



Needle mass, fine root and stem wood production in response to silvicultural treatment, tree size and competitive status in radiata pine stands

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Abstract

The effect of silvicultural regime, tree size and competitive status on needle mass, root fine production and allocation of carbon to stem wood was analyzed. Three stands with different agroforestry treatments were compared with one managed traditionally. Data were obtained through destructive sampling of 36 trees and analyzed by ANOVA and regression analysis. The analysis allowed us to conclude that foliage mass was not affected by the silvicultural treatment, tree size or competitive status. Fine root biomass showed an inverse relationship with fertilization. Growth efficiency was not affected by the management treatment, tree size, or intraspecific competition. The greater stem wood allocation recorded in the agroforestry treatment than in the forestry regime, is interpreted as a response to two different types of competition. Competition for light appears to induce growth in height and diameter as a function of local environment conditions. Competition for nutrients appears to reduce allocation to fine roots and increase allocation to stem wood.

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1. Introduction

Tree growth is a function of: (i) the amount of leaf area present to absorb light and its display throughout the year; (ii) the potential carbon fixation rate per unit leaf area and (iii) the extent to which photosynthesis is limited by site resources. These factors affect the photosynthetic processes, as well as respiration, determining carbon resources available for growth of stem

wood and other organs (Dewar et al., 1994). However, the detailed processes that explain allocation of growth are still not fully understood and different theories exist (Waring and Running, 1998). One theory suggests that allocation of carbohydrates is based on a priority for survival that first must provide for the maintenance of living tissue. Thereafter, the ranking in priority for long-lived perennials is toward: (i) the production of photosynthetic tissue (buds, foliage); (ii) the activity and growth of fine roots; (iii) reproductive organs (flowers and seeds); (iv) extension of branches, stem and large diameter roots (Waring, 1987; Oliver

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and Larson, 1996). The last priority, in theory, if carbohydrates are available, is to diameter growth and production of defensive compounds (Waring and Schlesinger, 1985; Oliver and Larson, 1996). Based on the low priority of carbon allocation to stem wood, a growth efficiency index (GEI) has been proposed as a measure of tree vigor. This is defined as the annual growth of stem wood per unit of leaf area (Waring et al., 1980), which integrates the photosynthetic efficiency of the canopy and partitioning of resources to aboveground organs (Vose and Allen, 1988). This index is sensitive to changes in competition (Perry, 1985), cultural practices, such as irrigation or fertilization (Linder and Axelsson, 1982), and tree resistance to native diseases and insects (Mitchell et al., 1983).

Biomass allocation has also been interpreted by the pipe model theory, originally developed by Shinozaki et al. (1964). This theory considers a tree a conductive tube system linking foliage with roots, with the evolutionary advantage to favor dominance while meeting requirements for mechanical support. This theory is based on the concept that the water conducting sapwood area should be proportional to the amount of foliage in a tree's crown (Margolis et al., 1995). Using this model, along with the functional balance theory, Valentine (1985) and Mäkelä (1986) demonstrated that a higher proportion of stem growth occurs in suppressed trees than in dominant trees. Therefore allocation patterns in trees are reflected in stem growth, with rapid increment in young trees, moderate growth by mature trees, and decreasing growth with advanced age (Mäkelä, 1990). For this observed pattern in stem growth, the pipe model theory serves well with its underlying assumption of stability in the ratio of foliage area to sapwood area (Mäkelä, 1990; Bartelink, 1998). However, this model is inadequate to explain growth allocation, because its parameters are complex functions that reflect local environmental conditions as well as genetic properties of a species (Rennols, 1994).

In this study, we determine empirically how growth is affected by silvicultural treatment, and the extent that, tree size, and competition among trees and pasture grasses, affect growth efficiency and the fraction of photosynthate allocated to stems in plantations of *Pinus radiata* D. Don, in a semiarid region of Chile.

2. Material and methods

2.1. Study site and experimental design

An agroforestry experiment was established by Corporación Nacional Forestal, in Tanumé, community of Pichilemu, VI Region, Chile (34°9'S–34°15'S latitude; 72°53'W–72°59'W longitude). Soils of this area are classified as Alfisol, suborder Xerafls, typical of a subhumid temperate climate, with six months of drought. The annual average precipitation at the study site is ~700 mm, with a minimum average temperature of 8.6 °C in July and a maximum average temperature of 15.4 °C in January, based on data obtained from a nearby meteorological station at Tanumé (2.5 km distance).

