

UNDERSTOREY VEGETATION AND THE CROWN ARCHITECTURE OF *PINUS RADIATA* SEEDLING AND CLONAL TREES IN AN AGROFORESTRY SYSTEM

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ABSTRACT

Crown characteristics of 4-year-old *Pinus radiata* D. Don originating from seedlings and clonal trees propagated by tissue culture, and growing in the presence and absence of an understorey of lucerne (*Medicago sativa* L.), in an agroforestry experiment were investigated to explain differences in foliage efficiency between the treatments.

There was no difference in the tree height between selected sample trees for any of the treatments, but the diameter at breast height (1.4 m above ground-level) and the total tree biomass were larger for the clonal trees than for the trees originating from seedlings in the no-understorey treatment. The distribution of biomass within the crown showed marked differences between treatments. Branch basal area and the number of medium-sized branches were greater for the clonal trees than for the seedling trees, and foliage area per unit branch basal area was lower for the clonal trees than the seedling trees. Internode length was longer and the crown shape ratio higher for the clonal trees than the seedling trees. These differences in crown architecture resulted in differences in foliage area distribution within the crown, possibly leading to differences in the fraction of solar radiation intercepted.

The allocation of above-ground biomass was changed, resulting in an increase in the stem wood fraction and a decrease in the branch fraction for trees growing with the lucerne understorey, compared with trees with no understorey present. Foliage area per unit branch basal area was lower for trees grown with the lucerne understorey than in the no-understorey treatment and these changes were more pronounced for the seedling than for the clonal trees. These results confirm that the competitive effects of understorey vegetation result in changes in the growth patterns of trees, including the allocation of biomass to above-ground components.

Keywords: biomass allocation; competition; foliage distribution; canopy architecture; agroforestry.

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INTRODUCTION

A plantation programme based on the selection of superior clonal trees of *Pinus radiata* offers the possibility of large gains in growth compared with trees derived from seedlings (Shelbourne 1991). However, clonal trees grown from cuttings by tissue culture may show differences in canopy architecture distinct from seedling trees of the same chronological age (Fielding 1970; Burdon & Bannister 1985; Eldridge & Spencer 1988) due to differences in physiological age. Crown architecture determines foliage display, foliage distribution, and canopy foliage area density. These, in turn, influence light interception, canopy transpiration, water and nutrient distribution, and subsequently carbon assimilation (Jahnke & Lawrence 1965; Kellomäki *et al.* 1984; Whitehead 1986; Grace 1988; Kuuluvainen *et al.* 1988). The distribution of foliage mass within the forest canopy and within individual crowns (Wang *et al.* 1990; Whitehead *et al.* 1990; Maguire & Bennett 1996) has been used to explain the differences in growth between individual trees (Pulkkinen 1991; Hees & Van Bartelink 1993).

Previous studies have also shown that characteristics of crown structure are highly correlated with tree productivity (Velling & Tigerstedt 1984; Knowles & West 1986; Kuuluvainen *et al.* 1988; Pulkkinen 1991). Many environmental factors are known to affect crown development in *P. radiata* (Linder *et al.* 1987; Carson & Inglis 1988; Raison *et al.* 1992; Burdon *et al.* 1997). Further, growth rate of *P. radiata* is reduced when water and nutrients are restricted by environmental conditions (Mead & Mansur 1993; Yunusa *et al.* 1995a) or when there is competition for resources by understorey vegetation (Richardson *et al.* 1996, 2002; Watt, Whitehead, Richardson, Mason, & Leckie 2003). This may also result in changes in growth rate and patterns of biomass allocation between tree components (Mead *et al.* 1984; Snowdon & Benson 1992; Gautam *et al.* 2003; Watt, Whitehead, Mason, Richardson, & Kimberley 2003). A number of studies have demonstrated that genotype, propagation method, and environment affect crown structure and tree growth (Kuuluvainen *et al.* 1988; Menzies & Klomp 1988; West 1988; Hinckley *et al.* 1992). To explain differences in productivity of trees propagated using tissue culture or as seedlings, it is necessary to determine the response of canopy architecture and tree growth to water and nutrient availability in relation to competition from understorey vegetation.

This study was carried out to compare the above-ground biomass production and allocation patterns in large trees originating from seed and a tissue culture clone in relation to understorey competition, and to investigate the variations in crown architecture resulting from the differences in biomass allocation. The results were used to explain the relationship between crown architecture and previously observed higher foliage efficiency (*E*, biomass increment per year per unit foliage mass) in the different treatments (Bandara 1997).

MATERIALS AND METHODS

Site, Trial Design, and Materials

The site, trial design, and materials have been described in detail by Mead *et al.* (1993). Briefly, the soil was Templeton silt loam, medium- to free-draining with 320 mm water-holding capacity in the top metre of the profile. The mean annual temperature was 11 °C and long-term mean (\pm standard deviation) annual rainfall was 660 \pm 40 mm. The *P. radiata*

trees were planted in 1990 in a split-plot design with three blocks. The main plots consisted of five understorey pasture treatments plus a no-understorey control treatment. For this study, lucerne, the most competitive of the understorey species (Mead *et al.* 1993), and the no-understorey treatments were selected for the measurements. Within these main plots were subplots consisting of trees from five types of planting material. Four of these were clones derived from tissue culture and the fifth was seedlings from the “850” selection. Clone 3, set 11/8: full sib of “875” clones 7×292, and the seedling trees were used in this study. The growth and form ratings (Hammond 1995) expected for the clonal and seedling trees were about 17 and 14, respectively. The clonal trees were 6 years old from seed when planted and 10 years old from seed when the measurements were made. The seedling trees were 4 years old when the measurements were made (5 years after germination). Tree spacing was 600 stems/ha, the trees had not been pruned, and crown inter-tree competition was not apparent. The pasture understorey was grazed by sheep in the spring and autumn and the maximum canopy height was 200–300 mm, so the competitive effects of the understorey were considered to be attributable solely to nutrients and water availability.

