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Biomass dynamics of *Erythrina lanceolata* as influenced by shoot-pruning intensity in Costa Rica

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Abstract

Pruning of agroforestry trees, while reducing shade of the crops, usually reduces both biomass production and nitrogen fixation. Short pruning cycles are often not sustainable on the long run, because tree production declines over subsequent pruning cycles. We compared biomass and labile carbohydrate dynamics of *Erythrina lanceolata* Standley (Papilionaceae) shade trees under total and partial pruning regimes in a vanilla (*Vanilla planifolia* L.) plantation in South-western Costa Rica. The highest biomass production was measured in the unpruned control, followed by trees with 50% of the leaf pruned every three months, while total pruning every six months resulted in the lowest biomass pruduction. In the more productive treatments, a higher proportion of the production was in branches. Because, the N content of woody branches was high, they were important for nitrogen cycling. In the partial pruning treatment more nitrogen was returned to the soil from litter and woody branches than from pruned leaf. Sugar concentrations were not different between treatments and the dynamics of non-structural carbohydrates (sugar and starch) seems to depend more on plant phenology than pruning treatment. However, the starch concentrations in the total pruning were lower than in the other treatments.

Introduction

In many agroforestry systems, trees and crops compete inevitably for light, nutrients and other resources. Pruning of the tree component is, particularly in alley cropping systems, a powerful approach to regulate this competition. Therefore, pruning is a common practice in a many traditional and modern agroforestry systems. However frequent pruning can lead to decreasing production and slow death of the trees (Duguma et al. 1988; Romero et al. 1993).

The effects of pruning, especially belowground, are not well understood. Nygren and Ramírez (1995) found that in leguminous *Erythrina poeppigiana* (Walp.) O.F.Cook pruning induced dieback of dinitrogen fixing nodules and the N_2-fixing *E. poeppigiana* trees were actually non- fixing for 5 months during a year. Nevertheless, scientific justifications for the use of legume tree based agroforestry systems rely largely on the idea that N_2 fixation and rapidly decomposing litter provide a cheap source of nutrients to the crop (Nair et al. 1999).

In addition, pruning treatments affect the total amount of firewood, green manure and/ or forage produced by the system. On the other hand pruning regimes are flexible: pruning intervals and intensities can be modified to match various production goals.

After a complete pruning, trees left without leaves depend on their non-structural carbohydrate reserves for regrowth. Conceptual models of tree growth after pruning claim that the amount of available carbohydrates will strongly influence the regrowth of the trees (Erdmann et al. 1993; Nygren et al. 1996; Berninger et al. 2000). In other words, trees with abundant carbohydrate reserves will regrow vigorously. Too frequent pruning will deplete the reserves and tree

growth will decline (i.e., the trees will be 'close to starvation').

In the present study, we compare biomass production and non-structural carbohydrate dynamics in pruned *Erythrina lanceolata* Standley, a tropical agroforestry tree used as shade and support plant for vanilla (*Vanilla planifolia* L.) in South-western Costa Rica. Trees of genus *Erythrina* L. (Papilionaceae: Phaseoleae) are common in Central American agroforestry systems, where they are used for shade, green manure production, living fences, forage and as medicinal plants (Kass 1994). *E. lanceolata* is one of the less studied yet commonly used species of the genus. It is a small tree adapted to humid climates with a natural distribution from Honduras to Panama (Holdridge and Poveda 1975).

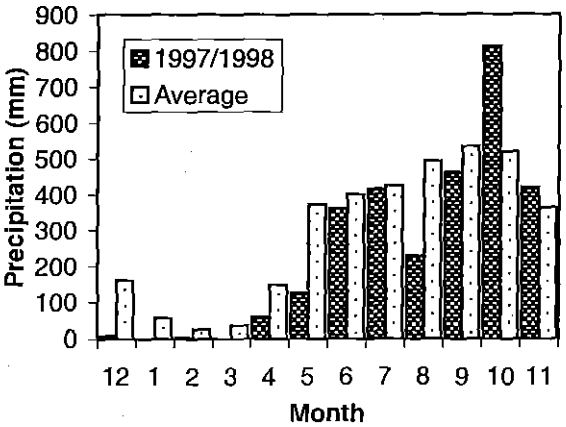

Figure 1. Rainfall in the experimental area (Quepos, Costa Rica; 9°26′ N, 84°09′ W, 20 m a.s.l.) during the season 1997/1998. (Averages refer to the 19 year period 1980–1999 from the Damas Meteorological station about 10 km from the site).