The agroforestry experiment was initiated at the beginning of 1983, in a radiata pine plantation, established at two initial densities: 625 and 1000 trees ha⁻¹ in units of 6 ha. In 1985, two types of pasture were created under the pine canopy: one with naturally established grasses and forbs, fertilized every 4 years and the other an artificial one, sowed with grass and fertilized annually. In a neighboring area, a forest stand was established with an initial density of 1600 trees ha⁻¹ (Table 1). Field work was carried out from the beginning of December 1999 to April 2000.

2.2. Data collection

2.2.1. Sampling

In each plot, diameter at breast height, 1.3 m (Dbh) was measured on all trees to obtain a stem diameter range for each treatment, which was divided into three

Table 1
Descriptions of treatments according to management of 16-year-old radiata pine, with initial and at age 16 tree densities, pasture type, and symbols representing different treatments

Management	Density (tree ha ⁻¹)		Pasture type	Treatment
	Initial	At age 16		
Agroforestry	625	187	Artificial	T1
	625	181	Natural improved	T2
	1000	185	Artificial	T3
Forestry	1600	489	Natural	T4

equal classes to represent intermediate, co-dominant and dominant crown classes (Smith et al., 1997). Later, three trees were selected randomly from each crown class, to obtain nine trees per treatment and 36 trees in total for destructive analyses. Before felling, Dbh and crown projection in all four cardinal directions were measured. After felling, total height (including stump height), and live crown height were measured. Disks of 2–3 cm width were cut at stump height (0.30 cm), Dbh, and every 3.5 m there above, including a disk at the base of the live crown. The disks were labeled, sealed in plastic bags, and stored at 2 °C for later analysis.

2.2.2. Needle mass and leaf area

To determine needle mass, the crown was divided vertically in thirds. Subsequently, all branches from each section were removed and weighed in the field to determine total fresh mass. A sample of three branches was selected randomly from each third of the crown to obtain dry mass conversions. From nine branches of each tree, all twigs were cut, the needles separated from twigs and branches, and the fresh mass of twigs then obtained by weighing. Randomly sampled needles were stored at 2 °C for later analysis. In the laboratory, samples were weighed fresh and then dried at 100 °C for 24 h, or until a constant weight was attained before weighing. Dry mass of the crown was estimated from the fractions of each component of the crown represented after making appropriate conversions from fresh to dry mass.

A subsample of fresh needles of each third of the crown of the sampled trees were kept at 2 °C until their leaf area could be determined using a Li-Cor 3100 measuring device. Subsequently, needles were dried at 100 °C for 24 h and weighed to the nearest 0.01 g to provide conversion from mass to projected leaf area (specific leaf mass). The sum of the sections corresponds to the projected leaf area.

2.2.3. Root biomass

Four stumps from previously felled trees in each treatment were randomly selected to determine root biomass, two from the intermediate class, and one from each from the other two classes. The potentially available areas for root mass were determined by the procedure described by Santantonio et al. (1977). The soil samples with roots were extracted using a steel

tube with a diameter of 10 cm and length of 30 cm. The samples were taken at depths of 30, 60 and 90 cm along four transects to neighboring trees at 1/2 and 1/4 distance from the stump (Santantonio et al., 1977). In the laboratory, samples were immersed in water and roots separated by flotation. All roots were sieved, dead roots removed, and the remaining classified as live fine (<2 mm) or coarse roots (between 2 and 5 mm). Fine roots were dried at 70 °C and weighed to 0.01 g.

2.3. Stem analysis and stem wood biomass

In the laboratory, diameters of the collected disks were measured following procedures described by Rodríguez et al. (2002). Total volume (m³) was calculated according to the geometric form of the stem (Husch et al., 1982). To determine wood density, disks were immersed in water to obtain fresh volume, dried at 100 °C for 48 h or until a constant weight, and then reweighed. Wood density (kg m⁻³) was determined by dividing the dry mass by the fresh volume. We obtained total dry mass of the sampled trees by adding together the mass of all sections. Stem growth (G_s , in kg per year) was calculated as an average for the 1997–1998 and 1998–1999 periods. At the same time, heartwood and total disk area were measured to calculate sapwood area at Dbh by difference.

