GROWTH, SURVIVAL AND SHOOT BORER DAMAGE IN MAHOGANY PLANTINGS IN THE LUQUILLO FOREST IN PUERTO RICO[1] /

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Resumen

Entre 1963 y 1981, se sembraron 1 275 ha en el bosque muy húmedo subtropical de las montañas de Luquillo usando un híbrido de Swietenia macrophylla *y* S. mahogani. *La medida de la sección sembrada en 1963 después de 20 años rindió los siguientes resultados: densidad de tallos, 373/ha; área basal, 28.2 m²/ha; biomasa maderable total por peso seco sobre el terreno 160.7 t/ha; biomasa total de hojas, peso seco, 9.0 t/ha; biomasa total sobre el terreno, 292.2 m³/ha. Estas cifras corresponden a tasas de incremento de 1.4 m²/ha/año en área basal, 8.0 t/ha/año en biomasa maderable total sobre el terreno, 8.5 t/ha/año en biomasa total sobre el terreno y 14.6 m³/ha/año en volumen maderable total sobre el terreno. Medidas previas hechas, según condiciones topográficas después de 18 años en la misma sección, demostraron un incremento promedial de 1.4 cm/año en diámetro y un incremento promedial de 1.0 m/año en altura con diferencias significativas en crecimiento por topografía y clase de copa. Las medidas hechas en las secciones sembradas en 1967 y 1974 también mostraron diferencias significativas en crecimiento por clase de copa y topografía pero con tendencia menos pronunciadas. Daños hechos por* Hypsipyla *se encontraron en 58, 11 y 18% de los árboles en las secciones sembradas en 1974, 1979 y 1980, respectivamente. Diferencias significativas por topografía se observaron solamente en la sección sembrada en 1974. Diferencias significativas en daños por* Hypsipyla *no fueron evidentes por clase de copa ni por clase de área basal en las secciones sembradas en 1974, 1979 y 1980. El porcentaje de supervivencia de árboles y arbolitos fue más bajo en la clase de copa suprimida que en las que recibieron luz en las secciones sembradas en 1974, 1979 y 1980. El porcentaje de supervivencia también fue más bajo en las secciones sembradas en 1974 y 1979 cuando el área basal se aumentó. El porcentaje de supervivencia fue más bajo en las posiciones topográficas que correspondieron a cimas y terrenos bajos en la sección sembrada en 1974, aunque esta tendencia no era evidente en las secciones de menos edad. Se sugieren prácticas para mejorar la siembra.*

Introduction

Reforestation began in the Luquillo Mountains of Puerto Rico in 1933 (Fig. 1). Previously cutover land used for subsistence agriculture was planted with about 30 timber species. After an assessment of the reforestation effort, the U.S. Forest Service initiated a program of plantation establishment and line planting using a hybrid of *Swietenia macrophylla* and *S. mahagoni* (Fig. 2). The total area planted in mahogany through 1981 was about

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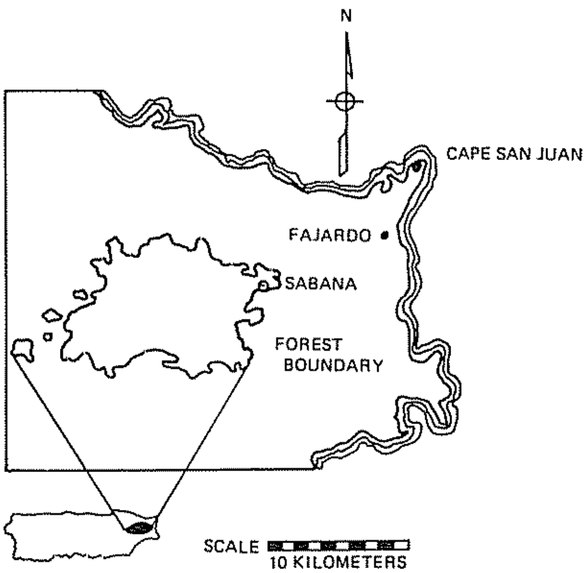

Fig. 1. Location of mahogany plantings in the Luquillo Mountains of northeastern Puerto Rico.

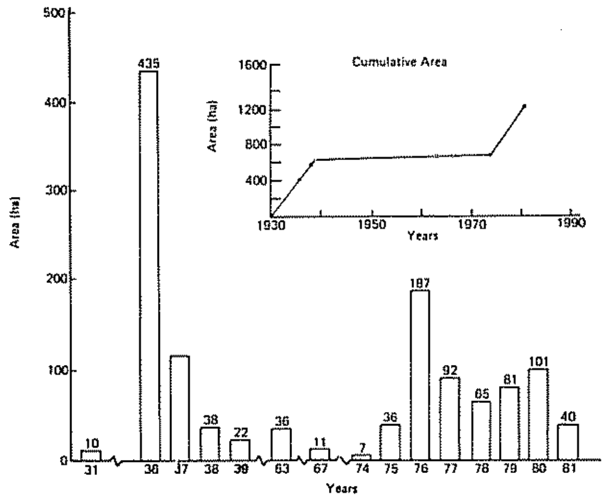

Fig. 2. Chronology of mahogany plantings in the subtropical wet forest of the Luquillo Mountains

1 275 ha. Trees planted in 1967 and later, about half the total, were line-planted in degraded secondary forest.

Enrichment planting is one method of improving the productivity of tropical forests. Several techniques exist as evidenced by the variety of terms used in the literature: conversion line-planting; strip planting; improvement planting; gap-, group, and inter- or under-planting. Some of these terms may be used interchangeably.

Conversion line-planting, the principal technique used on an areal basis in this study, involves the clearing of regularly spaced parallel lines through a degraded stand. These lines are usually about 2 m wide and spaced about 10 m apart, although closer spacings have been used on occasion. At maturity, the planted trees constitute a closed canopy. Conversion line-planting has been used most frequently in savanna woodlands, secondary forest with poor species composition, and degraded high forest (14).

