

Modeling the effect of physiological responses to green pruning on net biomass production of *Eucalyptus nitens*

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Summary Green pruning of *Eucalyptus nitens* (Deane and Maiden) Maiden increases instantaneous rates of light-saturated CO₂ assimilation (*A*), and changes patterns of total leaf area and foliage distribution. We investigated the importance of such changes on the rate of recovery of growth following pruning. A simple process-based model was developed to estimate daily net biomass production (*G_d*) of three-year-old plantation-grown trees over a 20-month period. The trees had been pruned by removal of 0, 50 or 70% of the length of green crown, equivalent to removal of 0, 55 or 88% of leaf area, respectively, when the plantation verged on canopy closure. Total *G_d* was reduced by only 20% immediately following the 50%-pruning treatment, as a result of both the high leaf dark respiration and low *A* in the portion of the crown removed compared to the top of the crown. Pruning at the time of canopy closure preempted a natural and rapid decline in *G_d* of the lower crown. Although leaf area index (*L*) was approximately 6.0 at the time of pruning, high light interception (95%) occurred with an *L* of 4.0. The 50%-pruning treatment reduced *L* to 3.5, but the physiological responses to pruning were sufficient to compensate fully for the reduction in intercepted radiation within 110 days of pruning. The 70%-pruning treatment reduced *L* to 1.9, and reduced *G_d* by 77%, reflecting the removal of branches with high *A* in the mid and upper crown. Physiological responses to the 70%-pruning treatment were insufficient to increase *G_d* to the value of unpruned trees during the study.

Model sensitivity analysis showed that increases in *A* following pruning increased *G_d* by 20 and 25% in the 50- and 70%-pruned trees, respectively, 20 months after pruning. Changes in leaf area/foliage distribution had a greater effect on *G_d* of 50%-pruned trees (47% increase) than did changes in *A*. However, the reduction in photosynthetic potential associated with the 70%-pruning treatment resulted in only small changes in leaf area/foliage distribution, which consequently had little effect on *G_d*. The effects of physiological processes occurring within the crown and in response to green pruning on *G_d* are discussed with respect to pruning of plantations.

Keywords: Beer's Law, carbon dioxide assimilation, foliage distribution, leaf area index, process-based model.

Introduction

The harvestable yield of a forest is a function of both net biomass production and partitioning of dry matter to harvestable plant parts (Cannell 1985). Traditionally, yield tables based on empirical measurements have been used to predict forest productivity. However, yield tables tend to be site and species specific, and, unless based on data from extensive field trials, are of limited use in predicting and understanding the impact of silvicultural treatments, such as pruning, on stand growth and productivity (Linder 1984). An alternative approach is to use mechanistic models that are based on observed or predicted physiological responses (Jarvis and Leverenz 1983, Waring 1983, Linder 1984). This approach requires an understanding of the total carbon budget of the plant and the effects of variation in environmental factors, such as temperature, nutrient and water availability and incident irradiance, on carbon uptake and loss (Jarvis and Leverenz 1983). In general, our knowledge of physiological processes in plants is restricted to single leaf measurements, and there is the potential for serious error when scaling up to the level of the whole plant or forest stand (Wang and Jarvis 1990). Although problems associated with scaling reduce the immediate predictive capacity of mechanistic models, they do not affect their intrinsic value or their usefulness in generating notional responses to treatments (Linder 1984, Cohen and Fuchs 1987, Cohen et al. 1987, Wang and Jarvis 1990, Dewar 1996, Landsberg and Hingston 1996).

The process of scaling CO₂ uptake from single leaf responses to the canopy level requires an understanding of radiation interception and the distribution of light in the crown (Monteith 1972, Jarvis and Leverenz 1983, Linder 1984, Sands 1995, Dewar 1996, Sands 1996). Total intercepted radiation and spatial distribution of light in the crown are a function of total leaf area, and of structural properties such as leaf area index, the vertical distribution of foliage, leaf angle and leaf transmittance (Jarvis and Leverenz 1983). The potential carbon losses from the plant also need to be considered. Respiration is the main source of carbon loss (Amthor 1994). As much as 75% of total carbon assimilated may be lost in respiration under some conditions (Evans 1975), although typically the

value is closer to 55% (Ryan et al. 1996). Ignoring photorespiration, which is largely a feature of photosynthesis itself (Evans 1975), the respiratory costs to the plant come from leaf dark respiration, and respiration involved in tissue maintenance and the construction of new tissue (Amthor 1994).

Green pruning is a silvicultural treatment used to increase wood quality in species that have persistent dead branches (Shepherd 1986). It involves removal of live branches, and hence leaf area, from the lower crown. A large decrease in height and diameter growth can occur as a result of this treatment (e.g., Sutton and Crowe 1975, Karani 1978, Majid and Paudyal 1992). Several physiological changes are known to occur following partial defoliation, such as increases in maximum rates of instantaneous photosynthesis, and changes in patterns of carbon allocation in the remaining crown (Caldwell et al. 1981, Heichel and Turner 1983, Reich et al. 1993). Although the overall effect of partial defoliation on net production has been investigated (e.g., Heichel and Turner 1983, McMurtrie et al. 1986, Grace et al. 1987, Reich et al. 1993, Nygren et al. 1996), the importance of specific physiological responses to defoliation in determining production have not been considered.

Eucalyptus nitens (Deane and Maiden) Maiden is an important hardwood plantation species in Australia. When grown in plantations, it retains rather than sheds dead branches, and serious problems with wood quality are often encountered. Thus, green pruning is necessary for the production of sawlogs from this species. It is planted at up to 1000 stems ha⁻¹, from which approximately 250 stems ha⁻¹ are selected for pruning. The species can tolerate removal of 50% of the length of green crown, but more severe pruning treatments reduce both height and diameter increment (Pinkard and Beadle 1998a). Green pruning of this species results in increased rates of photosynthesis throughout the crown (Pinkard et al. 1998), and changes in leaf area/foliage distribution (Pinkard 1997). However, it is not known whether these responses influence whole-crown net carbon uptake. We have taken a modeling approach to determine the effect of pruning on net production of individual trees and the extent to which physiological responses to pruning explain observed growth responses (Pinkard and Beadle 1998a). A single tree model was used to test the hypothesis that physiological responses to pruning reduce the effect of pruning on growth. The first objective was to determine the effect of pruning on the estimated daily net biomass production of different portions of the crown over a period of 20 months. The second objective was to investigate the importance to daily and cumulative net production of changes in instantaneous rates of photosynthesis, leaf area and foliage distribution.

Materials and methods

Site and treatment description

The experiment was conducted in a three-year-old *E. nitens* plantation in southern Tasmania, Australia. The plantation was established on an ex-pasture site with a podsolc soil type derived from Triassic sandstone, and consisting of a sandy loam A horizon of approximately 60 cm depth overlying a clay

B horizon. It was planted in September 1990 with seedling stock (a Mount Toorongo seedlot of the Upper Toorongo provenance), and fertilized with 200 and 100 kg ha⁻¹ of elemental nitrogen and phosphorus, respectively. The stocking density was 1430 stems ha⁻¹ (between-tree spacing of 3.5 × 2 m). 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. The plantation was verging on canopy closure, with branches of adjacent trees almost touching.

