr de Pérez Zeledón y Santa Clara de Ciudad Quesada. Sin embargo, el ensayo en Turrialb fue afectado severamente por un hongo, presumiblemente *Phyllosticta* sp. (Evans, 1984 Commonwealth Mycological Institute. Com. pers.), y dejó muy pocos árboles sobrevivientes para las evaluaciones; el sitio en San Isidro fue afectado en dos ocasiones por un incendi accidental, lo que perjudicó la expresión de las posibles diferencias entre procedencias. E sitio remanente está ubicado en los terrenos del Instituto Tecnológico de Costa Rica er Santa Clara de Ciudad Quesada, a 10°21' de latitud norte, 84°22' de longitud oeste, y a una altitud de 170 msnm. La precipitación media anual en el sitio es de 3400 mm, y la temperatura media anual de 25,7 °C.

El diseño experimental consistió de bloques incompletos al azar con cinco bloques, y parcelas de 36 árboles con un espaciamiento de 3 x 3m, en las cuales se evaluaron únicamente los 16 árboles centrales. Debido a limitaciones con el material, no todas las procedencias están representadas en todas las repeticiones; ocho procedencias están repetidas cinco veces, dos están repetidas cuatro veces, y las cuatro restantes están repetidas entre una y tres veces.

Análisis

El ensayo fue analizado para los datos de altura total, dap y sobrevivencia a los seis y medio años de edad, para las procedencias repetidas cuatro o cinco veces, utilizando valores de árboles individuales.

Cuadro 14. Identificación, ubicación y algunos datos climáticos de las procedencias de *E. urophylla* establecidas en Santa Clara, Costa Rica..

Procedencia	Abrev en los cuadros	Código CSIRO*	Latitud (°N)	Longitud (°E)	Altitud (msnm)	Precipitación media anual (mm)
Mt. Mandiri, Isla Flores	MAN	12895	08°15'	122°58'	490	
Mt. Lewotobi, Isla Flores	LEW	12896	08°32'	122°48'	475	
Mt. Wuko, Isla Flores	WUK	12897	08°33'	122°35'	830	
Mt. Boleng, Isla Adonara	BOL	12898	08°21'	123°15'	890	
S.W. Isla Lembata	LEM	802770N	08°26'	123°30'	500-950	950
Remexio, Isla Timor	REM	802793N	08°38'	125°41'	800-1150	1750
Maubisse, Isla Timor	MAU	802795N	08°47'	125°48'	1200-1540	1750
Región N.W., Isla Pantar	NWP	802800N	08°22'	124°13'	350-600	950
Región Central, Isla Wetar	WET	802801N	07°52'	126°09'	350	750
Región Central, Isla Alor	CAL	802803N	08°17'	124°42'	600-1000	900
Región E.,Isla Alor	EAL	802804N	08°18'	124°50'	600-900	1100
Mt. Moena, Isla Alor	MOE	802806N	08°22'	124°34'	700-800	1300
Mt. Egon, Isla Flores	EGO	802807N	08°39'	122°26'	300-700	
Región W., Isla Alor	WAL	802808N	08°20'	124°27'	450-700	

* Organizaciones de Investigación Científica e Industrial de la Mancomunidad.

Resultados

El Cuadro 15 muestra los promedios de crecimiento en altura total (m) y dap (cm), y los porcentajes de sobrevivencia por procedencia a los seis y medio años de edad.

La sobrevivencia en general fue alta y no mostró diferencias significativas entre procedencias, con porcentajes superiores al 70% en todos los casos. En cuanto a altura total y dap, las procedencias Remexio de la Isla Timor, Región oeste de la Isla Alor, Mt. Lewotobi de la Isla Flores y S.W. Isla Lembata mostraron el mejor comportamiento en este sitio, aunque debido a la pérdida de los otros sitios, no se pueden hacer conclusiones acerca de la estabilidad de las procedencias, o la existencia de interacciones genotipo-ambientales; se requiere más investigación para llegar a conclusiones más definitivas.

Cuadro 15. Promedios de altura total (m) y dap (cm), y porcentaje de sobrevivencia de 10 procedencias de *E. urophylla* a los 6,5 años de edad en Santa Clara, Costa Rica.

Proc.	Altura total (m)	Proc.	dap (cm)	Proc.	Sobrev. (%)
REM	23,7	WAL	20,5	LEM	96
WAL	23,7	LEM	19,0	LEW	93
LEW	23,6	LEW	18,4	MAN	90
LEM	22,8	REM	18,2	MAU	90
MOE	21,3	MOE	17,5	MOE	89
MAN	20,2	MAN	16,5	BOL	88
CAL	20,2	CAL	16,4	WUK	88
WUK	19,9	BOL	16,3	CAL	80
BOL	18,9	WUK	15,9	WAL	75
MAU	17,9	MAU	14,3	REM	73

Sin embargo, esta ha sido la primera introducción documentada de *E. urophylla* a Costa Rica, y el ensayo ha mostrado un excelente crecimiento y comportamiento de algunas procedencias de la especie, lo cual da una idea del potencial de estas fuentes para plantaciones en las zonas húmedas del país. Las mejores procedencias mostraron un incremento medio anual (IMA) en altura total de 3.6 m y un incremento medio anual en dap de 3,2 cm. Estos valores son similares a los obtenidos con las mejores procedencias de *E. grandis* a los cinco años de edad en Turrialba (IMA en altura total de 3,8 m e IMA en diámetro de 3,3 cm; Sección 2), y a los valores de IMA en altura total de 3,5 m e IMA en diámetro de 2,6 cm informados por Navarro (1985) para *E. deglupta* en una plantación de ocho años en Turrialba.

En 1988, a los ocho años de edad, se eliminaron las procedencias más pobres de este ensayo, y se realizó un aclareo, seleccionando los mejores árboles de las mejores procedencias, para establecer un rodal semillero, el cual ya se encuentra en su fase de producción.

4. PRUEBA DE PROCEDENCIAS DE *Gmelina arborea*

Este ensayo forma parte de los ensayos internacionales coordinados por el Centro de Semillas de Dinamarca/DANIDA, e incluye una procedencia derivada de Jarí, Brasil, y siete procedencias nativas. Como comparador en este ensayo, se incluyó una procedencia derivada de Manila, Costa Rica. La identificación, ubicación y algunos datos climáticos de las procedencias se muestran en el Cuadro 16.

El ensayo fue establecido en 1982 en los terrenos de la Empresa Celulosa de Turrialba, S.A., en Pavones, Turrialba, Costa Rica. El sitio se ubica a 9°56' de latitud norte, 83°37' de longitud oeste, y a una altitud de 520 msnm. La precipitación promedio anual en el sitio es de 3364 mm, y la temperatura media anual de 22,6°C.

El diseño experimental consistió de bloques al azar con cinco bloques, y parcelas de 36 árboles con un distanciamiento de 3 x 3 m, en las cuales se evaluaron únicamente los 16 árboles centrales.

Cuadro 16. Identificación, ubicación y algunos datos climáticos de las procedencias de *Gmelina arborea* evaluadas en Turrialba, Costa Rica..

Procedencia	Identificación y abreviación en los cuadros	Latitud	Longitud	Precipitación media anual (mm)	Altitud (msnm)
Manila, Siquirres, C.R.	BSF1018	10°10'N	83°25'O	3286	15
Sao Miguel 72-14, Jari, Brasil	DAN4040	00°52'S	52°32'O	2476	66
Sankosh-1, West Bengal, India	DAN4045	26°25'N	89°20'E	4800	46
Maredumilli, Andhra Pradesh, India	DAN4058	17°40'N	81°42'E	1500	NI
Lambasingi, Andhra Pradesh, India	DAN4065	17°52'N	82°30'E	1500	NI
Andhra Pradesh, India	DAN4066	NI*	NI	NI	NI
Sri Lanka "A"	DAN4067	NI	NI	NI	NI
Sri Lanka "B"	DAN4068	NI	NI	NI	NI
Kao Yai, Saraburi, Tailandia	D100380	14°37'N	100°15'E	1150	250

* NI: No se suministró la información

Análisis

El ensayo fue analizado utilizando valores de árboles individuales para las variables altura total, diámetro basal, altura a la primera rama, frecuencia de ramificación, rectitud del fuste, dominancia del eje, bifurcación y sobrevivencia. La altura total y la altura a la primera rama están expresadas en metros; el diámetro basal en centímetros; la frecuencia de ramificación está expresada como el número de veces que el árbol se bifurcó o desarrolló una rama gruesa; la rectitud del fuste está basada en una escala arbitraria de 1 a 9, siendo 9 el mejor; la dominancia del eje está basada en una escala arbitraria de 1 a 7, donde las categorías 1 a 3 representan la pérdida del eje principal, y en las categorías restantes este se mantiene con diferentes grados de dominancia; la bifurcación está expresada como el porcentaje de árboles bifurcados por parcela y la sobrevivencia como porcentaje de árboles vivos. Las escalas de evaluación están basadas en las recomendaciones de DANIDA para la evaluación de los ensayos de procedencias (Lauridsen *et al.* 1987)

Resultados

El Cuadro 17 muestra los promedios para las variables altura total, diámetro basal y sobrevivencia a los cuatro años de edad, y el Cuadro 18 muestra los promedios para frecuencia de ramificación, rectitud del fuste, altura a la primera rama, dominancia del eje y bifurcación, evaluadas a los tres años de edad.

Cuadro 17 Promedios de altura total en metros (Alt), diámetro basal en cm (Dbas), y porcentaje de sobrevivencia (Sobrev), para las procedencias de *G. arborea* los 4 años de edad en Turrialba, Costa Rica.

Proc	Alt	Proc	Dbas	Proc	Sobrev
BSF1018	20,5 a*	DAN4067	22,0 a	DAN4068	100 a
DAN4040	20,0 ab	DAN4040	21,6 a	D100380	100 a
DAN4067	19,2 ab	BSF1018	21,5 a	DAN4066	97 a
DAN4068	18,5 ab	D100380	21,2 a	DAN4040	97 a
D100380	18,2 b	DAN4066	21,1 a	DAN4065	93 a
DAN4066	18,0 bc	DAN4045	20,6 a	DAN4058	92 a
DAN4045	16,2 cd	DAN4068	19,5 a	BSF1018	91 a
DAN4058	15,1 d	DAN4058	18,6 a	DAN4067	91 a
DAN4065	14,4 d	DAN4065	18,0 a	DAN4045	89 a

* Letras diferentes indican diferencias significativas al cinco por ciento (Prueba de Duncan)

Cuadro 18. Frecuencia de ramificación (Fram), rectitud del fuste (Rect), altura a la primera rama en metros (Apr), dominancia del eje (Dom) y porcentaje de bifurcación (Bifc) para las procedencias de *G. arborea* a los 3 años de edad en Turrialba, Costa Rica.

Proc	Fram	Proc	Rect	Proc	Dom	Proc	Apr	Proc	Bifc
DAN4045	1,7 a*	BSF1018	5,2 a	BSF1018	4,5 a	BSF1018	5,1 a	DAN4065	13 a
BSF1018	1,8 ab	DAN4040	4,8 ab	DAN4067	4,1 a	DAN4066	5,1 a	DAN4058	16 a
DAN4066	1,9 ab	DAN4067	4,7 ab	DAN4040	3,9 a	DAN4067	4,7 ab	DAN4067	19 a
DAN4040	2,0 ab	D100380	4,5 b	DAN4065	3,7 a	DAN4040	4,7 ab	BSF1018	20 a
DAN4067	2,0 ab	DAN4045	4,4 b	DAN4066	3,7 a	DAN4045	4,6 ab	DAN4040	22 a
D100380	2,4 bc	DAN4068	4,4 b	D100380	3,2 a	DAN4068	4,6 ab	D100380	25 a
DAN4068	2,5 bc	DAN4066	4,3 b	DAN4058	3,2 a	D100380	4,4 ab	DAN4066	27 a
DAN4058	2,5 bc	DAN4058	3,7 c	DAN4045	3,0 a	DAN4058	4,2 bc	DAN4045	39 a
DAN4065	2,7 c	DAN4065	3,4 c	DAN4068	2,2 a	DAN4065	3,5 c	DAN4068	44 a

* Letras diferentes indican diferencias significativas al cinco por ciento (Prueba de Duncan)

La sobrevivencia fue alta para todas las procedencias, y no mostaron diferencias significativas, con porcentajes entre 89 y 100%. Para las variables altura total y diámetro basal, es evidente la superioridad de tres procedencias: la procedencia derivada de Manila, Costa Rica (BSF1018), la procedencia derivada de Jarí, Brasil (DAN4040) y la procedencia nativa de Sri Lanka "A" (DAN4067). Estos resultados son similares a los informados por Valerio (1986), quien evaluó el ensayo a los tres años, y sugieren que las diferencias relativas entre procedencias se mantienen a partir de esa edad, lo que permitiría una selección temprana de procedencias con un alto nivel de confianza. Estas mismas procedencias, y en particular, la procedencia Manila, presentaron buenos hábitos de ramificación, fustes más rectos y limpios y baja incidencia de bifurcaciones.

Resulta interesante el comportamiento de las procedencias derivadas de Manila y Jarí, que ocuparon las mejores posiciones para la mayoría de las variables, tanto de producción como de forma. Ambas procedencias tienen un origen similar (Valerio, 1986), y son una mezcla de cuatro procedencias derivadas de Africa. En estas plantaciones es lógico suponer que las presiones de selección natural y artificial en su nuevo ambiente, han favorecido los individuos de mejor crecimiento y forma, resultando en el desarrollo de razas locales mejor adaptadas a las condiciones de Costa Rica.

Basado en estos resultados, el Proyecto de Mejoramiento Genético Forestal del CATIE ha iniciado un programa de selección de árboles individuales en las plantaciones locales, para establecer pruebas de descendencias (F1), huertos semilleros clonales, y estudios de clonación de genotipos superiores, para explotar la superioridad mostrada por la procedencia derivada local. La procedencia Manila ha sido introducida también en la zona de Hojancha, Costa Rica, donde ha mostrado un crecimiento y forma excepcionales. Esto da cierta indicación de la alta estabilidad de esta procedencia, y la posibilidad de desarrollar razas locales para zonas secas y húmedas partiendo de la misma población base. Al mismo tiempo, se debe considerar la posibilidad de introducir más material de la procedencia Sri Lanka "A", para aumentar la base genética de la especie en el país, y abrir mayores posibilidades de mejoramiento a largo plazo.

5. PRUEBA DE PROCEDENCIAS DE *Acacia mangium*

Este ensayo forma parte de los ensayos internacionales coordinados por CSIRO, Australia, e incluye 15 procedencias nativas. La identificación, ubicación y algunos datos climáticos de las procedencias se muestran en el Cuadro 19.