Conversion line-planting has reforestation potential in tropical regions (24). In the Caribbean Islands, particularly the smaller islands where water resources are critical to growing populations, the technique maintains ground cover and protects the soil while seedlings take hold. Moreover, establishment cost is about a third of that for plantations, provided that spacing is not too close.

Although a considerable area of mahogany has been line-planted in Puerto Rico, the technique has never been evaluated. The objectives of this study were:

1) to evaluate diameter, height, basal area, biomass, and volume growth of the 1963 and 1974 plantings;

2) to evaluate survival and shoot borer attack on the 1974, 1979, and 1980 plantings;

3) to determine the influence of environmental variables (light, topography, and surrounding basal area) on growth, survival, and shoot borer damage; and

4) to assess the conversion line-planting technique for future use in Puerto Rico.

Study area

The study area is located between 130 and 300 m elevation in the subtropical wet forest life zone (4) of the Luquillo Mountains. In this area, rainfall averages 2 300 mm/yr, mean annual temperature is 23°C, and mean relative humidity is about 75% (2). The soils are deep acid clays (Table 1).

Historically, almost all of the study area had been farmed. When purchased for inclusion in the Luquillo Forest between 1935 and 1948, much of the property was covered with heavy brush and contained many

Table 1. Summary of site information and silvicultural practices for mahogany plantings.

Compartment number	Age (yrs)	Elevation (m)	Soil type	Area (ha)	Silviculture practices
1963	18	180-200	Catalina	36	Planting – direct seed; spacing – 3 x 3 m; existing overstory poisoned gradually before seeding; three seeds planted in each spot; 2-4 D and 2-4-5 T applied first two years to control weed and climber growth; repeated early thinnings; 30% removal of trees in 1975.
1967	15[1]	130-220	Catalina	10	Planting – bareroot; seedlings < 1 m tall; spacing - 2.5 x 11 m; planted in cleared lines below secondary forest canopy; weeded about 3 times per year for 5 years; overstory gradually poisoned with herbicide; no release thinning.
1974	8.2[1]	150-220	Catalina	7	Planting – bareroot; spacing – 2.5 x 11 m; planted in cleared lines below secondary forest canopy; weeded 2-3 times per year; overstory gradually poisoned with herbicide, probably Tordon; no release thinning.
1979	3.25[1]	150-300	Yunque	16	Planting – bareroot; spacing – 2.5 x 11 m; planted in cleared lines below secondary forest canopy; weeded 2-3 times per year; overstory gradually poisoned with herbicide Tordon.
1980	2.25[1]	130-200	Coloso	8	Planting – bareroot; seedlings averaged 0.3-1.0 m tall at time of planting; spacing – 2.5 x 11 m; planted in cleared lines below secondary forest canopy; weeded 2-3 times per year; overstory gradually poisoned with herbicide Tordon.

1 Includes one year duration of seedling in nursery

trees classified as small and large poles. When line-planting was initiated in 1967, the area still did not have species composition adequate for long-term management.

Methods

Establishment and tending methods varied between the first and later planting (Table 1). In the 1963 planting, the overstory was poisoned gradually, seeds were planted at 3 x 3 m spacing, and herbicides were applied to control weeds. Repeated early thinnings based on tree form and spacing were used to liberate the planted stock. In later plantings, bareroot seedlings were used at 2.5 x 11 m spacings and lines were maintained by weeding or cutting with a machete.

Most measurements were made in 1981 (Table 2). In each compartment dated 1967 through 1980, a beginning line was randomly designated, and every other row was measured. In the 1963 compartment, the first measurements were made along topographic features (ridge, midslopes, lower concave slopes, and bottomlands).

Height was measured to the nearest 0.1 m by an optical rangefinder in the 1963 and 1967 compartments and by extension pole in the 1974 compartment. A cloth diameter tape was used to measure tree diameter (d.b.h.) to the nearest 0.1 cm at 1.4 m above the ground for the 1963, 1967, and 1974 compartments. Crown classes were identified as: emergent (E), trees that extended well above the average height of the canopy; dominant (D), trees in the canopy with overhead and side light; codominant (C), trees in the canopy with overhead light; intermediate (I), trees below the general level of the canopy that received direct light at midday; lateral (L), trees below the general level of the canopy that received

Table 2. Tree and site measurements conducted on each of the plots.

Measurement	Compartment number				
	1963	1967	1974	1979	1980
Height	x	x	x	–	–
Diameter	x	x	x	–	–
Crown class	x	x	x	x	x
Topographic position	x	x	x	x	x
Basal area at stem	–	x	x	x	x
Shoot borer attack	–	–	x	x	x
Mortality	–	–	x	x	x
Number of live trees	85	232	214	672	643
Number of observations[1]	85	318	367	1 198	957
Percent survival	–	73	58	56	67

1 Topographic positions and basal areas were taken at each planting site including those where trees or seedlings had died

light in the early morning or late afternoon, but not at midday; and suppressed (S), understory trees overtopped at all times by surrounding vegetation. Not all crown classes were represented in all compartments. Growth differences by topographic position, surrounding basal area classes, and crown class were determined by repeated t-tests (22).

Basal area was measured with a BAF-10 prism at each tree, and frequently included other planted mahoganies on older plots. Shoot borer attack was recorded as positive or negative, but no tally of number of attacks per tree was made. In cases of mortality, basal area and crown class were recorded at the point of the dead or missing stem.

In addition, 24 *Swietenia* trees ranging from 1.9 to 49.2 cm d.b.h. were felled to determine biomass by compartments. Trees were randomly selected within diameter class limits to provide a range of sizes. Total tree height and d.b.h. were measured on each tree. Biomass was partitioned into trunks, leaves, and branches, with trunks defined as the main stem of the tree from ground level to the point of major bifurcation, or branching. The remaining woody portions were classified as branches that varied considerably in size. Wet weights were determined in the field. Four sample discs of the trunk and six of branches >2.5 cm were taken at different points along the tree. Branches <2.5 cm and leaves were sampled separately. All samples were ovendried at 70°C for about six weeks, at which time no decrease in the dry weight was observed. Sample dry weight/wet weight proportions were then used to determine the biomass for each of three groupings of woody material and leaves. In the development of regression equations, dry weight was expressed as a function of the d.b.h.^{2} tree height. In transformation of the estimates of the logarithmic equation back to arithmetic units, bias was corrected by adding half the sample variance to the intercept term (1).