Biomass Measurements

Twelve sample trees (representing the two planting material types, the two understorey treatments and three replicates) were selected for detailed measurements of crown architecture. The sample trees were selected to give a range in diameter at breast height (1.4 m above ground level) D , for each treatment. Before these trees were felled for estimation of biomass, 30 fascicles from each age class and from each tree were collected from all over the crown. These fascicles were stored in a refrigerator and used later for specific needle area measurements (following Beets 1977). Tree heights, crown diameters, and mean branch tip height for each branch cluster were measured using a telescopic measuring pole in the field. The selected trees were then felled and brought to the laboratory and set upright for measurements of maximum crown width. An average-sized sample branch from each branch cluster of sample trees was selected for detailed measurements. In order to estimate the foliage area and its distribution for these sample branches, measurements of height of the branch cluster, horizontal distance from the tree stem to the proximal end of the branch, basal diameter (50 mm from the point of attachment), and length for each age class of foliage were recorded. Also, the distance from the base of the sample branch, basal diameter, and length for each age class of foliage were measured for all second-order branches. Second-order branches were removed and separated into age classes, and their fresh mass was recorded. The first-order sample branches were then separated into age classes and their fresh mass was recorded. All the components of these sample branches (branch portions separated by age classes) were oven dried at 65°C, separated into foliage and branch wood, and weighed. All remaining branches in each cluster were then removed and branch basal diameters were measured. The foliage and branches were separated into age classes and fresh mass was recorded for each branch cluster. Finally, to obtain the dry mass of stem wood and stem bark, the total stem was first weighed green, then 30-mm-thick discs were taken at 400-mm intervals along the tree stem and weighed. These subsamples were separated into wood and bark, dried at 65°C, and weighed. Total dry mass of stem and crown components was calculated using the ratio of fresh to dry mass from the subsamples.

From the dry mass of foliage and specific needle area, estimated from the fascicle samples collected before trees were felled, the foliage area was calculated and presented on an all-surfaces-area basis (Grace 1987).

The vertical distribution of foliage area for a tree was reconstructed from each sample branch. Foliage area density was calculated in 100-mm vertical intervals, based on the geometric space occupied by the branch, the position of first- and second-order branches, and foliage mass. Using this foliage area distribution for the sample branch, foliage area distribution for branch clusters was calculated for 100-mm vertical intervals, knowing the position of each branch in each cluster.

A split-plot design was used for all the analysis of variance (ANOVA), with understorey treatment as a main plot and planting materials as the subplots.

Branch Diameter Distribution

Branches of each tree were classified into six diameter classes. Class 1 comprised branches 0–10 mm diameter; Class 2, 11–20 mm; Class 3, 21–30 mm; Class 4, 31–40 mm; Class 5, 41–50 mm; and Class 6, ≥ 51 mm. The Weibull distribution was fitted to the branch diameter class distribution for each tree, where the frequency of branches (f) for each branch diameter class (d) given by Rennolls *et al.* (1985) is:

$$f(d) = \frac{c}{a} \left[\frac{d-b}{a} \right]^{c-1} \exp \left[- \left[\frac{d-b}{a} \right]^c \right] \quad (1)$$

The three parameters a , b , and c are used to describe the shape of the distribution where a is a scale parameter related to the range of branch diameter classes, b is a location parameter describing the minimum value of the distribution or the minimum of the diameter class, and c determines the skewness of the distribution.

The parameters were estimated for each tree and ANOVA was used to test for significant differences between treatments. Further, these parameters were subjected to covariance analysis with D as a covariate, to study whether tree size influenced the branch diameter distribution.

Stem Internode Length

All the internodes in each sample tree were classified into three internode length classes. Class 1 was internodes 0–300 mm; Class 2, 310–600 mm; and Class 3, >600 mm. Differences in the numbers of internodes for each internode classes between treatments were tested using ANOVA.

Branch Basal Area and Foliage Area Relationship

Branch foliage area and branch basal area were related by linear regression, and the differences between treatments in intercepts and slopes from the relationships were tested using ANOVA. Branch basal area was regressed against the natural logarithm of branch length and comparison of the parameters between treatments was undertaken using ANOVA.

Vertical Foliage Area Distribution

To analyse the vertical foliage area distribution for each tree and remove the effects of differences in tree size, foliage area at a given height was normalised against the maximum

vertical foliage area and the height of each interval was normalised for total tree height. An exponential curve was fitted to the data (Kellomäki *et al.* 1980; Wang *et al.* 1990). The normalised foliage area distribution is expressed as

$$F = (p + qh) r^h \quad (2)$$

where F is the normalised foliage area at normalised height h , and p , q , and r are the parameters. The location of the maximum value of the function (F_m) or the position of maximum foliage area within a normalised crown was calculated from

$$F_m = -\frac{p}{q} - \frac{1}{\ln r} \quad (3)$$

Differences in the parameters p , q , and r and F_m were tested using ANOVA.

In this paper, the conventional $p \leq 0.05$ was not used as the criterion for significant differences because there were only 4 and 2 degrees of freedom for the subplots and main plot errors, respectively. We considered $p < 0.1$ a useful indicator of a treatment effect (Steel & Torrie 1980) but have included the actual probability of significant differences so that readers can make their own interpretation. All statistical analyses were done using the GenStat statistical package (GenStat 2000).

RESULTS

Details of Sample Trees

Mean heights of the 12 sample trees ranged from 4 to 6 m but treatment effects were not significant. However, these trees were highly variable in both diameter and mass (Table 1), there being significant interactions between planting material and understorey treatments

TABLE 1—Characteristics and biomass distribution for the sampled trees. Values shown are means with standard deviations in parentheses. The probabilities of significance are shown as T: tree types and U: understorey treatment.

