



# **Silvicultural Design Support for Farm Forestry**

**RIRDC/L&WA/FWPRDC Joint Venture Agroforestry Program**

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Silviculture (the growing and tending of trees in agroforestry) models currently used in industrial forestry are not very helpful because many of the assumptions inherent in them do not apply to a lot of common situations.

This research describes a new model called AGGRO, specifically designed for farm forestry applications. It provides indicative yields for a range of farm forestry scenarios. It is informed by the many valuable silvicultural experiments conducted in Australia, and passes this wealth of information onto small growers. It aims to remove some of the uncertainty impeding the adoption of farm forestry, and make it possible for land managers to consider tree growing as an economic part of the farm enterprise.

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# Foreword

The re-incorporation of trees into farming systems is a means of ameliorating land degradation, maintaining long-term sustainability of agricultural enterprises and increasing farm productivity. However, uncertainty about the financial returns from establishing and managing trees, and the outcomes of silvicultural actions like thinning and pruning, can impede tree planting.

Models widely used in industrial forestry in Australia are of little use to farm forestry situations because many of the assumptions do not apply in situations where trees are widely-spaced or planted in belts, or use silvicultural management such as thinning or pruning. These models are also difficult to apply on sites where a forest crop has not previously been grown.

This publication describes a new model called AGGRO, specifically designed for farm forestry applications. It provides indicative yields for a range of farm forestry scenarios. It is informed by the many valuable silvicultural experiments conducted in Australia, and passes this wealth of information onto small growers. It aims to remove some of the uncertainty impeding the adoption of farm forestry, and make it possible for land managers to consider tree growing as an economic part of the farm enterprise.

This project was funded by the Joint Venture Agroforestry Program (JVAP), which is supported by three R&D Corporations - Rural Industries Research and Development Corporation (RIRDC), Land & Water Australia (L&WA), and Forest and Wood Products Research and Development Corporation (FWPRDC). The Murray-Darling Basin Commission (MDBC) also contributed to this project. The R&D Corporations are funded principally by the Australian Government. State and Australian Governments contribute funds to the MDBC.

This report is an addition to RIRDC's diverse range of over 1800 research publications. It forms part of our Agroforestry and Farm Forestry R&D program, which aims to integrate sustainable and productive agroforestry within Australian farming systems. The JVAP, under this program, is managed by RIRDC.

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The modelling work presented within this report builds on and extends modelling work (PROMOD, Battaglia and Sands 1997) developed in the Cooperative Research Centre for Sustainable Production Forestry and CSIRO Forestry and Forest Products.

Thanks also to Dale Worledge, Daryl Mummery, Ros Pilbeam, all staff at WA Plantation Resources in Manjimup, Sven Ladiges and Ann Wilkinson for technical and logistic support. Thanks also to Drs Miko Kirschbaum and Don White for their helpful comments on portions of the manuscript.

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# Executive Summary

## What the report is about

This research developed the AGGRO model as a tool to support farm forestry development. A cutdown version of the model has since been incorporated into the Farm Forestry Toolbox (available from [www.privateforests.tas.gov.au](http://www.privateforests.tas.gov.au)).

## Who is the report targeted at?

While the AGGRO model itself passes on a wealth of information to small growers about indicative yields for a range of farm forestry scenarios, informed by the many valuable silvicultural experiments conducted in Australia, the detailed science presented in this report informs researchers and scientists with an interest in the technical details underpinning model development.

## Background

The AGGRO model was developed through this research in recognition that models used in industrial forestry are not well suited to farm forestry situations, which typically fail to predict growth realistically and do not account for silvicultural management, like thinning and pruning. The model is informed by a significant body of information collected from silvicultural experiments conducted throughout Australia. It provides farm foresters and researchers with more reliable information to guide tree planting and management.

## Aims/Objectives

The primary objective of this study was the development of a user-friendly PC package (the AGGRO model) for the prediction of wood volume for a range of planting designs (including wide-spaced and strip plantings) and thinning of *Eucalyptus globulus* and *E. nitens* given only a few simple and easily obtained site descriptors. The model developed also predicts branch biomass and average tree size and so gives some indication of end product suitability.

## Methods used

Field work and analysis were undertaken to better define the physiological and growth response of plantation grown *Eucalyptus globulus* trees to wide-spacing. This information was then used to underpin AGGRO, a simple, easy-to-use predictive model within an Excel spreadsheet format. This model was subsequently verified for growth predictions of *E. globulus* and *E. nitens*.

## Results/Key findings

The AGGRO model is a powerful tool that encapsulates not only the knowledge generated in this report, but years of research by many scientists. It puts at the fingertips of the farm forester a powerful scenario generation tool.

The major outcomes of the model predictions are reported according to:

- impact of spacing on growth and form
- patterns of light interception by tree crowns
- nitrogen distribution in tree crowns
- spacing effects on nitrogen and photosynthesis
- modelling production
- implications for farm forestry.

## **Implications for relevant stakeholders**

The research outlines the types of question that can be explored and how silvicultural regimes and planting layouts can be tailored to site characteristics. The detailed physiological and mensurational work in this project has developed a considerable knowledge base on the responses of photosynthetic and morphological traits. This information is inevitably complex. However, the work has shown that by embedding this knowledge into a simple-to-use decision support system, the implications of this research can become accessible to end-users.

## **Recommendations**

This project recommended the incorporation of AGGRO into the Farm Forestry Toolbox, which includes an economic evaluation tool. Together, these tools will enable farm foresters to evaluate the economic consequences of plantation project development and management options on their lands with greater confidence. An agreement between JVAP and the Cooperative Research Centre for Sustainable Production Forestry and Private Forests Tasmania was reached at the conclusion of this project, and a cutdown version of AGGRO has now been incorporated in Version 6 of the Farm Forestry Toolbox.

# 1. Introduction

## 1.1 Background to the Study Problem

Process-based models now play an important role in industrial forestry. Models such as PROMOD (Battaglia and Sands 1997) and 3PG (Landsberg and Waring 1997) are used widely for site selection, yield prediction and to a lesser extent silvicultural management (e.g. Sands *et al.* 2000, Pinkard and Battaglia 2001). The uptake of these particular models by forestry management reflects their transparency (*sensu* Passioura 1973), ease of use and parameterisation and ability to provide robust predictions with limited site-specific data.

The relative simplicity of these models is the reason these models have been used by the industrial sector rather than more complex models (e.g. MAESTRO Wang and Jarvis 1990, TREEGRO Weinstein *et al.* 1991, EDINBURGH-ITE Thornley 1991) that portray the soil-tree-atmosphere system in a more realistic manner (*sensu* Battaglia and Sands 1998). However, the naivety of many of the assumptions embedded within these ‘simple’ models reduces the range of questions to which these models can be applied appropriately. Principal among these assumptions are those of light interception and the distribution of nitrogen and photosynthetic capacity within the forest canopy. It is assumed by these models that: 1) the forest canopy can be treated as a ‘big-leaf’ through which light is attenuated using the Monsi-Saeki equation (analogous to the Beer-Lambert law in physics for the attenuation of light through a murky medium); 2) that either canopy nitrogen and photosynthetic activity is distributed with light in the canopy (as in PROMOD, for example); or 3) that light-utilisation efficiency is unaffected by plantation spacing and tree arrangement (as in 3PG, for example). It appears from the efficacy of models such as PROMOD and 3PG that the simplifications do not result in major errors in prediction in close-spaced, monoculture-plantations, or if the errors are large they are masked by other sources of error. However, in situations where tree canopy-cover is less uniform these assumptions may become less acceptable and predictions less reliable.

Increasingly trees are planted as part of on-farm business for industrial wood production and the emerging market in carbon credits raises the prospect of such plantations being used as carbon offsets. Annual plantings rose from around 30 000 ha in 1995 to around 100 000 ha in 2001 (Wood *et al.* 2001). The majority of these plantations were on cleared farmland, often under joint venture arrangements. Decision-support tools such as the Farm Forestry Toolbox and CAMFor (Richards and Evans 2000) provide partial and practical assistance for such activities. Trees are also being deployed into the agricultural landscape as part of revegetation activity to create sustainable landscapes. Included in these activities are treebelts on sloping land to use lateral water movement, tree belts in alley designs to access soil water from land occupied by crops or pastures and widely spaced tree plantings to maintain hydrological balance while allowing the benefits of shelter and animal husbandry. These later applications with heterogeneous canopy-cover provide substantial challenges for the existing tools (the Farm Forestry Toolbox contains PROMOD and CAMFor utilises the production side of 3PG). A good example of this is seen in Figure 1.1 below in which 3PG is calibrated to predict growth at regular spacings but fails to predict tree growth at wide spacing.

Silvicultural interventions, such as pruning and thinning, are applied to both widely and closely spaced stands of trees. These activities substantially disrupt the canopies of trees and require the prediction of growth in heterogeneous light environments. A wide-spaced or heavily thinned plantation when combined with a pruning regime that utilises farm labour during the quieter times of year may be a serious economic proposition if saw or veneer logs fetch a premium price. On high value cropping or dairy land, for example that typical of north-western Tasmania, trees may not be able to compete with alternative land-uses on a broad-acre basis, but the addition of trees as widened shelterbelts may provide both an increase in production from the agricultural land-use and yield a return from timber production. In dry landscapes the use of thinning, perhaps in association with pruning, can be used to minimise the risk of catastrophic drought death of plantations as occurred in

southwest Western Australia in the mid-1990's (Dutkowski 1995). In these dry landscapes where trees rely on ground-stored water through the summer months, there is effectively a maximum growth rate that can be sustained by the available water. Control of plantation leaf area index through wide spacing or thinning is one of the few feasible ways to ensure that growth rates do not exceed sustainable limits. In none of these situations is it currently possible to predict wood yield or quality using empirical growth models unless trees have been grown at similar spacings and under the same weather conditions previously. As we have discussed, application of the existing management-oriented process-based models is unreliable.

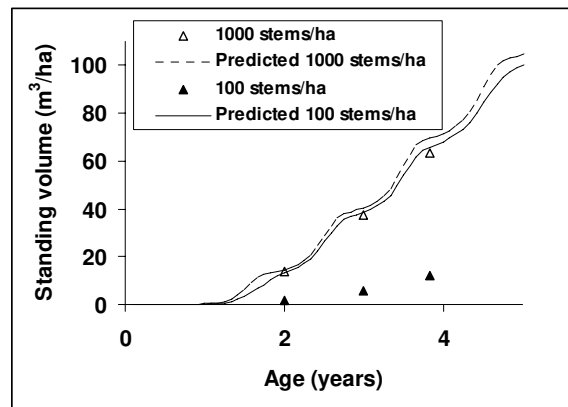


**Figure 1.1.** Observed volume growth for two spacings at Kamman, Western Australia (data and description contained in subsequent chapters) and predictions of volume growth made with 3PG.

## 1.2 Study Objectives

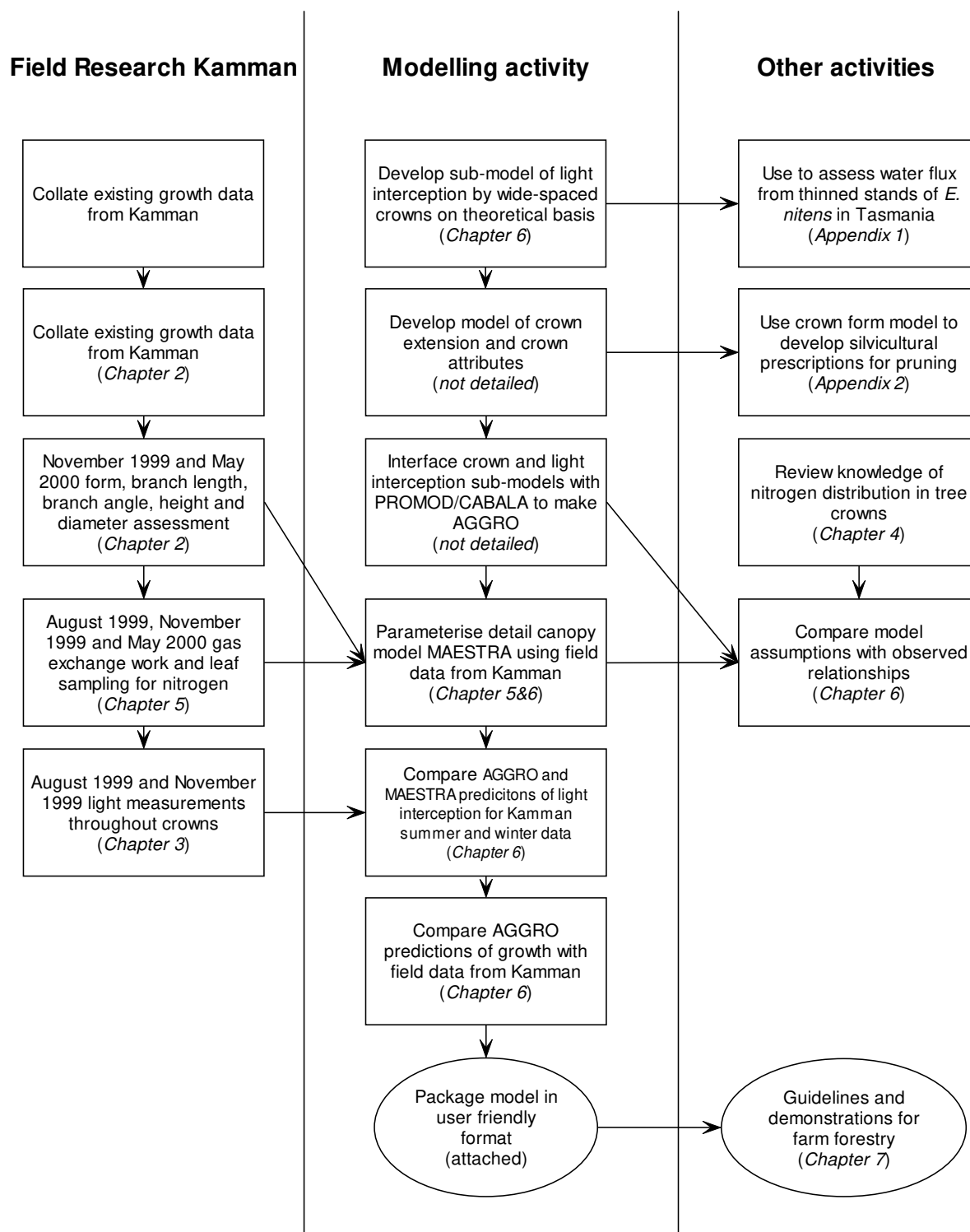
The primary objective of this study was the development of a user-friendly PC package for the prediction of wood volume for a range of planting designs (including wide-spaced and strip plantings) and thinning of *Eucalyptus globulus* and *E. nitens* given only a few simple and easily obtained site descriptors. The model developed also predicts branch biomass and average tree size and so gives some indication of end product suitability.

The process-based forest-growth model chosen to underpin this study was the CRC for Sustainable Production Forestry model PROMOD and its later reformulation into the more complex model CABALA. The model presented in this work represents a simplification of this later model, specifically adapted for farm forestry applications.

A key step to achieving this objective was to better understand the effects of spacing and crown arrangement on the light environment within crowns and how this affected physiological processes. This data was an important part of validating assumptions made by the model and enables the limits to model use to be defined. Suitable data is not readily available of sufficient quality and covering the range of tree arrangements necessary for model and concept testing so we carefully monitored processes, tree growth and tree form at an experimental plantation at Kamman, near Manjimup, Western Australia. At the Kamman agroforestry trial established in 1996 by Bunnings Tree Farms (now WAPRES), *Eucalyptus globulus* trees are laid out in a traditional block planting (4 x 2 metre spacing), as single trees (10 x 10 metre spacing), as single rows and as triple rows. All rows are oriented in a north-south direction. Five replicate blocks of each treatment are present. This experiment provided an ideal opportunity to measure the necessary process, growth and environmental data for model validation.

As part of delivering the project outputs the model developed in this work was used to describe growth curves for a range of farm forestry situations and silvicultural options.

## 1.3 Research Plan and Rationale to the Work



## 2. How Tree Form Changes with Spacing and Why: Implications for Farm Foresters<sup>1</sup>

### 2.1 Introduction

Trees are planted on agricultural land for many reasons. Consequently, a variety of planting arrangements and tree densities are used. The value, volume and merchantability of timber from farm tree plantings are affected by layout and stem density, as are the silvicultural requirements for specific end products. Most of the technical and scientific information available, however, is related to block-plantings and not well suited to the full suite of farm forestry planting designs.

Spacing and planting layout influence tree growth and form (Schönau and Coetzee 1989, Gerrand *et al.* 1997, Deans and Milne 1999, Neilsen and Gerrand 1999). In plantations, reducing stocking by thinning or through low initial stocking, respectively, releases trees from or delays the onset of intra-specific competition. This results in increased growth rates in individual trees (Gerrand *et al.* 1997, Medhurst *et al.* 2001) but may reduce overall stand volume at harvest (Hamilton and Christie 1974, Neilsen and Gerrand 1999). Increased spacing also has a major impact on the acceptability of timber for products such as saw log or veneer as it is associated with increased branch size and a greater number of large branches (Schönau and Coetzee 1989, Deans and Milne 1999, Neilsen and Gerrand 1999). Other characters such as wood density and strength, visually graded wood quality, crown shape and stem taper can also be affected (Persson *et al.* 1995, Deans and Milne 1999). Consequently, the trade-off between growth and form needs to be considered when managing stands for specific products. The few published plantation recommendations that are available can provide useful information to farm foresters. Many of these, however, are not applicable beyond the context of a given density, closed canopies and a restricted range of species. Determining relationships between factors such as planting layout and density, the consequent environment, tree form and growth is a powerful means of anticipating the effects of tree layout. These links, however, are rarely made or explained when spacing experiments are discussed, but in many cases would allow the effect of spacing on tree form and volume to be anticipated.

Many of the planting arrangements used in farm forestry are not tractable to current modelling procedures, and most current forestry growth models are designed for conventional plantations. Many process-based models assume that: canopy closure has occurred (Stage 1973); stand densities are constant; only one species is present (Zhang *et al.* 1996); nitrogen concentration within the crown follows particular distribution profiles (Sands 1995) and allometric relationships are constant along the length of stems, among stems and between stands (Landsberg and Waring 1997). These assumptions do not necessarily continue to apply following thinning or pruning or in farm forestry situations such as strip plantings and wide spacings. These types of planting layouts or silvicultural interventions result in discontinuous canopies that require complex calculations to estimate light interception and result in tree forms, and thus allometric relationships, that vary with spacing. Multiple species plantings include pasture or crops, which may compete with trees for resources. Empirical models are difficult to apply to sites where a tree crop has not previously been grown or to novel silvicultural regimes. These limitations are also present in many current agroforestry models. The Hybrid-PARCH model (Mobbs *et al.* 1998) for example, assumes a homogenous tree canopy. The silvopastoral model ALWAYS (Bergez *et al.* 1999) is similarly inflexible. ALWAYS also assumes the absence of competition for nitrogen (N) between pasture and trees, based on the incorrect supposition that trees

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<sup>1</sup> Based on a manuscript developed by F.L. Henskens, M. Battaglia, M.L. Cherry and C.L. Beadle and published in *Trees* 15, 365-777.

extract their required N from lower soil depth unavailable to the sward. Consequently, the predictive facility available to farm foresters from existing process-based and empirical models is limited.

### **2.1.1 Objectives**

In this report we examine relationships among tree form, growth, light environment and canopy photosynthetic processes and discuss how these change with planting layout in the common farm forestry species Tasmanian blue-gum (*Eucalyptus globulus*). With the use of a simple equation describing plantation growth we show how an understanding of these processes can be used to anticipate the effect of planting layout on tree growth and form. The implications of these findings for modelling typical farm forestry situations are discussed.

## **2.2 Methods**

### **2.2.1 Site details**

Experiments were conducted between August 1999 and May 2000 in a plantation of *Eucalyptus globulus* near Manjimup in southwest Western Australia. The plantation was established on a former pasture site in 1996, with rows running at 340° to 160° (approximately north-south). It contained seven different planting configurations arranged in five replicate blocks. Of these configurations, four were chosen as covering the range of those deployed in farm forestry practice. These were: a) conventional block-planting (2 x 4 m, 1 250 stems ha<sup>-1</sup>); b) triple rows set at 12 m intervals (2.5 x 4 m, 600 stems ha<sup>-1</sup>); c) single rows set 10 m apart (2.5 x 4 400 stems ha<sup>-1</sup>); and d) isolated trees set 10 m apart (100 stems ha<sup>-1</sup>). Physiological and biomass measurements were concentrated on three trees per treatment randomly selected from height trees in blocks one and four. These were the only blocks that were completely accessible to the elevated work-platform.

### **2.2.2 Volume**

Tree heights were determined from a subsample of 10 trees per treatment per block. Bunnings Tree Farms (now Western Australian Plantation Resources) supplied 1998 stem height and diameter data. Stem diameters were recorded for all trees of each treatment in all blocks in August 1999 and March 2000. The volume of trees measured for height was estimated using the tree volume equations included in the Farm Forestry Toolbox (<http://www.privateforests.tas.gov.au/toolbox.htm>). Following destructive sampling in May 2000, predicted volumes were found to agree with observed data (no significant difference at 5% and 0.1% levels). Volumes of the remaining trees were calculated using a log (volume) to log (stem basal area) regression relationship, corrected for bias, established from the trees measured for height after the method of Snowdon (1991) and Wilkinson and Neilsen (1995). Equations (S.G. Candy, Forestry Tasmania, pers. comm. 1999) were applied to these data to estimate stand volumes, mean dominant height (*MDH*) and current annual increment of planting layouts.

### **2.2.3 Form**

Tree form and green heights (distance from the ground to the first leaf-bearing branch) were recorded from all trees in all blocks. Tree form was assessed in August 1999 using a modification of the visual ranking method of Raymond and Cotterill (1990). Branch thickness was scored on a 0-5 scale where zero indicates the tree had very thin branches for the site and five denotes very thick branches. Photographs of typical examples of each thickness class were taken to standardise ranking. Branch angle was scored on a similar scale with zero denoting that all branches were horizontal while a score of five indicated that more than half the branches were at a steep angle. Stem straightness was assessed in terms of three characteristics; wobble or cork screw, deviation from vertical and the degree of butt sweep. A composite of these characteristics was evaluated according to the final crop selection criteria developed for *Eucalyptus nitens* by Neilsen and Gerrand (1999).

In May 2000, after completion of all other measurements, the three trees from the block planting, single row and isolated tree treatments were destructively sampled. Diameters, fresh weight, angle from vertical, length and green leaf weight of each branch were recorded. Stem cross-sections cut at

regular intervals and painted with dimethyl yellow were used to determine the area of the sapwood and heartwood zones.

#### **2.2.4 Light**

A single target tree per treatment was randomly selected from the three measurement trees. These trees were divided into three height zones of equal length in August 1999. Height zones were divided into four aspects: north, south, east and west. Each of these was further subdivided into three canopy positions according to distance from the stem (inner, middle and outer). This gave a total of 36 measurement locations per tree.

Light environment was recorded in target trees from block one. Light intensity was measured using Skye PAR quantum sensors (SKP 215, Skye instruments, Powys, UK) placed at 24 of the 36 locations in the tree canopies over 48-h periods in August and November 1999. At the upper and middle canopy height zones, sensors were placed at the outer and middle positions of each aspect plus two other inner canopy positions while in the lower canopy, sensors were attached at the middle position of each aspect. Sensors were secured to platforms placed at the bottom of each height zone along north-south, east-west axes. Sensors were connected to a data logger (Campbell Scientific Inc., Logan, Utah, USA) and instantaneous light readings logged every three minutes over a 24-hour period. A single sensor recorded incident light intensity outside the canopy. Light transmission data are presented as a percentage of the incident light. To simplify comparisons, only data from three hours around midday (1100 to 1300 hours Western Standard Time (WST)) when the sun was directly above the sensors are presented.