Finally, an 0.4 ha plot in the 1963 plantation was measured in 1983. All topographic positions were included as the plot ranged from bottomland to ridge. Diameter and height of 151 mahogany trees were recorded to determine standing biomass via regression. Total standing volume was estimated by dividing biomass by 0.55 g/cm^3, which is the specific gravity for the hybrid mahogany (16) The same regression equations and specific gravity were used to determine biomass and volume for the 1967 and 1974 plantings.

Results

Diameter and Height Growth

The mean diameter and mean height growth over the 18-year measurement period in the 1963 mahogany planting were 1.40 cm/yr and 1.0 m/yr, respectively (Figs. 3 and 4). Comparable mean diameter and mean height growth data in the 1967 plantation were 0.77 cm/yr and 0.7 m/yr, and in the 1974 plantings, 0.61 cm/yr and 0.7 m/yr, respectively (Figs. 3 and 4).

Diameter growth was influenced by topography (Fig. 3). In the 1963 plantings, diameters were significantly larger on bottomlands and lower concave slopes, and significantly smaller on ridges. Differences were not as pronounced in the 1967 plantings, where diameter on the ridges was significantly smaller than on at least one other topographic position.

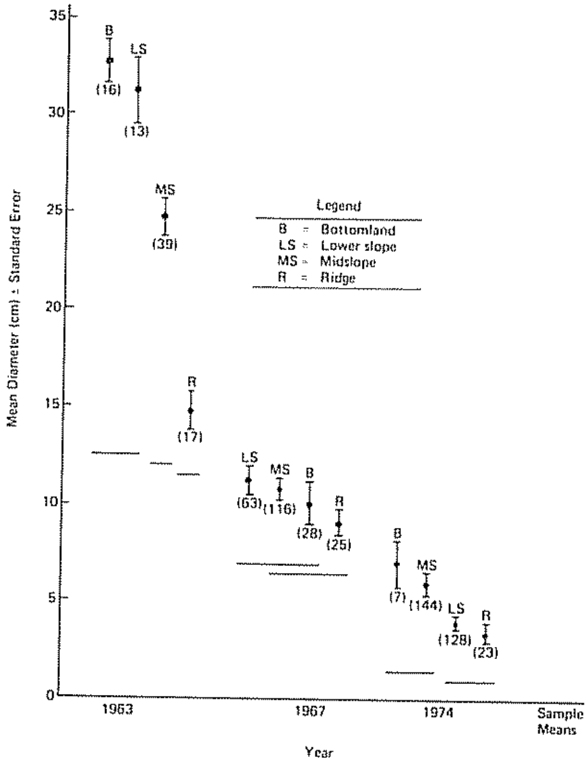

Fig 3 Differences in mean diameter of surviving mahogany by topography for plantings established in 1963, 1967, and 1974 Topography is indicated above the standard error bars and the number of trees sampled is indicated below Horizontal lines connect means that are not significantly different at the 95% level Means without reference to topography are given on the right margin

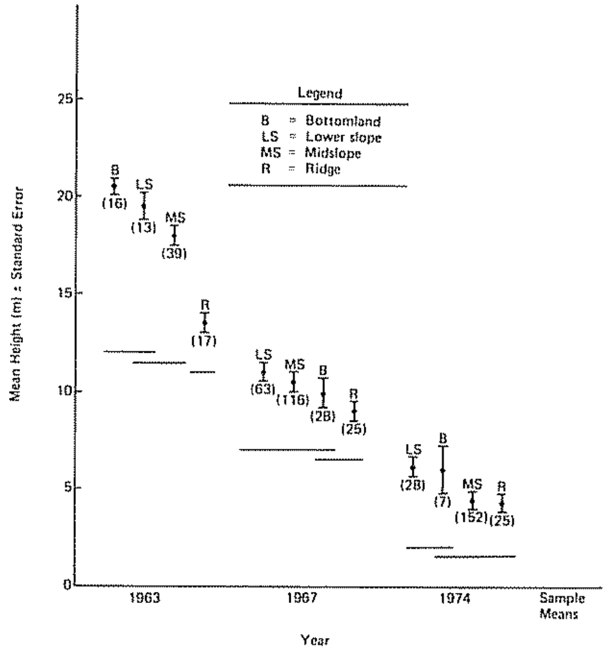

Fig 4 Differences in mean height of surviving mahogany by topography for plantings established in 1963, 1967, and 1974 The potography is indicated above the standard error bars and the number of trees sampled is indicated below. Horizontal lines connect means that are not significantly different at the 95% level. Means without reference to topography are given on the right margin

Height growth was also influenced by topography (Fig. 4). In the 1963 plantings, trees were significantly shorter on ridges than on other topographic positions. In the 1967 and 1974 plantings, trees were shortest on ridges, although the differences were not as pronounced.

The basal area around individual trees also influenced diameter and height growth in the 1974 planting (Figs. 5 and 6). Mean diameter growth and height growth were significantly more rapid in the 0-9.9 m^2/ha basal area class, intermediate in the range of 10-19.9 m^2/ha, and significantly slower in basal area classes > 20 m^2/ha. In the 1967 planting, the same general trends were apparent, but the differences in most instances were not statistically significant.

Crown class was also significantly correlated with diameter growth (Fig. 7). In the 1963 plantings, dominants grew significantly faster than codominants, which, in turn, grew significantly faster than intermediate trees. In the 1967 planting, significantly different growth rates were found among all crown classes ranging from emergents through suppressed trees. In the 1974 planting, trees in the intermediate crown class grew significantly faster than those receiving lateral light, and these trees in turn grew significantly faster than suppressed ones.