	No-understorey		Lucerne		Significance
	Seedling	Clone	Seedling	Clone	
Tree height (m)	4.3 (± 0.08)	5.8 (± 0.12)	4.2 (± 0.19)	4.7 (± 0.90)	
Mean diameter, D (mm)	66 (± 2.6)	96 (± 3.4)	79 (± 3.1)	74 (± 5.2)	T = 0.047 U × T = 0.018
Total tree mass (kg)	28.4 (± 9.73)	51.7 (± 7.41)	15.1 (± 2.53)	16.1 (± 7.32)	U = 0.024 U × T = 0.036
Foliage mass (kg)	11.1 (± 5.36)	16.7 (± 1.94)	5.1 (± 1.45)	4.9 (± 2.18)	U = 0.023
Branch mass (kg)	11.5 (± 2.62)	19.7 (± 3.26)	4.8 (± 0.79)	5.4 (± 0.25)	U = 0.024 T = 0.018 U × T = 0.029
Stem wood mass (kg)	5.0 (± 0.61)	13.5 (± 2.19)	4.5 (± 0.63)	4.8 (± 2.23)	U = 0.032 T = 0.012 U × T = 0.016
Bark mass (kg)	0.9 (± 0.21)	1.8 (± 0.16)	0.7 (± 0.09)	1.1 (± 0.75)	

for *D* and total tree mass. The diameter of clonal trees in the no-understorey treatment was significantly larger than that for the seedling trees, but seedling and clonal trees had similar diameters in the lucerne understorey treatment. Mean total tree dry mass for the seedling and the clonal trees in the no-understorey was 28 kg and 52 kg, respectively. Both the seedling and the clonal trees weighed about 15 kg in the lucerne understorey treatment.

There was no significant difference ($p=0.176$) in foliage mass between the seedling and the clonal trees (Table 1), but trees in the lucerne understorey had 64% less foliage mass than trees in the no-understorey treatment. The seedling trees in the no-understorey treatment had 12 kg of branches and the clonal trees had 71% more branch mass than the seedling trees. Both the seedling and the clonal trees in the lucerne understorey treatment had about 5 kg of branch wood (interaction $p=0.029$). Similarly, the seedling trees in the no-understorey treatment had 5 kg of stem wood and the clonal trees had 170% more stem wood than the seedling trees. Both the seedling and the clonal trees in lucerne understorey treatment had about 5 kg of branch wood (interaction $p=0.016$). There was no significant difference between treatments in bark mass ($p=0.256$).

Proportional Allocation of Biomass

Total dry mass for the clonal trees was greater than that for the seedling trees but there was no significant difference in the proportion of foliage ($p=0.432$) due to higher variability in foliage mass for the seedling trees (Table 1) and proportions of branches ($p=0.859$) (Fig. 1). The seedling and the clonal trees in the no-understorey treatment allocated 18% and 26% of total biomass, respectively, to stem wood, but both types allocated 30% to stem

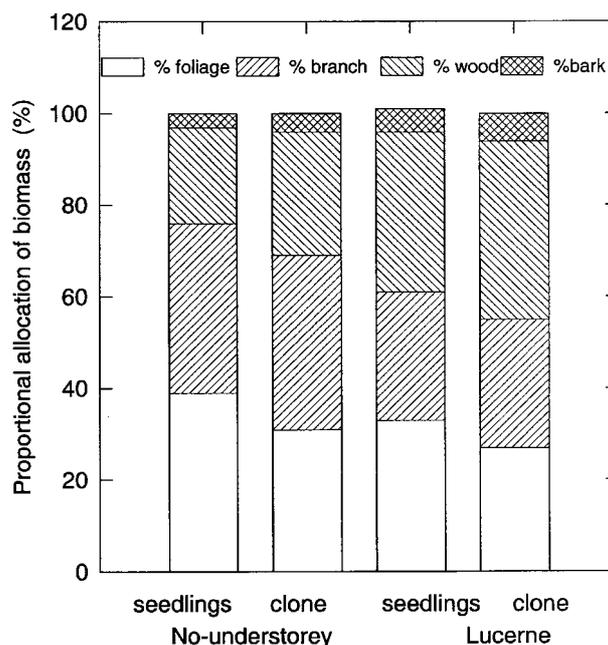


FIG 1—Proportional allocation of biomass to foliage, branch, stem wood, and stem bark in sample trees for each treatment.

wood in the lucerne understorey treatment (interaction $p=0.086$) (Fig. 1). Presence of the lucerne understorey also resulted in changes in the proportional allocation to branch wood ($p=0.004$). Trees in the lucerne understorey treatment had 33% of their total mass allocated to branch wood, compared to 40% in the no-understorey treatment (Fig. 1). The biomass proportion allocated to foliage was not significantly altered by the understorey treatment ($p=0.112$).

Crown Characters

The clonal trees had a higher crown shape ratio (C , ratio of tree height to crown width) than the seedling trees ($p=0.001$) (Fig. 2). Furthermore, all trees grown with lucerne understorey had relatively narrow crowns ($p=0.015$). The number of internodes longer than 600 mm was greater for clonal trees ($p=0.081$) than for seedling trees in the no-understorey treatment (Fig. 3). The effect of understorey treatment on the number of internodes in each class was not significant ($p=0.642$).

