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PRUNING EFFECTS ON ROOTS OF NITROGEN FIXING TREES IN THE HUMID TROPICS

By

Patrick Ewart Kent Chesney

Dissertation for the
Degree of
Doctor of Philosophy

Turrialba, Costa Rica
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This thesis is dedicated:

To the J's of my life: Jannice, Jamal & Jamella.

To my mother,
and
To the memory of my late father.

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This thesis is the synthesis and discussion of the following five articles:

Article I	N and root length dynamics in a tropical agroforestry system with periodically pruned *Erythrina poeppigiana*
Article II	Fine root and nodule dynamics of periodically pruned hedgerow trees in a tropical alley cropping system
Article III	Dynamics of non-structural carbohydrate reserves in pruned leguminous trees
Article IV	Effect of shoot pruning on starch content in roots of two leguminous species
Article V	Regrowth dynamics of periodically pruned leguminous trees

The articles follow the synthesis, in the same sequence as presented here.

CHESNEY, P.E.K. 2000. Pruning Effects on Roots of Nitrogen Fixing Trees in the Humid Tropics. Ph.D. Thesis. CATIE.

Key words: alley cropping, allocation, *Erythrina poeppigiana*, fine roots, *Gliricidia sepium*, histology, nitrogen, nodule, non-structural carbohydrates, phosphorous, regrowth.

Abstract

In alley cropping systems in the humid tropics, fast growing, leguminous trees are completely shoot pruned at half-yearly intervals to reduce tree-crop competition for light and to provide organic inputs for crop nutrition. Research experiences with maize and tomato alley cropping recommend increased frequency of pruning to increase marketable yield. Complete pruning of trees causes fine root and nodule turnover resulting in tree-crop competition for soil nitrogen (N) as trees recover. Increased frequency of complete pruning may exacerbate these effects. As an alternative, partial pruning may have a more conservative effect on fine roots and nodules but little is known about the merits of this practice. The present study was carried out under humid tropical conditions in Turrialba, Costa Rica. The objectives of the study were to 1) evaluate the effects of complete and partial shoot pruning on soil N, N accumulated in biomass, and fine root and nodule dynamics of *Erythrina poeppigiana*, and 2) elucidate the physiology of recovery of completely and partially pruned *E. poeppigiana* and *Gliricidia sepium* trees. Net N mineralisation and nitrification rates were measured in field-incubated soil in *E. poeppigiana* amended plots. Micro-kjeldahl N accumulation in pruned tree biomass was computed. The production and turnover of fine roots and nodules were determined by applying the compartment flow model to fine root and nodule biomass measured in sequentially taken soil cores. The recovery of pruned trees was followed up to 12 weeks after pruning by monitoring root and stem tissue starch (Lugol) and soluble carbohydrate (HPLC) changes as well as resprouting rates. The study showed that pruning intensity did not affect net N mineralisation or nitrification rates. Partially pruned 2- and 8-year-old trees cycled 187 kg and 256 kg N $ha^{-1}a^{-1}$, respectively in shoot biomass, which was 50% more than that cycled in completely pruned trees. This difference may be attributed largely to the conservative effect of partial pruning on fine root and nodule production. Over a 5-month regrowth period, mean fine root length was 821 m vs. 489 m $tree^{-1}$ for partially versus

completely pruned 2-year-old trees, respectively; for 8-year-old trees, corresponding values were lower by 40%. Partial pruning increased fine root turnover by 50%, and nodule turnover by 120% over complete pruning in 2-year-old trees. However, fine root and nodule production, which began at 10 weeks after pruning, was sufficient to compensate for losses due to senescence. The physiology of tree recovery was affected more by the timing of pruning than by pruning intensity. Pruning during the wetter period in December did not deplete non-structural carbohydrate reserves (starch) in roots. Pruning during the drier period in March reduced starch levels, more in stems than in roots. Starch depletion was apparent at six weeks after pruning when sprout development was most vigorous. In *G. sepium*, starch re-synthesis in roots reached 70 percent of its initial level by 12 weeks after pruning; at this time, replenishment in *E. poeppigiana* was commencing. Management of *E. poeppigiana* trees in alley cropping systems in the humid tropics of Costa Rica by partial rather than complete pruning maintains fine root capacity for N uptake, increases N cycling, and contributes more organic matter to soil. Pruning management of both *E. poeppigiana* and *G. sepium* should consider that these species require a regrowth period longer than 12 weeks to replenish carbohydrate reserves in their roots. Moreover, pruning during the dry period depletes more non-structural carbohydrate reserves than pruning during the wet period.

CHESNEY, P.E.K. 2000. Efectos de la Poda Sobre las Raíces de los Arboles Fijadores de Nitrógeno en el Trópico Húmedo. Tesis de Ph.D., CATIE, Turrialba.

Palabras claves: cultivo en callejones, distribución, *Erythrina poeppigiana*, raíces finas, *Gliricidia sepium*, histología, nitrógeno, nódulos, carbohidratos no estructurales, fósforo, regeneración.

Resumen

En el sistema de cultivo en callejones en los trópicos húmedos los árboles leguminosos de rápido crecimiento son totalmente podados a intervalos de seis meses, para reducir la competencia árbol-cultivo por luz y como suministro materiales orgánicos para la nutrición del cultivo. El incremento en la frecuencia de poda para mejorar los rendimientos comerciales fue recomendado a partir de experiencias de investigación en cultivo en callejones con maíz y tomate. La poda completa de los árboles causa pérdida de raíces finas y de los nódulos, resultando en competencia árbol-cultivo por el nitrógeno (N) del suelo, durante el periodo de recuperación de los árboles. Este efecto podría aumentar si incrementa la frecuencia de la poda. Como una alternativa, la poda parcial podría tener un efecto mas conservador sobre las raíces y nódulos, sin embargo, el conocimiento actual de esta practica es incompleto. El presente estudio se llevó a cabo en condiciones de trópico húmedo en Turrialba, Costa Rica. Los objetivos fueron: 1) evaluar los efectos de la poda completa y parcial sobre N acumulado en la biomasa, y la dinámica del N en suelo, las raíces finas y nódulos de árboles de *Erythrina poeppigiana*, y 2) determinar la fisiología de recuperación de árboles podados de *Erythrina poeppigiana* y *Gliricidia sepium*. Por el método de incubación se midió la tasa de mineralización y de nitrificación en parcelas de *E. poeppigiana*. La acumulación de N en biomasa aérea se determinó por el método micro-kjeldahl. Se usó el modelo de flujo de la biomasa de raíces finas y nódulos en compartimientos para determinar la producción y renovación de las mismas. La recuperación de los árboles podados, durante 12 semanas de crecimiento de los rebrotes, fue determinada a través los cambios en la concentración de almidón (método Lugol) y carbohidratos solubles (método HPLC). La tasa de rebote se midió a través del numero de brotes activos comparados con el numero de brotes desarrollados. El estudio mostró que la intensidad de la poda no afectó significativamente la mineralización de N, ni la nitrificación. Los árboles de dos y ocho años de edad podados parcialmente produjeron 187

kg y 256 kg N ha^{-1} de biomasa, respectivamente, que fue un 50% más que al aplicar poda completa. Esta diferencia puede atribuirse principalmente al efecto conservativo de la poda parcial en la producción de nódulos y raíces finas. Durante un periodo de 5 meses, el promedio de raíces finas fue de 821 m vs. 489 m $árbol^{-1}$ para árboles de dos años con poda parcial vs. poda completa, respectivamente. Los árboles de 8 años presentaron valores menores en un 40%. La poda parcial aumentó la senescencia de las raíces finas y los nódulos en 50% y 120%, respectivamente, en comparación con la poda completa. Sin embargo, la producción de raíces finas y nódulos empezó un proceso de recuperación a las 10 semanas después de la poda. Esto fue suficiente para compensar las perdidas debido a la senescencia. La fisiología de la recuperación del árbol fue mas afectado por el periodo de la poda que por la intensidad de ella. La aplicación de la poda durante la época lluviosa en Diciembre, no resultó en la disminución de los carbohidratos reservados (almidón) en las raíces. La aplicación de la poda durante la época seca en Marzo, resultó en mayor disminución del nivel de almidón en el tallo que en las raíces. La disminución del contenido de almidón ocurrió a las seis semanas después de la poda, cuando el desarrollo del rebrote era más vigoroso. La concentración inicial de almidón en las raíces fue re-abastecida en un 70 por ciento a las 12 semanas después de la poda en *G. sepium;* en ese momento, el re-abastecimiento de almidón en *E. poeppigiana* estaba comenzando. Se puede lograr mayor conservación del sistema de adquisición de nutrientes y el mejoramiento en el reciclaje de N en árboles de *E. poeppigiana* con la poda parcial comparado con la poda completa. La recuperación de los árboles resultó en una mayor disminución de los carbohidratos reservados cuando la poda se llevó a cabo durante la época seca que en la época lluviosa. Se necesitó mas de 12 semanas para permitir el relleno de las reservas en las raíces. Este estudio mostró que el manejo de los árboles de *E. Poeppigiana*, en sistemas agroforestales en el trópico húmedo de Costa Rica, es mucho mejor cuando se aplica poda parcial comparado con la poda completa, dado que permite mantener la capacidad de absorción de N, aumenta en el reciclaje de N y la contribución de materia orgánica al suelo. El manejo de la poda de *E. poeppigiana* y *G. sepium* debe considerar que estas especies requieren un periodo mas largo de rebrote, superior a las doce semanas, para rellenar las reservas de carbohidratos en las raíces. Además, la poda durante la época seca produce una reducción mayor de las reservas carbohidratos si se compara con la poda durante la época lluviosa.

CHESNEY, P.E.K. 2000. Schneitelwirkung auf Wurzeln von Leguminosenbaumarten in den humiden Tropen. Dissertation, CATIE, Turrialba.
Stichwörter: Agroforstsysteme, *Gliricidia sepium, Erythrina poeppigiana*, Feinwurzeln, Histologie, Lebendpfosten, Kohlenhydrathaushalt, Stickstoff, Phosphor

Zusammenfassung

Im tropischen Schneisenanbau werden schnellwüchsige Baumleguminosen traditionell halbjährlich geschneitelt, um die Lichtkonkurrenz zwischen Bäumen und den landwirtschaftlichen Kulturpflanzen zu reduzieren und dabei Nährstoffe über den biologischen Kreislauf dem System wieder zuzuführen. Häufiges Schneiteln der Bäume ist mit einem Verlust an Feinwurzeln und Wurzelknöllchen verbunden; dies fuehrt zu einer Konkurrenz um Bodenstickstoff (N) zwischen Bäumen und Kulturpflanzen. Aus früheren Untersuchungen mit Mais und Tomaten ist bekannt, dass häufiges Schneitel aus phytosanitärer und produktionstechnischer Sicht zur Ertragsmaximierung notwendig ist. Die aktuelle Kenntnis über den Schneiteleffekt auf die Baumwurzeln ist unzureichend, um Entscheidungen bezüglich des optimalen Zeitpunktes und der Intensität des Schneitelns zu treffen. Diese Studie untersuchte den Effekt vollständigen und partiellen Schneitelns auf Feinwurzeln, Wurzelknöllchen, N-Mineralisierung und Kohlenhydrathaushalt von *Erythrina poeppigiana* and *Gliricidia sepium* als Lebendpfosten für Tomaten in Turrialba, Costa Rica. Netto Stickstoffmineralisations- und Nitrifikationsraten wurden an im Feld inkubiertem Boden bestimmt, der Parzellen mit *E. poeppigiana* Applikation entnommen wurde. Die Akkumulation von Mikro-Kjeldahl N in der geschneitelten Baumbiomasse wurde berechnet. Die Produktion und der Umsatz von Feinwurzeln und Wurzelknöellchen wurde mittels des "compartment flow model" bestimmt, das auf die Feinwurzel- und Wurzelknöellchenbiomasse angewandt wurde, die in periodisch entnommenen Bohrkernen gemessen wurde. Die Erholung geschneitelter Bäume wurde bis zu 12 Wochen nach dem Schneiteln beobachtet indem Aenderungen im Staerkegehalt des Wurzel- und Stammgewebes sowie von loeslichen Kohlenhydraten (HPLC) und Wachstumsraten der Sprosse festgehalten wurden. In einem einjährigen Schneitelzyklus wurden die Bäume viermal geschneitelt. Die partiell geschneitelten zwei und acht Jahre alten Bäume akkumulierten je 187 kg und 256 kg N ha^{-1} in der oberirdischen Biomasse, 50% mehr als

die vollständig geschneitelten Bäume. Dieser Unterschied wurde vor allem auf den konservierenden Effekt des partiellen Schneitelns auf die Produktion der Feinwurzeln und Wurzelknöllchen zurückgeführt. Während eines fünfmonatigen Schneitelintervalls hatten zweijaehrige partiell geschneitelte Baeume eine Feinwurzellänge von 821 m je Baum im Gegensatz zu 489 m je Baum bei vollständig geschneitelten Bäumen akkumuliert; bei achtjähren Bäumen lagen die Werte um 40% niedriger. Der Feinwurzelumsatz, bestimmt nach dem "compartment flow model", für partiell im Vergleich zu vollständig geschneitelten zwei jaehrigen Bäumen lag bei 24 bzw. 16 g je Baum, und der Wurzelknöllchenumsatz bei 47 bzw. 103 g je Baum, bei einer entsprechenden Feinwurzelproduktion von 38 bzw. 11 g je Baum und Wurzelknöllchen-produktion von 58 bzw. 115 g je Baum. Die Stärkekonzentration in Wurzeln sowie Stamm war sechs Wochen nach dem Schneiteln signifikant reduziert gegenüber ungeschneitelten Bäumen. Die ursprüngliche Stärkekonzentration in den Wurzeln war bei *G. sepium* 12 Wochen nach dem Schneiteln zu 70% wieder aufgefüllt, während ein Anstieg der Kohlenhydrate bei *E. poeppigiana* erst jetzt einsetzte. Partielles im Gegensatz zu vollständigem Schneiteln kann die Nährstoffaufnahme und den Kreislauf von *E. poeppigiana* erhalten. Nicht-strukturelle Kohlenhydratreserven werden durch das Nachwachsen des Baumes stärker erschöpft, wenn das Schneiteln während der Trockenzeit durchgeführt wird im Vergleich zur Regenzeit. Die Erschöpfung dieser Reserven in den Wurzeln benoetigt eine Erholungsphase von mehr als 12 Wochen. Partielles im Gegensatz zu vollständigem Schneiteln von *E. poeppigiana* im Schneisenanbau in den humiden Tropen Costa Rica erhaelt die Kapazitaet der Feinwurzeln zur N-Aufnahme, foerdert N-"cycling" und fuehrt dem Boden mehr organische Substanz zu. Das Schneitelregime von *E. poeppigiana* als auch *G. sepium* sollte berücksichtigen, dass diese Arten eine Erholungsphase von mehr als 12 Wochen brauchen, um die Kohlenhydratreserven in den Wurzeln wiederaufzufuellen. Schneiteln während der Trockenzeit erschöpft die Reserven an nicht-strukturellen Kohlenhydraten in einem stärkeren Ausmass als Schneiteln während der Regenzeit.

List of abbreviations

CATIE	Centro Agronómico Tropical de Investigación y Enseñanza
CFM	Compartment flow model
CP	Complete pruning
DM	Dry matter
FRB	Fine root biomass
FRL	Fine root length
GLM	General linear model
HPLC	High-Performance Liquid Chromatography
NA	Number of activated buds
NS	Number of sprouts
PP	Partial pruning
REGWQ	Ryan-Elinot-Gabriel-Welsch multiple range test
RLD	Root length density
RML	Root mass: length ratio
SAS	Statistical analysis system
SD	Standard deviation
SE	Standard error
WAP	Weeks after pruning
WAS	Weeks after sowing
WAT	Weeks after transplanting

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1. INTRODUCTION

1.1 Problem statement

Alley cropping is the growing of annual crops in alleys between rows of planted fast growing, N-fixing leguminous trees (Kang and Wilson, 1987). The trees are managed by periodical pruning[1] to prevent shading of the associated crop (Rao *et al* 1998), and the nutrient-containing pruned materials are usually incorporated as green manure or applied as mulch to support crop nutrition and to protect the soil. In Costa Rica, it is common practice to completely prune alley cropping trees at half-yearly intervals. However, research experiences with maize (*Zea mays* L.) (Kass *et al* 1992) and tomato (*Lycopersicon esculentum* Mill.) (Schlönvoigt and Chesney 1999; Chesney *et al* 2000a,b) alley crops recommend increased pruning frequency to increase yield and lower fruit losses.

The effects of complete pruning applied more frequently than twice a year, or alternatively less severe forms of pruning, on nutrient acquisition systems, or the importance of non-structural carbohydrate reserves to tree pruning tolerance are not well studied in tropical agroforestry species. Although partial pruning of shade trees is practiced in coffee (*Coffea arabica* L.) farms in Turrialba and in the Central Valley of Costa Rica, (Somarriba *et al* 1996), very little is reported on the merits of this practice.

1.2 Pruning of nitrogen fixing trees

Pruning application in agroforestry enhances resource (mainly light) supply (Cannell 1983), and use of the resource is by competitive interaction between species (Anderson and Sinclair 1993). In alley cropping, tree-crop competition for light exceeds or nullifies the positive contributions to soil fertility made by the service trees (Rao *et al* 1998). Analysis of alley cropping data from Turrialba, Costa Rica (Kass 1987) has shown negative (-3%), or near neutral (1%) estimates of overall interaction effect[2] for commonly used *Erythrina poeppigiana* (Walp.) O.F. Cook and *Gliricidia sepium* (Jacq.) Kunth ex Walp. hedgerow trees, respectively (Sanchez 1995).

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[1] Shoot pruning is the removal of selected vegetative shoots from trees (Larson 1980); a management activity commonly referred to as green pruning in the forestry literature (Dictionary of Forestry 1998). Green pruning may be complete or partial. Throughout this thesis, reference to pruning is understood to mean shoot pruning.

Pruning trees to achieve positive ecological interactions aboveground inevitably results in negative ecological interactions belowground, a phenomenon explained by the functional equilibrium hypothesis (Brouwer 1982). Complete pruning at half yearly intervals has increased the turnover of nodules (Nygren and Ramírez 1995) and fine roots (Lehman and Zech 1998) of trees, increasing the likelihood of interspecific nutrient competition during tree recovery (Kass *et al* 1997). In addition, increased pruning frequency has reduced shoot biomass and increased tree mortality (Romero *et al* 1993), probably due to negative carbon balance (Lawson and Mobbs 1998). Quantification of the effects of frequent complete versus partial pruning on fine roots, nodules and nitrogen and the internal plant factors affecting the tree's tolerance to pruning will contribute to refining tree management for enhanced alley cropping applications in the humid tropics.

Managing trees on farms has importance for Central America where an estimated four million hectares of mainly treeless hillsides farmed with annual crops (Lindarte and Benito 1993) suffer soil and mineral element erosion, and consequent dependence on inorganic sources for plant nutrition (Pimental *et al* 1995). The current high adoption of alley cropping (Current *et al* 1995) is encouraging to the increase of tree cover in agricultural fields.

1.3 Objectives

The **general objective** of the study was to elucidate the effects of pruning on nutrient acquisition systems of two common alley cropping trees, *E. poeppigiana* and *G. sepium*, that provide organic inputs to vegetable crops (Figure 1). The **specific objectives** were to determine the effect of complete and partial pruning on:

1. fine root, nodule and nitrogen dynamics in *Erythrina poeppigiana* trees.

2. the dynamics of non-structural carbohydrate reserves in roots and stems during early regrowth of *E. poeppigiana* and *G. sepium* trees.

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[2] A positive value means net complementarity and a negative value means net competition to the detriment of crop yields; net complementarity is the desired outcome of agroforestry (Sanchez 1995)

1.4 Hypotheses

1. Accumulated N in shoot biomass, available soil N and fine root length will be influenced by shoot pruning intensity.

2. The magnitude of production and turnover of fine roots and nodules will depend on pruning intensity.

3. Pruned trees will mobilise non-structural carbohydrate reserves in roots for early shoot regrowth; the intensity of pruning being directly related to the rate of depletion of these resources.

Figure 1. Live stake-tomato agroforestry practice with *Erythrina poeppigiana* stake 3 x 2 m and tomato variety Dina Panama 1.5 x 0.5 m.

2. LITERATURE REVIEW

2.1 *Functional relationship between shoots and roots*

> "The success of agroforestry systems may be favoured by maintenance of non-equilibrium conditions derived from such practices as pruning and soil amelioration....." (Kass *et al* 1997).

The 'functional equilibrium' hypothesis proposed by Brouwer (1962, 1983) contends that plants display a tendency to maintain a constant balance between growth rates of shoots and roots. This balance is regulated by the demand for plant resources such as non-structural carbohydrates and nitrogen (N). When N limits growth, root growth is relatively favoured and when the limiting factor is non-structural carbohydrate, which can occur after shoot pruning, aboveground growth is relatively favoured. The typical plant response in the restoration of, or the establishment of a new functional equilibrium between shoots and roots, is to mobilise non-structural carbohydrate reserves in the stem (Erdmann *et al* 1993) or roots (Von Fircks and Sennerby-Forsse, 1998) to support resprouting and early shoot growth.

2.2 *Nutrient acquisition systems: fine roots and nodules*

The acropetal flow of mobilised non-structural carbohydrates has been associated with the turnover of nodules and fine roots (Eissenstat and Yanai 1997). There is evidence that half-yearly complete pruning of agroforestry trees in the humid tropics causes about 50-75 % turnover of fine roots (Nygren and Campos 1995; Muñoz and Beer, in press) and almost complete turnover of nodules (Fownes and Anderson 1991; Nygren and Ramírez, 1995; Nygren and Cruz, 1998). While the photosynthetic system of *E. poeppigiana* matures, re-nodulation of tree roots is delayed for 10-16 weeks (Vaast and Snoeck 1999) during which time the likelihood of tree-crop competition for soil N increases (Kass *et al* 1997). Recent evidence has shown that partial pruning may have a less drastic effect on nodule turnover (Nygren and Cruz 1998); and possibly fine roots, probably through exploitation of non-structural carbohydrate reserves in stems rather than from comparatively higher reserves in roots during regrowth of trees (Erdmann *et al* 1993).

Root and nodule mass provide a useful measure of plant investment in root systems (Caldwell and Virginia 1991; Fitter 1991) and root length is associated with absorptive capacity of root systems (Nye and Tinker 1977; Marschner 1997). Estimates of fine root production and turnover are critical to tree pruning studies. Soil coring remains the most practical and frequently used method to obtain root samples (Caldwell and Virginia 1991). The compartment flow model (CFM) has been applied for estimating the production and turnover of fine roots (Santantonio and Grace 1987; Mäkela and Vanninen 2000) and nodules (Nygren and Ramírez 1995). It has been shown to be the most accurate estimation method in comparison to the maximum-minimum and balancing-transfer methods (Publicover and Vogt 1993; Lehman and Zech 1998).

According to the CFM approach, the change in nodule and fine root biomass can be determined from the successive samplings, and the decomposition rate can be determined independently. The total production (P_i) and senescence (S_i), during the time interval i between the samplings can be estimated by solving a system of difference equations. Let M and N denote the biomass and necromass, respectively, of nodules or fine roots, and D_i the necromass decomposed during interval i. Assuming that the decomposition follows a negative exponential decay function, the necromass remaining at the end of interval i (N_t) is:

$$N_t = N_0 \cdot \exp(-k \cdot t_i) \tag{1}$$

where, N_0 is the initial necromass, t_i the length of the time interval i, and k the decay coefficient. It can be shown that with these assumptions, the total senescence during the interval i is (Santantonio and Grace 1987; Nygren and Ramírez 1995):

$$S_i = \frac{t_i \cdot k \cdot (N_t - N_0 \cdot \exp(-k \cdot t_i))}{1 - \exp(-k \cdot t_i)} \tag{2}$$

and total production and decomposition during the interval i can be calculated:

$$D_i = N_0 - N_t + S_i \tag{3}$$

$$P_i = M_t - M_0 + S_i \tag{4}$$

where, subscripts 0 and t refer to the biomass or necromass at the beginning and end of interval i, respectively. The equations (1) - (4) hold both for nodules and fine roots, but the

decay coefficient k is specific for the decaying material, and must be determined separately for nodules and fine roots.

Main conclusions: Complete pruning causes drastic changes in nodule and fine root growth and can lead to tree-crop competition for N during tree regrowth; partial pruning may conserve fine roots and nodules.

2.3 *Effect of pruning on nutrient cycling*

In unfertilised alley cropping, the main source of N may be from mineralisation of pruned materials (Palm 1995). Unlike natural litter fall, pruning does not allow for N remobilisation in leaves to stems or roots for storage and senescing roots do not re-translocate nutrients (Nambiar 1987). Thus both pruned biomass materials and senescing roots and nodules are potentially nutrient-rich organic sources that are quite important for internal nutrient cycling (Huck 1983). Frequent pruning can increase N in shoot regrowth (Peoples *et al* 1996) probably due to higher N partitioning to shoots (Sanginga *et al* 1994).

Leaves of *E. poeppigiana* and *G. sepium* trees are of high quality (Palm 1990, 1991) and they readily decompose (Haggar *et al* 1993; Budelman 1987) liberating high quantities of nutrient elements. Total tissue N content of *E. poeppigiana* biomass from three prunings a year was 173 kg ha^{-1} $year^{-1}$ (Russo and Budowski 1986). Periodically pruned trees can cycle up to 90% of nutrients (Beer 1988) and 70-80 % of total N may be in prunings of *E. poeppigiana* (Nygren 1995). Senescing nodules of *E. poeppigiana* trees pruned twice a year can contribute approximately 9 kg N ha^{-1} in 6 months (Nygren and Ramírez 1995). Trees must maintain the ability to absorb available N, to avoid leaching losses in high rainfall areas. This aim may be achieved with partial pruning (Vanlauwe and Sanginga 1995) possibly through its conservative effect on fine root length.

Biomass can be measured directly (destructive), or predicted (non-destructive) using process based models (Harrington and Fownes 1993, Droppelmann and Berliner 2000). Direct measurement is more laborious but involves less computation time. In this study, direct measurement by sub-sampling was used and the pruned material applied both as green manure and mulch. Aboveground tree biomass serves as an important store for N, which is then made available to plants through mineralisation of biomass added to soil (Marschner 1997).

Due to the strong effect of site environmental factors on soil N transformation rates, field methods are preferred to laboratory methods to assess the N supplying power of a soil. Net accumulation of inorganic N in the absence of plant roots can be estimated using closed-top, solid cylinder and bury-bag methods in sites where a water table does not exist near the soil surface (Hart *et al* 1994).

Main conclusions: Shoot growth in pruned trees is at the expense of nodule and root growth. N assimilated in plants is derived from inorganic N pools, to which pruned tree material and senescent roots and nodules are periodic contributors.

2.4 *Physiological demands of shoot regrowth*

Shoot regrowth is dependent on the mobilisation of non-structural carbohydrate reserves to drive early energy demanding processes (Lambers *et al* 1999). Starch is considered the most important non-structural carbohydrate reserve (Kozlowski and Keller, 1966), whose role has been studied extensively in horticultural crops (Loescher *et al* 1990). Data for trees used in agroforestry are few especially in connection to pruning.

There is evidence that non-structural carbohydrate reserves, mainly starch (Adams *et al* 1986) provide the energy for resprouting in pruned trees (Eissenstat and Yanai 1997; Kandiah 1979), the organ source of which may be stem (Erdmann *et al* 1993) or roots (Miyanishi and Kellman 1986; von Fircks and Sennersby-Forsse 1998). In roots, post-prune starch activity takes place in vascular tissues (Selvendran and Selvendran 1972; Gholz and Cropper 1991), to which root diameter is of functional importance (Wargo 1975). Histochemistry has been used to study seasonal changes in starch content in roots and stems of temperate hardwoods (Wargo 1975, 1976; Essiamah and Eschrich 1985) as well as the effects of coppicing on root starch mobilization (von Fircks and Sennerby-Forsse 1998). It can help in elucidating the role of root diameter in root starch dynamics.

Plant tolerance to defoliation has been associated with rapid regrowth of foliage following defoliation (Richards and Caldwell, 1985). Foliage regrowth is affected by the allocation of metabolically active nutrients (N, P) to maximise C fixation and growth (Loescher *et al* 1990). Also, the number and rate of bud development are important.

Main conclusions: Non-structural carbohydrates reserves, mainly starch, and N and P, are important to tree recuperation. The organ source of starch is species specific.

3. MATERIALS AND METHODS

3.1 Overview of research

From September 1998 to February 1999 a preliminary field experiment assessed the agronomic performance of a live-stake agroforestry practice and the results have been reported elsewhere (Schlönvoigt and Chesney 1999; Chesney *et al* 2000a, b). In September 1998, inventory vertical and horizontal fine root distribution was determined from coring procedure to facilitate planning of root sampling for the study of fine root and nodule dynamics. Field plots were fallowed from February to May 1999. From May 1999 to June 2000, two field experiments were conducted at CATIE, and the related laboratory analyses were undertaken at CATIE and 'Universidad Nacional', Heredia, Costa Rica. Experiment 1 elucidated the effects of pruning on N, fine root and nodule dynamics in *E. poeppigiana* during a one-year pruning cycle in which pruning intervals were based on crop needs. Experiment 2 investigated the physiology of regrowth of *E. poeppigiana* and *G. sepium* trees during two pruning cycles each of three months duration. Experiments 1 and 2 were carried out in separate experimental plots at the La Montaña experimental farm.

3.2 Description and history of the experimental site

The La Montaña experimental farm of CATIE, Turrialba, Costa Rica (9^0 53' N, 83^0 43' W, 602 m.a.s.l) is part of ecological zone described as a very humid pre-montane forest (Holdridge, 1987). The soil is a Eutric Cambisol of fine halloysitic isohyperthermic materials derived from alluvial deposits of volcanic origin (Kass *et al* 1995). The climate[3] is classified as Köppen Af, mean annual precipitation is 2636 mm, soil moisture regime is udic, and a drier period occurs between February and April. Mean monthly temperature is 22 ^{0}C.

The study site was cropped to sugar cane (*Saccharum oficinarum* L.) and coffee (*Coffea arabica* L.) prior to the establishment of an alley cropping experiment in January 1991. Vegetatively propagated *E. poeppigiana* CATIE clone 2708, and *G. sepium*, (living fence provenance, Atlantic lowland region of Guapiles, Costa Rica), and generatively propagated *Calliandra calothyrsus* Meissn., selected from CATIE Seed Bank, were planted

in plots measuring 384 m^2 each. Tree spacing was 6 x 2 m, 6 x 0.5 m and 6 x 1 m, respectively. Tree species along with a treeless control treatments, were arranged in a randomised completely block design with three replications.

Previous research included, 1992-1996: crop variety tests (Limón 1993), land preparation, planting density, (Quintanilla 1995), soil chemistry and physics (Heredia 1996); 1997: nutrient cycling and competition in a bean (*Phaseolus vulgaris* L.) alley crop (Henriksen, 1999). After 1997, alley width was halved to 3 m with the inclusion of rows of stakes (*E. poeppigiana, G. sepium*) taken from mature trees in the same plot or seedlings (*C. calothyrsus*, from the CATIE Seed Bank); within-row spacing was thinned to 2 m. In this thesis, the trees planted in 1991 will be referred to as 8-year-old trees, and the trees planted in the original alleyways in 1997 will be referred to as 2-year-old trees. Trees were completely pruned to 1 m height once every six months (1992 to 1995) or once a year (1996) with additional topsoil (0-20 cm) root pruning in 1997. Pruning height was increased to 1.5 m for tomato staking and pruning frequency increased to three a year in 1998.

3.3 Inventory fine root distribution

In September 1998, core (auger cylinder diameter = 8 cm; L = 25 cm) samples were taken at 20, 50 and 100 cm distance from hedgerow each to 20, 40 and 60 cm soil depth, within a 1.5 m^2 unit soil area. A modal 8-year-old *E. poeppigiana* or *G. sepium* tree occupied the centre of the area. Fine roots (<2 mm) were washed in 0.5 mm sieve under running tap water; live root length was measured by WinRhizo Pro® (Regent Instruments, Quebec, Canada) and oven dried (50 ^{0}C for 48 h) for biomass. Fine root length density (cm cm^{-3}) was computed.

3.4 Experiment 1: N, fine root and nodule dynamics (Articles I, II)

The effects of complete and partial pruning on N accumulation in foliar biomass, net N mineralisation and net nitrification rates, fine root length and biomass, and nodule biomass, were studied in a split plot in time design with three replications. Mainplot factor

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[3] Specific meteorological data during field experiments are included in the *Materials and Methods* section of the source articles included in Part II

was pruning intensity, A (A_0 = complete i.e. removal of all shoots; A_1 = partial i.e. retention of one branch corresponding to 5% of total shoot biomass) (Figure 2). Subplot factor was pruning date, B (B_1 = May 1999; B_2 = Aug 1999; B_3 = Nov 1999; B_4 = Jan 2000; B_5 = May 2000) (Figure 3). The basic statistical model was:

$$Y_{ijk} = \mu + r_i + A_j + \gamma_{ij} + B_k + AB_{jk} + \varepsilon_{ijk}$$

where, Y_{ijk} represent the response variable (biomass, fine root, nodule or N) in the *i*th block of a randomised complete block design, on the *j*th mainplot treatment with the *k*th subplot treatment. Where $i = 1,2,3$, replications; $j = 1,2$, A pruning intensity; $k = 1,\ldots,5$, B pruning date; γ_{ij} and ε_{ijk} are random error components (Steele and Torrie 1980).

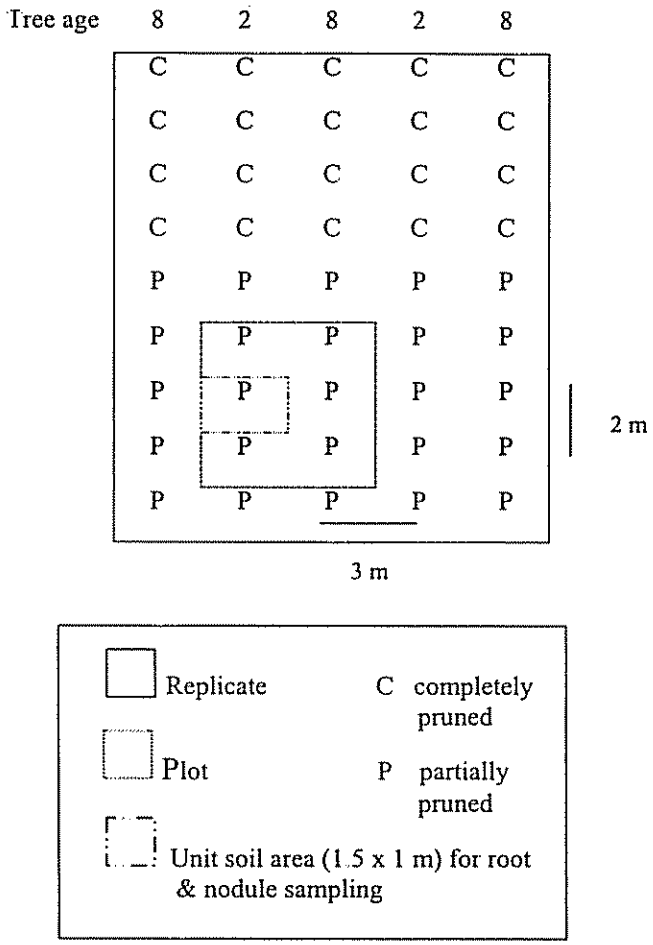

Figure 2. Layout of mainplot factor levels and an example of a unit soil area in one replicate, Turrialba.

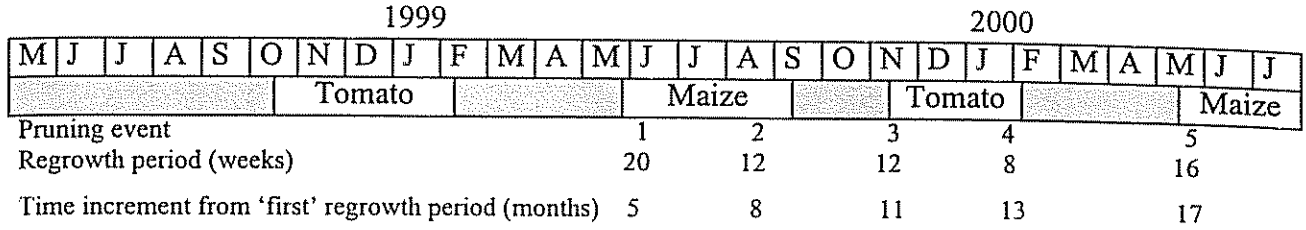

Figure 3. Chronogram of cropping and pruning (shaded cells are weed fallows).

Pruned biomass, tissue N accumulation, soil N and fine root length dynamics *(Article I)*

Pruned biomass and tissue N accumulation

On each pruning date, plot totals of fresh weights of pruned branches and leaves were measured. Nine branches with intact leaves were randomly selected and weighed with and without leaves to determine the proportion of leaf to branch biomass per plot. Oven dried (65 ^{0}C) mass was determined in 0.5 kg fresh weight sub-samples of chopped leaves, woody and non-woody branch parts to convert fresh biomass to dry biomass for each branch part. Tissue N concentration was determined by semi-micro kjeldahl (Weaver *et al* 1994) in oven-dried branch parts. N accumulation in biomass was computed as the sum of the product of oven-dried branch part and its N concentration.

Soil N dynamics

Net N mineralisation and nitrification rates in topsoil (0-20 cm) were determined using the closed-top solid cylinder field incubation method (Hart *et al* 1994). Sampling was carried out during the 1999-2000-tomato crop at pre-plant and during vegetative and flowering phases. Topsoil available N was measured after extraction with 2N KCl (Weaver *et al* 1994) on samples taken during the 1999 maize and 1999-2000 tomato crops.

Fine root length dynamics

Topsoil core samples were taken from a unit soil area of 1.5 m^2 at 2, 6, 10, 14 and 22 weeks after pruning (WAP) in August 1999. In May 2000, when tree regrowth was 16 weeks old, core samples were taken at soil depths of 0-20, 20-40, 40-60 cm. Samples were

washed in 0.5 mm sieve and live fine roots were measured for total length as described above.

Production and turnover of fine roots and nodules (Article II)

Fine root and nodule production and turnover in pruned 2- and 8-year-old trees were estimated by applying the compartment flow model (CFM) to fine root and nodule biomass and necromass measured in sequentially taken soil cores as described above. The decomposition rate constant k = 0.053 (Nygren and Ramírez 1995) was applied to the nodule data for estimation of turnover. Decomposition rate of fine roots was measured using standard mesh bag technique (McClaugherty and Aber 1982), and the decay coefficient constant k was fitted to equation $N_t = N_0 \cdot \exp(-k \cdot t_i)$ by the least squares method in SAS (Statistical Analysis System, Cary, NC).