El ensayo fue establecido en 1984 en cuatro sitios en Costa Rica: Santa Clara de Ciudad Quesada, Buenos Aires de Puntarenas, Colorado de Guanacaste y Puriscal. El ensayo de Colorado presentó una alta mortalidad inicial, mientras que los árboles en Buenos Aires fueron afectados a la edad de dos años por un hongo (aún no identificado), que causó la muerte regresiva de muchos de ellos. El sitio 1: Santa Clara se ubica a 10°21' de latitud norte, 84°32' de longitud oeste, y a una elevación de 170 msnm. La precipitación promedio anual en el sitio es de 3400 mm, y la temperatura media anual de 25,7 °C. El sitio 2: Puriscal se ubica a 9°51' de latitud norte, 84°22' de longitud oeste, y a una elevación de 960 msnm. La precipitación promedio anual y la temperatura media anual en este sitio son de 2470 mm y 22,3°C.

El diseño experimental que se utilizó en ambos sitios consistió de bloques al azar con cinco bloques, y parcelas de 36 árboles con un distanciamiento de 3x3m, en las cuales se evaluaron únicamente los 16 árboles centrales. Debido a las limitaciones con el material, en el ensayo de Santa Clara se establecieron 14 procedencias, y solamente seis en el de Puriscal.

Análisis

Cada sitio fue analizado separadamente utilizando valores de árboles individuales, para las variables altura, dap y sobrevivencia, además del porcentaje de árboles bifurcados por parcela.

Resultados

Los Cuadros 20 y 21 muestran los promedios de altura total y dap, y los porcentajes de sobrevivencia y bifurcación a los cuatro años para el sitio de Santa Clara, y a los tres años para el sitio de Puriscal.

Cuadro 19. Identificación, ubicación y altitud de las procedencias de *Acacia mangium* estudiadas en Costa Rica.

Procedencia	Código CSIRO*	Latitud (°S)	Longitud (°E)	Altitud (msnm)
Rex Range NR Nossman, Queensland (Qld)	CSR12992	16°30'	145°32'	30
Cowley Beach Road, Qld.	CSR13232	17°41'	146°05'	5
Walsh's Pyramid, Qld.	CSR13233	17°06'	145°48'	20
Trinity Inlet, Qld	CSR13234	17°02'	145°48'	20
Mourilyan Bay, Qld.	CSR13235	17°35'	146°05'	20
Tully Mission Beach Rd, Qld.	CSR13238	17°56'	146°302	70
Syndicate Rd. Tully, Qld.	CSR13239	17°55'	145°52'	50
Ellerebeck Rd. Cardwell, Qld.	CSR13240	18°14'	145°58'	60
Broken Pole Creek, Qld.	CSR13241	18°21'	146°03'	50
Abergowrie, SF, Qld.	CSR13242	18°26'	146°01'	60
Claudie River, Qld.	CSR13229	12°44'	143°13'	60
W. of Morehead, Papúa Nueva Guinea	CSR13459	08°45'	141°10'	30
Oriomo River, Papúa Nueva Guinea	CSR13460	08°50'	143°08'	10
Piru Ceram, Indonesia.	CSR13621	03°04'	128°12'	150
SE Mossman, N.Qld.	CSR13846	16°31'	145°24'	60

* Organizaciones de Investigación Científica e Industrial de la Mancomunidad

Cuadro 20. Promedios de altura total (m) y dap (cm), y porcentajes de sobrevivencia y de árboles bifurcados para 14 procedencias de *Acacia mangium* a los 4 años de edad en Santa Clara, Costa Rica

Proced.	Altura total (m)	Proced.	dap (cm)	Proced.	Sobrev. (%)	Proced.	Incidencia de bifurcación (%)
CSR13242	13,3 a*	CSR13459	13,7 a	CSR13242	95 a	CSR13621	8 a
CSR13459	11,8 ab	CSR13229	13,6 ab	CSR13241	94 a	CSR13235	11 ab
CSR13229	11,2 bc	CSR13460	12,5 abc	CSR12992	94 a	CSR13229	15 ab
CSR13460	11,0 bc	CSR13242	12,2 abcd	CSR13233	92 a	CSR13238	15 ab
CSR13241	10,4 bc	CSR13240	11,7 abcde	CSR13234	91 a	CSR13234	19 abc
CSR13232	10,1 bcd	CSR13621	11,6 bcde	CSR13240	87 ab	CSR13459	20 abc
CSR13239	9,9 bcd	CSR13241	11,2 cde	CSR13232	84 ab	CSR13239	21 abc
CSR13240	9,6 bcd	CSR13232	11,0 cde	CSR13229	68 bc	CSR13233	21 abc
CSR13621	9,3 cd	CSR13235	10,9 cde	CSR13460	67 bc	CSR13460	24 abc
CSR12992	9,2 cd	CSR13238	10,8 cde	CSR13239	67 c	CSR13240	25 abc
CSR13238	9,1 cd	CSR13234	10,5 cde	CSR13459	58 c	CSR12992	26 abc
CSR13235	9,0 cd	CSR13239	10,3 de	CSR13238	55 c	CSR13232	29 bc
CSR13234	9,0 cd	CSR12992	10,3 de	CSR13621	48 c	CSR13242	30 bc
CSR13233	7,8 d	CSR13233	9,6 e	CSR13235	40 c	CSR13241	42 c

* Letras diferentes indican diferencias significativas al cinco por ciento (Prueba de Duncan)

Cuadro 21. Promedios de altura total (m) y dap (cm), y porcentaje de sobrevivencia y de árboles bifurcados para 6 procedencias de ***Acacia mangium*** a los 3 años de edad en Puriscal, Costa Rica

Proced.	Altura total (m)	Proced.	dap (cm)	Proced.	Sobrevivencia (%)	Proced.	Incidencia de bifurcación (%)
CSR13229	6,1 a*	CSR13229	8,2 a	CSR13242	95 a	CSR13846	14 a
CSR13242	6,1 a	CSR13459	7,7 a	CSR13459	85 a	CSR13621	38 a
CSR13459	6,0 a	CSR13242	7,5 a	CSR13229	84 a	CSR13233	39 a
CSR13233	5,8 a	CSR13233	7,5 a	CSR13621	73 ab	CSR13459	45 a
CSR13846	5,5 a	CSR13846	7,4 a	CSR13233	73 ab	CSR13242	50 a
CSR13621	5,1 a	CSR13621	5,4 b	CSR13846	50 b	CSR13229	63 a

* Letras diferentes indican diferencias significativas al cinco por ciento (Prueba de Duncan)

Con excepción de las variables altura total e incidencia de bifurcación, en el sitio 2, todas las demás variables mostraron diferencias significativas entre procedencias. El análisis combinado también detectó la presencia de interacciones genotipo-ambiente para las variables altura, dap y porcentaje de bifurcación en las procedencias comunes a ambos sitios, por lo que no se puede hablar de una única procedencia superior para ambos sitios.

Sin embargo, teniendo presente las restricciones debidas a la representación limitada de algunas procedencias en Puriscal, se puede notar el buen comportamiento general de la procedencia Morehead de Papúa Nueva Guinea (CSR13459), y de las procedencias Abergowrie y Claudie River (CSR13242 y CSR13229) de Queensland.

Los resultados de este ensayo ilustran una vez más la magnitud de las diferencias que pueden obtenerse entre procedencias de una misma especie. En Santa Clara, las diferencias entre la mejor y la peor procedencia en altura total y dap, fueron respectivamente, del 71 y del 43%. En Puriscal, las diferencias para esta mismas variables fueron del 20 y del 52%.

En este caso, la elección entre las mejores procedencias estará determinada en gran medida por la disponibilidad de semilla, ya que, por ejemplo, no ha sido posible hasta la fecha obtener semilla de las procedencias de Papúa Nueva Guinea, ni de la procedencia Abergowrie de Queensland. En 1988, el Proyecto de MGF importó semilla de Claudie River para el establecimiento de plantaciones piloto, con cuatro objetivos principales: evaluar la especie bajo condiciones normales de plantación, aumentar la base genética de la especie en el país, desarrollar plantaciones semilleras, y proveer una población base para selecciones de segunda generación.

Si bien algunas procedencias mostraron un comportamiento excelente en los sitios evaluados, y la especie ha mostrado su potencial en parcelas experimentales en muchos otros sitios del país (CATIE, 1986; Jiménez y Picado, 1987), es necesario conocer más acerca de la enfermedad que afectó los árboles en Buenos Aires antes de poder recomendar alguna procedencia en particular para plantaciones a mayor escala. Posiblemente, estudios más detallados sobre la enfermedad, y la exploración de posibilidades de contar con procedencias tolerantes o resistentes, será la base de las investigaciones con esta especie en los próximos años.

6. ACCIONES FUTURAS

El Grupo de Mejoramiento Genético del CATIE (Proyecto Mejoramiento Genético Forestal/MGF, Proyecto Arboles de Uso Múltiple/MADELEÑA) continúa trabajando con 22 especies maderables y de uso múltiple, que han mostrado buen crecimiento y adaptabilidad en las regiones de Centro América con potencial para plantaciones forestales. El Grupo de Mejoramiento Genético mantiene un programa de establecimiento de ensayos de procedencias, para aquellas especies y regiones donde la información es insuficiente. El Proyecto Madeleña está concentrado en el establecimiento de ensayos de procedencias, y establecimiento y manejo de rodales y plantaciones semilleras en Centro América, como una alternativa inmediata al problema de abastecimiento de semilla de origen y calidad genética conocidos. Por su parte, el Proyecto MGF ha iniciado un programa de selección, y/o introducción de fenotipos individuales, para el establecimiento de ensayos de descendencias, huertos semilleros clonales y bancos de conservación. Asimismo, se realizan estudios de clonación, para la propagación y utilización de los mejores ideotipos de estas poblaciones.

Los ensayos generalmente se evalúan a un año para sobrevivencia y altura total, a los tres años para sobrevivencia, altura total y dap, y se realiza una evaluación intensiva a los cinco años, donde se incluyen además, características del fuste y ramificación. A partir de este momento, se decide la estrategia a seguir para cada ensayo, dependiendo de las necesidades de la especie que está siendo estudiada. Sin embargo, generalmente los ensayos de procedencias se continúan evaluando hasta el final del turno de rotación, cuando se realiza la evaluación final que incluye, además de las variables mencionadas, características de la madera. Con base en la información de la evaluación al quinto año, se inicia el establecimiento de plantaciones piloto con las mejores procedencias, con tres objetivos principales: evaluar el potencial de las procedencias bajo condiciones normales de plantación, aumentar la base genética de la especie, y crear "plantaciones semilleras de procedencia" (provenance seed stand), para el suministro de semilla de calidad genética superior.

Los ensayos de descendencias, por su parte, pueden ser transformados inmediatamente en "huertos semilleros de plántulas" (seedling seed orchards), mediante selección de los mejores árboles dentro de las mejores familias. El diseño experimental utilizado en estos ensayos, permite una distribución adecuada de los individuos que conformarán finalmente el huerto. Los bancos de conservación pueden ser aclareados con base en la información de las pruebas de descendencias, y convertidos igualmente en huertos semilleros de plántulas, o conservados como tales si el objetivo primario es conservación de genes y genotipos. La conversión de estos ensayos en huertos semilleros es factible si las condiciones en las cuales están establecidos, favorecen la producción abundante de semilla.

Otra función de los ensayos y de las plantaciones piloto, es la de proveer material para selecciones avanzadas de individuos superiores, los cuales se integrarán a las poblaciones de producción de semilla genéticamente mejorada.

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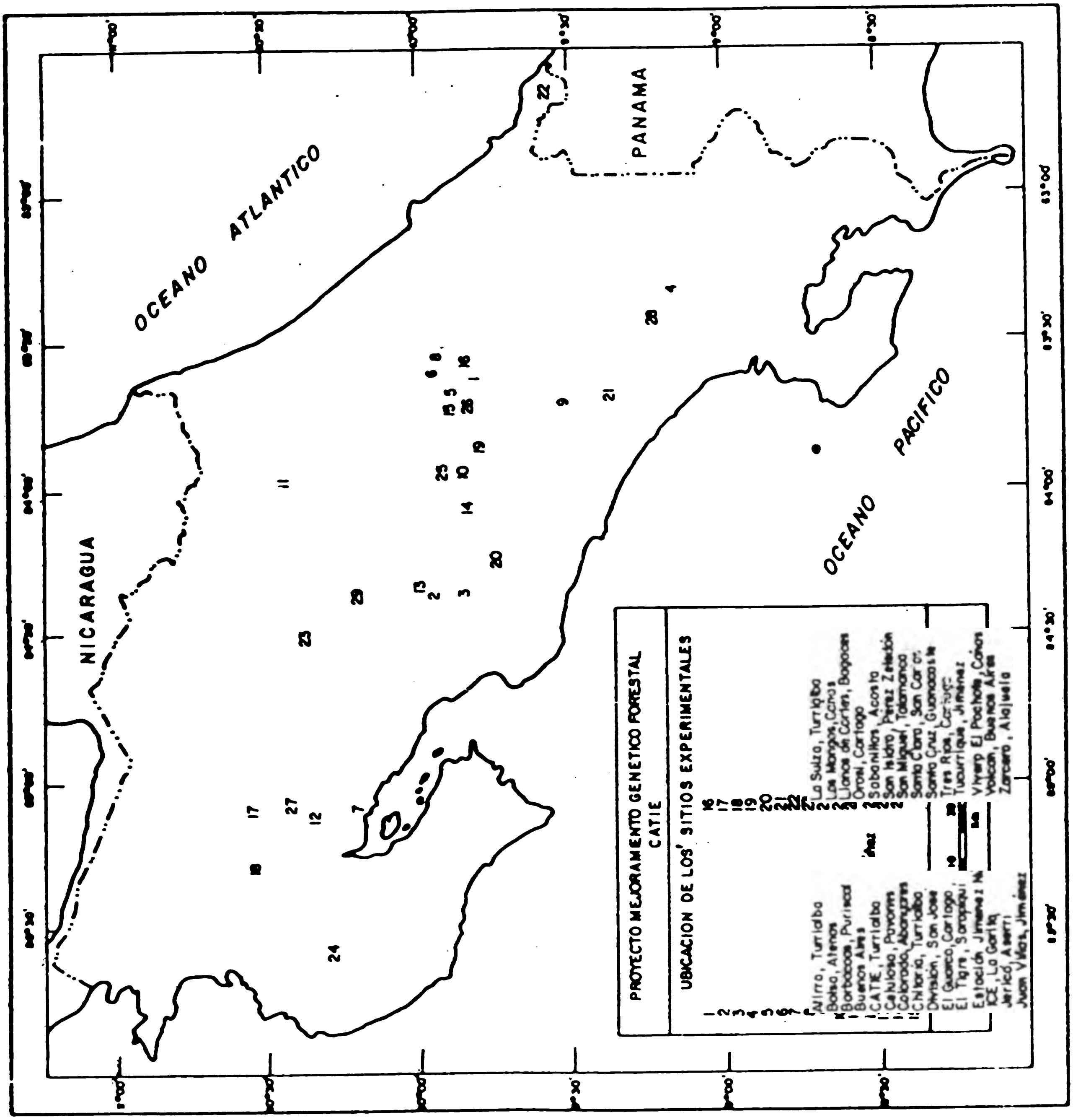
Anexo 1.


