Aboveground biomass partitioning and crown architecture of *Eucalyptus nitens* following green pruning

E.A. Pinkard and C.L. Beadle

Abstract: The effects of green pruning on aboveground biomass partitioning and crown architecture were explored in a 3-year-old *Eucalyptus nitens* (Deane and Maiden) Maiden plantation. Responses were measured in five height zones and three foliage age classes over a 20-month period following removal of 0, 50, or 70% of the green crown length. Development of foliage in the upper crowns of 50%-pruned trees was faster and total leaf area at the end of the experiment was greater than in unpruned trees. Leaf area development of 70%-pruned trees was similar to that of unpruned trees. Larger apical leaves, with a lower specific leaf area (SLA), developed following 50% pruning. However, 70% pruning resulted in smaller leaves, and SLA increased in some crown positions. Pruning reduced branch diameter and length in the upper crowns. However, branches of 50%-pruned trees had an increased ratio of foliage to wood dry mass. These responses to green pruning may have increased the carbon-fixing capacity and the efficiency of carbon utilisation of the remaining crown. Following 50% pruning, responses were sufficient to maintain stem dry mass increment at a level similar to that of unpruned trees. However, following 70% pruning, stem and branch dry mass increment was reduced.

Résumé : Les effets de l'élagage des branches vivantes sur la répartition de la biomasse aérienne et l'architecture de la cime ont été étudiés dans une plantation d'*Eucalyptus nitens* (Deane and Maiden) Maiden âgée de 3 ans. Les réactions ont été mesurées dans cinq zones de hauteur et trois classes d'âge du feuillage sur une période de 20 mois suite à l'enlèvement de 0, 50 ou 70% de la longueur de la cime vivante. Le développement du feuillage dans la partie supérieure de la cime des arbres élagués à 50% était plus rapide et la surface foliaire totale à la fin de l'expérience était plus grande que chez les arbres non élagués. Le développement de la surface foliaire n'était pas différent chez les arbres élagués à 70% et les arbres non élagués. De plus grandes feuilles apicales, avec une plus faible surface foliaire spécifique, se sont développées après un élagage à 50%. Cependant, l'élagage à 70% a entraîné la production de feuilles plus petites et la surface foliaire spécifique a augmenté à certains endroits dans la cime. L'élagage a réduit la longueur et le diamètre des branches dans la partie supérieure de la cime. Cependant, les branches des arbres élagués à 50% avaient un plus fort ratio de la masse sèche des feuilles sur la masse sèche de matière ligneuse. Ces réactions à l'élagage de branches vivantes pourraient avoir augmenté la capacité de fixation du carbone ainsi que l'efficacité de l'utilisation du carbone dans la partie restante de la cime. Chez les arbres élagués à 50%, cela était suffisant pour maintenir l'accroissement en masse sèche de la tige au même niveau que chez les arbres non élagués. Par contre, après un élagage à 70%, l'accroissement en masse sèche des branches et de la tige était réduit.

[Traduit par la Rédaction]

Introduction

Green pruning is a silvicultural treatment employed to increase production of knot-free timber, particularly in species that do not readily shed dead branches (Shepherd 1986). It involves the removal of live branches to a predetermined height above ground. Hence, there is the potential to reduce whole-plant carbon fixation, and the increase in the ratio of zones of carbon utilisation to zones of carbon assimilation may result in considerable reductions in growth. Both short- and long-term loss of height and diameter growth have been reported in many tree species following pruning (e.g., Sutton and Crowe 1975; Karani 1978; Bredenkamp et al. 1980; Majid and Paudyal 1992).

Numerous studies have demonstrated that trees compensate to some extent for loss of leaf area resulting from pruning or browsing-induced defoliation (Helms 1964; Bassman and Dickmann 1982, 1985; Hoogesteger and Karlsson 1992; Reich et al. 1993). However, there is a level of defoliation above which complete compensation cannot occur. This is the level at which growth is first affected, and it varies widely between species (e.g., Fujimori and Waseda 1972;

Received November 10, 1997. Accepted July 5, 1998.

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Dakin 1982; Heichel and Turner 1983; Bassman and Dickmann 1985; Majid and Paudyal 1992). When developing management prescriptions for silvicultural treatments such as pruning, it is critical that responses to loss of leaf area and the potential impact of those responses on growth are understood.

A number of responses are reported following partial defoliation. All have the potential to increase the carbon-fixing capacity of the remaining crown and reduce the impact of partial defoliation on growth and yield of harvestable plant parts. For example, increases in the light-saturated rate of net CO_2 assimilation have been observed following partial defoliation of plants of many life forms (Helms 1964; Heichel and Turner 1983; von Caemmerer and Farquhar 1984; Senock et al. 1991; Ovaska et al. 1993; Reich et al. 1993). The magnitude of this response often has been found to increase with the severity of defoliation (Heichel and Turner 1983; Reich et al. 1993). Changes in patterns of biomass partitioning also have been measured. For example, increased leaf area development (Heichel and Turner 1983; Coughenour et al. 1990), delayed leaf senescence (Trumble et al. 1993), and changes in distribution of foliage in the crown have been reported (Coughenour et al. 1990). In addition, leaves may increase in size, and the ratio of area to weight (specific leaf area) may change (Hodgkinson 1974; Alderfer and Eagles 1976; von Caemmerer and Farquhar 1984).

Eucalyptus nitens (Deane and Maiden) Maiden is an important plantation species in southeastern Australia. It retains dead branches and pruning is essential for the production of sawlogs and veneer from the species. Sawlog plantations generally are established with a high initial stocking density (>1000 stems·ha^{-1}), and approximately one third of stems are selected for pruning (Gerrand et al. 1997). The challenge is to develop a pruning regime that will maximise production of knot-free timber without reducing growth. An earlier experiment (Pinkard and Beadle 1998*a*) demonstrated that height and diameter growth of *E. nitens* was not affected by removal of 50% of the length of green crown when pruning was done at the time of canopy closure. However, removal of 70% of the crown length reduced diameter and, to a lesser extent, height growth. Light-saturated rates of CO_2 assimilation increased following pruning, irrespective of foliage age or crown position (Pinkard et al. 1998). The magnitude and duration of the response increased with pruning severity. It was estimated that the response increased net biomass production of 50%-pruned and 70%-pruned trees by 20 and 25%, respectively (Pinkard 1997), which partly explained growth responses observed in the field.

This paper describes an experiment that investigated the impact of green pruning on patterns of aboveground biomass partitioning and crown architecture. Both harvested and standing trees were used to measure responses over a 20-month period. The objectives were to explore the impact of different severities of pruning on leaf and branch development and leaf morphology and to determine changes in partitioning of biomass between aboveground components following pruning. In addition, the impact of pruning on crown area, leaf area density, and branching pattern was explored.