Materials and Methods

Study site

The field research was conducted in the experimental farm of the Costa Rican Ministry of Agriculture and Animal Husbandry (MAG) close to Quepos, Puntarenas, Costa Rica (9°26′ N, 84°09′ W, ~30 m a.s.l.). The climate is hot and humid most of the year but there is a three months dry season. According to the database of Instituto Meteorológico Nacional, San José, Costa Rica, (www.imn.ac.cr on 24 Sep. 1999), The monthly average of maximum temperatures varied from 30 °C (November) to 32 °C (February through April) and minimum from 21 °C (January) to 23 °C (April through June). Most of the fieldwork was conducted in 1998, when the dry season was exceptionally long and dry compared to the 15 years' average (Figure 1) (an 'El Niño' year). The soil was a sandy loam of alluvial origin. The water table was below two meters depth in the wet season. The surface soil was acidic (pH = 5.3) and had a low nitrogen and phosphorous availability (1.5 g N kg^{-1} using the Kjeldal method, and 9.1 mg P l^{-1} using the Olsen method). The soil type was an Inceptisol.

E. lanceolata was planted as a shade and support tree in 1993. Trees were planted as large stakes. The trees were planted at the density of 2 × 3 m. The whole plantation area was 2,300 m^2. About a quarter of the area was reserved for testing vanilla varieties new to the region and the rest was used for commercial vanilla cultivation. The trees in the commercial plantation were partially pruned once or twice a year, and the trees in the variety trial plot were pruned with a lower intensity. The pruning treatments started 6 month before the start of the experiment.

In June 1997, the plantation was divided into four plots with about 100 trees in each plot. Four pruning regimes of *E. lanceolata* were assigned to the plots: (i) complete pruning every six months (T-6), (ii) complete pruning every three months (T-3), (iii) partial, ca. 50%, pruning every three months (P-3), and (iv) an unpruned control (C) (pruned the last time 2 years before the start of the experiment). The biomass dynamics of the trees were followed during 11 months from December 1997 to November 1998. Sampling was concentrated in a core-plot of 12 trees growing in the centre of each plot. Around each core-plot there were at least three rows of trees with identical pruning treatments. The experiment was unreplicated in order to have plots big enough to avoid edge effects between the treatments, and hence statistical data represent pseudoreplications which have to be treated with caution.

Fine root and nodule sampling

The fine root and nodule biomass of *E. lanceolata* was sampled monthly from December 1997 through Nov. 1998 except in July and Oct. 1998. Fine roots (< 2mm) were sampled according to the methodology of Schroth and Zech (1995). In each sample plot, 12 cores were taken in the field with a stainless steel sampling tube (with an internal diameter of 6.5 cm). The random sampling locations were selected by

throwing a non-rolling object with closed eyes into a random direction. Each core was divided into three depths (0–15, 15–30 and 30–45 cm). For each depth, the 12 samples were joined and the soil was well mixed. Thereafter, fine roots were separated from a subsample 1/3 of the soil (defined by mass) for estimating the root biomass in the soil (Schroth and Kolbe 1994).

The nodules were sampled using a stratified sampling approach. The plot was divided into two sampling areas: A 1 m wide strip along the tree rows and the 2 m wide inter-row space. Fifteen random samples per sampling zone and plot were taken with a 6.5 cm auger to the depth of 15 cm. The soil samples were pooled by sample area and washed on a 2.5 mm sieve. The recovered nodules were oven-dried at 70 °C for 48 h. Nodule biomass per unit area was calculated using the surface area weighted average for both strata.

Aboveground biomass

Litter was collected weekly in each plot from three baskets (or 0.25 cm each) per sample plot for estimating the litterfall. Leaf and branch biomass was calculated using a regression of branch leaf and branch wood biomass on branch diameter. During each sampling the diameter of all branches of the sample plot was measured. In December 1997, March 1998, June 1998, and November 1998, a subsample of branches in each plot was destructively harvested for determining the regressions. The branches were selected randomly and contained all branch diameter classes. Leaf was defined as leave blades plus the leaf petioles. Branch wood included green and non-lignified parts of the branch. In order to eliminate biases caused by heteroscedasticity, the data was log-transformed for both diameter and biomass values. General linear models were used to account for sampling date and treatment effects in the data and the final models were selected using the adjusted r^2 criterion. All calculations were done in SAS (SAS Institute, Cary, North Carolina, ©1995/1999).

The regressions were applied for completely non-destructive estimation of leaf and branch biomass (Nygren et al. 1993), i.e. we applied the regression to all branches in the stand. The estimated biomasses were summed up to stand biomass. Leaf production was calculated as change in leaf biomass plus litterfall. Results were expressed per unit area and time.