Stand Development

Regressions of total aboveground woody biomass, leaf biomass, and total aboveground biomass yielded coefficient of determination (r^2)values of 0.95 or greater (Figs. 8, 9, and 10). Numbers of trees, basal area, biomass, and volume estimates for each compartment are given in Table 3.

Shoot Borer Damage

Shoot borer damage was greatest in the 1974 plantings, with an infestation rate of nearly 58% on the surviving trees (Table 4). The 1980 plantings showed nearly 18% of the trees affected by shoot borer, exceeding the 11% infestation rate suffered by the seedlings in the 1979 planting.

The percentage of trees affected by the shoot borer was not significantly correlated with crown class in the 1974, 1979, or 1980 plantings (see Table

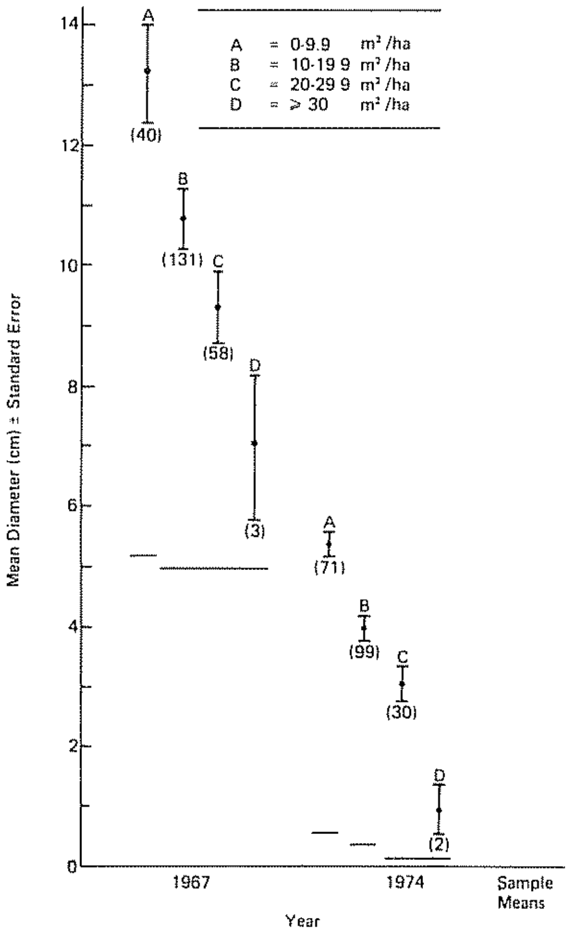

Fig. 5. Differences in mean diameter of surviving mahogany by basal area class of surrounding secondary forest for plantings established in 1967 and 1974. Letters above the standard error bars indicate the basal area classes and the number of trees in indicated below. Horizontal lines connect means that are not significantly different at the 95% level. Means without reference to basal area class are given on the right margin.

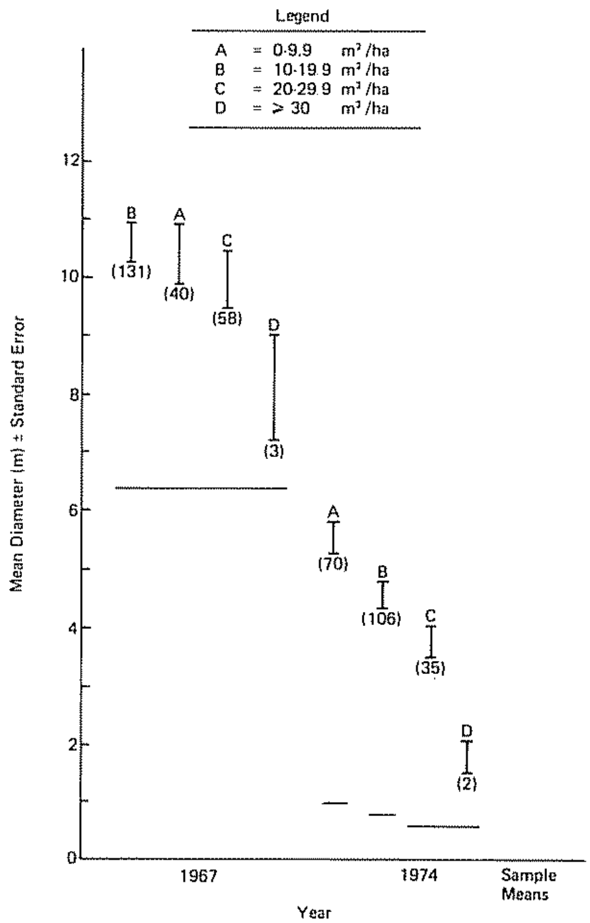

Fig. 6. Differences in mean height of surviving mahogany by basal area class of surrounding secondary forest for plantings established in 1967 and 1974. Letters above the standard error bars indicate the basal area classes and the number of trees in indicated below. Horizontal lines connect means that are not significantly different at the 95% level. Means without regard to basal area given on the right margin.

4, Footnote 1). A similar lack of significant differences was observed when the plantings were categorized in classes according to the basal area. When the shoot borer damage was categorized according to topographic position, no significant trends were observed in the 1979 or 1980 plantings. The 1974 planting, however, showed significantly less damage on ridges than on other types of topography.

Survival

Survival of trees and saplings ranged from 56% in the 1979 plantings to about 67% in the 1980 plantings (Table 5). Significant differences in survival were observed by crown class, with those crown classes receiving direct light, either overhead or lateral, surviving at a higher rate. Basal area of the surrounding secondary forest also influenced survival in the 1974 and 1979 plantings, although the differences were not significant (Table 6). Survival was greatest for trees with the lowest surrounding basal areas.

Survival percentage of trees and saplings differed significantly according to topography in the 1974 plantings, with the lowest survival rates on ridge and bottomland sites (Table 7).

Discussion

Growth and Development

The occurrence of mahogany progeny intermediate in form between *S. macrophylla* and *S. maha-*

Table 3. Stem density, basal area, biomass, and volume estimates for hybrid mahogany established in 1963, 1967, and 1974 determined by regression equation.