Nine adjacent plots of similar sized trees were selected. Each plot was three trees long by three trees wide. The pruning treatments were randomly allocated to the central tree in these plots, and the remaining eight trees acted as an unpruned buffer to simulate a selective pruning regime. In January 1994, trees were pruned to remove either 0, 50 or 70% of the length of green crown, which is equivalent to the removal of 0, 55 or 88% of leaf area, respectively. Only the lower crown was removed. Crowns of these trees were divided into four height zones: 0–50, 50–70, 70–90 and >90% of height at the time of pruning. The heights of these zones were fixed with respect to the ground. Instantaneous rates of light-saturated CO₂ assimilation (A , μmol CO₂ m⁻² s⁻¹) and leaf dark respiration (r , μmol CO₂ m⁻² s⁻¹), and changes in leaf area/foliage distribution were measured in each height zone (Pinkard 1997, Pinkard et al. 1998). Fitted values of light-saturated A (A_{\max}) for measurements at 0, 6, 13 and 20 months after pruning are given in Table 1. Leaf area and foliage distribution for measurement times are summarized in Table 2. All tree-level calculations detailed below were made for individual trees within pruning treatments and then the mean value was calculated for each treatment.

Annual means of weekly measurements of maximum and minimum temperatures in a Stephenson screen were 19.7 and 4.0 °C, respectively, and mean annual rainfall was 957 mm (1991–1995). Daily maximum and minimum temperatures and solar radiation were compiled for a sample year from a weather station at Esperance (43°18' S, 147°01' E), approximately 25 km southwest of the experimental site (Figures 1A and 1B). Annual means of weekly measurements of maximum and minimum temperatures at Esperance were 19.5 and 3.7 °C, and rainfall was 1412 mm (1984–1991). Mean vapor pressure deficit ranged from 0.36 kPa in July to 0.70 kPa in December. At both locations, rainfall is distributed uniformly throughout the year, with a slight peak in spring (September–November). The weather data used in the modeling spanned the year 1987, which was not the year that the field experiment was conducted, but was the only year for which a complete set of records was available.

Experimental design

The experimental design can be described by a two-strata model, in which pruning treatments were allocated between trees, and height zones were allocated within trees:

$$X_{i,j} = M + B_i + C_{i,j}, \quad (1)$$

Table 1. Apparent quantum yield, Φ , leaf dark respiration, r_1 ($\mu\text{mol m}^{-2} \text{s}^{-1}$), the shape of the light response curve, θ , and foliar nitrogen (N) content (g m^{-2}) (from Pinkard et al. 1998) for mature foliage of pruned and unpruned trees 10 months after pruning. The A_{max} is presented for four measurement times. Measurements were made at PFDs varying from 0 to 1500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and a leaf temperature of 25 °C. Values are means of three leaves per treatment, and numbers in brackets are least squares standard errors ($P < 0.05$).

| Pruning treatment | % Height | Φ | θ | r_1 | Foliar N | A_{max} | | | |
|-------------------|----------|---------------|-------------|-------------|-------------|------------------|-----------|-----------|-----------|
| | | | | | | Pre-prune | 6 Months | 13 Months | 20 Months |
| 0 | 0–50 | 0.047 (0.006) | 0.99 (0.07) | 2.39 (0.27) | 1.10 (0.29) | 9.9 (1.6) | 7.3 (0.6) | 6.4 (0.5) | 4.1 (0.4) |
| 0 | 50–70 | 0.045 | 0.93 | 1.77 | 1.77 | 17.1 | 13.3 | 8.3 | 7.6 |
| 0 | 70–90 | 0.041 | 0.93 | 1.98 | 2.07 | 17.3 | 17.2 | 11.2 | 11.5 |
| 0 | > 90 | 0.043 | 0.93 | 2.24 | 2.65 | 17.4 | 20.3 | 18.9 | 17.9 |
| 50 | 50–70 | 0.044 | 0.84 | 2.10 | 2.14 | 17.1 | 15.6 | 12.7 | 9.4 |
| 50 | 70–90 | 0.041 | 0.89 | 1.94 | 2.42 | 17.3 | 19.2 | 16.6 | 18.2 |
| 50 | > 90 | 0.053 | 0.85 | 2.46 | 2.83 | 17.4 | 22.7 | 23.2 | 21.7 |
| 70 | 70–90 | 0.039 | 0.92 | 1.39 | 2.68 | 17.3 | 18.3 | 14.6 | 16.9 |
| 70 | > 90 | 0.048 | 0.88 | 2.35 | 2.33 | 17.4 | 22.3 | 21.2 | 19.7 |

Table 2. Mean leaf area per height zone (m^2), and cumulative leaf area index (L) of pruned and unpruned trees at four measurement times. The extinction coefficient (k_i) calculated 13 months after pruning is also presented. Numbers in brackets are least squares standard errors ($P < 0.05$).

| Pruning treatment | % Height | Leaf area (m^2) | | | | L | | | | k_i |
|-------------------|----------|----------------------------|------------|-----------|-----------|-------------|-----------|-----------|-----------|-------------|
| | | Pre-pruning | 6 Months | 13 Months | 20 Months | Pre-pruning | 6 Months | 13 Months | 20 Months | 13 Months |
| 0 | 0–50 | 30.5 (1.3) | 16.6 (2.6) | 2.7 (1.6) | 2.7 (1.5) | 6.1 (0.4) | 7.8 (0.9) | 7.1 (0.6) | 4.1 (0.5) | 0.53 (0.08) |
| 0 | 50–70 | 13.0 | 11.2 | 12.5 | 9.4 | 2.9 | 4.1 | 4.7 | 3.6 | 0.77 |
| 0 | 70–90 | 8.0 | 11.2 | 12.6 | 13.0 | 2.2 | 2.9 | 4.5 | 2.7 | 0.76 |
| 0 | > 90 | 2.3 | 2.8 | 10.6 | 11.4 | 1.1 | 0.9 | 2.2 | 1.3 | 0.94 |
| 50 | 0–50 | 35.0 | – | – | – | 6.3 | – | – | – | – |
| 50 | 50–70 | 17.1 | 19.1 | 12.9 | 13.6 | 3.5 | 4.6 | 5.5 | 4.9 | 0.68 |
| 50 | 70–90 | 11.6 | 11.0 | 11.4 | 11.6 | 2.0 | 2.3 | 4.2 | 3.3 | 0.79 |
| 50 | > 90 | 2.6 | 4.5 | 14.1 | 18.4 | 1.1 | 1.2 | 3.3 | 2.5 | 0.76 |
| 70 | 0–50 | 31.0 | – | – | – | 6.6 | – | – | – | – |
| 70 | 50–70 | 23.3 | – | – | – | 3.9 | – | – | – | – |
| 70 | 70–90 | 6.3 | 11.9 | 12.2 | 12.2 | 1.9 | 2.1 | 3.3 | 2.7 | 0.87 |
| 70 | > 90 | 1.4 | 2.9 | 9.4 | 12.3 | 0.2 | 0.6 | 2.4 | 1.5 | 0.76 |