3.6 *Experiment 2: Physiology of tree regrowth (Articles III, IV, V)*

The effect of pruning on the dynamics of non-structural carbohydrate reserves in roots and stems of resprouting trees was studied in a split plot in time design during December 1999 to March 2000 (wet period) and March to June 2000 (dry period). Mainplot factor was pruning intensity, A (A_0 = complete i.e. removal of all shoots; A_1 = partial i.e. retention of one branch with intact leaves corresponding to 5% of total shoot biomass). Subplot factor was sampling date, B (B_0 = at pruning (0 WAP); B_1 = 2WAP; B_2 = 6 WAP; B_3 = 12 WAP) (Figure 4). The statistical model was:

$$Y_{ijk} = \mu + A_j + \gamma A_{i(j)} + B_k + AB_{jk} + \varepsilon_{ik(j)}$$

Where, Y_{ijk} represent the observation (starch, soluble carbohydrates) in a completely randomised design, on the *j*th mainplot treatment with the *k*th subplot treatment. Let i = 1 to 5, or 1 to 4, repetitions, j = 1,2, A pruning intensity; k = 1,..,4, B pruning date; and $\gamma A_{i(j)}$ and $\varepsilon_{ik(j)}$ being random error components (Steel and Torrie 1980). The number of treatment repetitions was five (wet period) or four (dry period). Different experimental units were used during each period.

Starch and soluble carbohydrate dynamics (Article III):

During 1700-1800 h on each sampling date, root and stem tissues were collected, freeze dried by lyophilization and ground under liquid N. Starch was determined by the Lugol method after extraction with 0.1 mol l^{-1} pH 7.2-phosphate buffer (Caraway 1959). Soluble carbohydrates (fructose, glucose, saccharose) were analyzed by HPLC after hot water extraction (Lim 1986).

Histochemical analysis of starch content in roots of different diameter (Article IV)

The statistical model described above was expanded to include root diameter as an additional classification variable:

$$Y_{ijkl} = \mu + A_j + \gamma A_{i(j)} + B_k + AB_{jk} + \lambda Ab_{ik(j)} + C_l + AC_{jl} + BC_{kl} + ABC_{jkl} + \varepsilon_{il(jk)}$$

Where, Y_{ijk} represent the observation (starch) in a completely randomised design, on the *j*th mainplot treatment with the *k*th subplot treatment. Let $i = 1$ to 5, or 1 to 4, repetitions, $j =$ 1,2, A pruning intensity; $k = 1,..,4$, B sampling date; $l = 1,2,3$, C diameter; and $\gamma A_{i(j)}$, $\lambda Ab_{ik(j)}k$, and $\varepsilon_{il(jk)}$ being random error components (Steel and Torrie 1980). The number of treatment repetitions was five (wet period) or four (dry period). Different experimental units were used during each period.

Between 1700-1800 h on each sampling date (Figure 4), roots of different diameters (< 2, 2-10 and >10 mm) were collected, fixed in a solution of formalin, acetic acid and alcohol, sectioned and stained (CIRAD 1989). Starch granules were visually estimated according to an ordinal scale method after Wargo (1975, 1976).

Accumulation of N and P during regrowth (Article V):

This study was conducted in the field plots used for the chemical determination of non-structural carbohydrates. Biomass was determined per pruning intensity and replication using the direct measurement method. Tissue N (semi-micro kjeldahl) and P (nitric and perchloric acid digestion) concentrations (SSSA 1994) were determined in oven-dried (65 ^{0}C) leaves, branches and stems of differentially pruned trees at 12 WAP during both wet and dry periods. N and P accumulation in biomass was computed as the sum of the product of oven-dried tree part and its N or P concentration.

Figure 4. Single tree plot of *Erythrina poeppigiana* with root barrier delimiting 2 x 2 m area, and randomly allocated sampling dates B_0 to B_3.

3.7 Statistical analyses

All data sets were tested for homogeneity of variance and for normality; data sets were transformed if non-normal before applying analysis of variance procedures. Data were analysed by PROC GLM procedure in SAS (Statistical Analysis System, Cary, NC 1996). Means of significant effects were compared with REGWQ ($p \leq 0.05$) Orthogonal polynomial functions were applied to biomass data from experiment 1 to determine whether pruned biomass means were linearly related to the pruning date and whether there was a significant curvature in the trend of the means (Hoshmand 1994).

Nutrient (N and P) data are presented as means of composite samples (combined repetitions). Analysis of variance was conducted separately for each species and for each tree age.

4. RESULTS

4.1 Inventory fine root distribution

For both species, mean fine root length density and biomass were lower at greater soil depths. For *E. poeppigiana* trees, fine root length density and biomass were higher at the tree proximity zone of 1 m to the tree row than at 0.5 m (Figure 5). For *G. sepium*, while fine root length density was highest at the tree proximity zone of 1 m to the tree row than at 0.5 or 0.2 m; biomass was lowest in this zone (Figure 6). *G. sepium* had less fine root length at greater soil depth than *E. poeppigiana*.

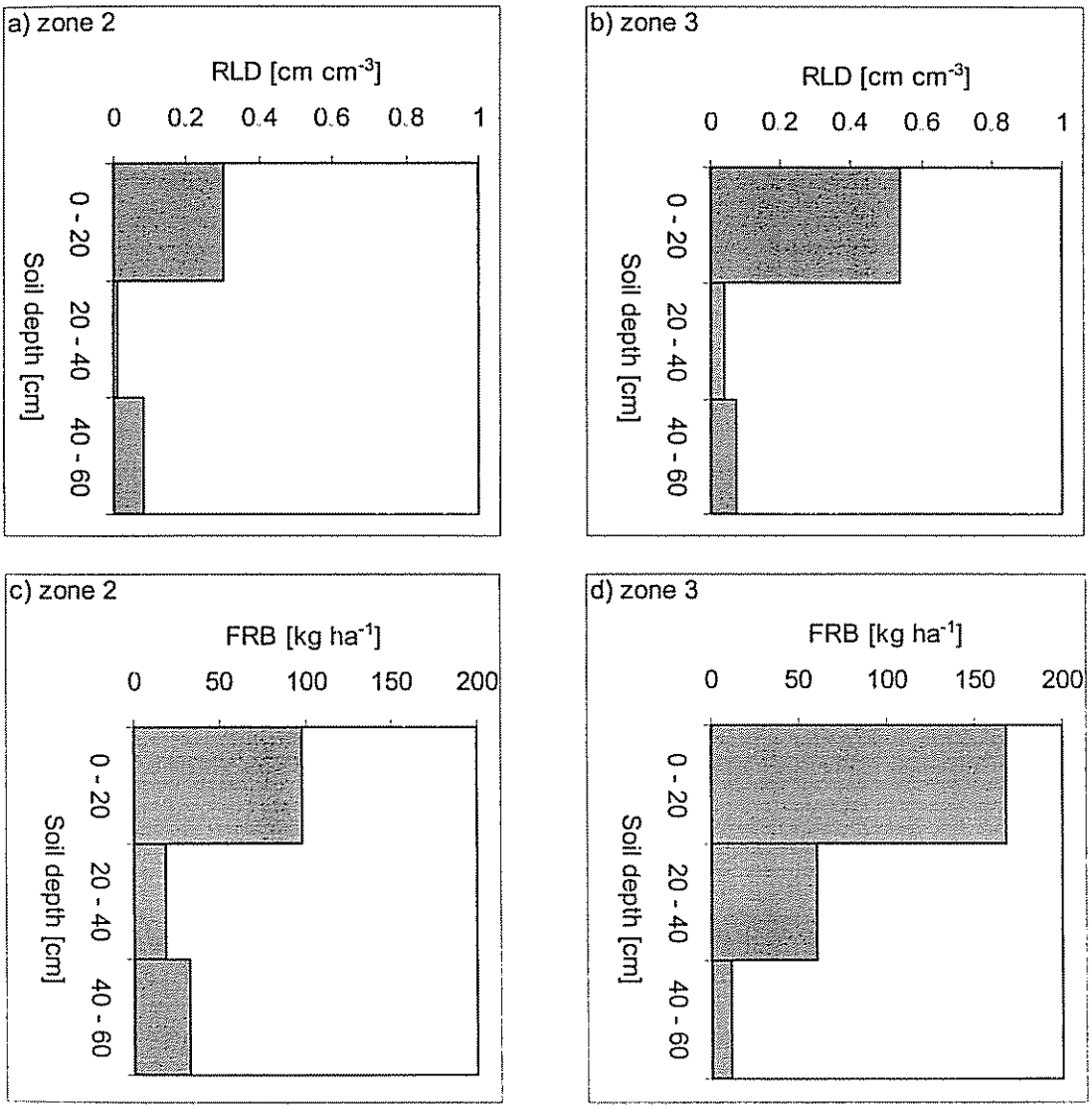

Figure 5. Distribution of fine root length density (RLD) and fine root biomass (FRB) of *Erythrina poeppigiana* at distances of 50 (zone 2) and 100 (zone 3) cm from tree row.

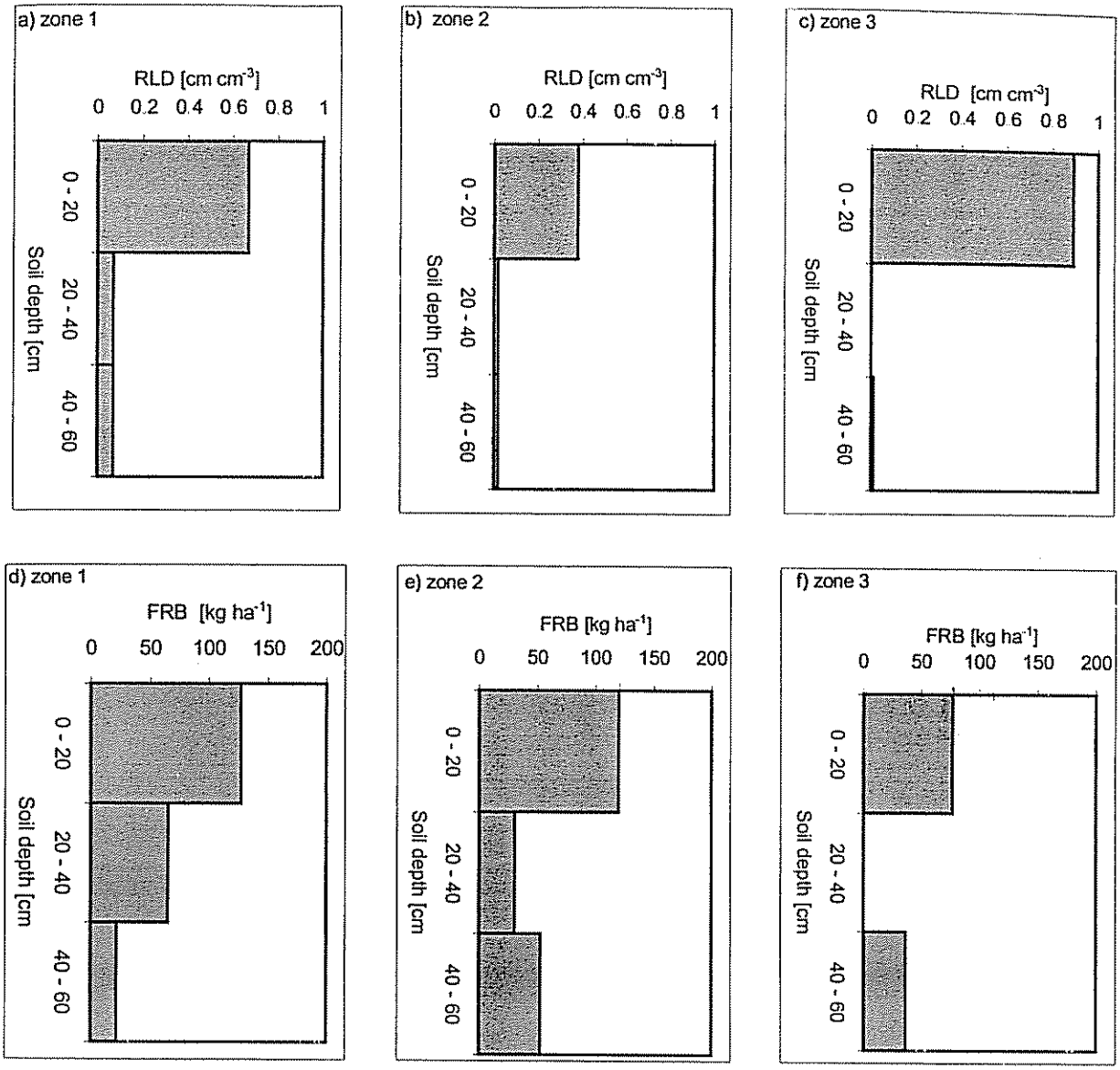

Figure 6. Distribution of fine root length density (RLD) and fine root biomass (FRB) of *Gliricidia sepium* at distances of 20 (zone 1), 50 (zone 2) and 100 (zone 3) cm from tree row.

4.2 *Experiment 1: N, fine root and nodule dynamics (Articles I, II)*

Pruned biomass and tissue N accumulation (Article I)

Plots of pruned biomass against pruning date showed that the relationship could best be described by a quadratic orthogonal polynomial function (Figure 7). Linear and quadratic effects were found to be highly significant for the pruning date treatments (Table 1). The quadratic function showed that the decrease in total biomass became less for each

increment in time. The rate of change of total biomass per time increment showed that for 2- and 8-year-old trees the minimum values for significant biomass change along the curvature were 14.7 months and 15.4 months, respectively. These values correspond to the period February-March 2000, when environmental conditions improved.

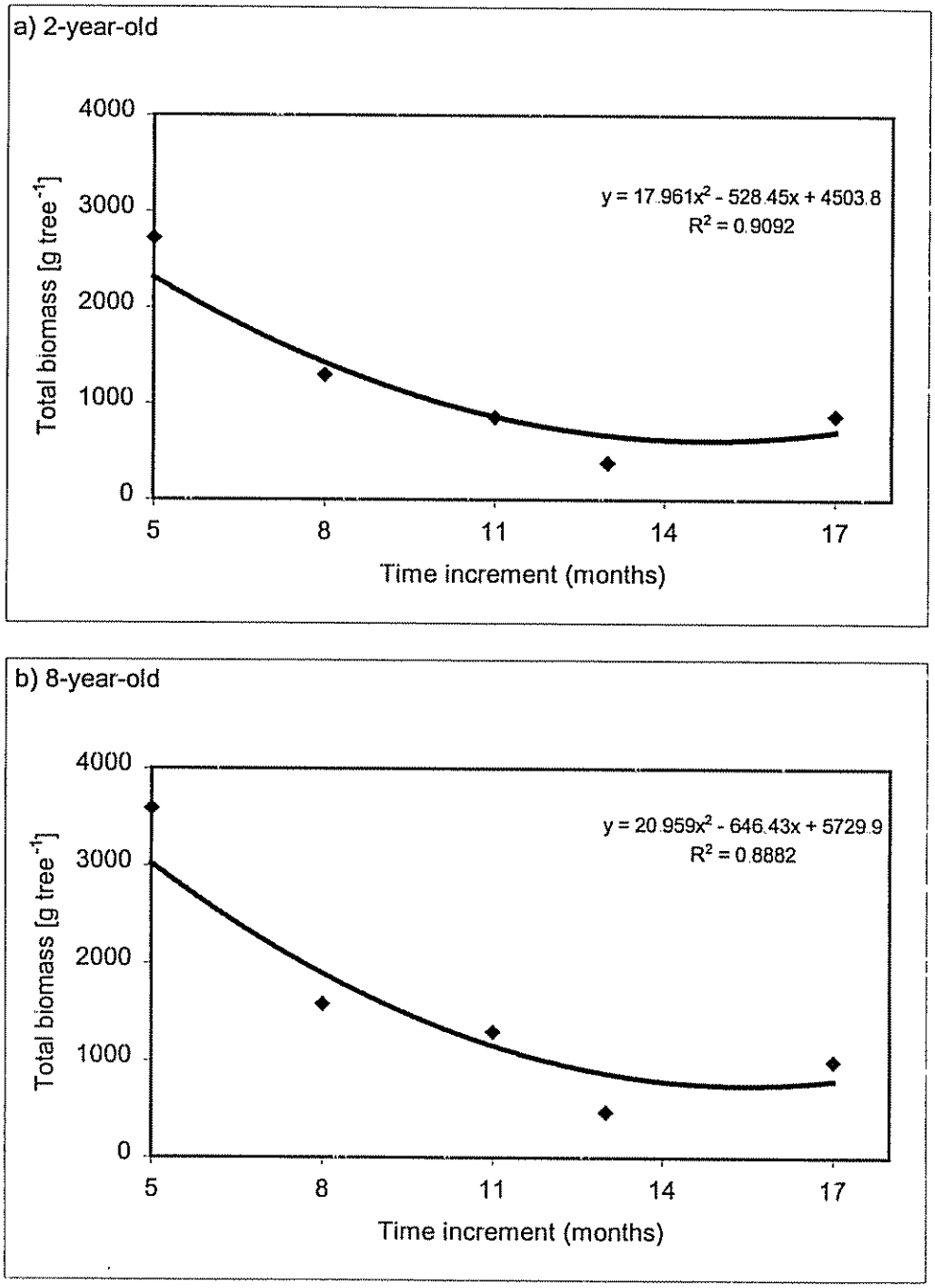

Figure 7. Relation between total pruned biomass and increment in time of 2-year-old and 8-year-old *Erythrina poeppigiana* trees, Turrialba. Increments in time are regrowth periods.

Table 1. Analysis of variance of the effects of pruning intensity, sampling date and the interaction between pruning intensity and sampling date on shoot biomass of 2- and 8-year-old *Erythrina poeppigiana* trees, Turrialba.

Source of variation	2-year-old			8-year-old		
	df	MS	Pr > F	df	MS	Pr > F
Blocks	2	108613		2	475053	
Pruning intensity	1	438637	0.1980	1	1689609	0.1592
Error (a)	2	121684		2	350236	
Pruning date	4	4805745	0.0001	4	8525869	0.0001
Linear	(1)	12718541	0.0001	(1)	23847502	0.0001
Quadratic	(1)	6162590	0.0001	(1)	8696259	0.0001
Others	(2)	170925	0.0734	(2)	779858	0.0100
Interaction	4	180668	0.0388	4	65076	0.7228
Error (b)	16	55543		16	125293	
Total	29			29		
r^2	0.96			0.95		

Between August 1999 and May 2000, partial pruning increased total N accumulated in pruned biomass by more than 50% over complete pruning (Table 2). Differences in accumulated N were due to the differences in the amounts of biomass (Article I) since leaf N concentration was similar for completely versus partially pruned trees; 3.6% vs. 3.7% (2-year-old) or 3.8% and 4% (8-year-old), respectively.

Soil N dynamics

Higher foliage biomass and N in the partial pruning treatment did not result in significantly higher net mineralisation and nitrification rates compared to complete pruning treatment. During crop development, mean net N mineralisation rates increased significantly from pre-plant 2.5 mg to 16.7 mg N kg^{-1} during vegetative development. Time course change in net nitrification rates was opposite to net mineralisation rates. Mean net nitrification rates decreased significantly from 4.3 mg N kg^{-1} soil during vegetative development to 0.3 mg N kg^{-1} soil during early fruit development. Mean net N mineralisation and net nitrification values in *E. poeppigiana* plot and treeless soil were not significantly different. Soil NO_3-N value of 4 kg ha^{-1} in *E. poeppigiana* plot during early December 1999, is about 14 times lower than preseason soil NO_3-N of 57 kg ha^{-1} measured during May 1999.

Table 2. Effects of shoot pruning *Erythrina poeppigiana* trees on total nitrogen pool in pruned total biomass, Turrialba, 1999-2000.

Age of stake (years)	Pruning Intensity	Total N (kg N ha^{-1})					Total [z] (mean [y])
		May 99	Aug 99	Nov 99	Jan 00	May 00	
2	Complete	119	42	32	13	36	123 (31)
	Partial	109	57	47	27	56	187 (47)
8	Complete	154	53	46	21	40	160 (40)
	Partial	169	82	78	29	67	256 (64)
	Mean	138	59	51	23	50	183 (46)

[z] in kg ha^{-1} yr^{-1} for the period August 1999 to May 2000; [y] in kg ha^{-1}. Dates from May 99 to May 00 correspond to regrowth periods of 20, 12, 12, 8 and 16 weeks, respectively.

Fine root length dynamics

Absorption of soil available N could be increased by the conservative effect of partial pruning on fine root length. Mean fine root length was 821 m and 489 m tree^{-1} for partially pruned 2- and 8-year-old trees, respectively. Corresponding values for 2- and 8-year-old complete pruned trees were 364 m and 184 m (Figure 8). In addition, partial pruning conserved 2 to 3 times more fine roots throughout the measured soil profile (0-60 cm) one year after the pruning regime was imposed (Figure 9).

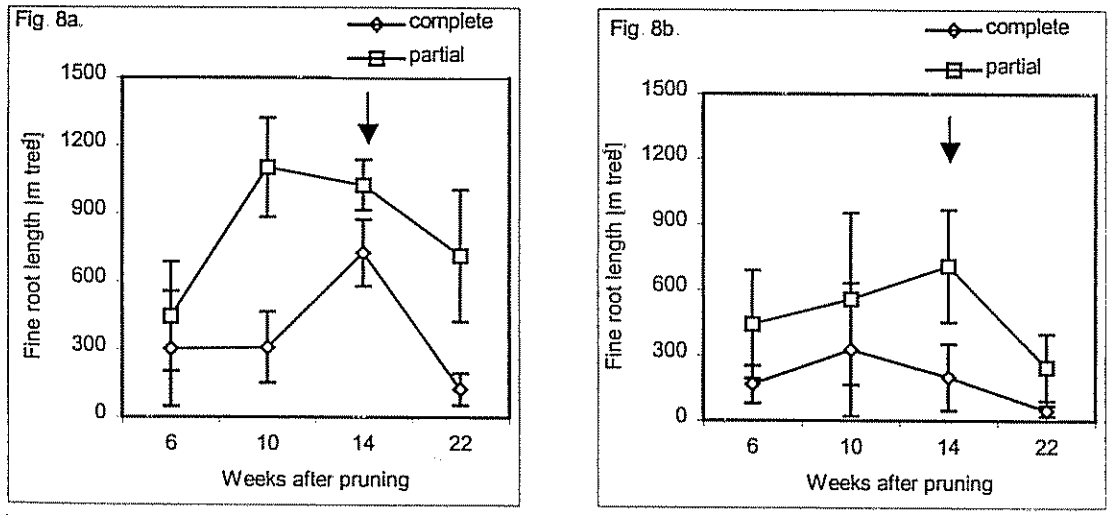

Figure 8. Effect of complete and partial pruning on fine root length dynamics in a) 2-year-old, and b) 8-year-old *Erythrina poeppigiana* tree. Bars are standard errors. The arrows indicate the pruning date 15 November 1999.

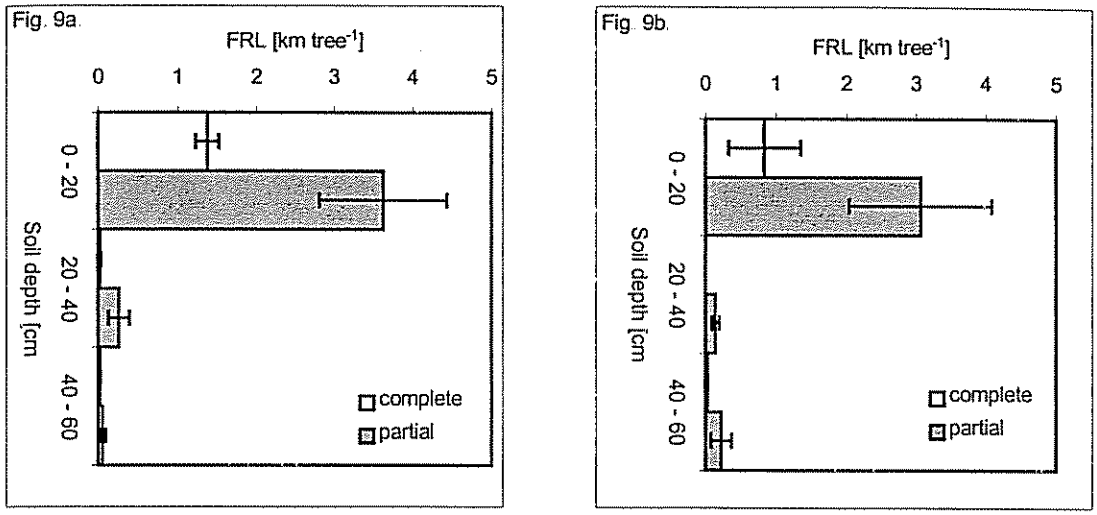

Figure 9. Effect of complete and partial pruning on fine root length (FRL) distribution in a) 2-year-old, and b) 8-year-old *Erythrina poeppigiana* trees after a regrowth period of 16 weeks. Complete and partial pruning were imposed one year previous. Bars are SEM.

Production and turnover of fine roots and nodules (Article II):

Partial pruning produced three times more fine root biomass and two times more nodule biomass compared to complete pruning of 2-year-old trees (Table 3). Almost all of the senescent roots and nodules were added to the soil organic matter pool. The CFM resulted in erroneous estimates of fine root production and turnover for 8-year-old trees.

Table 3. Total production, senescence and decomposition of fine roots and nodules in pruned *Erythrina poeppigiana* from 6 to 22 WAP, compartment flow model.

Tree age	Pruning Intensity	Production	Senescence	Decomposition
		[g tree^{-1}]		
		Fine roots, k = 0.00826[z]		
2	Complete	11.2	15.8	17.6
	Partial	38.1	24.5	16.6
8	Complete	-11.0	-6.2	8.0
	Partial	-3.1	-0.55	10.9
		Nodules, k = 0.053[y]		
2	Complete	58.2	47.4	50.4
	Partial	114.9	102.9	95.4
8	Complete	26.8	26.7	36.5
	Partial	26.4	17.7	26.7

[z] derived from this study (Article II); [y] Nygren and Ramírez 1995.

4.4 Experiment 2: Physiology of tree regrowth (Articles III, IV, V)

Based on observations made during the 12-week pruning cycles, regrowth of pruned trees can be divided into the following three distinct stages:

a. 1-2 WAP: greening of buds and initiation of sprouts.
b. 2-6 WAP: vigorous development of buds into sprouts and shoots.
c. > 6WAP: leaf expansion and elongation of shoots.

Starch and soluble carbohydrates dynamic in E. poeppigiana (Article III)

Stem starch concentrations were lower in pruned trees compared to unpruned trees during both periods (Table 4). The effect of sampling date on starch concentration was significant for both root and stem, particularly during the dry period. Mean root and stem starch concentrations decreased to one-third their initial concentration by 6 WAP thus explaining the date effect (Table 4). The decline in root starch concentration coincided with increases in stem sugar concentration indicating mobilization of non-structural carbohydrates during the regrowth stage of vigorous sprouting.

Starch and soluble carbohydrate dynamics in G. sepium (Article III)

Roots of completely pruned trees had the lowest mean starch concentration, and highest mean sugar concentration levels during both periods (Table 5). Starch concentration in roots and stems increased with time during the wet period, the opposite trend to what occurred during the dry period. Pruning during the dry period reduced root and stem starch concentration to one-third their initial concentrations by 6 WAP, but starch concentration in roots increased to 70% of its initial concentration by 12 WAP. Mobilization of carbohydrates in completely pruned trees occurred during the period of vigorous stem resprouting.

Histochemical analysis of starch content in roots of different diameter (Article IV)

Histochemical analysis detected changes in starch content in ray and axial parenchyma tissues in response to pruning, and generally corroborates results from chemical starch analyses reported above. Unpruned trees had significantly more root cells filled with starch granules than partially or completely pruned trees. The effect of pruning

increased during the dry period (Table 6). Larger diameter roots stored significantly more starch than smaller diameter roots. Fine roots of pruned trees were almost devoid of starch.

Table 4. Means and F-test significance for the effects of pruning intensity and sampling date on starch and soluble carbohydrate concentration in the dry matter (DM) roots and stems of *Erythrina poeppigiana,* Turrialba.

Source of variation		Root		Stem	
		Wet period	Dry period	Wet period	Dry period
		Starch concentration (mg g^{-1} DM)			
Pruning Intensity					
	Unpruned	32.2 a	33.2 a	26.0 a	22.5 a
	Partial	29.3 a	33.5 a	14.2 b	15.4 b
	Complete	23.6 a	24.6 a	9.8 b	18.8 b
	Mean	28.4	30.4	16.7	18.9
	Pr > F	0.1252	0.2825	**0.0039**	**0.0471**
Sampling Date (WAP)					
	0	21.6[z]	45.6 a	6.8[z]	23.5 a
	2	30.9 a	42.9 a	14.0 b	30.7 a
	6	26.4 a	15.7 b	21.2 a	11.2 b
	12	27.8 a	18.4 b	14.8 b	10.2 b
	Mean	28.4	30.6	16.7	18.9
	Pr > F	0.7390	**0.0001**	**0.0337**	**0.0001**
Interaction	Pr > F	0.4006	0.2181	**0.0004**	0.0646
		Soluble carbohydrate concentration (mg g^{-1} DM)			
Pruning Intensity					
	Unpruned	62.5 a	83.9 a	55.7 a	62.9 a
	Partial	60.1 a	55.1 a	63.9 a	64.5 a
	Complete	59.1 a	53.2 a	51.2 a	75.5 a
	Mean	60.6	64.1	56.9	67.6
	Pr > F	0.9204	0.1801	0.2903	0.8168
Sampling Date (WAP)					
	0	60.4[z]	82.3 a	79.9[z]	55.1 b
	2	56.2 a	44.9 b	51.2 a	80.2 a
	6	65.3 a	n.a.	56.8 a	n.a.
	12	60.7 a	n.a.	63.0 a	n.a.
	Mean	60.7	n.a.	57.0	n.a.
	Pr > F	0.4551	**0.0254**	0.2172	**0.0424**
Interaction	Pr > F	0.3647	0.2448	0.1904	0.7906

Means in the same column followed by the same letter are not significantly different (REGWQ $p \leq 0.05$); [z] average of three trees measured at beginning of study; n.a. - measurements were not taken during this period.

Table 5. Means and F-test significance for the effects of pruning intensity and sampling date on starch and soluble carbohydrate concentration in the dry matter (DM) root and stem of *Gliricidia sepium*, Turrialba.

Source of Variation		Root		Stem	
		Wet period	Dry period	Wet period	Dry period
		Starch concentration (mg g^{-1} DM)			
Pruning Intensity					
	Unpruned	29.2 a	52.4 a	19.3 a	21.7 a
	Partial	27.9 a	29.7 b	14.0 ab	18.2 ab
	Complete	15.2 b	14.8 c	11.4 b	14.3 b
	Mean	24.1	32.3	14.9	18.1
	Pr > F	**0.0091**	**0.0001**	**0.0382**	0.0512
Sampling Date (WAP)					
	0	9.3[z]	41.1 a	9.2[z]	27.1 a
	2	14.0 b	41.4 a	14.2 b	26.5 a
	6	18.4 b	17.1 b	19.1 a	9.2 b
	12	39.9 a	28.7 ab	11.3 b	9.5 b
	Mean	24.1	32.1	14.9	18.1
	Pr > F	**0.0001**	**0.0006**	**0.0094**	**0.0001**
Interaction	Pr > F	0.7578	0.5832	0.1287	**0.0171**
		Soluble sugar concentration (mg g^{-1} DM)			
Pruning Intensity					
	Unpruned	48.2 b	24.5 b	41.9 a	41.2 a
	Partial	53.5 b	43.7 b	42.6 a	60.5 a
	Complete	78.0 a	80.9 a	48.4 a	40.2 a
	Mean	59.9	49.7	44.3	47.3
	Pr > F	**0.0360**	**0.0045**	0.2839	0.2662
Sampling Date (WAP)					
	0	43.4[z]	53.2 a	31.8[z]	45.0 a
	2	65.2 a	48.1 a	35.8 a	49.7 a
	6	69.3 a	n.a.	48.0 a	n.a.
	12	45.1 b	n.a.	49.1 a	n.a.
	Mean	59.9	n.a.	44.3	n.a.
	Pr > F	0.0510	0.3257	0.1038	0.5920
Interaction	Pr > F	0.6800	**0.0071**	**0.0199**	0.7566

Means in the same column followed by the same letter are not significantly different (REGWQ $p \leq 0.05$); [z] average of three trees; n.a. – not available.

Accumulation of N and P during regrowth of E. poeppigiana [Article V]

In unpruned treatments, increased tree height during the dry period was associated with higher allocation of DM to branches, and accumulation of N in leaves. P accumulation in stems, branches and leaves was proportionate. Partial pruning treatment increased N and

P allocation to leaves and branches over that in completely pruned trees. Twelve-week pruned biomass from partially pruned trees could contribute 2 to 3 times more DM, N and P to the tree-crop-soil system than that from complete pruning.

Accumulation of N and P during regrowth of G. sepium (Article V)

In unpruned trees, DM and P were allocated to stems during the wet period but branches increased in DM during the drier period and had more P accumulated in their tissues. In both partially and completely pruned trees, tissue N and P increased in leaves during the dry period (Article V). Biomass regrowth was very poor in pruned trees and therefore the values obtained for nutrient cycling were negligible and are not reported.

Table 6. Means and F-test significance for the effects of pruning intensity, root diameter and sampling dates on cellular starch content of *Erythrina poeppigiana* and *Gliricidia sepium*, Turrialba.

Source of variation		*E. poeppigiana*		*G. sepium*	
		Wet period	Dry period	Wet period	Dry period
Pruning intensity (Prune)					
	Unpruned	3.7 a	4.4 a	3.7 a	4.2 a
	Partial	2.2 b	3.1 b	2.7 b	3.4 b
	Complete	1.9 b	1.9 c	2.6 b	1.9 c
	Mean	2.6	3.1	3.0	3.2
	Pr > F	**0.0004**	**0.0001**	**0.0133**	**0.0001**
Sampling Date (WAP)					
	0	n.a.	4.1 a	n.a.	3.8 a
	2	2.6 a	3.1 b	3.1 a	3.5 ab
	6	2.5 a	2.8 b	3.0 a	2.4 c
	12	2.7 a	2.5 b	3.0 a	2.8 bc
	Mean	2.6	3.1	3.0	3.2
	Pr > F	0.5073	**0.0043**	0.8884	**0.0065**
Diameter (mm)					
	< 2	1.2 c	1.8 c	1.2 c	1.4 c
	2-10	2.6 b	3.4 b	3.1 b	3.7 b
	> 10	4.0 a	4.3 a	4.7 a	4.4 a
	Mean	2.6	3.2	3.0	3.2
	Pr > F	**0.0001**	**0.0001**	**0.0001**	**0.0001**
Prune x Date	Pr > F	0.5781	0.0615	0.6713	**0.0018**
Prune x Diameter	Pr > F	**0.0010**	**0.0001**	**0.0024**	**0.0001**

Means in the same column followed by the same letter are not significantly different (REGWQ $p \leq 0.05$); n.a. = not available.

5. DISCUSSION

5.1 *Inventory fine root distribution*

The superficial fine root distribution pattern corroborates what Nygren and Campos (1995) reported for *E. poeppigiana* and van Noordwijk and Purnomosidhi (1995) for *G. sepium*. This distribution pattern may be attributed to the presence of more favourable chemical conditions in topsoil (Article 1). Higher biomass in fine roots at greater soil depth indicates higher construction and/or maintenance cost (Fitter 1991) probably due to penetration resistance. At soil depths greater than 20 cm, physical impediments such as stones were observed. Fine root distribution to greater soil depth could be important in uptake of nutrients, an important addition to topsoil nutrient stores in *E. poeppigiana*-amended soil. Higher length density at the tree proximity zone of 1 m may be due to less soil interference during preparation for planting; planting strips were usually at 75 cm distance form the tree row.

5.2 *Experiment 1: N, fine root and nodule dynamics (Articles I, II)*

Pruned biomass and tissue N accumulation

Pruning of *E. poeppigiana* trees four times in one year predictably led to lower biomass output. This present study showed that while biomass decreased at each pruning event, more evident at pruning interval of two months, the annual biomass output, ca. 8 Mg ha^{-1} yr^{-1}, from partially pruned trees was comparable to that when trees were completely pruned twice a year in alley cropping systems (Kass *et al* 1992) or three times a year in coffee plantations (Russo and Budowski 1986) in Turrialba. Complete pruning applied at half-yearly intervals did not reduce biomass output during the short term (Beer 1988); however, this pruning frequency will lead to negative tree-crop interaction in tomato alley cropping. Pruning in January after two months of regrowth, when environmental conditions were sub-optimal for growth, did not only decrease biomass output but also had a negative effect on subsequent tree recovery. Recovery in the period immediately following this pruning event was much slower in 8-year-old trees than in 2-year-old trees. Nygren (1995) suggested that reduced biomass output might be due to slow recovery of carbohydrate reserve and re-nodulation after pruning. *E. poeppigiana* trees do require 10-16 weeks to

renew N_2 fixation (Vaast and Snoeck 1999) and produce new nodules (Nygren and Ramírez 1995).

In terms of N cycling, the direct consequence of reduced biomass was reduced N accumulation in foliage tissue of trees, given that tissue N concentration was similar across pruning events. Trees cycled the least amount of N during the period of minimum biomass output in January due either to low photosynthesis or to fewer fine roots available for N capture and uptake, or both. Partial pruning increased biomass output and tissue N accumulation probably due to faster growth rates of the retained branch. This process may have been facilitated by maintenance of fine root and nodule function through maintenance of axes between these belowground organs and the retained branch for the movement of photosynthate, water and N (Wilson 1990). In addition, it seems likely that the hypothesis of branch autonomy for C fixation and use (Sprugel *et al* 1991) may explain rapid development of the retained branch in the partial pruning treatment. Greater capacity for N uptake in partially pruned *E. poeppigiana* trees and the reduction of nitrates in the leaves of this species (Orebango *et al* 1982; Muthuchelian 1993) may explain the faster growth rates that led to higher biomass output under partial pruning management than under complete pruning. The amount of N cycled in biomass from the present study exceeds the 173 kg ha^{-1} yr^{-1} reported by Russo and Budowski (1986) when trees were completely pruned at four-month intervals.

Soil N dynamics

Seasonal differences in soil N availability were observed. Soil NO_3-N was higher in May, at the beginning of the rainy season, and lower levels in December, during the rainy season. Preseason soil NO_3-N level measured in May was similar to that considered sufficient to support maize in the USA (Bundy and Meisinger 1994) and Africa (Barrios *et al* 1998). Higher available soil N in at the beginning of the rainy season may be attributed to higher mineralisation rates while lower available soil N during the rainy season may be attributed to lower nitrification rates (Article I). Therefore, crop nutrition during the rainy period requires fertilizer application particularly during the tomato flowering when nitrification rates is very low. Similar net N mineralisation and nitrification fluxes in both *E. poeppigiana* plots and treeless soil suggest that the benefits of biomass addition in the

tree plots to soil N were nullified by high rainfall. During the drier period in May, soil NO_3-N concentration in treeless soil was one-half that in *E. poeppigiana*-amended soil.