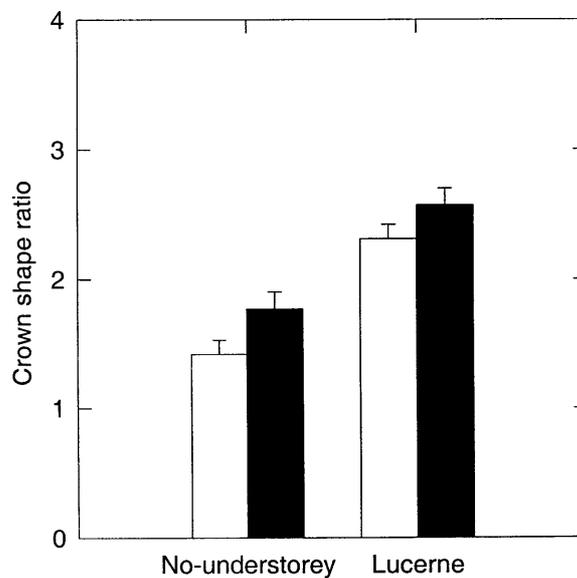


FIG. 2—Crown shape ratio (tree height/crown width) for seedling (open bars) and clonal (filled bars) trees grown with no understorey and lucerne. Standard deviations are shown above each bar.

Branching Structure

There was no difference in the number of branches per tree between planting material types ($p=0.312$) or between understorey treatments ($p=0.141$) (Table 2). In contrast to branch number, the clonal trees had a higher number of branch clusters ($p=0.041$) and twice the branch basal area (105%) of the seedling trees in the no-understorey treatment. Competition from the lucerne understorey reduced branch basal area by 67% in the clonal trees and by 34% in the seedling trees (interaction $p=0.035$), resulting in similar branch basal area for both types. Covariance analysis with D did not explain a significant

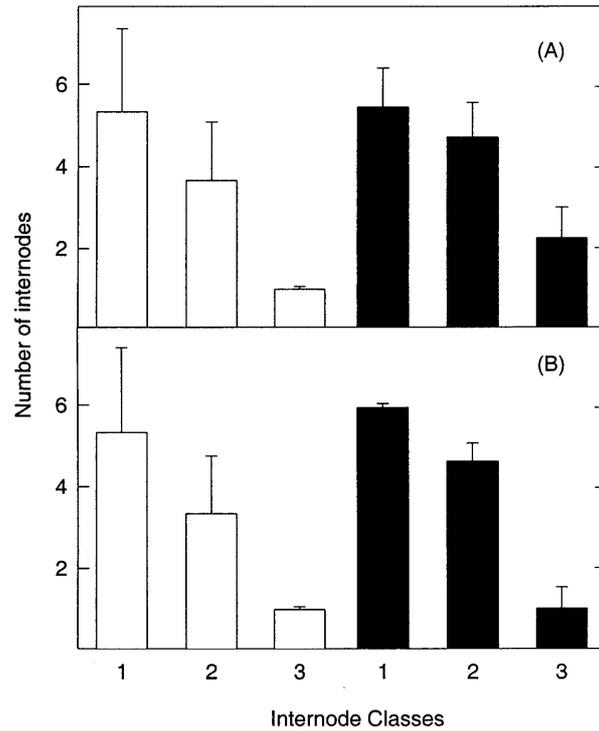


FIG. 3—Mean number of stem internodes for each internode class for seedling (open bars) and clonal (filled bars) trees grown (A) with no understorey and (B) with the lucerne understorey. Stem internode classes refer to Class 1, 0–300 mm; Class 2, 310–600 mm; and Class 3, > 600 mm. Standard deviations for each internode class are shown above each bar.

TABLE 2—Total number of first-order branches, number of branch clusters, and total branch basal area per tree. Values shown are means with standard deviation in parentheses. The probabilities of significance are shown as T: tree type and U: understorey treatment.

	No-understorey		Lucerne		Significance
	Seedling	Clone	Seedling	Clone	
Number of branches	71 (±5.9)	80 (±10.4)	60 (±7.5)	65 (±14.6)	
Number of branch clusters	11 (±1.0)	14 (±1.5)	10 (±1.2)	12 (±1.2)	T = 0.041
Total branch basal area per tree (m ² × 10 ⁴)	242 (±67.2)	498 (±101.9)	160 (±15.8)	166 (±76.3)	U = 0.018 T = 0.030 U × T = 0.035

proportion of the variation of branch basal area ($p=0.395$), indicating that these changes were not directly related to the differences in stem size.

Branch Diameter Class Distribution

The values of parameters in the Weibull function describing branch size distribution (Equation 1) are given in Table 3 and the data in Fig. 4 were constructed using the mean parameter values for each treatment. There were no significant differences between treatments in the parameters a ($p=0.171$) and b ($p=0.102$) (Table 3). There was a significant interaction ($p=0.044$) between planting materials and understorey treatment for values of the parameter c , which determines the skewness of the distribution. The seedling trees in the no-understorey treatment had a mean value of $c=0.84$, while the clonal trees had a mean value of $c=1.89$. The values for c were higher in trees with the lucerne understorey for both the seedling (3.84) and the clonal trees (2.50). Covariance analysis with D showed that

TABLE 3—Mean and standard deviation (in parentheses) for the parameters in Equation 1 by fitting to data for branch diameter classes distribution. The probabilities of significance are shown as T: tree type and U: understorey treatment.