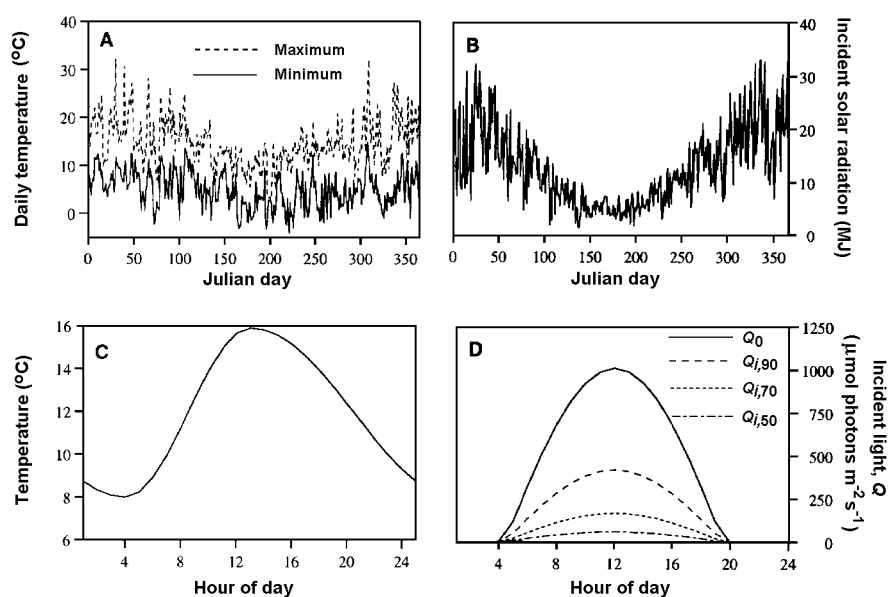


Figure 1. (A) Daily maximum and minimum temperatures, and (B) incident solar radiation, at Esperance during 1987; and modeled diurnal variation in (C) temperature and (D) solar radiation above the crown (Q_0) and at the base of each height zone (Q_{i90} , Q_{i70} , Q_{i50}) on a typical summer day ($Q_{\text{day}} = 15.8 \text{ MJ m}^{-2}$).

where $X_{i,j}$ is the response (e.g., photosynthetic) of the j th height zone of the i th tree; M is the overall mean, B is the plot strata (or between-tree effect); and C is the split-plot strata (or within-tree effect). The particular treatment allocations are given by:

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

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

where P_m is the m th pruning treatment, and H_n is the n th height zone, and e is the error term.

The model

The model estimates net biomass production on a daily basis for single *E. nitens* crowns between the ages of three and five years. It was developed to estimate the effect of green pruning at three years of age on net biomass production, and to ascertain the relative importance of various physiological responses to pruning on production. It comprises submodels to calculate leaf area development, CO₂ assimilation and respiration and the distribution of light in the crown on a daily basis, and diurnal and seasonal variations in temperature and light. Model inputs include: (1) daily maximum and minimum temperature and solar radiation; (2) observed changes in the distribution of leaf area in four height zones in the crown following pruning; (3) photosynthetic light response parameters at the base of the four height zones; (4) observed changes in A_{\max} following pruning at the base of the four height zones; and (5) light attenuation through the crown.

The model assumes that water and nutrients are non-limiting to growth. It estimates net production in four height zones within the crown, as well as for the whole crown. It assumes that leaf area is distributed homogeneously within each height zone, and that photosynthetic parameters are constant through a height zone. Changes in leaf area, leaf area index (L) and photosynthetic parameters with time are linearly interpolated between known points (field observations). Within a height zone, the model apportions leaf area and L equally to 10-cm-deep horizontal crown layers.

Model inputs

Leaf area development The area of apical (expanding) foliage per crown is small (Pinkard 1997). In addition, although A_{\max} differed between old (> 2 years old) and mature (< 2 years old but fully expanded) foliage (Pinkard et al. 1998), there was no difference in A at low irradiances. Because old foliage was only present in the 0–50% and 50–70% height zones, low irradiances minimized these differences. Thus, we assumed that all foliage was mature.

Total single-sided leaf area (s , m²) observed in the four height zones 0, 6, 13 and 20 months after pruning, is given in Table 2. Cumulative leaf area index (L) was calculated at the base of the four height zones at each measurement time, as total single-sided leaf area divided by projected ground area (P_a , m²) (Beadle 1985). The value P_a was calculated from the mean of four measurements of crown radii (north, east, south,

west) made at the base of each height zone. The generalized linear model analysis of variance procedure GLM (1990; SAS Institute Inc., Cary, NC) was used to determine differences in L related to pruning treatment and height zone.

Distribution of light in the crown Twelve months after pruning, eight quantum sensors (QS; Delta-T Devices, Cambridge, U.K.) were placed in pairs at the base of each height zone, at approximately half crown radius. These sensors were randomly moved between and within trees, giving a total of 27 sampling locations. Data were collected for a period of 10 days at each location. A single sensor was located above the canopy, from which continuous data were collected. Data were recorded from these sensors with a Campbell 21X automatic logger (Campbell Scientific, Logan, UT) that was programmed to record every 5 s and store means every 5 min. The mean for each hour was determined later. Sensors were calibrated at the beginning and end of the measurement period, with a Skye 210 PAR 'Special' Sensor (Skye Instruments Ltd., Powys, Wales), and field values were converted to $\mu\text{mol m}^{-2} \text{s}^{-1}$. The calibration was made with four Wotan xenon quartz globes as the light source. Photon flux densities, Q , ranging between 0 and 2000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ were obtained with a series of neutral density filters. The fraction of light at any point in the crown, Q_f , was calculated for each height zone as the irradiance at height i in the crown (Q_i) divided by the irradiance above the canopy, Q_o . Mean Q_f was calculated between and within days.

The relationship between Q_f and L was explored by regression analysis (PROC NLIN procedure of the SAS statistical software package; SAS Institute Inc., Cary, NC). The equation explaining this relationship was used to estimate Q_f in the crowns of pruned and unpruned trees for each day of the experimental period, based on observed values of Q_o .

The distribution of light in the crown can be expressed approximately by Beer's Law (Monsi and Saeki 1953):

$$Q_i = Q_o e^{-kL}, \quad (2)$$

where k is the canopy extinction coefficient. The transformed version of Equation 2 was used to calculate k at the base of each height zone (k_i). The SAS module, GLM, was used for analysis of variance of differences in k_i related to pruning treatment and height zone. The calculated k_i for each height zone was used in the model (Q_x in Equation 3).

CO₂ Assimilation An open-flow gas analysis system (LCA2; Analytical Development Corporation, Hoddesdon, U.K.) was used to measure instantaneous net CO₂ assimilation (A). Leaves were enclosed in a Parkinson (Hoddesdon, U.K.) PLC-B illuminated leaf chamber (area = 6.25 cm²). The light source consisted of four Wotan 150 W xenon quartz globes. A range of photon flux densities (Q_s) were produced by placing neutral density filters over the leaf chamber to shade the leaf surface progressively from a Q of 1500 to 0 $\mu\text{mol m}^{-2} \text{s}^{-1}$. A non-rectangular hyperbola was fitted to each curve (Battaglia and Sands 1997):

$$A = \frac{2\Phi Q_x A_{\max}}{\Phi Q_x + A_{\max} \sqrt{(\Phi Q_x + A_{\max})^2 - 4\theta\Phi Q_x A_{\max}}} - r, \quad (3)$$

where Φ is the slope of the relationship at low Q_x ; Q_x is Q ($\mu\text{mol m}^{-2} \text{s}^{-1}$) incident on the leaf and is presumed to be equivalent to Q_i/k_i (after Sands 1995); A_{\max} is light-saturated A ; r is leaf dark respiration; and θ is the shape of the photosynthetic light response curve. Analysis of variance was then used to determine differences between pruning treatments and height zones for each parameter (PROC GLM procedure of the SAS statistical software package). Estimated parameter values for mature foliage are presented in Table 1. The only parameter that varied with both pruning treatment and time was A_{\max} and values of A_{\max} are given in Table 1 for the four measurement times. Daily values of A_{\max} were estimated by linear interpolation.