2.4. Growth allocation

To interpret growth allocation, growth efficiency and stem growth relative to foliage growth were compared. The GEI was estimated according to Waring et al. (1980), as $G_{EI} = G_s/A_f$ (kg wood m⁻² foliage per year), where A_f is the projected leaf area. The relative stem wood growth allocation index (λ) was estimated as $\lambda = G_s/G_s + G_f$, according to Vanninen and Mäkelä (2000). Indicators of tree size were foliage biomass (W_f), leaf area (A_f), total height (H), diameter at breast height (Dbh), live crown length (L_c), and stem height from the ground to the base of the live crown (H_b). Indicators of competitive status were the ratio of leaf area/sapwood area (A_f/S_a), relative height (H_{rel}), live crown ratio ($R_c = L_c/H$), the relation between total height and diameter at breast height (H/Dbh), foliage density in relation to crown volume (F_v), and crown surface area (F_s). F_v and F_s were estimated

assuming a conic shape of the crowns with a height H and a radius equal to the mean crown radius where the crown was widest (Assmann, 1970).

2.5. Statistical analysis

To test the effect of the treatments on biomass components, multivariate analysis of variances (MANOVAs) and analysis of covariance (ANCOVA) techniques were used. Logarithmic transformation for Dbh and biomass components were applied. The analysis of variance (ANOVA) detected significant differences in Dbh between treatments, marking an effect of initial density. This indicates the necessity to use Dbh as a covariable in the following MANOVA models.

The allometric equations were calculated using regression models with indicator variables, which allows to separate the effect of each treatment and its interaction with Dbh. The general model of the allometric equation is

$$Y = \beta_0 + \beta_1 \log(\text{Dbh}) + \beta_2 \text{Treat}_1 + \beta_3 \text{Treat}_2 + \beta_4 \text{Treat}_3 + \beta_5 \text{Treat}_1 \log(\text{Dbh}) + \beta_6 \text{Treat}_2 \log(\text{Dbh}) + \beta_7 \text{Treat}_3 \log(\text{Dbh}) + \varepsilon$$

where Y is the biomass component (kg), Dbh the covariable, $\beta_0, \beta_1, \dots, \beta_7$ are the regressions coefficients, $\text{Treat}_1, \text{Treat}_2$ and Treat_3 are the dicotomic (0, 1) that are used to codify treatment effect, $\text{Treat}_1 \log(\text{Dbh}), \text{Treat}_2 \log(\text{Dbh}), \text{Treat}_3 \log(\text{Dbh})$ the interaction effects between treatment and Dbh, and ε the random error with a supposedly normal distribution.

A non-significant interaction is detected graphically. Parallel mean profiles for the treatments indicate that there is no interaction. In this case, the difference in biomass between treatments does not depend on the size of the tree. If there is no interaction, the general model is reduced to

$$Y = \beta_0 + \beta_1 \log(\text{Dbh}) + \beta_2 \text{Treat}_1 + \beta_3 \text{Treat}_2 + \beta_4 \text{Treat}_3 + \varepsilon$$

In this case, the analyses are given using the reduced model, which allows estimation of the confidence intervals of the treatment differences. Let μ_i be the population means for the i th treatment. The confidence intervals for the pairwise differences $\mu_i - \mu_j$ were

calculated using Scheffé's simultaneous estimation method (Neter et al., 1996).

To determine treatment effect on growth efficiency and allocation, ANOVA and regression models were used. To compare means, a Tukey's test was run. All analyses were done with the software 'Statistica'.

3. Results

3.1. Needle and root fine production and stem wood growth

Total biomass per tree in the agroforestry treatment (T3) was 2.2–2.5 times larger than in the pure forestry treatment. Although no significant difference was observed in aboveground biomass among the different treatments, fine root mass was significantly lower in T3 than in other treatments.

We used ANCOVA models only after adjusting for Dbh as a co-variable to determine whether there were significant differences of the biomass components among treatments. The ANCOVA indicated that needle mass and stem wood mass did not differ significantly among treatments (Tables 2 and 3). In all treatments, needle and stem wood mass were highly correlated with tree size because $\log(\text{Dbh})$ is a very significant component of all the regression models (Fig. 1a and b, respectively).