Estimate (units)	Compartment number					
	1963[1]		1967		1974	
	Standing trees	Mean annual growth	Standing trees	Mean annual growth	Standing trees	Mean annual growth
Density (trees/ha)	373	–	265	–	204	–
Basal area (m^2/ha; m^2/ha/yr)	28.2	1.41	2.9	0.21	0.4	0.06
Total aboveground woody biomass (t/ha; t/ha/yr)[2]	160.7	8.0	12.6	0.90	1.2	0.16
Leaf biomass (t/ha)[2]	9.0	–	1.0	–	0.1	–
Total aboveground biomass (t/ha; t/ha/yr)[2]	170.7	8.5	13.7	0.98	1.2	0.17
Total aboveground woody volume (m^3/ha; m^3/ha/yr)	292.2	14.6	22.9	1.64	2.2	0.31

1 Does not include trees thinned in 1975 or previous years.

2 Dry weight biomass.

Table 4. Percent of shoot borer damage to surviving trees in line plantings established in 1974 and 1980[1].

Compartment number	Percent damaged	Number measured
1974	57.5[2]	214
1979	11.2	672
1980	17.7	643

1 For each year, Chi-square was used to compare shoot borer attack by crown class (intermediate vs. lateral light vs. suppressed), basal area class (0-9.9 vs. 10-19.9 vs. 20-29.9 vs. >30 m^2/ha) and topographic position (ridge vs. straight slope vs. concave slope vs. bottomland). Except for topographic comparisons in 1974, none of the differences was significant.

2 Comparison of shoot borer attack by topographic positions showed significant differences at the 95% level; ridge 52.0% (25 trees), straight slope 56.5% (154 trees), concave slope 64.3% (28 trees) and bottomland 71.4% (7 trees).

goni is common when parent trees are in close proximity. Preliminary observations of the intermediate variety indicate that it has both the vigorous growth of *S. macrophylla* and the desirable wood characteristics of *S. mahagoni* (13, 15). These features, together with ready availability of seed locally, have resulted in its use for line-planting in Puerto Rico since the program's inception.

The mean diameter growth of 1.4 cm/yr and mean height growth of 1.0 m/yr for the hybrid (Figs. 3 and 4) are rapid and confirm earlier growth observations for *S. macrophylla* in the Luquillo Forest. Plantings of the latter made in 1932 averaged 1.3 cm/yr in diameter growth during the first 27 years (26).

More rapid diameter growth on lower slopes and bottomlands compared with other topographic positions also substantiates earlier studies for *S. macrophylla* in Luquillo (18). Deeper soils probably account of these differences (3). Elsewhere on the island, *S. macrophylla* grew well in the sink-holes of the limestone hills and in the narrow river valleys and concave slopes on serpentine soils in Maricao Forest, but was not adapted to areas with degraded

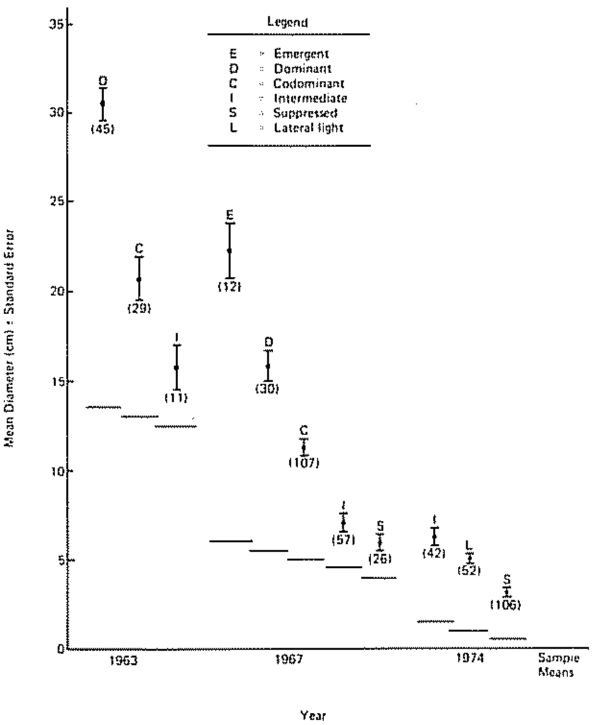

Fig 7. Differences in mean diameter of surviving mahogany by crown class for plantings established in 1963, 1967, and 1974. Letters above the standard error bars indicate the crown classes and the number of trees in indicated below. Horizontal lines connect means that are not significantly different at the 95% level. Means without regard to crown class are given on the right margin.

soils (19). The entire complex of edaphic factors associated with topography appears to be a good indicator of growth potential for mahogany.

In contrast, *S. mahagoni* was found unsatisfactory for high rainfall areas of the Luquillo Forest or the Cordillera Central (18). In Luquillo, only a few good trees were found on ridges where growth was better than on other topographic positions. Elsewhere on the island, *S. mahagoni* grew satisfactorily on slopes in karst topography, narrow river valleys and concave slopes on serpentine soils in Susua and Maricao Forests, and on the sandy coastal soils in Guanica and Mona Island (19). In subtropical moist forest at Guajataca, a plantation of *S. mahagoni* had a basal area of 18.6 m^2/ha and average diameter increment of 0.9 cm/yr after 15 years (25).

Greater mean diameter and mean height associated with lower surrounding basal areas (Figs. 5 and 6) and greater exposure to light (Fig. 7) demonstrate the effect of competing vegetation on mahogany growth. Mortality and stunted growth beneath *Syzygium jambos*, a non-native tree, was particularly noticeable in the field. This species has a dense crown and completely shades the understory. One of the necessary conditions and technical guidelines regarding the establishment and tending of line-plantings (14) is that, for most rapid growth, there must be no upper canopy, but instead only poisoned large trees or low secondary forest in the line-planted areas. The

Table 5. Percent survival of mahogany trees and saplings by crown class for line plantings established in 1974, 1979, and 1980.