The light response parameters Φ , A_{\max} and r vary with temperature (Jones 1983), and were adjusted using the following formulae (Sands 1995, Sands 1996, Battaglia and Sands 1997):

$$\Phi(T) = \Phi(1 - \Phi_1(T - T_o)), \quad (4)$$

where Φ_1 is the strength of the temperature dependence of Φ , T is actual temperature, and T_o is a reference temperature (20 °C):

$$A_{\max}(T) = \max\left\{0.01, A_{\text{opt}} \left(1 - \frac{1}{2} \frac{(T - T_{\text{opt}})^2}{t_{1/2}}\right)\right\}, \quad (5)$$

where A_{opt} is the value of A_{\max} at optimum temperature T_{opt} , $t_{1/2}$ is the temperature change from T_{opt} required to reduce A_{\max} to half the optimum value, and:

$$T_{\text{opt}} = (1 - \tau)T_{\text{pref}} + \tau T, \quad (6)$$

where T_{pref} is the acclimation temperature at which the optimum temperature and acclimation temperature are identical (Battaglia and Sands 1997), and τ determines how strongly T_{opt} tracks T . In *E. nitens*, A_{\max} acclimates to seasonal changes in temperature (Battaglia et al. 1996). The model accounts for this by using actual measurements of A_{\max} from throughout the year. Temperature-adjusted gross leaf dark respiration (r , $\text{g}_{\text{DM}} \text{tree}^{-1} \text{day}^{-1}$) was given by:

$$r(T) = r e^{a(T - T_o)}, \quad (7)$$

where $a = 0.069$, which results in a Q_{10} of 2 (Gifford 1994).

Daily temperature and light Temperature variation throughout the day was calculated on an hourly time step, with the minimum temperature occurring one hour before dawn, and maximum temperature one hour after solar noon (Australian Bureau of Meteorology, Hobart, Tasmania, personal communication). Equations 8–10 were applied to calculate nighttime, morning and afternoon temperature variation, respectively:

$$T_{\text{night}} = T_{\text{mean}} + \frac{1}{2} T_{\text{range}} \sin\left(\frac{\pi(h - t_{\min} + (24 - t_{\text{period}}/2))}{24 - t_{\text{period}}}\right), \quad (8)$$

$$T_{\text{AM}} = T_{\text{mean}} + \frac{1}{2} T_{\text{range}} \sin\left(\frac{\pi(h - (t_{\min} + t_{\text{period}}/2))}{t_{\text{period}}}\right), \quad (9)$$

$$T_{\text{PM}} = T_{\text{mean}} + \frac{1}{2} T_{\text{range}} \sin\left(\frac{\pi(h - t_{\max} + (24 - t_{\text{period}}/2))}{24 - t_{\text{period}}}\right), \quad (10)$$

where T_{mean} is the mean daily temperature, T_{range} is the daily temperature range, t_{\max} is time at which maximum daily temperature occurs, t_{\min} is the time at which minimum daily temperature occurs, t_{period} is the difference between t_{\max} and t_{\min} , and h is the time of the day (hours). Diurnal variation in Q was calculated on an hourly time step as (Monteith 1972):

$$Q_o = \frac{2.2 \times 10^6}{3600} \frac{\pi Q_{\text{day}}}{2t_d} \cos\left(\frac{\pi h}{t_d}\right), \quad (11)$$

where Q_{day} (MJ m^{-2}) is total Q_o ($\mu\text{mol m}^{-2} \text{s}^{-1}$) for the day; t_d is daylength in hours; and if $t_d > t_d/2$, then $Q_o = 0$. Daylength was corrected for time of year and for latitude. Figures 1C and 1D show diurnal temperature variation, and variation in Q above the canopy and at the base of each height zone, for a typical day in summer (daylength = 15 hours; maximum $Q = 1010 \mu\text{mol m}^{-2} \text{s}^{-1}$ [$Q_{\text{day}} = 15.8 \text{ MJ m}^{-2}$]; maximum air temperature = 15.9 °C; minimum temperature = 8 °C).

Gross daily carbon assimilation (A_c), leaf dark respiration (R_l) and net production (G_d) Gross A and r were calculated for the leaf area within each crown layer on an hourly time step, and summed for each height zone. Total daily values were then calculated and converted from $\mu\text{mol m}^{-2} \text{s}^{-1}$ to $\text{g dry matter day}^{-1}$, using a dry matter conversion factor (dmc) of $30 \times 10^{-12} \text{ g}_{\text{DM}} \mu\text{mol m}^{-2} \text{CO}_2$. Total gross dry matter production (A_c , $\text{g}_{\text{DM}} \text{tree}^{-1} \text{day}^{-1}$) and leaf dark respiration (R_l , $\text{g}_{\text{DM}} \text{day}^{-1}$) in the four height zones were then calculated for each day of the 612-day experimental period.

In addition to leaf respiration, respiration associated with maintenance of woody tissue and construction of new tissues was accounted for. Only leaf respiration was measured. The maintenance respiration coefficient, R_m , was given a value of 0.35 (from Ryan et al. 1996) and adjusted for temperature with the equation:

$$R_m(T) = R_m e^{a(T_{\text{av}} - T_o)}. \quad (12)$$

In this equation, T_{av} is the 10-day running mean temperature, and $a = 0.069$ as in Equation 7. The construction respiration coefficient, R_c , was given a value of 0.25, and was assumed to be independent of temperature (Penning de Vries 1975, Battaglia and Sands 1997). The respiration costs were used to calculate carbon use efficiency, Y , of each height zone (see Battaglia and Sands 1997):

$$Y = \frac{(1 - R_m - \frac{R_l}{A_c})}{1 + R_c} \quad (13)$$

Net daily biomass production, G_d ($\text{g}_{\text{DM}} \text{day}^{-1}$), was then calculated:

$$G_d = YA_c \quad (14)$$

Mean daily Y was calculated for the period of the experiment, and analysis of variance was used to determine differences between pruning treatments and height zones.