#### **2.2.5 Photosynthesis**

Photosynthetic measurements were taken from the three measurement trees in each treatment. Light-saturated net photosynthetic rate ( $A_{\max}$ ) was measured using a portable infrared gas analysis system (CIRAS-1, PPSsystems, Hertshire, UK) fitted with a Parkinson PLC leaf chamber (leaf area 2.5 cm<sup>2</sup>). The leaf chamber was illuminated using a PPSsystems light unit fitted with a quartz halogen class M projection globe. An electric fan was incorporated into the light source to dissipate heat generated by the globe. Measurements were taken from at least two leaves at each of the 36 sampling locations per tree. Additional measurements were taken from the very top of the canopy. The canopy depth sampling positions (canopy position in the results) roughly corresponded to foliage age classes. At the outer canopy, measurements were made on leaves between the fifth and seventh node from the apex. These leaves were classified as apical. Mid-canopy leaves were mature (< two years old but fully expanded). Leaves from the inner portion of the canopy (within 10 cm of main stem) were classified as old (> two years of age). Measurements were made in August 1999, November-December 1999 and May 2000. All measurements were made at the widest point of healthy, entire leaves under ambient CO<sub>2</sub> (ca 350 ppm) with a flow rate of 200 ml min<sup>-1</sup>. The incident photosynthetically active photon flux density (*PPFD*), unless otherwise stated, was 1520  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . All measurements were made between 0900 and 1500 hours (WST).

The response of photosynthesis (*A*) to varying light intensity was measured in November-December 1999 and May 2000 under ambient CO<sub>2</sub>. These measurements were made in the block plantation, single row and isolated tree treatments. Light response curves were obtained from 13 of the 36 measurement locations (including the top) in the trees in which light was measured. Response curves were started at a *PPFD* of 1740  $\mu\text{mol m}^{-2} \text{s}^{-1}$  and reduced in 10 steps to 0  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . At each step leaves were left a few minutes until *A* was constant. An adjustable power supply was used to provide light intensities above 1000  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . Neutral density filters were used to produce *PPFD*s between 0 and 840  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . The order in which trees were sampled was randomly allocated at the beginning of each experimental component. Each measurement period spanned 10-12 days.

## 2.2.6 Data analysis and calculations

Total tree branch cross-sectional area is the sum of branch cross-sectional areas derived from branch diameter. Stem sapwood cross-sectional area (SSA) was calculated from stem diameter at breast height over bark, since heartwood formation had not yet commenced. Leaf green weights were converted to leaf area using specific leaf area (SLA) relationships determined from subsamples of leaves (after Medhurst *et al.* 1999). Relationships between individual branch cross-sectional area and area and weight of leaves on the branch were the same for each treatment. These relationships were used to estimate the leaf area and biomass of each branch, and the results summed to give total tree leaf area and biomass. The relationship between total leaf area and SSA was also uniform across treatments and used to calculate the leaf area of other trees. Similarly constant relationships were found among branch diameter or cross-sectional area and branch length and branch weight. These relationships were used to determine total tree branch biomass. Stem volumes were converted to biomass assuming a basic density of 503 (after Beadle *et al.* 1996, who report a basic density of  $503 \pm 16 \text{ kg m}^{-3}$  for six-year-old *E. globulus*) allowing above-ground allocation patterns and biomass increments to be calculated. The branch cross-sectional area to SSA ratio was used to examine the effect of spacing on the "branchiness" of trees (after Berninger *et al.* 1995).

The length of the longest branch at each aspect in the lower canopy was used to estimate canopy basal area. The fraction of the area covered by trees ( $c$ ) in each treatment was calculated by multiplying the canopy basal area (based on the diameter of the canopy) by the stocking rate and dividing by the plot area. Leaf area index ( $L^*$ ) was the sum of tree leaf areas in the stand divided by stand canopy basal area.

For photosynthetic measurements, leaf dark respiration ( $r_l$ ) light compensation point ( $PFD_0$ ),  $A_{\max}$  and the light intensity at which  $A_{\max}$  occurred were determined from light response curves where  $PPFD$  was zero,  $A$  was zero and where  $A$  was saturated, respectively. Total annual photosynthetic production was the product of annual above-ground maintenance respiration ( $R_m$ ) plus annual above-ground biomass increment.

Growth, individual branch diameter, angle, length, fresh weight and leaf area, total tree leaf area and photosynthetic data and relationships between parameters were analysed using GENSTAT 5.0 ANOVA and regression procedures. Branch thickness class, branch angle class and stem straightness data were analysed using GENSTAT 5.0, CLASS.PRO logistical regressions.

## 2.3 Results

### 2.3.1 Growth

The block and triple row plantings produced the tallest trees with predicted site indices (age 15 years) of 37-38 m and mean dominant height ( $MDH$ ) (age 5 years) of around 17 m (Table 2.1). Single row and isolated tree configurations had a site index of about 34 m and  $MDH$  of between 15 and 16 m. Average stand height, however, did not vary significantly with spacing. The effect of spacing on basal area did not become apparent until canopy closure in denser stands from 1999 onwards. Isolated trees had the greatest basal areas per tree ( $17.5 \text{ cm}^2$  in 1999 and  $31.4 \text{ cm}^2$  in 2000). Trees planted in single rows had smaller basal areas ( $14.2$  and  $23.3 \text{ cm}^2$ , respectively) but block plantation and triple row treatments produced the lowest basal areas of around  $11.3$ - $13.8$  and  $16.0$ - $20.3 \text{ cm}^2$  in 1999 and 2000, respectively (Table 2.1). Consequently, the volume and overall growth of individual trees were greatest in open, widely-spaced configurations and least in the block layout. Stand volume and annual increment on a ground area basis, however, decreased with declining stocking rate because the decrease in tree numbers off-set the increase in tree size (Table 2.1).

**Table 2.1.** The effect of spacing on height, basal area, volume and growth parameters.

| Spacing    | SPH  | Site index (m)    | MDH (m)           | Mean height (m)   | Tree basal area (cm <sup>2</sup> ) |                  |                  | Mean tree volume (m <sup>3</sup> ) |                   |                   |
|------------|------|-------------------|-------------------|-------------------|------------------------------------|------------------|------------------|------------------------------------|-------------------|-------------------|
|            |      | (15 y)            | (5 y)             | 2000              | '98                                | '99              | '00              | '98                                | '99               | '00               |
| Block      | 1250 | 37.9 <sup>a</sup> | 17.9 <sup>a</sup> | 12.8 <sup>a</sup> | 56 <sup>a</sup>                    | 113 <sup>a</sup> | 160 <sup>a</sup> | .015 <sup>a</sup>                  | .040 <sup>a</sup> | .068 <sup>a</sup> |
| Triple row | 600  | 37.4 <sup>a</sup> | 17.7 <sup>a</sup> | 12.9 <sup>a</sup> | 67 <sup>b</sup>                    | 138 <sup>b</sup> | 203 <sup>b</sup> | .018 <sup>b</sup>                  | .050 <sup>b</sup> | .088 <sup>b</sup> |
| Single row | 400  | 34.8 <sup>b</sup> | 15.9 <sup>b</sup> | 12.7 <sup>a</sup> | 62 <sup>ab</sup>                   | 142 <sup>b</sup> | 233 <sup>c</sup> | .017 <sup>b</sup>                  | .051 <sup>b</sup> | .102 <sup>c</sup> |
| Isolated   | 100  | 33.8 <sup>b</sup> | 15.3 <sup>b</sup> | 12.4 <sup>a</sup> | 64 <sup>b</sup>                    | 175 <sup>c</sup> | 314 <sup>d</sup> | .017 <sup>b</sup>                  | .065 <sup>c</sup> | .143 <sup>d</sup> |

| Spacing    | Stand volume (m <sup>3</sup> ha <sup>-1</sup> ) |                   |                   | Annual volume increment (m <sup>3</sup> ha <sup>-1</sup> ) |                   |
|------------|-------------------------------------------------|-------------------|-------------------|------------------------------------------------------------|-------------------|
|            | '98                                             | '99               | '00               | '99                                                        | '00               |
| Block      | 13.7 <sup>a</sup>                               | 37.4 <sup>a</sup> | 63.3 <sup>a</sup> | 23.7 <sup>a</sup>                                          | 25.9 <sup>a</sup> |
| Triple row | 10.4 <sup>a</sup>                               | 28.0 <sup>a</sup> | 48.3 <sup>a</sup> | 17.6 <sup>a</sup>                                          | 20.4 <sup>a</sup> |
| Single row | 5.1 <sup>b</sup>                                | 19.1 <sup>b</sup> | 37.9 <sup>b</sup> | 11.0 <sup>b</sup>                                          | 18.8 <sup>a</sup> |
| Isolated   | 1.6 <sup>b</sup>                                | 5.6 <sup>c</sup>  | 12.2 <sup>c</sup> | 4.1 <sup>c</sup>                                           | 6.0 <sup>b</sup>  |

### 2.3.2 Tree form

Planting layout had a clear impact on the incidence of thick branches and on branch diameter ( $P < 0.001$ ). Open configurations had the most trees with heavy branches (class 5, Fig. 2.1a). The isolated layout produced very few trees with thin branches (Classes 0 and 1) and was the only treatment to have branches with diameters  $\geq 40$  mm (Fig 2.1a,b). In contrast the block plantations had the highest proportion of trees with thin branches (Class 0) and had no branches with diameters  $> 30$  mm. Over all, the number of trees with branches  $> 35$  mm in diameter and the number of large branches decreased with increasing planting density (Fig 2.1b,c).

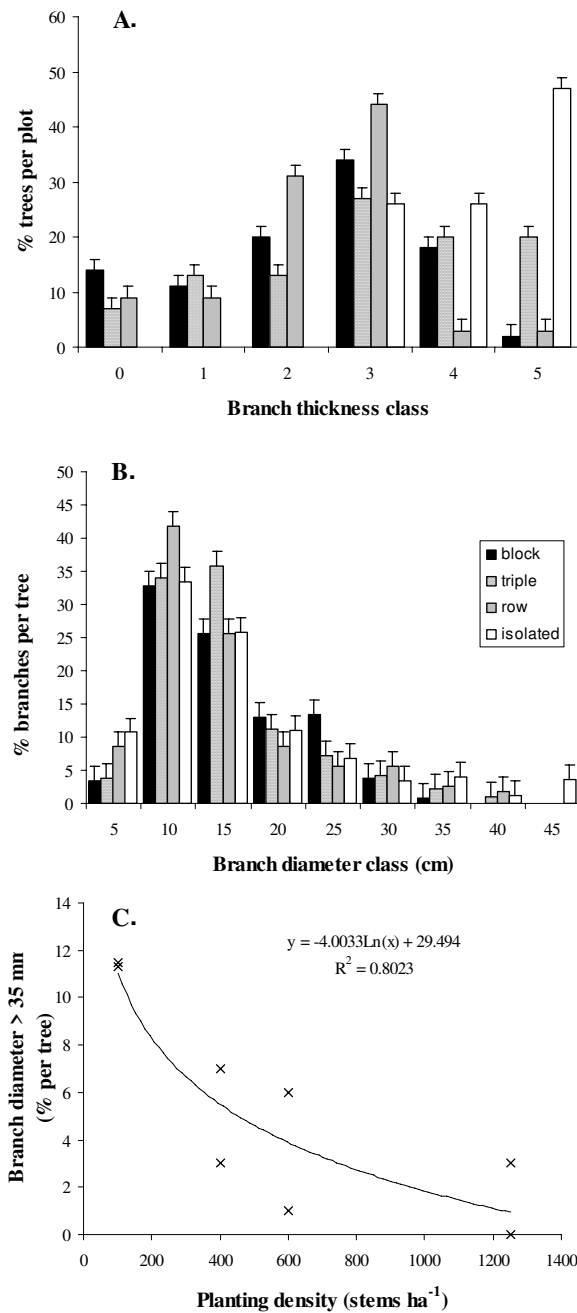


**Figure 2.1.** The effect of spacing on **A)** heaviness of branching (tree basis), where 0 = very thin branches for site, 5=very thick branches, **B)** branch diameter (branches per tree), and **C)** the occurrence of branches with diameters over 35 mm.

About 6-9% of trees in all treatments had only flat branches (class 0), but only the triple row and block layouts had trees with more than half of their branches at steep angles (class 5, Fig. 2.2a). Similarly in terms of the angles of individual branches, the branches of trees grown in block layouts were steeper than those of either single row or isolated trees ( $37.3^\circ$  compared to  $47.5^\circ$  and  $49.7^\circ$  from vertical, respectively). Spacing had little effect on fork and ramicorn numbers (Fig. 2b) or stem straightness criteria (data not presented). Irrespective of planting layout, most trees had no forks or ramicorns. Similarly butt sweep was absent from at least half of the trees in all treatments. Few trees, however, had stems without any significant deviation and moderate to severe wobble or corkscrew was common across all treatments. Less than 5% of all trees would be regarded as acceptable for sawlog or veneer products simply on stem straightness criteria. This was further reduced to about 2% when trees

possessing more than one branch with a diameter > 35 mm were excluded. The generally poor form probably reflects the high soil fertility associated with this ex-pasture-cropping site.

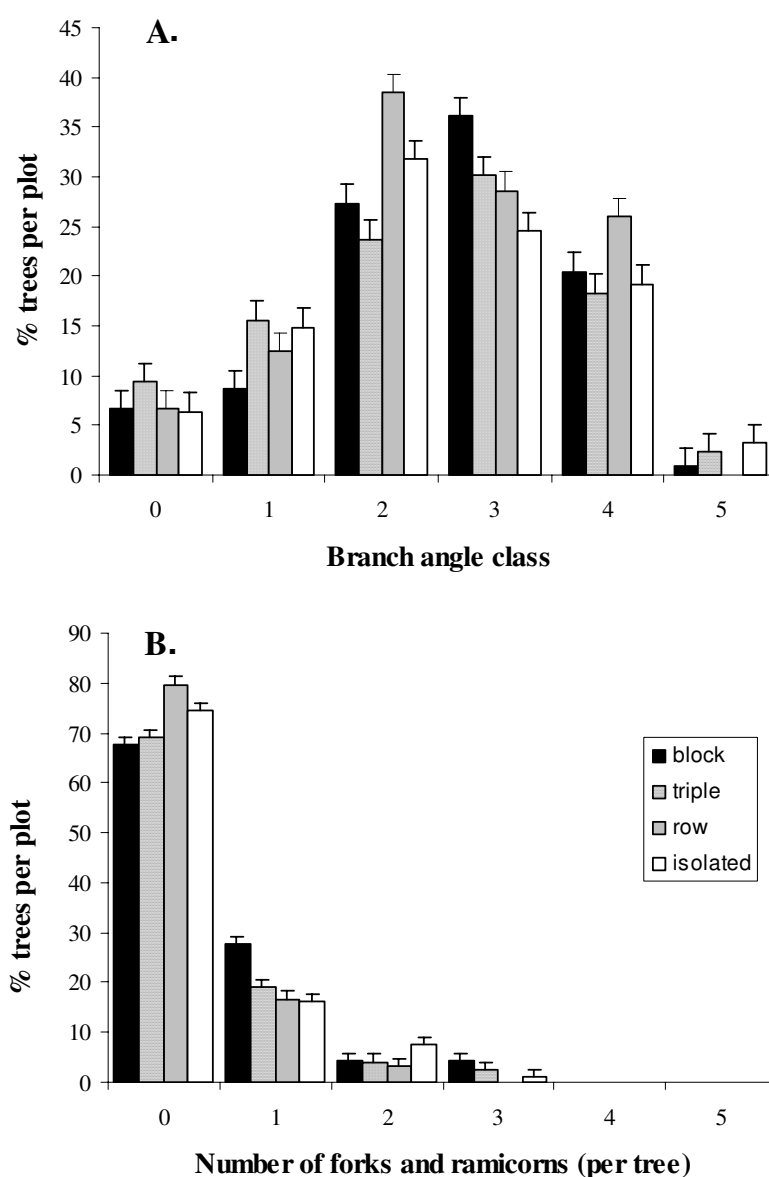


**Figure 2.2.** The effect of spacing on **A)** branch angle class: where 0 denotes all branches horizontal, 5 that > 50% were at steep angles, and **B)** the number of forks and ramiforms per tree.

### 2.3.3 Allometric relationships, crown architecture and partitioning

Planting layout had a major effect on the structure of tree crowns. Trees in more densely planted treatments retained few branches in the lower third of the canopy. This was reflected in the greater height to the green canopy, the shorter, narrower crown (crown basal area of 7.58 m<sup>2</sup> compared with 29.14 m<sup>2</sup>) and the lower number of branches in block planted compared to isolated trees (Table 2.2). More closely spaced trees had less leaf area per tree than trees grown in more open configurations. Total tree leaf area increased from 52.5 m<sup>2</sup> in block plantation trees to 93.2 m<sup>2</sup> in single rows to 149.2 m<sup>2</sup> in isolated trees. When leaf area is projected onto a stand ground area basis, however, block plantings had significantly greater  $L^*$ 's than more widely spaced layouts (Table 2.2).

**Table 2.2.** The influence of spacing on canopy architecture

| Spacing    | Green height (m)  |                   | Branch number    | May allocation to: |                   |                   | Mean canopy basal area (m <sup>2</sup> ) | Mean tree leaf area (m <sup>2</sup> ) | L*                |
|------------|-------------------|-------------------|------------------|--------------------|-------------------|-------------------|------------------------------------------|---------------------------------------|-------------------|
|            | Nov               | May               |                  | stems              | branches          | leaves            |                                          |                                       |                   |
| Block      | 0.95 <sup>a</sup> | 2.73 <sup>a</sup> | 104 <sup>a</sup> | 0.75 <sup>a</sup>  | 0.13 <sup>a</sup> | 0.11 <sup>a</sup> | 7.58 <sup>a</sup>                        | 52.5 <sup>a</sup>                     | 6.56 <sup>a</sup> |
| Single row | 0.25 <sup>b</sup> | 0.46 <sup>b</sup> | 110 <sup>a</sup> | 0.62 <sup>b</sup>  | 0.20 <sup>b</sup> | 0.19 <sup>b</sup> | 12.02 <sup>a</sup>                       | 93.2 <sup>ab</sup>                    | 3.73 <sup>b</sup> |
| Isolated   | 0.20 <sup>b</sup> | 0.16 <sup>b</sup> | 152 <sup>b</sup> | 0.49 <sup>c</sup>  | 0.27 <sup>c</sup> | 0.24 <sup>c</sup> | 29.14 <sup>b</sup>                       | 149.2 <sup>b</sup>                    | 1.49 <sup>c</sup> |

The distribution of this leaf area also varied between spacing treatments (Fig. 2.3). Strong interactions were found among tree spacing and height zone and aspect ( $P < 0.001$ ). In isolated trees most of the leaf area was located in the lower third of the canopy on the northern and western aspects (Fig. 2.3c). In the block planting, the middle canopy and the southern aspect had the greatest leaf area (Fig. 2.3a). The leaf area supported by each branch was strongly related to branch length and cross-sectional area ( $R^2 = 0.83$  and  $0.87$ , respectively, Fig. 2.4a,b,c,d).

Leaf area ( $R^2 = 0.82$ ) and branch cross-sectional area ( $R^2 = 0.74$ ) were linearly related to SSA (Fig. 2.5a,b). Total tree branch cross-sectional area and the ratio of branch area to SSA (“branchiness”) were greatest in isolated trees (Fig. 2.5c). Branchiness declined from an average of around 0.98 and 1.19 in single row and isolated trees to  $0.65 \text{ m}^3 \text{ m}^{-3}$  in block stands (from Fig. 2.5c). These changes correspond to alterations in the distribution of above-ground biomass with spacing (Table 2.2). A greater proportion of above-ground biomass was found in branches in isolated trees than in block planted trees, with a corresponding decline in the proportion of above-ground biomass in stemwood.

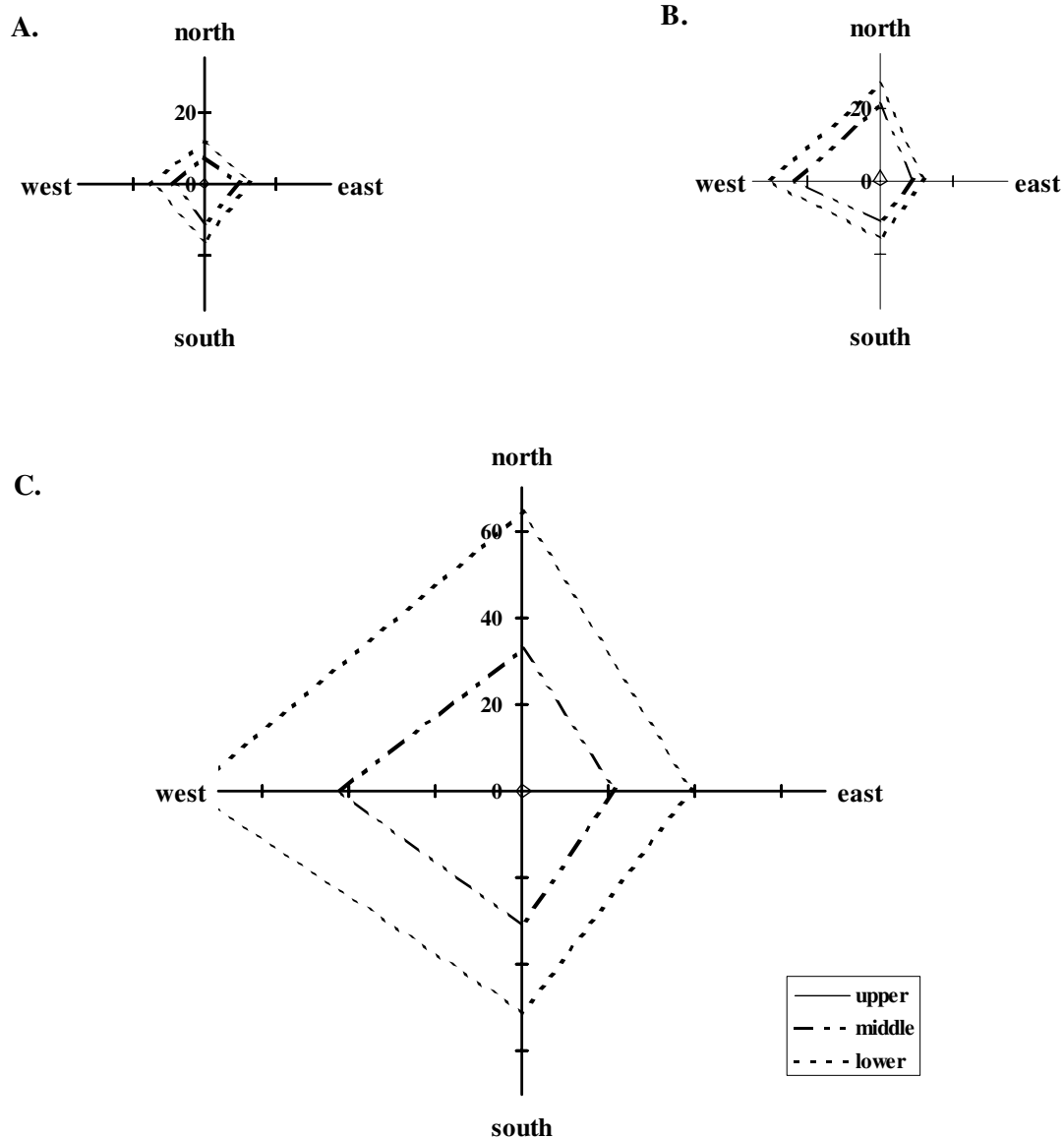


**Figure 2.3.** Cumulative leaf area distribution ( $\text{m}^2$ ) above the light sensors at upper, middle and lower thirds of the canopies of measurement trees in **A)** block plantations, **B)** single rows and **C)** isolated trees.