Compartment number	Crown classes							
	Intermediate		Lateral light		Suppressed		Totals	
	No. of sites[1]	Percent survival	No. of sites[1]	Percent survival	No. of sites[1]	Percent survival	No. of sites[1]	Percent survival
1974	68	60.3	72	73.6	227	52.4	367	58.3[3]
1979	145	75.2	156	69.9	897	50.5	1 198	56.1[3]
1980	320	75.0	–	2	637	63.4	957	67.4[3]

1 Number refers to total planting sites where observations were made. Percent survival refers to number of sites where living trees were found.

2 For the 1980 measurements, only intermediate and suppressed crown classes were used to classify the seedlings.

3 Chi-square values are significant at the 95% level: for 1974, 7.0; for 1979, 16.8; and for 1980, 4.1.

Table 6. Percent survival of mahogany trees and saplings according to surrounding basal area classes for line plantings established in 1974, 1979, and 1980.

Compartment number	Basal area classes (m^2/ha)									
	0-9.9		10-19.9		20-29.9		≥30		Totals	
	No. of sites[1]	Percent survival	No. of sites[1]	Percent survival	No. of sites[1]	Percent survival	No. of sites[1]	Percent survival	No. of sites[1]	Percent survival
1974	105	66.7	171	61.4	85	41.2	6	33.3	367	57.8
1979	34	67.6	421	59.1	624	55.1	119	46.2	1 198	56.0
1980	46[2]	58.7	321	69.5	496	66.9	94	67.0	957	67.4

1 Number refers to total planting sites where observations were made. Percent survival refers to number of sites where living trees were found.

2 Nine of these trees were located on a landslide overgrown by ferns. If these nine observations are eliminated, survival in this basal area class increases to about 73%.

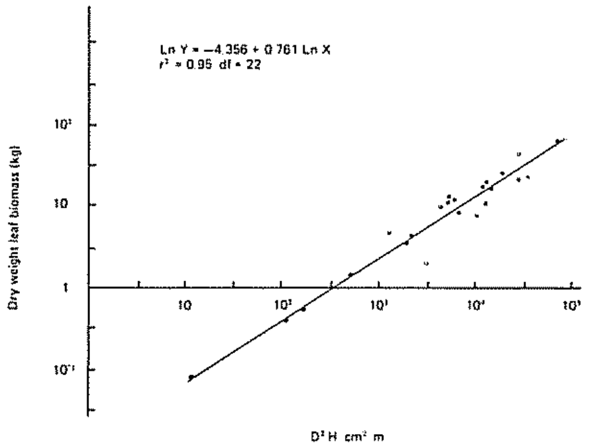

Fig 8. Regression equation for leaf biomass. The ovendry weight is expressed as an allometric function of tree diameter and height.

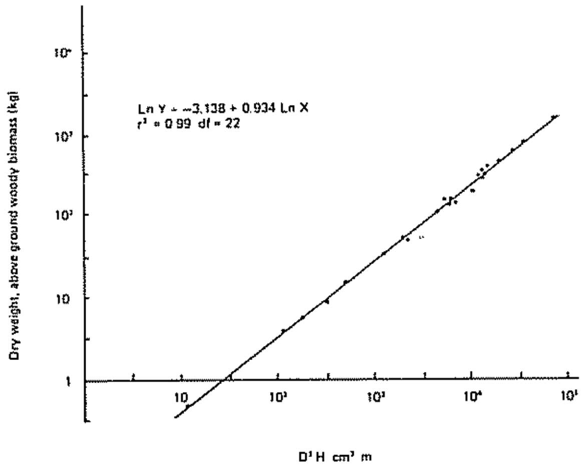

Fig. 9. Regression equation for aboveground woody biomass. The ovendry weight is expressed as an allometric function of tree diameter and height.

favorable survival and growth of the 1963 plantings were due to adequate weed control and early, repeated thinnings.

Twenty-five percent of the trees in the 1974 planting and 62% in both the 1979 and 1980 plantings are surrounded by basal areas > 20 m^2/ha (Table 6 – add trees below respective basal area classes and divide by total trees). Moreover, from 62% to 75% of the trees in the same plantings are in the suppressed crown class (Table 5 – add trees below suppressed crown class and divide by total trees). For best growth, release from competing vegetation is required in these plantations.

Total aboveground standing volumes and volume increments for the different compartments in the Luquillo Forest showed considerable variation (Table 3). The 1963 data compare favorably with those for *S. macrophylla* on 16 sites in 5 countries of Central America and the Caribbean (6). Standing volumes on four 8 to 10 year– old sites averaged 70 m^3/ha with a mean annual increment (MAI) of 7.7 m^3ha/yr. On 10 sites 11 to 20 years old, average

Table 7. Percent survival of mahogany trees and saplings by topographic position in line plantings established in 1974, 1979, and 1980.

Compartment number	Topographic position								Totals	
	Ridge		Midslope		Concave Slope		Bottomland			
	No. of sites[1]	Percent survival	No. of sites[1]	Percent survival	No. of sites[1]	Percent survival	No. of sites[1]	Percent survival	No. of sites[1]	Percent survival
1974	73	34.2	231	65.3	46	60.9	17	41.2	367	57.7[2]
1979	272	54.4	738	55.5	161	62.1	27	55.6	1 198	56.2
1980	104	72.1	800	66.9	49	65.3	4	75.0	957	67.4

1 Number refers to total planting sites where observations were made. Percent survival refers to number of sites where living trees were found.