Fine root length dynamics

Changes in fine root length showed a pattern more associated with nodules (Nygren and Ramírez 1995; Vaast and Snoeck 1999). Increased fine root length after 10-14 weeks of regrowth was probably related to basipetal flow of carbon, suggested by Nygren (1995) to occur during at this time. Two-year-old trees have the capacity to explore more topsoil than 8-year-old trees and therefore are potentially more competitive in this soil layer. Partially pruned trees could more efficiently exploit nutrients at greater soil depth than completely pruned trees due to the presence of more fine roots at greater soil depths in the former. Nutrient conservation through increased uptake and accumulation in aboveground tissues is particularly important when crop roots are absent or insufficiently developed, and mineralisation rates of soil organic matter are high (Schroth 1995).

Production and turnover of fine roots and nodules (Article II):

Over a five-month period, fine root and nodule turnover from partial pruning of 2-year-old trees could potentially add 212 kg DM ha^{-1} to the soil organic matter pool compared to 105 kg DM ha^{-1} for complete pruning. The importance of root turnover to SOM pool was recognized for quite a long time (Nye and Tinker 1977). Erroneous estimates in the case of 8-year-old trees may be attributed to the low value for the decay coefficient k, which resulted in low senescence estimate that transferred mathematically to production and decomposition estimates (eqs. 3 and 4). The decomposition study was carried out under high rainfall conditions and may explain slow decomposition rates. The CFM therefore has a limitation when applied to fine root biomass measured in established *E. poeppigiana* in high soil moisture environments.

Production of fine roots and nodules compensated for losses due to senescence. New nodule production at 10-14 WAP agrees with findings of Nygren and Ramirez (1995). New fine root production during this period represents an addition to the knowledge base about root dynamics of *E. poeppigiana* under humid tropical conditions. Similar average

net change in nodule biomass in partially and completely pruned trees, suggest that the retention of one branch has a similar effect on nodule survival as pruning of all branches.

5.3 *Experiment 2: Physiology of tree regrowth (Articles III, IV, V)*

Starch and soluble carbohydrates dynamics in E. poeppigiana (Article III)

During the 12-week pruning cycle, the effect of pruning intensity was first seen in stems indicating that resprouting in pruned trees utilized starch from the nearest available carbohydrate storage site. Increased demand for energy by more vigorously resprouting trees during the drier period coincided with significant decreases of root starch reserves at 6 WAP. Decline in stem starch to levels lower than root starch in severely pruned plants was reported (Ericsson *et al* 1980; Tschaplinski and Blake 1994). Starch reserves in roots were not replenished at the end of the 12-week period, indicating either that concentration levels were still above a critical minimum level or trees were maintaining high aboveground growth rates and therefore no excess soluble carbohydrates was available for storage as starch.

Starch and soluble carbohydrates dynamics in G. sepium (Article III)

Like *E. poeppigiana*, the most noticeable change in starch concentration occurred during the dry period at 6 WAP when vigorous sprout and shoot development occurred. An important species difference was observed in starch re-synthesis. *G. sepium* replenished root starch to 70% its initial concentration in just six weeks after the initial level was reduced by a similar amount. In *E. poeppigiana*, root starch replenishment was just commencing. This difference indicates that *G. sepium* with its smaller stem capacity for storage of non-structural root reserves auto conserved starch in its root tissues, a process that occurred at the expense of fine root survival, absence of nodulation and slow above-ground regrowth. Lower non-structural carbohydrate reserves in completely pruned compared to partially pruned trees could create N deficiencies through its negative effect on new root growth (Loescher *et al* 1990).

Histochemical analysis of starch content in roots of different diameter (Article IV)

Higher respiration rates in fine roots (Lambers 1985) could explain the significant

difference in starch content between fine roots and roots of larger diameter. Histochemical root starch data showed a similar trend as the Lugol starch analysis. Given that small roots are more numerous than coarser roots, their role in starch storage may be just as important as the comparatively fewer coarse roots with their higher starch content (Article IV). The histological technique was able to identify starch depletion in roots much earlier than the Lugol method. More root cells were emptied of starch granules as early as 2 WAP, when nodule and fine root mass were senescing and resprouting was initiated.

Accumulation of N and P during regrowth of E. poeppigiana [Article V]

Growth in unpruned trees took place mainly through branch extension and these branches were allocated greater amounts of N and P than other organs. In partially pruned trees, allocation of N was mainly to leaves. Comparatively more N and P were allocated to branches of partially pruned trees than to branches of completely pruned trees. This allocation pattern might partly explain the lignification of branches of partially pruned trees compared to those of completely pruned trees over 12-week regrowth periods. Completely pruned trees sequestered more N and P in stems during 12-week regrowth period. It therefore means that pruned trees take much longer than 12 weeks to recycle the approximately 90% of nutrients in their aboveground biomass (Beer 1988). In pruned trees, the timing of pruning did not seem to have had an effect on N and P allocation. However, lower DM in partially pruned trees pruned in March than in December was probably due to phenological leaf fall and temporary interruption of growth during the drier period of March (Article III).

Accumulation of N and P during regrowth of G. sepium [Article V]

In unpruned trees, N was proportionately allocated to all organs but P seemed to accumulate more in branches with increased branch biomass. In pruned trees, very little regrowth took place during the wet period, hence the presence of higher N and P in stem tissues. During the dry period, when slightly more DM was in branches and leaves, N and P allocation increased proportionately more in leaves than in branches.

6. CONCLUSIONS

6.1 Experiment I: Biomass, N, fine root and nodule dynamics (Article I, II)

The retention of a branch on the pruned stump increased biomass output as well as N accumulation in biomass. However, continual pruning at three month intervals will not yield the quantity of organic inputs required for crop nutrition. At least one of the regrowth periods should be longer than three months to allow for tree recovery.

The fine root distribution pattern of decreasing fine root length density at greater soil depth and increasing fine root length density at greater distance from the tree row was characteristic for both species. Root length density was strongly superficial presenting potential competition with crop roots. Pruning did not change this general pattern, but root length at greater soil depth was higher with partial pruning and tree maturity. Partial pruning increased nutrient absorption capacity of trees and contributed more to soil organic matter through higher pruning residue and higher turnover rates of nodules and fine roots than complete pruning. N-fixation potential, as determined by nodule production, was higher in partially pruned trees. Production of fine roots and nodules was sufficient to compensate for losses due to senescence.

6.2 Experiment II: Physiology of tree regrowth (Articles III, IV, V)

Mobilization of non-structural carbohydrate reserves during resprouting increased during the dry period and was highest at vigorous sprout growth at 6 WAP. On the contrary, starch accumulated in roots during the wet period. Higher starch mobilization in completely pruned trees during resprouting may affect the C balance in these trees more that in partially pruned trees. Replenishment of root starch before 12 WAP was species specific. At 12 WAP, replenishment was almost completed in *G. sepium*, and it was just beginning in *E. poeppigiana*. Starch concentration was lower in roots of *G. sepium* than in roots of *E. poeppigiana*. Complete pruning during the dry period depleted more starch in roots of *G. sepium* compared to partial pruning, but in *E. poeppigiana*, the effect of these two pruning intensities on starch concentration was not significantly different.

The effect of pruning intensity on starch was first observed in stems and *E. poeppigiana* with stems of larger diameter would have greater storage capacity and a better

response to energy needs of resprouting than *G. sepium*. Histochemical techniques detected starch changes in roots of different diameter as influenced by aboveground tree disturbance. Roots of larger diameter stored more starch and fine roots were almost devoid of starch.

Allocation of N and P to shoot biomass was affected by pruning intensity, and phenology during the dry period. These metabolically active elements were higher in leaves and branches of partially pruned trees in comparison with those of completely pruned trees.

7. IMPLICATIONS AND MANAGEMENT OF TREES

7.1 Potential and management of Gliricidia sepium as a live stake for tomato

Frequently pruned *G. sepium* did not recover well after pruning nor did it nodulate (personal observation) at the field site. In experiment 1, poor recovery after pruning may have been caused by pruning at 1.5 m height, which left a very slender orthotropic branch for the staking of tomato. Since this species 'auto conserved' non-structural carbohydrates in roots at the time when buds on the slender stake were developing, the buds probably were starved of mobilized carbon from roots resulting in slow sprout development. It was shown that root starch increased during the wet period and during the dry period, roots replenished starch to near initial concentration at just 12 WAP. As a consequence of the above, biomass output and associated N cycling was far below the potential of this species which precludes any meaningful analysis of the potential of *G. sepium* as a live stake for tomato agroforestry based on the results of this study.

7.2 Potential and management of Erythrina poeppigiana as a live stake for tomato

E. poeppigiana generally recuperated well after pruning but recuperation to higher biomass output and N accumulation require modifications to the currently employed pruning strategy. The results of two independent studies conducted at the same site under similar environmental conditions have shown that at all levels of biological organization, partial pruning treatment significantly increased biomass, N and P cycling and nutrient absorptive capacity of trees.

In the management of a tomato-maize rotation in alleys of *E. poeppigiana*, this study showed that four prunings of these trees in one year will not optimise the production

of organic inputs for tomato crop nutrition. While maize grown at the end of the rains in May-June can be sustained on mineralised N, a large part of the recommended application of 100 kg N at the end of flowering phenophase in tomato will have to be obtained from external inputs. The timing of pruning could however be shifted to increase biomass output and N accumulation for cycling and crop fertilization.

Given the heavy rainfall periods during December and January in Turrialba and the imperative to harvest tomato during the drier periods, it is suggested that planting should be done in December. During November to December period, the rate of aboveground biomass production in trees is slower than in other periods, and non-structural carbohydrate reserves in roots increases. Partial pruning of trees at this time will conserve more fine roots for greater soil exploration and nutrient uptake than will complete pruning. Mid-season pruning in February will avoid the more severe effect of drier conditions in March on resprouting and depletion of non-structural carbohydrate reserves. In addition, sufficient foliage would have developed to facilitate maximization of C fixation during the dry month of March. Midseason pruning could be complete pruning as it avoids the phenological changes associated with having mature branches as in partial pruning, during the drier period. Phenological influences have the effect of reducing overall biomass output when pruning in March, when the least amount of monthly rainfall occurs.

Tomato fruit maturity in March-April may require irrigation and calcium nutrition but this depends on rainfall and soil type. This topic was outside the scope of this study, but it is an important consideration. Trees pruned in February have four months to recover under favourable environmental conditions before the recommended maize planting in June. Preseason pruning in June at the commencement of the rainy season coincides with high soil N availability that could sustain a maize crop grown to physiological maturity. To complete the cropping/pruning cycle, preseason pruning for the next tomato crop in December will provide expected high biomass and accumulated N after six months of regrowth, the recommended interval in current pruning management of this species.

It is therefore recommended that pruning frequency should be three times a year. Timing of pruning to optimize N cycling and crop yields should be in December and February for the tomato crop, and in June for the maize crop.

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N and fine root length dynamics in a tropical agroforestry system with periodically pruned *Erythrina poeppigiana*[*]

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Abstract

The effect of pruning all branches (complete pruning) or retaining one branch (partial pruning) on the dynamics of N cycling in aboveground biomass, N supplying power of an amended Eutric Cambisol, and fine root length, was studied in an *Erythrina poeppigiana* (Walp.) O.F. Cook - tomato (*Lycopersicon esculentum* Mill.) alley cropping practice in Turrialba, Costa Rica during 1999-2000. Over the one year pruning cycle, in which trees were completely or partially pruned four times, respective aboveground biomass production was 4.4 Mg or 7 Mg ha^{-1} (2-year-old trees) and 5.5 Mg or 9 Mg ha^{-1} (8-year-old trees); N cycled in aboveground biomass was 123 kg or 187 kg ha^{-1} (2-year-old trees) and 160 kg or 256 kg N ha^{-1} (8-year-old trees); mean fine root length was 489 m or 821 m (2-year-old-trees), 184 or 364 m (8-year-old-trees). Pruning intensity did not significantly affect net N mineralisation and net nitrification rates during the tomato-cropping season. Pre-plant mean net N mineralisation rate of 2.5 mg N kg^{-1} soil 30 $days^{-1}$ was significantly lower than 16.7 mg N kg^{-1} soil 21 $days^{-1}$ or 11.6 mg N kg^{-1} soil 28 $days^{-1}$ at the end of vegetative development and flowering, respectively. Mean net nitrification rates of 3.5 mg N kg^{-1} soil 30 $days^{-1}$, and 4.3 mg N kg^{-1} soil 21 $days^{-1}$, at pre-plant and end of vegetative development, respectively, were significantly higher than 0.3 mg N kg^{-1} soil 28 $days^{-1}$ at end of flowering. In humid tropical low-input agroforestry practices that depend on organic inputs from trees for crop nutrition, retention of a branch on the pruned tree stump appears to be a good alternative to

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removal of all branches for reducing N losses through higher N cycling in aboveground biomass, and for conserving fine root length for higher N uptake.

Introduction

The tomato (*Lycopersicon esculentum* Mill.) on live stake agroforestry practice has shown promise when organic inputs for crop nutrition is provided by *Erythrina poeppigiana* (Walp.) O.F. Cook trees (Schlönvoigt and Chesney 1999; Chesney *et al* 2000). The main input from *E. poeppigiana* is the more than 250 kg N ha^{-1} yr^{-1} cycled in aboveground biomass (Beer 1988; Kass *et al* 1993) of trees that are managed by complete shoot pruning at half-yearly intervals to enhance light supply to the associated crop. Increased fluxes in senescent nodules (Nygren and Ramírez 1995) and fine roots (Muñoz and Beer, in press; Nygren and Campos 1995), due to pruning, are additional N sources.

However, half-yearly complete pruning of *E. poeppigiana* trees delays the renewal of N_2 fixation (Vaast and Snoeck 1999) and new nodule biomass production (Nygren and Ramírez 1995) for 10-16 weeks. During this lag period, regrowing trees may reabsorb soil N (Kass *et al* 1997). Research with other species has shown that complete pruning can increase N losses (Vanlauwe and Sanginga 1995), and influence other below ground processes such as net N mineralisation and net nitrification rates (Haggar *et al* 1993), and distribution of nitrates (Jama *et al* 1998) and fine root length (van Noordwijk *et al* 1996).

Experiences with maize (*Zea mays* L.) (Kass *et al* 1993) and tomato (Chesney *et al* 2000) alley cropping recommend pruning of *E. poeppigiana* trees more frequently than twice a year. Complete pruning at a frequency of three times a year reduced aboveground biomass production (Russo and Budowski 1986; Romero *et al* 1993) thus limiting the potential of this species to provide adequate amounts of organic inputs for crop nutrition. As a tree management alternative, pruning part of the canopy of the service tree instead of all shoots may satisfy the primary pruning function, and in addition, may increase pruning N availability (Vanlauwe and Sanginga 1995) possibly through conservation of nutrient acquisition systems (Nygren and Cruz 1998).

Leaving one or two branches on the pruned tree stump is a traditional partial pruning practice of *E. poeppigiana* shade trees in Costa Rican coffee (*Coffea arabica* L.) farms (Somarriba *et al* 1996). This technique called 'lung branch' pruning in tea (*Camellia sinensis*

(L.) O. Kuntze) culture, dates back to the 1930s (Kandiah *et al* 1984). It is presumed that the retained branch ensures a supply of photosynthates to developing new shoots. The functional advantages of partial pruning of leguminous service trees over complete pruning in humid tropical agroforestry systems have not been reported. A field study was carried out to elucidate the effects of complete and partial shoot pruning on the dynamics of available soil N and fine root length in an *E. poeppigiana* - tomato live-stake agroforestry practice under humid tropical conditions in Turrialba, Costa Rica.

Materials and methods

The study environment

The study was carried out in the La Montaña experimental farm of CATIE, Turrialba situated in a very humid pre-montane forest ecozone (Holdridge, 1987) with a medium fertility Eutric Cambisol (Kass *et al* 1995) (Table 1). Meteorological variables (average±SD) measured during field data collection from May 1999 to May 2000, were monthly precipitation 325±181 mm; daily temperature maxima 30.3±1.3 ^{0}C; daily temperature minima 15.2±1.7 ^{0}C, and relative humidity 87.8±2.0 %.

The experimental plots were established in January 1991 to compare different maize and bean (*Phaseolus vulgaris* L.) varieties associated with *E. poeppigiana*, *Calliandra calothyrsus* Meissn., *Gliricidia sepium* (Jacq.) Kunth ex Walp. and treeless control treatments. Further description will be confined to *E. poeppigiana* plots. The initial spacing was 6 x 2 m. In 1997, row width was halved to 3 m (1666 trees ha^{-1}) with the planting of rooted stakes, taken from the same plots. Throughout this article, the trees planted in 1991 will be referred to 8-year-old trees, and the trees planted in the original alleyways in 1997 will be referred to as 2-year-old trees.

Between 1992 and 1996, trees were managed by half-yearly complete shoot pruning carried out at the beginning of each of two cropping seasons. Pruned material was chopped into small pieces and added to the alleys and fertilised bean and maize were grown in rotation up to 1996. From 1998 onward, bean was replaced by tomato in the rotation and fertiliser use was discontinued. Pruning height of live stakes was raised from 0.75 m to 1.5 m to allow for connecting trees with wire at 1.3 m height for the staking of tomatoes.

Experimental design

The effect of complete and partial pruning on N cycling in foliar biomass, net N mineralisation rates, net N nitrification rates and fine root length were studied in a split plot in time design with three replications. Mainplot factor was pruning intensity (complete i.e. removal of all shoots; and partial i.e. retention of one branch corresponding to 5% of total shoot biomass). Subplot factor was pruning date (May, August, November of 1999, January and May 2000; applied without re-randomisation). Sampling and analyses were separate for tree age except for the net N mineralisation and net nitrification study. Soil N and maize yield data were collected from treeless plots to compare with those from *E. poeppigiana*-amended plots.

Plot management

Cropping seasons were May-August 1999 (maize) and November 1999-January 2000 (tomato). Plots were fallowed in the intervals between crops. Crops of maize var. Diamantes 8843 sown 15 June 1999 at a density of 26, 666 plants ha^{-1}, and tomato var. Dina Panama transplanted at 22 days on 26 November 1999 at a density of 13, 333 plants ha^{-1}, were established uniformly in the alleys formed by tree rows. Trees were pruned two weeks before planting and at crop flowering phenophase. Pre-plant N-containing pruned materials were chopped into small pieces; one-half (Table 2) along with dolomitic lime (0.5 Mg ha^{-1} $CaCO_3.MgCO_3$) was incorporated into the planting strips while the other half was applied as mulch. Mid-season (flowering) pruned material was applied as mulch. Plots were manually weeded at monthly intervals.

Pruned biomass and N accumulation

On each pruning date, total fresh weight of pruned shoots was measured. Shoots were separated into leaves, woody and non-woody branch parts and 0.5 kg sub-samples of each part was oven-dried (65 ^{0}C) to constant dry weight for dry mass determination. Composite (combined replications) dried sub-samples were analysed for total N by semi-micro kjeldahl (SSSA 1994). Accumulated biomass N was computed as the sum of the products of dry weight and N concentration in each compartment.

Soil nitrogen dynamics

Net N mineralisation and nitrification rates

Mineralisation rates were studied during the tomato crop at pre-plant (two weeks before to two weeks after pruning) and during vegetative (from planting to 21 days later) and flowering (end of vegetative phase to 28 days later) phases in *E. poeppigiana*-amended and treeless soil. The closed-top solid cylinder field incubation method (Hart *et al* 1994) was used. At the beginning of each phase, three cylinders per plot were removed immediately after insertion. The top 20 cm of soil were mixed, extracted with 2N KCl and analysed for initial concentration of NH_4 and NO_3 (SSSA 1994). The remaining tubes in the field were removed at the end dates of each phase and the process repeated. Net mineralisation and nitrification rates were calculated according to Hart *et al* (1994).

Available N (NH_4, NO_3)

During the maize crop, sampling was once over at one week after sowing (WAS) since pre-season inorganic N was reported to relate quite well with maize yield in N deficient soils (Barrios *et al* 1998). During the tomato crop, sampling commenced two weeks after transplanting (WAT) and continued thereafter weekly for six consecutive weeks. On each sampling date, six topsoil (0-20 cm) auger samples were randomly taken from the planting rows and analysed for NH_4-N and NO_3-N as described above.

Fine root length dynamics

Inventory coring of a modal 8-year-old tree to 60 cm soil depth in September 1998 revealed that 80% of fine roots of *E. poeppigiana* was distributed in the topsoil. For the present study, 10 topsoil core (auger cylinder: ∅ = 8 cm; L = 25 cm) samples were taken randomly from within the unit soil area, a rectangle measuring 1.5 m^2 with the tree in the centre of the rectangle, at 6, 10, 14 and 22 weeks after pruning (WAP) in August 1999. The sampling periods were selected based on observation of nodule dynamics by Nygren and Ramírez (1995). Sampling in the unit soil area to 20, 40 and 60 cm soil depth was carried out in May 2000 to determine the effect of pruning intensity on vertical distribution of fine roots.

Roots were washed free from soil in 0.5 mm sieves and sorted into live and dead fractions with the aid of a stereomicroscope and criteria of colour, texture and appearance of the central cylinder. Live fine roots (< 2 mm) were measured for root length using WinRHizo Pro® (Régent Instruments, Quebec, Canada). Fine root length was corrected from the sample area of 1.5 m^2 to the 6-m^2 area each tree occupies.

Plant biomass

At 12 WAS, physiologically mature maize plants with intact roots, were harvested from two cross-alley areas (each 6 m^2) per plot, separated into root, stem, leaves, cob and flower and 0.5 kg sub-samples of each plant part oven dried (65 ^{0}C) to constant weight for dry mass determination. The tomato crop was lost to severe fungal disease infection; a situation favoured by unusual heavy rainfall of 570 mm in December and 689 mm in January during flowering and fruiting, respectively.

Statistical analyses

Foliar biomass, fine root length and nitrogen data were examined for homogeneity of variances and normality. For analysis of biomass data, individual trees in each plot were treated as sub-samples and diameter at 10 cm was used as co-variable. Data were analysed using SAS/GLM (SAS Institute, Cary, North Carolina) procedure for split plot in time design with three replications. Mean comparisons were by REGWQ ($p<0.05$).

Results

Pruned biomass and N accumulation

Over the one-year pruning cycle, partial pruning treatment significantly increased aboveground biomass by approximately 50% over complete pruning (Table 3). Total biomass production from partially versus completely pruned trees was 4.4 Mg vs. 7 Mg ha^{-1} in 2-year-old trees, and 5.5 Mg vs. 9 Mg ha^{-1} in 8-year-old trees, respectively. Biomass decreased significantly over the observation period with lowest production in January 2000 (Table 3), when precipitation was highest and average solar radiation lowest (Figure 1). Plots of mean pruned biomass against pruning date showed that the relationship could best be described by a quadratic orthogonal polynomial function (Figure 1). The rate of change of biomass by

time showed that for 2- and 8-year-old trees, the minimum values for significant biomass changes along the curvature were 14.7 months and 15.4 months, respectively. These values correspond to the February to March 2000 dry season. The interaction between pruning intensity and pruning date was non-significant.

The proportion of leaf to branch biomass increased when the preceding pruning interval was less than 20 weeks and was generally higher in completely pruned trees compared to partially pruned trees (Table 3). Completely pruned trees did not produce woody branch tissue until a regrowth period of 16 weeks; branch tissue at August 1999 to January 2000 pruning events was entirely non-lignified. Partially pruned trees developed approximately three-quarters of its new growth on the retained branch that was lignified at all pruning events; stem borne shoots were non-lignified.

Over the one-year pruning cycle, N cycled in total aboveground biomass of completely versus partially pruned trees was 123 kg vs. 187 kg ha^{-1} (2-year-old trees) and 160 kg vs. 256 kg ha^{-1} (8-year-old trees), respectively (Table 4). N cycled in 10-week biomass regrowth cut in January 2000 was lower than the overall mean value. Differences in accumulated N were due to differences in the amounts of biomass since leaf N concentration was similar: 3.6% and 3.7% for completely and partially pruned 2-year-old tree, and 3.8% and 4% for completely and partially pruned 8-year-old tree, respectively.

Soil nitrogen dynamics

Net N mineralisation and nitrification rates

Pruning did not significantly affect net mineralisation and nitrification rates. Net N mineralisation rates significantly increased after planting to a peak of 16.7 mg kg $soil^{-1}$ 21 $days^{-1}$ at the end of the vegetative stage and decreased by non-significant amounts during early fruit development (Table 5). Net nitrification rates decreased by significant amounts to 0.3 mg kg $soil^{-1}$ 28 $days^{-1}$ during early fruit development (Table 5). Comparison of net N mineralisation and net nitrification rates in *E. poeppigiana*-amended soil with treeless soil did not show any significant differences ($p = 0.9180$). Time course changes were also similar (Table 5). The interaction between soil amendment and sampling date was non-significant ($p = 0.2975$).

Available N (NH_4, NO_3)

At 1 WAS, soil NH_4-N concentration was significantly lower in *E. poeppigiana*-amended maize plots containing partially pruned trees compared to those with completely pruned trees, but pruning intensity effect was non-significant for soil NO_3-N concentration (Table 6a). Mean soil NO_3-N concentration of 26.7 mg kg^{-1} soil was more than 12-fold higher than soil NH_4-N concentration and represented approximately 57 kg NO_3-N ha^{-1} (ρ = 1.077 t m^{-3}) present in the topsoil at that time. In treeless soil, NO_3-N concentration was 14.1 mg ka^{-1} corresponding to 30 kg NO_3-N ha^{-1}.

During the tomato crop, NH_4-N concentration at 2 WAT was about twice as high and NO_3-N concentration was 12-fold lower than corresponding values during the maize crop (Table 6b). Soil inorganic N (NH_4+NO_3) concentration decreased by non-significant quantities over the measurement period (Table 6b). During the first 3 WAT, NO_3-N concentration increased while that of NH_4-N decreased, thereafter both N forms decreased in soil under completely pruned trees but fluctuated in soil under partially pruned live stakes. Soil water content remained unchanged over the observation period.

Fine root length dynamics

Mean fine root length was significantly lower in completely pruned compared to partially pruned trees for both tree ages. Respective values were 489 m vs. 821 m for 2-year-old-trees, and 184 vs. 364 m for 8-year-old-trees (Figure 2). Maximum fine root length was observed between 10-14 WAP. Decline in root length at 22 WAP may be attributed to the effect of pruning in November 1999; the slope of the curve was steeper in completely pruned trees compared to partially pruned trees. In May 2000, one year after the pruning regime was imposed, and 16 WAP, more than 90% (2-year-old trees) or 75% (8-year-old trees) of fine roots was distributed to topsoil (Figure 3). Partially pruned trees conserved more than two to three times more fine roots than completely pruned trees, a difference that was significant in 2-year-old trees but non-significant in 8-year-old trees.

Plant biomass

At 12 WAS, approximately 12 g $plant^{-1}$ more maize biomass (mainly in stem, leaf and cob) were produced in plots with partially pruned trees compared to maize biomass in

completely pruned tree plots (Figure 4). Maize biomass from partially pruned tree plots and treeless plots were similar. There was a significant block effect on leaf, stem and total biomass suggesting that growth conditions were unfavourable in some blocks.

Discussion

Pruned biomass and N accumulation

The results of this study clearly showed that partial pruning doubled total biomass output over complete pruning. The average biomass of 8 Mg ha^{-1} yr^{-1} from 2- and 8-year-old partially pruned trees is comparable to values reported by Kass *et al* (1993) for *E. poeppigiana* when pruning intensity was complete and pruning frequency, half-yearly. The decline in pruned biomass at shorter regrowth periods even when a branch was retained, confirmed that regrowth periods longer than 16 weeks (Nygren 1995) are necessary to maintain the biomass productivity of *E. poeppigiana*. Unfavourable environmental conditions of high precipitation and low solar radiation may have contributed to observed low biomass and N cycled in biomass harvested in January 2000. Recovery (increasing biomass) began during February-March when environmental conditions for growth were more favourable.

The development of about 75% of new shoot growth on the retained branch may support the hypothesis that branch autonomy for C uptake and export is independent of C needs of other developing shoots on the stem (Sprugel *et al* 1991). New stem borne shoots may have met their C needs during resprouting from carbohydrate and nutrient reserves in the stem as observed in other species (Erdmann *et al* 1993). Branch tissues in partially pruned trees were lignified at all regrowth periods, but branch tissue lignification in completely pruned trees did not occur until a minimum regrowth period of four months when a dry period occurred, further explaining the biomass difference.

Higher N cycling in partially pruned trees than in completely pruned trees may be attributed to both faster growth through branch autonomy for C and high activity NO_3^- reduction in the leaves of *E. poeppigiana* (Orebango *et al* 1982; Muthuchelian 1993). In completely pruned trees, NO_3^- reduction may have initially taken place in roots, an energetically costly process (Marschner 1997) that may increase root and nodule turnover; evidence of this alternative pathway in *E. poeppigiana* is not available.

Soil nitrogen dynamics

Mineralisation of organic matter is perhaps the main source of available inorganic N at the study site. The presence of microbially available C and N sources in the leaves of *E. poeppigiana* (Palm and Sanchez 1990, 1991) facilitated rapid net mineralisation of added material during the vegetative phase and maintenance of high levels towards the end of tomato flowering phenophase. Mazzarino and colleagues (1993) found that after nine years of alley cropping in Turrialba, soil C and N and microbial C and N were higher in *E. poeppigiana* alley crop plots compared to other treatments. They found that soil microbial biomass C was greatest during rapid crop growth and lowest at end of cropping period probably due to C cycling from root exudates and root mortality.

Given that the mineralisation of organic N controls the amount of N cycled in soil, higher soil NO_3-N than NH_4-N at the start of the rainy season in May 1999 indicates that substrate NH_4-N for nitrification was not a limiting factor and that NH_4 pool was readily nitrified accounting for accumulation of NO_3 in the soil. Under low rainfall conditions, NO_3-N can be used as an index of N availability for the Turrialba site. Veldkamp and colleagues (1999) made a similar observation for pasture and forest ecosystems in Costa Rica. Lower nitrification rates during the high rainfall period in December, may be attributed to the adverse effect of environment on population and/or activity of nitrifying bacteria (Davidson *et al* 1990). Also, much of the NO_3-N might have been leached to lower soil depths. Under high rainfall conditions, total inorganic N may be used as an index of N availability at this site. Similar net N mineralisation and nitrification fluxes in both *E. poeppigiana*-amended and treeless soil suggest that the benefits of soil amendment were nullified by high rainfall. During the drier period in May, soil NO_3-N concentration in treeless soil was one-half that in *E. poeppigiana*-amended soil.

It is probable that completely pruned trees competed with maize plants for available soil N during the maize crop since maize plants in plots with completely pruned trees produced 320 kg ha^{-1} less total maize biomass than those in partially pruned tree plots. Maize leaf, stem and cob biomass were comparatively lower in completely pruned tree plots. NO_3-N levels may have increased during crop development when added pruning material further decomposes and releases N. While this study did not examine the relationship between preseason N and maize yield, recent findings indicate that pre-season N can be used to

predict maize grain yields in a maize alley crop in N deficient soils (Barios *et al* 1998; Ikerra *et al* 1999).

E. poeppigiana leaves decompose rapidly (Palm and Sanchez 1990, 1991) and release N even faster (Haggar *et al* 1993), making it imperative that pruning management should reduce leaf: woody branch ratio if N loss under high rainfall conditions is to be reduced. Observations of tomato fine root distribution showed very superficial (soil depth 0-10 cm) rooting with very little horizontal spread beyond 20 cm from the base of the plant. Therefore, mid-season application of the pruned residue to the soil surface may put much of the mineralised N out of reach of tomato roots during the reproductive stage. Partially pruned trees with higher leaf biomass also had higher fine root lengths suggesting higher absorptive capacity for available N.

Fine root length dynamics

Greater fine root length increases the capacity of a plant to absorb available soil N (Marschner 1997). Partial pruning, which retained some leaf area on the pruned stump, also maintained part of the nutrient acquisition system for uptake and transport. Fine root length dynamics as affected by complete pruning approximated nodule dynamics reported by Nygren and Ramirez (1995). Partial pruning did not change the pattern of fine root decrease after pruning and recovery at 10-14 WAP.

Frequent pruning did not result in redistribution of fine roots to greater soil depths although partially pruned 8-year-old trees had higher capacity for nutrient uptake at these depths. Superficial rooting pattern of *E. poeppigiana* may be related to better conditions for root growth in the topsoil compared to greater soil depths. Topsoil had higher soil organic matter and exchangeable cations than greater soil depths (Table 1).

The retention of a branch on the pruned stump increased total aboveground biomass, N cycled in aboveground biomass, and more fine roots were conserved compared to complete removal of all shoots. The branch selected for retention should have a strong crotch to prevent breakage since most new shoot is formed on the branch. Frequent shoot pruning at intervals less than 16 weeks maintained the tree in perpetual renewal, and the regrowth strategy depended on the intensity of pruning. Completely pruned *E. poeppigiana* trees produced biomass with very little branch lignification, as well as fewer roots, resulting in

reduced biomass production and lower recovery of internally cycled N. Partially pruned trees grew faster probably as a result of branch autonomy for C, in addition to stem borne shoot growth. More N was recovered, a process helped by higher fine root survival and production.

Per unit length of fine root (ratio of N content of pruned biomass to fine root length for November 1999, January and May 2000), older trees accumulated more N than younger trees and completely pruned trees than partially pruned trees. This observation shows that greater root length does not confer a greater advantage in terms of uptake and accumulation of N. However, partially pruned trees or juvenile trees may contribute more dry matter and nutrients to the soil organic matter pool through turnover, in addition to reducing loss of soil N. How much fine roots is required for efficient N cycling in pruned trees could not be answered from the results of this study.

On an *E. poeppigiana*-amended Eutric Cambisol in the humid tropics, the retention of a branch on the pruned tree stump (partial pruning) appears to be a good alternative to complete removal of shoots (complete pruning) for reducing N losses by cycling higher amounts of N in aboveground biomass, and for conservation of fine root length for higher N uptake. Tomato crop N requirement during the reproductive phenophase may have to be fertiliser supported.

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Table 1. Chemical properties of *Erythrina poeppigiana*-amended alluvial Eutric Cambisol, Turrialba, Costa Rica, January 1999. Data are means ± standard deviations of three replications each with six composite sub-samples randomly taken. Gravimetric moisture content was 27.3%.

Soil depth (cm)	pH (H_2O)	Extract-able acidity	Ca	Mg	K	ECEC	SOM %	P	NH_4^+	NO_3^-
		cmol l^{-1}						mg kg^{-1}		
0-20	5.14± 0.16	0.36± 0.19	4.75± 0.07	1.61± 0.13	0.33± 0.09	7.05± 0.06	5.12± 0.28	14.3± 7.4	2.40± 0.36	4.98± 0.72
20-40	5.26± 0.04	0.22± 0.06	4.37± 0.81	1.23± 0.1	0.2± 0.07	6.03± 0.88	3.76± 0.5	10.3± 3.0	-	-
40-60	5.51± 0.14	0.15± 0.08	4.46± 0.46	1.22± 0.18	0.16± 0.11	5.99± 0.52	2.38± 0.39	10.6± 3.3	-	-
Mean	5.3± 0.19	0.24± 0.15	4.53± 0.5	1.35± 0.23	0.23± 0.11	6.35±0. 73	3.75± 1.23	11.7± 4.7		

Table 2. N added with *Erythrina poeppigiana* prunings.

Month of pruning	Tree age	N (kg ha^{-1})
August	2	24
	8	35
November	2	20
	8	31

Table 3. Effect of shoot pruning *Erythrina poeppigiana* trees on pruned total biomass and proportion of leaf to total biomass, Turrialba, 1999-2000. Data are means ± standard deviations.

Age of Stakes (years)	Pruning Intensity	Pruned total biomass and the proportion that is leaf [z]					Mean[y] (Total)[yx]
		May 99	Aug 99	Nov 99	Jan 00	May 00	
		Total biomass (Mg ha^{-1})					
2	Complete	4.8±0.7	1.7±0.4	1.2±0.2	0.4±0.1	1.1±0.9	**1.1 b** (4.4)
	Partial	4.2±0.6	2.6±0.8	1.7±0.7	0.9±0.4	1.8±0.4	**1.7 a** (7.0)
	Mean	4.5	**2.1a**	**1.4b**	**0.6c**	**1.5b**	1.4
8	Complete	5.7±1.0	2.1±0.5	1.6±0.5	0.6±0.2	1.2±0.7	**1.4 b** (5.5)
	Partial	6.2±1.7	3.2±1.0	2.7±0.9	1.0±0.2	2.1±0.9	**2.2 a** (9.0)
	Mean	6.0	**2.6 a**	**2.1 a**	**0.8 c**	**1.6 b**	1.8
		Proportion of total biomass that is leaf biomass (%)					
2	Complete	43.9	48.5	76.1	79.2	76.1	70.0
	Partial	47.8	43.9	65.0	64.1	67.6	60.2
8	Complete	48.4	47.6	76.3	77.8	74.3	69.0
	Partial	49.1	49.5	71.9	67.2	72.7	65.3

[z] biomass at 20, 13, 12, 10 and 16 weeks regrowth corresponding to May 99, Aug 99, Nov 99, Jan 00 and May 00, respectively; [y] applies to August 99 through May 00; [x] in Mg ha^{-1} yr^{-1}.

Means in the same column (pruning intensity) or in the same row (pruning period) followed by the same letter are not significantly different, REGWQ ($p \leq 0.05$).

Table 4. Effect of shoot pruning *Erythrina poeppigiana* trees on total nitrogen (kg N ha^{-1}) obtained from pruned biomass, Turrialba, 1999-2000.

Tree age (years)	Pruning Intensity	Total N[z]					Mean[y] (Total)[yx]
		May 99	Aug 99	Nov 99	Jan 00	May 00	
2	Complete	119	42	32	13	36	31 (123)
	Partial	109	57	47	27	56	47 (187)
8	Complete	154	53	46	21	40	40 (160)
	Partial	169	82	78	29	67	64 (256)
	Mean	138	59	51	23	50	46 (183)

[z] biomass at 20, 13, 12, 10 and 16 weeks regrowth corresponding to May 99, Aug 99, Nov 99, Jan 00 and May 00, respectively; [y] applies to August 99 through May 00; [x] in kg ha^{-1} yr^{-1}.

Table 5. Effect of shoot pruning on *Erythrina poeppigiana*-amended topsoil (0-20 cm) net mineralisation and nitrification rates during different stages of tomato development, Turrialba, 1999-2000. Data are means ± SEM.