Materials and methods

Site

The experiment was conducted in a 3-year-old *E. nitens* plantation in southern Tasmania (43°28′S, 147°01′E). The plantation was at an altitude of 100 m above sea level. It was established on an ex-pasture site with a podsolic soil type derived from Triassic sandstone and consisting of a sandy clay A horizon of approximately 60 cm depth overlying a clay B horizon. The site was planted in September 1990 using seedling stock (a Mount Toorongo seedlot of the Upper Toorongo provenance) and fertilised with 200 and 120 kg·ha^{-1} of elemental nitrogen and phosphorus, respectively. The phosphorus was applied just before planting and the nitrogen in two instalments of 100 kg·ha^{-1} at the beginning of the first and second growing seasons. The stocking density was 1430 stems·ha^{-1}, with a spacing within and between rows of 2 and 3.5 m, respectively.

A weather station was located 30 m from the experiment. Annual averages of weekly readings of maximum and minimum temperatures in a Stephenson screen were 19.7 and 4.0°C, respectively (1991–1995), and mean annual rainfall was 957 mm.

At the start of the experiment, in January 1994, mean tree height and diameter at 1.3 m above ground were 9.5 m and 11.6 cm, respectively. Growth rates were close to the maximum recorded for the species in Australian plantations. The ratio of total tree height to the length of green crown was 0.95. The plantation was verging on canopy closure, with branches of adjacent trees almost touching.

Treatments and experimental design

Experimental work was undertaken in 24 nine-tree plots that were three trees long by three trees wide. Pruning treatments were randomly allocated to the central tree in these plots. The remaining trees in each plot acted as an unpruned buffer to simulate a selective pruning regime. In January 1994, trees were pruned to remove 0, 50, or 70% of the length of green crown. Only the lower crown was removed. Treatment trees in 15 of the plots were randomly selected for harvesting. In addition, nine adjacent plots were selected for measurement of responses over time.

Tree crowns were divided into four height zones. These zones corresponded to 0–50, 50–70, 70–90, and 90–100% of crown length at the time of pruning, and their heights were fixed with respect to the ground. Thus, as trees grew, it became necessary to include an additional height zone (>100%). Within the height zones, foliage was classed as old (>2 years of age), mature (<2 years old but fully expanded), or apical (expanding). It was relatively easy to determine foliage age classes, as leaf size changed in a consistent pattern throughout the growing season. The boundaries of these zones were constantly reassessed to allow for growth of new leaves, leaf aging, and leaf senescence.

The experimental design can be described by a two-strata model in which pruning treatments were allocated between trees and height zones and foliage age classes were allocated within trees (McPherson 1990). The overall model structure is described by

$$[1] \qquad Y_{i,j,k} = M + A_i + [B_{i,j} + (C_{i,j,k})]$$

where $Y_{i,j,k}$ is the response of the *k*th foliage age class at the *j*th height zone of the *i*th tree, *M* is the overall mean, *A* is the plot stratum (or between-tree effect), *B* is the split plot stratum (or within-tree effect), and *C* is the split-split plot. The particular treatment allocations are given by

$$A_i = P_m + e_{i,m}$$

$$B_{i,j} = H_n + (PH)_{m,p} + e_{i,m,n}$$

$$C_{i,j,k} = F_p + (HF)_{m,p} + (FPH)_{m,n,p} + e_{i,m,n,p}$$

where P_m is the mth pruning treatment, H_n is the nth height zone, F_p is the pth foliage age class, and e is the residual error at the particular stratum level.

Sampling

In August 1994, 6 months after pruning, two trees per treatment were harvested. Total tree height was measured, and the crowns were divided into the five height zones. All branches in each height zone were removed flush with the trunk using pruning shears, wrapped in plastic, and stored at 3°C until processed (maximum of 5 days). A second harvest was conducted in August 1995, 18 months after pruning. This proceeded as outlined above, except that three trees per treatment were harvested, and a subsample of five branches per height zone per tree was collected for processing. Each subsample was based on the distribution of branch size in that zone.

Branches were divided into foliage age classes, and total branch length was measured. Branch diameters were measured to the nearest 0.5 mm, 4 cm from the branch base. Leaves were then removed, keeping the foliage age classes separate for each branch. Leaves and branches were dried at 40°C for 72 h (to constant weight) and weighed. A 10% subsample was then dried at 80°C for 48 h, and the ratio of 80°C to 40°C weights was used to calculate the dry mass of remaining material (Gregoire et al. 1995). Following leaf removal, 10 leaves per foliage age class were randomly collected for analysis of specific leaf area (SLA, the ratio of single-sided leaf area to leaf dry mass) and mean leaf size. Areas of fresh leaves were measured using an area meter (Delta-T Devices Ltd, Cambridge, U.K.), and mass was determined after drying at 80°C for 48 h. The SLA's were used to estimate leaf area from dry mass.

Three standing trees of similar size per treatment were chosen for detailed study of crown architecture and patterns of carbon allocation over time. They are referred to in the following as “standing trees”. The crowns of these trees were divided into the five height zones. Branch diameters were measured 4 cm from the branch junction with the stem 0, 3, 6, 9, 13, 18, and 20 months after pruning. Total tree height and stem diameter at 1.3 m above ground level were measured immediately before pruning and 13 and 20 months after pruning. The angle from vertical of all branches on each tree was measured 13 months after pruning. Mean crown radius at the base of each height zone at that time was calculated from the average of four measurements (to the north, south, east, and west).

Data analysis

Harvested trees

The proportions of apical, mature, and old foliage per branch were calculated. Total branch biomass (foliage plus wood) and the ratio of foliage to wood dry mass per branch were calculated in each height zone. Differences between treatments were determined using the analysis of variance procedure GLM in SAS (SAS Institute Inc. 1990). Analysis of variance also was used to explore differences between treatments in leaf size and SLA.

Branch diameters were converted to cross-sectional area (CSA) assuming that branches were completely round. Allometric relationships were developed between CSA and leaf area per branch, CSA and branch length, and CSA and branch dry mass using group linear regression analysis (McPherson 1990; McPherson and Thompson 1993). The groups included in the analyses were pruning treatment, height zone, and harvest, and the model structure was as described above. The GLM procedure in SAS was used for the analyses. The ratio of leaf area to CSA was calculated for each branch.

Standing trees

The regression equations derived for the harvested trees were used to estimate leaf area per branch, branch dry mass, and branch length of the standing trees. Parameters derived from the first harvest were used to estimate values 3, 6, and 9 months after pruning, and parameters for unpruned trees from this harvest were used to estimate values immediately prior to pruning. Parameters derived from the second harvest were used to estimate values 13, 18, and 20 months after treatment.