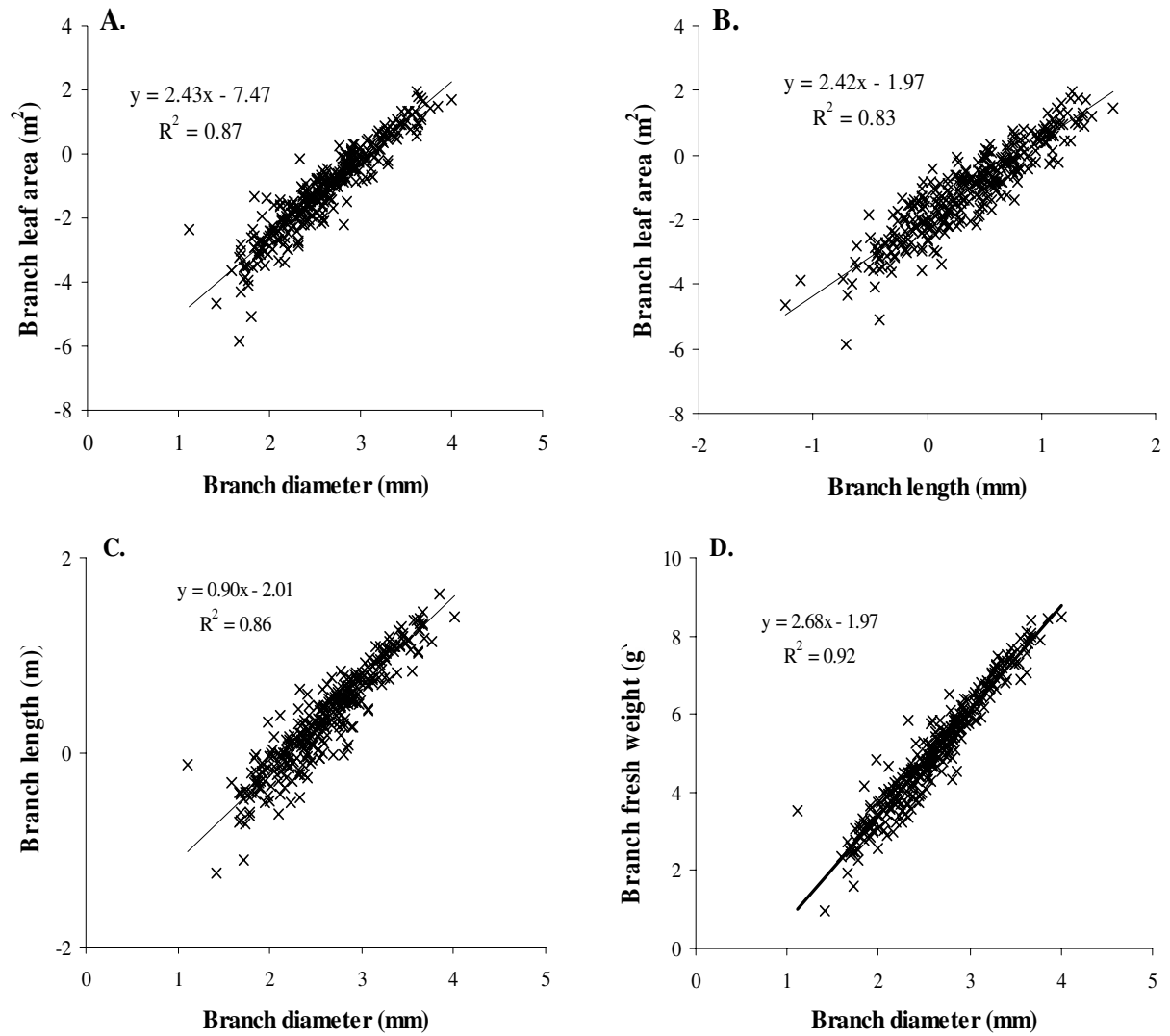


**Figure 2.4.** Branch and leaf area relationships: **A)** branch diameter and branch leaf area, **B)** branch length and branch leaf area, **C)** branch diameter and branch length and **D)** branch diameter and branch fresh weight.

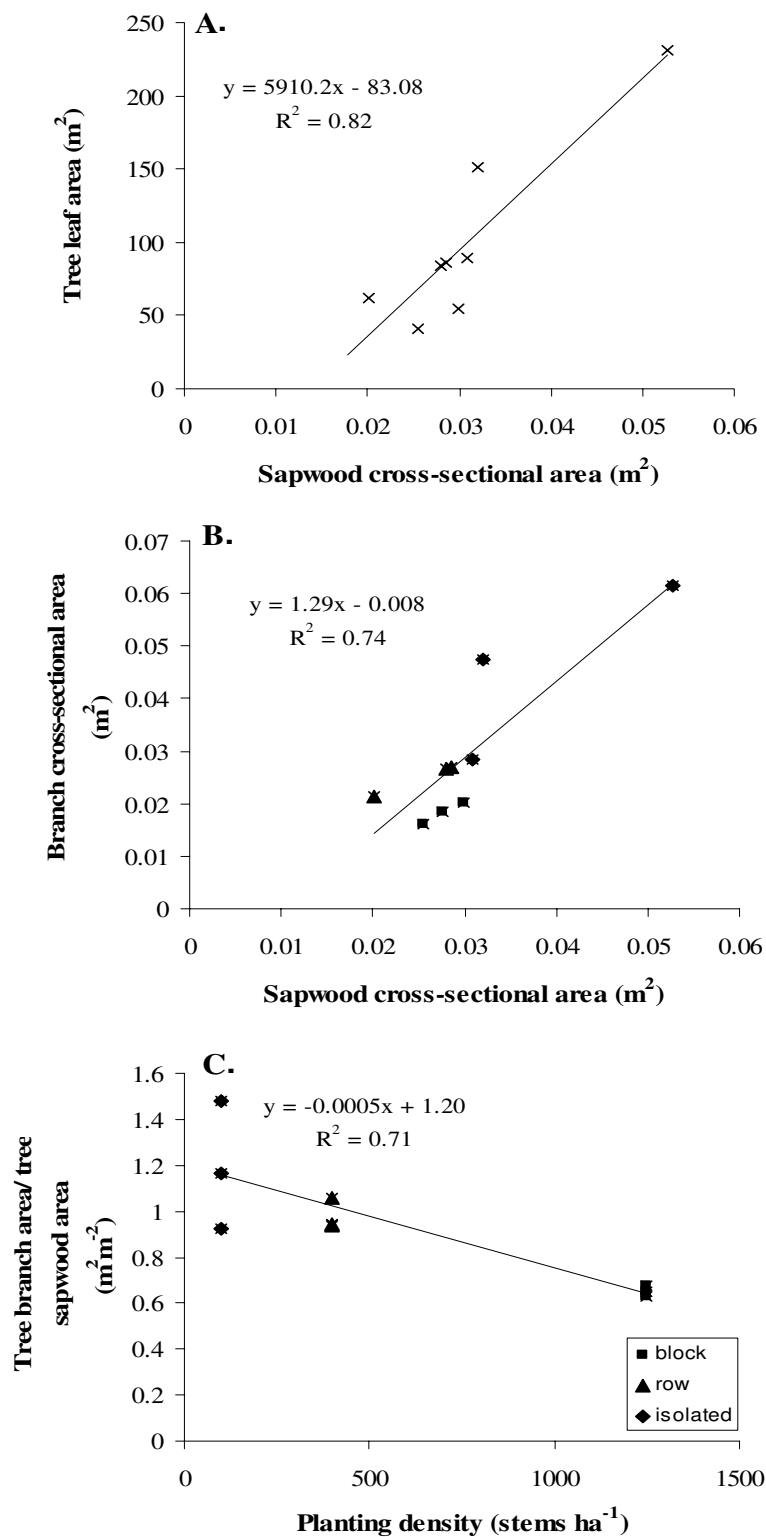


**Figure 2.5.** Sapwood cross-sectional area (SSA), leaf and branch cross-sectional area relationships: A) SSA and total tree leaf area, B) SSA and branch cross-sectional area and C) the change in branch area/sapwood cross-sectional area ratio with planting density.

### 2.3.4 Light environment

Planting density had a marked impact on light availability. In the upper zone and outer positions of the canopy at the north, south, east and west aspects, block planted trees received only 20, 13, 59 and 27% of available light, respectively. In contrast, these positions in isolated trees received 67, 36, 89 and 63% of available light, respectively (Table 2.3). The effect of spacing on the light environment in tree canopies was highly dependent on position within the canopy in terms of aspect, height above the ground, canopy depth, and on time of day and time of year (Table 2.3). The proportion of light transmitted, and hence the light available to lower leaves, decreased with decreasing height and increasing canopy depth, irrespective of treatment. Light levels were very low at the bottom of block planted canopies in August (2-5% of available light). Light transmission at the base of these canopies rose to 7-32% of available light in November, illustrating both the seasonal shift in light angles and the influence of canopy lift. Light transmission was observed to decrease in single row and isolated trees during November. This was because branch expansion above the platforms on which sensors were placed effectively moved the sensors further into the canopy.

**Table 2.3.** Light transmission at various positions within tree canopies as a proportion (%) of available light in the open.

| Position |        |          | AUGUST |        |          | NOVEMBER |        |          |
|----------|--------|----------|--------|--------|----------|----------|--------|----------|
| Aspect   | Height | Distance | Block  | Single | Isolated | Block    | Single | Isolated |
| North    | Upper  | Outer    | 20     | 33     | 67       | 61       | 31     | 44       |
| North    | Upper  | Middle   | 11     | 27     | 48       | 51       | 31     | 38       |
| North    | Mid    | Outer    | 10     | 27     | 18       | 24       | 21     | 22       |
| North    | Mid    | Middle   | 9      | 20     | 25       | 27       | 19     | 32       |
| North    | Lower  | Middle   | 2      | 14     | 11       | 11       | 24     | 3        |
| South    | Upper  | Outer    | 13     | 13     | 36       | 9        | 21     | 41       |
| South    | Upper  | Middle   | 23     | 13     | 43       | 12       | 5      | 33       |
| South    | Mid    | Outer    | 4      | 12     | 25       | 5        | 3      | 46       |
| South    | Mid    | Middle   | 2      | 26     | 17       | 6        | 3      | 32       |
| South    | Lower  | Middle   | 2      | 13     | 22       | 7        | 6      | 12       |
| East     | Upper  | Outer    | 59     | 18     | 89       | 39       | 36     | 40       |
| East     | Upper  | Middle   | 29     | 24     | 46       | 30       | 22     | 24       |
| East     | Mid    | Outer    | 16     | 63     | 15       | 16       | 40     | 29       |
| East     | Mid    | Middle   | 14     | 29     | 16       | 14       | 21     | 21       |
| East     | Lower  | Middle   | 3      | 32     | 33       | 32       | 17     | 5        |
| West     | Upper  | Outer    | 27     | *      | 66       | *        | 18     | 47       |
| West     | Upper  | Middle   | 18     | 18     | 40       | 44       | *      | 57       |
| West     | Mid    | Outer    | 16     | 37     | 44       | 47       | *      | 57       |
| West     | Mid    | Middle   | 11     | 24     | 23       | 41       | 14     | 40       |
| West     | Lower  | Middle   | 4      | 16     | 17       | 21       | 22     | 40       |

### 2.3.5 Net assimilation

Light saturated net photosynthetic rate ( $A_{\max}$ ) at the top of the canopy was around  $20 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  irrespective of treatment. At other canopy positions, however,  $A_{\max}$  varied with planting layout ( $P < 0.001$ ), decreasing as density and competition for light increased from isolated trees to single rows and block spacing (Table 4). In all treatments,  $A_{\max}$  declined with decreasing height and greater proximity to the stem. These gradients were much more acute in isolated trees ( $P < 0.001$ ), particularly in May 2000. In isolated trees  $A_{\max}$  decreased from  $16.9\text{--}20.7 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  to  $3.4\text{--}16.1 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  between outer and inner canopy regions. In block planted trees the corresponding decline in  $A_{\max}$  was from  $7.9\text{--}18.4$  to  $5.1 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ . Assimilation rates at outer portions of the canopies of isolated trees varied from around  $19 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  in the upper zone to about  $16 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  in the lower zone. In block planted trees the corresponding rates were approximately 17 and  $8 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ , respectively.

Light compensation point ( $PFD_0$ ) and leaf dark respiration rate ( $r_l$ ) were also affected by spacing (Table 5). While the leaves of isolated trees had greater  $A_{max}$  values than block planted trees, higher light intensities were required to achieve saturation ( $P < 0.05$ ). Light compensation point increased with increasing  $A_{max}$  ( $R^2 = 0.69$ ,  $P < 0.05$ ). Similarly, though the relationship was weaker ( $R^2 = 0.30$ ,  $P < 0.01$ ),  $r_l$  increased with increasing  $A_{max}$ .

**Table 2.4.** The influence of spacing and position in the canopy on  $A_{max}$  in November 1999 and May 2000.

| Spacing    | Height | November 1999 |        |       | May 2000 |        |       |
|------------|--------|---------------|--------|-------|----------|--------|-------|
|            |        | outer         | middle | inner | outer    | middle | inner |
| Block      | upper  | 16.8          | 14.6   | 13.3  | 18.4     | 15.0   | 13.8  |
|            | mid    | 11.6          | 8.7    | 8.4   | 10.9     | 9.1    | 8.0   |
|            | lower  | 7.9           | 6.0    | 5.7   | 8.4      | 5.7    | 5.1   |
| Single row | upper  | 13.2          | 14.0   | 11.6  | 18.1     | 14.4   | 12.6  |
|            | mid    | 13.6          | 11.1   | 8.9   | 15.2     | 11.7   | 13.3  |
|            | lower  | 8.8           | 9.6    | 7.0   | 8.5      | 8.9    | 9.0   |
| Isolated   | upper  | 19.3          | 17.5   | 15.2  | 20.7     | 16.6   | 16.1  |
|            | mid    | 16.9          | 13.4   | 12.4  | 19.3     | 13.7   | 11.8  |
|            | lower  | 15.7          | 10.4   | 6.9   | 18.5     | 13.0   | 3.4   |

**Table 2.5.** The influence of position in the canopy on maximum net  $CO_2$  assimilation rate ( $A_{max}$ ,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) the light intensity at which  $A_{max}$  was achieved (saturating  $PFD$ ), light compensation point ( $PFD_0$ ,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) and leaf dark respiration ( $r_l$ ,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) in block planted (Block) and isolated trees (Isolated).

| Position         | $A_{max}$ |          | Saturating $PFD$ |          | $PFD_0$ |          | $r_l$ |          |
|------------------|-----------|----------|------------------|----------|---------|----------|-------|----------|
|                  | Block     | Isolated | Block            | Isolated | Block   | Isolated | Block | Isolated |
| Top              | 23.0      | 22.9     | 1400             | 1400     | 18      | 35       | -0.8  | -1.4     |
| West upper outer | 22.4      | 21.0     | 1100             | 1100     | 18      | 18       | -0.7  | -1.1     |
| West mid outer   | 15.8      | 19.8     | 1100             | 1100     | 18      | 18       | -0.6  | -0.7     |
| West mid middle  | 9.8       | 17.0     | 610              | 910      | 0       | 18       | -0.6  | -0.4     |
| West lower outer | 10.5      | 21.1     | 840              | 1500     | 9       | 50       | -0.6  | -2.2     |
| East mid outer   | 15.0      | 20.3     | 1100             | 910      | 14      | 18       | -0.3  | -1.7     |
| East mid middle  | 11.9      | 14.7     | 910              | 1100     | 9       | 35       | -0.4  | -1.2     |
| East mid inner   | 8.8       | 9.3      | 610              | 910      | 9       | 129      | -0.3  | -1.0     |
| East lower outer | 11.5      | 21.4     | 840              | 1100     | 14      | 18       | -0.6  | -1.8     |

## 2.4 Discussion

Initial tree spacing and planting layout have a profound influence on subsequent tree growth and form (Schönau and Coetzee 1989, Gerrand *et al.* 1997, Neilsen and Gerrand 1999). Many of these changes are explicable when the effects of planting layout on light environment and the effect of light environment on tree growth are considered. Useful generalisations can be made that resolve some of the trade-offs between stand growth and product outcomes.

Many of the results revealed in our study, and indeed those of many other studies, can be understood from the following equation which describes annual stemwood growth:

$$\Delta W_s = \eta_s Q_i c \varepsilon (1 - e^{-kL/c}) - R - T, \quad (2.1)$$

where  $\Delta W_s$  is the change in stem biomass,  $\eta_s$  is the proportion of stand gross primary production allocated to stemwood,  $Q_i$  is the incident radiation per unit land area,  $\varepsilon$  is the efficiency with which radiation is converted to biomass,  $c$  is the fraction of the area covered by the stand,  $k$  is the light extinction coefficient within the stand,  $L^*$  is the stand leaf area index,  $R$  is stand respiration and  $T$  is stand litterfall and biomass turnover. This equation is an approximation because projected stand

area ( $c$ ), and tree geometry will have a more complex effect on production and light interception than implied in equation 1, but it nevertheless provides a useful focus for explanations of the effect of planting layout. Consequently, the following discussion will examine the effect of spacing, illustrated by our current experimental data, on each of the main terms in equation 1.

#### **2.4.1 Stemwood biomass increment, $\Delta W_s$**

Wide spacing maximised individual tree growth but overall stand production was reduced (Table 1). These results are consistent with those generally observed. The actual magnitude of response, however, varies with species, site quality, age and uniformity of tree size (Opie *et al.* 1984, Schönauf and Coetzee 1989, Vanninen *et al.* 1996, Gerrand *et al.* 1997, Bernardo *et al.* 1998, Neilsen and Gerrand 1999, Power *et al.* 2000, Medhurst *et al.* 2001). Bernardo *et al.* (1998), for example, reported a strong individual tree growth response to increased spacing and a decline in stand growth. The average tree weight in *E. pellita* stands rose around 40 kg, while that of *E. urophylla* grown at the same contrasting densities rose 60 kg. Stand weight decreased by 12 Mg ha<sup>-1</sup> in *E. pellita* and 22 Mg ha<sup>-1</sup> for *E. urophylla* with increased spacing. These differences strengthened with increasing age (Bernardo *et al.* 1998). Some understanding of these effects of thinning and initial spacing can be gained by reference to equation (1) and the distribution of light within and between spacing treatments (Fig. 3).

#### **2.4.2 Light interception ( $Q_{ic}$ ) and stand leaf area ( $L^*$ )**

The size and arrangement of plant canopies determines the amount of light that they intercept (Caldwell *et al.* 1986, Beadle 1997, Valladares 1999). Biomass production, under a given set of conditions, is related to the amount of light intercepted by canopies (Cannell 1989, Kupperts 1994, Beadle 1997). Widely spaced trees intercepted more light than block plantation trees because there was no side shading and because they had larger leaf areas (Tables 2.2 and 2.3). Individual tree growth rates are consequently higher with wider spacing. Projected stand area ( $c$ ) however, was lower in plantings with isolated trees compared with block plantations and unlike stands of isolated trees, block plantations had closed canopies. Individual trees in blocks had total leaf areas of around 52.5 m<sup>2</sup> and occupied only 7.58 m<sup>2</sup> of ground space (canopy basal area) compared with leaf areas of 149.2 m<sup>2</sup> and canopy basal area of 29.14 m<sup>2</sup> for isolated trees. In block plantings, however,  $c$  was 95%, resulting in a stand  $L^*$  of 6.6. In contrast  $c$  was only 29% in isolated trees and  $L^*$  was 1.5 (derived from Tables 1 and 2). Consequently, although the amount of leaf area and light intercepted per tree increased  $Q_{ic}$ ,  $L^*$  was less for isolated trees on a stand basis. Summing the radiation intercepted by individual trees in each treatment (calculated as the inverse of mean transmission at the base of the canopy at solar noon) and then multiplying by the stocking rate can further demonstrate this. Assuming a maximum incident  $PPFD$  of 2 500  $\mu\text{mol m}^{-2} \text{s}^{-1}$  at solar noon in summer, block-planted and isolated trees intercept 2 175  $\mu\text{mol m}^{-2} \text{s}^{-1}$  or 114 190  $\mu\text{mol m}^{-2} \text{s}^{-1}$  and 2 000  $\mu\text{mol m}^{-2} \text{s}^{-1}$  or 298 400  $\mu\text{mol m}^{-2} \text{s}^{-1}$  of light per tree, respectively. Thus block-planted trees intercept around 2 718 750  $\mu\text{mol ha}^{-1} \text{s}^{-1}$  while isolated trees intercept only 200 000  $\mu\text{mol ha}^{-1} \text{s}^{-1}$ .

These results have several practical implications for farm foresters. Maximum stand growth is only achieved when density is relatively high. Conversely mean tree growth is greatest when density is low enough to minimise or avoid competition. Any planting layout therefore involves a trade-off between stand volume production and maximal individual tree growth (Long 1985). For *E. globulus* in our study, and *E. nitens* in previous studies (Gerrand *et al.* 1997, Nielsen and Gerrand 1999, Medhurst *et al.* 2001), the increase in volume increments with wider spacing was driven by increased expansion of stem basal area rather than by height growth. Tree height was generally insensitive to spacing (Table 1). Consequently, increased spacing will result in increased piece-size but not greater log length (Nielsen and Gerrand 1999). If the aim is to produce trees of a certain diameter for high value products such as sawlog or veneer, the requisite tree girths will be achieved sooner with wider spacing. In sawlog plantations, managers generally aim to achieve the requisite stem diameter in the shortest possible time (Gerrand *et al.* 1997). To do this they manipulate tree spacing through thinning. Thinning delays or reduces intra-species competition with the aim of maintaining the optimal growth of selected trees, generally those with the best form, rather than the overall volume of the stand

(Deadman and Hay 1987, Long and Smith 1989, Shoulders 1989, Medhurst *et al.* 2001). If, however, a high volume of timber is required for wood-chip or similar products, then higher stand densities are appropriate (Schönauf 1984, Long 1985, Shoulders 1989, Gerrand *et al.* 1997, Neilsen and Gerrand 1999).

### 2.4.3 Stem partitioning, $\eta_s$

Isolated trees had more branches and these tended to be of greater diameter and length than those of block-planted trees (Table 2). The portion of above-ground biomass located in branches also rose while the fraction in stem sapwood decreased from about 75% in block-planted trees to 49% in isolated trees. Although root biomass and stem biomass as sapwood were not measured, these data indicate that stem sapwood biomass decreased with increasing spacing. Greater branch numbers in isolated trees reflected both the retention of live branches and a lower green canopy (Table 2.2). As with growth rate, branch production and retention are driven by the relationship between light availability and leaf area (King 1994, Hilbert and Messier 1996, King *et al.* 1997). Increased shoot formation in response to high irradiance allows plants to increase the leaf area in sunlit spaces (Takenaka 1994, 1997, Ballare *et al.* 1997). This increased leaf area requires an increased volume of conducting tissues and more mechanical support afforded by greater branch areas (Whitehead 1978, Mäkelä 1986, Berninger *et al.* 1995). In the current study the larger canopy basal areas of isolated trees were an immediate consequence of their longer branches (Table 2.2). Across all treatments the relationship between branch length and leaf area meant that longer branches had greater leaf areas (Fig. 2.4b). Branch diameter was simply related to branch length. That is, branches are thicker because they are longer and require greater mechanical support (Fig. 2.4c). Thus, increased branch diameter is associated with greater leaf areas and both the number of trees with branches over 35 mm and the number of branches with diameters over 35 mm declined as a function of increasing stand density (Fig. 2.1b,c). The link with assimilate allocation is made explicit by the strong relationship between branch biomass (fresh weight) and branch area ( $R^2 = 0.92$ , Fig 2.4d). That is, the greater the leaf area present, the greater the amount of biomass allocated to support that leaf area in the form of branches. Consequently, isolated trees had a greater incidence of heavy branches (Fig.1) and greater branch area per tree.