Regression analysis showed an inverse relationship between fine root biomass and tree size for all treatments (Fig. 1c). However, trees of all sizes in T3 have significantly less fine root biomass than their counterparts in all other treatments (Table 2).

Table 2
Mean value for foliage, fine root, stem wood and total mass per tree (kg) for 16-year-old radiata pine

Treatments	Component ^{a,b}			
	Foliage	Fine root	Stem wood	Total
T1	94 (70) a	15 (3) a	517 (40) a	626 (330) a
T2	82 (44) a	14 (2) a	474 (24) a	570 (386) a
T3	99 (55) a	7 (2) b	527 (17) a	633 (230) a
T4	36 (29) a	16 (3) a	220 (14) b	273 (198) b

^a Values in parenthesis indicate standard deviations.

^b Rows with different letters indicate significant differences at $P < 0.05$.

Table 3
Allometric equation coefficients for different tree components for 16-year-old radiata pine ($n = 36$)

Component	Variation source	β	SSE β	T(11)	P	R^2	SSE
Needles	Intercept	-251.909	116.7204	-2.158	0.0396	0.87	20.43
	log(Dbh)	87.578	35.4220	2.472	0.0197		
	Treat ₁	-368.284	156.2631	-2.356	0.0256		
	Treat ₂	-217.741	150.5288	-1.446	0.1591		
	Treat ₃	-344.001	173.2024	-1.986	0.0568		
	Treat ₁ log(Dhb)	107.812	45.5089	2.369	0.0249		
	Treat ₂ log(Dhb)	69.282	43.9131	1.577	0.1258		
	Treat ₃ log(Dhb)	101.729	49.5516	2.052	0.0495		
Stem wood	Intercept	-2.6254	0.5052	-5.196	0.0000	0.98	0.08
	log(Dbh)	2.4243	0.1533	15.809	0.0000		
	Treat ₁	0.3569	0.6764	0.527	0.6018		
	Treat ₂	0.8032	0.6516	1.232	0.2279		
	Treat ₃	1.9613	0.7498	2.615	0.0141		
	Treat ₁ log(Dhb)	-0.1220	0.1970	-0.619	0.5406		
	Treat ₂ log(Dhb)	-0.2574	0.1901	-1.354	0.1865		
	Treat ₃ log(Dhb)	-0.5470	0.2145	-2.550	0.0165		
Fine roots	Intercept	38.1569	2.8625	13.329	0.0000	0.95	0.94
	log(Dbh)	-6.7776	0.8707	-7.783	0.0000		
	Treat ₁	0.7254	0.7309	0.992	0.3422		
	Treat ₂	0.0091	0.7287	0.012	0.9902		
	Treat ₃ *	-6.0793	0.7517	-8.086	0.0000		

* Significance of treatment ($P < 0.05$; Tukey's test).

3.2. Growth efficiency and relative stem wood allocation indices

The GEI histogram for all treatments presented an exponential pattern, which required a natural logarithm transformation to adjust the regressions (Fig. 2).

The GEI for all treatments in the agroforestry management system was negatively correlated with size variables such as W_f , A_f , and Dbh. Furthermore, in T3 a negative correlation with H_t was found. For all treatments a negative correlation with A_f/S_a was found. However, in T1 and T2 GEI was positively correlated with H/Dbh , and in T3 negatively correlated with H_{rel} and R_c . Both variables H_{rel} and R_c are related to competitive status. In T4 a negative correlation with A_f and A_f/S_a was found. At the same time, λ did not present a correlation with size or with the competitive status variables in T1, T3 and T4. T2 showed a positive correlation with tree size through Dbh, H_t , L_c , and with competitive status through H_{rel} .

The GEI did not show differences between forestry and the agroforestry treatments (Fig. 2). However, intermediate and co-dominant trees had a larger

GEI than dominant trees in T1 and T2. Significant differences in T3 were found among all crown classes. The largest GEI observed was in the intermediate class and the lowest in the dominant class. At the same time, no significant differences were found in GEI among crown classes in T4 (Fig. 2).

Relative stem growth allocation (λ) was significantly greater in the agroforestry treatment than in the forestry treatment, and no difference was detected among various agroforestry treatments (Fig. 2). When looking at crown class, the differences detected for λ were only significant for T3, being greater in the dominant crown class.