Leaf area was summed for each height zone. Branch increment for the period of the experiment was calculated. Projected crown area at the base of each height zone was calculated from crown radius. The stem within each height zone of the nine trees was divided into 10-cm lengths, and crown volume was calculated for each section and then summed for the height zone. Leaf area density (LAD, square metres of leaf area per cubic metre of crown volume) was then calculated. Stem volume of standing trees was estimated using the Opie volume equation (Opie 1976). Stem dry mass was calculated from this assuming a basic density of 400 kg·m^{-3} (Waugh 1996). Relative growth rate (R, kilograms per month), unit leaf rate (E, square metres per kilogram per month), and leaf area ratio (F, square metres per kilogram) were calculated using the following equations (Beadle 1985):

$$[2] \qquad R = \frac{\ln W_2 - \ln W}{t_2 - t_1}$$

$$[3] \qquad E = \frac{(W_2 - W_1)(\ln s_2 - \ln s_1)}{(s_2 - s_1)(t_2 - t_1)}$$

$$[4] \qquad F = \frac{s}{W}$$

where W is dry mass (kilograms) at time t and s is leaf area (square metres).

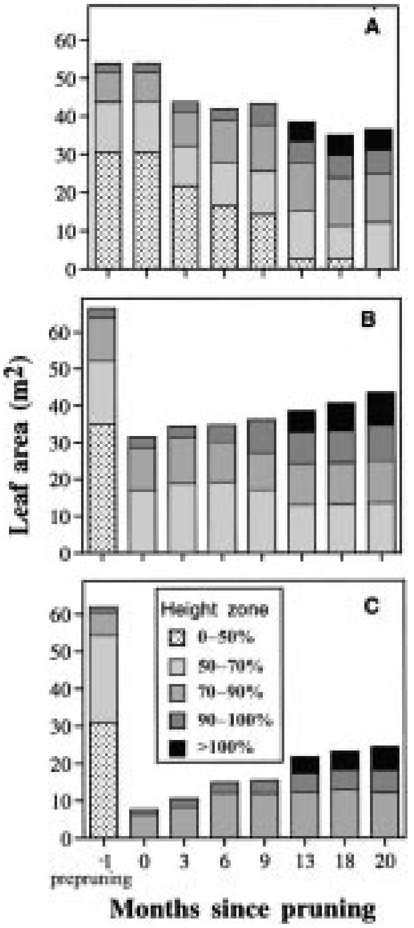
Analysis of variance was used to determine differences between treatments in leaf area per height zone, branch increment, branch angle, projected crown area, LAD, R, E, F, and dry mass. The GLM procedure in SAS was used.

Results

Leaf development

The 0, 50%-pruning, and 70%-pruning treatments were equivalent to removal of 0, 55, and 88% of leaf area, respectively. In unpruned trees, total leaf area gradually decreased with time from 53 m^2 before pruning to 38 m^2 20 months later (Fig. 1A). This was due to a reduction of leaf area in the 0–50% and, to a lesser extent, 50–70% height zones. There were slight increases in total leaf area coinciding with the two spring seasons encompassed by the experiment (9 and 20 months). Total leaf area of 50%-pruned trees increased from 31 m^2 immediately after pruning to 43 m^2 at the end of the experiment (Fig. 1B). After 13 months, unpruned and 50%-pruned trees had a similar total leaf area, and by the end of the experiment, 50%-pruned trees had greater leaf area than did unpruned trees. This was a result of greater leaf area development in the 90–100 and >100% height zones, and less loss of foliage in the 50–70% height zone, of 50%-pruned trees than unpruned trees. In 70%-pruned trees, total leaf area increased from 8 m^2 immediately after pruning to 24 m^2 20 months later (Fig. 1C). At the end of the experiment, leaf area in each height zone of

Fig. 1. Mean total leaf area per height zone of (A) unpruned, (B) 50%-pruned, and (C) 70%-pruned standing *E. nitens* trees growing in southern Tasmania estimated over the 20 months of the experiment. Height zones are based on height at the time of pruning. The >100% height zone was added 10 months after pruning.



these trees was similar to that in the corresponding zones of unpruned trees.

Six months into the experiment, pruned trees had a greater proportion of apical (expanding) foliage per branch in the 90–100 and >100% height zones than did unpruned trees (Fig. 2). Eighteen months after pruning, the percentage of old foliage per branch in the 50–70% height zone of 50%-pruned trees was approximately half that of unpruned trees (Figs. 2D and 2E).

The size of leaves prior to pruning was not determined. However, apical leaves were consistently larger throughout the crowns of 50%-pruned trees 6 months after pruning (Fig. 3A), suggesting greater leaf expansion. In contrast, apical leaves of 70%-pruned trees were smaller in the >100% height zone (Fig. 3A). The 70%-pruned trees also had smaller mature leaves throughout the crown (Fig. 3B). Eighteen months after pruning, old leaves of 50%-pruned trees were 30% smaller than those of unpruned tees (Fig. 3F).

SLA was relatively constant throughout the crowns of unpruned trees 6 months after pruning, but decreased slightly with height 18 months after pruning (Table 1). The 50%-pruning treatment resulted in significantly lower SLA's

Fig. 2. Percentage of old (>2 years old), mature (<2 years old but fully expanded), and apical (expanding) foliage per branch in the five height zones of (A and D) unpruned, (B and E) 50%-pruned, and (C and F) 70%-pruned *E. nitens* growing in southern Tasmania harvested (A–C) 6 and (D–F) 18 months after pruning.

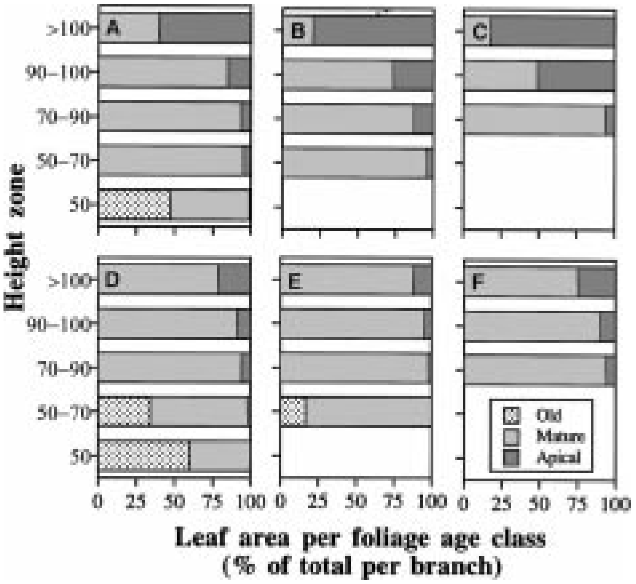


Fig. 3. Mean leaf size of apical (A and D) expanding, (B and E) mature (<2 years old but fully expanded), and (C and F) old (>2 years old) *E. nitens* foliage measured (A–C) 6 and (D–F) 18 months after 0, 50, or 70% pruning. Error bars indicate least squares standard errors.