Sensitivity of G_d to r

Gross leaf dark respiration (R_l) was calculated based on observed values of r and interpolated between the base of each height zone, but values in the lower crown were higher than expected (e.g., Pereira et al. 1986, Battaglia et al. 1996, Pinkard and Beadle 1998b). Many models assume that r is proportional to foliar nitrogen (N) content (e.g., Wang and Jarvis 1990, Sands 1995, Dewar 1996). Consequently, a sensitivity analysis was undertaken to compare the effect on G_d of assuming that r was proportional to foliar N content, and using observed values of r . Foliar N contents were taken from Pinkard et al. (1998) (Table 1), and were from the same leaves used to measure light response parameters. The ratio of r :N was determined. Two sets of simulations were carried out: one with observed values of r , and one with values estimated from foliar N concentration. The G_d from the two outputs was summed and converted to volume increment. It was assumed that partitioning of dry matter belowground was 0.50 (estimated by Battaglia and Sands 1997 for *Eucalyptus globulus* Labill. growing at a nearby site). In an earlier experiment it was found that, for *E. nitens* harvested at three years of age, partitioning of aboveground dry matter to stem was 0.65 (unpublished data), and this value was used to partition biomass between stems and leaves plus branches. Wood density was given a value of 400 kg m^{-3} (Waugh and Yang 1994). Results were compared to observed volume increment calculated based on the height and diameter values of Pinkard and Beadle (1998a) and the volume function of Opie (1976).

Influence of changes in A_{max} and leaf area/foliage distribution on G_d

The relative importance to G_d of changes in leaf area/foliage distribution and instantaneous photosynthesis in response to pruning were explored by sensitivity analysis. Artificial tree crowns with identical leaf area, foliage distribution, light response parameters and total height were generated by computer. The crowns of these identical trees were manipulated to simulate removal of 0, 50 or 70% of the length of green crown, based on observed responses. Four simulations were then run for the 612-day period of the experiment. (1) No change in leaf area/foliage distribution or A in response to pruning. In all treatments, changes in A and leaf area were manipulated to simulate the changes with time measured in unpruned trees (minus the portions of the crown removed by 'pruning'). (2)

Changes in A but not leaf area/foliage distribution. Assimilation rates of 'pruned' trees were manipulated to simulate changes with time measured on pruned trees in the field. Changes in leaf area were as per Simulation 1. (3) Changes in leaf area/foliage distribution but not A . Leaf area/foliage distribution of 'pruned' trees was manipulated to simulate changes with time measured in pruned trees in the field. Changes in A were as per Simulation 1. (4) Changes in both A and leaf area/foliage distribution. Both A and leaf area/foliage distribution of 'pruned' trees were manipulated concurrently to simulate those measured in the field.

Results

Cumulative leaf area index (L) and distribution of light in the crown

At the start of the field experiment, L of unpruned trees was 6.1. It increased to a maximum six months after pruning, and then gradually declined to 4.1 by the end of the experiment. A seasonal trend was not obvious, but it may have been masked by changes associated with canopy closure. The 50%-pruning reduced L from 6.3 to 3.5, and the 70%-pruning reduced L from 6.6 to 1.9 (Table 2); the pre-pruning means for L were not statistically different between treatments. In the pruned treatments, maximum L was measured 13 months after pruning.

The relationship between L and Q_f was described by the equation:

$$Q_f = L_i^{-0.174} \quad (r^2 = 0.82, P = 0.0001), \quad (15)$$

where L_i is cumulative leaf area above height i (Figure 2). The same relationship applied to all pruning treatments ($P > 0.05$). Approximately 95% of light was intercepted by an L of 4.0,

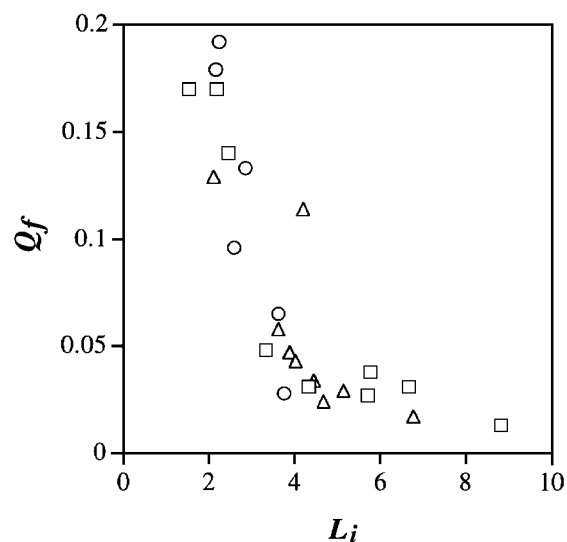


Figure 2. Relationship between cumulative leaf area index (L_i) and fraction of light at any point in the crown (Q_f), measured for unpruned (□), 50%-pruned (△), and 70%-pruned (○) trees 12 months after pruning.

resulting in low irradiances in the lower crowns of unpruned trees. Consequently, there was only a slight reduction in intercepted Q as a result of the 50%-pruning treatment, although the 70%-pruning treatment had a greater effect on intercepted Q .

The extinction coefficient, k_i , at the base of the crowns of unpruned trees was 0.53. It did not differ significantly between pruning treatments, but increased with height in the crown ($P < 0.05$) (Table 2), suggesting that the relationship between Q_i and L did not follow Beer's Law.

Carbon use efficiency, Y

Carbon use efficiency, Y , increased with height in the crown (Table 3), from 0.18 in the 0–50% height zone to 0.44 in the 90–100% height zone ($P < 0.05$). It did not differ between pruning treatments ($P > 0.05$). The low value in the 0–50% height zone reflected the high leaf dark respiration rates (r_i) measured at the base of the height zone (Table 1).

A_c , R_i , and G_d

Irrespective of pruning treatment, there was considerable variation in G_d , A_c and R_i with season, and winter values were up to 30% lower than summer values (Figures 3A–I), reflecting low temperatures and incident light during winter (Figures 1A and 1B). In the unpruned treatment, however, this trend was masked to some extent by the reduction in total R_i because of leaf senescence associated with canopy closure (crown lift).

In unpruned trees, the 0–50% height zone contributed approximately 40% of total A_c at the start of the experiment (Figure 3B). However, because of high rates of R_i (Figure 3C), this height zone only contributed 20% to total G_d (Figure 3A). Within 125 days (4 months), the contribution was negligible and sometimes negative (negative data not shown) as A_c approximated R_i in this height zone. In the 50–70% height zone G_d also declined with time, but not to the same extent as in the 0–50% height zone.

The 50%-pruning treatment reduced G_d , A_c and R_i by 35, 38 and 71%, respectively (Figures 3D–F). The relative contribution of the 50–70% height zone of this treatment to total A_c and G_d gradually declined with time (Figures 3D and 3E), whereas R_i remained relatively constant (Figure 3F). As a consequence, by the second winter period (approximately 450 days into the experiment), G_d in this zone was often zero and sometimes negative (data not shown). The 70%-pruning treatment reduced A_c , R_i and G_d by 83, 93 and 77%, respectively (Figures

3G–I). Irrespective of pruning treatment, G_d remained relatively constant with time in the 70–90% height zone, and increased with time in the 90% height zone as leaf area increased.

Figure 4 presents G_d for the three pruning treatments, expressed in relative terms as a percentage of the pre-pruning value of G_d . In unpruned trees, maximum G_d estimated in the second summer period was 20% less than the pre-pruning value, as a result of a high respiration cost. The relative G_d of 50%-pruned trees reached the same value as that of unpruned trees approximately 110 days after pruning, and remained at a value similar to unpruned trees for the rest of the experiment. Although relative G_d of 70%-pruned trees increased from 0.23 immediately after pruning to 0.61 during the second summer period, values never reached those of unpruned or 50%-pruned trees except during the first winter when respiration costs were much lower for 70%-pruned trees than for the other treatments.