Parameter	No-understorey		Lucerne		Significance
	Seedling	Clone	Seedling	Clone	
a	1.43 (± 0.736)	3.10 (± 0.983)	3.23 (± 1.98)	2.04 (± 0.964)	
b	0.69 (± 0.281)	0.28 (± 0.721)	-0.83 (± 1.967)	0.23 (± 1.179)	
c	0.84 (± 0.729)	1.89 (± 0.210)	3.84 (± 2.583)	2.50 (± 1.522)	U = 0.246 T = 0.754 U \times T = 0.044

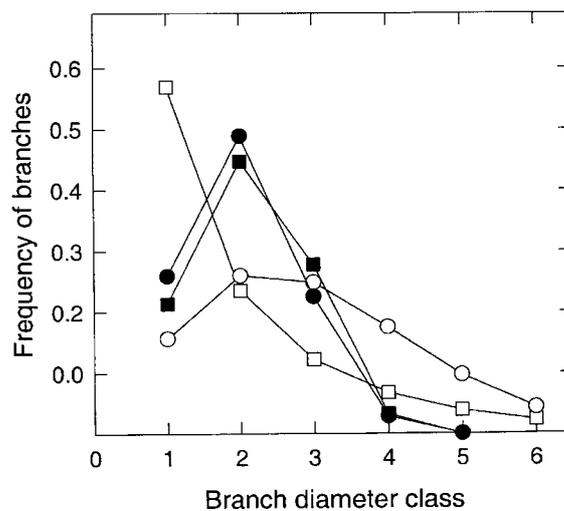


FIG. 4—Frequency of branches in each diameter class for (□) seedling trees with no understorey, (○) clonal trees with no understorey, (■) seedling trees with lucerne understorey and (●) clonal trees with lucerne understorey. Branch diameter classes refer to Class 1, 0–10 mm; Class 2, 11–20 mm; Class 3, 21–30 mm; Class 4, 31–40 mm; Class 5, 41–50 mm; and Class 6, > 51 mm. The plots are constructed using the mean parameter values of the Weibull function in Table 3.

diameter did not explain a significant proportion of the variation in parameters a , b , and c ($p=0.409$, $p=0.174$, and $p=0.144$, respectively), indicating that these were poorly related to the stem size of the trees.

Branch Basal Area and Foliage Area Relationship

The regressions of branch basal area against foliage area in the no-understorey treatment indicated that there was no significant difference ($p=0.269$) between treatments in the intercept (Fig. 5 and Table 4), but there was a significant interaction between understorey and planting material type ($p=0.005$) for the slope. The slope coefficient for the

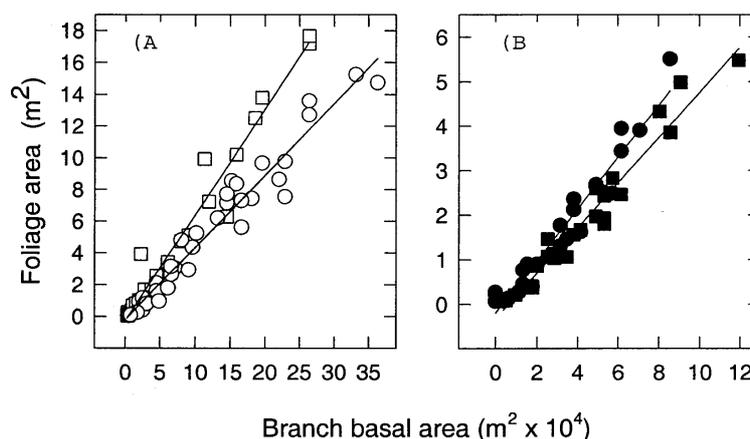


FIG. 5—The relationship between branch basal area and foliage area for (A) the no understorey and (B) lucerne understorey treatments. The symbols are the same as those in Fig. 4 and the lines are drawn from linear regression. Estimated parameters are given in Table 5 and data points include all three sample trees in each treatment.

TABLE 4—Mean parameter and standard errors (in parentheses) of the regressions for branch basal area against foliage area and branch basal area against the natural logarithm of branch length. The probabilities of significance refer to: (T) tree type and (U) understorey treatment.

	No-understorey		Lucerne		Significance (p)
	Seedlings	Clone	Seedlings	Clone	
Branch basal area and foliage area relationship					
intercept (m^2)	-0.29 (± 0.246)	-0.44 (± 0.557)	-0.31 (± 0.095)	-0.14 (± 0.074)	
slope ($m^2 m^{-2}$)	0.67 (± 0.059)	0.48 (± 0.049)	0.51 (± 0.016)	0.56 (± 0.057)	U = 0.161 T = 0.041 U \times T = 0.005
Branch basal area and branch length relationship					
intercept (m)	0.71 (± 0.035)	0.67 (± 0.058)	0.55 (± 0.040)	0.64 (± 0.039)	U = 0.008 T = 0.381 U \times T = 0.029
slope ($m m^{-2}$)	0.99 (± 0.058)	1.14 (± 0.059)	0.88 (± 0.066)	0.97 (± 0.074)	U = 0.011 T < 0.001

clonal trees did not differ between understorey treatments. However, for the seedling trees, the value of the coefficient was higher in the no-understorey treatment and lower in the lucerne understorey treatment than the equivalent values for clonal trees.

Branch Basal Area and Branch Length

There was a significant interaction ($p=0.029$) between planting material type and understorey treatment for the intercept of the relationship between branch basal area and the natural logarithm of branch length (Fig. 6 and Table 4). The seedlings and the clonal trees in the no-understorey treatment had a similar intercept but the seedling trees had lower intercept in the lucerne understorey treatment than that for the clonal trees. Also, the seedling trees had a lower ($p<0.001$) slope, than that for the clonal trees, and the lucerne understorey resulted in a lower slope ($p=0.011$) for both types.