NICARAGUA
OCEANO ATLANTICO
PANAMA
OCEANO PACIFICO
PROYECTO MEJORAMENTO GENETICO FORESTAL
CATIE
UBICACION DE LOS SITIOS EXPERIMENTALES
1 Atirro, Turrialba
2 Bolsa, Atenas
3 Barbacoas, Puriscal
4 Buenos Aires
5 CATIE, Turrialba
6 Celulosa, Pavones
7 Colorado, Abangares
8 Chitaria, Turrialba
9 División, San José
10 El Guarco, Cartago
11 El Tigre, Sarapiquí
12 Estación Jiménez N
13 ICE, La Garita
14 Jericó, Aserrí
15 Juan Viñas, Jiménez
16 La Suiza, Turrialba
17 Los Mangos, Cañas
18 Llanos de Cortés, Bagaces
19 Orosi, Cartago
20 Sabanillas, Acosta
21 San Isidro, Pérez Zeledón
22 San Miguel, Talamanca
23 Santa Clara, San Carlos
24 Santa Cruz, Guanacaste
25 Tres Ríos, Cartago
26 Tucurrique, Jiménez
27 Vivero El Pochote, Cañas
28 Volcán, Buenos Aires
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Anexo 2.

LISTA DE ENSAYOS ESTABLECIDOS EN COSTA RICA POR EL PROYECTO MEJORAMIENTO GENETICO FORESTAL, CATIE

Exp N°	Nombre	Rep. N°	Sitio N°	Lote N°	Nombre del sitio	Fecha plant.	Arboles/ parcela	N° bloq	N° de fuentes de semilla
48(68)	Variedades de Pinus caribaea	1	609	008	Florencia Sur, CATIE, Turrialba	10-06-68	110	1	4
		2	641	001	Hacienda Atirro, Turrialba	06-07-68	110	1	4
		3	604	010	Bajo San Lucas, CATIE, Turrialba	21-08-68	100	1	4
		4	610	024	Florencia Norte, CATIE, Turrialba	28-10-68	100	1	4
8(73-1)	Procedencias de P. caribaea	1	614	007	Puente Cajón, CATIE, Turrialba	03-01-73	49	1	10
		2	614	007	Puente Cajón, CATIE, Turrialba	03-01-73	49	1	10
		3*	610	026	Florencia Norte, CATIE, Turrialba	05-01-73	49	1	10
		4	615	001	San Juan Sur, CATIE, Turrialba	06-01-73	49	1	10
		5	613	001	Noche Buena, CATIE, Turrialba	10-01-73	49	1	10
112(77-1)	Procedencias de P. caribaea	1	642	002	Celulosa, Pavones Turrialba	09-77	7	5	12
		2	610	002	Florencia Norte, CATIE, Turrialba	09-77	7	5	12
		3*	703	003	ICE, La Garita, Alajuela	10-77	7	5	12
		4	306	001	Finca M. Beita, Volcán, Buenos Aires	31-03-78	7	4	12
		5	311	001	UNA, San Isidro de Perez Zeledón	09-77	7	5	12
		6	214	004	ITCR, Santa Clara, Ciudad Quesada	09-06-83	36	5	12
		7	454	001	Est. Exp. UCR, Santa Cruz, Guanacaste	23-06-83	36	5	12

ANEXO 2. Cont.

Exp. N°	Nombre	Rep N°	Sitio N°	Lote N°	Nombre del sitio	Fecha plant.	Arboles/ parcela	N° bloq.	N° de fuentes de semilla
113(73-1)	Procedencias de P. caribaea	1	614	009	Puente Cajón, CATIE, Turrialba	21-03-78	49	3	10
115(78-3)	Procedencias de P. oocarpa	1	642	002	Celulosa, Pavones, Turrialba	18-10-78	10	5	16
		2	615	003	San Juan Sur, CATIE, Turrialba	01-12-78	10	5	16
		3	311	002	UNA, San Isidro de Pérez Zeledón	10-05-79	10	5	16
		4*	410	017	Est. Exp. Enrique Jiménez Núñez, Cañas	30-05-79	10	5	16
117(77-2)	Descendencias de Cordia alliodora	1	610	014	Florencia Norte, CATIE, Turrialba	02-07-76	1	15	25
		2a		001	Finca La Cruz, Chitaria, Turrialba	22-09-87	6	10	39
		2b		002	Finca La Cruz, Chitaria, Turrialba	08-09-87	6	8	26
		3		001	ANAI, San Miguel, Talamanca	20-08-87	6	7	55
		5		003	Finca La Cruz, Chitaria, Turrialba (BC[1])	03-12-87	1	24	50
118(78-5)	Procedencias de C. alliodora	1	609	014	Florencia Sur, CATIE, Turrialba	07-08-79	49	5	8
		2	627	001	Col. Agrop. La Suiza, Turrialba	17-10-79	25	5	6
		3*	311	005	UNA, San Isidro de Pérez Zeledón	19-10-82	36	5	13
		4	642	012	Celulosa, Pavones, Turrialba	20-08-83	36	5	12
		5	214	003	ITCR, Santa Clara, Ciudad Quesada	19-05-83	36	5	14

ANEXO 2. Cont.

Exp. N°	Nombre	Rep N°	Sitio N°	Lote N°	Nombre del sitio	Fecha plant.	Arboles/ parcela	N° bloq	N° de fuentes de semilla
115(78-6)	Descendencias de P. caribaea	1*	415	018	Est. Exp. Enrique Jimenez Núñez, Cañas	06-79	6	5	41
		2	409	001	Vivero For. IDA, El Pochote, Cañas	09-79	6	5	32
136(79-3)	Especies y Procedencias de Eucalyptus	1	612	015	La Isla, CATIE, Turrialba	28-04-80	36	5	23
139(79-6)	Procedencias de Araucaria hunsteinii y A. cunninghamii	1	614	011	Puente Cajón, CATIE, Turrialba	07-07-81	49	2	4
142(79-9)	Procedencias de E. grandis	1*	408	001	IDA, Finca Llanos de Cortés, Bagaces	08-80	36	5	12
		2	306	002	Finca W. Beita, Volcán, Buenos Aires	26-06-81	36	5	10
		3	307	003	Finca P. Beita, Volcán, Buenos Aires	30-06-81	36	3	6
144(79-1)	Procedencias de P. oocarpa (Reforestación de pastizales degradados en La Suiza)	1	635	001	Finca Sánchez, La Suiza, Turrialba	20-07-79	49	1	15
		2	636	002	Finca Thiele, La Suiza, Turrialba	22-06-79	49	1	15
145(79-1)	Procedencias de E. tereticornis	1*	408	002	IDA, Finca Llanos de Cortés, Bagaces	08-80	36	5	14
151(80-7)	Procedencias de E. urophylla	1	214	002	ITCR, Santa Clara, Ciudad Quesada	19-08-81	36	5	14
		2	311	004	UNA, San Isidro de Pérez Zeledón	29-07-81	36	5	4
		3	609	006	Florencia Sur, CATIE, Turrialba	04-11-81	25	5	3
156(82-2)	Procedencias y Descendencias de P. caribaea y P. oocarpa	1a	716	001	ECAC, Balsa de Atenas	03-08-82	5	10	
		1b	716	002	ECAC, Balsa de Atenas	03-08-82	5	10	
		2a	646	003	Hda. Juan Viñas, Turrialba	31-07-84	5	10	41
		2b	610	035	Florencia Norte, CATIE, Turrialba	30-10-84	5	10	45

ANEXO 2. Cont.

Exp. N°	Nombre	Rep N°	Sitio N°	Lote N°	Nombre del sitio	Fecha plant.	Arboles/ parcela	N° bloq.	N° de fuentes de semilla
188(82-1)	Procedencias de Gmelina arborea	1	672	012	Celulosa, Pavones, Turrialba	01-09-84	36	4	9
201	Procedencias de Acacia mangium	1	214	006	ITCR, Santa Clara, Ciudad Quesada	06-12-84	36	5	146
		2*	319	001	PINDECO, Buenos Aires	01-11-84	36	5	6
		3*	482	001	Colorado de Guanacaste	13-09-84	36	5	6
		4	513	001	Cortezal de Barbacoas, Puriscal	08-08-84	36	5	6
		5			Bajo Chino, CATIE, Turrialba (PS^{2}-2)	07-01-89	1111	1	1
211	Rodales y huertos semilleros de P. tecunumanii	1	622	001	El Guarco, Cartago (RS^{3}-1)	18-06-86	397	1	1
		2	513	003	Cortezal de Barbacoas, Puriscal (RS^{3}-2)	03-07-85	394	1	1
		3	622	002	El Guarco, Cartago (BS^{4}-1)	10-86	1	14	12
		4	623	001	Vivero Anderson, Cartago (BS^{4}-2)	10-86	1	14	11
		5		001	Sabanillas, Acosta (PP^{5}-1)	08-08-87	1444	1	1
		6		001	Jericó, Aserrí (PP^{5}-2)	04-09-87	2000	1	1
		7		001	ITCR, Finca Los Lotes, Tres Rios (PP^{5}-3)	23-10-87	1111	1	1
		8		001	Finca Durman Esquivel, Orosi, Cartago (PP^{5}-3)	03-88	2000	1	1
213	Descendencias de P. tecunumanii	1		001	COOPACRIMAR, Zarcero	08-89	5	5	50
		2		002	COOPACRIMAR, Zarcero	08-89	1	10	30
		3		001	Finca R. Kandler, Division (BC^{1})	26-07-89	1	10	50

ANEXO 2. Cont.

Exp N°	Nombre	Rep N°	Sitio N°	Lote N°	Nombre del sitio	Fecha plant	Arboles/ parcela	N° bloq.	N° de fuentes de semilla
214	Descendencias de P. tecunumanii	1		001	INCSA, Jesús María, Turrialba	05-08-88	6	5	45
		1		001	Finca S. Pignani, Orosi, Cartago	11-10-88	6	9	53
215	Descendencias de P. caribaea	1*		001	Santa Cruz, Guanacaste	23-06-88	6	9	51
216	Descendencias de Pochota quinata	1		001	Finca Los Mangos, Cañas	08-06-88	6	9	71
222	Descendencias de E. grandis	1		001	Finca Zúñiga Araya, Tucurrique, Alvarado	10-89	5	7	98
		2		001	Finca M. Chávez, Atirro, Alvarado (BC^1-1)	11-89	1	20	96

* Repetición abandonada por alta mortalidad

1: Banco de conservación

2: Plantación semillera

3: Rodal semillero

4: Huerto semillero

5: Plantación piloto

RESULTADOS DEL PROYECTO MEJORAMIENTO GENETICO FORESTAL DEL CATIE, SUS APLICACIONES Y EFECTOS ESPERADOS. Corea Eugenio, Cornelius Jonathan y Mesén Francisco. Centro Agronómico Tropical de Investigación y Enseñanza. 1992.

La reforestación en Costa Rica ha aumentado significativamente en los últimos años, sustentada básicamente en una enorme inversión por parte del estado, organismos de ayuda internacional y del sector privado. Sin embargo, gran parte de las plantaciones no están dando los resultados esperados con las consiguientes pérdidas ecológicas y económicas, y el importante efecto colateral de desestímulo a la reforestación. La experiencia y la investigación en Costa Rica y en muchos países tropicales ha demostrado claramente que una de las principales razones para el fracaso o la baja productividad de las plantaciones forestales ha sido el uso de germoplasma inadecuado. Una mala selección puede producir, especialmente a mediano y largo plazo, más problemas que casi cualquier otro factor.

El primer y, probablemente, más importante paso de un programa de reforestación es la selección correcta de la especie y de la procedencia dentro de la especie. Sin embargo, esta decisión necesita una base científica y generalmente no se cuenta con la información suficiente.

Reconociendo esta necesidad, el Proyecto Mejoramiento Genético Forestal del CATIE (PMGF) inició en 1977 el establecimiento de una gran cantidad (más de 50 ensayos a la fecha) de ensayos de procedencias con 16 especies. Las especies incluidas fueron seleccionadas con base en los resultados de ensayos con más de 100 especies exóticas y nativas establecidos por el CATIE, la DGF y la OET en varias partes del país (1, 2, 3).

En la ponencia se presenta los resultados de los ensayos de procedencias de mayor edad de varias especies y se estiman y discuten los efectos que podrían tener en los proyectos de reforestación la aplicación de dichos resultados. Al mismo tiempo se brindan recomendaciones sobre la forma de obtener la semilla de las procedencias superiores. Es inaceptable que después de 15 años de costosa investigación los resultados no se apliquen porque la semilla no está disponible o no se sabe como conseguirla.

Hasta la fecha los resultados mas importantes por especie son las siguientes:

Acacia mangium

En un ensayo con 14 procedencias establecido en Santa Clara de San Carlos se encontró a los 4 años de edad que las procedencias más productivas son Abergowrie (CSR13242) y Claudie River (CSR13229) de Queensland, Australia, junto con la procedencia West of Morehead (CSR13459) de Papúa Nueva Guinea. La diferencia en producción de volumen con corteza entre la procedencia Abergorie y el promedio del resto de las procedencias es de 103%. Resultados similares se han obtenido en un ensayo con 6 procedencias en Puriscal donde las mismas tres procedencias han mostrado un crecimiento superior.

Cordia alliodora

De acuerdo a dos ensayos de procedencias establecidos en Turrialba se han identificado a los 3 años de edad como procedencias sobresalientes las procedencias San Francisco (K1532077) de Honduras y Florencia de San Carlos, Costa Rica. Las diferencias en volumen entre estas procedencias y el promedio de las procedencias restantes es de 139% y 115%, respectivamente.