Sensitivity of G_d to r

The mean ratio of r :N was approximately 1:1 when calculated for the whole crown. It was equivalent to $2.63 \text{ g C g}^{-1} \text{ N year}^{-1}$, which is similar to the value of $2.23 \text{ g C g}^{-1} \text{ N year}^{-1}$ reported by Sheriff and Nambiar (1991) for *E. globulus*. When the model was run with observed values of r , predicted volume increment ranged between 70 and 100% of observed values (Table 4), suggesting that the model adequately represented the system. However, when the model was run assuming that the ratio of r :N was constant through the crown, there was a closer match between observed and predicted volume increments for unpruned and 70%-pruned trees (~10% improvement in prediction).

Importance of changes in A_{max} or leaf area/foliage distribution in determining G_d

The results of the sensitivity analysis differed slightly from those presented in Figure 4. Figure 4 summarizes estimated G_d of individual field-grown trees that differed in height, leaf area and foliage distribution. The sensitivity analysis involved estimation of G_d based on theoretical individual tree crowns that were identical at the start of the simulations. Cumulative G_d estimated for field trees and from the simulations differed by 4, 1 and 16% for 0, 50 and 70%-pruned trees, respectively (Table 5). The large difference associated with 70%-pruned trees reflected loss of dominance in one of the field-grown trees.

In the sensitivity analysis, Simulation 1 predicted that, if there were no changes in A or leaf area/foliage distribution resulting from pruning, the relative G_d of 50%-pruned trees would gradually increase and reach the value of unpruned trees within 420 days (14 months) of pruning (Figure 5A). However, the initial reduction in G_d resulting from this treatment would lead to approximately 12% lower cumulative G_d by the end of the experimental period (Figure 5B); consequently, a reduction in height and diameter growth might be expected. This simulation predicted that the relative G_d of 70%-pruned trees would never recover to the value of unpruned trees over the period of the experiment (Figure 5A), and cumulative G_d would be

Table 3. Carbon use efficiency (Y) averaged from daily values estimated for the 612-day period of the experiment. There were no significant differences between pruning treatments ($P > 0.05$), but there was a significant height zone effect ($P < 0.01$).

| Height zone | Carbon use efficiency |
|-------------|-----------------------|
| 0–50% | 0.18 ¹ |
| 50–70% | 0.33 |
| 70–90% | 0.39 |
| 90–100% | 0.44 |

¹ Least squares standard error = 0.035.

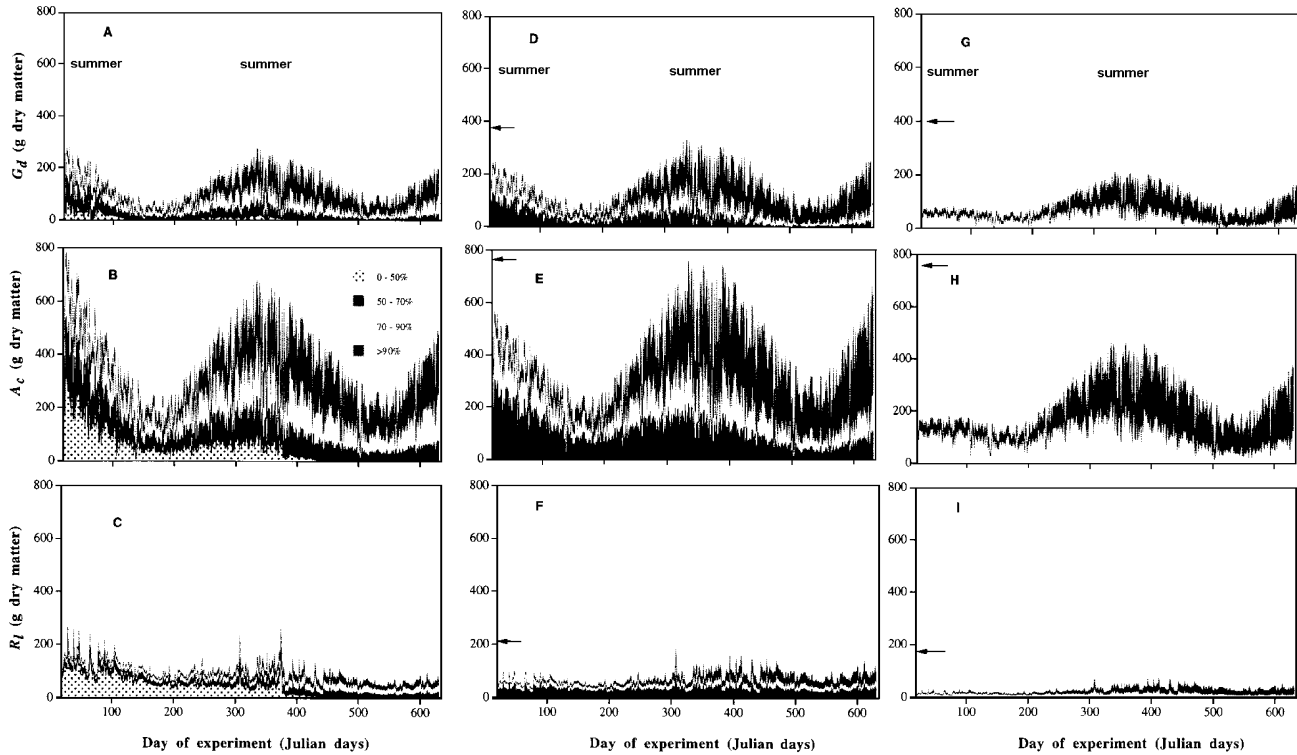


Figure 3. Daily (A) net biomass production (G_d), (B) gross CO_2 assimilation (A_c), and (C) leaf dark respiration (R_l) of unpruned trees; (D) G_d , (E) A_c , and (F) R_l of 50%-pruned trees; and (G) G_d , (H) A_c , and (I) R_l of 70%-pruned trees. Values were estimated on a daily basis for the 612-day period of the experiment. Arrows indicate the pre-pruning values.

approximately 33% less than that of unpruned trees at the end of the experiment (Figure 5B).

Simulation 2 predicted that changes in A alone would result in the relative G_d of 50%-pruned trees reaching a value similar to that of unpruned trees within 125 days (four months) of pruning, and greater relative G_d than unpruned trees during the second summer period (Figure 5C). The crowns of 70%-pruned trees would have a relative G_d similar to, but never

greater than, unpruned trees within 460 days (15 months) of pruning (Figure 5C). Cumulative G_d of 50%-pruned trees would increase to the same value as unpruned trees within 420 days (14 months), but cumulative G_d of 70%-pruned trees would still be 17% less than that of unpruned trees at the end of the experiment (Figure 5D).