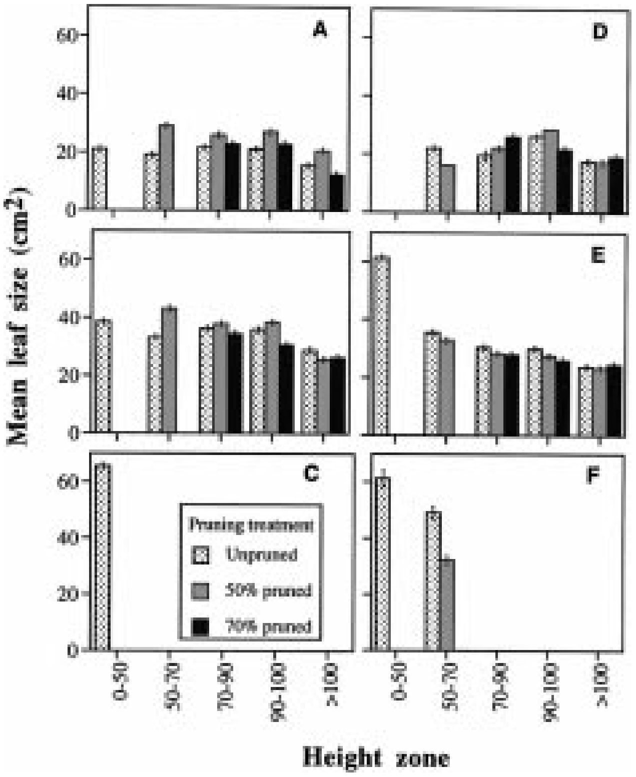


Table 1. Specific leaf area (leaf area:leaf dry mass) of unpruned, 50%-pruned, and 70%-pruned *E. nitens* growing in southern Tasmania.

Height zone (%)	Foliage age class	Specific leaf area ($m^2 \cdot kg$ dry $mass^{-1}$)		
		Unpruned	50% pruned	70% pruned
6 months after pruning				
0–50	Old	4.68 (0.26)		
	Mature	4.65		
	Apical	5.39		
50–70	Mature	5.09	4.82 (0.26)	
	Apical	5.19	4.55	
70–90	Mature	4.73	4.79	4.42 (0.26)
	Apical	4.62	4.79	5.56
90–100	Mature	4.55	4.40	5.36
	Apical	4.39	4.42	5.10
>100	Mature	4.68	4.30	4.58
	Apical	4.65	4.11	4.62
18 months after pruning				
0–50	Old	5.25 (0.29)		
	Mature	5.59		
50–70	Apical	5.84	5.45 (0.29)	
	Mature	5.45	5.57	
	Apical	5.13	5.29	
70–90	Mature	5.26	5.07	4.89 (0.29)
	Apical	4.38	4.38	4.57
90–100	Mature	5.32	4.62	4.79
	Apical	5.33	4.59	4.03
>100	Mature	4.79	4.66	4.44
	Apical	3.91	3.59	3.86

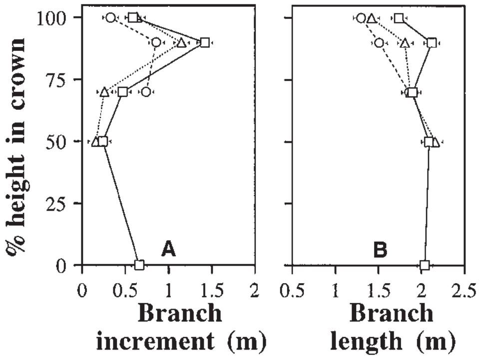
Note: Values are presented for trees harvested 6 and 18 months after pruning for five height zones (0–50, 50–70, 70–90 90–100, and >100%, based on height at the time of pruning) and three foliage age classes. Numbers in parentheses indicate least squares standard errors within a pruning treatment ($p < 0.05$).

in some height zones and foliage age classes 6 months after treatment. The response to 70% pruning was less consistent at this time. While the SLA of mature foliage in the 70–90% height zone was less in 70%-pruned trees than in unpruned trees, apical foliage in that height zone and mature and apical foliage in the 90–100% height zone had a greater SLA than unpruned trees ($p < 0.05$). Where differences between treatments existed 18 months after pruning, SLA was always less in pruned than in unpruned trees.

Branch development

Branch increment over the period of the experiment and mean branch length at the end of the experiment are illustrated in Fig. 4. In the 90–100 and >100% height zones, branch increment and mean branch length were less in 70%-pruned trees than in unpruned trees ($p < 0.05$). Branch increment in the 70–90 and 90–100% height zones of 50%-pruned trees was also less than in unpruned trees. However, mean branch length was only reduced in the 90–100% height zone, as a result of slightly longer branches in the 70–90% height zone of 50%-pruned trees at the start of the experiment. Irrespective of pruning treatment, greatest branch elongation occurred in the 90–100% height zone. In 50%-pruned and 70%-pruned trees, branches were longest at the base of the crown, but in unpruned trees, branch length was relatively constant with height.

Fig. 4. (A) Mean branch increment and (B) mean branch length estimated from standing *E. nitens* trees 20 months after pruning at a site in southern Tasmania. Values are shown for unpruned (squares), 50%-pruned (triangles), and 70%-pruned trees (circles). Error bars indicate least squares standard errors.



Biomass production and partitioning

Relative growth rate and unit leaf rate were not affected by 50% pruning (Table 2). However, 70% pruning reduced both relative growth rate and unit leaf rate by 64%. The 50%- and 70%-pruning treatments reduced the leaf area ratio by 54 and 86%, respectively, but by the end of the experiment, differences between treatments were no longer observed.

Table 2. Relative growth rate, unit leaf rate, and leaf area ratio immediately after pruning and 20 months after pruning for unpruned, 50%-pruned, and 70%-pruned *E. nitens* growing in southern Tasmania.

Pruning treatment (%)	Relative growth rate ($kg \cdot month^{-1}$)	Unit leaf rate ($m^2 \cdot kg^{-1} \cdot month^{-1}$)	Leaf area ratio ($m^2 \cdot kg^{-1}$) Immediately	Leaf area ratio ($m^2 \cdot kg^{-1}$) After 20 months
0	0.036 (0.005)	0.027 (0.006)	2.48 (0.22)	0.86 (0.14)
50	0.026	0.016	1.13	0.95
70	0.013	0.009	0.33	0.74

Note: Numbers in parentheses are least squares standard errors ($p < 0.05$).

Table 3. Total dry mass per branch (foliage plus wood) and the ratio of foliage dry mass to wood dry mass per branch of unpruned, 50%-pruned, and 70%-pruned *E. nitens* growing in southern Tasmania.