Root cartography

Spatial distribution of fine roots was measured twice in the border of the sample plot. One sampling was done during the dry season (March 1998) the other two months after the onset of the rains (late June 1998). The ditches were 1.5 m deep and had the length of half a row interval (1.5 m). The ditches were dug immediately before the sampling. Root impacts were counted on the wall going from the tree to the middle of the inter-row. We placed a metal net with a mesh-size on 18 × 18 mm on the wall. For each cell the presence or absence of life roots was determined. Results presented here are for fine roots (diameter 0–5 mm).

Carbohydrate measurements

Carbohydrate concentrations were measured for branches, stems and coarse roots. Samples were cut (branches, some coarse roots) or taken with a Pressler borer (some coarse roots, stems) from the tree. A subsample of the chipped (using a garden chipper), homogenized branch material was used for the carbohydrate analysis. Samples were refrigerated as soon as possible (less than 2 hours after sampling) and were stored in 99% ethanol in less than 8 hours after sampling. Analysis followed the procedure for analysis of food carbohydrates used in Costa Rica. In short: fresh samples were homogenized in a vortex mixer. Soluble sugars and starch were analysed separately. Sugars were extracted using hot water. Chlorophyll and other pigments were precipitated using potassium ferrocyanid and zinc acetate. Sugars were analysed spectrophotometrically using the anthrone reaction. From the residues of the sugar extractions starch was hydrolysed using hot HCl, and the resulting glucose was analysed spectrophotometrically using the anthrone reaction. Concentrations were converted from fresh to dry mass using the water content of parallel samples.

Statistical analyses

Data was analysed using the SYSTAT (Kruscall Wallis test) and SAS statistical packages. General linear models and analysis of variance were made using the procedure GLM that corrects for unbalanced designs. Given mean values are weighted least square means, that are corrected for unbalanced designs.

Results

Aboveground biomass

The aboveground biomass equations differed between dates and treatments for leaf biomass, while there were no differences between dates and treatments for branch biomass. The leaf biomass r^2 values were only moderate. The final r^2 was 0.68. For the leaf biomass, inclusion of sampling date and pruning treatment improved the adjusted r^2.

The best-fit leaf biomass model had the form:

$$W_f = (a_0 + a_s + a_{tr})D^{b_0 + b_s}$$

where W_f is the leaf biomass, a_0 is a constant (8.95), a_{tr} is the pruning treatment effect (–0.37 for the control, 1.19 for the partial treatment, 0.42 and total pruning), a_s is the seasonal effect to account for the different sampling times (1.64 for 12/97,0.677 for 3/98, 1.11 for 6/98 and 1.0 for 11/98), b_0 is a constant (2.60), and b_s is the seasonal effect of the nonlinearity of the curve(–2.018 for 12/97, –1.142 for 3/98, –0.081 for 6/98 and 0 for 11/98). Sampling time and pruning treatment effects were incorporated or not incorporated depending on changes in the adjusted r^2. Figure 2a displays leaf biomass as a function branch diameter.

For branches sampling time and treatment effects failed to improve the adjusted r^2. The best-fit model for the branch biomass (W_B) was:

$$W_b = a_b D^{b_b}$$

where a_b and b_b are parameters with the values 9.44 g and 3.311, respectively. The r^2 of the equation was 0.93. Figure 2b displays the branch biomass as a function of branch diameter.

During the dry season the allometric relations gave lower leaf biomasses (Figure 2). Especially the exponent of the equation changed strongly, indicating that larger branches had less leaf in the dry than in the wet season. This is probably linked to the phenology of *E. lanceolata*, which has a lower leaf biomass during the dry season.

Aboveground biomass growth was slow during the dry season. After the onset of rains there was a considerable growth of leaf and branch biomass (Figure 3). Leaf biomass was higher in the control and P-3 treatments than in the T-6 pruning regime during the whole experiment. The branch biomass in the control was much higher than in the other treatments. The trees under T-3 pruning regime died after the pruning in March 1998, or in less than a year after establishing the treatment. We assume that the extreme dry season in combination with the stress from pruning was responsible for the death of the trees, because similar pruning treatments were previously used in the region (A. Chacón pers. comm.).