4. Discussion

4.1. Needle production, fine root and stem growth

Foliage mass and leaf area could both be predicted accurately from measurement of Dbh. Allometric relations constructed between Dbh and needle production showed a particularly high correlation (Fig. 1a).

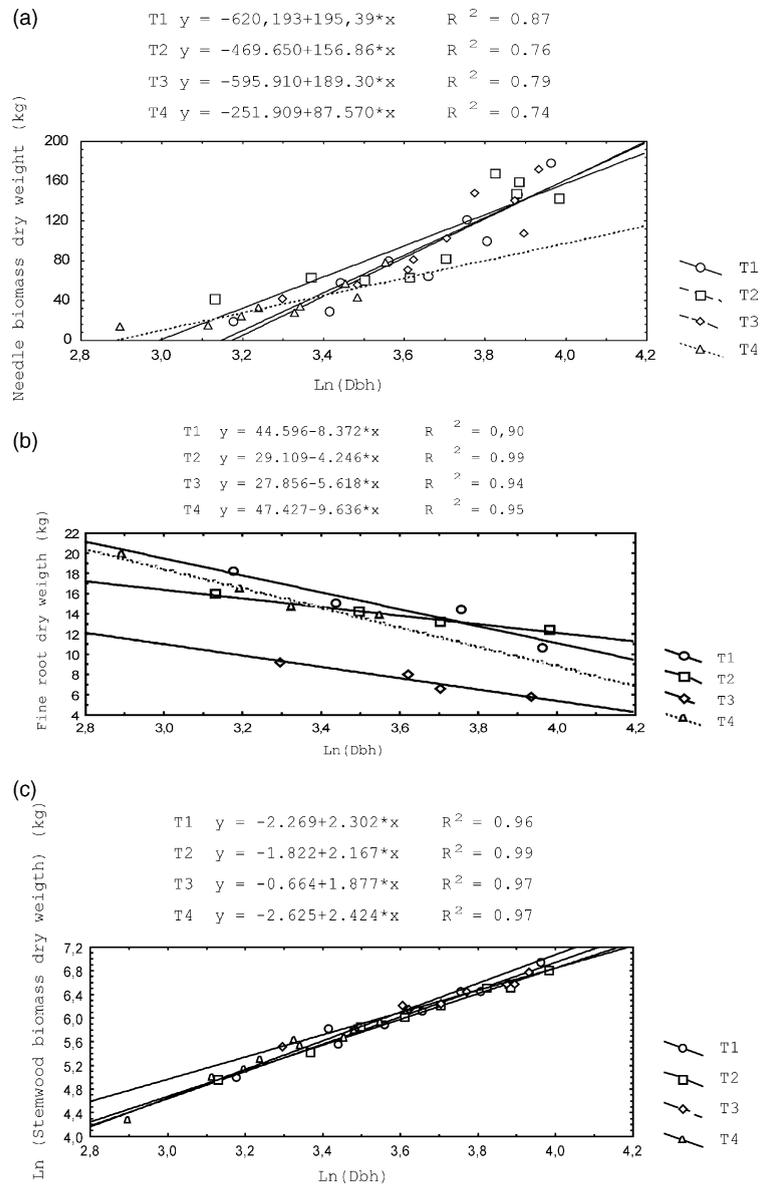


Fig. 1. Dispersion graphs for allometric relations between Dbh and biomass for each tree component in 16-year-old radiata pine. Equation coefficients are shown in Table 3 (variables were transformed to natural logarithms).

Similar high correlations between Dbh and foliage mass have been reported for other species (e.g. St. Clair, 1993; Bartelink, 1996; Naidu et al., 1998). Dbh represents the culmination of all previous growth at that height, while crown biomass, and especially the biomass of needles, is determined by more current conditions, in particular in response to thinning (Bartelink, 1996). However, the slope–intercept log(Dbh)

and biomass needle line in T4 related to T1–T3 (Fig. 1a) denotes the influence of the relationship between photosynthesis per unit of leaf area and stocking density (Perry, 1984).