In Simulation 3, it was predicted that changes in leaf area and foliage distribution alone would reduce the time taken for relative G_d of 50%-pruned trees to reach the value of unpruned trees from 420 to 120 days. However, although this physiologi-

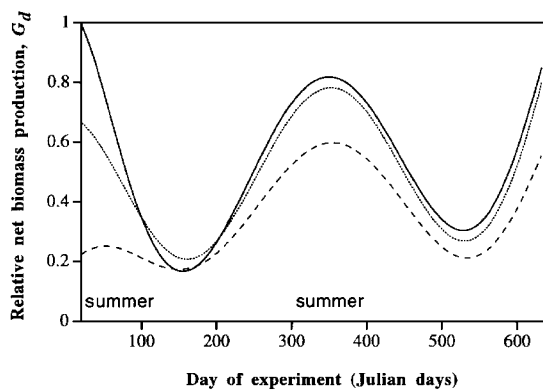


Figure 4. Observed relative net biomass production (G_d) of unpruned (—), 50%-pruned (···) and 70%-pruned (---) trees. Values are relative to G_d immediately before pruning.

Table 4. Estimated and observed mean cumulative volume increment for the first 365 days of the experiment. The estimate was made from G_d and assumed that partitioning of belowground dry matter was 0.50. Partitioning of aboveground dry matter to stem was 0.65 for three-year-old trees (Pinkard and Beadle, unpublished data). Numbers in brackets are least squares standard errors.

| Pruning treatment | Volume increment ($\text{m}^3 \text{ha}^{-1}$) | | |
|-------------------|--|------------------------|-------------|
| | Estimated ¹ | Estimated ² | Observed |
| Unpruned | 52.3 (8.0) | 58.0 (8.0) | 63.8 (8.0) |
| 50%-pruned | 63.5 (5.9) | 64.9 (5.9) | 64.6 (26.6) |
| 70%-pruned | 42.0 (12.8) | 39.1 (12.8) | 31.9 (11.0) |

¹ Estimated using observed values of r .

² Estimated assuming a constant ratio of r :foliar N.

Table 5. Cumulative G_d (kg tree^{-1}) estimated for field trees and from Simulations 1, 2, 3 and 4 (S1, S2, S3 and S4, respectively) over the 20 months following pruning.

| Pruning treatment | Cumulative G_d (kg tree^{-1}) | | | | |
|-------------------|--|------|------|-------|-------|
| | Field trees | S1 | S2 | S3 | S4 |
| Unpruned | 92.2 | 96.4 | 96.4 | 96.4 | 96.4 |
| 50%-pruned | 113.1 | 80.2 | 98.1 | 108.5 | 112.2 |
| 70%-pruned | 72.7 | 61.6 | 79.0 | 68.2 | 86.6 |

cal response would increase relative G_d of 70%-pruned trees, it would not increase it to the value of unpruned trees within the period of the simulation except for a short period during the first winter (Figure 5E). It was predicted that cumulative G_d of 50%-pruned trees would increase to a value approximately 22% greater than that of unpruned trees in this scenario. A small increase (~6%) in cumulative G_d of 70%-pruned trees still resulted in G_d being substantially lower than that of unpruned trees at the end of the experiment (Figure 5F).

In Simulation 4, it was predicted that the combined physiological responses would result in the relative G_d of 50%- and 70%-pruned trees reaching the value of unpruned trees within 120 and 130 days, respectively (Figure 5G). It was predicted

that cumulative G_d of 50%-pruned trees would be 27% greater, and cumulative G_d of 70%-pruned trees would be 5% less than that of unpruned trees at the end of the experimental period (Figure 5H).

Discussion

Effect of physiological responses on G_d

Following pruning of *E. nitens*, several physiological responses occur. Rates of instantaneous A_{max} increase (Pinkard et al. 1998) as a result of greater rates of biochemical reactions involved in carbon fixation (Pinkard and Beadle 1998b). Other responses to pruning included changes in leaf morphology, crown architecture, partitioning between foliage and wood, and leaf area and foliage distribution (Pinkard 1997). These physiological responses to pruning, however, have no impact on tree growth unless they increase G_d . It was found that physiological responses were important in increasing G_d following pruning. Similarly, Heichel and Turner (1983) found that physiological responses such as increased A_{max} and changes in leaf area following partial defoliation increased G_d of *Acer rubrum* L. and *Quercus rubra* L. by 19 to 67%. In *Pinus resinosa* Ait. similar physiological responses following

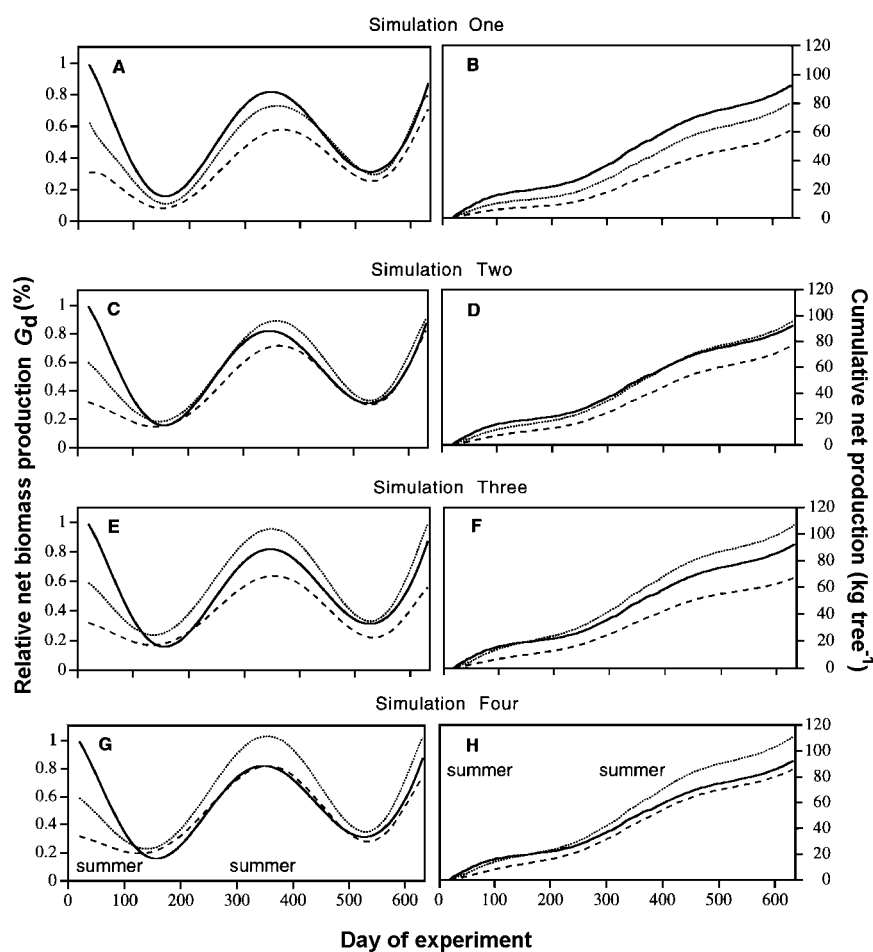


Figure 5. Simulated relative and cumulative net biomass production (G_d) of unpruned (—), 50%-pruned (···) and 70%-pruned (---) identical 'trees.' (A) Relative and (B) cumulative G_d with no change in A or leaf area; (C) relative and (D) cumulative G_d with changes in A only; (E) relative and (F) cumulative G_d with changes in leaf area and foliage distribution only; (G) relative and (H) cumulative G_d with changes in both A and leaf area and foliage distribution.