Gmelina arborea

En un ensayo con 9 procedencias (7 nativas y 2 derivadas) establecido en Javillos Turrialba (500 msnm) se encontró a los 3 años de edad que las procedencias derivadas Ja (72-14) Brasil y Manila (BLSF1018) Siquirres, Costa Rica son las más productivas. L diferencias en producción de volumen entre estas procedencias y el promedio de l procedencias restantes es de 47% y 41% respectivamente.

Eucalyptus urophylla

Los resultados a 6.5 años de edad de un ensayo de 10 procedencias establecido Santa Clara de San Carlos muestran que las procedencias S.W. Isla Lembata (802770N Región W. Isla Alor (802808N) y Mt. Lewotobi, Isla Flores (12896) son las que tienen mejor comportamiento. La diferencia en productividad de volumen entre S.W. Isla Lemba y el promedio de las restantes procedencias es de 49%.

Eucalyptus spp

Un ensayo combinado de especies (8) y procedencias (23) de *Eucalyptus s* establecido en Turrialba ha mostrado enormes diferencias en crecimiento tanto entre especi como entre procedencias a los 5 años de edad. Las especies probadas fueron *E. alba*, *camaldulensis*, *E. citriodora*, *E. cloeziana*, *E. deglupta*, *E. grandis*, *E. saligna* y *tereticornis*. Los mejores tratamientos fueron la procedencia Gympie (11761), Queenslan Australia, de *E. grandis* y la procedencia derivada Juan Viñas (Finca Peet) (BLSF 903) *E. saligna*. La diferencia entre estas procedencias y el promedio de las restantes es de 373 y 302% respectivamente.

Pinus caribaea, *P. oocarpa* y *P. tecunumanii*

Hasta la fecha se han establecido 13 ensayos de procedencias con estas especies en u gran diversidad de sitios, ubicados entre 100 y 1200 msnm. Los resultados de evaluaciones 7 años o más han mostrado que las procedencias Yucul, Nicaragua y Mountain Pine Ridg Belice, de *Pinus tecunumanii* son superiores a 13 procedencias probadas de *P. oocarpa* y a procedencias de *P. caribaea*. La procedencia Yucul de *P. tecunumanii* supera en 112% volumen sin corteza al promedio de las procedencias de *P. oocarpa*. Esta procedenc también supera en productividad a las mejores procedencias de *P. caribaea* generalmente un 25% a 40%. La unica excepción se da en las partes bajas, calientes y con estación se marcada de Guanacaste, donde las procedencias Guanaja, Honduras, Mountain Pine Ridg Belice y Poptún, Guatemala de *P. caribaea* tienen un mejor comportamiento.

Por otra parte, el potencial del mejoramiento genético forestal va más allá del qu ofrece la selección adecuada de especies y procedencias. Existen otras etapas más avanzada de selección y mejoramiento que permiten continuar obteniendo importantes ganancia genéticas y económicas. Entre ellas destaca la selección a nivel clonal y la aplicación de un silvicultura clonal a nivel operacional.

El desarrollo de la silvicultura clonal ha sido sin duda el logro más importante de la grandes empresas forestales en los últimos quince años, especialmente en Brasil y Colombia En algunos casos se ha logrado hasta triplicar la producción, al mismo tiempo que se mejor la calidad de los árboles. Sin embargo, la tecnología generada por estas compañías no est disponible y no es apropiada para el pequeño reforestador ni para programas de desarroll rural. Por esta razón, en cooperación con el Instituto de Ecología Terrestre (Escocia), PMGF ha desarrollado un sistema de propagación vegetativa simple y barato. El sistem consiste en propagadores con sub-irrigación, de fácil construcción, hechos de madera plástico, que no necesitan electricidad, agua de cañería o sistemas de riego, por lo que puede ser construidos e instalados a muy bajo costo en cualquier zona rural.

Usando los propagadores con sub-irrigación el PMGF ha realizado investigaciones para determinar métodos operacionales de enraizamiento de estacas juveniles de varias especies forestales prioritarias. Se han probado diferentes sustratos, niveles de aplicación de hormonas y diferentes longitudes del tallo y área foliar de la estaca. Hasta ahora se ha logrado obtener para la mayoría de las especies porcentajes de enraizamiento superiores al 80%, lo que se considera completamente aplicable a nivel operacional. En la ponencia se presentan los resultados de estas investigaciones para cada especie y las posibles implicaciones de su aplicación en programas de silvicultura clonal rural.

1. CAMACHO, M.P. 1981. Informe general del proyecto de ensayos de adaptabilidad y rendimiento de especies forestales en Costa Rica. Cartago, Costa Rica, ITCR-DGF. 287 p.

2. COMBE, J.; GEWALD, N.J. 1979. Guía de campo de los ensayos forestales del CATIE en Turrialba, Costa Rica. Turrialba, Costa Rica, CATIE. 378 p.

3. ESPINOZA, M.; BUTTERFIELD, R. 1989. Adaptabilidad de 13 especies nativas made-rables bajo condiciones de plantación en las tierras bajas húmedas del atlántico de Costa Rica. Preparado para la IV Reunión del Grupo de Trabajo de IUFRO S1.07-09 "Manejo y aprovechamiento de plantaciones forestales con especies de uso múltiple", 3 - 7 de abril de 1989, Antigua, Guatemala. DGF-OET, Heredia, Costa Rica. 19 p.

RESULTADOS DEL PROYECTO MEJORAMIENTO GENETICO FORESTAL DEL CATIE, SUS APLICACIONES Y EFECTOS ESPERADOS.

Eugenio Corea, Jonathan Cornelius y Francisco Mesén

(ANEXO DE RESULTADOS)

Cuadro 1. Volumen total para 14 procedencias de *Acacia mangium* a los tres años y dos meses de edad en Santa Clara, San Carlos, Costa Rica.

Procedencia	Código CSIRO	Volumen total (m3/ha)
Abergowrie, SF, Qld, Australia.	CSR13242	148
Claudie River, Qld, Aust.	CSR13229	110
West of Morehead, Papúa Nueva Guinea.	CSR13459	101
Broken Pole Creek, Qld, Aust.	CSR13241	97
Oriomo River, Papúa Nueva Guinea.	CSR13460	90
Ellerebeck Rd. Cardwell, Qld, Aust.	CSR13240	90
Cowley Beach Road, Qld, Aust.	CSR13232	81
Rex Range NR Nossman, Qld, Aust.	CSR12992	72
Trinity Inlet, Qld, Aust.	CSR13234	70
Syndicate Rd. Tully, Qld, Aust.	CSR13239	56
Walsh's Pyramid, Qld, Aust.	CSR13233	52
Piru Ceram, Indonesia.	CSR13621	47
Tully Mission Beach Rd, Qld, Aust.	CSR13238	45
Mourilyan Bay, Qld, Aust.	CSR13235	34

Cuadro 2. Volumen total para 6 procedencias de *Acacia mangium* a los dos años y siete meses de edad en Barbacoas, Puriscal, Costa Rica.

Procedencia	Código CSIRO	Volumen total (m3/ha)
Claudie River, Qld, Aust.	CSR13229	27
Abergowrie, SF, Qld, Australia.	CSR13242	26
West of Morehead, Papúa Nueva Guinea.	CSR13459	23
Walsh's Pyramid, Qld, Aust.	CSR13233	19
SE Mossman, North Qld, Aust.	CSR13846	12
Piru Ceram, Indonesia.	CSR13621	9

Cuadro 3 Promedios de altura total (m) y dap (cm), y porcentajes de sobrevivencia y de árboles bifurcados para 14 procedencias de *Acacia mangium* a los ~~4 años~~ de edad en Santa Clara, Costa Rica
3 años

Proced.	Altura total (m)	Proced.	dap (cm)	Proced.	Sobrev. (%)	Proced.	Incidencia de bifurcación (%)
CSR13242	13,3 a*	CSR13459	13,7 a	CSR13242	95 a	CSR13621	8 a
CSR13459	11,8 ab	CSR13229	13,6 ab	CSR13241	94 a	CSR13235	11 ab
CSR13229	11,2 bc	CSR13460	12,5 abc	CSR12992	94 a	CSR13229	15 ab
CSR13460	11,0 bc	CSR13242	12,2 abcd	CSR13233	92 a	CSR13238	15 ab
CSR13241	10,4 bc	CSR13240	11,7 abcde	CSR13234	91 a	CSR13234	19 abc
CSR13232	10,1 bcd	CSR13621	11,6 bcde	CSR13240	87 ab	CSR13459	20 abc
CSR13239	9,9 bcd	CSR13241	11,2 cde	CSR13232	84 ab	CSR13239	21 abc
CSR13240	9,6 bcd	CSR13232	11,0 cde	CSR13229	68 bc	CSR13233	21 abc
CSR13621	9,3 cd	CSR13235	10,9 cde	CSR13460	67 bc	CSR13460	24 abc
CSR12992	9,2 cd	CSR13238	10,8 cde	CSR13239	67 c	CSR13240	25 abc
CSR13238	9,1 cd	CSR13234	10,5 cde	CSR13459	58 c	CSR12992	26 abc
CSR13235	9,0 cd	CSR13239	10,3 de	CSR13238	55 c	CSR13232	29 bc
CSR13234	9,0 cd	CSR12992	10,3 de	CSR13621	48 c	CSR13242	30 bc
CSR13233	7,8 d	CSR13233	9,6 e	CSR13235	40 c	CSR13241	42 c

* Letras diferentes indican diferencias significativas al cinco por ciento (Prueba de Duncan)

(Fuente: Mesén, 1990)

Cuadro 4 Promedios de altura total (m) y dap (cm), y porcentaje de sobrevivencia y de árboles bifurcados para 6 procedencias de *Acacia mangium* a los 3 años de edad en Puriscal, Costa Rica

Proced.	Altura total (m)	Proced.	dap (cm)	Proced.	Sobrevivencia (%)	Proced.	Incidencia de bifurcación (%)
CSR13229	6,1 a*	CSR13229	8,2 a	CSR13242	95 a	CSR13846	14 a
CSR13242	6,1 a	CSR13459	7,7 a	CSR13459	85 a	CSR13621	38 a
CSR13459	6,0 a	CSR13242	7,5 a	CSR13229	84 a	CSR13233	39 a
CSR13233	5,8 a	CSR13233	7,5 a	CSR13621	73 ab	CSR13459	45 a
CSR13846	5,5 a	CSR13846	7,4 a	CSR13233	73 ab	CSR13242	50 a
CSR13621	5,1 a	CSR13621	5,4 b	CSR13846	50 b	CSR13229	63 a

* Letras diferentes indican diferencias significativas al cinco por ciento (Prueba de Duncan)

(Fuente: Mesén, 1990)

Cuadro 5. Volumen total a siete años de edad de 7 procedencias de *Cordia alliodora* y una de *C. gerascanthus* en Florencia Sur, Turrialba, Costa Rica.

Procedencia	Código	Volumen total (m3/ha)
San Francisco, La Ceiba, Honduras.	K1532077	75
Finca La Pineda, Matagalpa, Nicaragua.	K1521877	45
Finca La Fortuna, San Pedro, Honduras.	K1511977	43
Limón, Costa Rica.	3377	40
Finca El Chilero, Guatemala	K1451077	39
Estelí, Nicaragua.	K1461477	19
Tres Piedras, Choluteca, Honduras.	K1440977	17
Waswali, Nicaragua (*C. gerascanthus*).	K1471677	1

Cuadro 6. Volumen total a siete años de edad de 12 procedencias de *Cordia alliodora* en Celulosa, Javillos, Turrialba, Costa Rica.

Procedencia	Código	Volumen total (m3/ha)
Santa Clara, San Carlos, Costa Rica	BLSF1164	171
San Francisco, La Ceiba, Honduras	K1532077	136
Turrialba, Costa Rica	5178	127
Guápiles, Costa Rica	BLSF1166	110
Finca La Fortuna, San Pedro, Honduras	K1511977	104
Nueva Guinea, Nicaragua	K1673378	96
Finca La Pineda, Matagalpa, Nicaragua	K1521877	83
Finca Rincón Alegre, Guatemala	K1663078	73
Turrialba, Costa Rica	BLSF1165	62
Estelí, Nicaragua.	K1461477	54
Tres Piedras, Choluteca, Honduras	K1440977	41
Finca El Chilero, Guatemala	K1451077	37

* Finca Matamoros, Santa Clara de San Carlos.

Cuadro 7. Volumen total a siete años de edad de 14 procedencias de *Cordia alliodora* en Santa Clara, San Carlos, Costa Rica.

Procedencia	Código	Volumen total (m3/ha)
Nueva Guinea, Nicaragua	K1673378	65
Santa Clara, San Carlos, Costa Rica	BLSF1164	51
Finca Rincón Alegre, Guatemala	K1663078	47
Turrialba, Costa Rica	5178	46
San Francisco, La Ceiba, Honduras	K1532077	40
Finca La Fortuna, San Pedro, Honduras	K1511977	37
Tres Piedras, Choluteca, Honduras	K1440977	33
Estelí, Nicaragua	K1461477	33
Limón, Costa Rica	5278	33
San Carlos, Costa Rica	5378	30
Finca La Pineda, Matagalpa, Nicaragua	K1521877	29
Turrialba, Costa Rica	BLSF1165	22
Guápiles, Costa Rica	BLSF1166	15
Finca El Chilero, Guatemala	K1451077	11

* Finca Matamoros, Santa Clara de San Carlos.

Cuadro 8. Sobrevivencia (SOB), diámetro medio (DAP), altura total media (ALT) y volumen total (VOT) a siete años de edad de 7 procedencias de *Cordia alliodora* y 1 de *C. gerascanthus* en Florencia Sur, Turrialba, Costa Rica.

Procedencia	Código	SOB (%)	DAP (cm)	ALT (m)	VOT (m3/ha)
San Francisco, Hond.	K1532077	90,4	9,2	10,5	75,1
Finca La Pineda, Nic.	K1521877	80,0	8,0	8,7	44,9
Finca La Fortuna, Hond.	K1511977	78,4	8,1	8,6	43,3
Limón, Costa Rica.	3377	53,6	8,0	7,7	39,8
Finca El Chilero, Guat.	K1451077	71,2	8,2	8,5	39,1
Estelí, Nic.	K1461477	64,0	6,6	6,8	18,6
Tres Piedras, Hond.	K1440977	73,0	5,4	5,6	16,6
C. gerascanthus, Nic.	K1471677	37,6	1,2	2,7	0,7

Cuadro 9. Sobrevivencia (SOB), diámetro medio (DAP), altura total media (ALT) y volumen total (VOT) a siete años de edad de 12 procedencias de *Cordia alliodora* en Celulosa, Javillos, Turrialba, Costa Rica.