The consequences of spacing on  $\eta_s$  can also be examined by considering the relationship between the branch cross-sectional area and SSA at breast height. From the relationships among  $L^*$ , SSA, leaf area and branch area established in the current and previous studies, (Figs. 2.4, 2.5a,b, see also Whitehead 1978, Hunt *et al.* 1999) the total branch cross-sectional area supported by a stem is linearly related to sapwood area. The branch area/sapwood area relationship (after Berninger *et al.* 1995), however, is different for the block plantation (0.65) compared with the other planting designs (0.98-1.14). Changes in the branch area/sapwood ratio were interpreted by Berninger *et al.* (1995) in terms of evaporative demand and the hydraulic pipe model: that is trees growing in more evaporative conditions, such as more open grown trees, are generally exposed to higher vapour pressure deficit (VPD) due to a closer atmospheric coupling and therefore use more water per unit leaf area than trees in closed canopies. Open grown trees would be expected to have significantly higher branch areas/sapwood area ratios than more densely planted or less exposed trees in order to increase hydraulic resistance and reduce cavitation in branches. Our results tend to support this interpretation. There is also evidence, however, that mechanical constraints are an important factor in this relationship since the branch area: SSA ratio was correlated with planting density (Fig. 2.5c).

Carbon gain by the crown is balanced by its construction and maintenance costs (Givnish 1988). Its mechanical stability imposes a minimum requirement for tissue to support the canopy and its branches (Valladares 1999). Greater exposure to wind caused by increased spacing is, therefore, also linked to increased requirements for structural strength in stems and branches and this exerts a strong influence on tree size, shape and branching patterns (Speck *et al.* 1990, Ennos 1997). As branch or stem length increases so does the likelihood of irreversible bending or elastic toppling. Consequently, the fraction of biomass allocated to support increases rapidly with branch size (Mattheck 1991). The strength of a branch or stem scales with the square of its diameter. Similarly its mass increases with diameter

squared times length (Valladares 1999). In our study similar processes may be operating. Since declining  $\eta_s$  with increasing spacing is accompanied by increased allocation to branches, increased branch length and the greater incidence of thick branches, changes in  $\eta_s$  may be mediated both by increased requirements for conducting tissue and the greater requirement for mechanical support to resist wind loadings and support leaves. Since isolated trees had larger, denser canopies than trees in block planted stands, the ratio of branch area to sapwood area equally reflects changes in the light environment,  $VPD$  and requirements for mechanical support.

In practical terms, branch size and number are closely allied with branch angle in determining the size and frequency of knots and the potential end use of timber. Branches with diameters larger than 35 mm reduce the acceptability of trees for sawlog production. If unpruned they create large knots and seriously reduce the structural strength of timber (Gerrand *et al.* 1997, Neilsen and Gerrand 1999). These large branches are also more susceptible to decay following pruning (Neilsen and Gerrand 1999). Knot size is also determined by branch angle and steeper branches result in larger knots than flat branches. While branch angle is not explicitly included in equation (1), it influences light interception and is affected by stand density (Hilbert and Messier 1996, Valladares 1999). In this study, branches of block planted trees were at steeper angles than those of trees from more open layouts. In dense stands, the shape of the crown is constrained by competition for space, reduced light availability and by the greater cost of horizontal branches compared to vertical branches caused by their lower structural strength (Mattheck 1991, Bell 1993). Although more vertical orientations of foliage decreases the efficiency of light capture (Beadle 1997), in closed stands a large proportion of the total light received comes from low angles (Endler 1993). Conversely, in open stands, a greater proportion of light is received from directly overhead and in the absence of other limitations, more favourable light interception and photosynthesis make the energetic/metabolic costs associated with the formation and maintenance of horizontal branches less likely to be prohibitive. The prevalence of flat branches in isolated trees is also associated with longer leaf and branch retention than in the lower light environment at the base of the canopy of block stands. Across all treatments, lower branches were flatter than upper branches with angles from the vertical of 46° to 67° compared with 30° to 40°, respectively. In terms of the acceptability of timber for sawlogs, while trees from more widely spaced layouts produce branches at flatter angles than more closely spaced trees, they produce a greater proportion of thick branches. Consequently, wider spaced trees will require pruning sooner than trees in denser stands.

#### **2.4.4 Light utilisation efficiency, $\epsilon$**

The effect of spacing on net photosynthesis ( $A$  and  $A_{max}$ ) is captured within the term for light use efficiency ( $\epsilon$ ), which describes the efficiency with which radiation is converted to biomass via photosynthesis. While isolated trees had higher  $A_{max}$  and greater leaf areas, and consequently fixed greater quantities of  $CO_2$  than block plantation trees (Tables 4 and 5),  $\epsilon$  did not change between spacing treatments. The value for  $\epsilon$  is given by the relationship between light interception and annual above ground biomass increment (Fig. 2.6). There was a single linear relationship across all treatments with levels of intercepted radiation ( $R^2 = 0.90$ ). The slope of this line gives  $\epsilon$ , which was about 0.67 g MJ<sup>-1</sup>. This is well within the range of values of  $\epsilon$  (0.5 to 2.23) previously reported in a range of eucalypts in Australia (Beadle *et al.* 1995, Landsberg and Hingston 1996). In more water- and nutrient-limited environments greater access to resources might be expected to give isolated and single row trees higher values of  $\epsilon$  than in block plantations.

#### **2.4.5 Respiration, $R$**

Rates of leaf dark respiration and light compensation points are sensitive to density-induced changes to light environment (Table 5, see also Turnbull *et al.* 1993). The higher light levels required to reach  $PPFD_0$  and the greater  $r_1$  in isolated trees (Table 2.5) off-set their increased  $A_{max}$  compared with block-planted trees. This in part reflects that respiration rates for tissues within a tree vary with live cell number and metabolic activity. Expanding and upper canopy sun leaves, for example, have higher respiratory rates than fully-expanded and shade leaves from the lower canopy (Ryan *et al.* 1994). In

the current study, leaves from the outer layers at the bottom of isolated trees had much greater (three times)  $r_l$  than leaves from the same positions of block-planted trees.

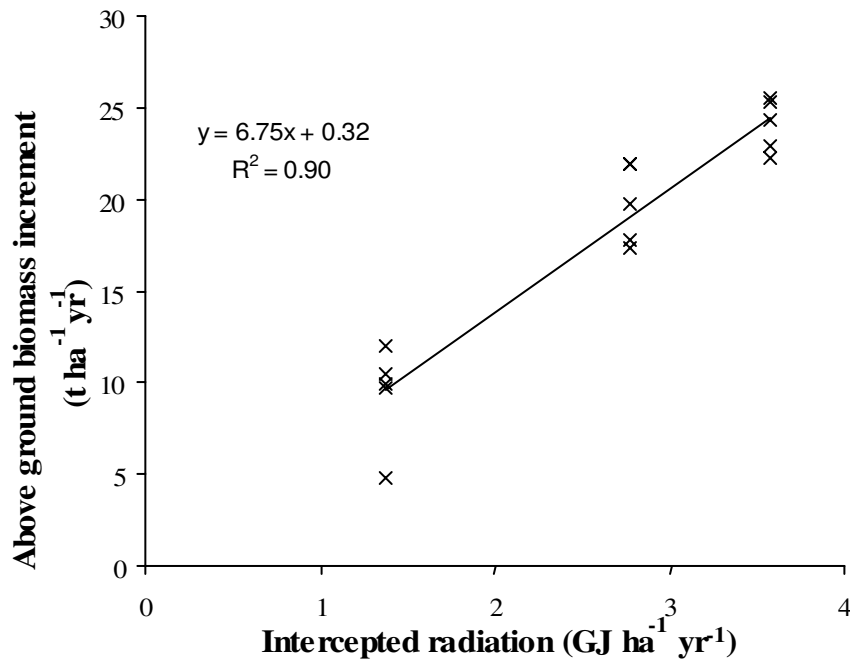


**Figure 2.6.** The relationship between annual above-ground biomass increment ( $\text{t ha}^{-1} \text{yr}^{-1}$ ) and intercepted radiation ( $\text{GJ ha}^{-1} \text{yr}^{-1}$ ). The slope of the relationship gives  $\varepsilon$ , the efficiency of the conversion of radiation to biomass ( $0.67 \text{ g MJ}^{-1}$ ).

As discussed previously, changes in spacing are coupled with different patterns of biomass distribution. The greater investment by isolated trees in leaves and branches simultaneously increases the amount of foliage that can be supported, the amount of light intercepted and incurs a greater respiratory load than in block-planted trees. This can be demonstrated from calculations of above-ground maintenance respiration ( $R_m$ ) using conversion factors derived for *Pinus radiata* (Ryan *et al.* 1996). Across all treatments leaf  $R_m$  accounted for about 90% of total  $R_m$ . Respective stem, branch and leaf  $R_m$  were 1.14, 17.69 and  $1.48 \mu\text{mol CO}_2 \text{s}^{-1} \text{tree}^{-1}$  in block-planted trees, but 1.11, 26.21 and  $2.52 \mu\text{mol CO}_2 \text{s}^{-1} \text{tree}^{-1}$  in single row trees and 1.34, 58.86 and  $5.56 \mu\text{mol CO}_2 \text{s}^{-1} \text{tree}^{-1}$  in isolated trees. Consequently, isolated trees each lose around  $43 \text{ kg DM yr}^{-1}$  more as  $R_m$  than block planting trees. On a stand basis, however, estimated annual  $R_m$  increased as stocking increased: in the current study block-planted stands lost  $23.9 \text{ t DM ha}^{-1} \text{yr}^{-1}$  in  $R_m$ , single row and isolated stands lost  $11.29$  and  $6.22 \text{ t DM ha}^{-1} \text{yr}^{-1}$ , respectively. While respiratory costs at stand level,  $R$ , are determined primarily by the volume of foliage, annual stemwood  $R_m$  per unit leaf area might be expected to increase as sapwood volume  $\text{ha}^{-1}$  increases (Lavigne *et al.* 1996). In pines, stemwood respiration was proportional to live-cell volume and annual stemwood growth while the ratio of annual respiration to photosynthesis increased linearly with stand biomass (Ryan 1990, Ryan *et al.* 1994). Consequently, although individual isolated trees lose a greater amount of fixed  $\text{CO}_2$  in  $R_m$  than trees from denser plantings, the much greater amount of biomass present in dense stands means that  $R$  will be greater and the ratio of stand photosynthesis to  $R$  less favourable than in open stands. In the current study,  $R_m$  accounted for 50% of total annual above-ground photosynthetic production ( $R$  plus biomass increment) in block-planted stands (mean annual above-ground biomass increment was  $24.03 \text{ t ha}^{-1} \text{yr}^{-1}$ , from Fig. 6) decreasing to 40% in stands of isolated trees (mean annual above-ground biomass increment was  $9.35 \text{ t ha}^{-1} \text{yr}^{-1}$ ). It does not follow, however, that  $R$  necessarily decreases with increased spacing as there is a trade-off between increased individual tree respiration due to spacing and total stand biomass production. In layouts where stand above-ground biomass is more similar to block plantings, but which are configured to receive more light (triple rows for example),  $R$  may not change.

#### **2.4.6 Turnover, $T$**

Although not measured directly, the amount of stand litterfall and biomass turnover probably changed with spacing. Litterfall and above-ground turnover of biomass was apparently less in stands of isolated trees than in denser stands. Block plantation trees shed their older, less productive lower leaves and the branches that bore them in response to low light levels at the base of their canopies. By May 2000, the first 2 m or more of the stems of block planted trees had no branches bearing green foliage (Table 2.2). In contrast, in isolated trees leaves and branches were present at ground level. Older leaves and branches were thus largely retained rather than contributing to litterfall.

## **2.5 Conclusion**

Light availability and competition for light was affected by planting layout. Planting designs that promoted competition for light produced trees with thin stems in relative terms and high values of  $\eta_s$ , few and/or thin branches, and narrow canopies with low depths. Branch angles, however, were steeper than in more open layouts. Though not demonstrated in the current study, high soil fertility may lead to generally poor form, but stem straightness will be improved with denser plantings. While individual tree leaf areas were lower than in more open stands, higher tree density meant that canopy closure was achieved sooner,  $L^*$  was greater and thus a greater proportion of available radiation was utilised on a ground area basis. Consequently, stand growth increments are higher in dense than in more open stands but  $R$  may also be greater. Widely spaced plantings produced trees with thicker stems. Allocation of biomass to stems was, however, reduced compared with block planted trees, since branches were more numerous, thicker and longer but flatter than those of densely planted trees. Wider spaced trees will, therefore, need to be pruned sooner and more heavily if sawlogs are to be obtained. Canopy closure will be delayed compared with dense stands or may not occur. Consequently, individual trees receive more light, have longer, wider and denser canopies and their growth and individual piece size will be greater than for densely planted trees, although their form and heavy branching may reduce the utility of the timber. By the same argument stand growth increments will be lower. The greater light availability under open stands, however, may allow other, simultaneous land uses such as grazing or the cultivation of crops. The benefit of increased land use flexibility may, in certain situations, offset the lower timber volumes obtained and increase overall farm profit.

# 3. Horizontal and Vertical Heterogeneity in the Light Environment and its Implications for Estimates of Carbon Fixation in Plantation Grown Eucalypts

## 3.1 Introduction

In forest stands as in all plant systems, light availability is an essential determinant of net primary productivity. Representations of the structure and the light environment within the crown are crucial components of mechanistic canopy CO<sub>2</sub> assimilation models (Landsberg 1986, Goudriaan 1986, Grace *et al.* 1987). Light availability within canopies is, however, a variable resource. Strong vertical gradients in light intensity have been identified in dense stands of a range of herbaceous plants and trees in which upper leaves receive more light than lower, shaded leaves (Egli and Schmid 1999, Schoettle and Smith 1999). Since Monsi and Saeki published their application of the Beer-Lambert law to predict light attenuation through plant canopies in 1953, models of light interception have largely focussed on describing these vertical gradients (Larsen and Kershaw 1996). Consequently, the canopy components of many simple models have also dealt primarily with vertical heterogeneity in leaf area distribution. The stand canopy is often assumed to be horizontally homogenous, and the interception of radiation is calculated on an area basis (Sellers *et al.* 1992, Sands 1995, 1996, Larsen and Kershaw 1996, Bartelink 1998). The rate of CO<sub>2</sub> assimilation is then integrated over canopy height on a daily or hourly basis (Goudriaan 1986). While this approach may give satisfactory predictions of stand growth for dense mono-specific, closed canopy stands it is not applicable to vegetation with discontinuous canopies, especially isolated crowns and mixed species (Palmer 1977, Oker-Blom 1986, Lantinga *et al.* 1999).

Horizontal discontinuity in the light environment and leaf area distribution within crowns has a significant impact on crown CO<sub>2</sub> assimilation. Variation and discontinuity in the distribution of leaf area and patchiness in irradiance within crowns are known to be an important feature of canopy structure even within closed canopy stands. Whitehead and co-workers (1990), for example, found that estimates of crown production that ignore the impact of foliage clustering on light over-estimated light interception by 20-30%. Similarly, Stenberg (1998) demonstrated that the grouping of foliage within crowns influenced the distribution of light interception and photosynthetic rate and ultimately influenced total stand biomass production. In widely spaced canopies the diurnal variation in light availability and interception is much greater than in closed stands (Palmer 1977, Jackson and Palmer 1979).

As indicated by Palmer (1977) and others (for example Ross 1981, Cescatti 1997a, Grindlay 1997, Bartelink 1998, Lantinga *et al.* 1999), in discontinuous systems a more detailed description of canopy structure is needed to account for the increased variation in the light environment. The impacts of these variations within the canopy are important in predicting and optimising stand production (Grindlay 1997, Papadopoulos and Pararajasingham 1997). The purpose of the current study was to empirically investigate variations in light availability on relationships among the distribution of light attenuation, light saturated rate of photosynthesis at ambient CO<sub>2</sub> ( $A_{\max}$ ) and to assess the influence of these on estimates of crown CO<sub>2</sub> fixation in *Eucalyptus globulus* in a three- to four-year-old plantation. We then used these empirical data to assess the performance of simple big-leaf tree growth models using a single light extinction coefficient (formulated in terms of leaf area index or leaf area density and beam path length). There are many more complex radiation models available including other big-leaf models especially in their two-leaf and sun/shade variants and the array model MAESTRA. The latter allows for a highly detailed and flexible description of the canopy light environment, leaf area distribution and accommodates differing planting layouts. These more

complex models, however, are data intensive and require a substantial range of measurements and derivation of empirical relationships, many of which may not be easily available to non-modelers. Big-leaf models that use a light extinction coefficient over the length of the canopy are still in common use despite their well-documented limitations.

## **3.2 Materials and Methods**

### **3.2.1 Light**

Irradiation data was collected as specified in the materials and methods portion of chapter one recorded in target trees from each treatment in block one. In the current chapter, light attenuation data is presented in terms of the ratio ( $I/I_0$ ) of irradiance intercepted at a given position to incident radiation measured outside the canopy one hour about solar noon and averaged over the entire daylight period. During summer, estimates of irradiance within the crown were corrected for internal reflectance (after James and Bell 2000) and diffuse radiation was assumed to have an extinction coefficient of 0.5 (after Iqbal 1983).

### **3.2.2 Photosynthesis**

Photosynthetic measurements were taken as described in chapter one. During November-December 1999, photosynthetic measurements were not taken during known periods of high vapour pressure deficit ( $D$ ) around solar noon. Except for light curves,  $A_{\max}$  data were discarded if stomatal conductance was below around  $150\text{--}200 \mu\text{mol m}^{-2} \text{s}^{-1}$ , which under full illumination corresponds to a  $D$  of around 1-1.5 kPa, beyond which point stomatal closure limits photosynthesis (White *et al.* 1999).

### **3.2. Nitrogen**

Five leaves were taken from each sampling position from three replicate trees of each treatment. Leaves were weighed, their images recorded using a flatbed scanner for leaf area analysis and air-dried at  $80^\circ\text{C}$  until weight was constant (48 h). The five dried leaves from each sampling position were bulked, ground through a 2 mm mesh and kept overnight at  $70^\circ\text{C}$  prior to sub-sampling for N analysis. Sub-samples (150 mg) were prepared for analysis according to the acid-hydrogen peroxide technique (after Lowther 1980) and total N was measured using a continuous flow colorimetric autoanalyser (McLeod 1992). The specific leaf area of leaves (single-sided area : weight ratio) was used to convert weight-based values of N concentration ( $N_w$ ) to area-based values ( $N_a$ ).

### **3.2.4 Crown dimensions**

Tree heights were measured in August and May. Branch diameters of standing measurement trees were measured in August and November. In May 2000, after completion of all other measurements, the three trees from the block planting, single row and isolated tree treatments were cut down. Diameter, fresh weight, angle from vertical, length, green leaf weight and the height from the ground of each branch were recorded. Projected branch lengths were calculated from branch angle and length. Projected branch length and the branch height were used to determine crown dimensions, total leaf area and the leaf area above each light sensor.

### **3.2.5 Limitation by water**

The potential of soil water to limit tree photosynthesis and growth was evaluated in November 1999 by measuring the pre-dawn water potential of three trees from each treatment in every block on the plantation using a standard pressure-bomb technique. The potential for deficits in atmospheric water vapour pressure ( $D$ ) to limit photosynthesis through stomatal closure was assessed (as given above) from calculations of  $D$  from observed relative humidity data ( $RH$ ) described below.

### 3.2.6 Data analysis and calculations

A nonrectangular hyperbola was fitted to each light curve (Battaglia and Sands 1997, Pinkard and Beadle 1998):

$$A = \frac{2\alpha I A_x}{(\alpha I + A_x) + \sqrt{(\alpha I + A_x)^2 - 4\theta\alpha I A_x}} - r_l \quad (3.1)$$

Where  $\alpha$  is the initial slope of the relationship at low  $I$ ;  $r_l$  is leaf dark respiration and  $\theta$  determines the shape of the photosynthetic light response curve; and  $A_x$  is light saturated  $A$ .

Light response curves were modelled for other, unmeasured canopy positions. Following von Caemmerer (2000), where not otherwise known,  $\alpha$  was assigned the value of 0.05 and the  $\theta$  value of 0.7. Leaf dark respiration was estimated from the linear regression of  $r_l$  against leaf  $N_w$ , spacing and month. Values for  $A_x$  were calculated as the sum of  $A_{\max}$  plus  $r_l$ . The parameters  $A_x$ ,  $\alpha$  and  $r$  are temperature dependent and were adjusted using the formulae given by Sands (1995, 1996) and Battaglia and Sands (1997).

For  $\alpha$ :

$$\alpha(T) = \alpha_1(T - T_0), \quad (3.2)$$

where  $\alpha_1$  is the strength of the temperature dependence of  $\alpha$ ,  $T$  is the actual temperature and  $T_0$  is a reference temperature (20°C).

For  $A_x$ :

$$A_x(T) = A_{opt} \left( 1 - \frac{1}{2} \frac{(T - T_{opt})^2}{T_{1/2}^2} \right), \quad (3.3)$$

where  $A_{opt}$  is the observed value of  $A_{\max}$  not the value predicted by Sands (1996) at optimum temperature  $T_{opt}$ ,  $T_{1/2}$  is the temperature change from  $T_{opt}$  required to reduce  $A_x$  to half the optimum value, and:

$$T_{opt} = (1 - \tau)T_{pref} + \tau T, \quad (3.4)$$

where  $T_{pref}$  is the acclimation temperature at which the optimum temperature and acclimation temperature are identical (Battaglia and Sands 1997),  $\tau$  determines how closely  $T_{opt}$  follows  $T$ . Leaf dark respiration ( $r_l$ ,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) was adjusted for temperature according to the equation:

$$r(T) = Q_{10} r_l \quad (3.5)$$

$$\text{where } Q_{10}(T) = Q_0^{(T - T_0)/10} \quad (3.6)$$

and following Pereira *et al.* (1986):

$$Q_0 = -0.038T_{av} + 3.268 \quad (3.7)$$

where  $T_{av}$  is the 10-day running average  $T$ . Diurnal temperature variation was modelled by assuming temperature varied sinusoidally between successive maxima and minima, with minimum temperatures assumed to occur at sunrise, and maxima at some time early in the afternoon. The basic equation is

$$T(h) = \frac{1}{2} \left( (T_1 + T_2) + (T_1 - T_2) \cos \left( \pi \frac{h - h_1}{h_2 - h_1} \right) \right), \quad (3.8)$$

where  $h$  is the time of day,  $T_1$  is a maximum or minimum which occurs at time  $h_1$ , and  $T_2$  is the next extreme temperature (i.e. minimum or maximum) which occurs at time  $h_2$ . Eqn. (3.8) is applied repeatedly over each period between successive maxima and minima, using the appropriate values for  $T_1$  and  $T_2$ . For example, between sunrise and early afternoon  $T_1$  and  $T_2$  are this morning's minimum and today's maximum temperatures, respectively, and between early afternoon and sunrise the next morning  $T_1$  and  $T_2$  are today's maximum and the next morning's minimum temperatures, respectively.

Similarly, the diurnal variation in relative humidity ( $RH$ ) was calculated from measured daily maxima and minima according to:

$$RH(h) = \frac{1}{2} \left( (R_1 + R_2) + (R_1 - R_2) \cos \left( \pi \frac{h - h_1}{h_2 - h_1} \right) \right), \quad (3.9)$$

where  $h$  is the time of day,  $R_1$  is a maximum or minimum which occurs at time  $h_1$ , and  $R_2$  is the next extreme of relative humidity (i.e. minimum or maximum) which occurs at time  $h_2$ . Relative humidity was assumed to be lowest at maximum temperatures. Eqn. (3.9) is applied repeatedly over each period between successive maxima and minima, using the appropriate values for  $R_1$  and  $R_2$ . For example, between sunrise and early afternoon  $R_1$  and  $R_2$  are this morning's maximum and today's minimum relative humidity, respectively, and between early afternoon and sunrise the next morning  $R_1$  and  $R_2$  are today's minimum and the next morning's maximum humidity, respectively. These relative humidity and temperature data were used to calculate the diurnal variation in vapour pressure deficit ( $D$ ) following Jones (1994).