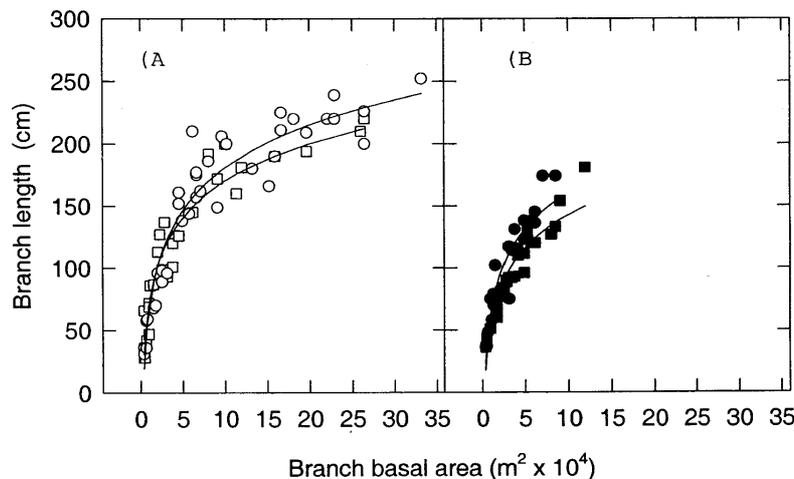


FIG. 6—The relationship between branch basal area and branch length for (A) the no understorey and (B) lucerne understorey treatment. The symbols are the same as those in Fig. 4 and the lines are drawn from non-linear regression. Estimated parameters are given in Table 5 and data points include all three sample trees in each treatment.

Vertical Distribution of Foliage Area

The normalised vertical foliage area distribution for all the treatments and the mean distribution curve (Equation 2) fitted for the data are illustrated in Fig. 7. The r^2 values for individual trees ranged from 0.57 to 0.75 for all treatments, but the r^2 value was not better for a particular treatment compared with any other. Analysis of variance for the three coefficients (p , q , and r in Equation 3) showed no significant differences between planting materials ($p=0.442$, $p=0.411$, and $p=0.452$ respectively) or between understorey treatments ($p=0.153$, $p=0.211$, and $p=0.130$ respectively) (Table 5). However, values for the parameter F_m indicated that the location of maximum foliage area within normalised tree crowns was higher for trees growing with lucerne understorey than for the no-understorey trees ($p=0.066$).

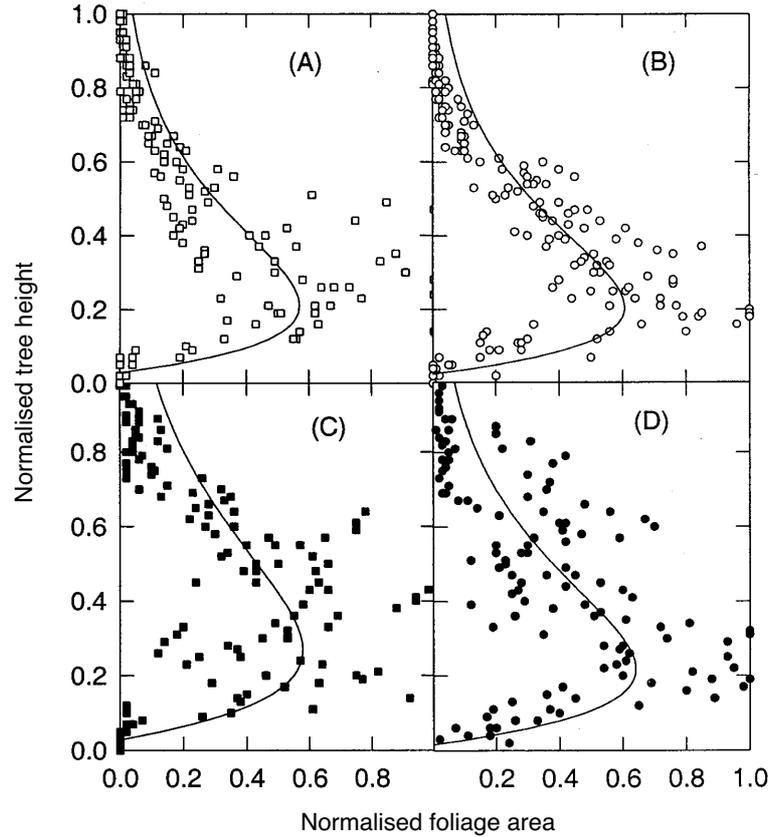


FIG. 7—Vertical distribution of foliage area in relation to relative height of the crown for (A) seedling and (B) clonal trees with no understorey, (C) seedling and (D) clonal trees with lucerne understorey. The lines were fitted using mean values of parameters from Equation 2. Data points include all three sample trees in each treatment. Estimated values of parameters for the predicted distribution are given in Table 5.

TABLE 5—Mean and standard errors (in parentheses) for the parameters in Equation 2. Non-significant differences at $p < 0.100$ are noted as ns.

Parameter	No understorey		Lucerne		Significance
	Seedlings	Clone	Seedlings	Clone	
p	-0.3 (± 0.22)	-0.3 (± 0.03)	-0.2 (± 0.03)	-0.2 (± 0.10)	ns
q	10.6 (± 2.91)	10.5 (± 0.86)	7.4 (± 0.87)	9.8 (± 3.32)	ns
r	0.004 (± 0.0031)	0.004 (± 0.0012)	0.02 (± 0.003)	0.01 (± 0.011)	ns
F_m	0.21 (± 0.211)	0.21 (± 0.009)	0.27 (± 0.016)	0.22 (± 0.009)	U=0.066

DISCUSSION

The growth rate of trees in the no-understorey treatment was comparable with other studies in *P. radiata* from high-quality sites (Beets & Pollock 1987). Even though diameter at breast height and total tree mass for the clonal trees in the no-understorey treatment were larger than values for the seedling trees, the seedling trees had similar foliage mass and lower branch mass. Beets & Pollock (1987) observed that allocation of dry matter production to the various components in *P. radiata* was largely related to age. With increasing age, allocation of biomass to foliage and fine roots decreased, while allocation to branches, stem bark, and stem wood increased. Therefore our differences in biomass allocation between the clonal trees and seedling trees (Fig. 1) may be due to differences in physiological age or maturation state of the clonal trees. The clonal trees were 10 years old at the time of sampling, compared to 5 years for the seedling trees