Procedencia	Código	SOB (%)	DAP (cm)	ALT (m)	VOT (m3/ha)
Sta Clara*, San Carlos, CR.	BLSF1164	86,3	14,3	12,4	171
San Francisco, Hond.	K1532077	82,5	13,1	12,3	136
Turrialba, Costa Rica	5178	88,8	12,6	11,6	127
Guápiles, Costa Rica	BLSF1166	78,8	11,7	11,2	110
Finca La Fortuna, Hond.	K1511977	85,0	11,6	11,3	104
Nueva Guinea, Nicaragua	K1673378	97,5	11,1	10,3	96
Finca La Pineda, Nic.	K1521877	80,0	11,4	10,4	83
Rincón Alegre, Guat.	K1663078	93,8	10,6	9,8	73
Turrialba, Costa Rica	BLSF1165	96,3	9,7	9,3	62
Estelí, Nicaragua	K1461477	86,3	9,6	8,8	54
Tres Piedras, Hond.	K1440977	65,0	9,3	8,9	41
Finca El Chilero, Guat.	K1451077	76,3	9,0	8,2	37

* Finca Matamoros, Santa Clara de San Carlos.

Cuadro 10. Sobrevivencia (SOB), diámetro medio (DAP), altura total media (ALT) y volumen total (VOT) a siete años de edad de 14 procedencias de *Cordia alliodora* en Santa Clara, San Carlos, Costa Rica.

Procedencia	Código	SOB (%)	DAP (cm)	ALT (m)	VOT (m3/ha)
Nueva Guinea, Nicaragua	K1673378	85,0	10,5	10,1	65
Sta Clara, San Carlos, CR.	BLSF1164	81,3	9,4	8,6	51
Rincón Alegre, Guatemala	K1663078	87,5	9,8	8,3	47
Turrialba, Costa Rica	5178	67,5	8,6	8,1	46
San Francisco, Honduras	K1532077	83,8	8,8	7,4	40
Finca La Fortuna, Hond.	K1511977	83,8	8,8	7,9	37
Tres Piedras, Honduras	K1440977	83,8	8,4	7,3	33
Estelí, Nicaragua	K1461477	82,5	8,4	8,0	33
Limón, Costa Rica	5278	78,8	8,4	8,3	33
San Carlos, Costa Rica	5378	77,5	7,9	7,3	30
Finca La Pineda, Nic.	K1521877	68,8	8,2	7,4	29
Turrialba, Costa Rica	BLSF1165	55,0	9,7	7,3	22
Guápiles, Costa Rica	BLSF1166	68,8	8,5	7,1	15
Finca El Chilero, Guat.	K1451077	93,8	6,9	5,6	11

* Finca Matamoros, Santa Clara de San Carlos.

Cuadro 11. Volumen total de un ensayo de 23 procedencias y 8 especies *Eucalyptus ssp.* a los 5 años de edad en CATIE, Turrialba, Costa Rica.

Especie	Procedencia	Código	Volumen total (m3/ha)
E. grandis	Gympie, Qld, Australia.	CSR11761	155
E. saligna	Finca Peet, Juan Viñas, C.R.	BLSF0903	131
E. tereticornis	N. Mt. Malloy, N. Qld, Aust.	CSR11952	92
E. grandis	Crediton, Qld, Aust.	CSR11891	82
E. grandis	Atherton, Qld, Aust.	CSR12002	56
E. saligna	S. Calliope, Qld, Aust.	CSR12064	44
E. deglupta	Turrialba, C.R.	BLSF1466	44
E. tereticornis	S. W. Mt. Garnett, Qld, Aust.	CSR12181	41
E. citriodora	Dawson Range, Qld, Aust.	CSR12012	34
E. citriodora	Atherton, Qld, Aust.	CSR12379	34
E. camaldulensis	Petford, N. Qld, Aust.	CSR12139	33
E. saligna	Gladfield, Qld, Aust.	CSR11894	33
E. saligna	N. Raymond Terr. Aust.	CSR11605	32
E. cloeziana	N.E. Gympie, Qld, Aust.	CSR10691	30
E. alba	S. Maningrida, N.T, Aust.	CSR11113	20
E. tereticornis	Mt. Poverty, N. Qld, Aust.	CSR11955	19
E. camaldulensis	Katherine, N.T, Aust.	CSR12181	18
E. camaldulensis	Gibb River, W.A, Aust.	CSR12346	16
E. citriodora	Orosi, Cartago, C.R.	BLSF1465	13
E. cloeziana	N. Paluma, N. Qld, Aust.	CSR10270	11
E. cloeziana	Cardwell, Qld, Aust.	CSR09785	4
E. alba	Greenvale, Qld, Aust.	CSR11957	4
E. alba	S. Cooktown, N. Qld, Aust.	11669CSR	2

Cuadro 12. Volumen total de 10 procedencias de *Eucalyptus urophylla* a lo 6,5 años de edad en Santa Clara, San Carlos, Costa Rica.

Procedencia	Código	Volumen total (m3/ha)
S.W. Isla Lembata, Indonesia.	CTFT802770N	397
Región W. Isla Alor, Ind.	CTFT802808N	375
Mt. Lewotobi, Isla Flores, Ind.	CSR12896	373
Mt. Moena, Isla Alor, Ind.	CTFT802806N	291
Remexio, Isla Timor, Ind.	CTFT802793N	288
Mt. Mandiri, Isla Flores, Ind.	CSR12895	248
Mt Boleng, Isla Adonara, Ind.	CSR12898	222
Mt. Wuko, Isla Flores, Ind.	CSR12897	222
Región Central, Isla Alor, Ind.	CTFT802803N	218
Maubisse, Isla Timor, Ind.	CTFT802795N	166

Cuadro 13 Promedios de altura total (m), dap (cm) y sobrevivencia (%) de 23 procedencias de *Eucalyptus* a los 5 años de edad en Turrialba, Costa Rica.

Especie	Proc.	Altura total (m)	Especie	Proc.	dap (cm)	Especie	Proc.	Sobrev. (%)
E. grandis	GYM	19,0 a*	E. grandis	CRE	16,5 a	E. teret.	MAL	82 a
E. grandis	CRE	19,0 a	E. saligna	JVI	14,3 a	E. grandis	GYM	80 a
E. saligna	JVI	18,2 ab	E. grandis	GYM	14,1 a	E. alba	MAN	79 a
E. grandis	ATH	16,1 abc	E. grandis	ATH	13,4 a	E. deglupta	TUR	69 ab
E. citrid.	DAW	14,8 abc	E. teret.	MAL	12,5 a	E. saligna	JVI	69 ab
E. citrid.	ATH	14,4 bcd	E. citrid.	ATH	11,7 a	E. teret.	CAR	65 abc
E. teret.	MAL	14,2 bcd	E. citrid.	DAW	10,9 a	E. teret.	POV	65 abc
E. saligna	RAY	13,5 bcd	E. saligna	RAY	10,8 a	E. cloez.	GYE	60 abc
E. saligna	CAL	13,1 cde	E. saligna	CAL	10,7 a	E. saligna	CAL	58 abcd
E. deglupta	TUR	13,0 cde	E. saligna	GLA	10,2 a	E. camald.	PET	51 abcd
E. camald.	PET	12,8 cde	E. teret.	CAR	9,9 a	E. saligna	GLA	49 abcd
E. citrid.	ORO	12,8 cdef	E. camald.	PET	9,9 a	E. camald.	KAT	47 abcd
E. saligna	GLA	12,6 cdefg	E. deglupta	TUR	9,8 a	E. camald.	GIB	46 abcd
E. teret.	CAR	12,5 cdefg	E. citrid.	ORO	9,4 a	E. alba	GRE	43 bcd
E. cloez.	PAL	12,0 cdefgh	E. cloez.	GYE	9,1 a	E. saligna	RAY	39 bcd
E. cloez.	GYE	11,8 cdefgh	E. camald.	KAT	8,6 a	E. grandis	ATH	38 bcd
E. camald.	KAT	10,1 cdefgh	E. cloez.	PAL	8,4 a	E. citrid.	DAW	38 bcd
E. camald.	GIB	10,0 cdefghi	E. camald.	GIB	8,3 a	E. alba	COO	33 bcd
E. teret.	POV	8,6 efghi	E. teret.	POV	8,1 a	E. citrid.	ATH	33 bcd
E. alba	MAN	8,4 fghi	E. alba	MAN	7,6 a	E. grandis	CRE	31 cd
E. cloez.	CAR	8,1 ghi	E. cloez.	CAR	5,9 a	E. cloez.	CAR	27 d
E. alba	GRE	7,6 hi	E. alba	GRE	5,4 a	E. cloez.	PAL	24 d
E. alba	COO	5,9 i	E. alba	COO	4,6 a	E. citrid.	ORO	23 d

* Letras diferentes indican diferencias significativas al cinco por ciento (Prueba de Duncan)

(Fuente: Mesén, 1990)

Cuadro 14 Promedios de altura total (m) y dap (cm), y porcentaje de sobrevivencia de 10 procedencias de *E. urophylla* a los 6,5 años de edad en Santa Clara, Costa Rica.

Proc.	Altura total (m)	Proc.	dap (cm)	Proc.	Sobrev. (%)
REM	23,7	WAL	20,5	LEM	96
WAL	23,7	LEM	19,0	LEW	93
LEW	23,6	LEW	18,4	MAN	90
LEM	22,8	REM	18,2	MAU	90
MOE	21,3	MOE	17,5	MOE	89
MAN	20,2	MAN	16,5	BOL	88
CAL	20,2	CAL	16,4	WUK	88
WUK	19,9	BOL	16,3	CAL	80
BOL	18,9	WUK	15,9	WAL	75
MAU	17,9	MAU	14,3	REM	73

(Fuente: Mesén, 1990)

Cuadro 15. Volumen total de 8 procedencias de *Gmelina arborea* a lo 3 años de edad en Celulosa, Javillos, Turrialba, Costa Rica.

Procedencia	Código	Volumen total (m3/ha)
Jari, Para, Brasil	DAN4040	146
Manila, Siquirres, C.R.	BLSF1018	140
"A" Sri Lanka	DAN4067	134
Andhra Pradesh, India	DAN4066	119
Kao Yai, Saraburi, Tailandia	D1003/80	107
Meredumilli, Andhra Pradesh, India	DAN4058	71
Sankosh-1, Bengala Occid., India	DAN4045	64
Lambasingi, Andhra Pradesh, India	DAN4065	59

Fuente: Valerio, 1986.

Cuadro 16 **Promedios de altura total en metros (Alt), diámetro basal en cm (Dbas), y porcentaje de sobrevivencia (Sobrev), para las procedencias de *G. arborea* los 4 años de edad en Turrialba, Costa Rica.**

Proc	Alt	Proc	Dbas	Proc	Sobrev
BSF1018	20,5 a*	DAN4067	22,0 a	DAN4068	100 a
DAN4040	20,0 ab	DAN4040	21,6 a	D100380	100 a
DAN4067	19,2 ab	BSF1018	21,5 a	DAN4066	97 a
DAN4068	18,5 ab	D100380	21,2 a	DAN4040	97 a
D100380	18,2 b	DAN4066	21,1 a	DAN4065	93 a
DAN4066	18,0 bc	DAN4045	20,6 a	DAN4058	92 a
DAN4045	16,2 cd	DAN4068	19,5 a	BSF1018	91 a
DAN4058	15,1 d	DAN4058	18,6 a	DAN4067	91 a
DAN4065	14,4 d	DAN4065	18,0 a	DAN4045	89 a

* Letras diferentes indican diferencias significativas al cinco por ciento (Prueba de Duncan)

(Fuente: Mesén, 1999)

Cuadro 17. Volumen total de 13 procedencias de *Pinus oocarpa*, 2 procedencias d *P. tecunumanii* y 1 de *P. caribaea* a los 6,5 años de edad, promedio de cuatro sitios* húmedos de Costa Rica.

Procedencia	Código	Volumen tot (m3/ha)
Yúcul, Nicaragua.(*P. tecu*)	K1280276	243
M. P. R. Belice (*P. tecu*)	1174	213
M. P. R. Belice (*P. cari*)	3073	193
Dipilto, Nicaragua *(P.ooca)*	K1160675	174
Villa Santa, Honduras *(P.ooca)*	K0850273	161
La Unión, Honduras *(P.ooca)*	K0781272	142
Cusmapa, Nicaragua *(P.ooca)*	K1170775	140
San Juan, Honduras *(P.ooca)*	K0980474	139
Mal Paso, Guatemala *(P.ooca)*	K1140475	130
Cerro El Bonete, Nicaragua *(P.ooca)*	K1030774	127
Pimientilla, Honduras *(P.ooca)*	K0990574	117
El Zamorano, Honduras *(P.ooca)*	K0860373	112
Valle Bonito, Honduras *(P.ooca)*	K1020374	103
El Pinalón, Guatemala *(P.ooca)*	K1130575	102
Lagunilla, Guatemala *(P.ooca)*	K1120875	100
Pueblo Viejo, Guatemala *(P.ooca)*	K1110775	48

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*Sitios San Isidro del General, La Suiza, Javillos y San Juan Sur de Turrialba

Cuadro 18. Diametro y altura total de 9 procedencias de *Pinus oocarpa* y 2 procedencias de *P. tecunumanii* a los 7 años de edad promedio en cuatro sitios* húmedos de Costa Rica.