Leaf green weight was converted to leaf area using specific leaf area ( $SLA$ ) relationships determined from subsamples of leaves (after Medhurst *et al.* 1999). Relationships between individual branch diameter and the area of leaves on the branch were used to estimate the leaf area and leaf biomass on each branch, and the results summed to give total tree leaf area (after Henskens *et al.* 2001). Leaf area index ( $L^*$ ) was the sum of tree leaf area (for a single sided leaf) divided by the vertical projection of the crown on to the ground. Branch distributions were used to estimate cumulative leaf area and the distribution of leaf area within individual crowns. Leaf area densities for individual cells and for the upper, middle and lower canopy layers were calculated by dividing the leaf area within each cell or layer by its volume.

The relationship between branch diameter and projected branch length was used to calculate the crown basal area of each canopy height zone. Each zone was divided into 12 cells by aspect (north, south, east, west) and proximity to the stem (outer, middle and inner) to give a total of 36 cells per tree. Leaf area within each cell was divided by the area of the basal surface of the cell to give a cellular  $L^*$  ( $L_i$ ) corrected for seasonal solar zenith angle. The fraction of radiation arriving at the centre of the bottom of each cell was assumed to be representative of the entire lower surface of the cell. The difference in the light flux density at the top ( $I_T$ ) and bottom centre ( $I_N$ ) of each cell was taken as an estimate of the absorption of light flux density absorbed by each cell. A unique light extinction coefficient ( $k$ ) was calculated for each cell in winter and summer using the Beer-Lambert law:

$$I_N = I_T e^{-kL_N} \quad (3.10)$$

where  $I_N$  is the light flux density at the  $N$ th position in the canopy,  $I_T$  is the light flux density incident on the top surface,  $L_N$  is leaf area index at the  $N^{\text{th}}$  layer and  $k$  the light extinction coefficient. The light extinction coefficients were corrected for diurnal and seasonal changes in solar zenith angle ( $k/\cos\theta$ , where  $\theta$  is the solar zenith angle). The light flux density within each cell was estimated by applying equation (10) to  $0.1 \text{ m}^{-2} \text{ m}^{-2}$  vertical slices of its  $L^*$ . An alternative formulation of the Beer-Lambert equation was used to examine sources of variation in canopy light extinction:

$$I_N = I_T e^{-G\sigma\rho} \quad (3.11).$$

$G$  is the canopy extinction coefficient or  $G$ -function (after Ross 1981),  $\sigma$  is leaf area density and  $\rho$  the vertical path length of light through the crown (height modified by solar elevation angle). In this formulation  $\rho$  varies with solar elevation so that if leaf area/angle has a spherical distribution  $G$  should be constant since hourly, daily and seasonal variations in solar elevation are subsumed into changes in  $\rho$ .

Diurnal canopy carbon (C) assimilation and C budgets for each cell were obtained by applying the light response equations to the appropriate observed diurnal light measurements. These were compared to budgets derived using the Beer-Lambert's law equation to derive a single  $k$  over the entire length of the crown and assuming a single big leaf with a horizontally and vertically uniform distribution of leaf area.

Differences in  $k$  and in  $G$ , photosynthetic data and the distribution and relationships among parameters were analysed using the S-PLUS forward and backward manual selection regression and ANOVA procedures (Mathsoft Inc.1999, S-PLUS 2000 Users Guide, Data Analysis, Products Division, Mathsoft, Seattle, WA pp. 620).

## 3.3 Results

### 3.3.1 Light environment

The light environment within the crowns of trees was strongly influenced by planting layout ( $P < 0.001$ ). Relative light flux densities ( $I/I_0$ ) were generally lower in block-planted trees and due to shading by neighboring trees, they intercept less light than isolated trees (Fig. 3.1). Light flux density within the crowns also varied according to aspect ( $P = 0.02$ ). These patterns, however, varied with spacing. For example, at solar noon in August, relative light flux densities were lowest on the northern and southern aspects of block-planted trees, but for isolated trees were highest in the southern portion of the crown (Fig. 3.1a,  $P < 0.05$ ). Similarly, during November in block-planted trees, the lowest light flux densities occurred on western and southern aspects, while in isolated trees the highest flux densities occurred on these aspects (Fig. 3.1b).

Irrespective of planting layout, relative light flux density within crowns showed two marked gradients (Fig. 3.1). The strength of the vertical gradient was influenced by both spacing and season. There was much less difference in light flux densities between the middle and lower portions of isolated trees than for block-planted trees, irrespective of season and a greater difference between flux densities in these layers in summer (November) than winter (August). The within-crown light environment was further complicated by the presence of strong horizontal gradients within each height zone ( $P < 0.001$ ). Across the crowns of block-planted and isolated trees relative light flux density declined with increasing proximity to the stem ( $P < 0.001$ ). Within this general pattern, there were smaller scale temporal and spatial variations in light intensity. Transistor light flecks and more stable patches of higher intensity light, termed light wells, produced strongly localised, discontinuous gradients in light intensity.

As shown above, light was attenuated rapidly through the upper canopy of block-planted and isolated trees (Fig. 3.1, 3.2). Relative light levels were low at the base of the canopy, though they tended to be higher in summer than in winter. A large, though highly variable proportion of light was intercepted in the upper canopy. On average, in block-planted trees between 55-80% of incident light was intercepted in the upper 1.0-1.5 m  $m^{-2}$  of  $L^*$ . This was observed irrespective of time of year or whether light interception ( $I/I_0$ ) was calculated on an instantaneous basis (over one hour about solar noon), summed over an entire day or averaged over each canopy layer (Fig. 3.2b). Relative light flux densities in the lower crown were greater when calculated over the whole day than at solar noon because of light shining between the rows, gaps in the canopy, sunflecks and greater sun angles, particularly during late afternoon. Light was attenuated more rapidly through the canopy during winter than during summer ( $P < 0.001$ ). Consequently, during winter  $k$  calculated over the entire crown according to equation (3.10), was 0.72 compared with 0.54 in summer in block-planted trees. The latter is close to the more commonly used average annual value for  $k$  of 0.5 (e.g. Battaglia and Sands 1997, Landsberg and Waring 1997). Similarly, for isolated trees a  $k$  of 1.20 compared with 0.79 was obtained in winter and summer, respectively. In contrast in block-planted and isolated trees variations in  $G$  between August and November (from 0.34 to 0.28 and 0.16 to 0.18, respectively) were not significant ( $P = 0.08$ ). Like  $k$ ,  $G$  varied strongly with spacing ( $P < 0.0001$ ). Unlike  $k$ , however, there was a significant interaction between time of year and spacing ( $P = 0.028$ ).

In winter (Fig. 3.2a), the upper canopy portion of the relative irradiance  $-L^*$  graph is not well described and light intensities in the lower portions may be under-estimated. A consequence of this, can be demonstrated by comparing observed light flux densities at various positions in the crown with those predicted by applying a single Beer-Lambert law equation (equation 10, a single  $k$ ) across the entire crown (Fig. 3.3). In the upper canopy, light flux densities predicted by a single  $k$  frequently exceeded those measured (Fig. 3.3a,d). This was particularly evident on the eastern aspect of the crown (Fig. 3.3d). In contrast, light levels at the bottom of the canopy were generally underestimated (Fig. 3.3c,f). Light flux densities in the mid-canopy also tended to be underestimated (Fig 3.3b,e). At all canopy levels and aspects there were brief periods when, due to irregularities in the crown, light sensors experienced full or close to full sunlight. These events were not, and could not be, predicted using the simple Beer-Lambert model and the occurrence of light flecks exacerbated the difference between the predicted and the observed light environment. As a result, the relationship between the observed and predicted light environment at any point in the canopy was relatively poor (Fig. 3.3). The use of a single  $G$ , similarly underestimated light flux densities within canopies and thus light interception by around 50-60% in block-planted and isolated trees. The proportion of irradiance in the lower canopy, for example, was predicted as 6% and 24% of total canopy irradiance in block-planted and isolated trees during summer. Lower canopy irradiance, however, was observed to account for 15% and 35% of total canopy irradiance in block-planted and isolated trees, respectively.

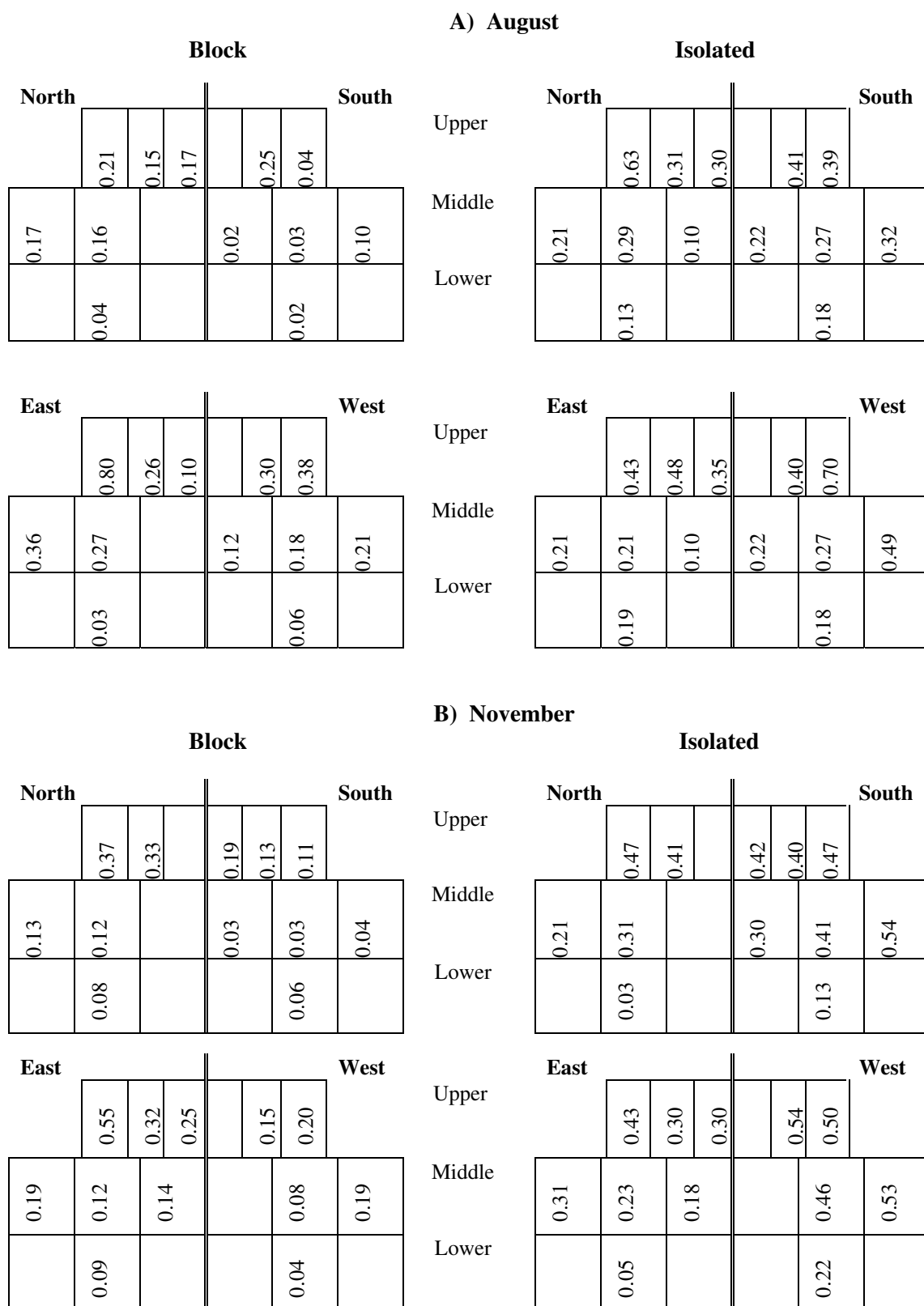


**Figure 3.1.** Horizontal and vertical variation in relative light intensity ( $I/I_0$ ) at the centre of the lower surface of cells at various positions through the canopies of block-planted and isolated canopies in **A)** August and **B)** November 1999.

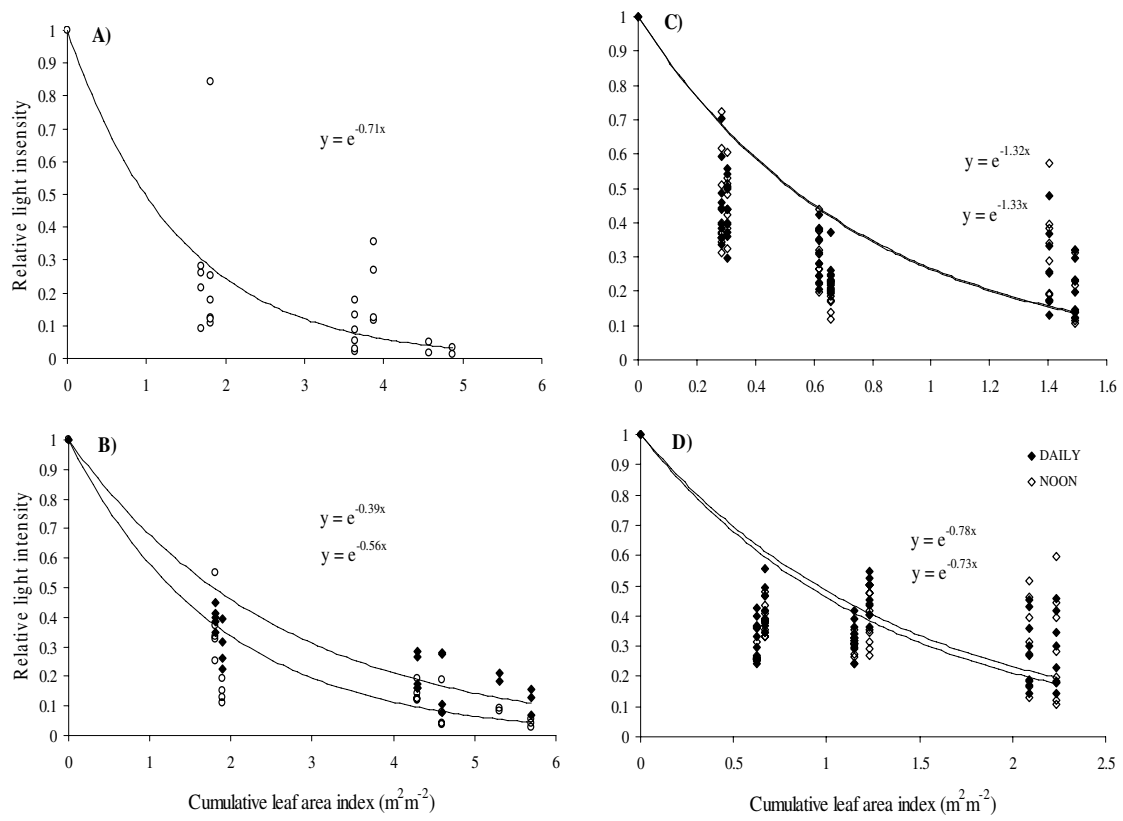


**Figure 3.2.** Relative light intensity ( $I/I_0$ ) averaged over one hour around solar noon (noon) and over the light period (daily) against cumulative leaf area index ( $\text{m}^2$  leaf area  $\text{m}^{-2}$  ground area) in the crowns of block-planted trees in A) August and B) November, and in isolated trees in C) August and D) November.

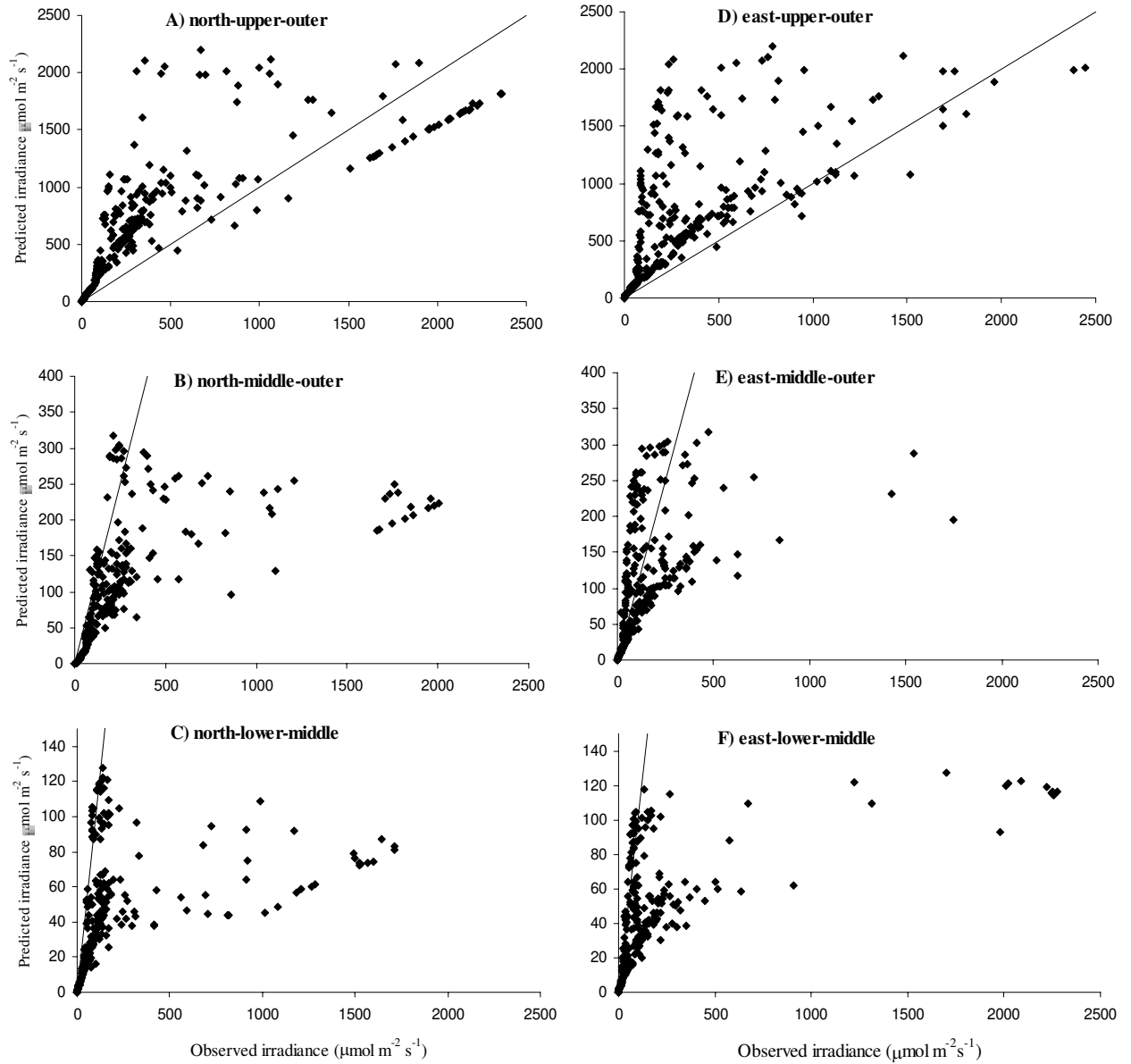


**Figure 3.3.** Observed light intensities ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) compared with values predicted by the Beer-Lambert law equation for positions in the canopy of block-planted trees in November. The solid line indicates the point at which observed and predicted light intensities are the same.

### 3.3.2 Photosynthesis

Photosynthetic responses to light within the crown varied along vertical (canopy height,  $P < 0.001$ , Fig. 4a) and horizontal gradients ( $P < 0.001$ , Fig. 3.4b). Photosynthesis in leaves lower in the crown or closer to the stem was saturated at lower light intensities than in leaves higher up the crown or further from the stem (Fig. 3.4). At an external  $p(\text{CO}_2)$  of  $350 \mu\text{bar}$  both  $r_l$  and  $A_x$  were affected by spacing, month and leaf N concentration, and for  $A_x$  also by canopy position (linear regressions  $R^2 = 0.71$  for both). The resulting regression equations for  $r_l$  were as follows:

$$\text{Block-planted, August: } r_l = 1.23 + 0.4N_w \quad (3.11)$$

$$\text{Isolated, August: } r_l = 0.92 + 0.47N_w \quad (3.12)$$

$$\text{Block-planted, November: } r_l = 2.26 + 0.47N_w \quad (3.13)$$

$$\text{Isolated, November: } r_l = 1.72 + 0.47N_w \quad (3.14)$$

where  $N_w$  is the percentage leaf nitrogen concentration on a weight basis.

Apparent quantum yield ( $\alpha$ ) showed a weak variation with height ( $P = 0.09$ ) while  $\theta$  did not vary systematically through the canopy.

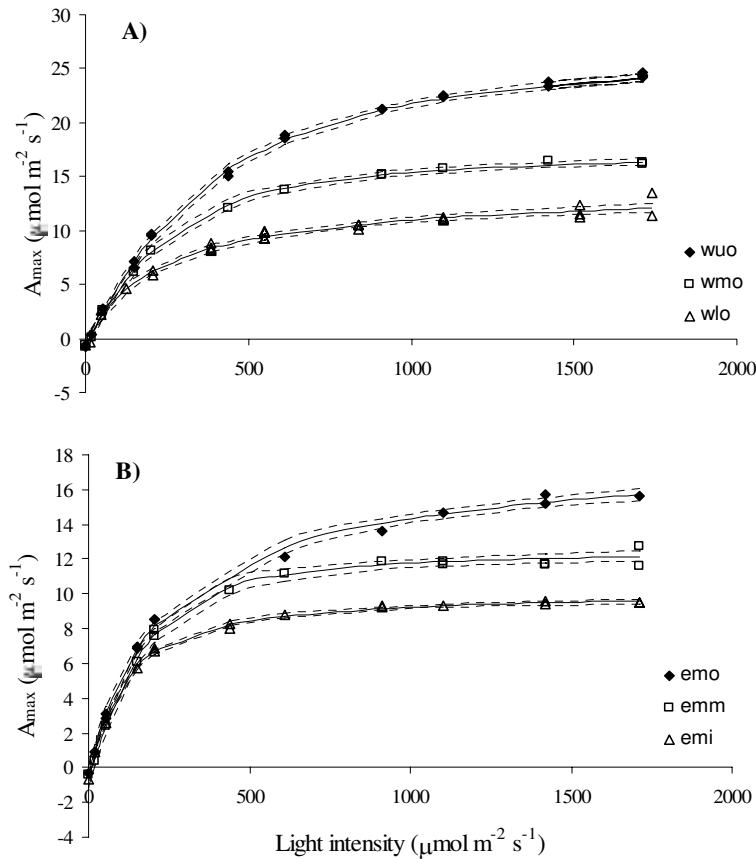


**Figure 3.4.** The response of net CO<sub>2</sub> assimilation rate ( $A_{\max}$ ,  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{s}^{-1}$ ) at  $p(\text{CO}_2)$   $350 \mu\text{bar}$  to light intensity ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) at three positions along **A**) a vertical gradient (west-upper-outer, west-middle-outer and west-lower-outer) and **B**) a horizontal gradient (east-middle-outer, east-middle-middle, east-middle-inner) in the canopy of block-planted trees. A solid line indicates the fitted values from the regression while broken lines represent the upper and lower 95% confidence intervals.

Daytime maximum vapour pressure deficits ( $D$ ) were potentially limiting to photosynthesis (values above 1 kPa) on four days during November (Table 3.1).