Pruning Intensity	Net mineralisation rates			Net nitrification rates		
	Pre-plant	Vegetative	Flowering	Pre-plant	Vegetative	Flowering
	mgN $kg^{-1}30d^{-1}$	mgN $kg^{-1}21d^{-1}$	mgN $kg^{-1}28d^{-1}$	mgN $kg^{-1}30d^{-1}$	mgN $kg^{-1}21d^{-1}$	mgN $kg^{-1}28d^{-1}$
Complete	2.0±0.33	16.2±6.63	11.4±7.5	4.1±1.2	1.6±1.3	-0.6±0.3
Partial	3.0±4.23	17.2±4.81	11.6±3.0	2.9±2.0	6.9±1.0	1.2±1.0
Mean[z]	2.5b	16.7a	11.5ab	3.5[a]	4.3[a]	0.3[b]
Treeless soil	-0.54±2.1	13.7±3.6	15.9±4.7	1.2±1.7	7.1±2.3	1.3±1.9
Mean[y]	1.0b	15.2a	13.7a	2.4[b]	5.7[a]	0.8[b]

Means in the same row followed by a different letter (net mineralisation rates) or superscript letter (net nitrification rates) are not significantly different, REGWQ ($p \leq 0.05$).
[z] Mean values for *E. poeppigiana*-amended soil; [y] mean values for *E. poeppigiana*-amended and treeless soil.

Table 6. Effects of shoot pruning *Erythrina poeppigiana* trees on topsoil (0-20 cm) inorganic N (mg kg^{-1}) concentration, Turrialba.

Table 6a. Maize plots, one week after sowing, June 1999.

Pruning Intensity	NH_4	NO_3	Total inorganic N
Complete	2.2 a	26.9 a	29.1 a
Partial	1.7 b	26.6 a	28.4 a
Mean	1.9	26.7	28.7
Treeless soil	1.5	14.1	15.6

Means in the same column followed by the same letter are not significantly different, REGWQ ($p \leq 0.05$).

Table 6b. Tomato plots, 2-7 weeks after transplanting, December 1999 to January 2000.

Weeks after planting	NH_4		NO_3		$NH_4 + NO_3$		Soil water (%)	
	complete	partial	complete	partial	complete	partial	complete	partial
2	3.9 a	4.1 a	2.1 a	2.1 b	6.1 a	6.2 a	28.5 a	29.7 a
3	2.6ab	3.0ab	3.9 a	3.4ab	6.5 a	6.4 a	29.7 a	30.0 a
4	1.8 b	2.4bc	3.6 a	3.5ab	5.4 a	5.9 a	29.7 a	29.6 a
5	1.9 b	1.7bc	3.6 a	3.9 a	5.5 a	6.4 a	29.2 a	30.8 a
6	0.9 b	1.2 c	3.0 a	2.9ab	3.9 a	4.1 a	29.1 a	29.5 a
7	1.4 b	1.5bc	2.8 a	3.1ab	4.2 a	4.6 a	29.1 a	29.7 a

Means in the same column followed by the same letter are not significantly different, REGWQ ($p \leq 0.05$).

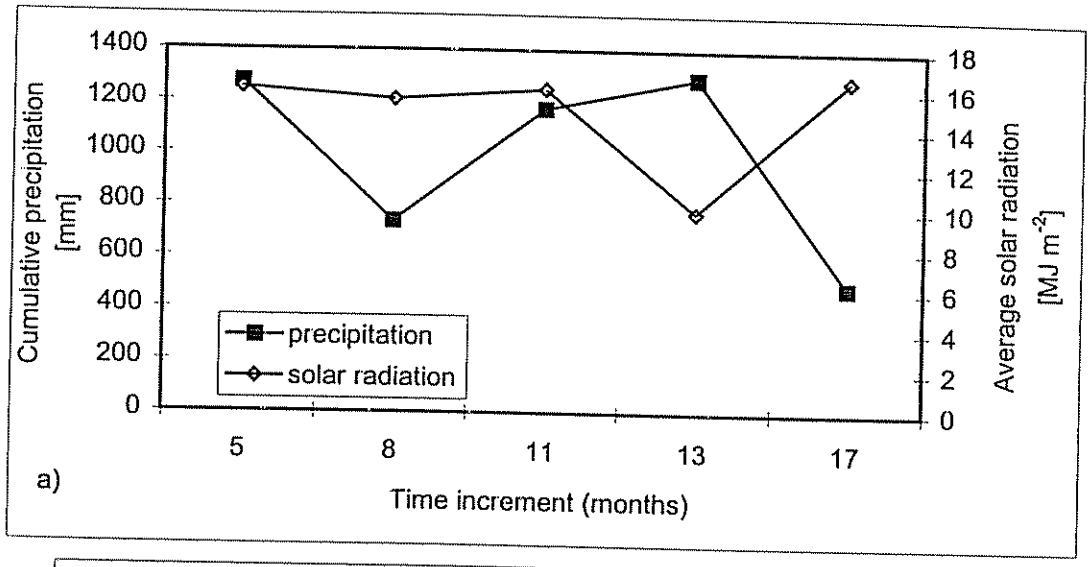
Figure Legends

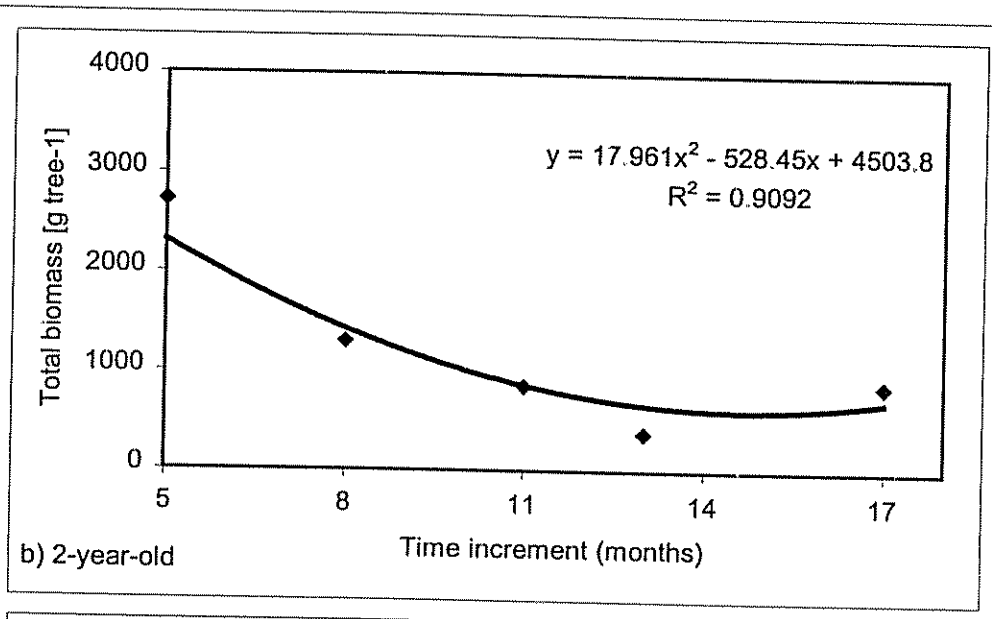
Figure 1. Plots of a) cumulative precipitation, average solar radiation, and b,c) aboveground biomass with pruning date (as increments in time) of *Erythrina poeppigiana* trees over the period May 1999 to May 2000, Turrialba.

Figure 2. Fine root length of *Erythrina poeppigiana* in topsoil (0-20 cm) of a) 2-year-old and b) 8-year-old trees when pruned completely or partially, Turrialba, September 1999 to January 2000. Bars are standard errors.

Figure 3. Fine root length distribution of 2-year and 8-year old *Erythrina poeppigiana* trees pruned after 16 weeks regrowth, May 2000. Bars are standard errors.

Figure 4. Biomass in maize plant compartments as influenced by pruning intensities of *Erythrina poeppigiana* trees and treeless soil, 12 weeks after sowing, Turrialba, August 1999.


Cumulative precipitation [mm]
1400
1200
1000
800
600
400
200
0
precipitation
solar radiation
18
16
14
12
10
8
6
4
2
0
Average solar radiation [MJ m-2]
5
8
11
13
17
a)
Time increment (months)


Total biomass [g tree-1]
4000
3000
2000
1000
0
y = 17.961x2 - 528.45x + 4503.8
R2 = 0.9092
5
8
11
14
17
b) 2-year-old
Time increment (months)

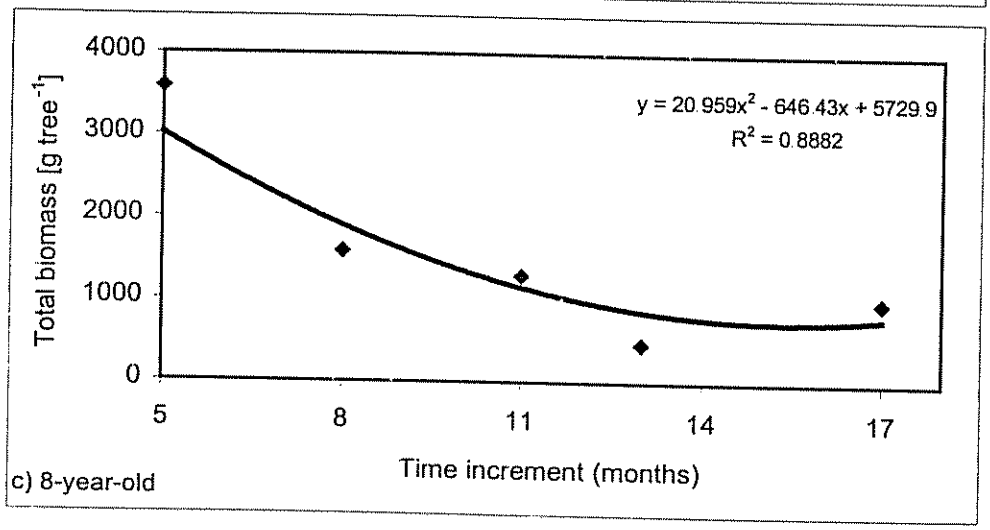

Total biomass [g tree-1]
4000
3000
2000
1000
0
y = 20.959x2 - 646.43x + 5729.9
R2 = 0.8882
5
8
11
14
17
c) 8-year-old
Time increment (months)

Fig. 1.

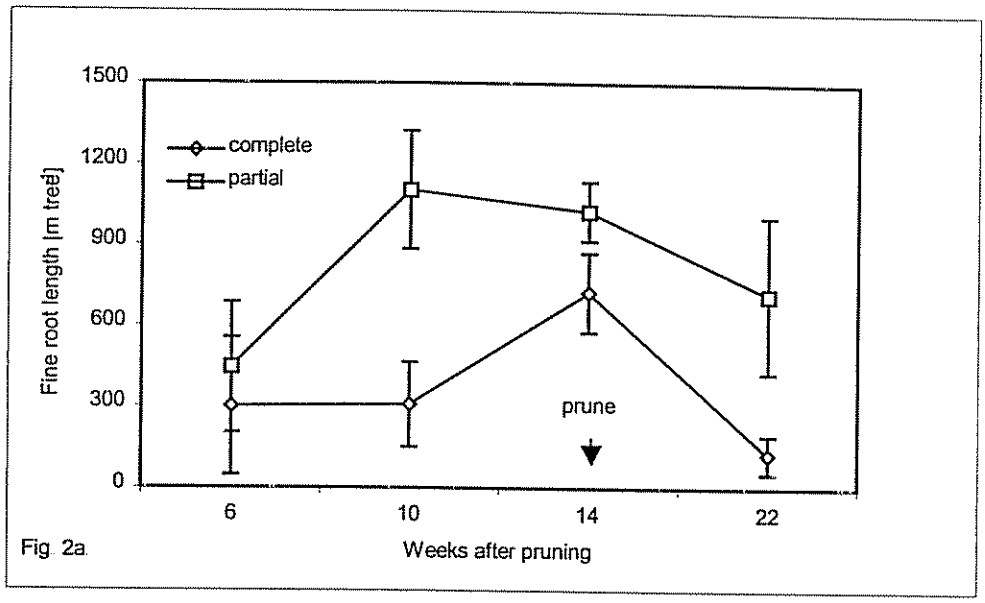


Fig. 2a.

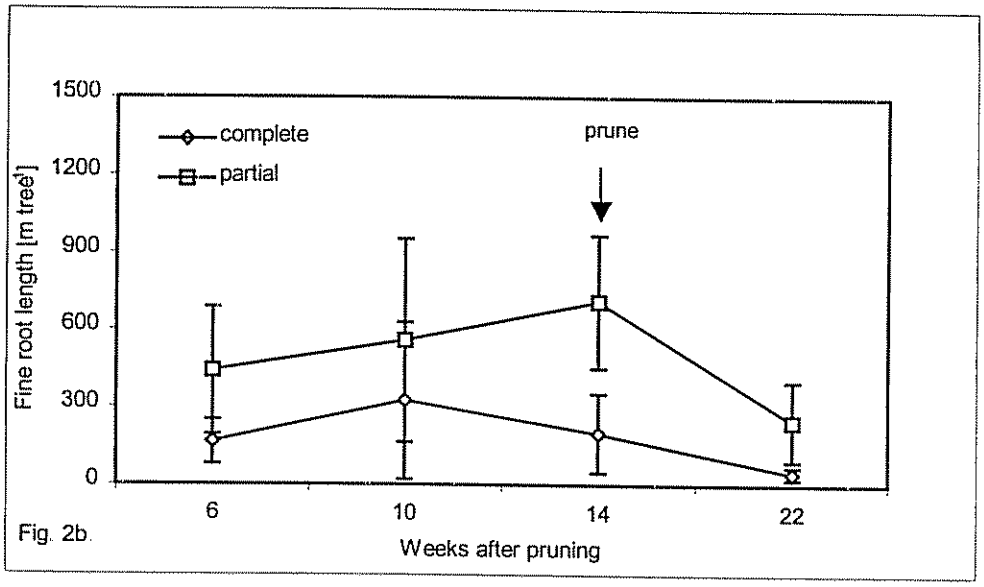
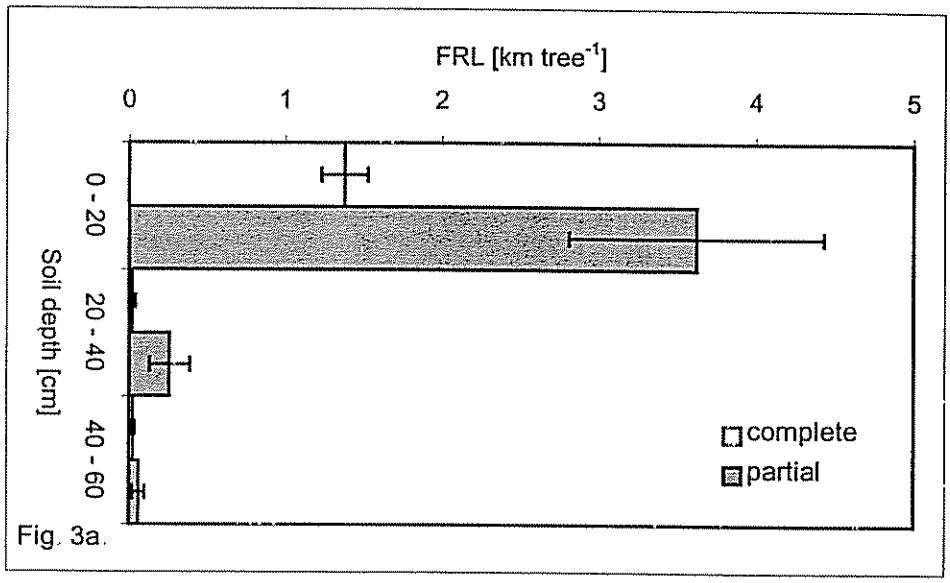


Fig. 2b.

Fig. 2.


FRL [km tree^{-1}]
0
1
2
3
4
5
Soil depth [cm]
0 - 20
20 - 40
40 - 60
complete
partial
Fig. 3a.

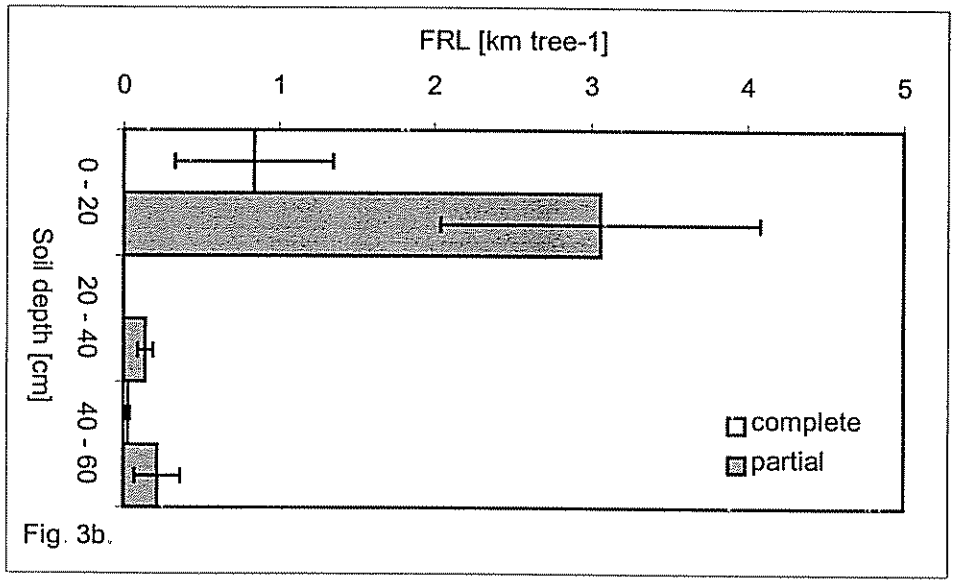

FRL [km tree-1]
0
1
2
3
4
5
Soil depth [cm]
0 - 20
20 - 40
40 - 60
complete
partial
Fig. 3b.

Fig. 3.

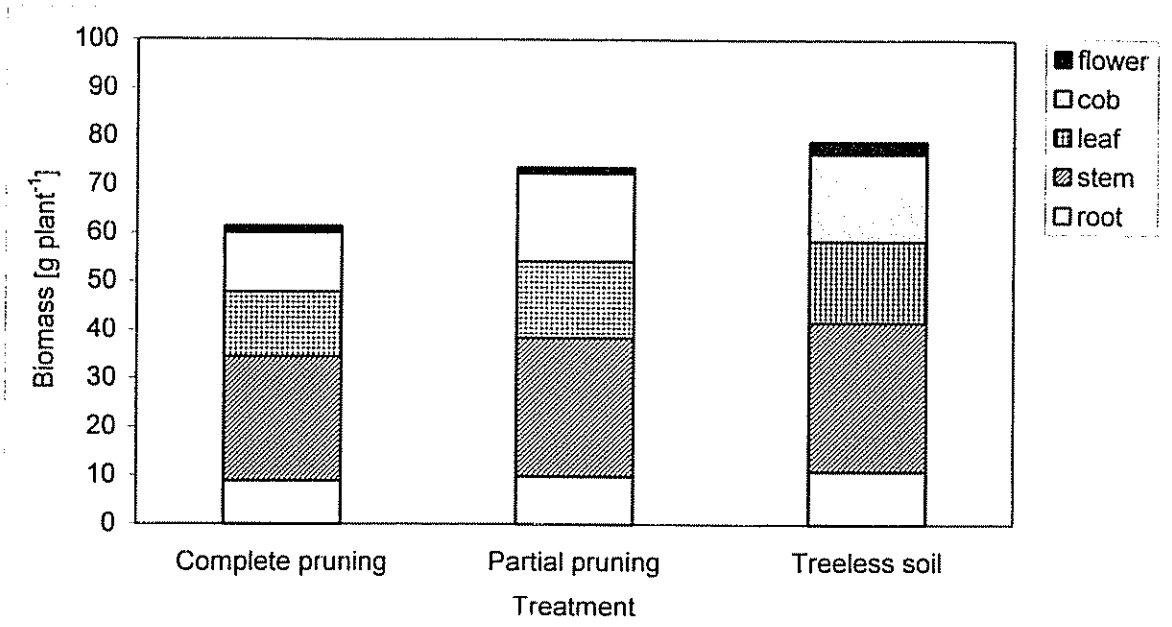

100
90
80
70
60
50
40
30
20
10
0
Biomass [g plant-1]
Complete pruning
Partial pruning
Treeless soil
Treatment
flower
cob
leaf
stem
root

Fig. 4.

Fine root and nodule dynamics of periodically pruned hedgerow trees in a tropical alley cropping system*

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Key words: defoliation, *Erythrina poeppigiana*, legume trees, pruning intensity, turnover

Abstract

Fine root and nodule production and turnover in pruned 2- and 8-year-old *Erythrina poeppigiana* (Walp.) O.F. Cook trees were estimated under humid tropical conditions by applying the compartment flow model (CFM) to fine root and nodule biomass and necromass measured in sequentially taken core samples. Shoot pruning intensities compared were complete pruning (i.e. complete removal of shoots) and partial pruning (i.e. retention of one branch on the pruned stump). The CFM provided reasonable estimates of nodule dynamics but did not apply well to fine root data. Over a five-month observation period, nodule production versus turnover in completely and partially pruned 2-year-old trees was 97 vs. 79 kg ha^{-1} and 191 kg vs. 171 kg ha^{-1}, respectively. Corresponding values in 8-year-old trees were 45 vs. 44 kg ha^{-1} and 44 vs. 29 kg ha^{-1}. Fine root production versus turnover in completely and partially pruned 2-year-old trees was 19 vs. 26 kg ha^{-1} and 63 vs. 41 kg ha^{-1}; estimated values in 8-year-old trees were negative. Senescent nodules and fine roots pass to soil organic matter via decomposition. Partially pruned 2-year-old trees added 75 kg ha^{-1} more decomposed nodules and 1 kg ha^{-1} less fine roots to soil than completely pruned trees. Partially pruned 8-year-old trees contributed 19 kg ha^{-1} less decomposed nodules and 5 kg ha^{-1} more decomposed fine roots than completely pruned 8-year-old *E. poeppigiana* trees. Nodule and fine root turnover was compensated for by new production at 10-14 weeks after pruning. The retention of a branch on the pruned *E. poeppigiana* tree stump allows better fine root and nodule survival, and contributes more to organic matter and N recycling compared to traditional complete pruning, due to higher tree biomass production.

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Introduction

Fast growing *Erythrina poeppigiana* (Walp.) O.F Cook has shown promise as a live stake for low-input tomato (*Lycopersicon esculentum* Mill.) production in the humid tropics of Costa Rica (Chesney *et al* 2000). In this practice, *E. poeppigiana* trees are shoot pruned to provide organic inputs for tomato crop nutrition. Shoot regrowth in *E. poeppigiana* forms a dense canopy (Muschler *et al* 1993) and its current management by complete pruning at half-yearly intervals as practiced in other agroforestry systems (Kass *et al* 1992; Beer *et al* 1998) did not prevent negative interaction with tomato. An additional pruning at tomato mid-season was recommended to mitigate environmental conditions favourable to disease development (Chesney *et al* 2000). The negative biophysical interactions aboveground and the required management to preserve the service attributes of agroforestry trees have recently been reviewed (Sanchez 1995; Rao *et al* 1998). However, the effects of aboveground tree management (pruning) on tree roots, although acknowledged as an important area for research (Vanlauwe and Sanginga 1995; van Noordwijk *et al* 1996), has been studied only in a few cases.

Managing perennial species by frequent pruning is possible because affected plants tend to restore the functional balance between above- and belowground plant organs (Brouwer 1983) through reducing root respiration, slowing or ceasing root growth or reallocating C from storage organs in roots and stems to shoot meristems (Eissenstat and Yanai 1997). The consequence of acropetal movement of C from roots and stems to shoot meristems is the death of roots and nodules, the latter being the first organ affected by reduced C supply (Marschner 1997).

It was shown that half-yearly complete pruning of *E. poeppigiana* trees resulted in complete turnover of nodules (Nygren and Ramírez 1995) and over 50% decrease in root mass (Nygren and Campos 1995; Muñoz and Beer, in press). Research with other species has shown similar plant response to pruning. In *Albizia lebbeck* and *Leucaena leucocephala*, the shoot removal reduced nodule dry weight by 58 and 19%, and root biomass by 40 and 20%, respectively, in a pot study (Kadiata *et al* 1998). Removal of the top one-third of the canopy in Valencia orange (*Citrus sinensis*) trees resulted in at least 20% loss of topsoil roots (Eissenstat and Duncan 1992). Fine root biomass decreased by approximately 25% in *Sesbania sesban* and 10% in *Leucaena leucocephala* during the first two weeks after

coppicing (Fownes and Anderson 1991). The observation that *E. poeppigiana* requires 10-16 weeks to renew N_2 fixation (Vaast and Snoeck 1999) and to increase nodule mass (Nygren and Ramírez 1995) implies that tree N requirement are met from other sources during this lag period (Kass *et al* 1997).

Minimising disruption to the nutrient acquisition system of *E. poeppigiana* when pruning frequency is more than twice a year may require a change in pruning intensity from complete removal of all shoots (complete pruning) to leaving a single branch (partial pruning). This option might be better than increasing the frequency of complete pruning or leaving too many branches at pruning. Complete pruning of *E. berteroana* at a frequency of more than three times a year resulted in decreased biomass production and increased tree mortality (Romero *et al* 1993); effects on roots were not determined. Leaving one or two branches is a traditional partial pruning practice in Costa Rican coffee (*Coffea arabica*) farms (Somarriba *et al* 1996) and it reportedly dates back to the 1930s in tea (*Camellia sinensis*). This technique, called 'lung branch' in tea pruning, is assumed to ensure a supply of photosynthates to developing new shoots (Kandiah *et al* 1984). Partial pruning reduces competition with the crop for light, the primary pruning function, and in addition, may increase available N (Vanlauwe and Sanginga 1995) and conserve nodules (Nygren and Cruz 1998).

The magnitude of disruption to the nutrient acquisition system of *E. poeppigiana* caused by pruning can be determined through measurements of fine root and nodule production and turnover. The compartment-flow model (CFM) has been applied for estimating the production and turnover of fine roots (Santantonio and Grace 1987) and nodules (Nygren and Ramírez 1995). It has been shown to be the most accurate estimation method for fine root production and turnover, in comparison to the maximum-minimum and the balancing-transfer methods, both in a Monte Carlo type test with simulated data (Publicover and Vogt 1993) and under field conditions (Lehmann and Zech 1998).

The aim of this study was to quantify the effects of complete and partial shoot pruning on the production and turnover of fine roots and nodules of *E. poeppigiana* in an agroforestry system with tomato under humid tropical conditions in Costa Rica.

Materials and Methods

The study environment

The study was conducted at the La Montaña experimental farm of CATIE (Centro Agronómico Tropical de Investigación y Enseñanza), Turrialba, Costa Rica (9°53' N, 83°43' W, 602 m a.s.l.). The ecological zone is a very humid pre-montane forest (Holdridge, 1987) with a medium fertility Eutric Cambisol according to the FAO/UNESCO soil classification (Kass *et al* 1995) (Table 1). Meteorological variables (average ± SD) measured during field data collection from August 1999 to January 2000, were monthly precipitation 473±148 mm; daily temperature maxima 30.3±1.5 ^{0}C; daily temperature minima 14.9±1.7 ^{0}C, and relative humidity 88.7±1.7 %.

The experimental plots were established in January 1991 to compare different maize and bean varieties associated with *E. poeppigiana*, *Calliandra calothyrsus* Meissn., *Gliricidia sepium* (Jacq.) Kunth ex Walp. or treeless control treatments. Further description will be confined to *E. poeppigiana*. The initial spacing was 6 × 2 m. In 1997, row width was halved to 3 m (1,666 trees ha^{-1}) with the planting of rooted stakes taken from the same plots. Throughout this article, the trees planted in 1991 will be referred to as 8-year-old trees, and the trees planted in the original alleyways in 1997 will be referred to as 2-year-old trees. Between 1992 and 1996, trees were managed by two complete shoot prunings per year and from 1998 onward, tree pruning height was raised from 0.75 m to 1.5 m to allow for connecting trees with wire at 1.3 m height for staking of tomatoes.

Experimental design

For the present study, *E. poeppigiana* plots were adapted to new treatments arranged in a split plot in time design. Mainplot factor was pruning intensity (complete i.e. removal of all shoots; and partial i.e. retention of one branch corresponding to 5% of total shoot dry weight). Subplot factor was pruning date (August 1999; November 1999; January 2000, applied without re-randomisation). The period May-August 1999 was maize season. Plots were fallowed from September-October 1999 and January-May 2000. On 26 November 1999, 22 days old tomato variety Dina Panama seedlings were transplanted at a spacing of 1.5 x 0.5 m (13,333 plants ha^{-1}) in the alleys formed by rows of *E. poeppigiana* trees. Field data were collected from August 1999 to January 2000 and in May 2000.

Fine root and nodule dynamics

Inventory coring of a modal 8-year-old tree to 60 cm soil depth in September 1998 revealed that 80% of fine roots and 100% of nodules of *E. poeppigiana* were distributed in the topsoil (0-20 cm). For the present study, 10 core (auger cylinder: ∅ = 8 cm; L = 25 cm) samples were taken randomly from the topsoil within the unit soil area, a rectangle measuring 1.5 m^2 with the live stake in the centre of the rectangle, at two weeks after pruning (WAP) in August 1999, and thereafter at 6, 10, 14 and 22 WAP. The sampling periods were selected based on observation on nodule dynamics by Nygren and Ramírez (1995). A once over sampling was carried out in May 2000.

Fine roots (< 2 mm) and nodules were washed free from soil in 0.5 mm sieves and were sorted into live and dead fractions with the aid of a stereomicroscope. Fine root samples not measured immediately after processing were stored at 5°C. Live fine roots were measured for total root length using WinRHizo Pro® image analysis system (Régent Instruments, Quebec, Canada) and both live and dead roots and nodules were measured for dry mass after oven drying (50 ^{0}C for 48 h). Fine root and nodule mass were corrected from the sample area of 1.5 m^2 to the 6-m^2 space each tree occupies. Ratio of live fine roots or nodules to leaf biomass at each pruning event was computed as an index of the tree recovery from disequilibria between below- and aboveground organs brought about by pruning.

Pruned biomass

On each pruning date, plot totals of fresh weights of pruned branches and leaves were measured. Nine branches with intact leaves were randomly selected and weighed with and without leaves to determine the proportion of leaf to branch biomass per plot. Oven dried (65 ^{0}C) mass was determined in 0.5 kg fresh weight sub-samples of chopped leaves, woody and non-woody branch parts to convert fresh biomass to dry biomass for each branch part.

Estimation of nodule and fine root production and turnover

The fine root and nodule production, turnover and decomposition between the samplings were determined by applying the CFM approach (Santantonio and Grace 1987; Nygren and Ramírez 1995). In our application, the model consisted of two compartments or state variables - standing crop of active and senescent nodules or fine roots - and three fluxes

or processes: production, turnover and decomposition. There is a flow of fine roots or nodules from one group to another; new active fine roots and nodules are formed in the production process, and the senescent fine roots and nodules are formed from the active ones in the process of turnover. The senescent fine roots and nodules pass to the soil organic matter through the process of decomposition.

The change in the standing crops of fine roots and nodules can be determined from the successive samplings, and the decomposition rate can be determined independently. The instantaneous process rates of production and senescence are unknown, but if we assume constant process rates between two successive samplings, then the total production (P_i) and senescence (S_i), during the time interval i between the samplings can be estimated by solving a system of difference equations. The assumption allows the process rates to vary from one sampling interval to another.

Let M and N denote the biomass and necromass, respectively, of fine roots or nodules, and D_i the necromass decomposed during interval i. Assuming that the decomposition follows a negative exponential decay function, the necromass remaining at the end of interval i (N_t) is:

$$N_t = N_0 \cdot \exp(-k \cdot t_i) \tag{1}$$

where, N_0 is the initial necromass, t_i the length of the time interval i, and k the decay coefficient. It can be shown that with these assumptions, the total senescence during the interval i is (Santantonio and Grace 1987; Nygren and Ramírez 1995):

$$S_i = \frac{t_i \cdot k \cdot [N_t - N_0 \cdot \exp(-k \cdot t_i)]}{1 - \exp(-k \cdot t_i)} \tag{2}$$

and total production and decomposition during the interval i can be calculated:

$$D_i = N_0 - N_t + S_i \tag{3}$$

$$P_i = M_t - M_0 + S_i \tag{4}$$

where, subscripts 0 and t refer to the biomass or necromass at the beginning and end of interval i, respectively. The equations (1) - (4) hold both for fine roots and nodules, but the decay coefficient *k* is specific for the decaying material, and must be determined separately for nodules and fine roots.

Decomposition rate of fine roots was measured using standard mesh bag technique (McClaugherty and Aber 1982), and the decay coefficient constant k was fitted to eq. (1) by the least squares method in SAS (SAS Institute, Cary, NC). The decomposition rate constant $k = 0.053\ d^{-1}$ was applied to the nodule data for estimating of turnover (Nygren and Ramírez 1995).

Results

Fine root dynamics

Fine root biomass increased to peaks of 35 g vs. 28 g $tree^{-1}$ at 14 WAP in partially and completely pruned 2-year-old trees, respectively (Figure 1a). In 8-year-old trees, corresponding values were 34 g $tree^{-1}$ at 14 WAP and 14 g $tree^{-1}$ at 10 WAP (Figure 1c). Pruning in November 1999 resulted in a steeper decline in fine root biomass in completely pruned trees than in partially pruned 2-year-old trees. Timing of fine root biomass decline with time was similar in partially pruned 2- and 8-year-old trees, but in completely pruned fine root biomass decline with time began before the second pruning. Interaction between pruning intensity and sampling date was non-significant (Table 2).

All measured sources of variation were non-significant for fine root necromass of 2-year-old trees. For 8-year-old trees, both pruning intensity and sampling date had a significant effect on fine root necromass. Necromass was higher in partially pruned trees. For both tree ages, fine root necromass was higher than fine root biomass at 6 WAP (Figures 1b,d), but values decreased by significantly four weeks later in 8-year-old trees (Figure 1d). Interaction between pruning intensity and sampling date was non-significant (Table 2).

Nodule dynamics

For 2-year-old trees, pruning intensity did not significantly affect nodule biomass, but sampling date had a significant effect on nodule biomass (Table 3). At 14 WAP, nodule biomass was 78 g $tree^{-1}$, an increase of 74 g $tree^{-1}$ in four weeks (Figure 2a). Pruning in

November 1999 resulted in a steep decline in nodule biomass in completely and partially pruned 2-year-old trees. As observed with fine root biomass in completely pruned 8-year-old trees, nodule biomass decline began before the second pruning in November 1999 (Figure 2c). Two-year-old trees had as much as four times more nodule biomass than 8-year-old trees. Interaction between pruning intensity and sampling date were non-significant (Table 3).

Pruning intensity did not significantly affect nodule necromass (Table 3). Sampling date had a significant effect ($p < 0.10$) on nodule necromass in 8-year-old trees; nodule necromass at 2 WAP was significantly higher than values at 22 WAP (Figure 2d). In 2-year old trees, plots of nodule necromass with sampling date (Figure 2b) show a pattern similar to changes in fine root biomass with time. Interaction between pruning intensity and sampling date was non-significant (Table 3).

Fine root decomposition rate

Approximately one-half of the fine root mass disappeared in 90 days and a quarter in the first 30 days (Figure 3). The decay coefficient, k, was estimated at 0.00826 d^{-1} ($r^2 = 0.73$). This value was used in the compartment flow calculations to estimate turnover of fine roots.

Estimation of fine root production and turnover

Over a 20-week observation period, fine root production and turnover estimates were higher in partially pruned than in completely pruned 2-year-old trees (Table 4). Decomposition estimates indicated that over the observation period, 70 - 100% of senescent fine roots from partially and completely pruned 2-year-old trees, respectively, were added to the soil organic matter. In the case of 8-year-old trees, the CFM failed to provide reasonable production and senescence estimates: several production and turnover values were negative or close to 0. This may indicate that the decay coefficient was not correctly estimated or some of the model assumptions did not hold in this case. Further, the failure of the CFM to estimate fine root production and turnover in 8-year-old trees suggest that caution should be applied for interpreting the results for 2-year-old trees.

Estimation of nodule production and turnover

Nodule production and turnover estimates were higher for partially than completely pruned 2-year-old trees. In 8-year-old trees nodule production was similar under both pruning intensities, but nodule turnover was higher in completely than in partially pruned trees (Table 4). Decomposition estimates indicate that over the observation period, all of senescent nodules from completely and partially pruned trees were added to the soil organic matter. Estimated production, turnover and decomposition were lower for 8-year-old trees compared to 2-year-old trees.

Fine root and nodule to foliage biomass ratio

Foliage fine root and nodule biomass presented in Table 6 were used to compute the live fine root or nodule to foliage biomass ratio. Live fine root to leaf dry matter ratio showed an increasing trend with time but the opposite was true for live nodule to leaf dry matter ratio (Figure 4). Generally, completely pruned trees had lower root to shoot ratio than partially pruned trees and 2-year-old trees had higher root to shoot ratio than 8-year-old trees. None of the ratios increased beyond 0.18; this value was for partially pruned 2-year-old trees. The ratios were lowest in completely pruned 8-year-old trees. At the end of the five-month period, average net change in fine root biomass was positive in partially pruned and negative in completely pruned 2-year-old trees; in 8-year-old trees, corresponding values were negative. Average net change in nodule biomass was higher in partially pruned than in completely pruned trees.

Discussion

Fine root dynamics

Partial pruning treatment tended to conserve fine roots in both 2- and 8-year-old *E. poeppigiana* trees. However, the values reported here were much lower than those observed by Nygren and Campos (1995) for the same species, probably due to different tree age and history of pruning. The conservative effect of partial pruning on fine root biomass may be due to the maintenance of a sequence of axes leading from leaves to the stem and the root

system for photosynthate allocation. This same sequence of axes serves as the direct channel for water transport in the opposite direction (Wilson 1990).

Fine root dynamics was similar to nodule dynamics reported by Nygren and Ramírez (1995) over a similar observation period. The increase in fine root biomass in completely pruned trees from 10 WAP suggests that acropetal movement of C may have recommenced or carbohydrate reserves supported fine root growth. In partially pruned trees, acropetal movement of C may not have been entirely disrupted. The second pruning after eight weeks regrowth in January 1999 produced the characteristic decline in completely pruned trees but partially pruned trees maintained a much higher fine root biomass. Generally, root biomass of 2-year-old trees showed a clearer response to pruning compared to 8-year-old trees, probably due to higher spatial variation in the latter.

Nodule dynamics

Retention of a branch on the pruned stump resulted in a low nodule biomass conservation. The pattern of change in nodule mass over time was similar to that reported by Nygren and Ramírez (1995). Nodules appear to be more sensitive to aboveground tree disturbance than fine roots. Nodule biomass declined to near zero at 10 WAP but new nodule growth was quite rapid over the next four weeks. Low nodule biomass in frequently pruned 8-year-old trees compared to 2-year-old trees suggests that N_2 fixation mechanism in the former is more disrupted than in the latter, or that the N requirement is supported mainly from uptake.

Estimation of fine root production and turnover

For the production and turnover fluxes, pruning intensity differences were observed in 2-year-old trees. The retention of a branch on the pruned stump increased fine root production probably due to the maintenance of axes connection between leaves and roots for photosynthate allocation as earlier described. The sum of senescent and decomposed fine roots was about 3-times higher than fine root production in completely and partially pruned trees.