That no significant differences were found in foliage mass among treatments (Table 2) is consistent with the findings of Beets and Whitehead (1996). Foliage mass, therefore, was insensitive to other

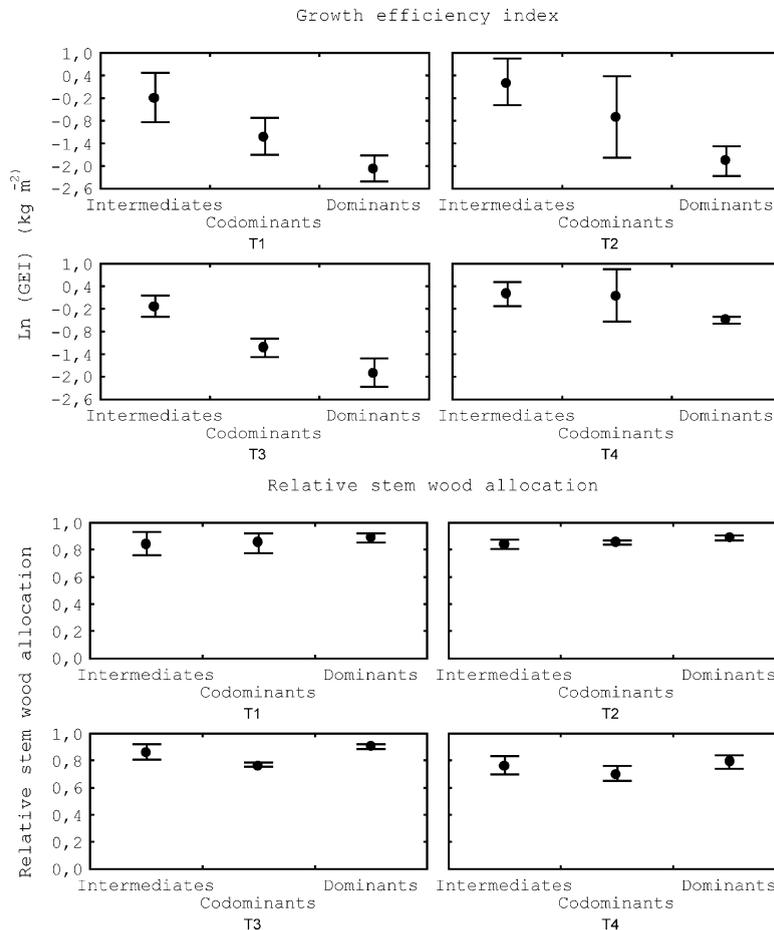


Fig. 2. GEI for the different treatments and crown classes (GEI was transformed to natural logarithm) and relative stem wood allocation (λ), for 16-year-old radiata pine. The symbol (●) indicates mean and the bars are standard deviation.

changes in carbon partitioning within the range of cultural practices covered in this study. Foliage growth is mainly dependent on environmental conditions during the prior growing season (Raison et al., 1992), and particularly water deficit for radiata pine (Bandara et al., 1999). The results of this study tend to support this interpretation because heavy leaf fall did not occur in 1997–1998, a growing season with only 28% of the annual mean precipitation (700 mm) recorded between 1983 and 1999. The absolute and relative growth of fine roots, which are responsible for the absorption of water and nutrients, were, as expected (Cannel and Dewar, 1994) decreased with fertilization associated with the agroforestry treatments. The relative response has been documented

in other studies, but the absolute values do not always decrease with fertilization (Linder and Axelsson, 1982; Marshall and Waring, 1985; Axelsson and Axelsson, 1986; Santantonio and Santantonio, 1987; Beets and Whitehead, 1996).

Stem and total growth in all the agroforestry treatments were greater than under forestry practices. Among agroforestry treatments, no significant differences were found (Table 2). In the context of this study, stem and total growth can be related to: (i) the response of crown structure resulting from the silvicultural treatments and the adaptation of the crown shape to its light regime (Kellomäki et al., 1985; Perry, 1985), (ii) the relation H/Dbh , which is not associated with productivity but with mechanical

stress (Albrektson and Valinger, 1985; Lundqvist and Valinger, 1996), (iii) site characteristics due to the sensitivity of trees to the current availability of site resources (Smith et al., 1997), and (iv) after crown closure, stem growth increases in response to a shift in carbon allocation from roots to stem (Oliver and Larson, 1996). This study showed that tree size and crown structure were affected by stocking. Stands with lower final density exhibited stem and total growth in single trees, regardless of the plantation design or type of pasture. Stem growth was significantly greater in the agroforestry than in the forestry treatments, which is explained by the lower fine root biomass typical of the agroforestry treatments (Table 2). The largest stem wood and total biomass were at expense of decreasing carbon allocation to fine roots in response to fertilization (Oliver and Larson, 1996). However, Table 2 shows that stem wood mass in T1 was the same as in T3, but T1 also had the same amount of fine root as T4. This results in a pattern of allocation between foliage, stem wood and fine root shows that depend on both resource availability (Axelsson and Axelsson, 1986) and crown structure.