**Table 3.1.** Maximum water vapour pressure deficits ( $D$ , kPa) experienced (between 1300 and 1500 hours) during measurement periods in August and November/December 1999.

| Date   | Maximum $D$<br>(kPa) | Date   | Maximum $D$<br>(kPa) |
|--------|----------------------|--------|----------------------|
| 12/08  | 0.34                 | 7/11   | 0.76                 |
| 13/08* | 0.51                 | 8/11   | 1.09                 |
| 14/08* | 0.60                 | 9/11   | 0.84                 |
| 15/08  | 0.70                 | 10/11  | 1.36                 |
| 16/08* | 0.27                 | 11/11  | 2.55                 |
| 17/08  | 0.75                 | 12/11  | 0.86                 |
| 18/08  | 0.40                 | 13/11  | 0.75                 |
| 19/08  | 0.24                 | 14/11  | 1.22                 |
| 20/08* | 0.50                 | 15/11  | 0.76                 |
|        |                      | 16/11* | 0.58                 |
|        |                      | 17/11  | 1.25                 |
|        |                      | 18/11* | 0.93                 |
|        |                      | 19/11* | 0.70                 |
|        |                      | 20/11* | 0.69                 |
|        |                      | 21/11* | 1.11                 |
|        |                      | 22/11  | 1.34                 |
|        |                      | 23/11  | 1.65                 |
|        |                      | 24/11  | 2.89                 |
|        |                      | 14/12* | 1.12                 |
|        |                      | 15/12* | 0.99                 |
|        |                      | 16/12* | 1.25                 |
|        |                      | 17/12* | 1.71                 |
|        |                      | 18/12  | 2.42                 |

\*days when photosynthetic data were collected

### 3.3.3 Leaf area

Block-planted trees had relatively high  $L^*$  of 4.9 and 5.7 m<sup>2</sup> m<sup>-2</sup> in August and November, respectively, compared with 1.5 and 2.2 m<sup>2</sup> m<sup>-2</sup> in isolated trees (Fig. 3.1). Between August and November 1999 the leaf area of block-planted trees increased from approximately 38 m<sup>2</sup> to 45 m<sup>2</sup> tree<sup>-1</sup> (Fig. 3.5, 3.6). Leaf area was irregularly distributed between aspects and height zones (Fig. 3.5, 3.6). In August, for example, a few larger branches in the middle of the northeast quadrant, and in November a few large branches, separated by smaller branches, in the south-west quarter of the middle and upper canopy accounted for the majority of the leaf area in those portions of these zones (Fig. 3.5, 3.6). In both August and November, most of the trees' leaf area was located in the middle canopy (Fig. 3.5, 3.6). Between August and November leaf area distribution shifted. The contribution of the lower canopy to total leaf area declined between August and November but the contribution of the upper canopy increased. This was because although leaf area was lost from the lower canopy, green branches remained close to the ground and there was little canopy lift despite increased tree height. This gave a longer green canopy with sparse leaf area in the lower third.

Leaf area densities were greatest in the upper portions of both block-planted and isolated trees irrespective of the time of year (Table 3.2). This was because the middle and lower layers of canopy had greater volumes. Unlike block-planted trees, leaf area densities in isolated tree canopies did not decline between the middle and lower portions of the crown as lower leaves were retained. Juvenile leaves were present at the middle and lower levels of trees from all treatments, particularly on the outer positions (Table 3). Juvenile leaves generally comprised a greater proportion of sample leaves

and tree leaf area, in isolated and row trees than in block-planted trees. Those on block-planted trees tended to be old, heavily thickened and senescent whereas those on row and isolated trees were young, green and thin with lower specific leaf area.

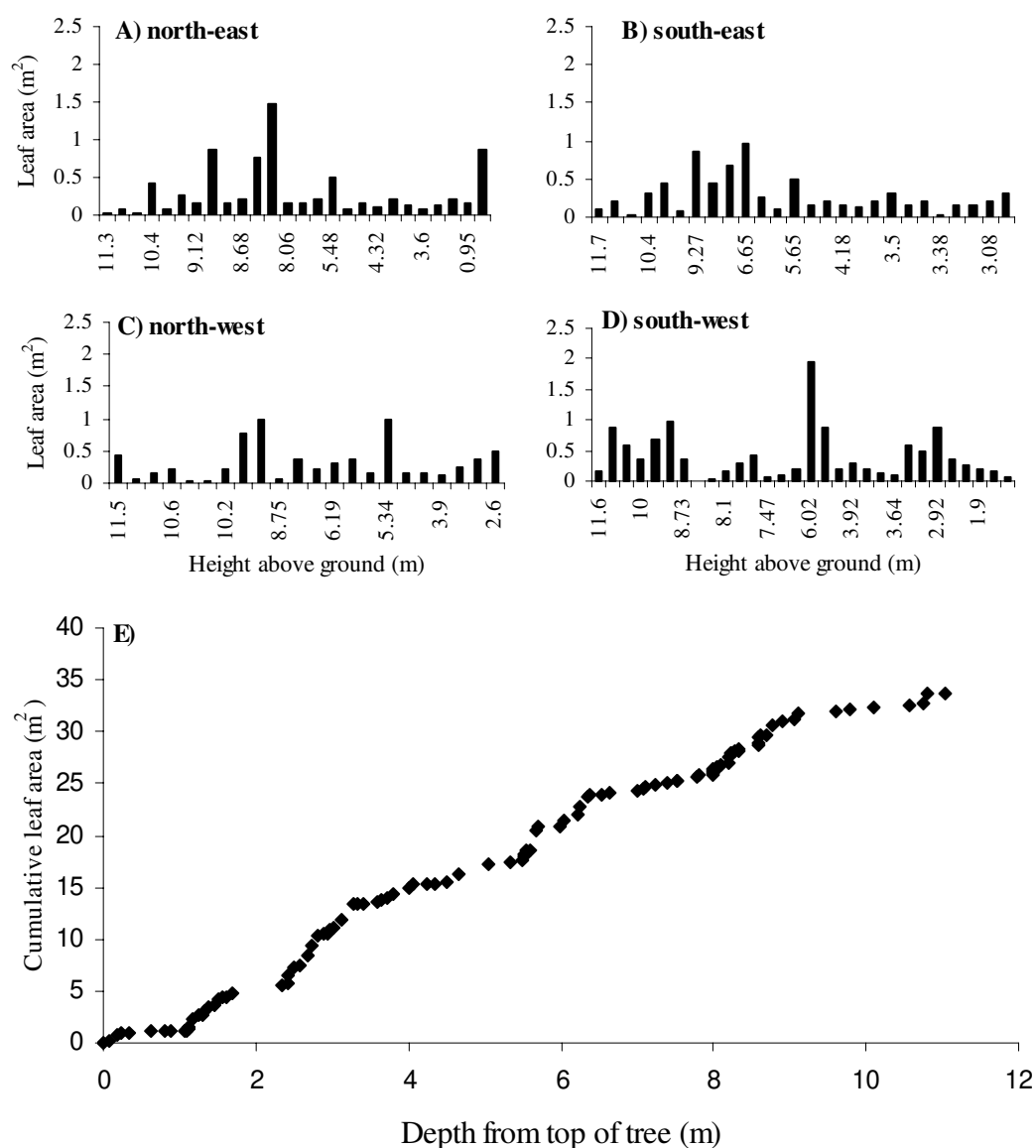


**Figure 3.5.** Leaf area distribution in block-planted tree crowns in August 1999 in terms of aspect **A)** north-east, **B)** south-east, **C)** north-west, **D)** south-west and **E)** cumulative leaf area from the top of the tree crown.

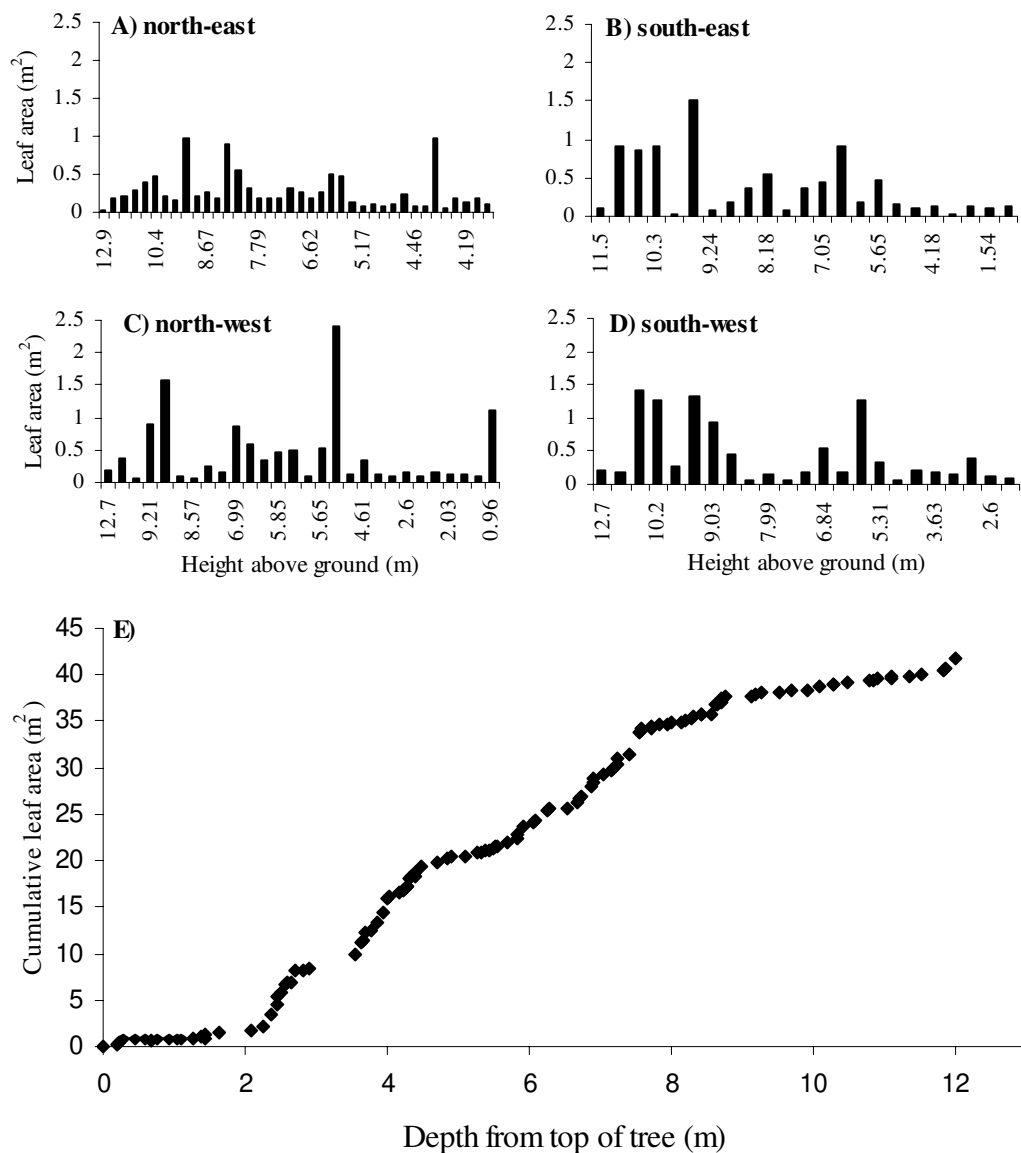


**Figure 3.6.** Leaf area distribution in block-planted tree crowns in November 1999 in relation to aspect **A)** north-east, **B)** south-east, **C)** north-west, **D)** south-west, **E)** cumulative leaf area from the top of the tree crown.

**Table 3.2.** The distribution of leaf area density (m<sup>2</sup> m<sup>-3</sup>) in three crown height zones of block-planted and isolated trees in August and November 1999.

|                      | Block-planted |          | Isolated |          |
|----------------------|---------------|----------|----------|----------|
|                      | August        | November | August   | November |
| <b>Upper canopy</b>  | 1.68          | 1.19     | 2.88     | 4.20     |
| <b>Middle canopy</b> | 0.99          | 0.78     | 1.08     | 0.64     |
| <b>Lower canopy</b>  | 0.42          | 0.40     | 0.94     | 0.61     |
| <b>Total canopy</b>  | 0.88          | 0.73     | 1.13     | 0.83     |

**Table 3.3.** The mean relative percentage of juvenile to mature foliage in leaf samples from different height zones in the canopies of block-planted, row and isolated trees (means from three trees per treatment from two blocks and four aspects and three canopy positions per height zone).

| Treatment | August          |                 |                 | November       |                  |                 |
|-----------|-----------------|-----------------|-----------------|----------------|------------------|-----------------|
|           | Block           | Row             | Isolated        | Block          | Row              | Isolated        |
| Upper     | 0               | 0               | 0               | 0              | 0                | 0               |
| Middle    | 23              | 38              | 12              | 0              | 20               | 15              |
| Lower     | 95              | 100             | 90              | 25             | 95               | 37              |
| Total     | 40 <sup>a</sup> | 46 <sup>b</sup> | 34 <sup>c</sup> | 9 <sup>d</sup> | 38 <sup>ac</sup> | 24 <sup>e</sup> |

Different letters indicate significant difference between means.

### 3.3.4 Carbon gain

In block-planted trees net CO<sub>2</sub> assimilation in the heavily shaded lower portions of the canopy occurred primarily during brief periods of high irradiance formed either by gaps in the canopy above or light-flecks (Fig. 3.7). In Figure 3.7, positive C fluxes of short duration due to light flecks are clearly identifiable as single points, whereas more stable light conditions gave rise as more or less solid lines. On the south and west aspects of the lower canopy, and south aspect of the middle canopy in particular, positive C balances occurred almost exclusively during light flecks (Fig. 3.7). Increased photosynthetic activity during light flecks was also a major contributor to achieving positive diurnal C balances in the middle canopy of block-planted trees. In contrast, light levels in the canopies of isolated trees were more consistently favourable to photosynthesis. Consequently, net CO<sub>2</sub> assimilation occurred at greater rates for longer periods. This reduced the importance of light flecks to achieving a net positive C balance (Fig. 3.7b,d).

Despite the low levels of irradiance at the bottom of the canopy of block-planted trees, the cumulative C balance at all height zones was positive during winter and summer (Table 3.4, 3.5). Net losses from the outer leaves in the south during winter and in the east during summer, were more than compensated for by higher assimilation rates in leaves on other aspects. During winter, however, these positive balances in the lower canopy were marginal (Table 3.4). The highest net CO<sub>2</sub> assimilation rates occurred in the upper canopy irrespective of the time of year (Table 3.4, 3.5). Despite having a greater leaf area than the upper canopy, the middle canopy zone contributed about 40% of the overall CO<sub>2</sub> fixed on a daily basis during winter and only around 30% during summer (Table 3.4, 3.5, Fig. 3.8).

The predictions of total canopy C fixation made using a single Beer-Lambert equation to estimate irradiance were similar to those observed using the cellular method, but only when the appropriate seasonal *k* or *G* was used (Table 3.4, 3.5). In winter, for example, daily C production was estimated as 23.7 g tree<sup>-1</sup> day<sup>-1</sup> using observed light data, 29.5 g tree<sup>-1</sup> day<sup>-1</sup> when a *k* of 0.72 was applied over the entire canopy. Using the summer *k* of 0.54, however, gave a significantly higher estimate of 33.5 g tree<sup>-1</sup> day<sup>-1</sup>. During summer, the predictions were more accurate. From observed light data, daily C fixation in November was around 109.6 g tree<sup>-1</sup> day<sup>-1</sup>, a single seasonal *k* of 0.54 gave 107.3 g tree<sup>-1</sup> day<sup>-1</sup> while the winter *k* of 0.72 significantly underestimated C production at 81.1 g tree<sup>-1</sup> day<sup>-1</sup> of fixed C. These estimates scale up to 37-50 t ha<sup>-1</sup> yr<sup>-1</sup> of C (Table 3.5).

The use of a single *k* or *G* to estimate irradiance within the canopy provided good estimates of both the contribution and the spatial distribution of C production in the upper canopy of block-planted trees, particularly for November (Fig. 3.8a,d). The predicted contribution and distribution of C production within the middle and lower canopy layers during winter, however, varied considerably from the observed data (Table 3.4, Fig. 3.8b,c). Carbon fixation in the middle canopy was over-estimated by approximately 40% and the amount of C fixed in the north and south aspects of this layer, was also over-estimated. Similarly, very little C was fixed in the southern portion of the lower canopy (Fig. 3.8c). During summer, the amount of C fixed in the lower canopy was overestimated by about 56%. Carbon production on the south aspect of this layer was again overestimated (Fig. 3.8f).

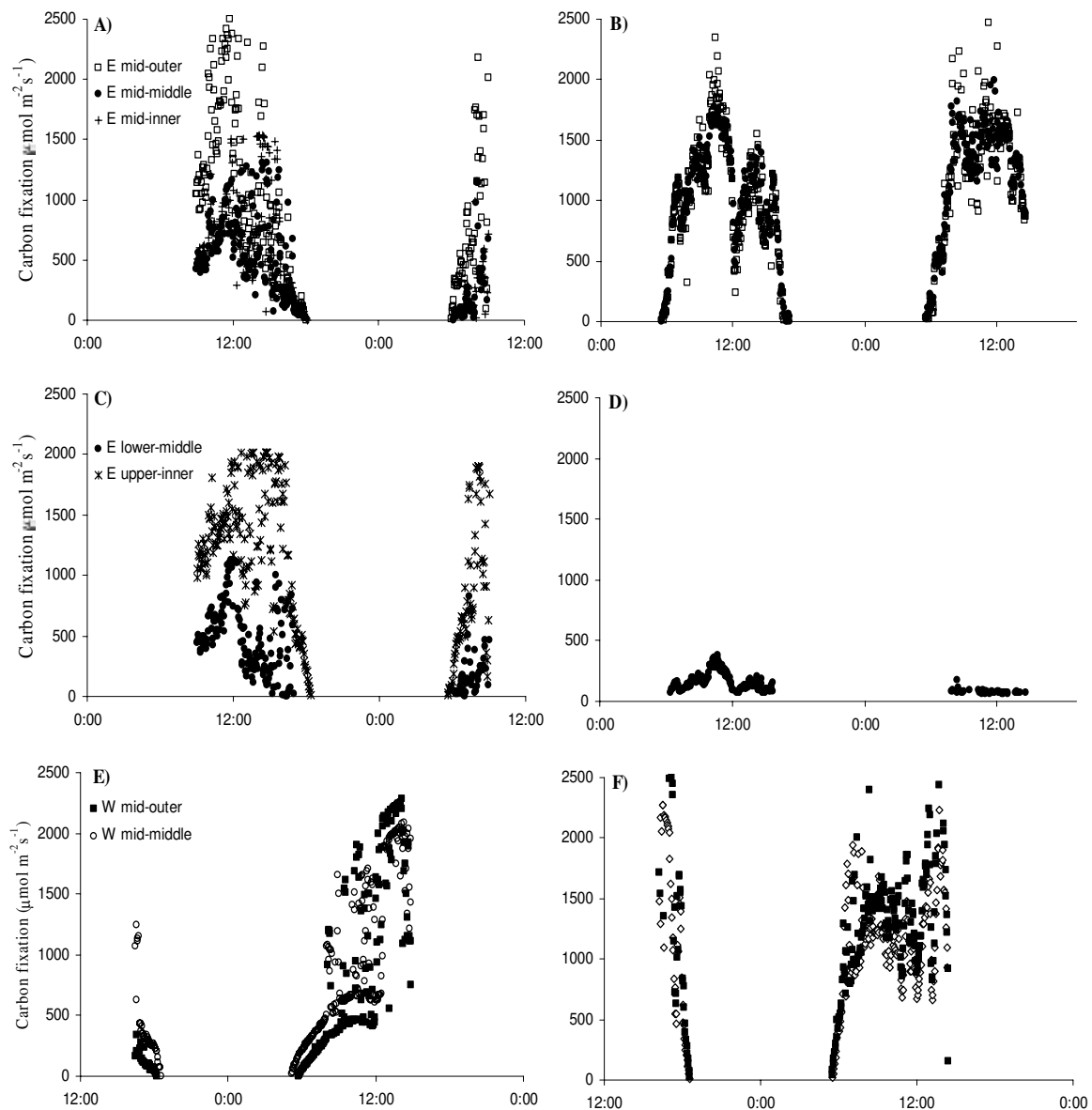


**Figure 3.7.** Time course of positive C fluxes at various canopy positions on the A) and C) eastern aspect of block planted and B) and D) eastern aspect of isolated trees, and E) western aspect of block-planted and F) western aspect of isolated trees during November 1999. Positive C fluxes due to light flecks appear as single points. Net photosynthesis under more stable light conditions produced more or less solid lines.

**Table 3.4.** Daily net CO<sub>2</sub> assimilation rate (mmol day<sup>-1</sup>) during a day in winter (August 1999) at various positions in the canopy of block-planted trees calculated from measured light data and from light data derived from the Beer-Lambert law for light attenuation using the observed value for *k* in August (0.72) and November (0.54).