The CFM resulted in obviously erroneous estimates in the case of 8-year-old trees. There are three possible reasons: (i) the estimation over a pruning violates the assumption on

constant process rates over an estimation period; (ii) sampling errors in fine root necromass are reflected in all estimates, and (iii) a too low value for the decay coefficient k, results in a too low senescence estimate that transferred mathematically to production and decomposition estimates (eqs. 3 and 4). All these factors may have affected the estimates on fine root dynamics for both 2- and 8-year-old trees, and the results for the young trees should thus be dealt with great caution.

Estimation of nodule production and turnover

The CFM provided reasonable estimates on nodule dynamics during the study period. The estimates of nodule production, senescence and decomposition were clearly higher for 2-year-old trees than 8-year-old trees. For these three nodule fluxes, pruning intensity differences were much clearer for 2-year-old trees than 8-year-old trees. About 6 g of C are directly consumed in fixation of 1 g of atmospheric N_2 to NH_3 (Vance and Heichel 1991), and ca. 2,3 g C is needed for assimilating the ammonia to amino acids or ureides before the fixed N is released to the xylem flow (Oaks 1992). It seems that 2-year-old trees with a more superficial root system and less C and N reserves, invest more C to nodule production than do 8-year-old trees in meeting their N needs. In this present study, C allocation to nodules occurred between 10-14 WAP when the photosynthetic capacity was restored in new foliage. The assumption on constant process rates was violated in the case of nodules as well, but the nodules are less prone to sampling errors than fine roots, and the nodule decay coefficient used has been cross-checked by litterbags and mathematical estimates on nodules attached to living roots in another research plot in La Montaña (Nygren and Ramírez 1995). Thus, we assume that nodule production, senescence and decomposition estimates are more reliable than the estimates for fine roots.

Fine root or nodule to leaf dry matter ratio

The magnitude of the root to shoot ratio generally agrees with that of Nygren and Campos (1995) for fine root mass to leaf biomass ratio, and with Nygren and Ramírez (1995) for active nodule to foliar biomass ratio in young *E. poeppigiana* trees. In this study, pruning intensity as well as tree age and regrowth period seemed to affect the biomass balance between below and aboveground organs. There is a comparatively greater shift in dry matter

allocation to leaves than to fine roots and nodules in completely pruned trees compared to partially pruned trees. This difference may be attributed to greater sink strength in young metabolically active leaves than in nodules and fine roots (Lambers *et al* 1998).

Over the longer regrowth period, from January to June 2000, both 2- and 8-year old trees allocated more dry matter to fine roots than to nodules in relation to dry matter allocation to leaves. Two-year-old trees displayed a greater tendency to restore biomass balance between below- and aboveground organs than 8-year-old trees. This tendency may explain lower biomass production in 2-year-old trees.

This study showed that partially pruned trees produced more fine roots, nodules, foliar biomass and recycled more N than did completely pruned trees. N_2 fixation was not completely disrupted in partially pruned trees. The CFM did not apply well to the data on fine root dynamics generated in this study. The response of *E. poeppigiana* trees in restoring the functional balance between root and shoot after pruning seems to favour biomass allocation to shoots at the expense of roots but the magnitude of the response may be affected by both tree age and pruning intensity.

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Table 1. Topsoil (0-20 cm) chemical properties of an alluvial Eutric Cambisol under *Erythrina poeppigiana* trees, Turrialba, 1999 January. Gravimetric moisture content was 27.3%.

pH (H_2O)	Extractable acidity	Ca	Mg	K	ECEC	SOM	P	NH_4^+	NO_3^-
	cmol l^{-1}					%	mg kg^{-1}		
5.14± 0.16	0.36± 0.19	4.75± 0.07	1.61± 0.13	0.33± 0.09	7.05± 0.06	5.12± 0.28	14.3± 7.4	2.40± 0.36	4.98± 0.72

Table 2. Analysis of variance of the effect of pruning intensity and sampling date on fine root biomass and necromass in *Erythrina poeppigiana*, Turrialba.

Source of variation	Fine root biomass			Fine root necromass		
	df	MS	Pr>F	df	MS	Pr>F
			Two-year-old trees			
Blocks	2	77.21		2	118.21	
Pruning intensity	1	1158.01	**0.0175**	1	0.87	0.9421
Error (a)	2	20.85		2	129.98	
Sampling date	3	324.13	0.3684	3	278.61	0.1335
Interaction	3	136.71	0.6986	3	121.87	0.4305
Error (b)	12	281.57		12	123.15	
Total	23			23		
R^2	0.45			0.53		
			Eight-year-old trees			
Blocks	2	487.89		2	168.15	
Pruning intensity	1	735.82	**0.0039**	1	76.90	**0.0362**
Error (a)	2	2.90		2	2.94	
Sampling date	3	103.17	0.6810	3	371.15	**0.0062**
Interaction	3	171.76	0.4911	3	27.84	0.6820
Error	12	201.18		12	54.45	
Total	23			23		
R^2	0.51			0.71		

Table 3. Analysis of variance of the effect of pruning intensity and sampling date on nodule biomass and necromass in *Erythrina poeppigiana*, Turrialba.

Source of variation	Nodule biomass			Nodule necromass		
	df	MS	Pr>F	df	MS	Pr>F
			Two-year-old trees			
Blocks	2	577.41		2	268.50	
Pruning intensity	1	154.81	0.5582	1	212.48	0.4466
Error (a)	2	319.13		2	240.70	
Sampling date	4	5920.50	**0.0022**	4	78.66	0.5631
Interaction	4	127.29	0.9625	4	68.56	0.6241
Error (b)	16	876.02		16	102.78	
Total	29			29		
R^2	0.65			0.52		
			Eight-year-old trees			
Blocks	2	15.92		2	92.29	
Pruning intensity	1	12.24	0.7938	1	15.57	0.7525
Error (a)	2	137.78		2	119.25	
Sampling date	4	39.37	0.7555	4	56.52	0.0518
Interaction	4	79.66	0.4583	4	13.42	0.5996
Error	16	83.39		16	19.02	
Total	29			29		
R^2	0.37			0.70		

Table 4. Total production, senescence and decomposition of fine roots in pruned *Erythrina poeppigiana* from 6 to 22 weeks after pruning, compartment flow model, k = 0.00826.

Tree age	Pruning Intensity	Production	Senescence	Decomposition
		[g tree^{-1}]		
2	Complete	11.2	15.8	17.6
	Partial	38.1	24.5	16.6
8	Complete	-11.0	-6.2	8.0
	Partial	-3.1	-0.55	10.9

Table 5. Total production, senescence and decomposition of nodules in pruned *Erythrina poeppigiana* from 2 to 22 weeks after pruning, compartment flow model, k = 0.053[z]

Tree age	Pruning Intensity	Production	Senescence	Decomposition
		[g tree^{-1}]		
2	Complete	58.2	47.4	50.4
	Partial	114.9	102.9	95.4
8	Complete	26.8	26.7	36.5
	Partial	26.4	17.7	26.7

[z] taken from Nygren and Ramírez (1995).

Table 6. Foliage, fine root, and nodule biomass [g tree^{-1}] of pruned *Erythrina poeppigiana*, Turrialba.

Pruning intensity	November 1999			January 2000			May 2000		
	foliage	root	nodule	foliage	root	nodule	foliage	root	nodule
				Two-year-old trees					
complete	514	28	82	170	9	13	489	65	21
partial	676	35	73	367	31	26	762	138	63
				Eight-year-old trees					
complete	749	8	1	280	6	1	526	18	7
partial	1145	34	10	388	17	9	926	95	37

Table 7. Average net change in fine root and nodule biomass during the 5-month-period.

Tree age	Pruning regime	Fine root biomass	Nodule biomass
		kg ha^{-1}	
2 years	Complete	-7.6	17.9
2 years	Partial	22.7	20.0
8 years	Complete	-8.1	0.3
8 years	Partial	-4.3	14.6

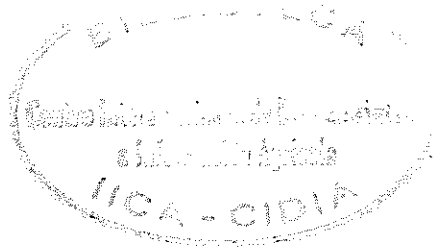
Figure legends:

Figure 1. Average ± SE of the standing crop of fine root biomass and necromass of *Erythrina poeppigiana* after pruning, Turrialba, Costa Rica. The arrow indicates the pruning date 15 Nov. 1999.

Figure 2. Average ± SE of the standing crop of nodule biomass and necromass of *Erythrina poeppigiana* after pruning, Turrialba, Costa Rica. The arrows indicate the pruning dates 18 Aug. and 15 Nov. 1999.

Figure 3. Average ± SE of fine root mass of *Erythrina poeppigiana* in litterbags, Turrialba, Costa Rica.

Figure 4. Evolution of root to shoot ratios in pruned 2- and 8-year-old *Erythrina poeppigiana* trees. Data points along the x-axis correspond to 12, 8 and 16 weeks regrowth. Cumulative precipitation during these regrowth periods was 1174, 1295 and 489 mm, respectively. Key to legend: CP = completely pruned tree; PP = partially pruned tree.



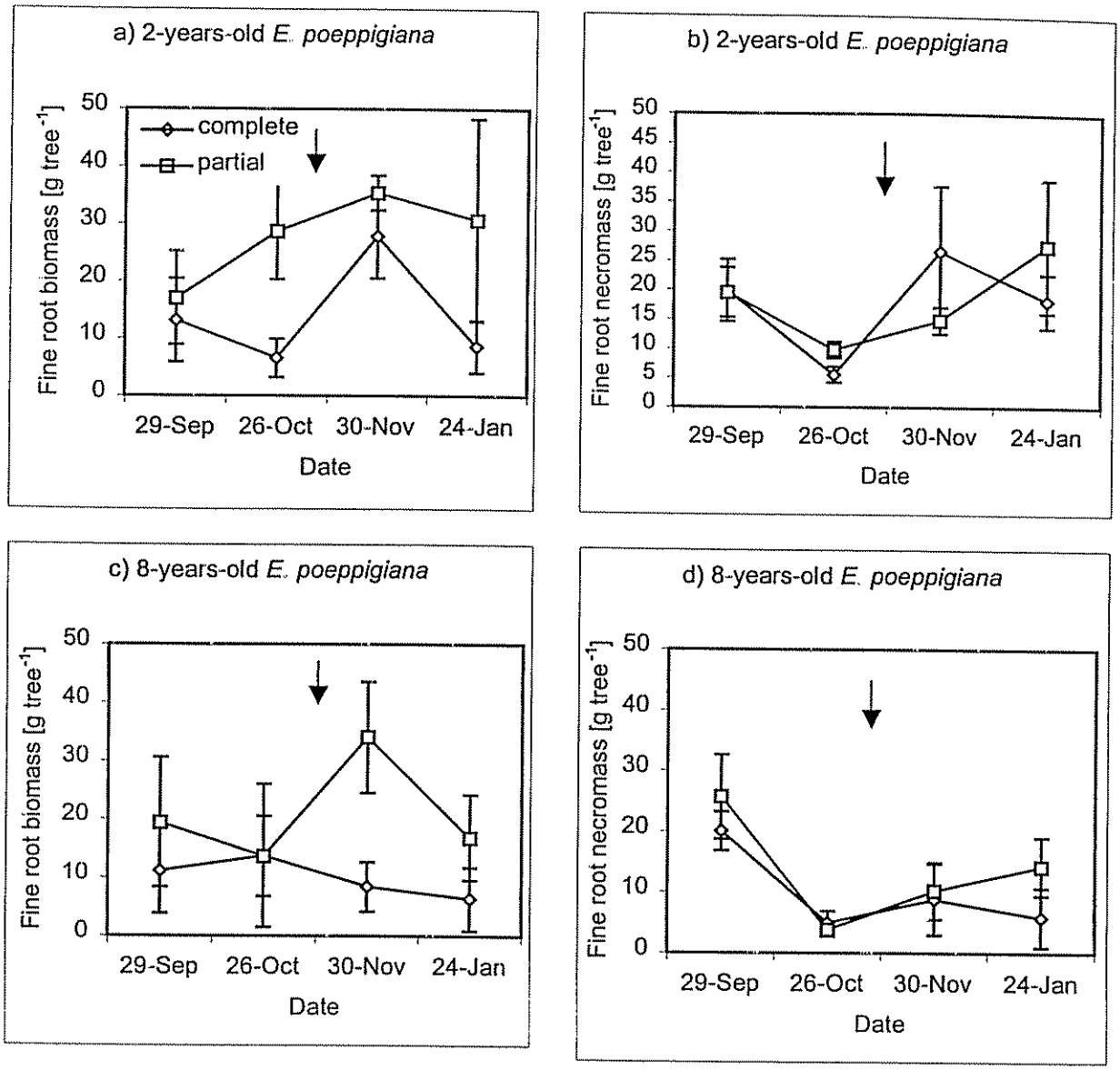

a) 2-years-old E. poeppigiana
Fine root biomass [g tree-1]
complete
partial
29-Sep
26-Oct
30-Nov
24-Jan
Date
b) 2-years-old E. poeppigiana
Fine root necromass [g tree-1]
c) 8-years-old E. poeppigiana
d) 8-years-old E. poeppigiana

Fig. 1

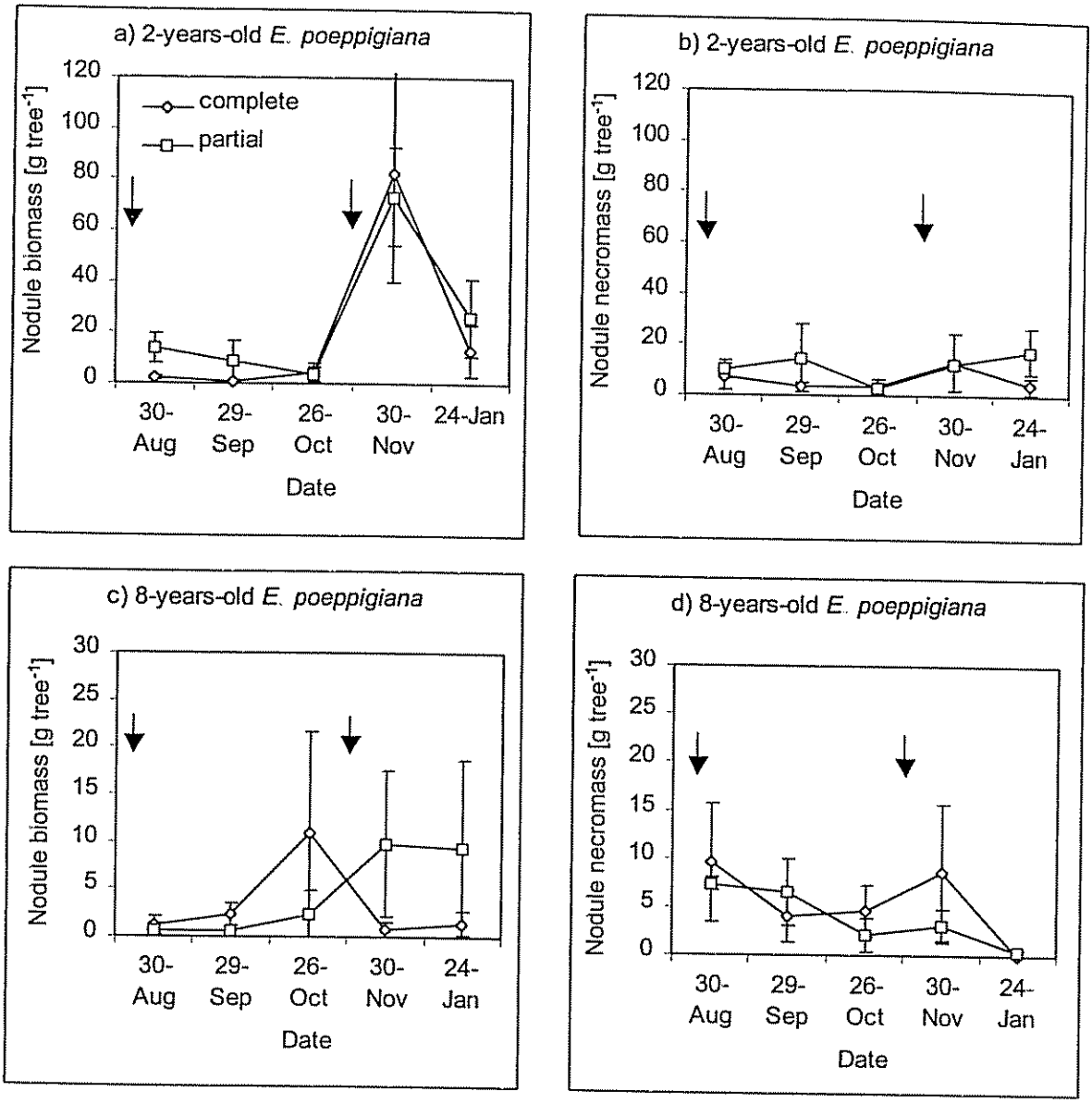

a) 2-years-old E. poeppigiana
Nodule biomass [g tree-1]
120
100
80
60
40
20
0
complete
partial
30-Aug
29-Sep
26-Oct
30-Nov
24-Jan
Date
b) 2-years-old E. poeppigiana
Nodule necromass [g tree-1]
120
100
80
60
40
20
0
30-Aug
29-Sep
26-Oct
30-Nov
24-Jan
Date
c) 8-years-old E. poeppigiana
Nodule biomass [g tree-1]
30
25
20
15
10
5
0
30-Aug
29-Sep
26-Oct
30-Nov
24-Jan
Date
d) 8-years-old E. poeppigiana
Nodule necromass [g tree-1]
30
25
20
15
10
5
0
30-Aug
29-Sep
26-Oct
30-Nov
24-Jan
Date

Fig. 2

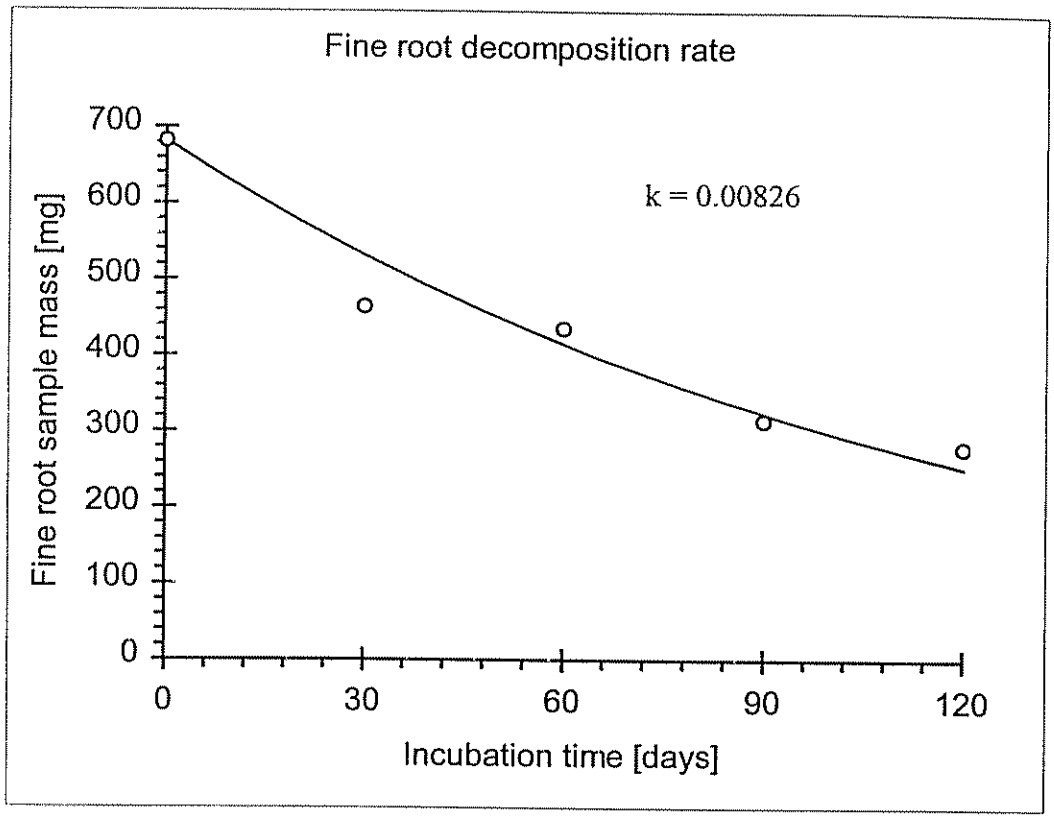

Fine root decomposition rate
k = 0.00826
Fine root sample mass [mg]
700
600
500
400
300
200
100
0
0
30
60
90
120
Incubation time [days]

Fig. 3.

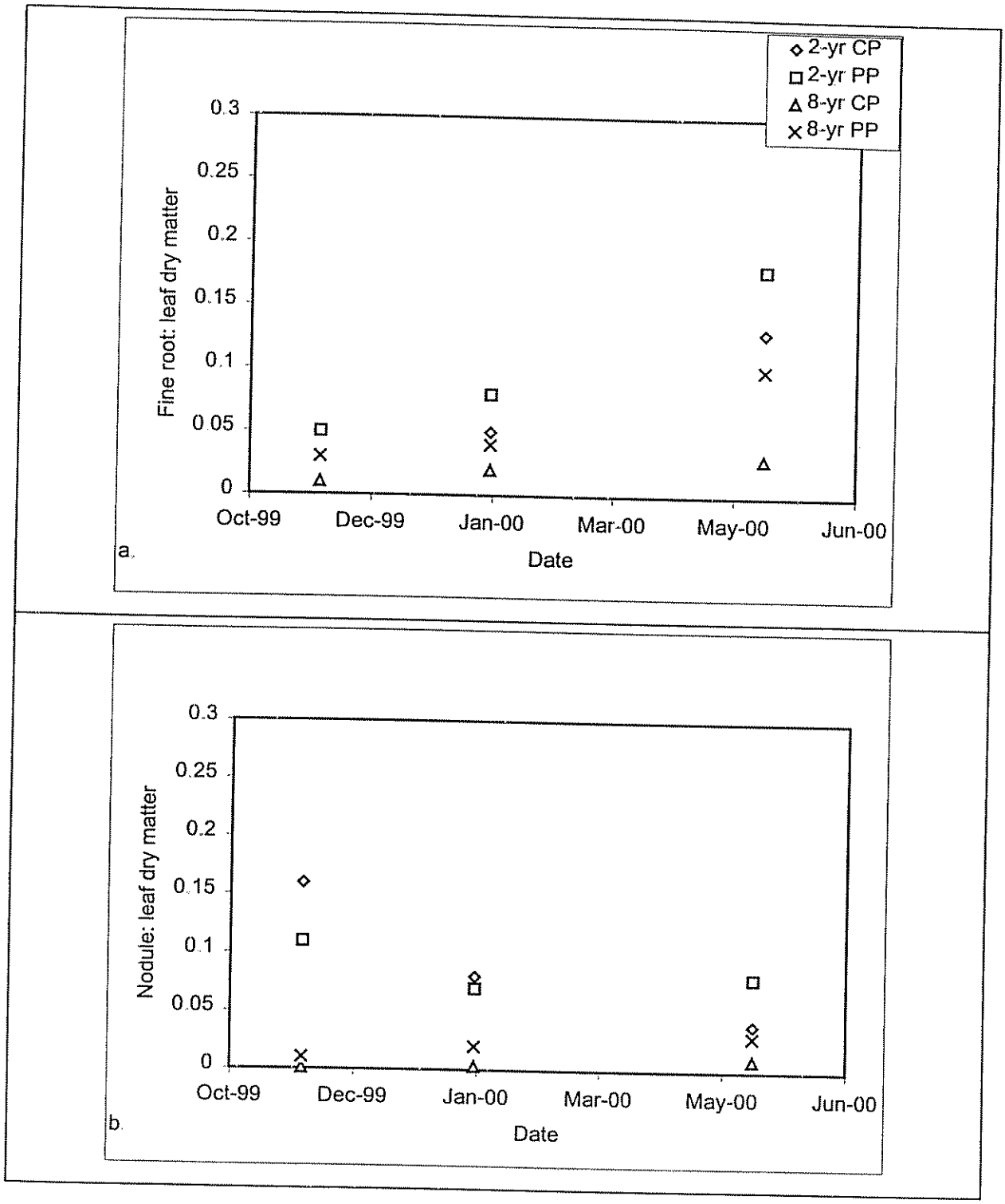

2-yr CP
2-yr PP
8-yr CP
8-yr PP
Fine root: leaf dry matter
0.3
0.25
0.2
0.15
0.1
0 05
0
Oct-99
Dec-99
Jan-00
Mar-00
May-00
Jun-00
Date
a.
Nodule: leaf dry matter
0.3
0.25
0.2
0.15
0.1
0.05
0
Oct-99
Dec-99
Jan-00
Mar-00
May-00
Jun-00
Date
b.

Fig. 4.

Dynamics of non-structural carbohydrate reserves in pruned leguminous trees*

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Summary:

In alley cropping, fast growing leguminous trees are pruned to reduce competition with crops for light and to provide organic inputs for crop nutrition. Tree regrowth depends on non-structural carbohydrate reserves in the remaining tree parts. In this study, starch and soluble carbohydrate dynamics in roots and stems of unpruned, completely pruned (all shoots removed) and partially pruned (one branch retained on the pruned stump) *Erythrina poeppigiana* and *Gliricidia sepium* trees were studied under humid tropical conditions in Turrialba, Costa Rica. Measurements were made at 0, 2, 6 and 12 weeks after pruning (WAP) during both wet and dry periods. In general, starch concentration was highest in unpruned trees. Starch concentration in roots was higher than that in stems. During early regrowth, the effect of pruning intensity was first observed in stems and starch reserves were more depleted in stems than in roots, a process more evident during the dry period. The critical tree regrowth stage for starch mobilisation was that of vigorous sprout development at 6 WAP particularly in completely pruned trees. If the proportion of sugar to starch concentration is taken as an indicator of metabolic activity then there was greater metabolic activity in stems than in roots of *E. poeppigiana*. Metabolic activity was high in both stems and roots of *G. sepium*. Starch re-synthesis in roots occurred at 12 WAP in *G. sepium*, and later than 12 WAP in *E. poeppigiana* roots. The implication for tree management would be to extend the regrowth period beyond 12 weeks to facilitate shoot growth with less root competition for fixed C in the former, and for acropetal movement of non-structural carbohydrates to replenish root stores in the latter.

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Key words: agroforestry, *Erythrina poeppigiana*, fine roots, *Gliricidia sepium*, nodules, resprouting, starch, soluble sugars

Introduction

Erythrina poeppigiana (Walp.) O.F. Cook and *Gliricidia sepium* (Jacq.) Kunth ex Walp. are common alley cropping species in the humid tropics. These fast growing leguminous trees are managed by twice-yearly complete shoot pruning to increase light supply (Muschler *et al* 1993) and to provide organic inputs for crop nutrition in various agroforestry systems (Beer 1990; Kass *et al* 1992; Romero *et al* 1993). Low input tomato (*Lycopersicon esculentum* Mill.) alley cropping (Schlonvoigt and Chesney 1999) requires mid-season pruning at eight weeks after planting or at 10 weeks after pre-plant pruning, to mitigate microclimate conditions favourable to disease development (Chesney *et al* 2000). Nygren (1995) suggested that complete pruning of *E. poeppigiana* trees at intervals less than 16 weeks might be insufficient for tree recovery due to slow non-structural carbohydrate replenishment. However, if proportionately more stem starch than root starch reserves is depleted during tree regrowth as was observed in *G. sepium* (Erdmann *et al* 1993) then regrowth can proceed without a severely affected nutrient acquisition system.

Biomass accumulation and rapid replenishment of tree reserves (Loescher *et al* 1990) increase the tolerance of woody perennials to pruning (Duguma *et al* 1988). Biomass accumulation is critical to the sustainability of low input agroforestry systems (Beer *et al* 1990). Shoot pruning affect the processes of photosynthesis and non-structural carbohydrate synthesis. Non-structural carbohydrate reserves, mainly starch (Kozlowski and Keller 1966; Adams *et al* 1986; Loescher *et al* 1990) provide the energy to drive regrowth of pruned trees (Quinlan 1969; Kandiah 1979; Harrington and Fownes 1993). Starch provides energy for respiration of active buds and synthesis of chlorophyll, proteins and structural compounds during early stages of leaf growth (Pollock, 1953), processes that influence the rate of resprouting and biomass output (Richards and Caldwell, 1985) of pruned trees.

The organ source of starch may be species specific. Erdmann *et al* (1993) reported that stem starch was depleted during regrowth of *Gliricidia sepium* (Jacq.) Walp. even though roots contained higher starch levels. In other species, such as *Salix viminalis* (von

Fircks and Sennerby-Forsse 1998), *Miconia albicans* and *Clidemia sericea*, (Miyanishi and Kellman 1986), root starch was critical to resprouting. Other factors that affect the regrowth of pruned trees include the severity of disruption to the photosynthetic capacity and the resprouting rate; the latter depends on the number of buds (Paukkonen and Kauppi 1998).

Minimising disruption to the tree when pruning frequency is more than twice a year may require a change in pruning intensity from complete removal of all branches (complete pruning) to retaining a single branch (partial pruning). This option might be better than increasing the frequency of complete pruning or leaving too many branches at pruning. Pruning of *E. berteroana* at a frequency of more than three times a year resulted in decreased biomass production and increased tree mortality (Romero *et al* 1993) probably due to negative C balance (Lawson and Mobbs 1998). Leaving one or two branches on the pruned stump is a traditional partial pruning practice in Costa Rican coffee (*Coffea arabica*) farms (Somarriba *et al* 1996) and it reportedly dates back to the 1930s in tea (*Camellia sinensis*). This technique, called 'lung branch' in tea pruning, is assumed to ensure a supply of photosynthates to developing new shoots (Kandiah *et al* 1984).

The physiological basis of regrowth after partial pruning of leguminous woody species of agroforestry importance has not been reported. This study was undertaken to determine the role of non-structural carbohydrate reserves during regrowth of *E. poeppigiana* and *G. sepium* subjected to partial and complete pruning. Starch and sugar concentration in stems and roots, and fine root length, mass and nodule mass were quantified to 1) elucidate the effects of pruning intensity on non-structural carbohydrate reserves and 2) to relate these effects to nutrient acquisition systems of *E. poeppigiana* and *G. sepium* trees.

Materials and Methods

The study environment

The study was carried out in a very humid pre-montane forest ecozone (Holdridge 1987) with a medium fertility Eutric Cambisol (Kass *et al* 1995). Meteorological variables (average±SD) measured during field data collection from Dec 99 to Mar 00 (wet period) vs. Mar to Jun 00 (dry period), were monthly precipitation 385±299 vs. 170±102 mm; daily

temperature maxima 29.1±0.8 vs. 29.9±1.2 ^{0}C; daily temperature minima 13.5±0.7 vs.16.1±2.9 ^{0}C, and relative humidity 87.9±3.5 vs. 86.8±1.8 %, respectively.

Experimental design

The field plot consisted of block plantings of 2 x 2 m spaced 2-year-old *E. poeppigiana* and *G. sepium* trees established from air-layered stakes. On 16 August 1999, 30 trees of each species were cut back to 1 m height to stimulate regrowth and multiple stems were thinned to one stem. Plastic barriers inserted to 0.5 m depth and delimiting a unit soil area of 1 m^2 for each tree separated roots of trees. Treatments were arranged in a split plot in time design. Mainplot treatment was pruning intensity, unpruned (intact tree), partial (retention of one branch on the pruned stump corresponding to 0.5m^2 leaf area), and complete (all shoots removed). Subplot treatment was sampling date (0, 2, 6, 12 WAP corresponding to 9 Dec 99, 24 Dec 99, 24 Jan 00, 3 Mar 00 and 24 Mar 00, 7 Apr 00, 8 May 00, 16 Jun 00, respectively. Number of treatment repetitions was five (wet period) or four (dry period). Observations started on 9 December 1999 and 24 March 2000; trees were excavated at 12 WAP on 3 Mar 00 (12 WAP_{wet}) and on 16 Jun 00 (12 WAP_{dry}).

Dynamics of root and stem non-structural carbohydrates

During 1700-1800 h on each sampling date, tissue samples were taken from stem (10-20 cm above soil) and roots, and were washed free of adhering soil. Tissue samples were plastic-bagged and kept under ice packs in the field. In the laboratory, frozen (-17 ^{0}C) samples were freeze-dried by lyophilisation (King 1971) followed by grinding under liquid nitrogen before chemical analyses.

Starch was determined by the Lugol method (Caraway 1959). Ground samples (100 mg) were extracted with 0.1mol l^{-1} pH 7.2-phosphate buffer in hot water baths (80 ^{0}C) for five minutes. Cooled samples were centrifuged at 4000 rpm for five minutes and 500 µl supernatant was analysed by spectrophotometry at 570 nm.

Soluble carbohydrates (fructose, glucose and saccharose) were analysed by HPLC (Lim 1986). Ground samples (200 g) were extracted with hot water at 80 ^{0}C for five minutes. Cooled samples were centrifuged at 4000 rpm for five minutes and 500 µl

supernatant was mixed with 1 ml acetonitrile and the mixture was centrifuged at 4000 rpm for five minutes. Aliquots of 1 ml of supernatant were then analysed by HPLC.

Resprouting and leaf area

Stem and branch borne sprouts, which are growing buds each with at least one normal foliage leaf or clearly elongated shoot (Paukkonen and Kauppi 1998), were counted at 1,2,3,4 and 6 WAP during the wet period, and weekly for four successive WAP during the dry period. Leaf area was determined in *E. poeppigiana* trees at 0, 6 and 12 WAP during the dry period only. On each sampling date, all the leaves per tree were counted and the area of each of 100 leaves (300 leaflets) per tree was measured. The leaf area was determined after applying form factors of Chacon-Espinosa (1990). Resprouting and leaf area data were used to explain observed changes in non-structural carbohydrate reserves during tree regrowth.

Fine root length, mass and nodule mass

On each sampling date, five-pooled topsoil core (cylinder L = 25 cm; ϕ = 8 cm) samples to 0-20 cm soil depth per plot were taken. Samples were washed free from soil in 0.5 mm sieve. Live roots were separated from dead roots with the aid of a stereomicroscope and criteria of colour, flexibility and integrity of central cylinder. Nodules were sorted into active and senescent classes. Total fine root (< 2 mm) length was measured using the WinRHizo Pro® image analysis system (Règent Instruments, Quebec, Canada) and root and nodule biomass determined as oven-dried (50 ^{0}C for 48 hours) mass.

Statistical analyses

Data sets were examined for homogeneity of variance and normality. Carbohydrate, root and nodule data were analysed using SAS/GLM and SAS/CORR procedures (SAS Institute, Cary, NC) for a split plot design. Mean comparisons were by the REGWQ ($p<0.05$) multiple range test.

Results

Dynamics of root and stem non-structural carbohydrates in E. poeppigiana:

The analysis of starch concentration during the wet period showed that the effects of pruning, sampling date and the interaction between pruning and date were non-significant for root starch, but were significant for stem starch concentration (Table 1). Plots of starch concentration with time (Figure 1) showed that stems of unpruned trees had significantly higher starch concentration (42 mg g^{-1} dry weight DW) at 6 WAP compared to starch concentration of 16 and 5 mg g^{-1} DW in partially pruned and completely pruned trees, respectively (Figure 1b). Mean starch concentration was 28 (root) and 17 mg g^{-1} DW (stem) during the wet period.

The analysis of starch concentration during the dry period showed that root starch was significantly affected by sampling date, and stem starch by both pruning and sampling date (Table 1). Mean root starch was highest (43-46 mg g^{-1}) during early (2 WAP) regrowth and decreased to one-third of its initial concentration at 6 WAP. Unpruned tree stems had the highest mean root starch concentration (22 mg g^{-1}) compared to 19 and 15 mg g^{-1} DW for completely and partially pruned trees, respectively. Mean stem starch decreased to one-third its concentration at 2 WAP by 6 WAP (Figure 1d). Mean starch concentration was 31 (root) and 19 mg g^{-1} DW (stem) during the dry period.

During the wet period, all sources of variation were non-significant for root and stem sugars (Table 1). Mean sugar concentration in roots and stems was 61 and 57 mg g^{-1} DW, respectively. During the dry period, root sugar decreased by 2 WAP and increased in stems at the same time. Saccharose was the main constituent (80%) of all measured sugars.

Sugar to starch ratio in roots was not affected by sources of variation. Mean sugar: starch ratio was 3.3. Sugar to starch ratio in stems was affected by pruning. Completely pruned trees with sugar to starch ratio of 9.8 was not significantly different to partially pruned trees (6) but was significantly different to unpruned trees 2.8. The critical period for higher starch mobilization in completely pruned tree stems appeared to be 6 WAP (Figure 3b).

Dynamics of root and stem non-structural carbohydrates in G. sepium:

During both wet and dry periods, pruning and sampling date significantly affected root and stem starch concentrations, while interaction between pruning and date was significant only for stem starch during the dry period (Table 2). During the wet period, mean starch concentration in roots of unpruned and partially pruned trees was not dissimilar but during the dry period, starch concentration in roots of unpruned trees was almost twice that of partially pruned trees. Roots of completely pruned trees had the lowest mean starch levels (15 mg g^{-1}) during both periods. During the wet period, root starch concentration increased 3-fold in 10 weeks at 12 WAP. However, during the dry period, time course changes were 41 mg (2 WAP) to 17 mg g^{-1} DW at 6 WAP. Starch concentration in roots replenished to 70% its initial concentration by 12 WAP. Mean root starch concentration was 24 (wet period) and 33 mg g^{-1} DW (dry period).

Stem starch concentration during wet and dry periods was lower in completely pruned trees compared to unpruned trees; values for partially pruned trees were intermediate. Under dry conditions, stem starch concentration decreased to one-third its initial concentration by 6 WAP. Mean stem starch concentration was the lowest in completely pruned trees from 2 WAP (Figure 2). Mean stem starch concentration during the wet and dry periods was 15 and 18 mg g^{-1} DW, respectively corresponding to 62 and 54% of values during the wet period.

Pruning had a significant effect on root sugar content, and interaction between pruning and date was significant for both root (dry period) and stem sugar (wet period) concentration (Table 2). In each of the wet and dry periods, sugar concentration was highest in roots of completely pruned trees but levels in stems were similar for the different pruning treatments. Sugar concentration was highest in stems of completely pruned trees at 6 and 12 WAP. Saccharose was the main constituent (80%) of all measured sugars.

Pruning and date significantly affected sugar to starch ratios in roots, while all sources of variation significantly affected sugar to starch ratios in stems. In roots, significantly higher sugar to starch ratio (8.4) was observed in completely pruned trees compared to statistically similar ratios of 3.5 and 2.6 for partially pruned and unpruned trees, respectively. Ratios decreased over time from 7 vs. 4.6 vs. 2.6 at 2, 6 and 12 WAP, respectively (Figure 3c). In stem tissues, completely pruned trees had higher sugar to starch

ratios (7.9) compared to ratios of 3.2 and 2.9 for partially pruned and unpruned trees, respectively. Ratios increased with time from 2.8 at 2 WAP to 7.8 at 12 WAP (Figure 3d); at this time, the sugar to starch ratio of completely pruned tree stems was five-times higher than that of unpruned and partially pruned trees.