Procedencia	Código	DAP (cm)	Altura tot (m)
M. P. R. Belice (*P. tecu*)	1174	21,0	16,6
Yúcul, Nicaragua.(*P. tecu*)	K1280276	20,7	16,7
Culmí, Honduras (*P. cari*)	K0573771	19,7	15,0
Alamicamba, Nic. (*P. cari*)	K1060674	19,3	15,0
Brus Laguna, Hond. (*P. cari*)	K0583871	19,1	14,6
M. P. R. Belice (*P. cari*)	3073	18,8	14,5
Melinda, Belice (*P. cari*)	K1071574	18,7	14,2
Río Coco, Nicaragua (*P. cari*)	K0222470	18,7	13,7
Guanaja, Honduras (*P. cari*)	K0242870	18,6	13,2
Poptún, Guatemala (*P.cari*)	K0252970	18,6	15,0
Los Limones, Hond. (*P. cari*)	K1242475	18,1	13,9

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*Sitios San Isidro del General, Volcan de Buenos Aires, Javillos y Turrialba

Cuadro 19 Promedios de dap (cm) de nueve procedencias de *P. caribaea* y dos procedencias de *P. tecunumanii* a los siete años de edad en los sitios 1 a 4, y a los tres años de edad en los sitios 5 y 6; porcentaje de sobrevivencia (Sobrev) en el sitio 6, Santa Cruz

1.Celulosa		2.Florencia		3.Volcán		4.San Isidro		5.Sta Clara		6. Sta Cruz		
Proc.	dap	Proc.	dap	Proc.	dap	Proc.	dap	Proc.	dap	Proc.	dap	Sobrev.
MPT	22,4 a	MPT	22,3 a*	YUC	25,3 a	CUL	23,8 a	MPT	11,9 a	POP	6,0 a	73
YUC	22,3 a	ALA	17,4 b	MPT	23,7 a	YUC	22,4 a	YUC	11,4 ab	GUA	5,8 a	83
CUL	21,6 a	MPC	16,3 bc	LIM	19,2 b	MPT	21,4 a	CUL	11,0 abc	MPC	5,5 ab	78
BRU	21,6 a	YUC	16,3 bc	ALA	18,5 b	ALA	20,9 a	ALA	10,8 bcd	BRU	5,3 abc	73
MEL	20,8 a	CUL	15,9 bc	BRU	17,5 b	RIO	20,7 a	BRU	10,2 cde	MEL	5,2 abc	57
RIO	20,2 a	GUA	15,1 bc	POP	17,5 b	MEL	20,3 a	GUA	10,2 cde	ALA	5,0 abc	35
POP	19,9 a	POP	14,8 bc	MPC	17,5 b	BRU	19,9 a	MPC	10,2 cde	CUL	4,9 abc	65
GUA	19,9 a	BRU	14,2 bc	CUL	17,5 b	MPC	19,3 a	POP	9,7 de	MPT	4,6 abc	22
MPC	19,5 a	RIO	13,9 bc	MEL	17,1 b	POP	10,9 a	RIO	9,5 e	RIO	3,8 bcd	57
ALA	19,1 a	MEL	13,5 bc	GUA	16,9 b	GUA	18,8 a	LIM	9,4 e	LIM	3,7 cd	46
LIM	17,2 a	LIM	12,9 c	RIO	16,8 b	LIM	18,1 a	MEL	9,2 e	YUC	2,4 d	58

* Letras diferentes indican diferencias significativas al cinco por ciento (Prueba de Duncan)

(Fuente: Mesén, 1990)

Cuadro 20 Promedios de altura total (m) de nueve procedencias de *P. caribaea* var *hondurensis* y dos procedencias de *P. tecunumanii* a los siete años de edad en los sitios 1 a 4, y a los tres años de edad en los sitios 5 y 6.

1.Celulosa		2.Florencia		3.Volcán		4.San Isidro		5.Sta Clara		6.Sta Cruz	
Proc.	Alt.	Proc.	Alt.	Proc.	Alt.	Proc.	Alt.	Proc.	Alt.	Proc.	Alt
YUC	18,3 a*	MPT	16,1 a	MPT	15,8 a	YUC	18,3 a	MPT	8,0 a	MPT	3,5 a
MPT	17,5 ab	MPC	13,6 b	YUC	15,4 a	MPT	17,2 a	YUC	7,9 a	POP	3,3 a
POP	16,6 abc	ALA	13,4 b	POP	14,0 b	MPC	17,0 a	ALA	6,8 b	GUA	3,3 a
CUL	16,6 abc	CUL	13,3 b	LIM	13,7 bc	POP	16,9 a	BRU	6,5 bc	MPC	3,1 ab
BRU	16,4 bc	POP	12,8 b	CUL	13,1 bc	ALA	16,8 a	CUL	6,2 bc	BRU	3,0 abc
MEL	16,1 bc	RIO	12,5 b	MEL	12,9 bc	BRU	16,6 a	GUA	6,1 cd	ALA	3,0 abc
RIO	15,9 bc	YUC	12,5 b	ALA	12,8 bc	RIO	16,5 a	MPC	6,0 cd	CUL	2,9 abc
ALA	15,9 bc	GUA	12,4 b	MPC	12,7 bc	CUL	16,4 a	RIO	5,5 de	MEL	2,5 bcd
MPC	15,6 cd	BRU	12,1 b	BRU	12,1 c	LIM	16,3 a	LIM	5,3 de	RIO	2,5 bcd
GUA	15,2 cd	LIM	12,1 b	GUA	10,0 d	MEL	15,7 a	POP	5,3 e	YUC	2,3 cd
LIM	14,2 d	MEL	11,6 b	RIO	9,7 d	GUA	14,9 a	MEL	5,2 e	LIM	2,0 d

* Letras diferentes indican diferencias significativas al cinco por ciento (Prueba de Duncan)

(Fuente: Mesén, 1990)

Cuadro 11 Promedios de altura total en metros (Alt) de trece procedencias de *P. oocarpa*, dos procedencias de *P. tecunumanii* y una procedencia de *P. caribaea* var. *hondurensis* a los 6,5 años de edad en cuatro sitios de Costa Rica. (Fuente: Corea, 1989)

7.Celulosa		8.San Juan Sur		9.San Isidro		10.La Suiza	
Proc.	Alt.	Proc.	Alt	Proc.	Alt.	Proc.	Alt
YUC	16,3 a*	YUC	15,3 a	MPT	12,6 a**	DIP	14,7 a**
MPT	15,9 a	UNI	15,1 a	YUC	12,4 a	YUC	14,2 ab
UNI	15,2 ab	VST	14,7 a	MPC	11,7 ab	MPT	14,1 abc
DIP	14,6 ab	DIP	14,6 a	DIP	11,6 ab	VST	13,0 abc
MPC	14,6 ab	PIM	14,6 a	UNI	11,4 ab	SJU	12,9 abc
VST	14,5 ab	CBO	14,4 a	MPA	11,3 ab	MPC	12,5 abcd
PIM	14,3 ab	ZAM	14,4 a	CUS	11,2 ab	VBO	12,5 abcd
SJU	14,2 ab	MPT	14,4 a	VST	11,1 ab	CBO	11,4 abcd
MPA	13,9 ab	MPC	14,2 a	ZAM	11,1 ab	CUS	10,9 abcd
ZAM	13,9 ab	CUS	13,9 a	CBO	11,0 ab	PIM	10,8 abcd
CUS	13,8 ab	VBO	13,9 a	LAG	11,0 ab	PVI	9,6 bcd
CBO	13,6 ab	MPA	13,9 a	SJU	10,7 ab	MPA	9,5 cd
LAG	13,3 ab	SJU	13,8 a	PVI	10,5 ab	PIN	9,4 cd
PIN	13,0 abc	PIN	12,8 a	PIN	10,3 ab	UNI	9,4 d
VBO	12,6 bc	LAG	12,7 a	PIM	9,4 b	LAG	8,2 d
PVI	9,9 c	PVI	12,6 a	VBO	9,1 b		

*,** Letras diferentes indican diferencias significativas al cinco por ciento (*Prueba de Bonferroni; **Prueba de Tukey)

Cuadro 12 Promedios de dap (cm) de trece procedencias de *P. oocarpa*, dos procedencias de *P. tecunumanii* y una procedencia de *P. caribaea* var. *hondurensis* a los 6,5 años de edad en cuatro sitios de Costa Rica. (Fuente: Corea, 1989)

7.Celulosa		8.San Juan Sur		9.San Isidro		10.La Suiza	
Proc.	dap	Proc.	dap	Proc.	dap	Proc.	dap
YUC	18,5 a*	YUC	20,3 a**	YUC	16,5 a**	MPC	16,9 a**
MPC	17,9 ab	DIP	19,2 ab	MPT	15,5 ab	YUC	16,3 ab
MPT	17,6 abc	MPT	19,9 ab	MPC	15,3 ab	DIP	16,0 abc
MPA	16,9 abc	MPC	18,9 ab	MPA	13,1 abc	MPT	15,0 abcd
DIP	16,8 abc	MPA	18,6 ab	DIP	12,6 abc	VST	14,1 abcd
UNI	16,7 abc	UNI	17,6 ab	CBO	12,1 abcd	VBO	14,1 abcd
VST	16,5 abc	CBO	17,0 ab	CUS	12,1 abcd	CBO	13,9 abcd
CUS	16,3 abc	VST	17,0 ab	UNI	11,8 bcd	SJU	13,7 abcd
PIM	15,5 abc	SJU	16,9 ab	VST	11,6 bcd	CUS	13,0 abcd
ZAM	15,4 abc	PIM	16,8 ab	LAG	11,5 bcd	PIM	12,4 abcd
PIN	15,3 abc	VBO	16,3 ab	PIN	11,1 bcd	PVI	12,0 abcd
SJU	15,2 abc	ZAM	16,1 ab	SJU	10,7 cd	MPA	11,5 abcd
LAG	14,9 abc	PIN	15,8 ab	ZAM	10,5 d	PIN	10,8 bcd
CBO	14,4 abc	CUS	15,6 ab	PVI	10,5 d	UNI	10,3 cd
VBO	13,5 bc	LAG	14,4 b	VBO	8,9 d	LAG	9,9 d
PVI	13,5 c	PVI	14,4 b	PIM	8,8 d		

*, ** Letras diferentes indican diferencias significativas al cinco por ciento *Prueba de Bonferroni, **Prueba de Tukey)

(Fuente: Corea, 1989)

Cuadro 23 Volumen sin corteza (m3ha^{-1}) de trece procedencias de *P. oocarpa*, dos procedencias de *P. tecunumanii* y una procedencia de *P. caribaea* var. *hondurensis* a los 6,5 años de edad en cuatro sitios en Costa Rica. (Fuente: Corea, 1989)

7.Celulosa			8.San Juan Sur			9.San Isidro			10.La Suiza		
Proc.	VSC		Proc.	VSC		Proc.	VSC		Proc.	VSC	
YUC	180,9	a*	YUC	207,6	a**	YUC	134,7	a**	YUC	131,6	a**
MPT	173,8	a	MPT	191,2	ab	MPT	102,8	ab	MPT	123,7	ab
MPC	149,7	ab	DIP	172,0	abc	MPC	82,0	ab	DIP	113,7	abc
UNI	128,9	abc	MPC	152,4	abc	DIP	74,3	bc	MPC	106,5	abcd
VST	122,7	abc	VST	144,8	abc	MPA	72,1	bc	SJU	97,6	abcd
DIP	113,9	abc	SJU	138,5	abc	CUS	63,0	bc	VST	95,8	abcd
SJU	101,7	bc	UNI	130,9	abcd	CBO	58,4	bc	CBO	74,2	abcd
CUS	100,4	bcd	CBO	116,9	abcd	VST	56,7	bc	VBO	72,8	abcd
PIM	96,6	bcd	CUS	115,9	abcd	LAG	51,2	bc	CUS	71,9	abcd
LAG	90,8	bcd	MPA	107,5	bcd	UNI	48,3	bc	PIM	68,3	abcd
PIN	87,5	bcd	ZAM	104,4	bcd	SJU	43,4	c	MPA	49,1	bcd
MPA	87,3	bcd	PIM	104,1	bcd	PIN	40,3	c	PVI	43,6	cd
ZAM	85,2	bcd	VBO	98,1	bcd	ZAM	37,0	c	PIN	43,6	cd
CBO	82,9	bcd	PIN	82,1	cd	PVI	35,8	c	LAG	31,5	d
VBO	70,8	cd	LAG	81,0	cd	PIM	30,0	c	UNI	31,3	d
PVI	30,9	d	PVI	32,2	d	VBO	26,0	c			

*, ** Letras diferentes indican diferencias significativas al cinco por ciento (*Prueba de Bonferroni, ** Prueba de Tukey)

Cuadro 24 Análisis combinado de los sitios 7 a 10 de *Pinus oocarpa* para altura total (m), dap (cm) y volumen sin corteza (VSC, m3ha^{-1}) a los 6,5 años de edad (Fuente: Corea, 1989)

Proc.	Altura total		Proc.	dap		Proc.	VSC	
YUC	14,7	a*	YUC	17,9	a	YUC	166,6	a
MPT	14,3	ab	MPC	17,1	ab	MPT	150,8	ab
UNI	13,8	abc	MPT	16,8	abc	MPC	122,8	bc
DIP	13,6	abcd	DIP	16,0	abcd	DIP	116,3	bc
MPC	13,5	abcd	MPA	15,4	abcde	VST	103,8	cd
VST	13,4	abcd	VST	14,7	bcdef	SJU	92,2	cd
ZAM	13,1	abcd	UNI	14,5	cdef	UNI	91,4	cd
MPA	13,0	abcd	CUS	14,2	def	CUS	87,7	cd
CBO	13,0	abcd	CBO	14,2	def	CBO	81,9	cd
CUS	13,0	abcd	SJU	14,0	def	MPA	81,5	cd
SJU	12,9	abcd	ZAM	13,6	def	PIM	72,9	d
PIM	12,8	bcd	PIN	13,4	ef	ZAM	70,2	de
LAG	12,3	cde	PIM	13,3	ef	LAG	66,6	de
PIN	12,0	de	LAG	13,0	ef	PIN	64,0	de
VBO	11,9	de	VBO	12,8	f	VBO	63,1	de
PVI	11,0	e	PVI	12,4	f	PVI	31,3	e

* Letras diferentes indican diferencias significativas al cinco por ciento (Prueba de Bonferroni)

(Fuente: Corea, 1989n)

Cuadro 5 Análisis de varianza y medias marginales poblacionales de supervivencia (SUP), altura (ALT), diámetro (DAP) y área basal (ABA) agrupadas según Bonferroni (alfa = 0,05)

SUP (%)			ALT1 (m)*			ALT2 (m)*			DAP (cm)			ABA (m²/ha)		
Proc.	Media	Bonf.	Proc.	Media	Bonf.	Proc.	Media	Bonf.	Proc.	Media	Bonf.	Proc.	Media	Bonf.
YUCN	85,2		YUCN	14,7		YUCN	14,6		YUCN	17,9		YUCN	37,6	
CUSN	83,1		MPTB	14,3		MPTB	14,3		MCHB	17,1		MPTB	33,4	
MPTB	81,6		UNIH	13,8		DIPN	13,9		MPTB	16,8		MCHB	31,3	
MCHB	78,1		DIPN	13,6		VSTH	13,3		DIPN	16,0		DIPN	27,2	
VSTH	77,0		MCHB	13,5		MCHB	13,2		MPAG	15,4		VSTH	24,4	
DIPN	76,8		VSTH	13,4		SJUH	12,9		VSTH	14,7		CUSN	22,7	
SJUH	76,7		ZAMH	13,1		UNIH	12,7		UNIH	14,5		UNIH	21,8	
PIMH	75,8		MPAG	13,0		CBON	12,6		CUSN	14,2		SJUH	21,8	
CBON	72,9		CBON	13,0		CUSN	12,5		CBON	14,2		MPAG	21,8	
UNIH	72,8		CUSN	13,0		PIMH	12,3		SJUH	14,0		CBON	21,2	
VBOH	72,5		SJUH	12,9		MPAG	12,1		ZAMH	13,6		PIMH	19,0	
LAGG	71,9		PIMH	12,8		VBOH	12,0		PING	13,4		ZAMH	17,5	
MPAG	69,9		LAGG	12,3		PING	11,4		PIMH	13,3		LAGG	17,2	
ZAMH	68,6		PING	12,0		LAGG	11,3		LAGG	13,0		PING	17,0	
PING	65,5		VBOH	11,9		PVIG	10,7		VBOH	12,8		VBOH	16,6	
PVIG	47,3		PVIG	11,0					PVIG	12,4		PVIG	8,8	

Análisis de varianza : probabilidad de una "F" mayor

Sit.	0.000	Sit.	0.000	Sit.	0.000	Sit.	0.000	Sit.	0.000
B(S)	0.016	B(S)	0.000	B(S)	0.000	B(S)	0.000	B(S)	0.017
Proc.	0.000	Proc.	0.000	Proc.	0.000	Proc.	0.000	Proc	0.000
P*S	-	P*S	0.126	P*S	0.004	P*S	-	P*S	-
Dren.	0.000	Dren.	0.004	Dren.	0.002	Dren.	0.033	Dren.	0.000

* Excluye el sitio La Suiza

* Excluye la procedencia Zamorano

(Fuente: Corea, 1989)

Cuadro 26 Análisis combinado de los sitios 1 a 4 para *P. caribaea* en altura total y dap a los 7 años de edad.