[illegible]

**Table 3.5.** Daily net CO<sub>2</sub> assimilation rate (mmol day<sup>-1</sup>) during a day in summer (November 1999) at various positions in the canopy of block-planted trees calculated from

measured light data and from light data derived from the Beer-Lambert law for light attenuation using an observed value of  $k$  for August (0.72) and for November (0.54).

| Lower           | Position               | NLO           | NLM   | SLO        | SLM   | ELO       | ELM   | WLO     | WLM   | Total  |       |       |       |        |
|-----------------|------------------------|---------------|-------|------------|-------|-----------|-------|---------|-------|--------|-------|-------|-------|--------|
| Measured        | Mmol day <sup>-1</sup> | 180.9         | 43.9  | 21.3       | 25.5  | -16.9     | 10.3  | 202.7   | 35.3  | 502.9  |       |       |       |        |
| k = 0.54        | Mmol day <sup>-1</sup> | 44.3          | 31.6  | 124.6      | 43.1  | -61.8     | -40.7 | 22.4    | 58.7  | 222.3  |       |       |       |        |
| k = 0.72        | Mmol day <sup>-1</sup> | -65.4         | -42.1 | -31.1      | 3.4   | -108.9    | -67.0 | -26.4   | 1.8   | -335.8 |       |       |       |        |
| Leaf area       | (m <sup>2</sup> )      | 1.62          | 0.97  | 0.75       | 0.60  | 0.98      | 0.59  | 1.39    | 1.11  |        |       |       |       |        |
| Middle          | Position               | NMO           | NMM   | NMI        | SMO   | SMM       | SMI   | EMO     | EMM   | EMI    | WMO   | WMM   | WMI   | Total  |
| Measured        | Mmol day <sup>-1</sup> | 240.1         | 276.2 | 276.2      | 260.4 | 116.9     | 70.3  | 517.5   | 136.4 | 85.6   | 410.2 | 420.5 | 111.7 | 2870.6 |
| k = 0.54        | Mmol day <sup>-1</sup> | 341.0         | 179.0 | 163.4      | 162.9 | 76.3      | 81.8  | 518.2   | 142.3 | 84.7   | 542.2 | 518.9 | 215.7 | 3026.5 |
| k = 0.72        | Mmol day <sup>-1</sup> | 193.0         | 65.5  | 83.9       | 107.5 | 53.7      | 58.3  | 276.0   | 25.8  | 42.0   | 364.1 | 367.7 | 151.9 | 1789.4 |
| Leaf area       | (m <sup>2</sup> )      | 2.67          | 2.67  | 0.89       | 1.79  | 1.79      | 0.60  | 2.37    | 2.37  | 0.79   | 2.10  | 2.10  | 0.70  |        |
| Upper           | Position               | NUO           | NUM   | NUI        | SUO   | SUM       | SUI   | EUO     | EUM   | EUI    | WUO   | WUM   | WUI   | Total  |
| Measured        | Mmol day <sup>-1</sup> | 511.6         | 440.1 | 190.6      | 750.5 | 593.1     | 375.1 | 493.8   | 404.7 | 113.7  | 845.2 | 822.3 | 217.8 | 5758.6 |
| k = 0.54        | Mmol day <sup>-1</sup> | 508.8         | 451.6 | 185.5      | 777.0 | 608.2     | 221.4 | 529.4   | 441.2 | 118.7  | 848.8 | 800.9 | 202.1 | 5693.7 |
| k = 0.72        | Mmol day <sup>-1</sup> | 472.2         | 418.2 | 171.7      | 739.6 | 582.7     | 211.8 | 489.8   | 410.2 | 111.1  | 802.8 | 763.2 | 194.0 | 5367.5 |
| Leaf area       | (m <sup>2</sup> )      | 1.40          | 1.40  | 0.47       | 1.98  | 1.98      | 0.66  | 1.40    | 1.40  | 0.46   | 1.98  | 1.98  | 0.66  |        |
| Overall C fixed |                        | mmol/tree/day |       | g/tree/day |       | kg/ha/day |       | t/ha/yr |       |        |       |       |       |        |
| Measured        |                        | 9132.1        |       | 109.6      |       | 137.0     |       | 50.0    |       |        |       |       |       |        |
| k = 0.54        |                        | 8942.6        |       | 107.3      |       | 134.1     |       | 49.0    |       |        |       |       |       |        |
| k = 0.72        |                        | 6821.2        |       | 81.8       |       | 102.3     |       | 37.3    |       |        |       |       |       |        |

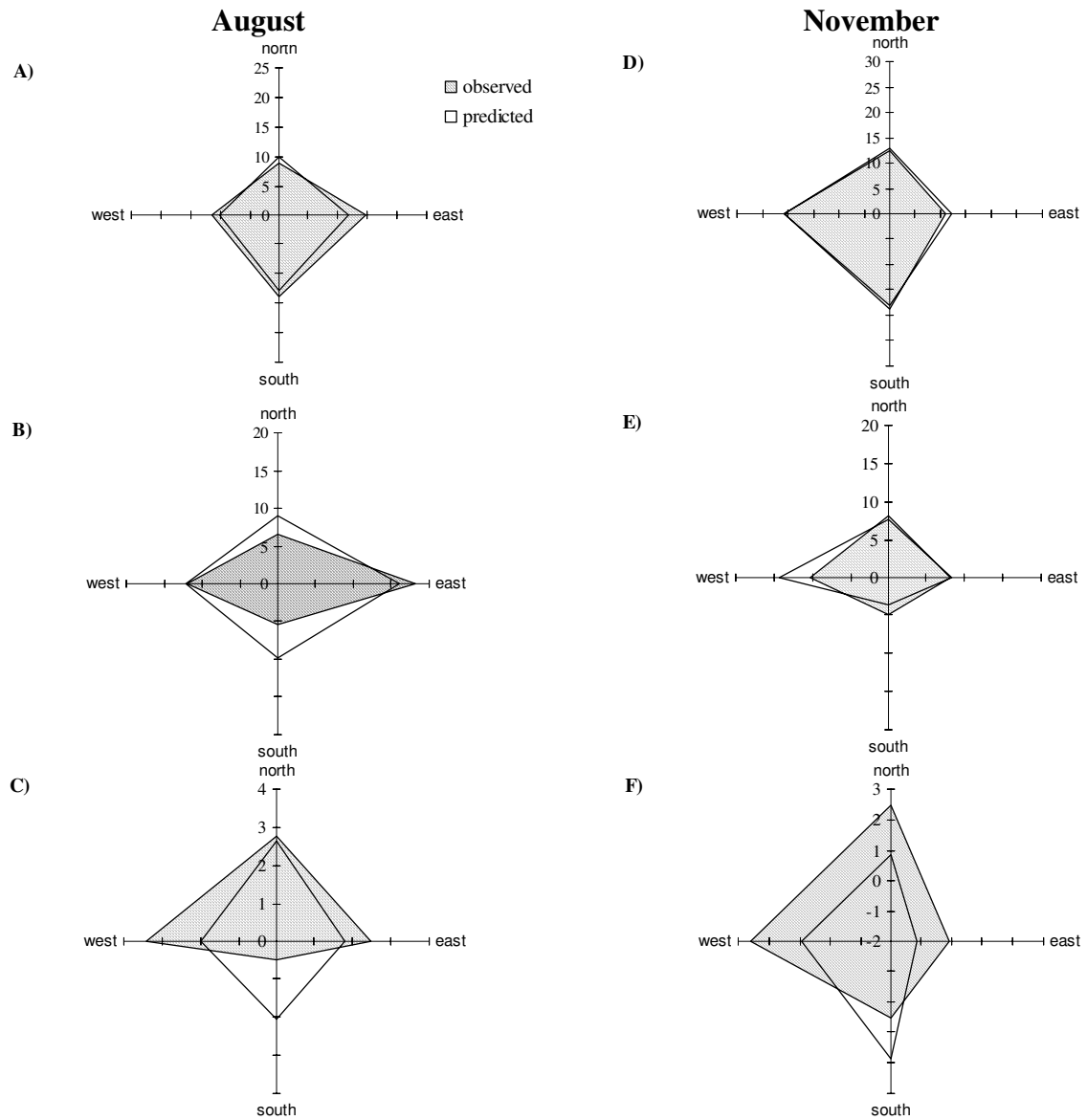


**Figure 3.8.** The proportional contribution to crown carbon budget of foliage in: **A)** upper canopy in August, **B)** middle canopy in August, **C)** lower canopy in August, **D)** upper canopy in November, **E)** middle canopy in November and **F)** lower canopy in November. Note that in **F)** the origin is about  $-2\%$  due to the negative carbon balance of portions of that crown zone at that time of year.

### 3.4 Discussion

The light environment in the crowns of three- to four-year-old plantation grown *E. globulus* observed in the current study reveal a similarly high degree of spatial and temporal heterogeneity as documented in the modelling literature by authors such as Palmer and co-workers (Palmer 1977, Jackson and Palmer 1979), Ross (1981), Norman (1983) and more recently Oker-Blom (1986) and Stenberg (1998). Vertical gradients in light intensity and thus photosynthetic production, as demonstrated in the crowns of block-planted and isolated trees (Fig. 3.1, Table 3.4 and 3.5), have been well documented in the canopies of a wide variety of vegetation (Jackson and Palmer 1979, Caldwell *et al.* 1986, Grace *et al.* 1987, Hirose and Werger 1987, Smith 1991, 1993, Le Roux *et al.* 1999). In the current study, light intensity declined through the upper third of the crown more rapidly than could be modelled adequately by a single  $L^*$  or by a single exponential function applied over the entire canopy, that is by a one-dimension radiation model (Fig. 3.2, 3.5, 3.6). In block-planted trees between 40-90% of incident radiation was intercepted in the upper third of the crown, leaving little light to travel through the remaining two-thirds of the crown (Fig. 3.2). Integrating  $I_N/I_0$  over longer time scales gave a significantly lower coefficient ( $k=0.39$  for a 24-h period compared with  $k=0.56$  for an hour about solar noon in November), but did not improve the fit for the upper portion of the crown. Averaging the light environment over each layer to better fit the predictions of the Beer-Lambert law (which predicts the theoretical average light intensity, Larsen and Kershaw 1996), gave a slightly lower value for  $k$  ( $k=0.73$  and  $0.55$  in August and November, respectively) but still did not fit the data adequately. Although graphically derived values for  $k$  and  $G$  were similar to those calculated from equations (3.10) and (3.11) using total  $L^*$  or overall  $\sigma$  and  $\rho$  and the proportion of incident light observed at the bottom of the crown ( $k_{\text{winter}}=0.72$ ,  $k_{\text{summer}}=0.54$ ), we conclude that, it is not appropriate to apply the Beer-Lambert equation over the entire length of *E. globulus* crowns in this study. Consequently, it is also not appropriate to apply the Beer-Lambert equation over the entire length of these crowns to infer spatial information, especially the distribution of light, C production or leaf area (in contrast to Smith *et al.* 1991, Smith 1993). The more detailed analysis afforded by a cellular approach demonstrated that, as might be expected from the highly heterogeneous light and leaf area distributions observed within crowns, light extinction coefficients varied strongly between cells. For example  $k=1.51$  in the eastern, outer portion of the upper canopy but  $0.56$  in the cell directly beneath it.

Rather than the single smooth exponential curve of light interception which underlies some common, one-dimensional, applications of the Beer-Lambert law (see for example Hirose and Werger 1987, Smith 1993, Sadras *et al.* 1993, Anten and Werger 1996, Hirose *et al.* 1997, Bartelink 1998), the distribution of  $I_N/I_0$  through *E. globulus* canopies in terms of  $L^*$  was effectively divided into at least two distinct curves. These represent the light environment in the upper portion of the crown and the lower two thirds of the crown respectively. This indicates that at least two separate phases of light interception are operating through the crowns. Although direct beam and diffuse radiation have different patterns of absorption through canopies (Goudriaan 1977, Ross 1981, de Pury and Farquhar 1997) this pattern was evident during winter when incident radiation was primarily diffuse and during summer when direct beam radiation predominated (Fig 3.2). This indicates that rapid attenuation in the upper crown of eucalypts has some structural cause. Some of the variation in light interception with time of year and through the canopy can be accounted for by changes in  $\rho$  and  $\sigma$  since  $G$ , which incorporates these terms, showed no statistically significant seasonal variation, in direct contrast to  $k$ . The significant variation in  $G$  with spacing can be largely attributed to differences in the influence of neighbouring trees on light availability. The significant interaction between spacing and time of year indicates that other sources of variation are important. These include horizontal variations in  $\sigma$  and clumping of leaves with planting layout and the distribution of leaf area and leaf angle (Tables 3.2, 3.3, 3.4 and 3.5) that varied both with spacing and time of year. The latter two factors are influenced by the distribution of juvenile leaves since the leaf angle and specific leaf area of juvenile and mature foliage of *E. globulus* differ significantly (James and Bell 2000). The juvenile foliage of *E. globulus* is more or less horizontally orientated in contrast to the vertical angles of mature leaves (James and Bell 2000). The proportion of semi-horizontal juvenile leaves and vertical mature leaves varied with

spacing, and in isolated and row trees, and at the lower third of block-planted trees and was observed to change with time of year, down the length of the canopy and with distance from the stem. The presence of more than one leaf angle class invalidates the assumption of a spherical distribution of leaf area and implies an elliptical distribution. These distributions require that a parameter characterising the distribution of leaf angle classes, ( $\chi$ ) be incorporated into  $k$  or  $G$  (Campbell and Norman 1989).

Comparing our light results with the more complex models of canopy organisation reviewed by Larsen and Kershaw (1996), the most simple models assumed a three-dimensional uniformity of leaf area (one of the basic assumptions of the Beer-Lambert law) or uniform distribution within cylindrical or parabolic crowns. Of the models tested by Larsen and Kershaw (1996), these simple leaf distributions predicted the most rapid attenuation of light in the upper third of the canopy, all be it only with 10-20% of light being attenuated in this region. In contrast to our observations, light intensity diminishes at a uniform rate throughout these simple crown models. The more complex models Larsen and Kershaw (1996) examined assume that the vertical leaf area distribution follows some form of normal distribution. Consequently, there is little leaf area in the top and bottom portions of the crowns. In these models, very little light is lost in the upper crown, with most being intercepted in the middle layers. While not following a normal distribution, this crown structure in which leaf area is concentrated in the middle of the canopy is similar to that observed in *E. globulus* crowns (Table 3.2, Fig. 3.5, 3.6). The pattern of light interception, however, is almost completely the reverse of those observed in *E. globulus* (Fig. 3.2). In *E. globulus*, the vertical distribution of leaf area is much more uneven than represented by any of the models reviewed by Larsen and Kershaw (1996). In addition to gaps in the stand and individual tree canopy, in both block-planted and isolated trees, leaf area densities were considerably greater in the upper third of canopy than in the remaining two-thirds (Table 2). Furthermore, a large proportion of the leaf area and the highest leaf area density in August or November is located along a small number of large branches, clustered together or separated by a number of smaller branches.

An important feature of the models reviewed by Larsen and Kershaw (1996) and those of Reynolds *et al.* (1992), Buwalda *et al.* (1993) and Bartelink (1998, 2000) for example, is the assumption of uniform horizontal distributions of leaf area. As is shown in Tables 3.4 and 3.5, the horizontal distribution of light and leaf area is not uniform in *E. globulus*. This partially accounts for the wide range of  $I_N/I_0$  values associated with the cumulative  $L^*$  of each canopy layer (Fig. 3.2). In the upper portion of the canopy, there is a high density of leaves and leaves are present along the entire length of branches. There are also a number of small branches closely grouped together (Fig. 3.5a). This agrees with work by Stenberg (1998) and de Castro and Fetcher (1999), who found that the slope of the relationship between  $L^*$  and light intensity declined as the degree of leaf clumping increased. In their models the most rapid decline in light intensity occurred with random and Poisson distributions of leaves. Uniformly distributed leaves cause the most rapid attenuation of light because there are fewer and smaller gaps in the canopy. As the degree of clustering increases, however, light attenuation decreases and beams of light may pass through numerous gaps in the canopy between clusters of leaves. Highly clumped leaf distributions cause very little attenuation and the relationship between light intensity and  $L^*$  becomes linear and almost flat (Oker-Blom 1986, Stenberg 1998, De Castro and Fetcher 1999). Light attenuation coefficients would consequently be low in crowns or sections of crowns with such distributions, as there is little difference between light at the top and bottom of the profile. In our study, this was observed to occur within cells at the bottom of *E. globulus* crowns indicating a high degree of clustering in these areas. In the middle and lower portions of the canopy, leaves were strongly concentrated to the middle and outer portions of the crown. Leaf density was lowest closest to the stem and at the bottom of the crown and leaves may be entirely absent from the inner third of the crown. Consequently, there is an inner cone-shaped zone in which leaves are sparsely distributed or absent. A similar distribution has been described in plantation grown *E. grandis* Hill *ex* Maiden (Leuning *et al.* 1991). In our study there was clustering about the vertical axis in the mid-canopy (Fig. 3.5, 3.6). Leaf area in this portion of the canopy was predominantly located along a few larger branches, separated by smaller branches (Fig. 3.5, 3.6). This

spatial arrangement effectively produces at least two different regions, each with a characteristic leaf area distribution and light attenuation patterns.

Seasonal changes in  $k$  are incorporated into a variety of complex radiation models (for example de Pury and Farquhar 1997) but omitted from a number of simpler models (for example Sellers *et al.* 1992, Dewar *et al.* 1998). In the current study,  $k$  was found to change through the year ( $P < 0.001$ ), from 0.72 in block-planted trees and 1.20 in isolated trees during winter to 0.54 and 0.79, respectively, in summer. Although seasonal variations in  $G$  were statistically insignificant, the  $G$  value used also had important consequences for the estimates of light availability in crowns. In rapidly growing *E. globulus*, the consequences for estimates of fixed C and interpretations of productivity of applying a single  $k$  derived at one time of the year across other seasons were significant. Canopy C fixation was underestimated by about 5 t ha<sup>-1</sup> yr<sup>-1</sup> using the winter  $k$  (0.72) year round. Applying the winter  $k$  to summer data underestimated summer C production by about 25% (Table 3.4, 3.5). The proportion of C fixed in the upper canopy was overestimated while the lower canopy was predicted to have a net negative C balance (Table 4). Use of the summer  $k$  (0.54) year round only slightly overestimates annual C production (by 1.7 t ha<sup>-1</sup> yr<sup>-1</sup>, about 10%) but during winter overestimates middle and lower canopy production by about 60% and 90%, respectively (Table 3.4).

Underestimates of lower and middle canopy C budgets when incorporated into growth and silvicultural support models could lead forest managers to schedule pruning earlier or more severely than actually warranted, potentially causing greater than expected losses in wood production. In plantation *E. nitens* (Dean and Maiden) Maiden, for example, Pinkard *et al.* (1999) found that when 50% of the length of the green canopy was removed, physiological responses to pruning were sufficient to compensate for the reduction in light interception within 110 days of pruning and biomass increments were subsequently equal to those of unpruned trees. Removal of 70% of the length of the green crown, however, removed branches with high  $A$  and biomass production was reduced by 77%. The growth increment of these trees did not fully recover during the 20-month course of the study.

As demonstrated in complex models, seasonal, yearly or longer term C production can easily be modified to include seasonal values for  $k$ . Problems could arise for analyses of the efficiency of radiation conversion to biomass ( $\epsilon$ ), calculated from the relationship of annual net primary production or biomass increment and intercepted radiation ( $Q_i$ ), where  $Q_i$  is estimated according to the equation:

$$Q_i = (1 - e^{-kL^*})I_x \quad (3.15)$$

As noted previously, seasonal changes in sun angles accounted for only some of the variation observed in  $k$  and  $G$  in three- to four-year-old *E. globulus*.

A major consequence of the heterogeneity in leaf area distribution and light attenuation is the penetration of light deep into the crown, even in stands with high  $L^*$ . These periods of high irradiance, termed light flecks, fall into three categories: those caused by gaps in the canopy (which change with sun position), by leaf movement and by cloud movement (Tang *et al.* 1988, Barradas *et al.* 1998). This means that the distribution of light within a crown constantly changes and leaves deep in the canopy will be subject to much higher light intensities than the Beer-Lambert law predicts (de Pury and Farquhar 1997). In the current study, this fundamental flaw of big-leaf models was amply demonstrated in block-planted *E. globulus* (Fig. 3.3). In Figure 3.3, the 1:1 line shows where light intensity calculated using the Beer-Lambert law over the entire canopy is the same as the observed light intensity at various positions in the crowns of block-planted trees. Even in the upper canopy, where this approach generally overestimates irradiance, there are instances, particularly on the northern and southern aspects, where less attenuation than predicted has occurred (sensors in full or close to full sunlight) and observed irradiance exceeds predicted values (Fig. 3.3a,d). Light flecks can make large contributions to the total amount of light intercepted by a canopy (Sims and Pearcy 1993, Kupperts and Schneider 1993, Kupperts *et al.* 1996, Barradas *et al.* 1998). In the current study, the impact of light flecks on the light environment was particularly evident at the bottom of the crown

where leaves experienced brief periods of high irradiance often close to full mid-day sunlight (around 1500-2500  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , Fig. 3.3c,f). In addition, light intensities throughout the canopy, particularly in the north and east portion, were frequently underestimated by the Beer-Lambert law for periods that did not appear directly attributable to light flecks but may correspond to penumbra (Fig. 3.3).

Leaves growing in low light environments can fully or partially acclimate to their general light environment so that photosynthesis saturates at lower light intensities than leaves in full sunlight (Anderson 1986, Hollinger 1989, Brooks *et al.* 1996). Acclimation to low irradiance involves the reduction in both electron transport ( $J$ ) and Calvin cycle capacities and an increase in the ability to absorb light (Anderson 1986, Evans 1989). The leaves of block-planted *E. globulus* clearly showed photosynthetic acclimation to prevailing light conditions as  $A_{\text{max}}$  declined along both vertical and horizontal gradients of decreasing light availability (Fig. 3.4). Acclimation to low light reduced the degree to which inner and lower canopy leaves utilise high light levels during sunflecks. The efficiency with which light flecks are utilised also depends on the photosynthetic induction state of leaves (Sims and Pearcy 1993). The period of time under saturating illumination required for photosynthetic rates to reach their maximum values is termed the induction period and varies with the period of exposure to low light or darkness (Chazdon and Pearcy 1991). In *Phaseolus vulgaris*, however, Barradas *et al.* (1998) found that leaves do not ever completely lose induction. They did suggest that light flecks of more than one-minute duration might also increase leaf temperature, thus increasing transpiration and altering the response to light. Light flecks none the less have a generally positive impact on C fixation in these shaded regions (Barradas *et al.* 1998). Photosynthesis in leaves in shaded regions generally operates in the steep, linear portion of the light response curve, but during light flecks proceeds at the light-saturated rates indicated by  $A_{\text{max}}$  (Fig. 3.4). In the lower crown of block-planted trees in the current study, positive C balances were achieved primarily during the short periods of elevated photosynthetic rates that characterise light flecks (Fig. 3.7). Elevated photosynthetic rates over periods of short duration were also significant in the middle canopy particularly on the more heavily shaded western aspect (Fig. 3.7a,c). In addition to coinciding with periods of high irradiance, these scattered incidences of elevated C fixation were much less prevalent in the high light environments of the upper canopy and the crowns of isolated trees and may therefore be confidently attributed to light flecks (Fig. 3.7).

While a one-dimensional application of the Beer-Lambert law, even when the appropriate  $k$  or  $G$  is employed, provides a clearly inadequate radiation model, it nonetheless produces estimates of net crown C fixation similar to empirical data (Table 3.4, 3.5). The total estimate of C production matches the empirical data well, especially for summer. The ability to predict the spatial distributions of irradiance and photosynthetic production through crown layers of block-planted trees throughout the year, however, varied substantially (Table 3.4, 3.5, Fig. 3.3, 3.8). Consequently, the observed distribution gives a different interpretation of light and photosynthetic dynamics within the stand. As discussed previously, the big-leaf approach overestimated C production in the mid and lower canopy layers by about 16-40% during winter but underestimated the contribution and amount of C fixed in the lower canopy in summer by more than 50% (Fig. 3.8c,f). In our study, good estimates of total canopy C production were obtained despite these discrepancies and the generally poor ability of a single  $k$  to accurately predict light levels within the canopy (Fig. 3.3). This was because in the upper canopy leaves were photosynthesising in the flat, light-saturated portion of the light response curve, so that very large inaccuracies in radiation would be needed to change  $A_{\text{max}}$  significantly. At the bottom of the canopy, leaf areas are generally small and photosynthetic rates relatively low so that inaccuracies in light predictions in this region may not greatly alter  $A_{\text{max}}$  or estimates of total crown C production.

### 3.5 Conclusion

We conclude that a one-dimensional big-leaf approach to modelling C fixation in *E. globulus* canopies provides workable estimates of total stand growth but only if an appropriate  $k$  or  $G$  is used. Its ability to provide an accurate description of the light environment and distribution of C fixation within block-planted stands could easily be improved by estimating light attenuation and C production in layers each with an appropriate  $k$ . The gradients in the light environment and distribution of photosynthetic activity within widely spaced trees tended to be stronger than those observed in block-planted trees because of side lighting (Fig. 3.1). Consequently, a simple, one-dimensional big-leaf approach may be unsuitable for modelling the light environment, leaf area distribution and crown C fixation in discontinuous canopies and especially, unevenly spaced trees. To be suitable for application across the range of agroforestry planting layouts, crown C production models will require a more detailed analysis of leaf area distribution, light environment and incorporate seasonal changes in  $k$  and/or  $G$ . While there exists a number of sun-shade, two-leaf and array models that improve on the simple big-leaf model analysis used in the current study, many are highly complex and data intensive. Further research is presented in a later chapter that compares the performance of these in their spatial representations of the light environment and distribution of C production within *E. globulus* crowns in block-planted, row and isolated tree stands.

## 4. Nitrogen Distribution in Eucalypt Canopies Reviewed

### 4.1 Introduction

Eucalypts evolved primarily in Australia, generally on poor soils, frequently with seasonal and interannual variation in nutrient and water availability and temperature constraints (Adams 1996). Eucalypts now enjoy a cosmopolitan distribution as an important plantation species across a broad range of environmental conditions. The economic importance of eucalypts, both as natural forests and in plantations, has given rise to extensive literature on their nutrition. This review focuses on nitrogen (N) in the canopy. Though not solely concerned with N, the reviews of Groves *et al.* (1996), Judd *et al.* (1996a), and Kriedemann and Cromer (1996) provide a comprehensive general introduction to the pre-1995 literature on this topic. These authors, particularly Groves *et al.* (1996), identified several important gaps in the knowledge at the time and areas requiring further research. These included a lack of both understanding of, and quantitative data on, N dynamics within eucalypts, how uptake, storage and internal redistribution are affected by seasonal and silvicultural factors and longer term changes in growth requirements, the significance of N storage and transfer from wood and bark in meeting photosynthetic requirements, a lack of field data particularly for established stands, a paucity of data on the relative importance of internal cycling and uptake compared with other forest ecosystems, the need for a more detailed knowledge of the physiologically-active forms of N and the biochemical processes associated with N mobilisation and transfer and how all these respond to environmental factors such as increased nutrient supply. Many of these have been at least partially addressed in the interim. Several widely held notions such as the contention that N supply often limits eucalypt growth in indigenous forests (see Groves *et al.* 1996 and references within) have also recently been re-examined (Attiwill and May 2001, Warren *et al.* 2000b).