4.2. Growth efficiency and relative stem wood allocation

No statistical evidence was acquired to conclude that management practices affected GEI. However, clear patterns in the agroforestry treatments were observed among crown classes with intermediate trees having significantly larger GEI than dominants in all treatments. This response may be attributable to the effects of thinning on stand structure (O'Hara, 1988). On the other hand, in forestry treatments no significant differences were found in GEI among crown class. Both results are consistent with the findings of others that shows GEI is relatively constant once stands reach their maximum leaf area index and only change when leaf area decreases (Waring, 1983). Table 3 shows that for all the size variables significantly correlated with GEI, the correlation is negative. Only T1 and T2 seem to be affected by competition through the H/Dbh ratio. These results suggest that in managed stands under competition for light, growth allocation between height and diameter is regulated by environmental conditions (Vanninen and Mäkelä, 2000), and reflect

tree response to mechanical stress (Albrektson and Valinger, 1985; Lundqvist and Valinger, 1996).

In all agroforestry treatments, λ was greater than in the forestry treatments, due to lower tree density and fertilization. The greater allocation to stem biomass observed was highly correlated with H_{rel} . This indicates shading of crowns between neighboring trees (Vanninen and Mäkelä, 2000) and confirms that in this treatment light competition is a consequence of the cluster design of the plantation. In the other treatments, λ was not correlated with size and competitive status, suggesting competition for water and/or nutrients were important in T3 and T4 treatments.

An interpretation of the general correlation found between λ and indices of competitive status, was that in managed stands competition for light has a different effect than competition for nutrients. In both cases, growth allocation differs. With competition for light, as in T1 and T2, height growth responds more than diameter growth (Nilsson and Hålgren, 1993). As a result, less dominant crown class trees respond relatively more in height growth, while still maintaining a constant A_f/S_a ratio (Axelsson and Axelsson, 1986; Nilsson and Albrektson, 1993; Vanninen and Mäkelä, 2000). In this study the A_f/S_a ratio did differ significantly between agroforestry and forestry treatments. This difference could be interpreted as adaptations of crown shape to the modified light regime (Kellomäki et al., 1985). On the other hand, the A_f/S_a ratio was not affected by fertilization, nor by other features associated with the agroforestry treatments. With light competition, growth allocation between height and diameter is regulated by local conditions and H/Dbh represents an accumulative index that integrates long-term effects of local conditions on growth patterns (Vanninen and Mäkelä, 2000).

However, under nutrient competition, as in T3 and T4, GEI and λ are not correlated with tree size or competitive status. The greater stem growth allocation in T3, compared to T4, is in response to a decrease in allocation to fine roots following fertilization (Table 2). This finding is in accordance with the priority theory (Waring and Schlesinger, 1985; Waring, 1987; Oliver and Larson, 1996; Waring and Running, 1998). It is also related to the rapid turnover of fine roots, associated with high demand for carbohydrates by fine roots when growing in soils lacking nutrients or water (Santantonio and Hermann, 1985).

5. Conclusions

Needle mass was not affected by the silvicultural treatments included in this study. However, tree stem and total biomass were significantly larger in the agroforestry than in the forestry treatments. This we attribute to a shift in allocation away from fine roots to stem wood in response to fertilization. Growth efficiency was not affected by the silvicultural treatment, tree size, nor competition. The greater allocation to stem wood observed in the agroforestry treatments is attributed to two types of competition. Under competition for light, height growth is the major priority constrained by mechanical stresses. Shifts in growth allocation between height and diameter, on the other hand, are more a function of by local site conditions (Albrektson and Valinger, 1985; Lundqvist and Valinger, 1996; Vanninen and Mäkelä, 2000). With reduced increased competition for nutrients, greater allocation to stem growth is observed as a result of reduced growth of fine roots.

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