Branch basal area per tree was greater for the clonal trees than that for the seedlings (Table 2) and covariance analysis with tree diameter, D , did not explain a significant amount of the variation in total branch basal area ($p=0.395$). This indicated that higher branch basal area in the clonal trees was not related solely to the larger stem size. The relationship between branch basal area and foliage area (Fig. 5) indicated that the area of foliage for a given branch basal area was less for clonal trees than that for seedling trees. Also, for a given branch basal area, branch length was longer for clonal trees than that for the seedling trees (Fig. 6). The length of branch at the base with no foliage present was less than 50 mm for all the treatments (data not shown). Therefore, for a given branch size, there was less foliage area per unit branch length on the clonal trees than for the seedling trees. The significant interaction between planting material and understorey treatment for the parameter c in the Weibull function (Table 3) indicated that the distribution patterns of branch diameters in the no-understorey treatment were different for the seedling and the clonal trees. The value of $c = 0.84$ in the seedling trees indicated that there was a negative exponential pattern of branch diameter distribution, with a large number of small branches. In contrast, the value of $c = 1.89$ for clonal trees indicated that the distribution was skewed with more branches in the intermediate size classes. Covariance analysis of c with tree diameter, D , showed that the branch diameter distribution differences between treatments were not strongly related to size differences between the trees. Also, for the clonal trees, the branches were distributed on a larger number of branch clusters (Table 2). There were more internodes longer than 600 mm on the clonal trees (Fig. 3).

In contrast to the clonal trees, the internode length of the seedling trees was shorter, there were fewer branch clusters, and a larger number of small branches (Table 2, Fig. 3 and 4). However, there was no significant difference in the vertical distribution of foliage area between planting material types. The difference between the seedling and the clonal trees in the distribution of branch basal area within the crown (Fig. 4), foliage distribution within the branches (Fig. 5), and the crown shape ratio (Fig. 2) resulted in differences in the horizontal distribution of foliage area in the tree crown.

The sample trees were selected from an experiment based on a split-plot design with understorey treatment as the main plot. Therefore, within the plots the environmental factors apart from solar radiation, such as water and nutrients, were expected to be similar for all trees. The amount of radiation intercepted by an individual tree is determined mainly by its crown architecture, particularly by the foliage distribution (Whitehead *et al.* 1990).

Knowles & West (1986) observed that competition for solar radiation within the tree could occur in *P. radiata* even at an early stage of growth. Therefore the faster growth rate and higher value of E (Bandara 1997) of the clonal trees compared with the seedling trees was likely due to less self-shading of foliage resulting from differences in branching structure. The higher crown shape ratio in the clonal trees (Fig. 2) also resulted in less self-shading in the clonal trees than the seedling trees, as narrow crowns intercept more radiation than wider crowns of the same size (Kuuluvainen & Pukkala 1987). Higher values of E in the clonal trees (Bandara 1997) are unlikely to be due to a higher light use efficiency, as studies at the site (Bandara 1997) and elsewhere (Linder 1985; Grace *et al.* 1987) have shown that light use efficiency remains constant when trees are supplied with adequate water and nutrients.

Lucerne understorey resulted in reduced tree growth compared to the no-understorey treatment (Mead *et al.* 1993; Peri *et al.* 2002) (Table 1). Foliage and branch mass were reduced proportionately more than the reduction in total above-ground mass and this was more pronounced in the clonal trees than in the seedling trees (Table 1). When trees were grown with the lucerne understorey, the competition for water and nutrients (Mead & Mansur 1993; Yunusa *et al.* 1995b) resulted in substantially less foliage and branch wood. The presence of the understorey resulted in marked soil water deficit in the later part of the growing season (reported by Yunusa *et al.* 1995b). Thus, changes in the crown characteristics of trees growing in the understorey treatment compared with those in the no-understorey treatment were most likely the result of water deficit and to a lesser degree nutrient stress at this site (Mead & Mansur 1993; Yunusa *et al.* 1995b). This conclusion is consistent with other studies at similar dryland sites for young (Watt, Whitehead, Richardson, Mason, & Leckie 2003) and old (Richardson *et al.* 2002) *P. radiata* stands.

The sample trees selected from the lucerne understorey treatment had the same number of branches, number of branch clusters, and stem internode classes as the trees in the no-understorey treatment (Table 2 and Fig. 3). This indicates that the developmental growth phase of the trees was not affected by the water deficit due to the presence of the understorey. Bollmann *et al.* (1986) showed that water stress was unlikely to affect needle initiation in the developmental phase. However, the presence of the understorey had an impact on the growth phase of the trees, resulting in lower foliage and branch stem and bark mass than trees in the no-understorey treatment (Table 1). There were also changes to biomass allocation within the crown, with trees in the lucerne understorey treatment allocating less biomass to branches. Furthermore, the distribution of branch diameters in the seedling trees became more skewed, resulting in more medium-size branches. The lucerne understorey also resulted in a low branch basal area for trees from both planting material types, with the reduction more marked in the clonal trees than in the seedling trees (Table 2). This supports findings by Watt, Whitehead, Mason, Richardson, & Kimberley (2003) in young *P. radiata* trees that the marked occurrence of drought due to the presence of understorey vegetation resulted in increased allocation of dry matter to stems at the expense of foliage and branches.

In comparison to the no-understorey treatment, the lucerne understorey resulted in less foliage area per unit branch basal area (Fig. 5) and the changes were more marked in the seedling than the clonal trees. This reduction in foliage area, attributed to seasonal water deficits in trees with the lucerne understorey (Yunusa *et al.* 1995b), was consistent with

those reported by Myers (1988). The values of C (Fig. 2) and F_m (Table 5) were higher for the trees growing with the lucerne understorey, resulting in an increase in foliage efficiency (Bandara 1997), probably due to differences in light interception.