Height zone (%)	Total dry mass per branch (foliage plus wood) (g) Unpruned	50% pruned	70% pruned	Foliage: wood dry mass ($g \cdot g^{-1}$) Unpruned	50% pruned	70% pruned
6 months after pruning						
0–50	263.02			1.12		
50–70	218.77	353.99		1.39	1.51	
70–90	152.05	157.76	100.69	1.69	1.54	1.82
90–100	105.44*a*	86.29*a*	17.14*b*	1.56*b*	2.22*a*	0.98*c*
>100	14.62*a*	18.45*a*	2.53*b*	0.81*b*	1.28*a*	0.48*c*
18 months after pruning						
50–70	322.85	285.75		0.95	0.81	
70–90	341.19	257.63	234.96	0.96	1.04	0.94
90–100	457.08*a*	117.19*b*	97.72*b*	0.81*b*	1.33*a*	0.86*b*
>100	112.20*a*	95.28*a*	65.61*b*	0.88*b*	1.99*a*	0.99*b*

Note: Values are presented for trees harvested 6 and 18 months after pruning for five height zones (0–50, 50–70, 70–90, 90–100, and >100%, based on height at the time of pruning). Letters following the values indicate significant differences between pruning treatments in the same height zone ($p < 0.05$) (least squares method).

The total dry mass of branches in the 90–100 and >100% height zones of 70%-pruned trees was 84% less than of unpruned trees 6 months after pruning (Table 3). The ratio of foliage to wood dry mass per branch also was considerably lower. Eighteen months after pruning, total branch biomass was still less in the 90–100 and >100% height zones of 70%-pruned trees, but there were no longer differences in the ratio of foliage to wood dry mass.

The 50%-pruning treatment had no impact on total branch biomass, except for a decrease in the 90–100% height zone 18 months after pruning (Table 3). However, there was a large increase in the ratio of foliage to wood dry mass in the 90–100 and >100% height zones of this treatment compared with unpruned trees, both 6 and 18 months after pruning.

In the 50–70% height zone, 50%-pruned trees had greater CSA (Figs. 5A and 5B) and also had greater leaf area per unit branch CSA (LA:CSA) 6 months after pruning (Fig. 5C). However, 18 months after pruning, LA:CSA in the 50–70% height zone was less in 50%-pruned trees than in unpruned trees (Fig. 5D). In the 90–100% height zone, CSA of pruned trees was less than that of unpruned trees, and the magnitude of the reduction increased with pruning severity (Figs. 5A and 5B). Six months after pruning, there was no difference in the LA:CSA of unpruned and 50%-pruned trees in that height zone, but 70%-pruned trees had a significantly lower LA:CSA. Eighteen months after pruning, both 50%- and 70%-pruned trees had less LA:CSA in the 90–100% height zone. Although in the >100% height zone, CSA of 70%-pruned trees was less than that of unpruned trees 6 months after pruning, LA:CSA did not differ between treatments.

At the tree level, pruning inevitably reduced the proportion of aboveground biomass in branches and leaves. Over the 20 months of the experiment, unpruned trees partitioned approximately 90% of new standing biomass to stems while reducing partitioning to leaves (Table 4). The 50%-pruned trees had a aboveground biomass increment similar to that of unpruned trees, but partitioned 25% less new standing biomass to stems and 20% more new standing biomass to leaves than did unpruned trees ($p < 0.05$). The aboveground biomass increment of 70%-pruned trees was significantly less than that of the other treatments ($p < 0.05$), but the percentage allocated to stems was similar to that of 50%-pruned trees. The 70%-pruned trees partitioned less new standing biomass to branches, and more to leaves, than unpruned and 50%-pruned trees in the 20 months following pruning.

Crown architecture

Thirteen months after pruning, greater branch angles (more horizontal branches) in the crowns of 50%-pruned trees resulted in greater projected crown area in the 50–70 and 70–90% height zones (Table 5). Branch length in these height zones did not differ significantly between unpruned and 50%-pruned trees ($p > 0.05$) (Fig. 4). The result was a lower LAD in the 50–70 and 70–90% height zones of 50%-pruned trees ($p < 0.05$). While branch angle in the

Table 4. Aboveground dry mass increment and allocation of standing biomass to stems, branches, and leaves and (% of total aboveground dry mass increment) of unpruned, 50%-pruned, and 70%-pruned *E. nitens* over the 20 months of the experiment.

	Stems		Branches		Leaves	
Pruning treatment (%)	Increment (kg·month^{-1})	% of total	Increment (kg·month^{-1})	% of total	Increment (kg·month^{-1})	% of total
0	1.04 (0.22)	89.95 (5.04)	0.24 (0.06)	18.81 (2.55)	–0.10 (0.04)	–8.77 (3.52)
50	1.01	65.43	0.35	22.95	0.18	11.83
70	0.56	62.09	0.14	15.69	0.18	22.21

Note: Numbers in parentheses indicate least squares standard errors ($p < 0.05$).

Table 5. Mean crown length, projected crown area, leaf area density, and branch angle in each height zone of unpruned, 50%-pruned, and 70%-pruned *E. nitens* growing in southern Tasmania 13 months from the start of the experiment.

Pruning treatment (%)	Height zone (%)	Crown length (m)	Projected crown area (m^2)	Leaf area density (m^2 leaf area·m^{-3} crown volume)	Branch angle (° from vertical)
0	50–70	1.72 (0.31)	6.47 (0.50)	1.09 (0.11)	40.2 (1.4)
	70–90	1.72	7.86	0.86	38.6
	90–100	1.18	7.27	0.77	36.7
	>100	3.97	3.33	0.75	35.8
50	50–70	1.81	10.37	0.80	42.4
	70–90	1.81	9.73	0.55	43.5
	90–100	0.91	7.04	1,68	46.8
	>100	5.28	3.20	0.59	45.5
70	70–90	1.84	7.01	0.85	36.4
	90–100	0.92	6.97	1.07	39.2
	>100	3.27	2.82	0.61	36.3

Note: Numbers in parentheses are least squares standard errors ($p < 0.05$).

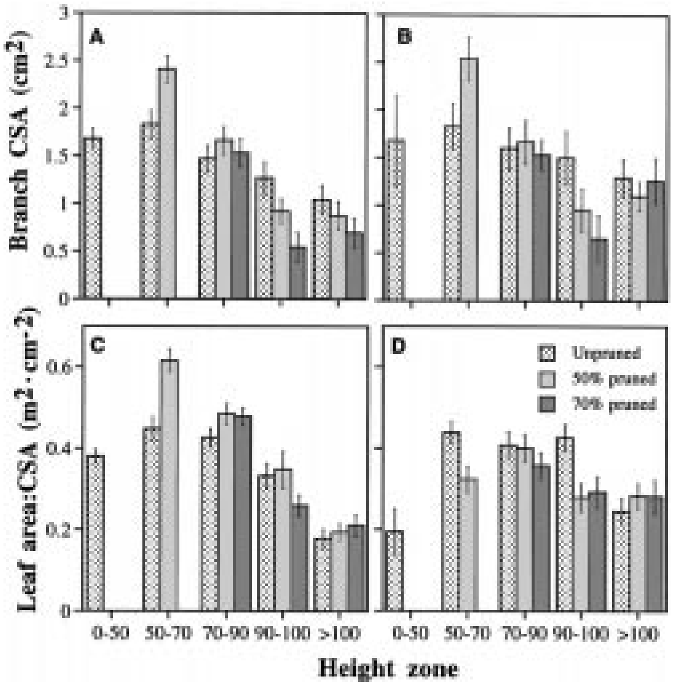
90–100% height zone was greater in 50%-pruned trees than in unpruned trees, branch length was shorter and there was no difference in projected crown area (Table 5). This, combined with a greater leaf area in 50%-pruned trees than in unpruned trees (Fig. 1), resulted in a higher LAD in the 90–100% height zone of 50%-pruned trees. A similar response was found in the 90–100% height zone of 70%-pruned trees.