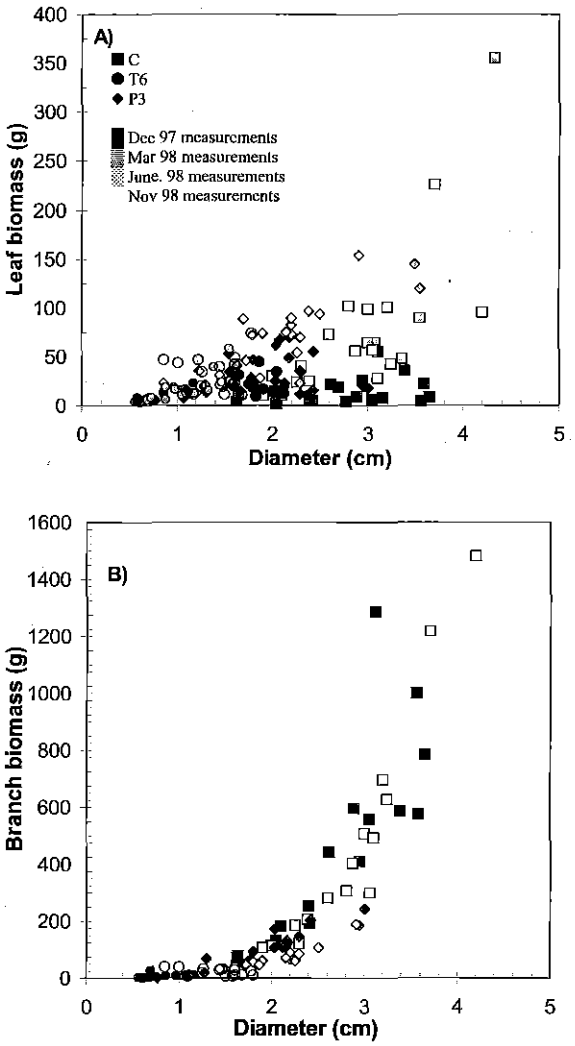

Figure 2. Leaf (a) and woody (b) biomass in a branch of *Erythrina lanceolata* as a function of branch diameter (Quepos, Costa Rica).

Litter production was a small proportion of all the productivity in all treatments (Figure 3). The leaf biomass in the partially pruned trees increased faster and was approximately equal to the control prior to the September 1998 pruning.

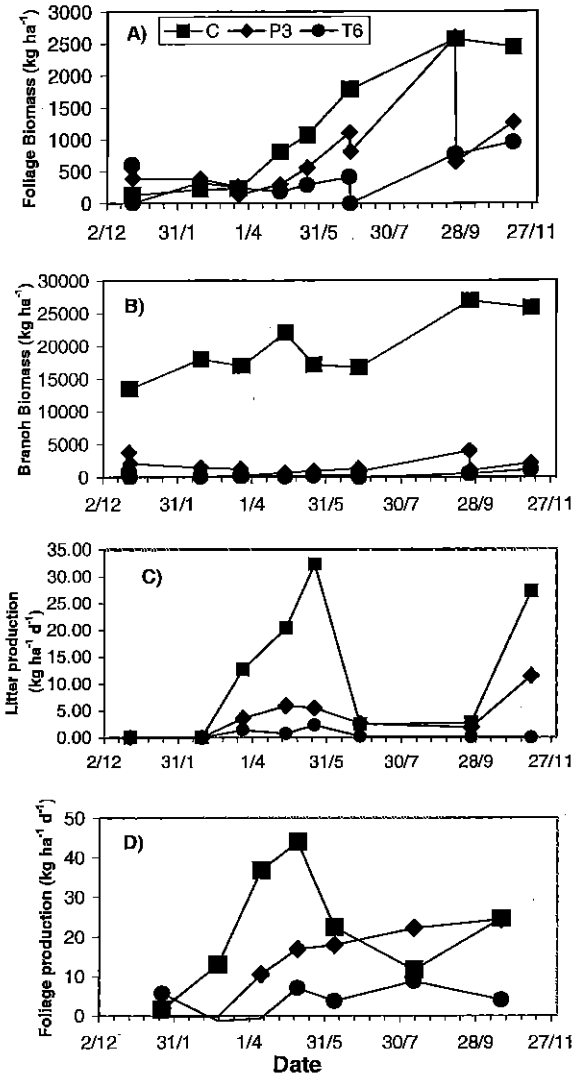

Figure 3. Development of standing leaf biomass (a), standing branch biomass (b), litter production (c), and leaf production (d) of *Erythrina lanceolata* shade trees during the one year in a vanilla plantation in Quepos, Costa Rica.

N concentrations were on the average 0.032 g[N] g^{-1} [DM] and 0.011 g[N] g^{-1} [DM] for leaf and branch wood, respectively. The N concentration of litter was 0.018 g[N] g^{-1} [DM] (Figure 4). The high N concentrations in branches made branch wood an important stock of N. Also pruning residues of N were an important source of N: in the pruning treatments 38% (P3) and (22%) of the N flux from the trees to the soil was from branch wood (Figure 4).