25% defoliation resulted in greater G_d than in foliated plants (Reich et al. 1993). In our study, it was possible through sensitivity analysis to estimate the relative importance of the main physiological responses to pruning (i.e., changes in A_{max} and in leaf area and foliage distribution), as well as the combined effect of these responses. Changes in A were important following both pruning treatments, and increased cumulative G_d by 20% in 50%-pruned trees, and 25% in 70%-pruned trees by the end of the experiment. However, changes in leaf area and foliage distribution had a much greater effect on G_d of 50%-pruned trees than did changes in A , and resulted in a G_d greater than that of unpruned trees by the end of the simulation period. Because total height and diameter were not affected by the treatment (Pinkard and Beadle 1998a), it is possible that dry matter partitioning was affected by the treatment (Cannell 1985, Pinkard 1997). Changes in leaf area and foliage distribution were minimal following 70%-pruning, reflecting a greater reduction in carbon-fixing capacity of the crown associated with this treatment compared to the 50%-pruning treatment. Thus, changes in leaf area and foliage distribution had only a small effect on cumulative G_d following 70%-pruning.

Can G_d explain growth responses?

Developing an understanding of G_d can be of considerable assistance in understanding growth responses to silvicultural treatments. The estimated impact of pruning on G_d was consistent with the growth responses measured in an earlier experiment in which 50%-pruning had no effect on height or diameter growth, whereas 70%-pruning decreased diameter, and to a lesser extent, height increment (Pinkard and Beadle 1998a). Height and diameter increment were not affected by 50%-pruning despite the initial decrease in G_d suggesting that stored carbon was utilized to maintain growth for the first four months after pruning. Similarly, Nygren et al. (1996) estimated that growth of *Erythrina poeppigiana* (Walpen) F. Cook was dependent on stored carbohydrate for a period of two months after pruning. Trees commonly maintain moderate carbohydrate reserves that are depleted at times of large demand (Cannell 1985), a strategy that has obvious survival advantages (Trumble et al. 1993).

However, it should be noted that the model was not developed to estimate stem growth, and volume estimates differed from observed values by up to 30%, most probably because of a lack of information on changes in biomass partitioning between roots and shoots following pruning. It is generally agreed that a balance is maintained between root and shoot biomass (e.g., Cannell 1985). Following treatments such as pruning, more biomass is partitioned to shoots at the expense of roots until a balance is restored between above- and below-ground biomass (Cannell and Dewar 1994). When estimating stem volume from net biomass production, we allocated 50% of biomass to roots irrespective of pruning treatment. In order to estimate the effect of pruning on stem growth more accurately, a more detailed understanding of how root:shoot partitioning changes is necessary.

Management implications

The impact of pruning is related to the degree to which radiation interception by the crown is affected (Chang 1968, Monteith 1972, Linder 1984). In this experiment, 95% of light was intercepted by an L of 4.0, although the maximum L value was 7.8. The 50%-pruning treatment reduced L to 3.5, and the physiological responses following this treatment increased G_d sufficiently to compensate for the small reduction in intercepted radiation associated with the treatment. The 70%-pruning treatment reduced L to 1.9, and physiological responses were insufficient to allow complete compensation. A pruning regime should not reduce L below a value that can be compensated for with physiological responses. This value will vary between species and sites, because L increases with increasing water and nutrient availability, and species vary in foliage distribution patterns (Chang 1968, Grier and Running 1977, Waring et al. 1977). In this experiment, L at the base of the crowns was approximately 6.0 at the time of pruning, thus 50% of the crown length could be removed. However, on sites with poor nutrient or water availability, it is probable that less severe pruning would affect growth because of a lower L .

The timing and severity of subsequent pruning will also be determined by the L of the stand, and by the rate of recovery of L following pruning. For example, in *E. nitens*, L of 50%-pruned trees increased to 5.5 13 months after pruning, and removal of the 50–70% height zone at that time only reduced L to 4.2. However, the L of 70%-pruned trees remained below 4.0 for the duration of the experiment.

In Australia, selective pruning regimes are applied to *E. nitens* plantations, in which approximately one-third of stems are pruned (Gerrand et al. 1997). The alternative management scenario, common in conifers (e.g., Sutton and Crowe 1975), is to prune all stems in the stand. In selective pruning regimes, there is considerable potential for pruned stems to be out-competed by unpruned neighbors (Sutton and Crowe 1975, Karani 1978), which was a possible long-term outcome for 70%-pruned trees. However, biomass production was only temporarily affected by 50%-pruning and the timing of pruning was probably critical. Pruning at the time of canopy closure preempted a natural and rapid decline in G_d of the lower crown. Pruning before canopy closure would be expected to increase the relative impact on G_d , because of greater irradiance in the lower crown at that time.

The model

The model allowed us to explore the effect of pruning on G_d , and the relative importance of physiological responses to pruning on G_d . Although volume estimates from biomass production indicated that the model adequately represented the system, the lack of information on changes in above- and below-ground biomass partitioning means that the model has limited application for accurately estimating the effects of pruning on stem volume in its present form.

Sensitivity analysis indicated that estimates were improved when it was assumed that the relationship between leaf dark respiration and foliar nitrogen content remained constant throughout the crown. Many canopy production models as-

sume that r is proportional to foliar N (e.g., Wang and Jarvis 1990, Sands 1995, Dewar 1996). The high r and ratio of $r:N$ observed at the base of the 0–50% height zone probably were not indicative of values throughout the height zone, and may have reflected changes in metabolic processes associated with senescence at the crown base (Larcher 1975). The model interpolated r between sampling positions in the crown, but the 10% improvement in volume predictions obtained when it was assumed that r was proportional to N suggests that samples from a larger number of crown positions would have improved accuracy.

Carbon use efficiency (Y) of the crowns was lower than the mean value used by other researchers (e.g., Battaglia and Sands 1997) when modeling production of eucalypts. This was related to the high leaf dark respiration rates measured in this experiment compared to rates measured for other species (Pereira et al. 1986, Battaglia et al. 1996). However, the observed values of r were similar to values measured in other experiments with *E. nitens* (Pinkard and Beadle 1998b).

Beer's Law has been widely used to model the light environment in plant canopies (e.g., Wang and Jarvis 1990, Sands 1995, Dewar 1996, Landsberg and Hingston 1996), the underlying assumptions of which are that light intercepting particles are infinitely small and randomly distributed through the extinction space; and the suspension medium is translucent (Larsen and Kershaw 1996). Larsen and Kershaw (1996) showed that, for a range of simulated patterns of foliage distribution, these assumptions did not affect the mean light extinction below the canopy base. However, variation in foliage distribution had a large effect on predicted light extinction in different crown positions. The estimated value of k_i at the base of unpruned *E. nitens* trees was similar to values presented for other eucalypt species (e.g., 0.57 for *Eucalyptus maculata* Hook., Jarvis and Leverenz 1983; 0.50 for *E. nitens* and *E. globulus*, Linder 1984). However, light extinction in other crown positions did not follow the pattern expected by Beer's Law. Although the mean prediction of light extinction obtained by Beer's Law may be accurate at the canopy level, use of Beer's law may be inappropriate for individual tree crowns or portions of crowns (Larsen and Kershaw 1996). In such cases, an understanding of light extinction in different portions of the crown, as used in the model described above, may be necessary for accurate estimates of G_d .

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