Discussion

In eucalypts, leaf biomass increases rapidly during the first few years of growth until canopy closure (Cromer and Williams 1982), after which it often declines (Beadle et al. 1995). This is consistent with the decrease in leaf area measured in unpruned *E. nitens* over the course of the experiment. The plantation was verging on canopy closure at the start of the experiment. The reduction in leaf area was confined to the 0–50 and 50–70% height zones and was most likely a result of senescence due to low light conditions in those portions of the crown (Thomas and Stoddart 1980). Development of foliage in the upper crown occurred at a slower rate than did loss from the lower crown during this time.

After pruning, total leaf area increased with time, mainly as a result of development in the 90–100 and >100% height zones. In 50%-pruned trees, this increase in the upper crown was greater than in unpruned trees, which, combined with a slower rate of attrition of leaves in the 50–70% height zone, resulted in slightly but significantly greater total leaf area in

Fig. 5. (A and B) Mean branch cross-sectional area (CSA) and (C and D) mean leaf area per unit branch CSA of *E. nitens* harvested (A and C) 6 and (B and D) 18 months after pruning at a site in southern Tasmania. Height zones are based on percentage height at the time of pruning. Error bars indicate least squares standard errors ($p < 0.05$).



this treatment than in unpruned trees at the end of the experiment. An increase in leaf area per se may not increase biomass production of the crown because of shading of lower foliage. However, in 50%-pruned trees, branch angles and projected crown area in the 50–70 and 70–90% height zones increased. The reduction in LAD that resulted from this and the decrease in branch length with height in the crown may have increased light penetration and CO_2 assimilation in those height zones. Similar relative growth rates were observed for unpruned and 50%-pruned trees. This is consistent with the results of an earlier experiment, which found similar height and diameter growth and volume increment for unpruned and 50%-pruned trees (Pinkard and Beadle 1998*a*). Leaf area development of trees in the 70%-pruning treatment was similar to that of unpruned trees. However, the lower unit leaf rate and the increase in leaf area ratio measured over the period of the experiment indicate that 70%-pruned trees partitioned more carbon to leaf area development at the expense of wood.

The maintenance of higher leaf area and a greater LA:CSA in the 50–70% height zone of 50%-pruned compared with unpruned trees is consistent with delayed leaf senescence (Hodgkinson 1974; Alderfer and Eagles 1976; Thomas and Stoddart 1980). The decrease in SLA and elevated light-saturated CO_2 assimilation rates measured in that zone following 50% pruning (Pinkard et al. 1998) support this conclusion (Thomas and Stoddart 1980). The delayed senescence may have been a result of improved illumination resulting from changes in crown architecture or of changes in concentrations of growth hormones such as cytokinins and abscisic acid (Wareing and Patrick 1975; Geiger 1987).

The increase in leaf area in 50%-pruned trees was accompanied by increases in apical leaf size 6 months after treatment. Increased leaf expansion is a commonly reported response to partial defoliation (Trumble et al. 1993). Eighteen months after pruning, however, old leaves in the 50–70% height zone of 50%-pruned trees were smaller than those of unpruned trees. *Eucalyptus nitens* foliage has a distinct juvenile phase, characterised by large, glaucous leaves. At the start of the experiment the 0–50% height zone was almost exclusively juvenile foliage, and there was a mix of juvenile and adult foliage in the 50–70% height zone. It is possible that there were differences between unpruned and 50%-pruned trees in the retention of juvenile foliage. However, foliage retention was not monitored in the experiment.

Changes in SLA reflect changes in the capacity of the leaf to absorb light and CO_2 (Hodgkinson 1974; Alderfer and Eagles 1976; Trumble et al. 1993). For example, it is common to find that SLA increases as light intensity decreases (Björkman 1981). In this experiment, SLA increased with depth in the crown, reflecting changes in the light environment. Six months after pruning, SLA had decreased in many crown positions in response to 50% pruning, and a similar response was measured, albeit later, following 70% pruning. This may have reflected structural and compositional changes due to altered source–sink–storage relationships and new irradiance regimes (Thorne and Koller 1974; Jurik et al. 1979).

Early in their development, branches are a strong sink for assimilate (Dickson and Isebrands 1991). As leaves develop, the sink strength decreases. When sufficient foliage has been produced, branches become autonomous with respect to carbon and export any surplus to other parts of the plant (Dickson and Isebrands 1991; Sprugel et al. 1991). The form of branches can have a considerable effect on their efficiency with respect to net carbon export from the branch per unit carbon invested (Cannell and Morgan 1990; Sprugel et al. 1991; Farnsworth and Van Gardingen 1995). As branch length increases, the requirement for carbon for support increases semiexponentially (Cannell et al. 1988; Ford et al. 1990). It has been demonstrated theoretically that shorter branches elongating little per growing season have the potential to export more assimilate than longer, vigorously growing branches and that the development of laterals increases the export of assimilate per unit carbon invested (Cannell and Morgan 1990; Ford et al. 1990). In this experiment, lateral development was not investigated. However, shorter branches were found in the 90–100 and >100% height zones of pruned trees in the final months of the experiment. In 50%-pruned trees, these zones also had a greater ratio of foliage to wood dry mass per branch than in unpruned trees. Height growth was not affected by 50% pruning (Pinkard and Beadle 1998*a*), indicating that sufficient carbon was exported to the shoot tip to maintain shoot expansion at a rate similar to that of unpruned trees. These results suggest that the development of new leaves and continued shoot expansion had greater priority for carbon utilisation than did branch development under conditions of carbon shortage (Sprugel et al. 1991).

In 70%-pruned trees, branches in the 90–100 and >100% height zones were not only shorter, but had a much lower ratio of foliage to wood dry mass. Following this treatment, net export of assimilate may not have increased. The reduction in the ratio of foliage to wood dry mass suggests that there was a considerable shortage of carbon for new growth. New woody tissue has a lower nutrient content than foliage, and greater partitioning to branch wood rather than leaves decreases the average nutrient content of newly developed biomass (Cannell 1985). Such a response may occur when there is limited carbon available for root activity.