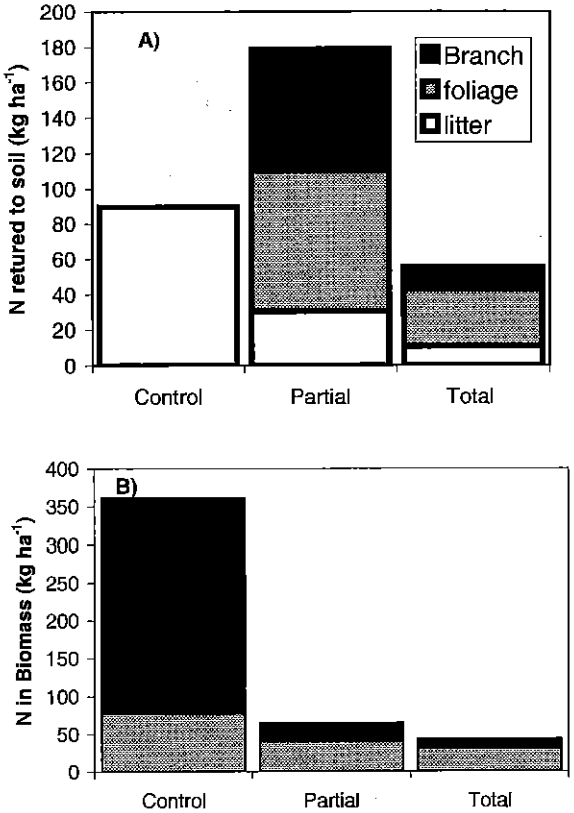

Figure 4. A) Nitrogen returned to the soil from different above ground biomass components in Quepos, Costa Rica. In the three pruning treatments Control, Partial pruning and Total pruning. (B) Nitrogen in the standing above ground biomass at the end of the experiment.

Root mapping

The number of root impacts was higher in the wet season than in the dry season and differed between treatments: the highest number of impacts was in the control (22.2 impacts m^2 dry season, 64 impacts m^2 wet season) followed by the partial pruning (12.4 impacts m^2 dry season, 21.3 impacts m^2 wet season). The number of impacts in total pruning treatment was lower (6,7 impacts m^2 dry season, 8.9 impacts m^2 wet season). Root mapping also indicated that there were a large number of fine roots in the lower soil layers below the depth of cores (Figure 5). The increase in root impact counts was much higher, also in relative terms, in the control and partial pruning treatments. More than half of the increase took place in the top 40 cm of the soil. In the control there was some increase in the lowest part of the soil profile (Figure 5).

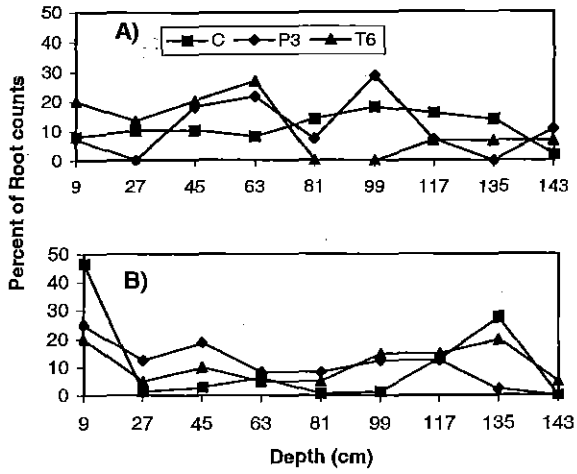

Figure 5. Root density as measured by impact points of *Erythrina lanceolata* under three pruning treatments as a function of depth in March 1998 (dry season) (a) and June 1998 (wet season) (b) in Quepos, Costa Rica.

Fine root biomass

Fine root biomass in the upper 45 cm of the soil profile was higher in the P-3 and control treatment than in the T-6 treatment. Fine root biomass increased at the beginning of the wet season. However, the timing of the increase was slightly different for the control and P-3 treatments (Figure 6). Average wet season (May to November) fine root biomass was 202 kg ha^{-1}. Nodule biomass ranged from 0 to 56 kg ha^{-1} (Figure 6). Surface fine root to leaf ratios are shown in Figure 7.

Carbohydrate concentrations

Sugar concentrations were significantly different between dates ($p < 0.001$) and between biomass compartments (root, stem, branch). Further, there were significant differences between biomass compartments. No clear reduction in sugar concentrations following a pruning was observed in either pruning treatment. Sugar concentrations were highest at the beginning of the wet season, decreased till September and increased towards November (Figure 8). Least square means of the sugar concentrations were 4.8% for roots, 4.3% for branches and 3.1% for stems. There were no significant differences between treatments in the sugar concentration.