Fine root and nodule parameters of E. poeppigiana:

During the wet and dry periods, fine root biomass (Figure 4a,c), fine root length (Figure 4e) and nodule biomass (Figure 5a,c) were highest in unpruned trees. Fine root biomass was lowest in completely pruned trees at 12 WAP. Fine root and nodule necromass were low and were not significantly affected by pruning intensity or sampling date. While fine root biomass and length increased in magnitude with time in unpruned trees, a descending trend to lowest values at 6 WAP was observed in pruned trees; values then increased at 12 WAP. In pruned trees, nodule biomass decreased towards zero at 6 WAP during both wet and dry periods. Nodule biomass decrease in unpruned trees was less strong (Figure 5a,c). Nodule necromass did not significantly differ among treatments (Figure 5b,d).

Fine root and nodule parameters of G. sepium:

Fine root length was the only parameter that differed significantly over time (Figure 6c). It declined with time irrespective of pruning treatments during the wet period.

Relationship among starch, soluble carbohydrates and root parameters in E. poeppigiana

In unpruned trees during the wet period, stem starch and soluble carbohydrates were negatively correlated with nodule and fine root biomass and with fine root length (Table 3a). In partially pruned trees, root and stem starch were uncorrelated with root parameters but root soluble carbohydrates were negatively correlated with fine root length and biomass. In completely pruned trees, root starch was positively correlated with nodule and root necromass; there were no correlations between soluble carbohydrates and root parameters.

During the dry period, root starch was positively correlated with nodule biomass in unpruned trees (Table 3b). In partially pruned trees, root and stem starch were positively correlated with nodule biomass, root length and root biomass. In completely pruned trees, root and stem starch were uncorrelated with root parameters.

Relationship among starch, soluble carbohydrates and root parameters in G. sepium:

In unpruned trees during the wet period, root soluble carbohydrates were negatively correlated with fine root biomass. In partially pruned trees, root starch was negatively correlated with fine root length and, in completely trees, stem soluble carbohydrates were negatively correlated with fine root length.

Discussion

Dynamics of root and stem non-structural carbohydrates of E. poeppigiana and G. sepium

In the present study, root and stem carbohydrate dynamics were generally similar for both *E. poeppigiana* and *G. sepium*. In general, starch concentration was higher in roots than in stems and during early regrowth, the effect of pruning intensity was first observed in stems. Unpruned trees had the highest starch concentration and completely pruned trees the highest soluble carbohydrate concentration. It appears that disruption to the photosynthetic apparatus through removal of source leaves is the critical factor in starch utilization. Partially and completely pruned *E. poeppigiana* trees mobilised similar amounts of starch in roots and stems during tree regrowth except during the wet period when more starch was depleted in stems of completely pruned trees. In *G. sepium*, complete pruning tended to deplete more starch than partial pruning. Ericsson and colleagues (1990) reported that starch concentration in roots was reduced following partial leaf removal, but total defoliation can provoke much stronger depletion of carbohydrates than partial defoliation (Tschaplinski and Blake 1990).

Starch reserves were more depleted in stems than in roots, a process more evident during the dry period. The more severe effect of pruning on non-structural carbohydrate in stems than in roots agrees with findings of Erdmann *et al* (1993). Starch concentration in root and stems did not fall below 2 WAP levels until 6 WAP, thus explaining the date effect. The critical tree regrowth stage for starch mobilisation was that of vigorous sprout

development at 6 WAP particularly in completely pruned trees (Figure 7). Roots of completely pruned trees had the least starch reserves probably due to greater sink strength at meristems (0-2 WAP) and elongating shoots (2-6 WAP). The difference in starch levels between partially and completely pruned trees could be greater assimilate demand in the latter where presence and activity of meristems would have greater respiratory demand for energy (Kozlowski 1992). The mechanism appears to be active growth of vegetative meristems to maintain an osmotic gradient as a sink for carbohydrates (Lawson and Mobbs 1998).

Stem starch decrease at 6 WAP coincided with highest resprouting; resprouting was a lot more rapid at during the dry period when trees would maximize C fixation (Figure 7). Decline in stem starch more than root starch in severely pruned plants has been reported (Ericsson *et al* 1980; Tschaplinski and Blake (1994). Vigorous sprout development may have depended on stem starch reserves for energy (Marshall and Waring 1985). On the other hand, refoliation of unpruned trees due to phenological changes coincided with increased starch mobilisation (Figure 8).

Retention of a branch on partially pruned trees did not increase soluble carbohydrate mobilization in roots. Higher sugar to starch ratio in stems of completely pruned trees at 6 WAP, coincided with decreases in sugar to starch ratio in roots and with stem resprouting.

Relation of non-structural carbohydrate dynamics to root parameters

In *E. poeppigiana*, the relationship between non-structural carbohydrates and root and nodule parameters appeared to be much stronger in unpruned and partially pruned trees than in completely pruned trees. The retention of photosynthetic capacity in partially pruned trees facilitated the maintenance of some fine root and nodule for water and nutrient uptake. In completely pruned trees, most of the starch reserves were probably used up to support resprouting, and coupled with the delayed restoration of photosynthetic capacity in new growth may have resulted in fine root and nodule senescence. Higher demand for starch during the dry period to support faster resprouting and refoliation resulted in insufficient carbohydrates for fine root and nodule maintenance or increase. Fine root and nodule turnover rates are therefore expected to be higher during this period.

In *G. sepium*, fine roots were conserved during the wet period when regrowth demand for starch was lower. During the dry period, when this demand increased, root growth was affected. Starch was depleted to support regrowth but trees, irrespective of pruning intensity, resynthesized starch at the expense of shoot and fine root growth. Replenishment of starch in roots of *G. sepium* to 70% of its initial concentration by 12 WAP agrees with findings of Tscaplinski and Blake (1994). Inadequate non-structural carbohydrate reserves in roots could create N deficiencies through its negative effect on new root growth (Loescher *et al* 1990). Increases in root starch at 12 WAP were associated with decreases in fine root length at this time particularly in partially pruned trees. In completely pruned trees, it appears that increased metabolic activity during resprouting (stem sugar increases) was responsible for loss in fine roots. The severity of pruning is therefore a determinant in fine root growth. In unpruned trees, reduced soluble carbohydrates in roots was associated with increases in fine root biomass, a possible conservative mechanism during the rainy season.

Roots stored more starch than stems in both species thus maintaining the potential to supply non-structural carbohydrates for regrowth. In *E. poeppigiana,* more starch might be expected to be stored in stems due to greater stem girth and higher dry matter in stem than in roots compared to *G. sepium*. Completely pruned trees will deplete more starch from roots to support energy demands of aboveground sinks. Reduced photosynthesis and greater depletion of carbohydrate reserves during regrowth of completely pruned tree stumps may affect the C balance more than in partially pruned trees. The tree management implication of starch re-synthesis in *G. sepium* roots at 12 WAP and in *E. poeppigiana* roots later than 12 WAP would be to extend the regrowth period beyond 12 weeks to facilitate shoot growth with less root competition for fixed C in the former and for acropetal movement of non-structural carbohydrates to roots in the latter.

Acknowledgement

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Table 1. Means and F-test significance for the effects of pruning intensity and sampling date on starch and soluble carbohydrate concentration in the roots and stems of *Erythrina poeppigiana* for the periods 12 December 1999 to 3 March 2000 (wet period) and from 24 March 2000 to 16 June 2000 (dry period), Turrialba.

Source of Variation		Root		Stem	
		Wet period	Dry period	Wet period	Dry period
		Starch concentration (mg g^{-1})			
Pruning Intensity					
	Unpruned	32.2 a	33.2 a	26.0 a	22.5 a
	Partial	29.3 a	33.5 a	14.2 b	15.4 b
	Complete	23.6 a	24.6 a	9.8 b	18.8 b
	Mean	28.4	30.4	16.7	18.9
	Pr > F	0.1252	0.2825	**0.0039**	**0.0471**
Sampling Date (WAP)					
	0	21.6[z]	45.6 a	6.8[z]	23.5 a
	2	30.9 a	42.9 a	14.0 b	30.7 a
	6	26.4 a	15.7 b	21.2 a	11.2 b
	12	27.8 a	18.4 b	14.8 b	10.2 b
	Mean	28.4	30.6	16.7	18.9
	Pr > F	0.7390	**0.0001**	**0.0337**	**0.0001**
Interaction	Pr > F	0.4006	0.2181	**0.0004**	0.0646
		Soluble carbohydrate concentration (mg g^{-1})			
Pruning Intensity					
	Unpruned	62.5 a	83.9 a	55.7 a	62.9 a
	Partial	60.1 a	55.1 a	63.9 a	64.5 a
	Complete	59.1 a	53.2 a	51.2 a	75.5 a
	Mean	60.6	64.1	56.9	67.6
	Pr > F	0.9204	0.1801	0.2903	0.8168
Sampling Date (WAP)					
	0	60.4[z]	82.3 a	79.9[z]	55.1 b
	2	56.2 a	44.9 b	51.2 a	80.2 a
	6	65.3 a	n.a.	56.8 a	n.a.
	12	60.7 a	n.a.	63.0 a	n.a.
	Mean	60.7	n.a.	57.0	n.a.
	Pr > F	0.4551	**0.0254**	0.2172	**0.0424**
Interaction	Pr > F	0.3647	0.2448	0.1904	0.7906

Means in the same column followed by the same letter are not significantly different (REGWQ $p \leq 0.05$).

[z] values are averages from three trees and were not included in statistical analysis; n.a. not available.

Table 2. Means and F-test significance for the effects of pruning intensity and sampling date on starch and soluble carbohydrate concentration in the root and stem of *Gliricidia sepium* for the periods 12 December 1999 to 3 March 2000 (wet period) and from 24 March 2000 to 16 June 2000 (dry period), Turrialba.

Source of Variation		Root		Stem	
		Wet period	Dry period	Wet period	Dry period
		Starch concentration (mg g^{-1})			
Pruning Intensity					
	Unpruned	29.2 a	52.4 a	19.3 a	21.7 a
	Partial	27.9 a	29.7 b	14.0 ab	18.2 ab
	Complete	15.2 b	14.8 c	11.4 b	14.3 b
	Mean	24.1	32.3	14.9	18.1
	Pr > F	**0.0091**	**0.0001**	**0.0382**	0.0512
Sampling Date (WAP)					
	0	9.3[z]	41.1 a	9.2[z]	27.1 a
	2	14.0 b	41.4 a	14.2 b	26.5 a
	6	18.4 b	17.1 b	19.1 a	9.2 b
	12	39.9 a	28.7 ab	11.3 b	9.5 b
	Mean	24.1	32.1	14.9	18.1
	Pr > F	**0.0001**	**0.0006**	**0.0094**	**0.0001**
Interaction	Pr > F	0.7578	0.5832	0.1287	**0.0171**
		Soluble carbohydrate concentration (mg g^{-1})			
Pruning Intensity					
	Unpruned	48.2 b	24.5 b	41.9 a	41.2 a
	Partial	53.5 b	43.7 b	42.6 a	60.5 a
	Complete	78.0 a	80.9 a	48.4 a	40.2 a
	Mean	59.9	49.7	44.3	47.3
	Pr > F	**0.0360**	**0.0045**	0.2839	0.2662
Sampling Date (WAP)					
	0	43.4[z]	53.2 a	31.8[z]	45.0 a
	2	65.2 a	48.1 a	35.8 a	49.7 a
	6	69.3 a	n.a.	48.0 a	n.a.
	12	45.1 b	n.a.	49.1 a	n.a.
	Mean	59.9	n.a.	44.3	n.a.
	Pr > F	0.0510	0.3257	0.1038	0.5920
Interaction	Pr > F	0.6800	**0.0071**	**0.0199**	0.7566

Means in the same column followed by the same letter are not significantly different (REGWQ $p \leq 0.05$).

[z] values are averages from three trees and were not included in statistical analysis; n.a. not available.

Table 3. Pearson correlates for starch, sugars and fine root and nodules in *Erythrina poeppigiana*

Table 3a. December 1999 to March 2000, Turrialba.

Root parameters	Pruning intensity											
	Unpruned				Partial				Complete			
	Root starch	Stem starch	Root sugar	Stem sugar	Root starch	Stem starch	Root sugar	Stem sugar	Root starch	Stem starch	Root sugar	Stem sugar
Nodule biomass	-013 0.6538	-0.65 **0.0088**	0.30 0.2727	-0.42 0.1174	0.28 0.3159	0.14 0.6044	-0.36 0.2073	-0.08 0.7832	-0.09 0.7531	0.20 0.4806	-0.19 0.4979	-0.36 0.2084
Nodule necromass	-0.12 0.6776	0.35 0.2004	0.01 0.9585	0.210 .4495	0.11 0.6821	-0.23 0.4016	-0.56 **0.0358**	-0.05 0.8468	0.54 **0.0378**	0.34 0.2194	-0.45 0.0910	-0.37 0.1948
Root length	0.27 0.3360	-0.25 0.3625	-0.33 0.2223	-0.70 **0.0035**	0.40 0.1422	-0.44 0.1020	-0.63 **0.0157**	-0.02 0.9953	0.43 0.1104	0.36 0.1908	0.12 0.6628	-0.12 0.6873
Root biomass	0.16 0.5711	-0.26 0.3446	-0.17 0.5346	-0.54 **0.0388**	0.43 0.1120	-0.27 0.3315	-0.61 **0.0184**	0.23 0.4000	0.50 0.0594	0.44 0.1015	-0.16 0.57	-0.21 0.4642
Root necromass	-0.21 0.4419	0.31 0.2534	0.63 **0.0401**	0.44 0.1005	-0.09 0.7440	0.24 0.3815	-0.12 0.6709	-0.64 **0.0094**	0.54 **0.0389**	0.51 0.0534	-0.19 0.5064	-0.04 0.9014

Table 3b. March to June 2000, Turrialba.

Root parameters	Pruning intensity					
	Unpruned		Partial		Complete	
	root	stem	root	stem	root	Stem
Nodule biomass	0.69 **0.0033**	0.07 0.7898	0.83 **0.0001**	0.76 **0.0006**	0.37 0.1567	0.31 0.2393
Nodule necromass	-0.43 0.0959	-0.39 0.1333	-0.23 0.3984	-0.24 0.3677	0.10 0.7038	0.22 0.4192
Root length	-0.39 0.1362	-0.03 0.9211	0.54 **0.0386**	0.64 **0.0072**	0.18 0.4977	0.02 0.9431
Root biomass	0.15 0.5848	-0.15 0.5835	0.75 **0.0014**	0.74 **0.0010**	0.22 0.4067	0.10 0.7024
Root necromass	-0.20 0.4628	-0.39 0.1348	-0.48 0.0709	-0.48 **0.0603**	-0.27 0.3114	-0.27 0.3077

Table 4. Pearson correlates for starch, sugars and fine root and nodules in *Gliricidia sepium* during December 1999 to March 2000, Turrialba.

Root parameters	Pruning intensity											
	Unpruned				Partial				Complete			
	Starch		Sugar		Starch		Sugar		Starch		Sugar	
	root	stem	root	stem	root	stem	root	stem	root	stem	root	stem
Root length	-0.41 0.1311	-0.13 0.6393	0.01 0.9802	0.18 0.5133	-0.67 **0.0065**	0.04 0.8716	0.21 0.4555	-0.27 0.3376	-0.33 0.2225	0.15 0.6046	-0.03 0.9144	-0.54 **0.0381**
Root biomass	0.20 0.4709	-0.13 0.6440	-0.60 **0.0230**	0.08 0.7662	-0.46 0.0841	-0.16 0.5618	0.26 0.3570	0.28 0.3079	-0.16 0.5563	0.07 0.7902	-0.01 0.9734	-0.24 0.3911
Root necromass	-0.14 0.6047	-0.11 0.6981	0.59 **0.0252**	0.50 0.0547	-0.09 0.7592	-0.11 0.7027	0.11 0.7019	0.14 0.6278	-0.19 0.4852	-0.11 0.7011	0.05 0.8516	-0.15 0.6020

Figure legends:

Figure 1. Changes in starch and sugar concentration in root (a, c, e) and stem (b, d, f) tissues of pruned *Erythrina poeppigiana*, Turrialba. Bars are standard errors.

Figure 2. Changes in starch and sugar concentration in root (a, c, e) and stem (b, d, f) tissues of pruned *Gliricidia sepium*, Turrialba. Bars are standard errors.

Figure 3. Changes in sugar to starch ratios in root and stem tissues of pruned *Erythrina poeppigiana* (a, b) and *Gliricidia sepium* (c, d), Turrialba. Bars are standard errors.

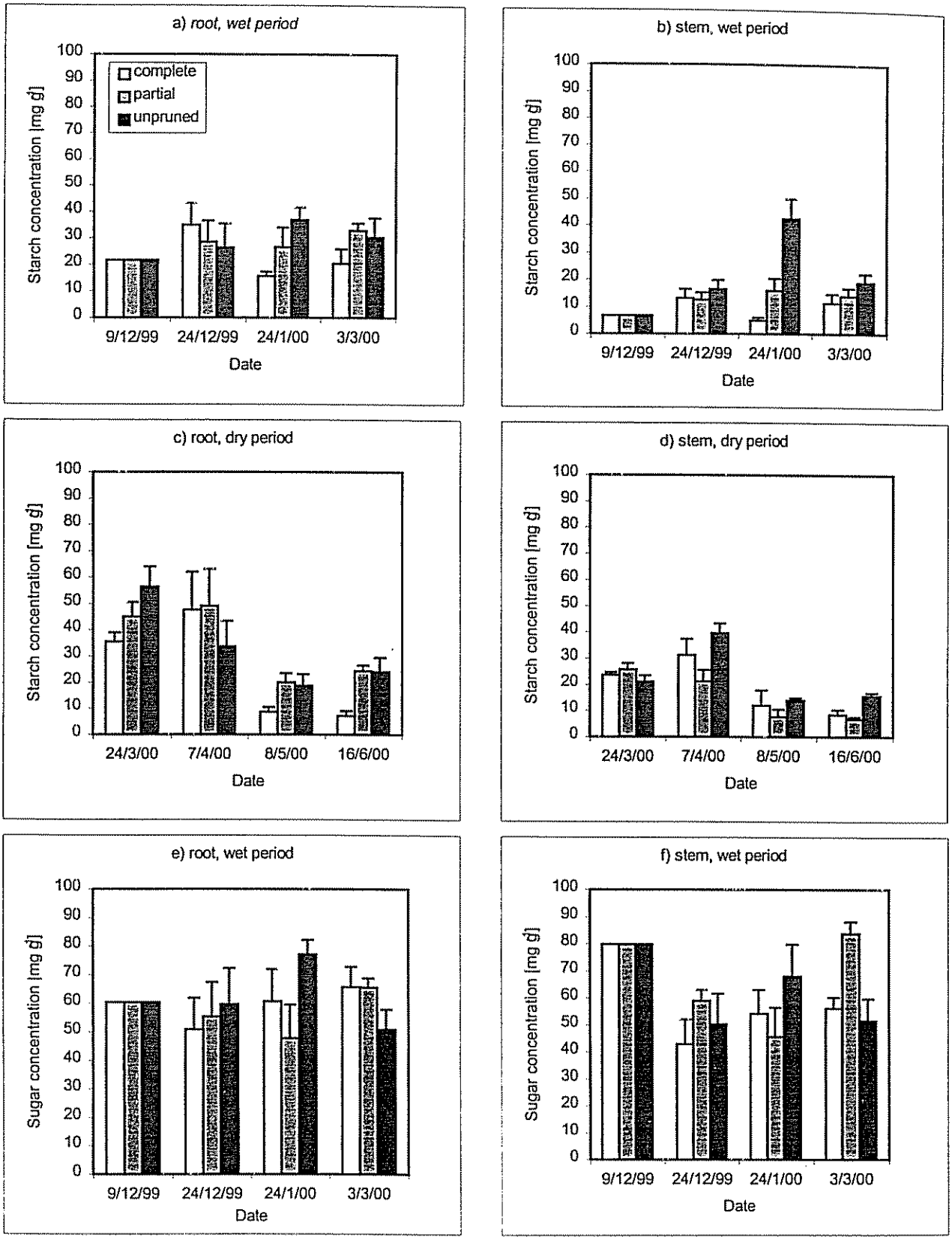
Figure 4. Plots of root parameters of *Erythrina poeppigiana* with date for a,c) fine root biomass, b,d) fine root necromass, e,f) fine root length, for wet and dry periods, Turrialba.

Figure 5. Plots of root parameters of *Erythrina poeppigiana* with date for a,c) nodule biomass, b,d) nodule necromass, for wet and dry periods, Turrialba. Bars are standard errors.

Figure 6. Plots of root parameters of *Gliricidia sepium* with date for a) fine root biomass, b) fine root necromass, c) fine root length, for the wet period, Turrialba. Bars are standard errors.

Figure 7. Evolution of total number of sprouts with time as affected by pruning treatments, a,b) *Erythrina poeppigiana*, c,d) *Gliricidia sepium*, Turrialba. Bars are standard errors.

Figure 8. Effect of pruning intensity on leaf area in *Erythrina poeppigiana*. Bars are standard errors.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Starch concentration [mg g]
complete
partial
unpruned
9/12/99
24/12/99
24/1/00
3/3/00
Date
b) stem, wet period
Starch concentration [mg g]
Date
c) root, dry period
Starch concentration [mg g]
24/3/00
7/4/00
8/5/00
16/6/00
Date
d) stem, dry period
Starch concentration [mg g]
Date
e) root, wet period
Sugar concentration [mg g]
Date
f) stem, wet period
Sugar concentration [mg g]
Date

Fig. 1

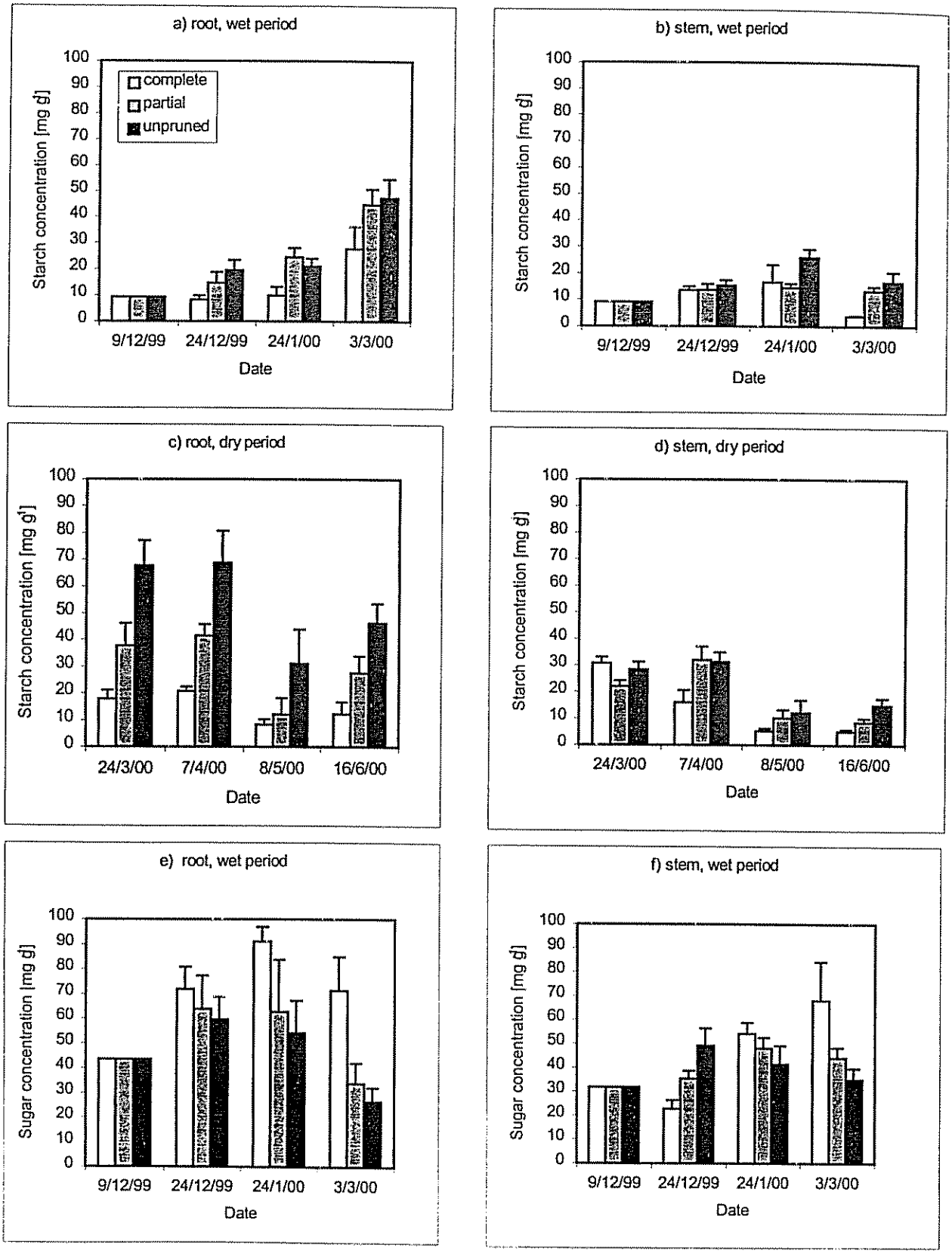

a) root, wet period
Starch concentration [mg g]
complete
partial
unpruned
9/12/99
24/12/99
24/1/00
3/3/00
Date
b) stem, wet period
Starch concentration [mg g]
9/12/99
24/12/99
24/1/00
3/3/00
Date
c) root, dry period
Starch concentration [mg g]
24/3/00
7/4/00
8/5/00
16/6/00
Date
d) stem, dry period
Starch concentration [mg g]
24/3/00
7/4/00
8/5/00
16/6/00
Date
e) root, wet period
Sugar concentration [mg g]
9/12/99
24/12/99
24/1/00
3/3/00
Date
f) stem, wet period
Sugar concentration [mg g]
9/12/99
24/12/99
24/1/00
3/3/00
Date

Fig. 2

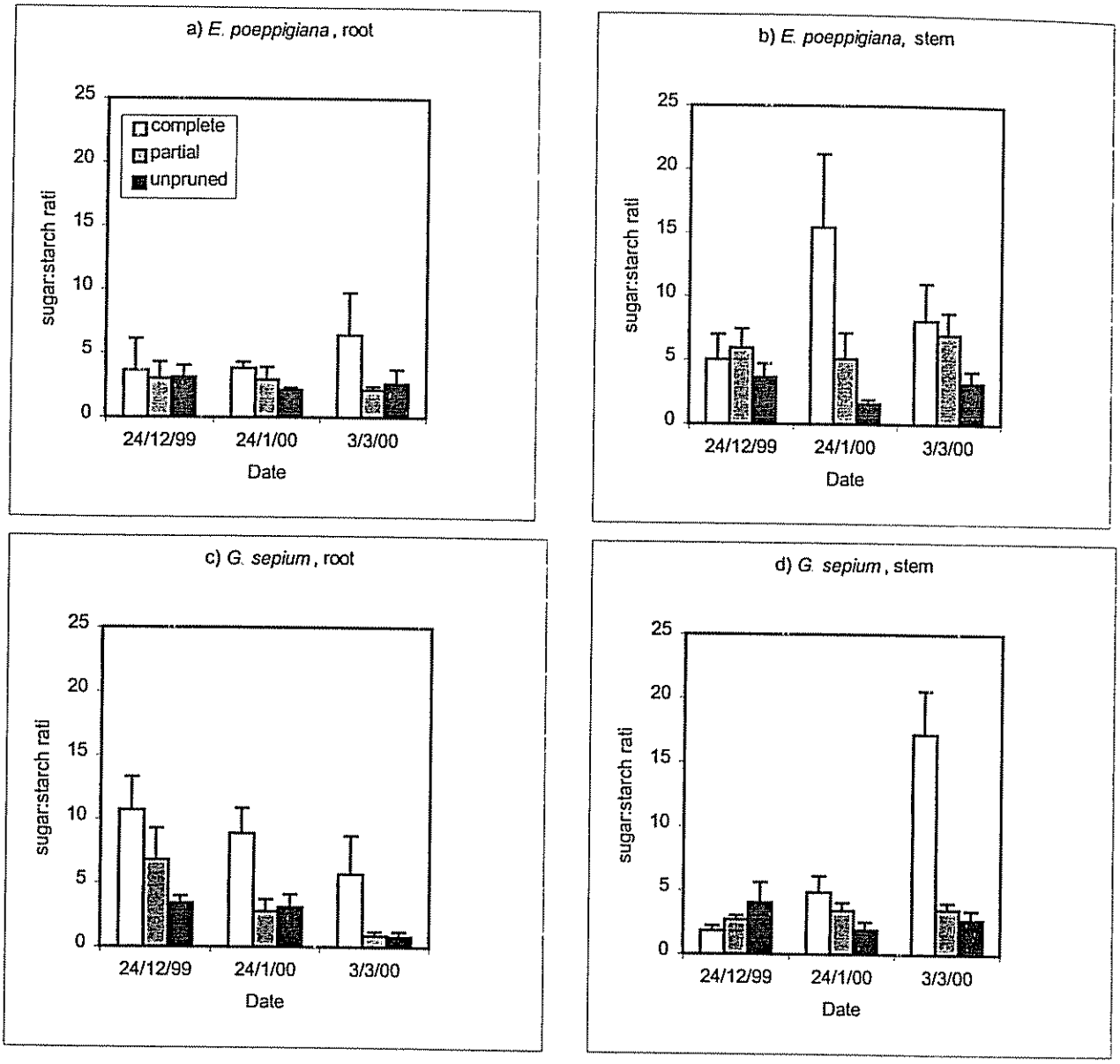

a) E. poeppigiana, root
complete
partial
unpruned
sugar:starch rati
25
20
15
10
5
0
24/12/99
24/1/00
3/3/00
Date
b) E. poeppigiana, stem
sugar:starch rati
Date
c) G. sepium, root
sugar:starch rati
Date
d) G. sepium, stem
sugar:starch rati
Date

Fig. 3

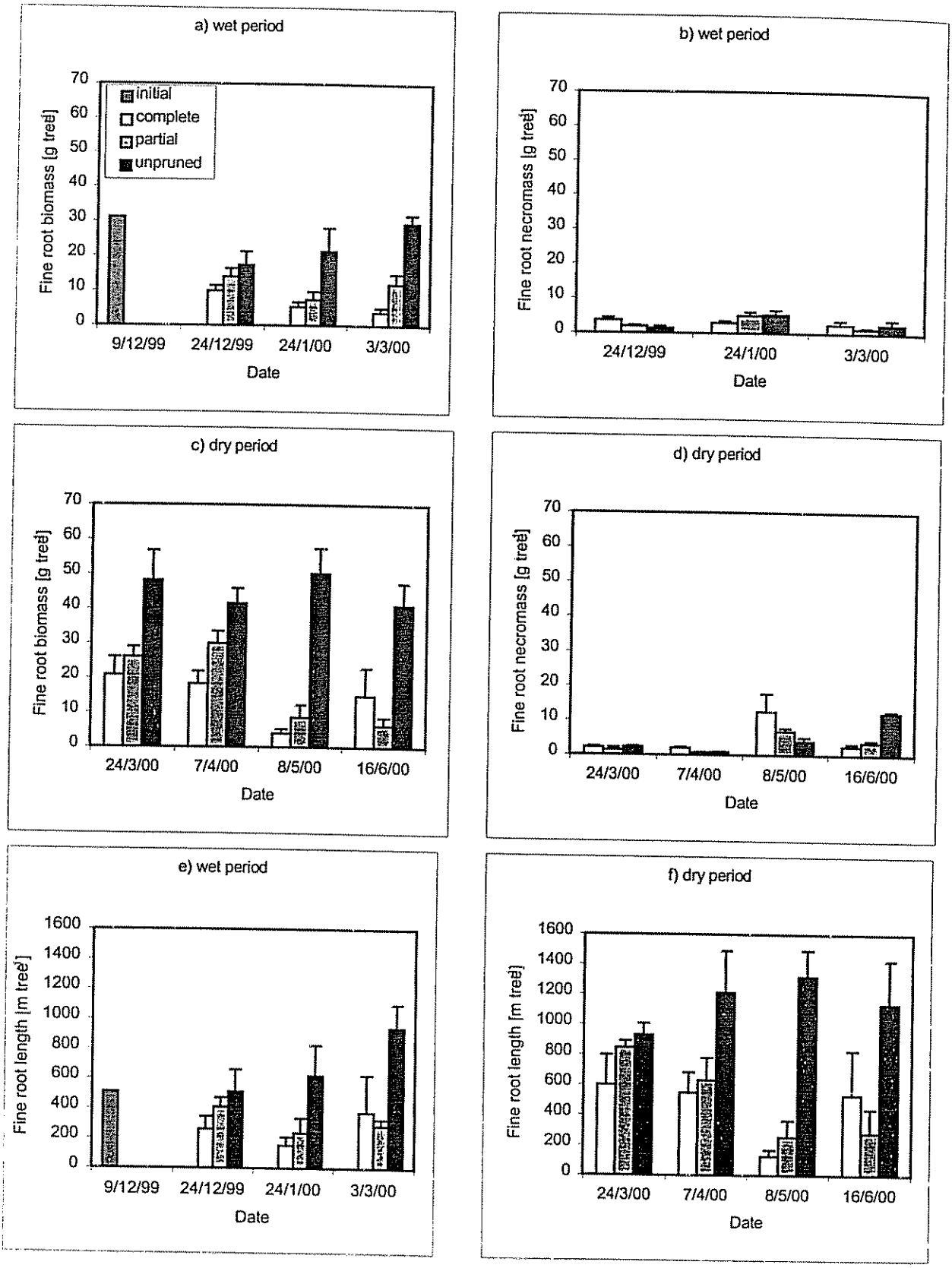

a) wet period
Fine root biomass [g tree]
initial
complete
partial
unpruned
9/12/99
24/12/99
24/1/00
3/3/00
Date
b) wet period
Fine root necromass [g tree]
24/12/99
24/1/00
3/3/00
Date
c) dry period
Fine root biomass [g tree]
24/3/00
7/4/00
8/5/00
16/6/00
Date
d) dry period
Fine root necromass [g tree]
24/3/00
7/4/00
8/5/00
16/6/00
Date
e) wet period
Fine root length [m tree]
9/12/99
24/12/99
24/1/00
3/3/00
Date
f) dry period
Fine root length [m tree]
24/3/00
7/4/00
8/5/00
16/6/00
Date

Fig. 4

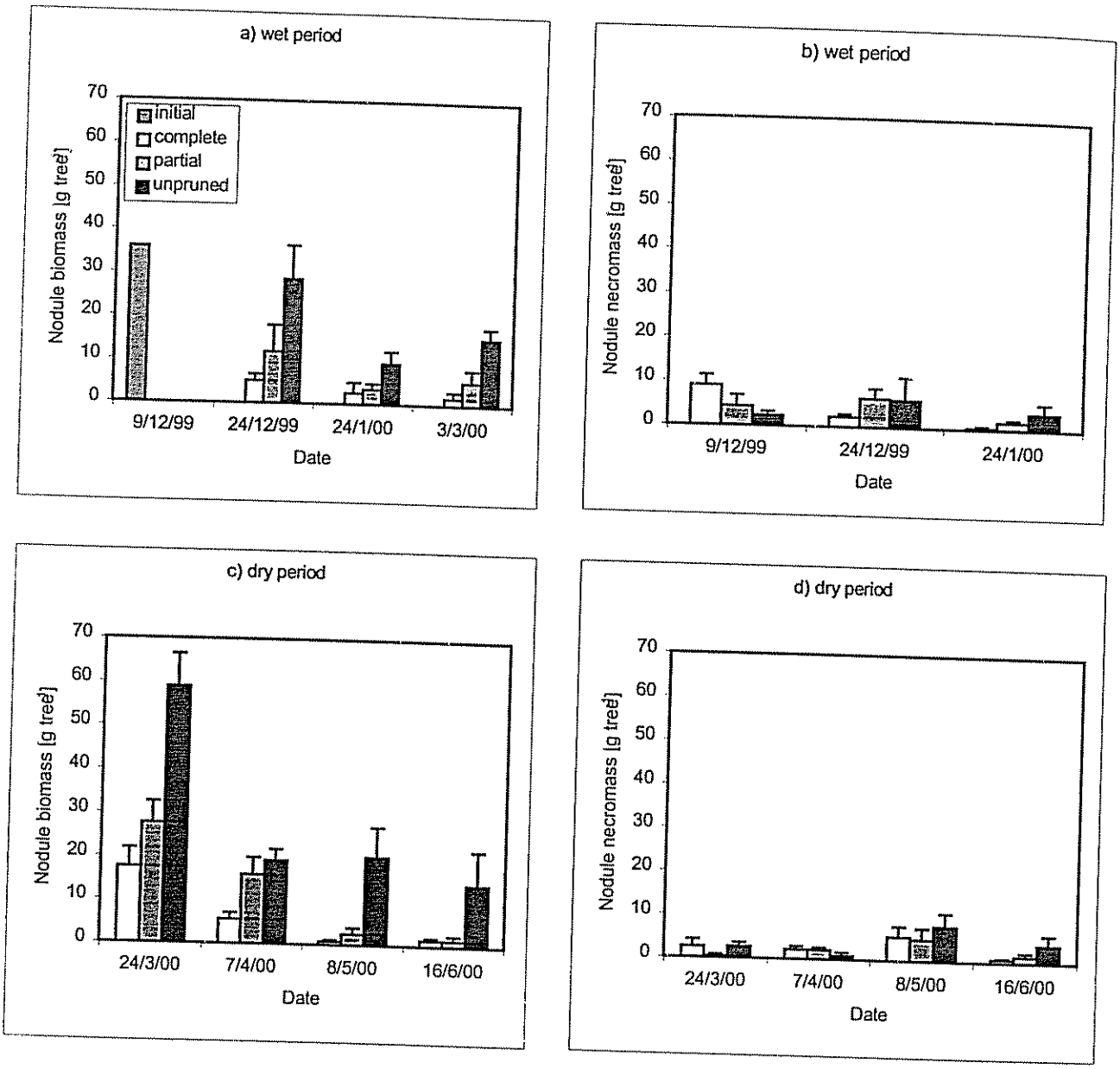

a) wet period
Nodule biomass [g tree]
initial
complete
partial
unpruned
9/12/99
24/12/99
24/1/00
3/3/00
Date
b) wet period
Nodule necromass [g tree]
9/12/99
24/12/99
24/1/00
Date
c) dry period
Nodule biomass [g tree]
24/3/00
7/4/00
8/5/00
16/6/00
Date
d) dry period
Nodule necromass [g tree]
24/3/00
7/4/00
8/5/00
16/6/00
Date

Fig. 5.