Functional relationships between biomass components have been implied by many studies (Waring et al. 1982; Bertram 1989; Fownes and Harrington 1992; Farnsworth and Van Gardingen 1995) and are generally explained in terms of two main hypotheses. The first is the pipe model theory (Shinozaki et al. 1964*a*, 1964*b*) that relates the production and distribution of biomass to the requirements for hydraulic support. The second suggests that resource allocation is a function of the structural costs for mechanical support (Cannell and Dewar 1994; Farnsworth and Van Gardingen 1995). The increase in LA:CSA in the 50–70 and 70–90% height zones of pruned trees suggests either that there were changes in hydraulic conductivity following pruning or that the relationship is primarily defined by support requirements. Further research is necessary to determine which (if any) of these theories explain observed relationships. The results suggest that the species generally is conservative in the apportioning of biomass between foliage and branches, an approach that allows changes in patterns of partitioning when carbon is in short supply without compromising mechanical or hydraulic requirments. The increase in LA:CSA and the ratio of foliage to wood dry mass may have been responsible for the greater branch angles measured in 50%-pruned trees (Cannell et al. 1988). The decrease in LA:CSA in the 90–100% height zone of 70%-pruned trees was primarily a consequence of reduced leaf area development rather than of changes in functional relationships per se.

As trees age, they allocate proportionately less biomass to leaves and more to stems (Givnish 1995). The increase in biomass partitioning to stems that occurred in unpruned trees during the first 12 months of the experiment is consistent with changes that would be expected following canopy closure (Givnish 1995; Hinckley and Schulte 1995). In 50%-pruned trees, there was change in partitioning to stem. The treatment preempted the natural decline in leaf area that occurred in unpruned trees. However, during the first 12 months of the experiment, 70%-pruned trees decreased partitioning to stems while increasing partitioning to leaves and branches. Plants partition resources in such a way as to optimise growth given the available resources (Mooney and Winner 1991). Results of this experiment suggest that in *E. nitens*, there is a minimum level of leaves and branches required for the maintenance of stemwood production. Below this level, carbon is diverted to increasing or maintaining leaf and branch development. The 70%-pruning treatment reduced the proportion of leaves and branches to below the minimum level.

Acknowledgements

This project was funded by the Forests and Forest Industry Council of Tasmania. We are grateful to Ray McLeod, Maria Cherry, and Sonia Hedenström for field and sampling assistance, Michael Battaglia for statistical advice, and Robin Cromer, Peter Snowdon, and two anonymous reviewers for valuable comments on the manuscript.

References

Alderfer, R.G., and Eagles, C.F. 1976. The effect of partial defoliation on the growth and photosynthetic efficiency of bean leaves. Bot. Gaz. **137**: 351–355.

Bassman, J.H., and Dickmann, D.I. 1982. Effects of defoliation in the developing leaf zone of young *Populus* × *euramericana* plants. I. Photosynthetic physiology, growth, and dry weight partitioning. For. Sci. **28**: 599–612.

Bassman, J.H., and Dickmann, D.I. 1985. Effects of defoliation in the developing leaf zone on young *Populus* × *euramericana* plants. II. Distribution of ^{14}C-photosynthate after defoliation. For. Sci. **31**: 358–366.

Beadle, C.L. 1985. Plant growth analysis. *In* Techniques in bioproductivity and photosynthesis. *Edited by* J. Coombs, D.O. Hall, S.P. Long, and J.M.O. Scurlock. Pergamon Press, Oxford. pp. 20–24.

Beadle, C.L., Honeysett, J.L., Turnbull, C.R.A., and White, D.A. 1995. Site limits to achieving genetic potential. *In* Eucalypt plantations: improving fibre yield and quality. Cooperative Research Centre for Temperate Hardwood Forestry, Hobart, Australia. pp. 325–335.

Bertram, J.E.A. 1989. Size-dependent differential scaling in branches: the mechanical design of trees revisited. Trees (Berl.), **4**: 241–253.

Björkman, O. 1981. Responses to different quantum flux densities. *In* Physiological plant ecology. 1. Responses to the physical environment. *Edited by* O.L. Lange, P.S. Nobel, C.B. Osmond, and H. Ziegler. Springer-Verlag, Berlin. pp. 57–108.

Bredenkamp, B.V., Malan, F.S., and Conradie, W.E. 1980. Some effects of pruning on growth and timber quality of *Eucalyptus grandis* in Zululand. S. Afr. For. J. **114**: 29–34.

Cannell, M.G.R. 1985. Dry matter partitioning in tree crops. In Attributes of trees as crop plants. *Edited by* M.G.R. Cannell and J.E. Jackson. Institute of Terrestrial Ecology, Huntingdon, U.K. pp. 160–193.

Cannell, M.G.R., and Dewar, R.C. 1994. Carbon allocation in trees: a review of concepts for modelling. Adv. Ecol. Res. **25**: 59–104.

Cannell, M.G.R., and Morgan, J. 1990. Theoretical study of variables affecting the export of assimilates from branches of *Picea*. Tree Physiol. **6**: 257–266.

Cannell, M.G.R., Morgan, J., and Murray, M.B. 1988. Diameters and dry weights of tree shoots: effects of Young's modulus, taper, deflection and angle. Tree Physiol. **4**: 219–231.

Coughenour, M.B., Detling, J.K., Bamberg, I.E., and Mugambi, M.M. 1990. Production and nitrogen responses of the African dwarf shrub *Indigofera spinosa* to defoliation and water limitation. Oecologia, **83**: 546–552.

Cromer, R.N., and Williams, E.R. 1982. Biomass and nutrient accumulation in a planted *E. globulus* (Labill.) fertilizer trial. Aust. J. Bot. **30**: 265–278.

Dakin, A.J. 1982. Pruning trial with Sugi. N.Z. J. For. **27**: 89–100.

Dickson, R.E., and Isebrands, J.G. 1991. Leaves as regulators of stress response. *In* Responses of plants to multiple stresses. *Edited by* H.A. Mooney, W.E. Winner, E.J. Pell, and E. Chu. Academic Press, New York. pp. 3–29.

Farnsworth, K.D., and Van Gardingen, P.R. 1995. Allometric analysis of Sitka spruce branches: mechanical versus hydraulic design principles. Trees (Berl.), **10**: 1–2.

Ford, E.D., Avery, A., and Ford, R. 1990. Simulation of branch growth in the Pinaceae: interactions of morphology, phenology, foliage productivity and the requirement for structural support, on the export of carbon. J. Theor. Biol. **146**: 15–36.

Fownes, J.H., and Harrington, R.A. 1992. Allometry of woody biomass and leaf area in five tropical multipurpose trees. J. Trop. For. Sci. **4**: 317–330.

Fujimori, T., and Waseda, O. 1972. Fundamental studies of pruning. II. Effects of pruning on stem growth. Bull. Gov. For. Exp. Stn. (Tokyo) No. 244.

Geiger, D.R. 1987. Understanding interactions of source and sink regions of plants. Plant Physiol. Biochem. **25**: 659–666.

Gerrand, A.M., Medhurst, J.L., and Neilsen, W.A. 1997. Research results for thinning and pruning eucalypt plantations for sawlog production in Tasmania. Report to the Forests and Forest Industry Council of Tasmania, Forestry Tasmania, Hobart, Australia.