Starch concentrations differed significantly between treatments ($p < 0.05$), biomass compartments ($p < 0.001$) and dates ($p < 0.01$). The proportion of

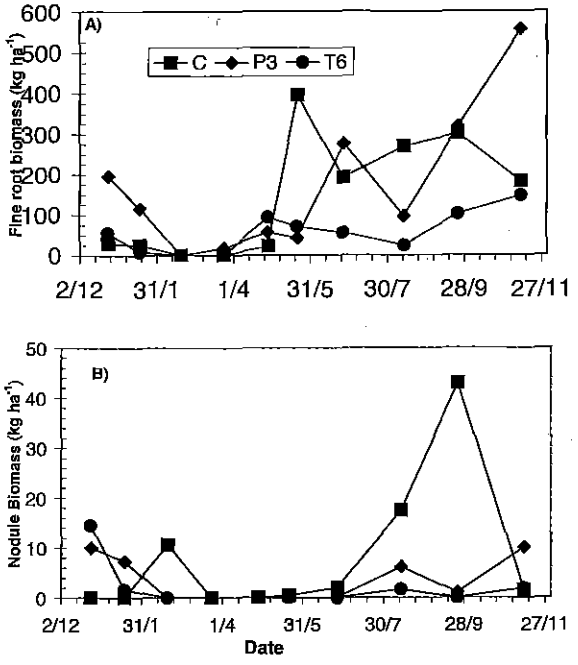

Figure 6. Root (a) and nodule biomass (b) development in *Erythrina lanceolata* as a function of time in Quepos, Costa Rica.

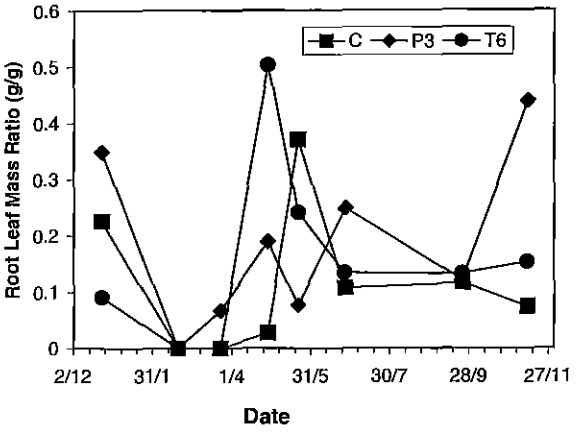

Figure 7. Fine root to leaf biomass ratios (kg kg^{-1}) in *Erythrina lanceolata* under three pruning treatments and their development over time in Quepos, Costa Rica.

the explained variance of the ANOVA was 0.37. The least square means of starch concentrations decreased in the order control, P-3, T-6 and T-3. Differences in the starch concentration between the P-3 and the control were not significant using a t-test, but differences between the T-6 and P-3 and control treatments were significant ($p < 0.01$ for control, $p < 0.05$ for the partial pruning). The least square means for the plots were 72.8 mg Starch/g for the Control, 69.2 mg/g for the partial pruning and 57.3 mg Starch /g for the total