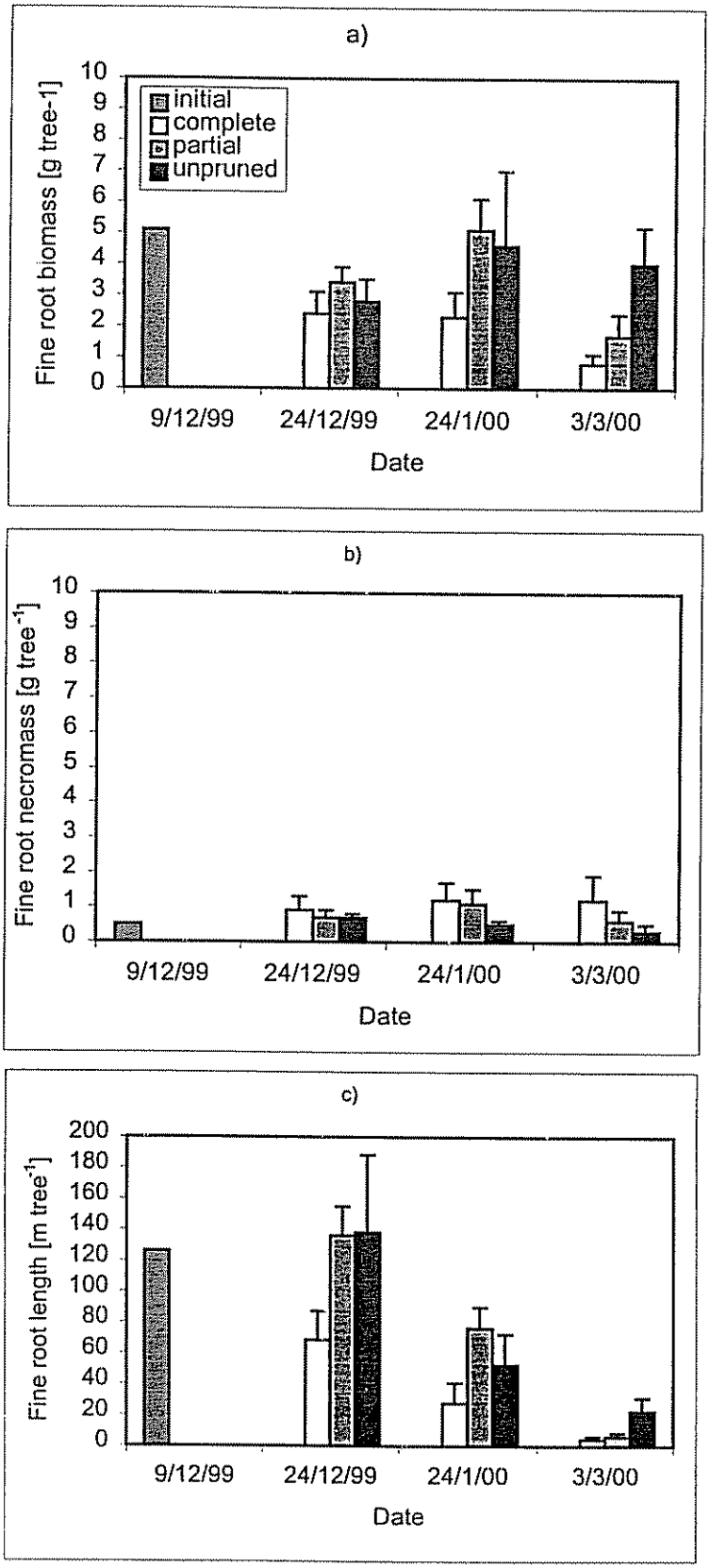
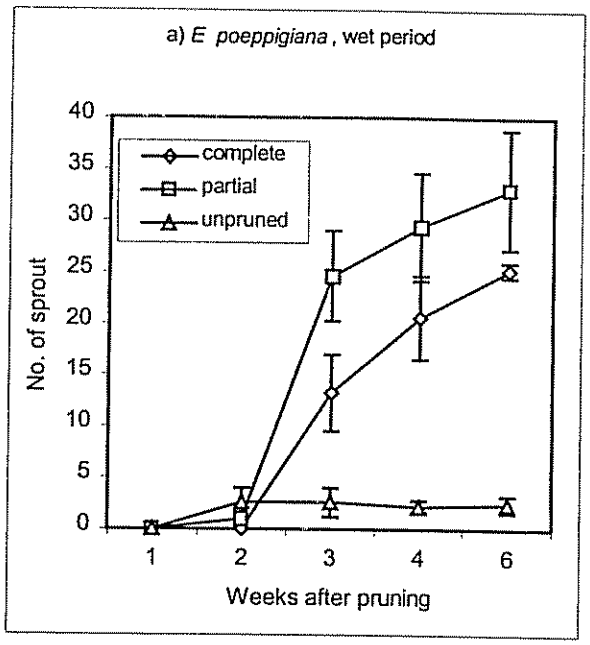
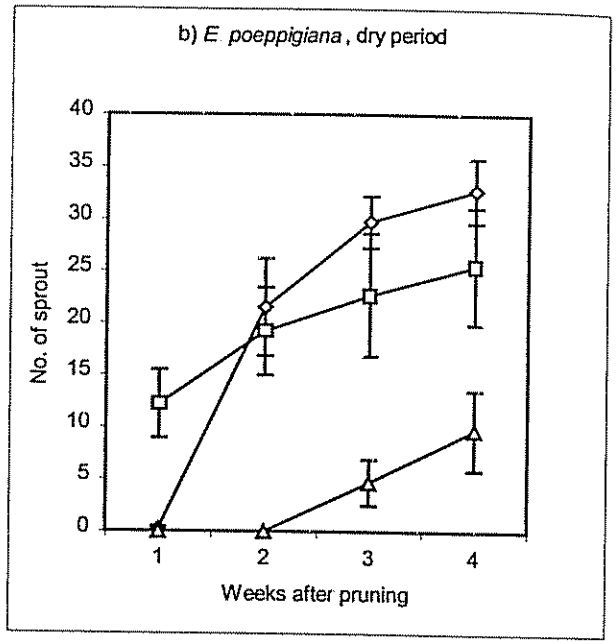
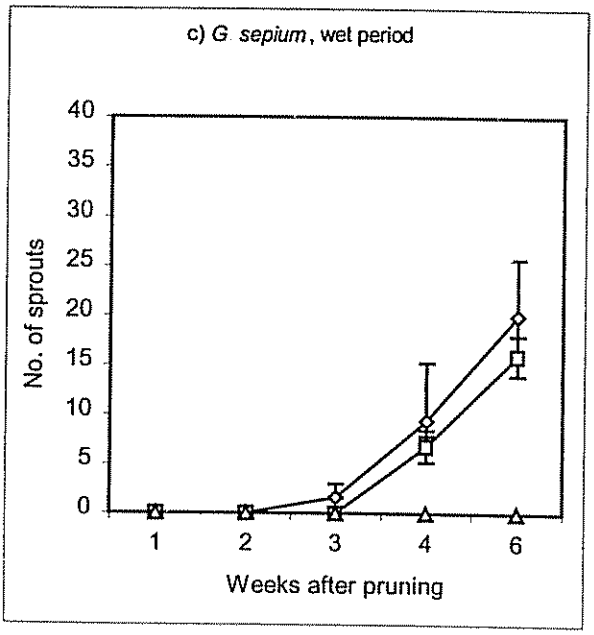
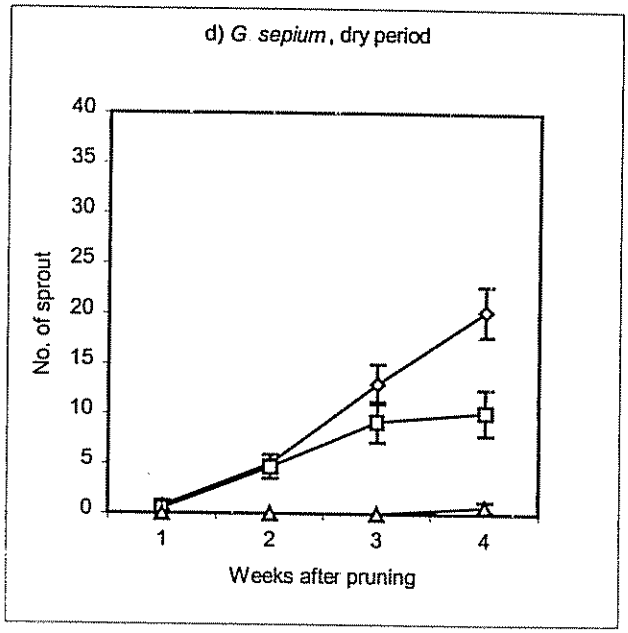

a)
Fine root biomass [g tree-1]
initial
complete
partial
unpruned
9/12/99
24/12/99
24/1/00
3/3/00
Date
b)
Fine root necromass [g tree-1]
9/12/99
24/12/99
24/1/00
3/3/00
Date
c)
Fine root length [m tree-1]
9/12/99
24/12/99
24/1/00
3/3/00
Date

Fig. 6


a) E poeppigiana, wet period
complete
partial
unpruned
No. of sprout
Weeks after pruning
0
5
10
15
20
25
30
35
40
1
2
3
4
6


b) E poeppigiana, dry period
No. of sprout
Weeks after pruning
0
5
10
15
20
25
30
35
40
1
2
3
4


c) G sepium, wet period
No. of sprouts
Weeks after pruning
0
5
10
15
20
25
30
35
40
1
2
3
4
6


d) G sepium, dry period
No. of sprout
Weeks after pruning
0
5
10
15
20
25
30
35
40
1
2
3
4

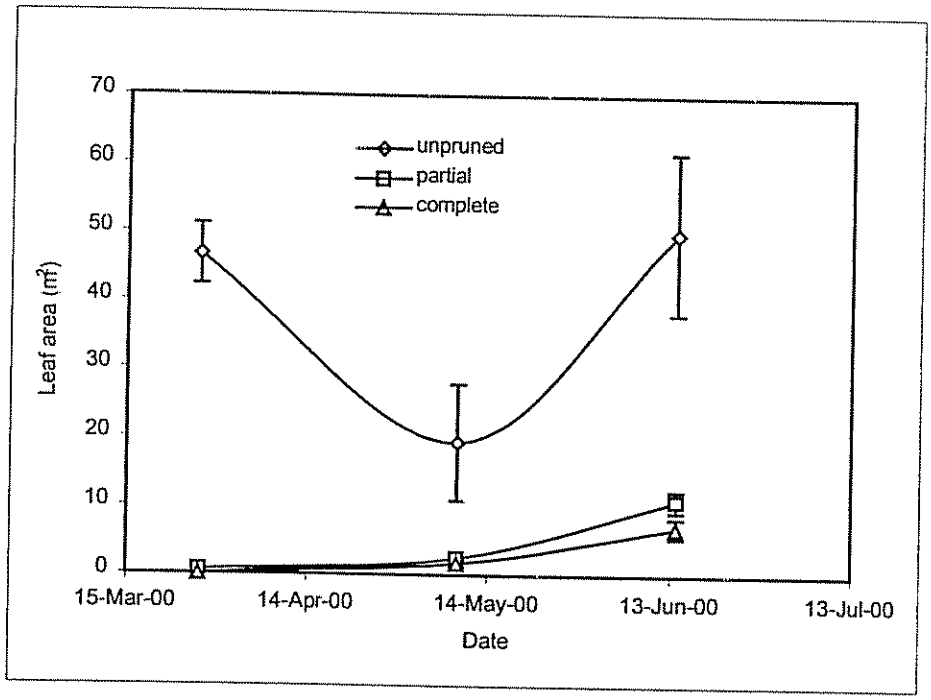

70
60
50
40
30
20
10
0
Leaf area (m²)
unpruned
partial
complete
15-Mar-00
14-Apr-00
14-May-00
13-Jun-00
13-Jul-00
Date

Fig. 8.

Effect of shoot pruning on starch content in roots of two leguminous species*

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Abstract

The effect of unpruned, partial (retention of one branch with ~0.5 m^2 leaf area) and complete (removal of all shoots) pruning on starch dynamics in roots of *Erythrina poeppigiana* and *Gliricidia sepium* was histochemically determined. Roots of three diameter classes were compared namely, fine (<2 mm), small to medium (2-10 mm), and coarse (>10 mm) roots. Abundant axial and radial parenchyma tissues were conspicuous in roots of both species. In general, starch content was highest in roots of unpruned trees and the difference in root starch content between partial and complete pruning treatments was apparent only during the dry season. During this period, roots of completely pruned trees had the lowest starch content at 6 and 12 WAP. Starch depletion occurred only during the dry period and from as early as 2 weeks after pruning (WAP). Larger diameter roots contained significantly higher starch content than smaller diameter roots. Fine roots of pruned trees were almost devoid of starch. The severity of pruning on root starch levels was more evident when pruning was done during the drier month of March than during the wetter month of December, indicating that timing of pruning is an important determinant of energy needs for regrowth.

Key words: axial parenchyma, defoliation, *Erythrina poeppigiana*, *Gliricidia sepium*, histochemistry, humid tropics, ray parenchyma

Introduction

Starch is considered the most important non-structural carbohydrate reserve in plants disturbed by disequilibria (Adams *et al* 1986). It accumulates whenever high levels of sugars build up and is transformed to sugars when sugars are low in amounts (Kozlowski and Keller 1966). Highest concentrations of starch are usually found in root tissues

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(Loescher *et al* 1990), usually in parenchymatous cells of the cortex, which are connected to conducting elements in phloem and xylem by radially running ray tissue (Tromp 1983).

Non-structural carbohydrate reserves are essential for maintaining respiration of all living cells when photosynthesis is low or has stopped (Kozlowski, 1992). In tea (*Camellia sinensis* (L.) Kuntze), Selvendran and Selvendran (1972) found that immediately after pruning starch content was high in inner xylem parenchyma. Von Fircks and Sennerby-Forsse (1998) working with a coppice lot of *Salix viminalis* found higher starch in roots of trees and starch accumulated in cortical cells of both root and stem as well as in ray parenchyma. Starch in roots of two shrubs (*Miconia albicans* and *Clidemia sericea*) was significantly depleted after a savannah fire in Belize (Miyanishi and Kellman, 1986). When measured at the end of the growing season, starch levels provide an adequate index of variation among cutting treatments in temperate species (Kays and Canham, 1991).

As plants resprout, respiration of dormant buds increases rapidly as dormancy is lost (Pollock 1953), and root cells of decapitated plants may be more depleted of starch than root cells of intact plants (Von Fircks and Sennerby-Forsse 1998). During early stages of leaf growth, synthesis of chlorophyll, proteins and structural compounds is high resulting in high catabolic rates to support development processes, thus constituting an important sink for root resources during regrowth (Kandiah, 1971). Requirement for respiration energy decreases rapidly as the photosynthetic system matures (Dickmann, 1971). Post-prune regrowth of woody plants is driven by sucrose translocated from roots to shoots (Wargo, 1975). If there is sufficient non-structural carbohydrate reserves in stems of pruned trees, then the trees may preferentially use stem starch for regrowth as was observed for *G. sepium* (Erdmann *et al* 1993) and *Citrus sinensis* (Kandiah *et al* 1984) although starch concentration was higher in roots than in stems.

Histochemical analysis of starch is a relatively simple and inexpensive method to determine changes in tissue starch content as influenced by season (Wargo 1975; Essiamah and Eschrich 1985) or shoot disturbance (Gregory and Wargo 1985; von Fircks and Sennersby-Forsse 1998). In this present study, starch changes in different diameter roots of pruned *Erythrina poeppigiana* (Walp.) O.F. Cook and *Gliricidia sepium* (Jacq.) Walp. were determined. These species are common woody perennials used in agroforestry to provide organic inputs to crop nutrition. They are managed by frequent shoot pruning.

Materials and Methods

The study was carried out in a very humid pre-montane forest ecozone (Holdridge 1987) with a medium fertility Eutric Cambisol (Kass *et al* 1995). Meteorological variables (average±SD) measured during field data collection from Dec 99 to Mar 00 (wet period) vs. Mar to Jun 00 (dry period), were monthly precipitation 385±299 vs. 170±102 mm; daily temperature maxima 29.1±0.8 vs. 29.9±1.2 ^{0}C; daily temperature minima 13.5±0.7 vs.16.1±2.9 ^{0}C, and relative humidity 87.9±3.5 vs. 86.8±1.8 %, respectively.

Experimental design

The field plot consisted of block plantings of 2 x 2 m spaced 2-year-old *E. poeppigiana* and *G. sepium* trees established from air-layered stakes. On 16 August 1999, 30 trees of each species were cut back to 1 m height to stimulate regrowth and multiple stems were thinned to one stem. Plastic barriers inserted to 0.5 m depth and delimiting a unit soil area of 1 m^2 for each tree separated roots of trees. Treatments were arranged in a split-split plot design Mainplot treatment was pruning intensity, unpruned (intact tree), partial (retention of one branch with 0.5m^2 leaf area), and complete (all shoots removed). Subplot treatment was sampling date (0, 2, 6, 12 weeks after pruning (WAP) corresponding to 9 Dec 99, 24 Dec 99, 24 Jan 00, 3 Mar 00 and 24 Mar 00, 7 Apr 00, 8 May 00, 16 Jun 00, respectively. Sub-subplot treatment was root diameter (2 mm, 2-10 mm and >10 mm). During the wet period, five repetitions were used, and during the dry period, four repetitions were used. Observations started on 9 December 1999 and 24 March 2000.

Sampling and histochemical preparation of roots:

On each sampling date, between 1700-1800 h, root tissues of each diameter class were excised and placed into vials containing a solution of formalin, alcohol and acetic acid (FAA). The tissue samples were dehydrated in an ascending series of alcohol treatments (50-70-80-90-95-100-100 %, one hour at each concentration). Dehydrated samples were placed into historesin (Reichert-Jung) at 4 ^{0}C for 48 hours and blocks of resin-encased samples were then microtome sectioned into 3 µ diameter slices. Tissue sections were then stained with Schift-Naphtol Blue Black (CIRAD 1989). Hard-to-microtome samples

(mainly *G. sepium*) were cut by hand and stained with an iodine solution (I_2KI). Slides were observed under the microscope at 10x magnification.

Analysis of stained slides

Transverse and longitudinally sectioned tissues were evaluated for starch granule content (%) in xylem parenchyma using an ordinal scale of 1=0%; 2=1-10%; 3=10-25%; 4=25-50%; 5=50-75%; 6>75% (Figure 1). This scale, a modified method of Wargo (1976), was applied to three diameter classes of roots namely fine roots (<2 mm), small to medium roots (2-10 mm) and coarse roots (> 10 mm) (Böhm 1979). Data sets were examined for homogeneity of variance and normality. Starch data were analysed using PROC GLM procedure (Statistical Analysis Systems, Cary, NC) for a split-split plot design.

Results

Anatomy of tree root

E. poeppigiana: Dermal tissue consists of a peridermis of variable thickness which encloses the ground tissue. The latter is made up of a thick layer of cortical parenchyma, large air spaces and small groups of fibres. Some cortical cells contain phenols with a brownish appearance. The vascular tissues are derived from a wide cambium layer. Vessels are wide, single or in groups with a large quantity of axial and radial parenchyma. Levels of starch in these parenchymatous cells vary depending on disturbance to aboveground organs. Bands of schlerenchyma cells are apparent in the vascular tissues and ground tissues (Figure 2a).

G. sepium: Dermal tissue consists of a thick peridermis. The ground tissues are cortical parenchyma cells with air spaces and a high content of phenols with a blue tint. Large quantities of fibres, whose walls are much larger than in *E. poeppigiana*, are present. The vascular tissues consist of phloem and xylem cells, the latter with abundant fibres with very thick walls making sectioning of these tissues very difficult. Like in *E. poeppigiana*, large quantities of axial parenchyma cells are present (Figure 2b).

Simple distinguishing features between the two species are the appearance of fibres, phenols and plugged vessels in *G. sepium*.

Starch dynamics in roots of E. poeppigiana

During the wet period, pruning intensity, diameter and the interaction between pruning and diameter significantly affected root starch content. Sampling date had no significant effect on root starch. (Table 1). Unpruned trees had significantly more root cell starch than partially or completely pruned trees. Starch content was directly proportional to diameter classes with larger diameter roots containing significantly more starch than smaller diameter roots (Figure 3).

During the dry period, all measured sources of variation except the pruning by sampling date interaction had highly significant effects on root starch content. Unpruned trees had significantly more starch as partially pruned trees. Completely pruned trees had the least amount of starch. Starch content was directly proportional to diameter classes with larger diameter roots containing significantly more starch than smaller diameter roots. Starch decreased over time particularly in completely pruned trees, beginning 2 WAP (Figure 3).

Starch dynamics in roots of G. sepium:

During the wet period, pruning intensity, diameter and the interaction between pruning and diameter significantly affected root starch content. Date had no significant effect on root starch content (Table 1). Roots of unpruned trees contained significantly more starch than partially or completely pruned trees. Larger diameter roots contained more starch than roots of smaller diameter.

During the dry period, all measured sources of variation had highly significant effects on root starch content (Table 1). Roots of unpruned trees contained significantly more starch than roots of partially pruned trees while roots of completely pruned trees contained lowest amounts of starch. Root diameter was proportional to starch content and starch decreased in significant quantities 6 WAP particularly in pruned trees (Figure 4). After 6 WAP, starch content increased in partially pruned trees but remained low in completely pruned trees.

Discussion

Anatomy of tree root

Both species seem to have an abundance of axial and radial parenchyma tissues potentially increasing the capacity for starch accumulation. Baretta-Kuipers (1982) remarked that the abundance of these tissues was a most conspicuous feature of wood tissue of stems of *Erythrina*; the wood anatomy of *Gliricidia* has not been reported.

Root starch dynamics in roots of E. poeppigiana:

The histochemical technique showed that carbohydrate reserves in tree roots follow predictable patterns related to the imbalance caused by disturbance (pruning) to aboveground organs. While unpruned trees conserved starch in small to coarse roots, starch levels in pruned tree roots were much lower, due to mobilization of starch to aboveground sinks, a process detected from 2 WAP during the dry period, when regrowth was faster. The severity of pruning on root starch levels was more evident when pruning was done during the drier month of March, indicating that timing of pruning is an important determinant of energy needs of regrowth (Kays and Canham 1991).

The high respiration rates of fine roots (Lambers 1985) resulted in insignificant amounts of starch in their tissues. Coarse roots were likely to store starch irrespective of pruning intensity and small roots were important to unpruned trees in storage of starch than they were in pruned trees.

Root starch dynamics in roots of G. sepium:

Unpruned trees maintained steady starch levels in coarse and small to medium roots during the observation periods. Root starch decreases in pruned trees may be attributed to demand of stronger sinks of stem meristems (von Fircks and Sennerby-Forsse 1998). Very low levels of starch in fine roots may be attributed to their high respiration rates (Lambers *et al* 1998). The timing of pruning was also important for use of root starch. Pruning during March was related to higher starch use in more severely pruned trees than in unpruned trees.

Generally, cutting in March associated with faster aboveground recovery and growth is associated with higher starch transformation than cutting during the relatively

slow growing period in December, the rainiest month in Turrialba. Starch content values for partially pruned trees were intermediate between those for unpruned and completely pruned trees. Although pruning reduced starch reserves, more in completely pruned trees than in partially pruned or unpruned trees, no tree mortality was observed suggesting that the C balance in both species was always positive or not negative for critically long periods.

Von Fircks and Senenrby-Forsse (1998) in their study with *Salix viminalis*, found that during the post dormant to shoot extension period, starch concentration in decapitated plants decreased more rapidly than in roots of intact plants. They found higher starch concentration in phloem and cortical cells than in xylem differing from sweet cherry (Keller and Loescher 1989) and eucalyptus (Kile 1981). In this study, starch was located mainly in xylem parenchyma.

This study demonstrated that histochemistry is a useful tool to elucidate the effects of pruning on root starch content in tropical leguminous species. In the two species evaluated, large carbohydrate reserves in coarse and small-medium roots, and strong sink strength of stem borne buds and sprouts may partly explain the capacity for rapid regrowth of these pruned tree species. Starch re-synthesis in partially pruned trees may occur much earlier than in completely pruned trees.

Acknowledgement

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Table 1. Means and F-test significance for the effects of pruning intensity, root diameter and sampling dates on cellular starch content of *Erythrina poeppigiana* and *Gliricidia sepium* for the periods 24 December 1999 to 3 March 2000 (wet period) and from 24 March to 16 June 2000 (dry period), Turrialba.

Source of variation		*E. poeppigiana*		*G. sepium*	
		Wet period	Dry period	Wet period	Dry period
		Ordinal scale units[z]			
Pruning intensity (Prune)					
	Unpruned	3.7 a	4.4 a	3.7 a	4.2 a
	Partial	2.2 b	3.1 b	2.7 b	3.4 b
	Complete	1.9 b	1.9 c	2.6 b	1.9 c
	Mean	2.6	3.1	3.0	3.2
	Pr > F	**0.0004**	**0.0001**	**0.0133**	**0.0001**
Sampling Date (WAP)					
	0	-	4.1 a	-	3.8 a
	2	2.6 a	3.1 b	3.1 a	3.5 ab
	6	2.5 a	2.8 b	3.0 a	2.4 c
	12	2.7 a	2.5 b	3.0 a	2.8 bc
	Mean	2.6	3.1	3.0	3.2
	Pr > F	0.5073	**0.0043**	0.8884	**0.0065**
Diameter (mm)					
	< 2	1.2 c	1.8 c	1.2 c	1.4 c
	2-10	2.6 b	3.4 b	3.1 b	3.7 b
	> 10	4.0 a	4.3 a	4.7 a	4.4 a
	Mean	2.6	3.2	3.0	3.2
	Pr > F	**0.0001**	**0.0001**	**0.0001**	**0.0001**
Prune x Date	Pr > F	0.5781	0.0615	0.6713	**0.0018**
Prune x Diameter	Pr > F	**0.0010**	**0.0001**	**0.0024**	**0.0001**
Diameter x Date	Pr > F	0.6053	**0.0191**	0.1387	**0.0018**
Prune x Date x Diameter	Pr > F	0.2482	**0.0038**	0.2899	**0.0001**

Means in the same column followed by the same letter are not significantly different (REGWQ $p \leq 0.05$).

[z] 1= 0%, 2 = 1-10%, 3 = 10-25%, 4 = 25-50%, 5 = 50-75%, and 6 >75%.

Figure legends:

Figure 1. Transverse sections of roots of *Erythrina poeppigiana* showing different starch (dark granules) content: a) 1=0%, b) 2=1-10%, c) 3=10-25%, d) 4=25-50%, e) 5=50-75%, and e) 6>75%. Arrow indicates starch granules in xylem parenchyma tissues.

Figure 2. Anatomical structure of transverse sections of leguminous tree roots.

Figure 2a. *Erythrina poeppigiana.*

Figure 2b. *Gliricidia sepium.*

Figure 3. Effect of pruning intensity and diameter classes on cellular starch content of *Erythrina poeppigiana* roots. Bars are standard errors.

Figure 4. Effect of pruning intensity and diameter classes on cellular starch content of *Gliricidia sepium* roots. Bars are standard errors.

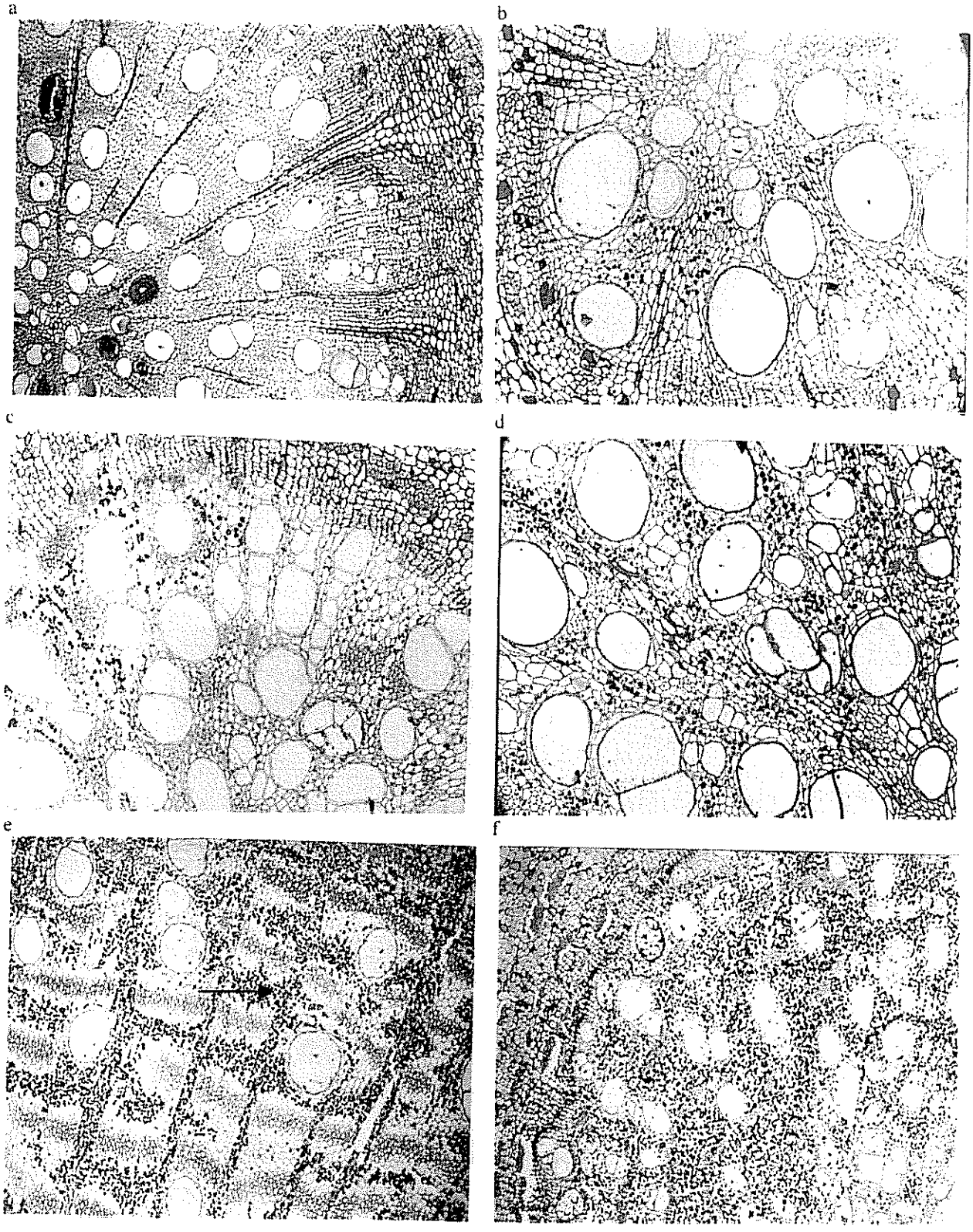
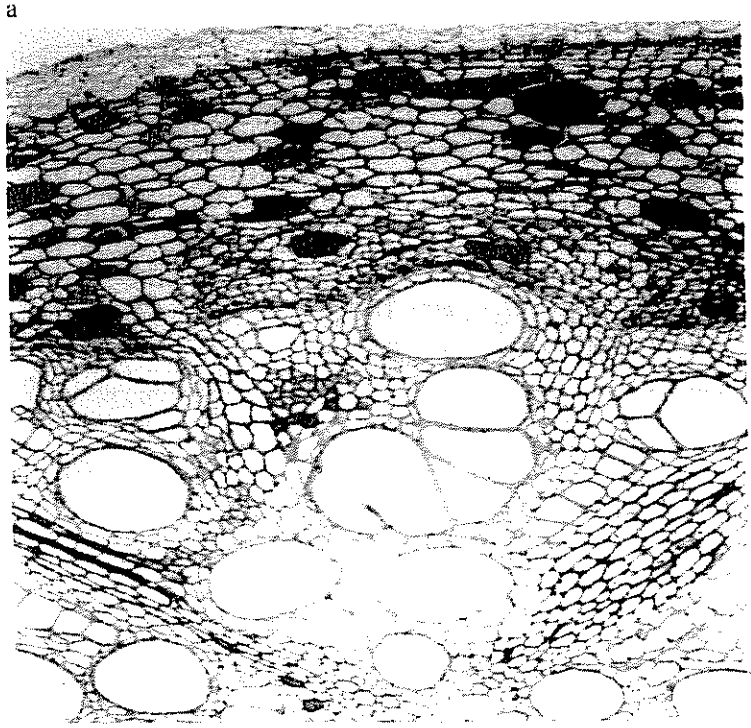


Fig. 1

a



b

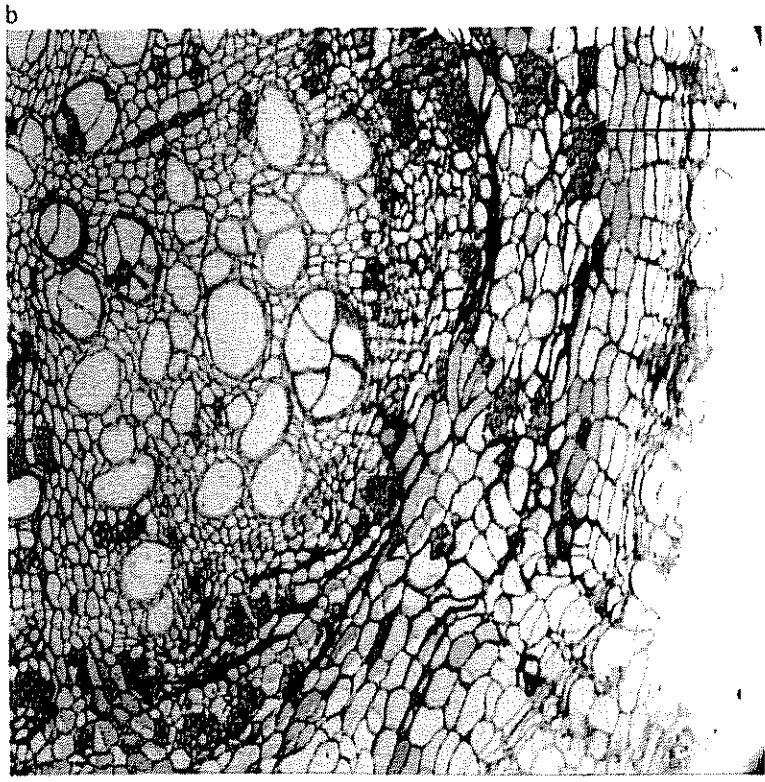
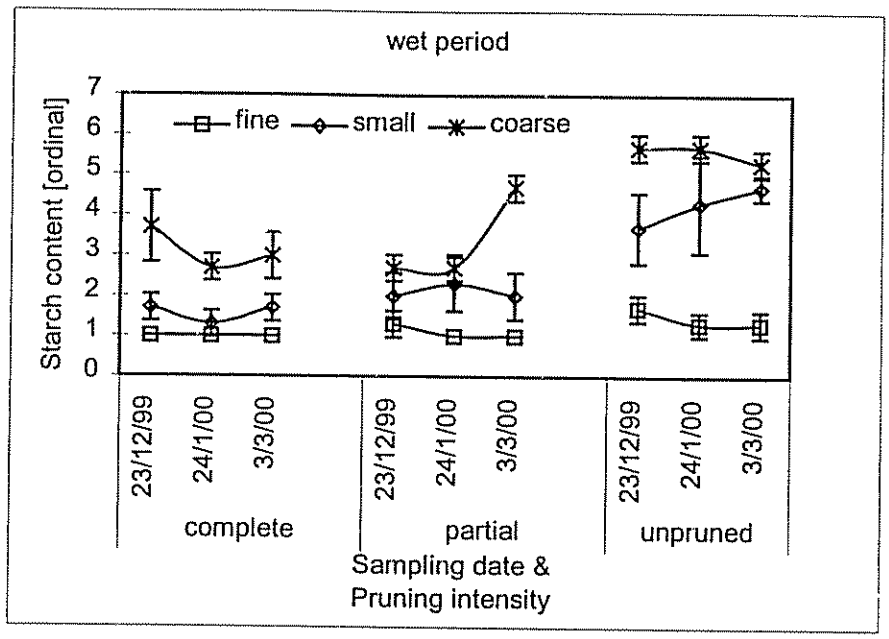


Fig. 2


wet period
Starch content [ordinal]
fine
small
coarse
0
1
2
3
4
5
6
7
23/12/99
24/1/00
3/3/00
complete
partial
unpruned
Sampling date &
Pruning intensity

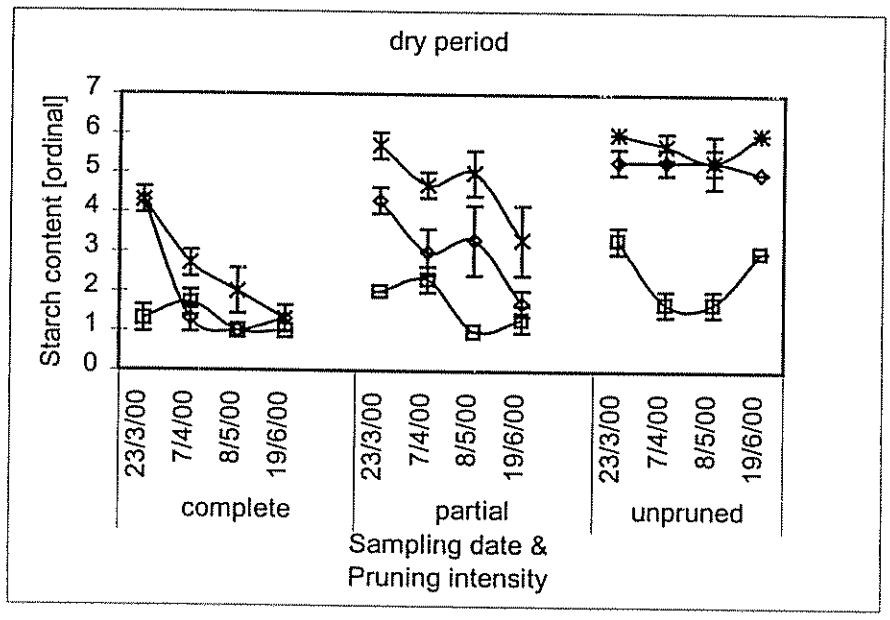

dry period
Starch content [ordinal]
0
1
2
3
4
5
6
7
23/3/00
7/4/00
8/5/00
19/6/00
complete
partial
unpruned
Sampling date &
Pruning intensity

Fig. 3

Regrowth dynamics of periodically pruned leguminous service trees*

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Summary:

In agroforestry practices in the humid tropics, fast growing leguminous trees are pruned to reduce tree-crop competition for light. The pruned material contains organic inputs for crop nutrition. To find out how these inputs might be affected by different pruning intensities, measurements were taken on dry matter (DM), total tissue nitrogen (N) and phosphorous (P) in leaves, branches, stems and roots of *Erythrina poeppigiana* and *Gliricidia sepium*. The pruning treatments evaluated were unpruned, complete (removal of all shoots) and partial (retention of one branch on the pruned stump) pruning carried out in an alley cropping experiment in Turrialba, Costa Rica. In *E. poeppigiana* trees, tissue N concentration in descending order was leaves>branches>roots>stems and that of tissue P concentration was leaves>branches>stems=roots for partially versus completely pruned trees, respectively. N and P accumulation in 12-week-old leafy branch regrowth of 2 Mg vs. 1.5 Mg DM ha^{-1} was 72 kg vs. 27 kg N ha^{-1} and 7 kg vs. 2 kg P ha^{-1} for partially versus completely pruned trees, respectively. In *G. sepium* trees, tissue N concentration in descending order was leaves>branches>roots>stems and that of tissue P concentration was branches>leaves>roots>stems. N and P accumulation in 12 week-old leafy branch regrowth of 0.2 Mg vs. 0.3 Mg DM ha^{-1} was 14 kg vs. 9 kg N ha^{-1} and 1.2 kg vs. 0.7 kg P ha^{-1} for partially versus completely pruned trees, respectively. *G. sepium* allocated more N and P to stems and expended twice as much DM per unit root length than did *E. poeppigiana*. Retention of a branch increased nutrient accumulation of pruned trees, particularly in *E. poeppigiana*, and hence higher nutrient inputs for associated crops.