Proc.	Altura total (m)	Proc.	dap (cm)
YUC	16,7 a*	MPT	21,0 a
MPT	16,6 a	YUC	20,7 a
POP	15,0 b	CUL	19,7 b
CUL	15,0 b	ALA	19,3 bc
ALA	15,0 b	BRU	19,1 bc
BRU	14,6 bc	MPC	18,8 bcd
MPC	14,5 bc	MEL	18,7 cd
MEL	14,2 bc	RIO	18,7 cd
LIM	13,9 cd	GUA	18,6 cd
RIO	13,7 cd	POP	18,6 cd
GUA	13,2 d	LIM	18,1 d

* Letras diferentes indican diferencias significativas al cinco por ciento (Prueba de Duncan)

(Fuente: Mesén, 1990)

Cuadro 27. Productividad bruta de las mejores procedencias por especie en los ensayos y porcentaje de superioridad sobre el promedio general.

Especie	Procedencia	Productividad bruta (m3/ha/año)	Superioridad sobre el promedio en el ensayo
Acacia mangium	Abergowrie, Aust.	47	90%
Acacia mangium	Claudie River, Aust.	11	40%
Cordia alliodora	San Francisco, Hond.	11	89%
Cordia alliodora	Santa Clara, C.R.	24	88%
Cordia alliodora	Nueva Guinea, Nic	9	85%
Eucalyptus grandis	Gympie, Aust.	31	276%
Eucalyptus urophyla	S. W. Isla Lembata, Aust.	61	42%
Gmelina arborea	Jari, Brasil	49	39%
Gmelina arborea	Manila, Siquirres	47	33%
Pinus tecunumanii	Yúcul, Nic.	37	26%*
Pinus tecunumanii	Yúcul, Nic	37	98%+

* Superioridad con respecto a *P. caribaea*
\+ Superioridad con respecto a *P. oocarpa*

Mejoramiento genético forestal para finqueros pequeños y medianos. I. Resultados y experiencias de 17 años de investigación del CATIE en Costa Rica

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Resumen

Se resumen los resultados y experiencias del Proyecto Mejoramiento Genético Forestal del CATIE desde su inicio en 1977, cubriendo los siguientes temas: experimentación "en finca" vs "en estación", magnitud de diferencias entre procedencias; traslado de semilla de especies nativas; selección de árboles plus; comportamiento de germoplasma importado vs. germoplasma local de especies exóticas; diseño experimental; incidencia de interacción genotipo-ambiente; niveles de variación genética y heredabilidad; resultados de ensayos genéticos, rentabilidad del mejoramiento genético forestal de escala pequeña.

Introducción

El Proyecto Mejoramiento Genético Forestal del CATIE inició sus actividades en 1977. Desde entonces, se ha generado una vasta cantidad de información, incluyendo no solamente resultados de ensayos de campo, sino también información de relevancia a la planificación y diseño de programas de mejoramiento. En el presente artículo se describen estas experiencias. En el artículo siguiente (Cornelius, 1995), se discuten las implicaciones de estas y otras consideraciones para el manejo de recursos genéticos forestales en América Central.

Experimentación "en finca" vs. "en estación experimental"

Prácticamente todos los ensayos del Proyecto MGF, más de cien hasta la fecha, han sido establecidos en diferentes tipos de finca. Las ventajas y desventajas de este tipo de experimentación con respecto a la experimentación en estaciones experimentales se resumen en el Cuadro 1. Esta modalidad de trabajo tiene importantes ventajas estadísticas, permite un enfoque más participativo que en el caso de los programas exclusivamente "en estación", y obviamente evita la necesidad de contar con una gran área experimental. En la experiencia del Proyecto, los factores más determinantes en el éxito de ensayos "remotos" son el interés del colaborador y las características de la especie. Las especies mas "delicadas" como *Bombacopsis quinata*, *Eucalyptus* spp. son más dificiles de manejar "a distancia" que las especies más robustas, como *Acacia mangium*, *Gmelina arborea* y *Vochysia guatemalensis*. Sin embargo, para cualquier especie el enfoque "en finca" depende para su éxito de la disponibilidad de vehículos y combustibles, a menos que se trate de un programa netamente local.

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Cuadro 1. Comparación de la experimentación genética forestal "en finca" vs. experimentación "en estación"

Atributo / función	Mejor "en estación"	Mejor "en finca"	Comentarios
1. Aspectos estadísticos			
precisión de experimentos	√	*	Sin embargo, las experiencias del Proyecto MGF demuestran que no existe la menor duda que experimentos "en finca" bien diseñados son perfectamente capaces de detectar diferencias entre genotipos.
representatividad con respecto a los sitios de plantación	*	√	Sin embargo, depende del manejo que se practica en la estación. A veces las estaciones experimentales forestales son muy parecidas las fincas forestales operacionales.
estimación de interacción genotipo-ambiente	*	√	A menos que existan varias estaciones en diferentes condiciones, no se puede estimar la interacción-genotipo ambiente con respecto a variaciones macroambientales.
2. Aspectos administrativos y financieros	√	*	
facilidad de control de mantenimiento etc.	√	*	Se puede visitar la estación todos los días, mientras frecuentemente pueden pasar meses entre visitas a fincas individuales. A veces los finqueros no cumplen con sus responsabilidades.
costos	*√	*√	Los ensayos "en finca" normalmente son mantenidos por los mismos finqueros, mientras en la estación los ensayos tienen que ser mantenidos por empleados del programa o proyecto. Sin embargo en el caso de ensayos "en finca" los costos de monitoreo y establecimiento son más altos.
seguridad	*√	*√	Existe más probabilidad de perder un ensayo individual "en finca" que "en estación". Sin embargo, en el caso de la experimentación "en finca" existe la posibilidad de perder varios ensayos a la vez debido a incendios, al precarismo, o a cambios en políticas institucionales
3. Demostración	*√	*√	Es más facil demostrar resultados "en estación" que en finca. Sin embargo, los resultados pueden tener menos credibilidad debido a que los sitios son menos representativos de condiciones operacionales. De todos modos muchos tipos de ensayos genéticos no se prestan para fines demostrativos. Para demostrar resultados es más efectivo usar parcelas demostrativas.
4. Producción de semilla	√	*	Normalmente es más fácil estimular alta producción y recolectar semilla "en estación" que en una multiplicidad de diferentes fincas.
5. Distribución y uso de semilla mejorada	*√	*√	Depende de las características específicas del programa. Si los usuarios (finqueros) están involucrados en el programa de experimentación y producción de semilla "en finca", es probable que se logre más fácilmente la aceptación del germoplasma producido que cuando la semilla se distribuye de un centro de producción lejano.

Diferencias entre procedencias: aspectos generales

La experiencia del Proyecto ha demostrado que existen importantes diferencias entre procedencias de las especies comúnmente plantadas en América Central. Es importante destacar que esta conclusión aplica no solo a las especies exóticas, sino también a las nativas. Algunos ejemplos de este fenómeno en las especies nativas se describen en el Cuadro 2. Otros ejemplos, incluyendo de especies exóticas, se incluyen en el Cuadro 7. La magnitud de variación entre procedencias no depende de si una especie es nativa o exótica, sino en gran medida de las diferencias ambientales entre los sitios de recolección de semilla. Cuando estas diferencias son grandes, puede haber grandes diferencias entre las procedencias, siempre y cuando las dos procedencias no estén tan cerca como para permitir un intercambio constante de polen y/o semillas.

Traslados de semilla de especies nativas

Con base a los resultados del Proyecto es evidente (Cuadro 2) que en América Central el traslado de semilla de especies nativas a zonas muy distintas a su procedencia puede provocar el fracaso de las plantaciones.

Cuadro 2. Ejemplos de diferencias importantes entre procedencias de especies nativas a América Central

Especies	Ubicación del ensayo[1]	Resultados
Alnus acuminata	Sta. Cruz de Turrialba	Una procedencia guatemalteca creció más lentamente y exhibió mayor susceptibilidad al ataque de *Scolytodes alni* que las procedencias costarricences incluidas (Cornelius y Masís, 1995)
Cordia alliodora	Guápiles, zona atlántica[2]	Las procedencias de la zona atlántica crecieron 95% más rápidamente que una procedencia de Nicoya (zona seca) durante los primeros 2 años (sin publicar)
Pinus patula ssp. *tecunumanii*	varios	La procedencia Yucul, Nicaragua de *Pinus patula* ssp. *tecunumanii* se demostró superior en crecimiento a otras fuentes de la misma especies de Belice (Corea, 1989) y Honduras (Cornelius, Hernández y Apedaile, 1995)
Vochysia guatemalensis	Sarapiquí, zona atlántica	Hasta los 42 meses dos procedencias costarricenses crecieron 10% más rápidamente en dap que procedencias guatemaltecas y hondureñas (Cornelius y Masís, 1994)

[1] Todo Costa Rica; [2] parcela demostrativa

La selección de árboles plus

El Proyecto ha iniciado todos sus programas de selección dentro de procedencias con un ciclo de selección de árboles plus. Se concentró principalmente en la selección por características de forma, especialmente rectitud del fuste. En el caso de la selección en plantaciones y rodales naturales coetáneos (*Alnus acuminata*), se procuró también que el diámetro fuera igual o mayor que el promedio del rodal. En la mayoría de los casos, se incluyó en los ensayos de progenie un testigo no seleccionado. En el Cuadro 3, se resumen algunos resultados de esta experiencia. En rodales naturales, hay poca evidencia de que la selección fenotípica, incluyendo la selección por forma, haya sido efectiva, mientras en el caso de la selección en plantaciones parece que la selección fenotípica sí ha sido efectiva. Estos resultados están de acuerdo con experiencia a nivel mundial (Cornelius, 1994b). Vale la pena recalcar que los datos en el cuadro 3 probablemente subestiman considerablemente las ganancias en productividad realizables a través de la selección de árboles plus, ya que no se aplicó una presión de selección muy fuerte.

Comportamiento de germoplasma importado vs germoplasma local de especies exóticas

En varios de los ensayos de procedencias y descendencias de especies exóticas del Proyecto han sido incluídos tantos lotes de semilla importados como fuentes locales. El comportamiento relativo del material importado y local y se resumen en el Cuadro 4. En todos los casos, el material local ha sido mejor que el material recién introducido. Esto no significa que no vale la pena probar nuevo material o que no vale la pena hacer pruebas de procedencias si ya existen fuentes locales. En otros casos, puede ser que la fuente local se originó de una procedencia nativa mala o, por lo menos, no de las mejores. Sin embargo, por otra parte estos resultados sugieren que no se deben despreciar fuentes locales, ni asumir que fuentes importadas - aunque sean de huertos semilleros - sean superiores en condiciones locales.

Diseño experimental

En casi todos los experimentos de campo establecidas por el Proyecto, se ha utilizado el diseño tradicional de bloques completos aleatorios. Cuando hay muchos (>45) tratamientos, este diseño requiere de bloques muy grandes, y frecuentemente es prácticamente imposible lograr homogeneidad ambiental dentro del bloque, particularmente en sitios experimentales "en finca". A pesar de esto, en la gran mayoría de los experimentos analizados hasta la fecha, se nota un efecto muy fuerte de bloque, lo cual implica que definitivamente vale la pena utilizar un diseño con bloques y no un diseño completamente aleatorizado.

Muchos de los ensayos de progenies del Proyecto tienen una área de 2,5 ha-3,0 ha, lo cual permite establecer suficientes (8-9) repeticiones aun con parcelas relativamente grandes (5-6, siguiendo las normas del Instituto Forestal de Oxford y CAMCORE, respectivamente). Sin embargo, recientemente ha sido más difícil encontrar áreas tan extensas, por lo cual se empezó a trabajar en áreas de 1,5-2,0 ha. Como respuesta a este cambio, se bajó a tres el número de árboles por parcela. La parcela más pequeña permite el establecimiento de más repeticiones por sitio, y también ofrece ventajas valiosas en cuanto a la ubicación de los bloques. Con bloques más pequeños, es mucho más fácil lograr la homogeneidad ambiental dentro del bloque.