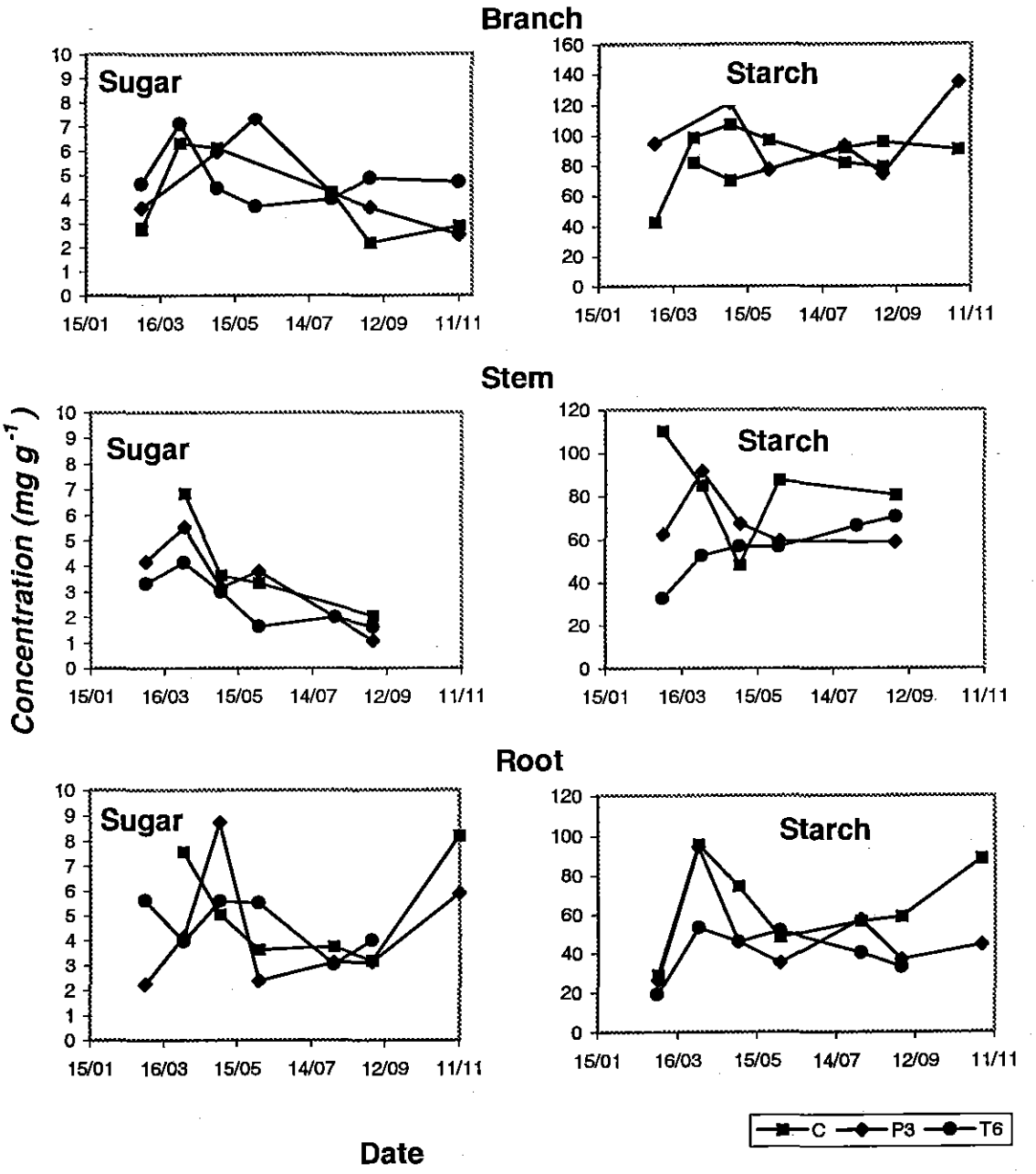

Figure 8. Time development of the concentrations of carbohydrates in branches (a), stems (b) and coarse roots (c) in Quepos, Costa Rica.

pruning. The least square means for the different plant parts were 45.8 mg Starch /g dry matter for roots, 64.3 mg Starch /g for the stem and 80.0 mg Starch/g for branches.

Discussion

Pruning treatments resulted in drastic changes in development of biomass production and allocation patterns. Total production was the highest in the control, followed by the P-3 treatment. Altogether, biomass production was in the lower range of the values reported by Nair et al. (1999) for tropical alley crop-

ping systems. Decreases in biomass production caused by pruning have been observed previously: Miah et al. (1997) showed that the biomass of Acacia mangium, A. auriculiformis and Gliricidia sepium was 27–38.5% lower than the control in pruned trees after two years of treatment. Sanginga et al. (1994) observed biomass decrease by 46% in young *G. sepium* due to pruning.

N concentrations in the leaf of *E. lanceolata* were quite high (3.5%), when compared to non-N_2-fixing trees. Palm and Sanchez (1990) reported similar values for an unidentified Erythrina sp., while Nygren and Campos (1995) measured higher values (4.6–5.1%) for *E. poeppigiana*. N concentrations in the branches were about a third of the leaf concentrations. This means that branches were an important sink of N (Figure 4). Leaf litter N concentration was about 40% lower than in pruned leaves. In other words, apart from leaf prunings, branches and litter had quantitative importance for N cycling in the system. Cut woody branches (excluding leaf) contributed 38% and 22% respectively of the N cycled through the trees in the P3 and T6 treatments, respectively while leaf recycled 44% of the N to the soil in the P3 and 58% in the T6 treatment.

During the dry season, tree growth and production were low. Especially after the December 1997 pruning, very low production rates were observed. This may be caused by an especially severe dry season. After the onset of the first rains production peaked in the control (Figure 3).