2 The Chi-square value, 10.1, was significant at the 95% level.

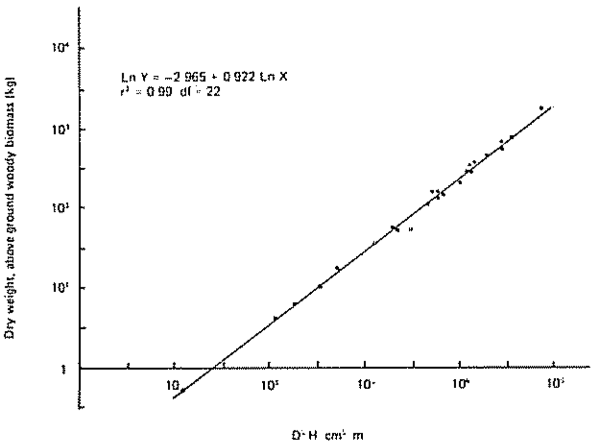

Fig 10 Regression equation for total aboveground biomass. The ovendry weight is expressed as an allometric function of tree diameter and height.

standing volume was 125 m^3/ha with an MAI of 88.6 m^3/ha/yr. On three sites ranging in age from 21 to 32 years, average standing volume was 234 m^3/ha with an MAI of 8.4 m^3/ha/yr. Considerable variation among the sites was apparent, with growth rates ranging from 3.1 m^3/ha/yr during 17 years to 21.0 m^3/ha/yr during 16 years.

The 1967 and 1974 compartments, however, were noticeably lower in standing volumes and growth rates, differences that may be attributable, in part, to varying initial planting densities, silvicultural techniques, and planting sites (Table 1). The portions of the 1963 compartment measured in this study were located on variable topography and had been properly tended during the early years, assuring a high survival rate. In contrast, survival rates in the 1967 planting were a little over 70%, and those in the 1974 planting only about 60%. Many of the 1974 trees were surrounded by high basal areas (Table 6) and were in the suppressed crown class (Table 5). All of these factors contribute to slower growth.

Shoot Borer Damage

The mahogany shoot borer, *Hypsipyla grandella*, generally lays its eggs on young shoots at the base of leaf petioles whence the larvae bore immediately into stem tissues and hollow out the shoots. The cycle lasts from 1 to 2 1/2 months, beginning the rainy season, with a minimum of two generations per year (5). The net effect is considerable retardation of stem growth and possible shoot deformities. From 1935 to 1943, an estimated one million *Cedrela* and *Swietenia* were damaged in Puerto Rico (5).

More extensive shoot borer damage in the 1980 plantings in comparison with the 1979 plantings was contrary to expectations. Normally, greater damage would be found in those seedlings exposed to attack for a longer period. Other factors being equal, cyclic variations of borer outbreak could account for this difference. Such variations might be contingent upon available food supply or density-dependent factors like shoot borer parasites (20). It is also possible that some of the 1980 seedlings were infested when planted.

The lack of correlation between shoot borer damage and environmental factors such as seedling crown class, basal area surrounding the seedling, and topographic position is not surprising (Table 4). Other authors have stated explicitly that shoot borer damage "is complete and widespread regardless of whether mahogany trees are located in the open or in heavy shade" (7) and that shade trees "were not very successful (in reducing shoot borer attack) if the mahogany was planted in pure lines" (21).

The apparent decrease in shoot borer attack on ridge sites in comparison with other topographic positions in the 1974 plantings (Table 4) may be explained by higher winds or possibly higher local "relief" of ridge trees within the forest. Wind speed is important in determining where moths fly after release (12). Slightly higher winds on ridges may help in dispersing the moths to better protected slopes and bottomlands. Several observations of infestation related to height above ground have shown that the moths are less likely to deposit eggs on trees taller than 6 to 10 m (8, 20). With pronounced topographic variation, moths might low a preference for lower sites. Another possible explanation is that the infestation rate is the same regardless of topography, but that tree survival on ridge sites is lower after infestation (Table 7).

Probably the best control method for the shoot borer is distant spacing within the secondary forest. As observed by Holdridge (11), mahogany and other Meliaceae seedlings like *Carapa* and *Cedrela* often grow up in thickets, providing a niche for the borer. Mahogany in plantations or dense line-plantings, then, presents ideal conditions for maintaining large borer populations. Over time, infestation rates may approach 60% or more as observed in the 1974 plantings (Table 4). Mixed plantations or imitated natural conditions for mahogany have been suggested as alternatives (10, 11, 17). Indeed, planting of Meliaceae alternately with other species in line plantings in Africa has provided some degree of shoot borer control (21). Open-grown *S. macrophylla*, near Santarem, Brazil, were heavily infested with shoot borer, whereas nearby mixed line-plantings had not a single incidence of infestation. Naturally occurring *S. macrophylla* may be as sparse as one tree/ha. These trees are economical to harvest because of their high value. Spacing mahogany at 11 x 15 m and interplanting with other commercial species in lines could yield about 60 trees/ha along with other commercial wood and might alleviate the shoot borer problem considerably.

Survival

Seedling survival is best when direct overhead or lateral light is available, and the surrounding basal area is less than 20 m^2/ha (Tables 5 and 6). The effects of basal area are particularly noticeable in the 1974 planting (Table 6). It appears that mortality in heavy shade occurs within a couple of years after outplanting.

S. macrophylla seedlings are extremely intolerant of strong light in the first few months (23), and young trees are intolerant of shade (15). Experience has shown that planting *S. macrophylla* under a shelterwood gives good results, but that the stand has to be opened rapidly for best growth (9).

In earlier mahogany plantings in Puerto Rico, seedlings between 0.3 and 2 m in height showed little difference in survival rate. However, it was felt that larger stock should be favored because it was less costly to weed and tend (9). Early growth of the transplants was not dependent upon seedling size, but rather on site and the amount of tending. Eroded soils and those continuously farmed in annual crops were less suitable than those maintained with ground cover, probably due to greater amounts of organic matter, better soil moisture retention, and favorable soil texture, all of which are associated with ground cover (9).

Silvicultural and Management Recommendations

Silvicultural Techniques

All of the autoecological information related to mahogany points to line-planting as the ideal method for its establishment. The problem of poor growth on eroded soils is averted because organic matter and soil texture are improved by the surrounding secondary forest. The presence of surrounding shade helps to control weeds around the planted seedlings and probably assists the tree in the development of a single main shoot, even if infested by shoot borers. Widely spaced line-plantings simulate the conditions in which mahogany successfully regenerates in the natural forest. Small gaps created by the death of larger stems, simulated by poisoning of overhead shade, provide the light and soil conditions required for successful growth and development.