Interactions between planting material type and understorey were observed for foliage area per unit branch basal area, branch basal area and branch length relationship, total branch basal area per tree, the pattern of branch diameter distribution, and total biomass allocated to stem wood proportion. Foliage area per unit branch basal area and branch length per unit branch basal area were reduced more in the seedling than in the clonal trees in the lucerne understorey treatment. Branch basal area per tree was reduced more in the clonal than in the seedling trees, but branch diameter distribution pattern was changed more in the seedling trees. So, the presence of the lucerne understorey reduced all these characters but the degree of change was different between planting materials. This indicates that the growth phase of trees, during which time the allocation of biomass to components occurs, is modified by environmental effects. For example, a competitive understorey, irrespective of whether seedlings or clonal materials are present, can lead to smaller branches. It has been observed that higher growth rates of *P. radiata* on fertile farm sites often produce larger branches, thus reducing the quality of wood produced (Knowles 1992; Maclaren 1993), and the effects are greater at wide tree spacing where there is little inter-tree competition. Managers often manipulate tree spacing to control the rate of growth of individual trees, crown development, branch size, and hence wood quality (Maclaren 1993). Our study shows that branch size distribution can be manipulated by the use of an appropriate understorey, rather than by maintaining a high number of trees per unit area to ensure small branch sizes.

Pinus radiata growth is determined principally by the availability of water and nutrients (Myers & Talsma 1992; Mead & Mansur 1993; Yunusa *et al.* 1995b), by intercepted radiation (Grace *et al.* 1987; Yunusa *et al.* 1995b), and by genetic factors (Burdon *et al.* 1997). Allocation of biomass into tree components is affected by genotype (Madgwick 1983), by water and nutrient availability (Snowdon & Benson 1992; Beets & Whitehead 1996), and by tree age (Beets & Pollock 1987). This study shows that the proportion of biomass allocated to wood and branches differs with planting material type and the presence or absence of understorey vegetation. Therefore, managers may be able to reduce the allocation of biomass to branches thus increasing the proportion of the stem wood. This change in allocation could partly offset the loss in stem growth in agroforestry systems due to understorey competition for water and nutrients. The study also illustrates the importance of evaluating agroforestry systems in detail, taking into account the effects of understorey on tree form and growth habits as well as productivity.

In conclusion, this study showed that tree characteristics determined during the developmental phase, such as number of branches and branch clusters, were different for clonal and seedling trees but not for the presence or absence of understorey vegetation. However, characteristics determined during the growth phase were altered by both planting material type and understorey treatment through differences in the proportional allocation of biomass to foliage, branches, and stem wood. Such changes can affect wood quality, since branch size is a strong determinant of timber quality. Forest managers therefore have two ways of regulating tree growth patterns without altering tree spacing — i.e., selection of improved planting materials (e.g., trees derived from physiologically aged cuttings or

tissue-cultured clones) and managing the understorey so that competition for water and nutrients results in higher allocation of biomass to stem wood without a reduction in productivity.

Analysis of the distribution of biomass within the crown has shown that, with similar proportions of foliage or branches in trees, there can be differences in biomass distribution within the crown. This can result in differences in radiation interception resulting in higher foliage efficiency. The value of foliage efficiency for the seedling trees was 25% lower than that for the clonal trees and in the lucerne treatment foliage efficiency was increased in the seedling trees by 43% and the clonal trees by 39% (Bandara 1997). These differences are likely to have important implications for pruning strategies in *P. radiata*. The removal of branches during pruning may have different effects on growth losses leading to the need for different pruning strategies for trees growing in an agroforestry system compared to those for trees growing in forest plantations (Bandara *et al.* 1999).

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ECONOMIC EVALUATION OF IMPLEMENTING IMPROVED STEM SCANNING SYSTEMS ON MECHANICAL HARVESTERS/PROCESSORS

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ABSTRACT

Use of mechanical harvesting/processing systems in timber harvesting is increasing worldwide, with advantages in terms of increasing productivity and safety. However, despite these systems giving operators access to advanced computer and measuring systems, their ability to extract the maximum value from a tree is, on average, less than motor manual log bucking systems. The productivity, cost, and value recovery of several simulated procedures for scanning and bucking *Pseudotsuga menziesii* (Mirb.) Franco (Douglas fir) and *Pinus ponderosa* Lawson & C. Lawson (ponderosa pine) trees were evaluated from a log seller's perspective. The procedures evaluated were (a) conventional operating where quality changes and bucking decisions were made by the machine operator, (b) an automatic full scan of the stem prior to optimisation and bucking, and (c) partial scanning where a portion of the stem was scanned and then qualities and dimensions were forecast before the optimal bucking took place. After subtracting costs, the net value improvement for the automated scanning procedures over the conventional procedure ranged from -7% to 8%. The best net value improvement for both species was obtained using the procedure that fully scans the stem prior to bucking. Breakeven capital investment costs for new scanning, forecasting, and optimisation equipment ranged between zero and US\$2,120,000 depending on tree species, markets, scanning speed, volume scaling rules, and scanning procedure.

Keywords: value recovery; mechanical harvesters/processors; productivity; cost; scanning.

INTRODUCTION

The adoption of mechanical timber harvesting systems is increasing worldwide. These systems allow stems to be delimited, bucked, sorted, and sometimes felled by a single machine. In Scandinavia, almost 90% of logging is carried out using mechanical harvesting systems (Nordlund 1996). Within the last 10 years, the number of harvesters and processors sold in eastern Canada increased from 200 to 900 (Godin 2000). In Australia, by the late 1980s mechanisation had almost eliminated motor-manual felling in *Pinus radiata* D. Don (radiata pine) thinning operations (Raymond 1988). Factors causing this shift from the traditional motor manual harvesting systems to mechanical harvesting systems include the