Givnish, T.J. 1995. Plant stems: biomechanical adaptation for energy capture and influence on species distributions. *In* Plant stems. Physiology and functional morphology. *Edited by* B.L. Gartner. Academic Press, London, U.K. pp. 3–41.

Gregoire, T.G., Valentine, H.T., and Furnival, G.M. 1995. Sampling methods to estimate foliage and other characteristics of individual trees. Ecology, **76**: 1181–1194.

Heichel, G.H., and Turner, N.C. 1983. CO_2 assimilation of primary and regrowth foliage of red maple (*Acer rubrum* L.) and red oak (*Quercus rubra* L.): responses to defoliation. Oecologia, **57**: 14–19.

Helms, J.A. 1964. Apparent photosynthesis of Douglas-fir in relation to silvicultural treatment. For. Sci. **10**: 432–442.

Hinckley, T.M., and Schulte, P.J. 1995. Stems in the biology of tissue, organism, stand and ecosystem. *In* Plant stems. Physiology and functional morphology. *Edited by* B.L. Gartner. Academic Press, London, U.K. pp. 410–425.

Hodgkinson, K.C. 1974. Influence of partial defoliation on photosynthesis, photorespiration and transpiration by lucerne leaves of different ages. Aust. J. Plant Physiol. **1**: 561–578.

Hoogesteger, J., and Karlsson, P.S. 1992. Effect of defoliation on radial stem growth and photosynthesis in the mountain birch (*Betula pubescens* spp. *tortuosa*). Funct. Ecol. **6**: 317–323.

Jurik, T.W., Chabot, J.F., and Chabot, B.F. 1979. Ontogeny of photosynthetic performance in *Fragaria virginiana* under changing light regimes. Plant Physiol. **63**: 542–547.

Karani, P.K. 1978. Pruning and thinning in a *Pinus patula* stand at Lendu Plantation, Uganda. Commonw. For. Rev. **57**: 269–278.

Majid, N.M., and Paudyal, B.K. 1992. Pruning trial for *Acacia mangium* Willd. plantation in Peninsular Malaysia. For. Ecol. Manage. **47**: 285–293.

McPherson, G. 1990. Statistics in scientific investigation. Its basis, application and interpretation. Springer-Verlag, London.

McPherson, G., and Thompson, D. 1993. A user's perspective on SAS. An introduction and guide to its statistical applications for students, researchers and administrators. University of Tasmania, Hobart, Australia.

Mooney, H.A., and Winner, W.E. 1991. Partitioning response of plants to stress. *In* Responses of plants to multiple stresses. *Edited by* H.A. Mooney, W.E. Winner, E.J. Pell, and E. Chu. Academic Press, New York. pp. 129–139.

Opie, J.E. 1976. Volume functions for trees of all sizes. For. Comm. Vic. For. Tech. Pap. No. 25. pp. 27–30.

Ovaska, J., Ruuska, S., Rintamaki, E., and Vapaavuori, E. 1993. Combined effects of partial defoliation and nutrient availability on cloned *Betula pendula* saplings. II. Changes in net photosynthesis and related biochemical properties. J. Exp. Bot. **44**: 1395–1402.

Pinkard, E.A. 1997. Photosynthesis and resource allocation in the crowns of *Eucalyptus nitens* (Deane and Maiden) Maiden following green pruning. Ph.D. thesis, Department of Plant Science. University of Tasmania, Hobart, Australia.

Pinkard, E.A., and Beadle, C.L. 1998*a*. Effects of green pruning on growth and stem shape of *Eucalyptus nitens* (Deane and Maiden) Maiden. New For. **15**: 107–126.

Pinkard, E.A., Beadle, C.L, Davidson, N.J., and Battaglia, M. 1998. Photosynthetic responses of *Eucalyptus nitens* (Deane and Maiden) Maiden to green pruning. Trees (Berl.), **12**: 119–129.

Reich, P.B., Walters, M.B., Krause, S.C., Vanderklein, D.W., Raffa, K.R., and Tabone, T. 1993. Growth, nutrition and gas exchange of *Pinus resinosa* following artificial defoliation. Trees (Berl.), **7**: 67–77.

SAS Institute Inc. 1990. SAS/STAT user's guide, version 6. 4th ed. SAS Institute Inc., Cary, N.C.

Senock, R.S., Sisson, W.B., and Donart, G.B. 1991. Compensatory photosynthesis of *Sporobolus flexuosus* (Thurb.) Rydb. following simulated herbivory in the northern Chihuahuan desert. Bot. Gaz. **152**: 275–281.

Shepherd, K.R. 1986. Plantation silviculture. Martinus Nijhoff Publishers, Lancaster. pp. 225–235.

Shinozaki, K., Yoda, K., Hozumi, K., and Kira, T. 1964*a*. A quantitative analysis of plant form — the pipe model theory. I: Basic analyses. Jpn. J. Ecol. **14**: 97–105.

Shinozaki, K., Yoda, K., Hozumi, K., and Kira, T. 1964*b*. A quantitative analysis of plant form — the pipe model theory. II: Further evidence of the theory and its application in forest ecology. Jpn. J. Ecol. **14**: 133–139.

Sprugel, D.G., Hinckley, T.M., and Schaap, W. 1991. The theory and practice of branch autonomy. Annu. Rev. Ecol. Syst. **22**: 309–334.

Sutton, W.R.J., and Crowe, J.B. 1975. Selective pruning of radiata pine. N.Z. J. For. Sci. **5**: 171–195.

Thomas, H., and Stoddart, J.L. 1980. Leaf senescence. Annu. Rev. Plant Physiol. **31**: 83–111.

Thorne, J.H., and Koller, H.R. 1974. Influence of assimilate demand on photosynthesis, diffusive resistances, translocation and carbohydrate levels of soybean leaves. Plant Physiol. **54**: 201–207.

Trumble, J.T., Kolodney-Hirsch, D.M., and Ting, I.P. 1993. Plant compensation for arthropod herbivory. Annu. Rev. Entomol. **38**: 93–119.

von Caemmerer, S., and Farquhar, G.D. 1984. Effects of partial defoliation, changes of irradiance during growth, short-term water stress and growth at enhanced $p(CO_2)$ on the photosynthetic capacity of leaves of *Phaseolus vulgaris* L. Planta (Heidelb.), **160**: 320–329.

Wareing, P.F., and Patrick, J. 1975. Source–sink relations and the partition of assimilates in the plant. *In* Photosynthesis and productivity in different environments. *Edited by* J.P. Cooper. Cambridge University Press, Cambridge, U.K. pp. 481–499.

Waring, R.H., Schroeder, P.E., and Oren, R. 1982. Application of the pipe model theory to predict canopy leaf area. Can. J. For. Res. **12**: 556–560.

Waugh, G. 1996. Properties of plantation-grown eucalypts. *In* Farm Forestry and Plantations Conference Proceedings. Australian Forest Growers, Mount Gambier, South Australia. pp. 83–93.