Shoot borer problems are enhanced in plantations of mahogany. Two main silvicultural strategies are available to reduce problems of low branching and retarded growth associated with infestations: densely plant an area with mahogany and select the best stems, or intersperse the mahogany with other fast-growing commercial species, making it more difficult for the shoot borer to locate the mahogany. The first alternative probably leads to an increase in the insect's population. Because infested trees may be adjacent to each other in the lines, selection involves not only release of stems with good form but also some poorly-formed trees. The second alternative reduces shoot borer infestation, but is not without problems. Growth rates and spacing requirements vary among timber species and may result in competition that favors one species over another. Differential growth rates and mixed species composition may also present problems at harvest time.

Chemical control of the shoot borer is most easily accomplished in the nursery phase, and keeping the seedlings there until they have reached one meter in height would not only reduce weeding costs after outplanting, but also could reduce the time available for shoot borer infestation since the insect is most active on stems less than 6-10 m tall.

Management Strategies

In Puerto Rico, line-planting methods could be improved. In the nursery phase, the shoot borer has not been adequately controlled. Often, seedlings are grown without proper shade and are outplanted when about 0.3 m tall. Tending after planting has not followed established guidelines (14). Many of the seedlings and saplings are shaded by the surrounding overstory, precluding rapid growth. Many stands appear to need thinning for most rapid development. Based on personal observations and the literature, the following management strategies for mahogany are recommended for Puerto Rico:

Nursery

1) control shoot borer infestation chemically;

2) provide seedlings with appropriate shade.

Outplanting and tending

1) orient planting lines from east to west within the forest to maximize sunlight; at the time of line-clearing, poison all large overstory trees shading the lines;

2) ft the seedlings when about one meter tall, using the larger size classes on lower slopes and bottomlands;

3) cut all *Syzygium jambos* trees, poison the stumps and cut back all sprouts, or do not plant beneath this species;

4) space lines 11 m apart, and space trees within the lines about 2.5 m apart;

5) follow established line-planting guidelines with modifications baed on results (14);

6) within one year of outplanting, reduce all surrounding basal area to under 15 m^2/ha;

7) experiment with mixed line-planting of mahogany with other timber species that have similar growth rates; subsequent thinnings within the lines should favor mahogany;

8) continue studies of the nursery phase, outplanting and tending, to better formulate rules for mahogany management in the Luquillo Mountains and elsewhere on the island.

Conclusions

The fast initial growth rates, utility, and market value of mahogany make it a desirable tree for many areas of Puerto Rico. Line-planted mahogany may be used to enrich secondary forests with poor species composition. An active reforestation and timber management program could provide local employment and improve the island's future balance of payments through import substitution (27).

Summary

Plantings initiated in 1963 on 1 275 ha of subtropical wet forest in the Luquillo Mountains using a hybrid of *Swietenia macrophylla* and *S. mahagoni* yielded the following data after 20 years: stem density, 373 trees/ha; basal area, 28.2 m^2/ha; total aboveground dry-weight woody biomass, 160.7 t/ha; total dry-weight leaf biomass, 9.0 t/ha; total aboveground dry-weight biomass, 170.7 t/ha; and total aboveground woody volume, 292.2 m^3/ha. These data correspond to growth rates of 1.4 m^2/ha/yr in basal area, 8.0 t/ha/yr in total aboveground woody biomass, 8.5 t/ha/yr in total aboveground biomass, and 14.6 m^3/ha/yr in total aboveground woody volume. Previous measurements made along topographic features after 18 years in the same compartment disclosed a mean diameter growth of 1.4 cm/yr and a mean height growth of 1 m/yr with significant differences by topography and crown class. Measurements taken in compartments that were planted in 1967 and 1974 also showed significant growth differences by crown class and topography, but with less pronounced trends. Moreover, growth declined as basal area around individual stems increased in these compartments. Shoot borer damage was found on 58, 11, and 18% of the trees in the compartments planted in 1974, 1979, and 1980, respectively. Differences by topography were significant only in the 1974 plantings. No significant differences in shoot borer damage by crown class or basal area class were evident in the compartments planted in 1974, 1979, and 1980. Percent survival of trees and saplings was lower in the suppressed crown class than for trees receiving light in all three compartments. Percent survival was also lower in the compartments planted in 1974 and 1979 when basal area increased, and on ridge and bottomland sites in the 1974 plantings, although this trend was not apparent in the younger plantings. Improved planting practices for mahogany are suggested.

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Notas y comentarios

Incendios forestales prehistóricos

Una caída promedio de lluvia de 3 530 milímetros por año no es suficiente para prevenir incendios en una selva tropical húmeda. Esta es la conclusión de un trabajo hecho por un equipo de científicos de cinco organizaciones de investigación de los Estados Unidos y Venezuela (**Science**, vol. 227, p. 53).

El equipo se internó en la selva lluviosa de Venezuela, en la cuenca amazónica. Allí, los investigadores colectaron 96 muestras de suelos en 11 lugares esparcidos en una área grande. Hicieron sondajes de suelos hasta una profundidad de un metro. Encontraron carbón de palo en 63 de las muestras. El siguiente paso fue determinar la edad del carbón de palo. El datado por radiocarbón mostró que el carbono contenido fue producido entre 250 ± 50 y 6 260 ± 110 años antes del momento del análisis.

Los incendios forestales podrían haberse producido por personas; había ciertamente signos de habitación humana en la región. Sin embargo, los pedazos de cerámica encontrados probaron tener una edad hasta de 3 750 años. Así, los incendios más antiguos pueden haber ocurrido antes de la presencia humana en la región. Como señalan los investigadores, "No se puede ahora suponer que las selvas lluviosas bajas de los trópicos han estado libres de perturbación por el fuego ... La ecología de las selvas lluviosas tropicales debe ahora ser considerada tanto en contexto antiguo como contemporáneo". **A.G.**