Surface fine root biomass was lowest in the dry season. It seems that most of the roots were in deep soil layers. However, surface fine root biomass increased after the onset of the rainy season. Root mortality started between the September and November sampling. Excavations in November 1998 showed that some, but few, roots were growing below 2 m depth. Low surface root biomass has been observed in *G. sepium* during the dry season (Lehmann and Zech 1998). Nygren and Campos (1995) showed that pruning depressed fine root biomass in *E. poeppigiana*.

During root sampling, we found only a few nodules below 0.15 m, although during the excavation of root systems (Salas et al. unpublished) we found nodules at 1.5 m depth. However, we assume that only few nodules were below our sampling depths. On the other hand, most of the fine root biomass escaped sampling in the dry season, because it was located below our sampling depth. Fine root biomass densities decreased in all samplings from the surface to 45 cm. This illustrates that root sampling using soil coring requires additional methods to check for root depth distributions, such as root mapping. These methods should preferably be repeated during different seasons. We, for example, decided our sampling depth based on a preliminary sampling in November 1997. At that time the results indicated that it was improbable that there were many fine roots below 45 cm depth.

Surface fine root to leaf biomass ratios were generally lower during the dry season, probably, because we failed to estimate deep fine root biomass. Growing season surface fine root to leaf biomass ratios were rather constant in the control and T-6 pruning regimes, but increased in the P-3. Simulation studies, using a growth model based on transport-resistance approach (Berninger et al. 2000), suggest a similar behaviour. Altogether surface fine root and leaf biomass were well correlated with each other. This agrees with theories on balanced growth in plants like the functional balance approach (Davidson 1969). The fact that leaf and surface fine root biomass are closely related indicates that also the competitive capacity of trees for above- and belowground resources correlate closely. Pruning diminishes the competition both below- and aboveground at the expense of a lower production of the shade trees. The root to foliage ratios were similar to those observed previously (i.e., Nygren and Campos (1995)). However, Nygren et al. (2000) observed that the input of branch biomass was reduced in *G. sepium* when pruned partially every two months, while differences in the input of leaf to the soil were not pronounced.

The control and P-3 treatment produced more biomass during the experiment. There also were qualitative differences in growth; aboveground production in the P-3 and T-6 treatments was half leaves and half branches, but about 2/3 of the production in the control consisted of branch growth. This agrees with theoretical investigations, based on the pipe model theory, which suggest that in larger trees production is geared towards woody growth (Mäkelä 1988; Nikinmaa 1992; Berninger and Nikinmaa 1997). However, in agroforestry research there are empirical results supporting and not supporting these ideas (e.g., Duguma et al. (1988) and Sanginga et al. (1994)). Branches and litter were important components of the N cycling of the system. Leaf litter and branches composed 10–18% and 20–38%, respectively, of the N returned to the soil (Figure 4). The branches were

important inputs of N and C to the soil, especially in the P-3 treatment. Altogether, the amount of nitrogen cycled through the trees was considerable, 90–230 kg[N] ha^{-1} a^{-1}. Nygren et al. (2000) described similar amounts of N accumulation in their experiments with *G. sepium*.

Sugar concentrations did not differ significantly between pruned and unpruned trees in about a month after pruning. Sugar concentrations were relatively constant throughout the observation period and seemed to follow more a yearly cycle than pruning treatments.

Erdmann et al. (1993) and Nygren et al. (1996) hypothesised that starch reserves limit the tree regrowth after pruning. We observed that starch concentrations were significantly lower in the less productive T-6 treatment, but no depletion of starch concentrations was observed after pruning. The studied trees were relatively big, and thus the total starch pool in a tree may have been so large that remobilisation of starch to initial regrowth did not affect significantly the concentration. García et al. (2001) have shown that the size of the total starch pool is more important for regrowth of *Gliricidia sepium* than high starch concentration. The lowest starch concentration in the T_6 treatment of *E. lanceolata*, which produced less biomass, may be a result of too intensive pruning. In *G. sepium*, the least productive pruning intensity also depleted most starch concentration (García et al. 2001).

The research showed that *Erythrina lanceolata* is a potential agroforestry tree, and its slow growth make it a good alternative as a support tree for climbing, shade tolerant crops like black pepper or vanilla. Partial pruning seems to be a suitable management practice for the species, leading to higher biomass production and N yield. Further, some shade is maintained all the time. Partial pruning also seems to be less disruptive for the dynamics of other biomass compartments. While partial pruning may be problematic in association with annual crops, it may be a feasible alternative for shade trees in perennial cropping systems. Due to the rather high N concentration in branches, pruned branches might be an important source of N, especially under partial pruning regimes.

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