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Keywords: allocation, dry matter, *Erythrina poeppigiana*, fine root, *Gliricidia sepium*, phosphorous

Introduction

The response of trees to shoot-root disequilibria caused by disturbance to shoots is generally to increase assimilate allocation to leaves (Wardlaw 1990) resulting in the establishment of a new 'functional equilibrium' between above- and belowground organs (Brouwer 1983). Frequent pruning may take this equilibrium to a level too low to permit the realization of the desired service attributes of the woody component, but this may depend on species and environment (Cannell 1989). According to Lambers *et al* (1998), N and P are the most important nutrients that limit plant growth. Generally, leaves have higher concentrations of N and P than woody stems; roots have intermediate concentrations.

The amount of nutrients acquired from the soil and incorporated into aboveground biomass is considered the nutrient requirement of a plant (Switzer and Nelson 1972). Nutrient requirement depends on uptake and internal distribution (Meier *et al* 1985), processes affected by species, environment, and C and nutrient allocation to woody and herbaceous tissues (Lambers *et al* 1998). Disturbance to trees can affect plant nutrient concentration by changing both allocation among organs and composition of individual tissues (Lambers *et al* 1998). Sanginga and colleagues (1994) reported that in pruned plants, stems accounted for most of the tree dry matter, leaves were the major sinks for N, and P followed dry matter distribution. They reported that unpruned plants allocated most dry matter to leaves and most P to branches.

In the humid tropics of Central America, *Erythrina poeppigiana* (Walp.) O.F. Cook and *Gliricidia sepium* (Jacq.) Kunth ex Walp. are common agroforestry service trees. These tree species require about 16 weeks to recover from complete pruning (Nygren 1995; Vaast and Snoeck 1999). Pruning at shorter intervals is necessary in some agroforestry practices to reduce negative tree-crop interactions (e.g. Chesney *et al* 2000). However, pruning at shorter intervals can decrease biomass (Romero *et al* 1993) and N yield (Duguma *et al* 1988) to a greater degree than pruning at longer intervals. Recently, partial pruning was proposed as an alternative to complete pruning to reduce N loss and to conserve tree function (Sanginga *et al* 1994).

Alternatives to complete pruning have received little research attention in agroforestry. In shaded coffee (*Coffea arabica*) systems in Costa Rica, it is common to prune *E. poeppigiana* leaving one or two apically dominant branches (Somarriba *et al* 1986), a practice known as 'podar con chimenea', similar to 'lung branch' pruning of tea (*Camellia sinensis*) in Asia (Kandiah *et al* 1984). During 1999-2000, a study was carried out in Turrialba, Costa Rica to compare the effect of partial versus complete pruning on tissue N and P concentration and accumulation in *E. poeppigiana* and *G. sepium* biomass.

Materials and Methods

The study environment

The study was carried out in a very humid pre-montane forest ecozone (Holdridge 1987) with a medium fertility Eutric Cambisol (Kass *et al* 1995). Meteorological variables (average±SD) measured during Dec 99 to Mar 00 (wet period) vs. Mar to Jun 00 (dry period), were monthly precipitation 385±299 vs. 170±102 mm; daily temperature maxima 29.1±0.8 vs. 29.9±1.2 ^{0}C; daily temperature minima 13.5±0.7 vs. 16.1±2.9 ^{0}C, and relative humidity 87.9±3.5 vs. 86.8±1.8 %, respectively.

Experimental design

The field plot consisted of block plantings of 2 x 2 m spaced 2-year-old *E. poeppigiana* and *G. sepium* trees established from air-layered stakes. On 16 August 1999, 30 trees of each species were cut back to 1 m height to stimulate regrowth and multiple stems were thinned to one stem. Plastic barriers inserted to 0.5 m depth and delimiting a unit soil area of 1 m^2 for each tree separated roots of trees. Treatments were arranged in a split plot in time design. Mainplot treatment was pruning intensity: unpruned (shoots intact), partial (retention of one branch with 0.5 m^2 leaf area) and complete (all shoots removed). Subplot treatment was sampling date (0, 2, 6, and 12 weeks after pruning (WAP) corresponding to 9 Dec 99, 24 Dec 99, 24 Jan 00, 3 Mar 00 and 24 Mar 00, 7 Apr 00, 8 May 00, 16 Jun 00, respectively. During the wet period, five repetitions were used, and during the dry period, four repetitions were used. For the wet and dry periods, observations began on 9 Dec 1999 and 24 Mar 2000, respectively. Trees were excavated at 12 WAP on 3 March 2000 (12 WAP_{wet}) and on 16 June 2000 (12 WAP_{dry}).

Dry matter

On 7 December 1999, two days before application of pruning treatments, three randomly selected trees out of the 30 experimental trees were sampled for DM distribution in leaves, branches, stems and roots. Component tree parts were weighed fresh and 0.5 kg chopped material sub-sampled for oven-dried (65 ^{0}C) mass. On 3 March 2000 (12 WAP_{wet}) and on 16 June 2000 (12 WAP_{dry}) trees were sampled for DM and samples were treated as described above.

Tissue N and P concentration

Composite (combined repetitions) oven-dried subsamples by treatment and tree part (leaves branches, stems, roots) were analysed for total N (semi-micro kjeldahl) and total P (wet digestion with nitric and perchloric acids 5:1) (Weaver *et al* 1994).

Resprouting rate

The resprouting rate (%) was computed from a modified method of Paukkonen and Kauppi (1998): [NS/(NA+NS)]*100 where number of sprouts (NS) and number of activated buds (NA) were counted on stems (all treatments) and retained branches or botanically similar branches in unpruned trees, weekly for 1,2,3,4 and 6 weeks after pruning (WAP) during the wet period and 1,2,3, and 4 WAP during the dry period.

Fine root length and mass

Fine roots from five-pooled topsoil (0-20 cm) core (cylinder L = 25 cm; ϕ = 8 cm) samples from each plot were washed free from soil in a 0.5 mm sieve. Live roots were separated from dead roots with the aid of a stereomicroscope. Total root length was measured using the WinRHizo Pro® image analysis system (Régent Instruments, Quebec, Canada) and root biomass determined as oven-dried (50 ^{0}C for 48 hours) mass. The root mass/root length (RML) ratio (mg m^{-1}) was computed as an index of the relationship between degree of soil penetration by a root system and belowground biomass allocation (Schroth and Zech 1995).

Statistical analyses

Data for each species were analysed separately. Data sets were examined for homogeneity of variances and normality and transformed if non-normal. DM, resprouting rate, and RML ratios were analysed using SAS/GLM procedures (SAS Institute, Cary, North Carolina, 1996) for a split plot design. Mean comparisons were by REGWQ ($p \leq 0.05$). Total N and P data are presented as means of composite samples. Significant correlations between selected above- and below-ground variables are reported.

Results

Dry matter, N and P distribution in E. poeppigiana:

Dry matter values in unpruned tree parts were significantly different to corresponding values for pruned trees (Table 1). In unpruned trees, DM shifted from being highest in stems during the wet period to being highest in branches during the dry period. In partially and completely pruned trees, stems were the major reservoir of total tree DM and leaves accumulated more DM than branches during both observation periods. Nitrogen accumulation was highest in physiologically active tissues. In unpruned and partially pruned trees, N accumulation was highest in leaves. In completely pruned trees, N accumulation was highest in stems even though N concentration was highest in leaves (Figure 1). Generally, branches formed the weakest sink for N. Tissue N concentration was in the descending order of leaves>branches>roots>stems. In unpruned trees, aboveground tree parts accumulated similar amounts of P during both periods. In pruned trees, P accumulation was highest in stems and lowest in branches. Higher P allocation to leaves than to branches was related more to biomass accumulation than to P concentration (Figure 1). Generally, tissue P concentration was in the descending order of leaves=branches> stems=roots, however, in completely pruned trees, P concentration was slightly higher in branches than in leaves (Figure 1).

Dry matter, N and P distribution in G. sepium:

Dry matter values in leaves and branches of unpruned trees were significantly different from corresponding values for pruned trees; DM values for stems were statistically similar (Table 2). Dry matter accumulation was higher during the dry period than during the

wet period. Stems were the major reservoir for DM followed by leaves. N accumulation was highest in stems of trees during the wet period, but accumulation changed during the dry period (Table 2). In unpruned trees, branch and leaf N accumulation was slightly higher than that of stems. In partially pruned trees, stems remained the main reservoir but in completely pruned trees, both stems and leaves were important. In pruned trees leaf N concentration was almost 3-fold higher than in stems (Figure 2). Tissue N concentration was in the descending order of leaves>branches>roots>stems. Phosphorous accumulation was highest in branches and lowest in leaves of unpruned trees (Figure 2). However, in pruned trees, P accumulation was highest in stems and lowest in branches. Tissue P concentration was in the descending order of branches>leaves>roots>stems.

Resprouting rate in E. poeppigiana:

Post-prune bud activation occurred a few days after pruning and resprouting began three weeks later on stems and two weeks on branches (Table 3). During the wet period, sprouting of all active stem borne buds was completed at 6 WAP, and during the dry period, trees tended towards full stem sprouting within four weeks. Branch sprouting in the partially pruned treatment was 64-68% of activated buds compared to 39-57% on a botanically similar branch in the unpruned treatment. Mean number of stem borne sprouts was 15 for partially pruned and 27 for completely pruned trees, and these were negatively correlated with branch DM (Table 5). The number of branch borne sprouts was 14 and 7 for trees partially pruned and unpruned, respectively.

Resprouting rate in G. sepium:

During wet period, sprouting of active buds was completed at 6 WAP in partially pruned trees and about 80% completed in completely pruned trees. During the dry period, sprouting was completed two weeks earlier than during the wet period (Table 4). Mean number of stem borne sprouts was 9 and 7 for complete and partial pruning, respectively. Subsidiary branching was not observed on the retained branch in the partial pruning treatment or on the selected branch in the unpruned treatment.

Fine root mass: length ratio in E. poeppigiana:

Neither pruning intensity nor time had a significant effect on root mass: length (RML) ratio (Figure 3). Mean biomass allocation to fine root was 37.5 to 40.2 mg m^{-1} fine root length. During the wet period when resprouting was slower, the number of stem borne sprouts was negatively correlated with fine root length and aboveground biomass was positively correlated with fine root biomass (Table 5). During the dry period when resprouting was more rapid, stem DM and number of stem sprouts were negatively correlated with fine root biomass 2 weeks after partial or complete pruning; while the number of branch borne sprouts was negatively correlated with fine root length 12 weeks after partial pruning was applied. Aboveground DM was positively correlated with fine root length and biomass. Stem DM was negatively correlated with root biomass in completely pruned trees.

Fine root mass: length ratio in G. sepium:

Pruning intensity was non-significant for RML ratio but when plotted against time, RML ratio was significantly higher at 12 WAP_{wet} (Figure 3). This increase in RML ratios may be attributed to lack of new fine root production. Mean fine root biomass allocation was 90.4 mg m^{-1} fine root length. DM was negatively correlated with root biomass; leaf (2 WAP_{wet}) and stem (12 WAP_{wet}) DM was positively correlated with fine root length (Table 6). There were no apparent direct effects of resprouting on root variables.

Discussion

Dry matter, N and P distribution in E. poeppigiana:

In unpruned trees, branch growth was mainly orthotropic and branches were the main sink for DM during the period of active growth. The retained branch in partially pruned trees assumed a more plagiotrophic growth habit under the weight of fast developing leafy sprouts, and proportionately more DM was allocated to this branch than to non-lignified sprouts on the main stem at the end of the 12-week observation period. Shoot regrowth of completely pruned trees formed a dense canopy. In partially pruned trees, new growth on the branch might have been supported from carbon fixation while stem regrowth might have been supported from stem or root derived carbon. The simultaneous sprouting

pattern suggests that branch autonomy for carbon production and use may be characteristic of *E. poeppigiana,* a feature that allows for rapid regrowth and higher DM production in a shorter period. Kandiah and colleagues (1984) showed that buds developed on pruned shoots independently of the presence of the 'lung branches'.

In *E. poeppigiana,* NO_3^- is reduced in the leaves (Orebango *et al* 1982; Muthuchelian 1993). Higher distribution of N to leaves of unpruned and partially pruned trees indicated that sink strength had a greater effect on internal correlational processes than sink size. In partially and completely pruned trees, stems were important in storage of N and P and play an important role in regrowth. Kozlowski and Winget (1964) suggested that shoot growth depends on mineral elements stored in aboveground tissues rather than recently absorbed elements. They use evidence from research results of Harley *et al* (1958) to show that shoot growth is correlated with the amount of N in storage tissues and that only negligible amounts of P^{32} are translocated from roots of apple tree shoots until leaves have attained considerable growth and shoots have elongated.

Dry matter, N and P distribution in G. sepium:

Dry matter production in *G. sepium* was comparatively less than *E. poeppigiana* but the pattern of post-prune distribution was similar. In unpruned and partially pruned trees, branch growth was mainly orthotropic with no subsidiary branching. Higher accumulation of N and P in branches of unpruned trees agree with the findings of Sanginga *et al* (1994) for this species. In this present study, the period of growth of unpruned trees was similar. In pruned trees, the observation period might have been too short for subsequent P translocation to branches during regrowth. In pruned trees, higher N and P in stems show that they play an important role in regrowth. The number of stem borne sprouts apparently did not affect aboveground distributions of DM, N or P.

Root mass: length ratio in E. poeppigiana:

Non-significant changes in RML ratios over time might have been due to the presence of sufficient non-structural carbohydrate reserves in stems to support resprouting. During the wet period, shoot growth was slower and biomass allocation to roots per unit root length was not affected even at 12 WAP. However, during the dry period, when growth

was faster, there was a tendency for biomass allocation to roots per unit root length to decrease. Sprout development in pruned trees during the dry period occurs at the expense of biomass allocation to roots.

Root mass: length ratio in G. sepium:

An important difference observed between these two species is the tendency for *G. sepium* to allocate a significantly higher amount of DM, N and P to root tissue than *E. poeppigiana*. This tendency may be associated with the ecophysiological adaptation of *G. sepium* to drier zones, where root growth increases relative to shoot growth. In partially pruned trees, branch DM at 12 WAP reduced fine root length from 2 to 12 WAP. Increases in RML ratio over time suggest that *G. sepium* was accumulating DM in roots at a time when resprouting was most vigorous. New shoot growth and root 'auto conservation' competed for fixed C or re-mobilized C. Mean RML ratio was twice that for *E. poeppigiana* over a similar observation period. The association between branch DM and root length and root biomass indicates the presence of a direct tissue connection.

Erythrina poeppigiana and *G. sepium* showed different responses to the shoot to root disequilibria caused by pruning. While unpruned trees yielded the most DM and allocated more DM to structural branches and stems than to leaves, pruned trees had more DM in stems, especially when severely pruned. In *E. poeppigiana*, partially pruned trees increased overall biomass by both stem borne sprouting and branch development while N allocation to leaves supported C fixation. In completely pruned trees more N and P in stems meant that C fixation could not be maximized in the short term due to N deficiency. Frequently pruned trees use stems for temporary N and P storage for utilization in regrowth. Plant responds to aboveground disturbance initially by reducing root biomass allocation and root length and later increasing them when photosynthetic capacity is restored.

If we consider nutrient requirement as the quantity of nutrients incorporated into biomass production (Switzer and Nelson 1972), determined by uptake and internal distribution (Meier *et al* 1985), then species with high requirements for nutrients may be better able to tolerate pruning. The nutrient requirement of 12 weeks old regrowth from partially pruned and completely pruned *E. poeppigiana* trees are 72 kg vs. 27 kg N ha^{-1} and 7 kg vs. 2 kg P ha^{-1} in 2 Mg vs. 1.5 Mg ha^{-1} of dry matter. For *G. sepium*, corresponding

values for pruning intensity are 14 kg vs. 9 kg N ha^{-1} and 1.2 kg vs. 0.7 kg P ha^{-1} in 0.2 Mg vs. 0.3 Mg ha^{-1} of dry matter. Retention of a branch increases the nutrient requirement of pruned trees and at a much higher degree in *E. poeppigiana* than in *G. sepium*. This trend implies that partial pruning rather than complete pruning is the better tree management option. Pruning will not compromise the potential of trees to resprout since stems serve as storage for C, N and P. These elements are important for regrowth. It follows therefore that tree with larger stems can better meet energy demands during early stages of regrowth.

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Table 1. Effect of shoot pruning on tissue dry matter, tissue N and P accumulation in unpruned and pruned *Erythrina poeppigiana* trees, Turrialba.

Pruning Intensity	12 WAP_{wet}			12 WAP_{dry}		
	leaves	branches	stems	leaves	branches	stems
	Dry matter [g $tree^{-1}$]					
Unpruned	1735a	2202a	5381a	4009a	8660a	7475a
Partial	1029b	662b	4860a	694b	518b	4367b
Complete	339c	145b	2773b	303b	121c	3276b
	Tissue N accumulation [g $tree^{-1}$]					
Unpruned	72	30	51	173	87	57
Partial	41	8	31	33	5	23
Complete	14	2	20	13	2	23
	Tissue P accumulation [g $tree^{-1}$]					
Unpruned	6.3	6.3	8.6	10.8	11.2	11.2
Partial	2.7	1.9	4.4	2.1	1.2	4.4
Complete	0.1	0.4	2.8	0.9	0.6	3.9

Means in the same column followed by the same letter are not significantly different, REGWQ (0.05).

Table 2. Effect of shoot pruning on tissue dry matter, tissue N and P accumulation in unpruned and pruned *Gliricidia sepium* trees, Turrialba.

Pruning Intensity	12 WAP_{wet}			12 WAP_{dry}		
	leaves	branches	stems	leaves	branches	stems
	Dry matter [g $tree^{-1}$]					
Unpruned	222a	627a	1256a	460a	1423a	1548a
Partial	55b	95b	1191a	273ab	237b	1484a
Complete	48b	13c	867a	174b	102c	1172a
	Tissue N accumulation [g $tree^{-1}$]					
Unpruned	7	12	13	17	19	15
Partial	2	1.6	11	10	4	16
Complete	2	0.2	6	7	2	7
	Tissue P accumulation [g $tree^{-1}$]					
Unpruned	0.4	2.2	1.3	1.1	2.7	1.5
Partial	0.1	0.2	1.1	0.6	0.5	1.8
Complete	0.1	0.03	0.7	0.5	0.2	0.8

Means in the same column followed by the same letter are not significantly different, REGWQ (0.05).

Table 3. Sprouting rates of active buds on stems and branches of unpruned and pruned *Erythrina poeppigiana*, Turrialba.

Pruning Intensity	Sprout origin	Regrowth period (weeks)				
		1	2	3	4	6
		wet period				
Unpruned	Stem			No buds		
	branch	0	0.19	0.19	0.39	0.28
Partial	Stem	0	0	0.59	0.74	1.0
	Branch	0	0.08	0.72	0.68	0.7
Complete	Stem	0	0	0.55	0.71	1.0
	Branch			No buds		
		dry period				
Unpruned	Stem			No buds		
	Branch	0	0	0.3	0.57	-
Partial	Stem	0	0.52	0.85	0.91	-
	Branch	0.25	0.49	0.65	0.64	-
Complete	Stem	0.01	0.7	0.86	0.96	-
	branch			No buds		

Table 4. Sprouting rates of active buds on stems of unpruned and pruned *Gliricidiaa sepium*, Turrialba.

Pruning InIntensity	Weeks after Pruning				
	1	2	3	4	6
		wet period			
Partial	0	0	0	0.49	1.0
Complete	0	0	0.08	0.32	0.82
		dry period			
Partial	0.11	0.64	0.81	1.0	-
Complete	0.30	0.50	0.67	0.96	-

Table 5. Correlations between above- and belowground tree variables in *Erythrina poeppigiana*, Turrialba.

WAP	Pruning Intensity	Comparison	r	p	n
		December 99 – March 00 (wet period)			
2	CP,PP	Number of stem sprouts vs. fine root length	-0.65	0.0406	10
6	CP,PP	Stem DM vs. fine root biomass	0.64	0.0469	10
12	CP	Branch DM vs. fine root biomass	0.95	0.0131	5
12	PP	Branch DM vs. fine root length	0.90	0.0344	5
12	CP,PP	Leaf DM vs. fine root biomass	0.81	0.0046	10
12	CP,PP	Stem DM vs. fine root biomass	0.75	0.0115	10
12	PP,UNP	Branch DM vs. fine root length	0.79	0.0067	10
12	PP,UNP	Branch DM vs. fine root biomass	0.83	0.0029	10
		March – June 00 (dry period)			
2	PP	Stem DM vs. fine root biomass	-0.96	0.0437	4
2	CP,PP	Number of stem sprouts vs. branch DM	-0.76	0.0282	8
2	CP,PP	Number of stem sprouts vs. root biomass	-0.83	0.0106	8
2	PP,UNP	Leaf DM vs. fine root length	0.79	0.0182	8
2	PP,UNP	Leaf DM vs. fine root biomass	0.90	0.0022	8
2	PP,UNP	Stem DM vs. fine root biomass	0.74	0.0340	8
2	PP,UNP	Branch DM vs. fine root biomass	0.83	0.0103	8
6	PP,UNP	Number of stem sprouts vs. branch DM	-0.76	0.0282	8
6	PP,UNP	Branch DM vs. fine root length	0.81	0.0135	8
6	PP,UNP	Branch DM vs. fine root biomass	0.83	0.0105	8
12	PP	Stem DM vs. fine root biomass	-0.96	0.0437	4
12	PP	Number of branch sprouts vs. fine root length	-0.95	0.0477	4
12	UNP	Leaf DM vs. fine root biomass	-0.98	0.0175	4
12	CP,PP	Number of stem sprouts vs. branch DM	-0.76	0.0282	8

CP = complete pruning; PP = partial pruning; UNP = unpruned.

Table 6. Correlations between above- and belowground tree variables in *Gliricidia sepium*, December 99 – March 00 (wet season), Turrialba.

Weeks after Pruning	Pruning Intensity	Comparison	r	p	n
2	complete	Leaf DM vs. fine root length	0.88	0.0462	5
2		Branch DM vs. fine root length	0.89	0.0415	5
6	partial	Branch DM vs. fine root length	-0.96	0.0084	5
6		Branch DM vs. fine root biomass	-0.91	0.0341	5
6		Stem DM vs. fine root length	0.95	0.0122	5
12	partial	Branch DM vs. fine root length	-0.96	0.0084	5
12		Branch DM vs. fine root biomass	-0.91	0.0341	5
12		Stem DM vs. fine root length	0.95	0.0122	5

Figure Legends

Figure 1. N and P concentrations in different parts of two-year-old *Erythrina poeppigiana* trees.

Figure 2. N and P concentrations in different parts of two-year-old *Gliricidia sepium* trees.

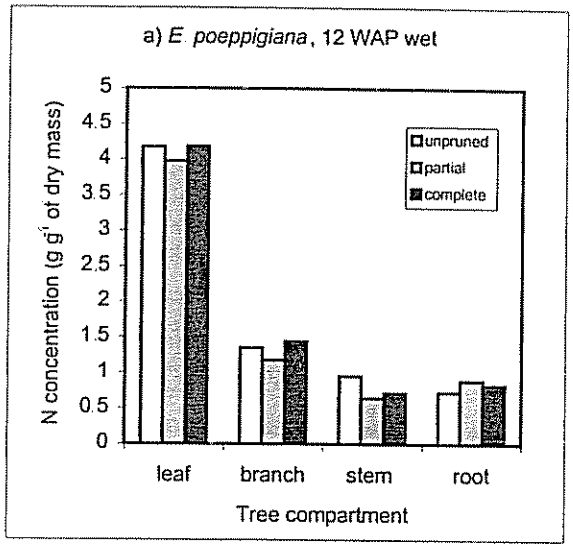
Figure 3. Fine root mass/length ratio over weeks after pruning of unpruned and pruned trees, Turrialba:

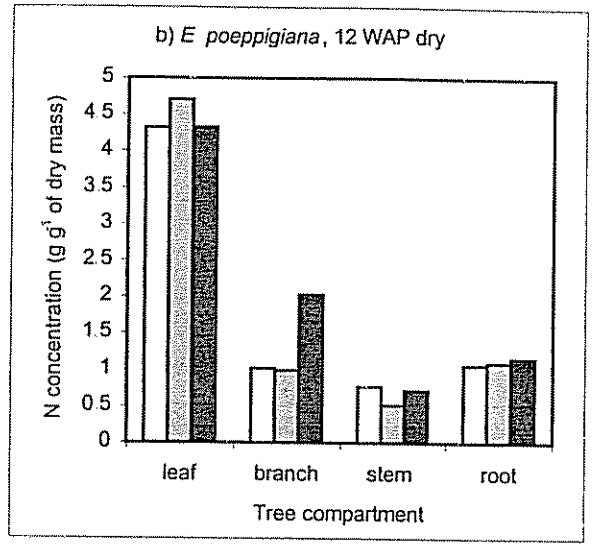
a) *Erythrina poeppigiana*, wet period

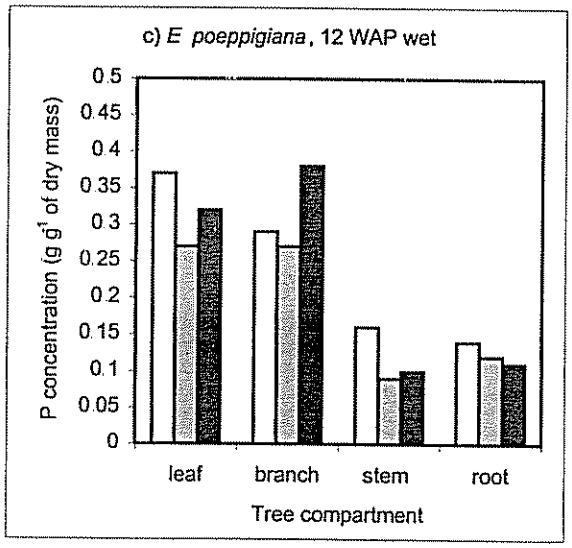
b) *Erythrina poeppigiana,* dry period

c) *Gliricidia sepium*, wet period

Bars are standard errors.


a) E. poeppigiana, 12 WAP wet
N concentration (g g-1 of dry mass)
5
4.5
4
3.5
3
2.5
2
1.5
1
0.5
0
unpruned
partial
complete
leaf
branch
stem
root
Tree compartment


b) E. poeppigiana, 12 WAP dry
N concentration (g g-1 of dry mass)
5
4.5
4
3.5
3
2.5
2
1.5
1
0.5
0
leaf
branch
stem
root
Tree compartment


c) E. poeppigiana, 12 WAP wet
P concentration (g g-1 of dry mass)
0.5
0.45
0.4
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
leaf
branch
stem
root
Tree compartment

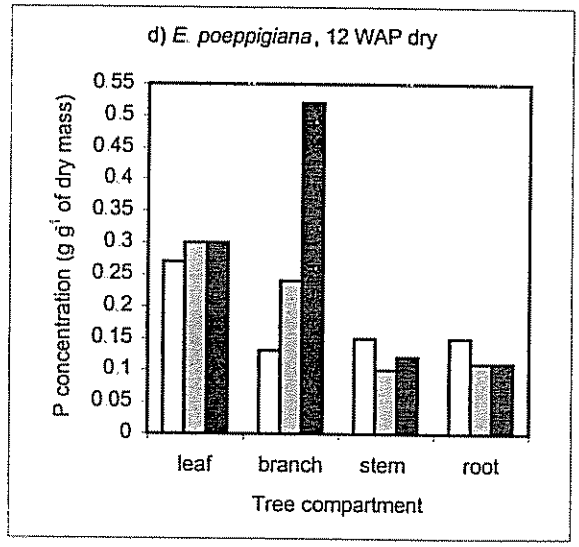
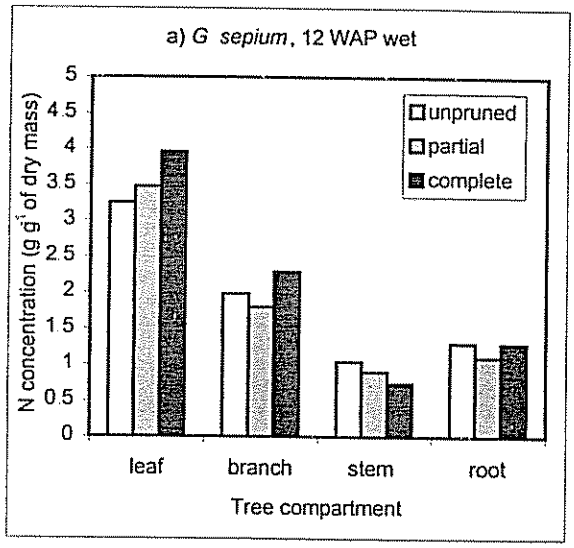
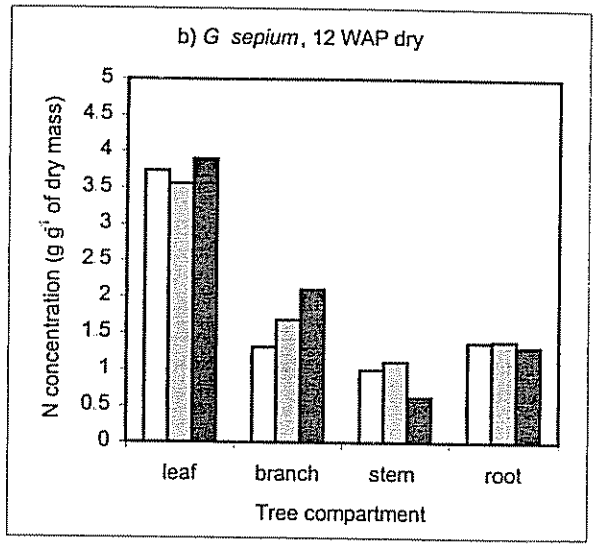
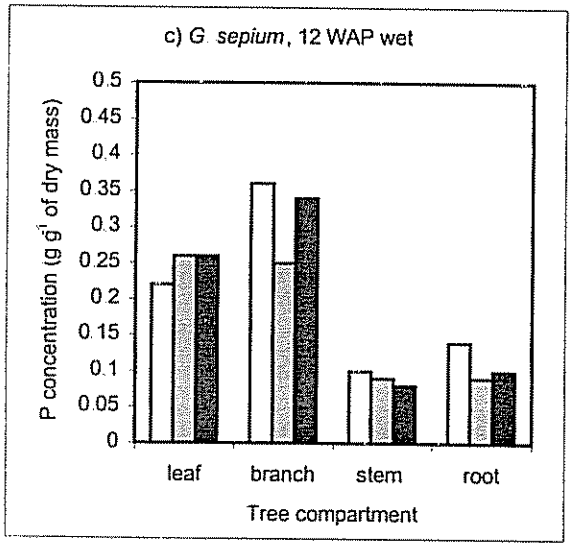

d) E. poeppigiana, 12 WAP dry
P concentration (g g-1 of dry mass)
0.55
0.5
0.45
0.4
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
leaf
branch
stem
root
Tree compartment

Fig. 1


a) G. sepium, 12 WAP wet
N concentration (g g-1 of dry mass)
unpruned
partial
complete
leaf
branch
stem
root
Tree compartment


b) G. sepium, 12 WAP dry
N concentration (g g-1 of dry mass)
leaf
branch
stem
root
Tree compartment


c) G. sepium, 12 WAP wet
P concentration (g g-1 of dry mass)
leaf
branch
stem
root
Tree compartment

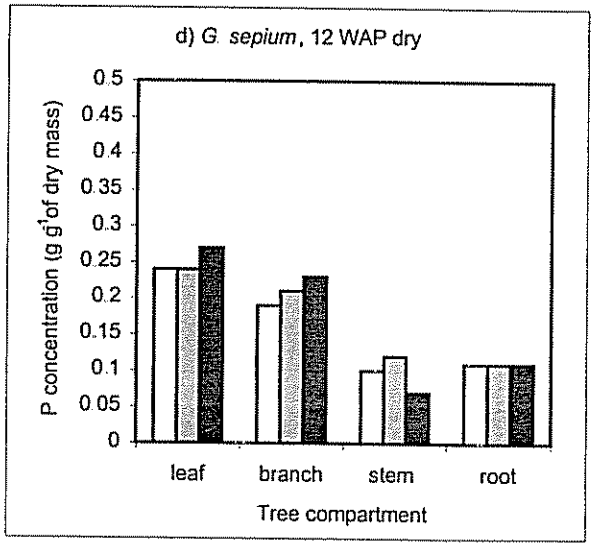
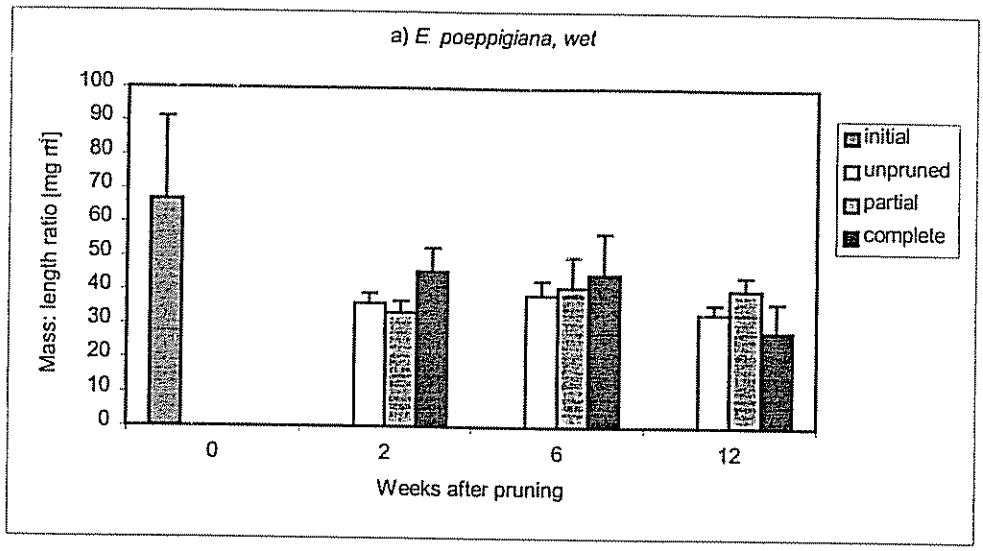
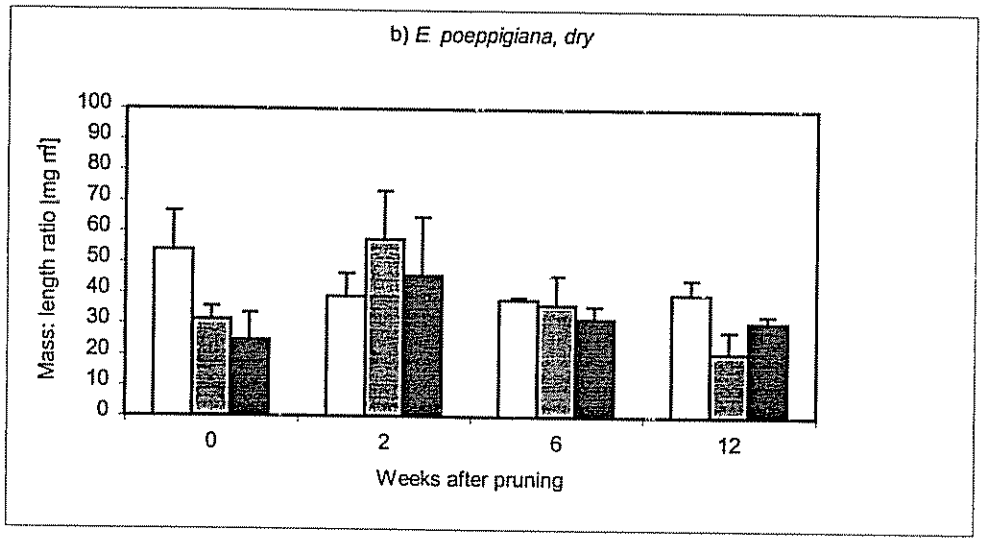

d) G. sepium, 12 WAP dry
P concentration (g g-1 of dry mass)
leaf
branch
stem
root
Tree compartment

Fig. 2


a) E. poeppigiana, wet
Mass: length ratio [mg m]
100
90
80
70
60
50
40
30
20
10
0
0
2
6
12
Weeks after pruning
initial
unpruned
partial
complete


b) E. poeppigiana, dry
Mass: length ratio [mg m]
100
90
80
70
60
50
40
30
20
10
0
0
2
6
12
Weeks after pruning

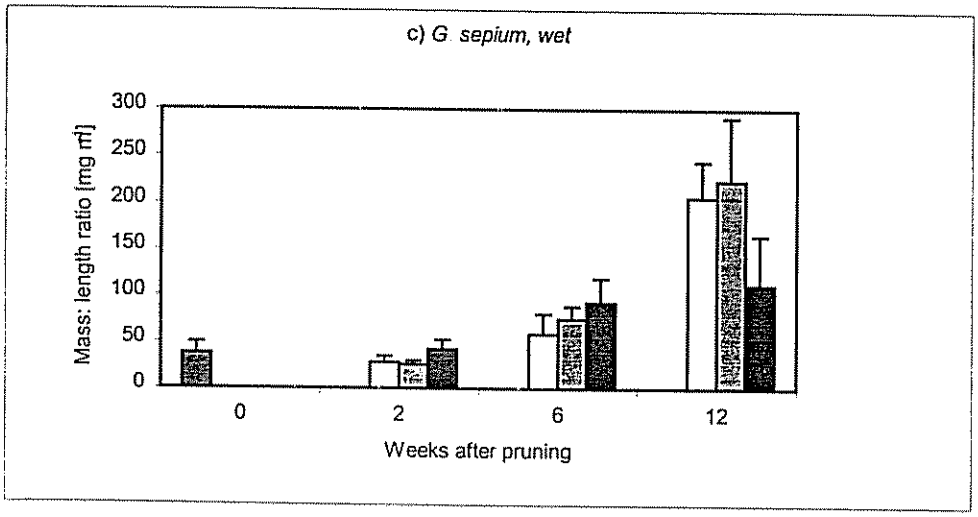

c) G. sepium, wet
Mass: length ratio [mg m]
300
250
200
150
100
50
0
0
2
6
12
Weeks after pruning

Fig. 3