Alrededor del 25% de los ensayos del Proyecto son ensayos de procedencias / descendencias tipo "bloque compacto", establecido en colaboración con CAMCORE u OFI. Aunque este tipo de ensayo proporciona mucha información de utilidad, también tiene defectos. Por lo general, el número de procedencias que se pueden incluir es poco - dado

Cuadro 3. Resultados de selección de árboles plus por el Proyecto MGF en Costa Rica

Especie / procedencia	Ensayo^1	Característica		Material seleccionado mejor (%)	Material no seleccionado mejor (%)
		seleccionada	medida		
1.Selecciones en poblaciones naturales					
Alnus acuminata, División	Sta. Cruz de Turrialba	dap y altura^2, rectitud del fuste	rectitud (34 meses)	igual	igual
"	"	dap y altura^2, rectitud del fuste	índice de volumen^3 (34 meses)	*	√ (22%)
Cordia alliodora, San Carlos	Talamanca	rectitud	rectitud (52 meses)	√ (11%)	*
Cordia alliodora, Talamanca	"	"	"	*	√ (27%)
Cordia alliodora, Turrialba	"	"	"	√ (12%)	*
Vochysia guatemalensis San Miguel	Sarapiquí	"	rectitud (42 meses)	igual	igual
2.Selecciones en plantacioness					
Alnus acuminata, Prusia	Sta. Cruz de Turrialba	dap y altura^2, rectitud del fuste	rectitud (34 meses)	√ (3%)	*
"	"	dap y altura^2, rectitud del fuste	índice de volumen^2 (34 meses)	√ (2%)	*
Cupressus lusitanica, población base C.R.	"	dap y altura^2, rectitud del fuste	índice de volumen^2 (28 meses)	√ (50%)	*
Eucalyptus deglupta, población base C.R.	varios	dap y altura^2, rectitud del fuste	altura, 16 meses	√ (5%)	*
Gmelina arborea, población base C.R.	varios	dap y altura^2, rectitud del fuste	dap, 19-32 meses	√ (3%)	*
"	"	"	rectitud, 19-32 meses	√ (7%)	*

[1] Todos Costa Rica; [2] promedio del rodal; [3] 0.5altura x d≤/4

que es necesario mantener las familias en parcelas separadas -, mientras por otra parte el número de familias por procedencia es normalmente demasiado bajo como para pemitir estimaciones definitivas de los parámetros genéticos. En general, hay tanto que ganar a nivel de procedencia que no se justifica fácilmente la omisión de la fase de ensayos de procedencias tradicionales.

Cuadro 4. Comportamiento relativo de fuentes importadas y locales de especies exóticas

Especies	Característica	Fuente local: descripción si es superior (√) o inferior (*)	Fuente importada: descripción si es superior (√) o inferior (*)	Referencia
Cupressus lusitanica	altura, 28 meses	progenie de 44 árboles plus √ (24%)	progenie de un huerto semillero clonal (Arcadia, Colombia) *	Cornelius y Baeza, 1995
Eucalyptus deglupta	altura, 16 meses	progenie de 48 árboles plus √ (6%)	progenie de un huerto semillero, Papúa *	Cornelius, Corea y Mesén, 1995
Eucalyptus saligna	índice de volumen²	procedencia local Juan Viñas √ (250%)	promedio global de las procedencias Gladfield, S. Calliope (Queensland) y N. Raymond Terrace, Nuevo Gales del Sur *	Mesén, 1990
Gmelina arborea	volumen por hectárea	procedencia local, Siquirres √ (52%)	promedio de seis procedencias de la India, Sri Lanka y Tailandia *	Valerio, 1986
	rectitud	procedencia local, Siquirres √ (21%)	promedio de seis procedencias de la India, Sri Lanka y Tailandia *	Valerio, 1986

¹todos Costa Rica; ² 0.5altura x d≤/4

La interacción genotipo-ambiente

En casi cualquier juego de ensayos genéticos, existe la interacción genotipo-ambiente, es decir que las diferencias entre genotipos incluidos no se mantienen exactamente igual sobre todos los sitios. Sin embargo, la única interacción de interés práctico se da cuando los genotipos que son los mejores en un sitio no son los mejores en uno o más otros sitios. En estos casos, la aplicación de resultados de experimentos en un solo sitio puede provocar pérdidas en productividad de las plantaciones. Por lo tanto, resulta interesante resumir las experiencias del Proyecto en cuanto a la ocuriencia de interacciones de este tipo. Estas experiencias, resumidas en en el Cuadro 5, indican que a veces no hay interacciones. En tales casos, se podría decir, con anterioridad, que se pudo haber utilizado sólo un sitio. El problema, sin embargo, es que la ocurriencia de la interacción genotipo-ambiente no es predecible, y por lo tanto **sólo después de realizar ensayos en varios sitios es posible concluir que hubiera sido posible prescindir de varios de ellos.** Por lo tanto es inescapable la conclusión que para lograr resultados definitivos y plenamente confiables se necesita más de un sitio, particularmente cuando la especie en cuestión se planta en diferentes condiciones macroambientales.

Niveles de variación genética y parámetros genéticos en especies estudiadas hasta la fecha

En general la heredabilidad en especies forestales para las características de interés prácticamente universales como rectitud del fuste, altura, dap y volumen por árbol está en el rango 0,1-0,3, mientras el coeficiente de variación genética aditiva (CVGA) típicamente tiene valores entre 5%-15% (Cornelius, 1994a). El CVGA mide la cantidad de variación genética como porcentaje del promedio genotípico, mientras la heredabilidad mide la magnitud de esta variación en relación a la variación total fenotípica. Hasta la fecha, el Proyecto ha producido estimaciones de estos parámetros para las siguientes especies: *Alnus acuminata*, *Cupressus lusitanica*, *Eucalyptus deglupta*, *Pinus caribaea* var. *hondurensis*, *Gmelina arborea* y *Vochysia guatemalensis*. Estas estimaciones se presentan en el Cuadro 6. Resulta interesante observar que. por lo general, las tendencias son muy parecidas a las tendencias generales mencionadas, aunque estas últimas se basan principalmente en especies coníferas. Sólo un valor de heredabilidad parece particularmente inusual (heredabilidad de 0,47 para rectitud, *Pinus caribaea*), y sólo dos valores de CVGA (22,5% para altura de *E. deglupta* en

Cuadro 5. Presencia de interacción genotipo-ambiente de importancia[1] en los experimentos del Proyecto MGF en Costa Rica

Especies	Tipo de ensayo / número de sitios	Característica y presencia o no de interacción importante[1]	Fuente	Notas
Acacia mangium	procedencia 2 sitios	altura, dap no	Mesén, 1990	
Eucalyptus deglupta	progenie 3 sitios	altura no	Cornelius et al. 1995	
Gmelina arborea	progenie 4 sitios	rectitud, dap no	Cornelius y Hernández, 1995	
Pinus caribaea var. *hondurensis*	procedencias 6 sitios	dap sí	Mesén, 1990	las procedencias de Guanaja, y Poptún fueron entre las peores globalmente pero eran las mejores en un sitio
Vochysia guatemalensis	procedencias 2 sitios	dap sí	sin publicar	en un sitio, las procedencias costarricenses crecieron más rápidamente, mientras en el otro sitio la procedencia de Honduras fue la mejor
"	"	rectitud no	sin publicar	

[1]=cuando los mejores genotipos en un sitio no son los mejores en otro

Cuadro 6. Estimaciones de heredabilidad y coeficiente de variación genética aditiva en experimentos del Proyecto MGF en Costa Rica

Especies	Característica	h≤	CVGA %	Fuente
Alnus acuminata	altura, 34 meses	0,29	9,6	Cornelius, Mesén, Corea y Henson, 1995
	rectitud, 34 meses	0,12	9,7	"
Cupressus lusitanica	altura, 28 meses	0,21	10,2	Cornelius, Apedaile y Mesén, 1995
	diámetro, 28 meses	0,12	15,9	"
Eucalyptus deglupta (sitio Canalete)	altura, 16 meses	0,15	16,2	Cornelius, Corea y Mesén, 1995
Eucalyptus deglupta (sitio San José de Upala)	"	0,19	14,6	"
Eucalyptus deglupta (sitio Tuis)	"	0,27	22,5	"
Pinus caribaea var. *hondurensis*	altura	0,12		Crockford et al., 1990
"	rectitud	0,47		"
Gmelina arborea (sitio Nicoya)	dap, 32 meses	0,19	8,3	Cornelius y Hernández, 1995
"	rectitud, 32 meses	0,23	19,1	"
Gmelina arborea (sitio Hojancha)	dap, 31 meses	0,31	20,8	"
"	rectitud, 31 meses	0,08	13,3	"
Gmelina arborea (sitio Santa Cruz)	dap, 29 meses	0,28	11,3	"
"	rectitud, 29 meses	0.07	9,3	"
Gmelina arborea (sitio Canalete)	dap, 19 meses	0,21	10,6	"
"	rectitud, 19 meses	0,29	16,0	"
Vochysia guatemalensis (procedencia Izabal, sitio La Guaria)	altura, 42 meses	0,08		Cornelius y Masís, 1995
"	rectitud, 42 meses	0,32		"

Tuis, y 20,8% para dap de *G. arborea* en Hojancha). Por lo tanto la experiencia hasta la fecha sugiere que podemos esperar ganancias genéticas parecidas a las alcanzadas en otras regiones.

Cuadro 7. Principales resultados de ensayos genéticos del Proyecto MGF del CATIE, 1977-1995 en Costa Rica

Especies	Resumen de resultados	Fuentes
Acacia mangium	Mejores procedencias: Claudie River / Iron Range (Queensland)	Mesén, 1990
Alnus acuminata	La procedencias guatemalteca Palestina de los Altos se mostró inferior a procedencias locales en crecimiento, forma y susceptibilidad a *Scolytodes alni*	Cornelius, Mesén,, COrea y Henson, 1995 Cornelius y Masís, 1995
Cedrela odorata	Las fuentes de la zona de bajura de Guanacaste son de muy lento crecimiento en zonas húmedas de la vertiente atlántica. La procedencia de San Carlos, Costa Rica, exhibe la mayor tolerancia al ataque de *Hypsipyla*	sin publicar

Cordia alliodora	Las fuentes de la vertiente pacífica tienen forma y crecimiento inferior, tanto en zonas húmedas como secas. Además la procedencia de Turrialba presentó crecimiento inferior en dicha zona	sin publicar
Cupressus lusitanica	en un ensayo en Sta. Cruz de Turrialba, hasta los 28 meses la fuente de Santa María de Dota creció 30% más lentamente que las procedencias al norte de Heredia	Cornelius y Baeza, 1995
Eucalyptus deglupta	las plantas con hojas de fuerte coloración morada tienden a crecer más lentamente que las de hojas verdes	Cornelius, Corea y Hernández, 1994. Cornelius, Corea y Mesén, 1995
Eucalyptus urophylla	las procedencias más productivas en un ensayo en San Carlos, Costa Rica fueron las de Mt. Lewotobi (Isla Flores), Remexio (Timor), Isla Alor (oeste) y Isla Lembata (suroeste)	Mesén, 1990
Gmelina arborea	la raza local (costarricense) mostró un comportamiento igual o superior a otras procedencias introducidas en un ensayo en Turrialba, Costa Rica	Mesén, 1990 Valerio, 1986
Pinus caribaea var. *honduresis*	la procedencia Guanaja, Honduras, mostró superioridad en crecimiento y forma a otras procedencias en un ensayo en Guanacaste, Costa Rica	Mesén, 1990
Pinus patula ssp. *tecunumanii*	la procedencia Yucul, Nicaragua, se demostró superior en forma y crecimiento en todos los sitios ensayados, excepto la bajura guanacasteca	Corea, 1989 Mesén, 1990 Corea et al. 1993b Cornelius et al. 1994
Vochysia guatemalensis	en un ensayo de Sarapiquí, Costa Rica, las procedencias de la zona atlántica de Costa Rica crecieron más rápidamente que las procedencias de Izabal, Guatemala, y La Ceiba, Honduras. Sin embargo la procedencia Guatemala tenía fustes más rectos	Cornelius y Masís, 1994

Resultados de ensayos de procedencias y descendencias

Los resultados de los ensayos de campo del Proyecto MGF han sido ampliamente presentados y difundidos a niveles nacionales (Boshier y Mesén 1987; Cornelius 1990, 1994); , regionales (Corea 1989; Corea, Cornelius y Mesén, 1992; Corea, Mesén y Cornelius 1993a, 1993b; Cornelius, Corea y Hernández, 1994; Cornelius y Hernández, 1995; Cornelius, Hernández y Apedaile, 1994; Cornelius y Masís 1994, 1995; Mesén 1990) e internacionales (Boshier, 1984; Byrd, 1984; Cornelius, Corea y Mesén, 1995; Cornelius, Mesén, Corea y Henson, 1995; Salazar y Mesén, 1990). Por limitaciones de espacio, no se detallarán estos resultados en el presente artículo. Sin embargo, en el Cuadro 7 se presentan en forma muy resumida algunos de los resultados de más relevancia general y aplicación inmediata a la escogencia de germoplasma en América Central.

Rentabilidad del mejoramiento genético forestal de escala pequeña

Durante los últimos tres años, el Proyecto MGF ha ido evolucionando hacia un papel más catalítico que ejecutivo. Obviamente, el apoyo de los donantes internacionales no seguirá para siempre, por lo cual se percibió la necesidad de empezar a capacitar y equipar diferentes grupos involucrados en la reforestación para que ellos mismos puedan ejecutar sus programas de mejoramiento, utilizando como punto de partida los ensayos genéticos y huertos establecidos por el Proyecto MGF dentro de sus zonas de acción. De esta manera, se pretende dar sostenibilidad y, por lo tanto, efecto a largo plazo, a los logros del Proyecto.

Como parte de este proceso, se realizó un análisis financiero del mejoramiento genético forestal de escala pequeña, tomando como ejemplo un programa de mejoramiento de *Gmelina arborea* implementado por el Centro Agrícola Cantonal de Hojancha (Hamilton, Chandler, Brodie y Cornelius, 1995). El programa consiste en un juego de tres ensayos de descendencias y un huerto semillero clonal. Con base en datos recopilados por el Proyecto y en otras fuentes suplementarias, se calculó que el valor presente de los costos del programa fue de aproximadamente $25.000. Posteriormente, se estimó el área anual de reforestación necesaria para justificar esta inversión, con base en 20 años de producción de semilla, ganancias genéticas de 5%, 10%, 15% y 20% con respecto a productividad de plantaciones sin mejorar, y precios actuales ($15/m^3) para madera en pie. Los resultados demostraron claramente que en muchos casos los programas de este tipo se justifican fácilmente en términos financieros: con ganancias genéticas de tan sólo 5%, una tasa anual de plantación de 125 ha justifica la inversión, mientras con ganancias genéticas de 20%, una tasa anual de reforestación de tan sólo 31ha es suficiente para justificar el programa de mejoramiento.

Tradicionalmente en América Central, el mejoramiento genético forestal ha consistido principalmente en el establecimiento de rodales semilleros como fuentes 'interinas' de semilla, a usarse hasta que esté disponible semilla de mejor calidad. Desafortunadamente, en muchos casos lo interino se ha convertido en algo más permanente, tal vez porque se haya percibido que el mejoramiento de más alto nivel todavía no se justifica. Los resultados del análisis financiero descritos aquí sugieren que esta percepción es errónea: sí se justifica el mejoramiento genético forestal de más alto nivel en América Central. En el artículo siguiente se considera cómo se debería hacer.

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