The current review focuses on N and more particularly N in the canopy since leaf N concentration ( $N_{\text{leaf}}$ ) has been shown to be broadly related to plant primary productivity, relative growth rates (for example Ingestad 1977, Agren 1985, 1988, Agren and Ingestad 1987, Greenwood *et al.* 1991) and biomass allocation and growth responses to N availability have been extensively examined across a wide range of species and situations. Consequently N content is a key variable in many plant growth and allocation models of varying complexity (for example Brouwer 1963, Agren and Ingestad 1987, Sands 1995, dePury and Farquhar 1997). More detailed examinations of these relationships across a diverse range of plant species, revealed strong, general correlations between  $N_{\text{leaf}}$  and photosynthetic capacity and between  $N_{\text{leaf}}$  and mean levels of irradiance (Field 1983, Field and Mooney 1986, Evans 1989). Others have studied the roles and movement of different forms of N within canopies and between organs (for example Pate *et al.* 1998, Pate and Arthur 2000). Still others have focussed on the impact of factors that influence growth, particularly irradiance, on N distribution within plants.

Parallel to, and at times over-lapping, these lines of enquiry are investigations of N movement within crowns and between plant parts. Major pools of interest to the current investigation are in photosynthetic processes (enzyme or amino acid-held N), storage and supporting growth. There is a considerable body of literature concerning N in storage transport or recirculation to support growth, particularly in fruit trees and forest species (for example Millard 1988, 1994) but as noted by Groves *et al.* (1996) and Kriedeman and Cromer (1996), until recently, very little on eucalypts.

Contrary to the conventional framework of discrete compartments or interacting pools of N, Warren *et al.* (2000a,b) found that in eucalypts, forms of N usually considered only in terms of photosynthesis, such as Ribulose-1,5-biphosphate carboxylase/ oxygenase (Rubisco), may also have a storage function. Similarly, recent, detailed isotope tracer studies in young *Eucalyptus globulus* trees have provided new insights into the movement of N within these crowns, and particularly relationships between branches (Pate *et al.* 1998). In other work, limitations about the way in which the light

environment within tree canopies is estimated in some current approaches to modelling canopy C production have been made apparent (for example, Larsen and Kershaw 1996, de Pury and Farquhar 1997).

Despite its centrality to modelling C production there are no recent reviews to draw together these developments and the influence of planting layout and silvicultural practices on canopy N distribution in general or in forestry trees and eucalypts due to their current and increasing importance in plantation forestry, in particular. Consequently, a review of N distribution in eucalypt canopies is both timely and overdue. The primary focus of this chapter is plantation species in plantation situations. Within this context the influence of various environmental and silvicultural factors on N distribution are considered, as are the roles of different forms of N and movement of N within the crown. This information from eucalypts is related to current hypotheses of N distribution and resource allocation and the implications for the treatment of N distribution in current growth models are discussed. Although it is conventional to treat the canopy or crown simply as being composed of foliage, in the current review the canopy or crown is considered to include the twig, branch and stem bark. The conventional simplification of the canopy as simply the leaf fraction is convenient. It, however, ignores significant photosynthetic contributions (generally as refixation of respired CO<sub>2</sub> rather than a positive C efflux) by bark and twigs to the canopy C economy, which have been well documented in a range of woody species (Sprugel *et al.* 1991, Pfanz 1999, Cernusak and Marshall 2000, Aschan *et al.* 2001). These portions are included where possible in the current review. Recently, evidence has emerged of significant bark photosynthesis in plantation grown *Eucalyptus nitens* and *E. globulus* (M. Battaglia 2002, pers. comm., unpublished data).

## 4.2 General Distribution Patterns Across Species

### 4.2.1 Allocation between canopy components

The N content of eucalypt trees and how it is distributed among the above-ground components varies between species and with age, stem density and site conditions (Table 4.1, 4.2 and references therein). As with other plants, eucalypt foliage is a major site of above-ground N allocation (Table 4.1). In their review of nutrient distribution, Groves *et al.* (1996) concluded that across a range of species the foliage of eucalypts typically contains about 20% of above-ground N while comprising only about 2% of the biomass. They contrasted this with other evergreen forest trees such as conifers (aged 36-150 years), in which according to Groves *et al.* (1996) the leaves generally are of greater importance in N storage than in eucalypts. The foliage typically accounted for around 7% of the above-ground biomass but contained around 40% of the above-ground N. Examining the original data, however, shows a rather more variable picture in which the foliage in the four conifer species referred to by Groves *et al.* (1996) comprises from 1.5 to 11.5% of above-ground biomass and 13-34% of above-ground N (Ovington and Madgwick 1959, Cole *et al.* 1967, Alban *et al.* 1978, Rolfe *et al.* 1978). In older eucalypts (30 years and over) stemwood and bark appeared to be more important sites of N storage than conifers. Eucalypt stems and bark containing 31-54% and 19-43% of above-ground N compared with 15-37% and 12-17% of above-ground N, respectively, in conifers (Table 4.1 and references above). Contradicting the assertion that branches are a more important site of nutrient allocation and storage in eucalypts than in conifers (Groves *et al.* 1996), the branches of these older eucalypts contained 7-17% of above-ground N (Table 4.1) in comparison to 21-43% in the conifers. This discrepancy possibly arises from the use of a wider data set than Groves *et al.* (1996), the tendency of the authors to aggregate and average data of very different origins and that because general statements about nutrient distribution do not necessarily hold for N or other individual nutrients.

**Table 4.1.** Allocation of N and biomass among above-ground plant parts in eucalypts.

| Species                                                                                                                                           | Site                    | Age<br>years | Treatment                                               | % N allocation |        |      |      | % biomass allocation |        |      |      | Reference                    |
|---------------------------------------------------------------------------------------------------------------------------------------------------|-------------------------|--------------|---------------------------------------------------------|----------------|--------|------|------|----------------------|--------|------|------|------------------------------|
|                                                                                                                                                   |                         |              |                                                         | leaf           | branch | bark | stem | leaf                 | branch | bark | stem |                              |
| <i>E.globulus</i>                                                                                                                                 | P                       | 2            | None                                                    | 82             | 7      | 4    | 7    | 46                   | 17     | 9    | 28   | Cromer <i>et al.</i> 1975    |
|                                                                                                                                                   | P                       | 4            | None                                                    | 62             | 12     | 9    | 15   | 17                   | 13     | 11   | 54   |                              |
|                                                                                                                                                   | P                       | 2            | 34kg ha <sup>-1</sup> N, 15kg ha <sup>-1</sup> P        | 70             | 11     | 6    | 13   | 34                   | 20     | 9    | 37   |                              |
|                                                                                                                                                   | P                       | 4            | 34kg ha <sup>-1</sup> N, 15kg ha <sup>-1</sup> P        | 61             | 12     | 10   | 15   | 16                   | 11     | 12   | 57   |                              |
|                                                                                                                                                   | P                       | 2            | 101kg ha <sup>-1</sup> N, 45kg ha <sup>-1</sup> P       | 73             | 9      | 7    | 11   | 33                   | 20     | 9    | 38   |                              |
|                                                                                                                                                   | P                       | 4            | 101kg ha <sup>-1</sup> N, 45kg ha <sup>-1</sup> P       | 58             | 11     | 11   | 17   | 16                   | 11     | 12   | 57   |                              |
|                                                                                                                                                   | P                       | 2            | 202kg ha <sup>-1</sup> N, 90kg ha <sup>-1</sup> P       | 73             | 11     | 6    | 10   | 33                   | 20     | 9    | 38   |                              |
|                                                                                                                                                   | P                       | 4            | 202kg ha <sup>-1</sup> N, 90kg ha <sup>-1</sup> P       | 59             | 11     | 10   | 17   | 17                   | 13     | 11   | 54   |                              |
| <i>E.radiata</i> &<br><i>E.dalrympleana</i><br><i>Pseudotsuga</i><br><i>menziesii</i>                                                             | Regen.                  | 50           | disturbance                                             | 24             | 7      | 19   | 50   | 5                    | 7      | 22   | 67   | Turner 1980                  |
|                                                                                                                                                   | F                       | 50           | +NP                                                     | 25             | 23     | 9    | 43   | 4                    | 8      | 9    | 79   |                              |
|                                                                                                                                                   | P                       |              |                                                         |                |        |      |      |                      |        |      |      |                              |
| <i>E.regnans</i><br><i>E.obliqua</i><br><i>E.diversicolor</i>                                                                                     | Regen.                  | 39           | Burnt pre-planting, no subs.                            | 12             | 17     | 31   | 40   | <1                   | 6      | 11   | 82   | Feller 1980                  |
|                                                                                                                                                   | F                       | 39           |                                                         | 7              | 8      | 32   | 54   | 1                    | 7      | 22   | 71   |                              |
|                                                                                                                                                   |                         | 39           |                                                         | 4              | 4      | 43   | 48   | 1                    | 6      | 20   | 73   |                              |
| <i>E.regnans</i>                                                                                                                                  | P                       | 4            | Urea: 56 g tree <sup>-1</sup> + 250 kg ha <sup>-1</sup> | 50             | 22     | 9    | 19   | 9                    | 21     | 8    | 62   | Frederick <i>et al.</i> 1985 |
|                                                                                                                                                   |                         | 7            | Urea: 60 g tree <sup>-1</sup>                           | 42             | 17     | 12   | 29   | 5                    | 15     | 8    | 72   |                              |
|                                                                                                                                                   |                         | 10           | mix: 56 g tree <sup>-1</sup> + urea 250                 | 39             | 17     | 9    | 34   | 5                    | 13     | 6    | 76   |                              |
|                                                                                                                                                   |                         | 13           | kg ha <sup>-1</sup>                                     | 44             | 15     | 11   | 30   | 5                    | 3      | 7    | 78   |                              |
|                                                                                                                                                   |                         | 17           | mix: 56 g tree <sup>-1</sup> + urea 250                 | 33             | 18     | 12   | 38   | 3                    | 2      | 10   | 83   |                              |
|                                                                                                                                                   |                         |              | kg ha <sup>-1</sup><br>none                             |                |        |      |      |                      |        |      |      |                              |
| <i>E.obliqua</i>                                                                                                                                  | Open F                  | 43.7         |                                                         |                |        |      |      | 2                    | 7      | 16   | 77   | Attiwill 1979                |
|                                                                                                                                                   |                         | 50.7         |                                                         |                |        |      |      | 2                    | 7      | 15   | 76   |                              |
|                                                                                                                                                   |                         | 60.7         |                                                         |                |        |      |      | 2                    | 8      | 14   | 77   |                              |
|                                                                                                                                                   |                         | 66.2         |                                                         |                |        |      |      | 2                    | 9      | 13   | 76   |                              |
| <i>E.grandis</i>                                                                                                                                  | P                       | 27           | No site preparation                                     | 21             | 15     | 19   | 45   | 2                    | 5.3    | 10   | 83   | Turner & Lambert 1983        |
| <i>E.obliqua</i><br><i>E.obliqua</i><br><i>P.radiata</i><br><i>P.radiata</i>                                                                      | F C-L                   | 70-80        | none                                                    | 22             | 9      | 25   | 44   | 2                    | 4.4    | 10   | 84   | Baker & Attiwill 1985        |
|                                                                                                                                                   | F B-L                   | 80-90        | none                                                    | 32             | 15     | 23   | 31   | 3                    | 11.    | 14   | 72   |                              |
|                                                                                                                                                   | P C-L                   | 24           | clearing                                                | 45             | 19     | 16   | 20   | 4                    | 0      | 8    | 76   |                              |
|                                                                                                                                                   | P B-L                   | 20           | clearing                                                | 49             | 20     | 16   | 15   | 6                    | 11.    | 8    | 73   |                              |
| <i>E.marginata</i><br><i>E.calophylla</i>                                                                                                         | F                       | 60           | Controlled low intensity burn                           | 21             | 19     | 21   | 39   | 3                    | 12     | 13   | 72   | Hingston <i>et al.</i> 1981  |
|                                                                                                                                                   | F                       | 60           | 4 yrs prior to study                                    | 24             | 18     | 20   | 37   | 3                    | 11     | 16   | 70   |                              |
| <i>E.diversicolor</i>                                                                                                                             | Regen.<br>F             | 11           | Clear felled, slash-burn prior                          | 67             | 8*     | -    | 25   | 16                   | 8*     | -    | 77   | Grove & Malajczuk 1985       |
| Hybrid <i>E.PFI</i><br>( <i>E.alba</i> x (hybrid<br>of <i>E.grandis</i> x<br><i>E.robusta</i> x<br><i>E.urophylla</i> x<br><i>E.botryoides</i> )) | P<br>clonal<br>material | 1.1          | Site burnt, ploughed, initial                           | 74             | 11     | 4    | 10   | 30                   | 22     | 8    | 38   | Laclau <i>et al.</i> 2000    |
|                                                                                                                                                   |                         | 2.1          | NPK 150 g cutting <sup>-1</sup> , weed                  | 61             | 11     | 7    | 21   | 14                   | 20     | 8    | 58   |                              |
|                                                                                                                                                   |                         | 4.2          | control in rows & inter-row                             | 31             | 13     | 11   | 45   | 4                    | 11     | 7    | 79   |                              |
|                                                                                                                                                   |                         | 5.2          |                                                         | 24             | 13     | 14   | 49   | 2                    | 9      | 6    | 83   |                              |
|                                                                                                                                                   |                         | 7.3          |                                                         | 23             | 11     | 13   | 54   | 2                    | 7      | 5    | 86   |                              |
| <i>E.grandis</i>                                                                                                                                  | P                       | 0.66         | None                                                    |                |        |      |      |                      |        |      |      | Cromer <i>et al.</i> 1993    |
|                                                                                                                                                   |                         | 0.66         |                                                         |                |        |      |      |                      |        |      |      |                              |
|                                                                                                                                                   |                         | 1.04         | None                                                    |                |        |      |      |                      |        |      |      |                              |
|                                                                                                                                                   |                         | 1.04         |                                                         |                |        |      |      |                      |        |      |      |                              |
|                                                                                                                                                   |                         | 1.44         | None                                                    |                |        |      |      |                      |        |      |      |                              |
|                                                                                                                                                   |                         | 1.44         |                                                         |                |        |      |      |                      |        |      |      |                              |
|                                                                                                                                                   |                         | 1.81         | None                                                    |                |        |      |      |                      |        |      |      |                              |
|                                                                                                                                                   |                         | 1.81         |                                                         |                |        |      |      |                      |        |      |      |                              |
|                                                                                                                                                   |                         | 2.40         | None                                                    |                |        |      |      |                      |        |      |      |                              |
|                                                                                                                                                   |                         | 2.40         |                                                         |                |        |      |      |                      |        |      |      |                              |
|                                                                                                                                                   |                         | 3.08         | None                                                    |                |        |      |      |                      |        |      |      |                              |
|                                                                                                                                                   |                         | 3.08         | N 1536 kg ha <sup>-1</sup> , P 461 kg ha <sup>-1</sup>  |                |        |      |      |                      |        |      |      |                              |

|                                                                |            |            |                       |                                                                                                                                                             |    |    |    |    |    |    |    |    |                             |
|----------------------------------------------------------------|------------|------------|-----------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------|----|----|----|----|----|----|----|----|-----------------------------|
| <i>E.camaldulensis</i>                                         | P          | 3.4        | 3mx1.5m               | Site cleared & bedded, single application 11 kgNha <sup>-1</sup> , 175 kgPha <sup>-1</sup> , 5.5 kgKha <sup>-1</sup> , 90 kg S ha <sup>-1</sup> at planting | 54 | 20 | 7  | 19 |    |    |    |    | Harrison <i>et al.</i> 2000 |
|                                                                |            | 3.4        | 3m x3m                |                                                                                                                                                             | 63 | 16 | 7  | 15 |    |    |    |    |                             |
|                                                                |            | 3.4        | 4m x3m                |                                                                                                                                                             | 56 | 15 | 8  | 22 |    |    |    |    |                             |
| <i>E.pellita</i>                                               |            | 3.4        | 3mx1.5m               |                                                                                                                                                             | 57 | 11 | 8  | 24 |    |    |    |    |                             |
|                                                                |            | 3.4        | 3m x3m                |                                                                                                                                                             | 50 | 11 | 15 | 24 |    |    |    |    |                             |
| <i>E.urophylla</i>                                             |            | 3.4        | 4m x3m                |                                                                                                                                                             | 58 | 9  | 7  | 26 |    |    |    |    |                             |
|                                                                |            | 3.4        | 3mx1.5m               |                                                                                                                                                             | 60 | 10 | 5  | 24 |    |    |    |    |                             |
|                                                                |            | 3.4        | 3m x3m                |                                                                                                                                                             | 58 | 14 | 6  | 23 |    |    |    |    |                             |
|                                                                |            | 3.4        | 4m x3m                |                                                                                                                                                             | 59 | 10 | 5  | 26 |    |    |    |    |                             |
| <i>E.globulus</i>                                              | Sand, pots | 29N        | Pretreatment          | Pretreatment 1.0 mol Nm <sup>-3</sup> as NH <sub>4</sub> NO <sub>3</sub><br><br>6.0 molNm <sup>-3</sup> as NH <sub>4</sub> NO <sub>3</sub>                  | 70 |    |    | 30 | 53 |    |    | 47 | Wendler <i>et al.</i> 1995  |
|                                                                |            | 30J        | Pretreatment          |                                                                                                                                                             | 72 |    |    | 28 | 52 |    |    | 48 |                             |
|                                                                |            | F13        |                       |                                                                                                                                                             | 82 |    |    | 18 |    |    |    |    |                             |
|                                                                |            | F27        |                       |                                                                                                                                                             | 88 |    |    | 12 |    |    |    |    |                             |
|                                                                |            | M18        |                       |                                                                                                                                                             | 86 |    |    | 14 |    |    |    |    |                             |
|                                                                |            | M31        |                       |                                                                                                                                                             | 81 |    |    | 19 |    |    |    |    |                             |
|                                                                |            | F13        |                       |                                                                                                                                                             | 84 |    |    | 16 |    |    |    |    |                             |
|                                                                |            | F27        |                       |                                                                                                                                                             | 88 |    |    | 12 |    |    |    |    |                             |
|                                                                |            | M18        |                       |                                                                                                                                                             | 78 |    |    | 22 |    |    |    |    |                             |
|                                                                |            | M31        |                       |                                                                                                                                                             | 74 |    |    | 26 |    |    |    |    |                             |
| <i>E.agglomerata</i> & <i>E.muelleriana</i> & <i>E.sieberi</i> | Mixed F    | 100 – 100+ | Periodic natural fire |                                                                                                                                                             | 17 | 23 | 23 | 38 | 2  | 22 | 16 | 60 | Hopmans <i>et al.</i> 1993  |

F = forest, P = plantation, C-L = clay loam, B-L = Boolarra loam, N = November, J = January, F = February, M = March

**Table 4.2** Nitrogen concentration in above-ground components of eucalypts

| Species                                                               | Site        | Age    | Treatment                                         | N (mg g <sup>-1</sup> ) |      |        |          |      |          | Reference                   |
|-----------------------------------------------------------------------|-------------|--------|---------------------------------------------------|-------------------------|------|--------|----------|------|----------|-----------------------------|
|                                                                       |             |        |                                                   | leaf                    | twig | branch | br. bark | stem | st. bark |                             |
| <i>E.globulus</i>                                                     | P           | 2      | None                                              | 17.3                    |      | 4.0    |          | 2.3  | 4.8      | Cromer <i>et al.</i> 1975   |
|                                                                       | P           | 4      | None                                              | 14.0                    |      | 4.0    |          | 1.1  | 3.4      |                             |
|                                                                       | P           | 2      | 34kggha <sup>-1</sup> N, 15kggha <sup>-1</sup> P  | 14.8                    |      | 4.0    |          | 2.6  | 5.2      |                             |
|                                                                       | P           | 4      | 34kggha <sup>-1</sup> N, 15kggha <sup>-1</sup> P  | 12.6                    |      | 3.2    |          | 0.9  | 2.7      |                             |
|                                                                       | P           | 2      | 101kggha <sup>-1</sup> N, 45kggha <sup>-1</sup> P | 13.1                    |      | 2.6    |          | 1.7  | 4.5      |                             |
|                                                                       | P           | 4      | 101kggha <sup>-1</sup> N, 45kggha <sup>-1</sup> P | 11.6                    |      | 3.0    |          | 0.9  | 2.9      |                             |
|                                                                       | P           | 2      | 202kggha <sup>-1</sup> N, 90kggha <sup>-1</sup> P | 13.7                    |      | 3.3    |          | 1.7  | 4.1      |                             |
|                                                                       | P           | 4      | 202kggha <sup>-1</sup> N, 90kggha <sup>-1</sup> P | 10.5                    |      | 2.5    |          | 1.0  | 2.8      |                             |
| <i>E.agglomerata</i><br><i>E.muelleriana</i><br><i>E.sieberi</i>      | F           | 100y + | None                                              | 9.02                    | 2.54 | 0.71   | 1.76     | 0.52 | 1.21     | Hopmans <i>et al.</i> 1993  |
|                                                                       |             | 100y + |                                                   | 10.52                   | 2.30 | 0.78   | 2.56     | 0.80 | 2.02     |                             |
|                                                                       |             | 100y + |                                                   | 9.64                    | 1.57 | 0.57   | 1.73     | 0.50 | 1.22     |                             |
| <i>E.globulus</i>                                                     | Boola P     | 6y     | No N                                              | 12.2                    | 3.6  | 1.6    |          | 0.5  | 2.2      | Bennett <i>et al.</i> 1997  |
|                                                                       | Boola P     | 6y     | 400 N                                             | 12.2                    | 3.6  | 1.6    |          | 0.6  | 2.1      |                             |
|                                                                       | Maryvale P  | 6y     | No N                                              | 11.7                    | 3.1  | 1.8    |          | 0.8  | 2.4      |                             |
|                                                                       | Maryvale P  | 6y     | 400 N                                             | 10.8                    | 2.8  | 1.6    |          | 0.7  | 2.2      |                             |
|                                                                       | Glencoe P   | 6y     | No N                                              | 11.5                    | 3.7  | 1.5    |          | 0.6  | 2.2      |                             |
|                                                                       | Glencoe P   | 6y     | 400 N                                             | 10.4                    | 3.3  | 1.6    |          | 0.7  | 2.0      |                             |
| <i>E.diversicolor</i><br><i>E.diversicolor</i><br><i>E.calophylla</i> | Red earth F | 39y    | None                                              | 11.1                    |      | 2.1    |          | 0.39 | 1.8      | Hingston <i>et al.</i> 1979 |
|                                                                       | YP F        |        |                                                   | 10.7                    |      | 1.7    |          | 0.55 | 1.7      |                             |
|                                                                       | YP F        |        |                                                   | 10.4                    |      | 2.3    |          | 0.67 | 1.7      |                             |
| <i>E. grandis</i>                                                     | P           | 9.25y  | None                                              | 15.6                    |      | 5.5    |          | 1.15 | 2.4      | Birk & Turner 1992          |
|                                                                       |             |        | Fert. over 6y                                     | 16.5                    |      | 4.3    |          | 0.85 | 2.7      |                             |
|                                                                       |             |        | Fert.+W+I over 6 yr                               | 16.3                    |      | 4.1    |          | 0.90 | 2.5      |                             |
| <i>E. diversicolor</i>                                                | F           | 8-11y  | None                                              | 13.2                    | 3.3  |        |          | 1.0  |          | Grove & Malajczuk 1985      |

F = forest, F# =only dominant forest species are listed, P = plantation, YP = yellow podsol

The general point made by Groves *et al.* (1996) that eucalypt foliage contains a disproportionately large amount of N relative to its biomass is valid. The values they cite are typical for eucalypts, however, pertain to “older” trees. Consequently these values may not be relevant for younger trees or plantations with short rotations since N and biomass allocation patterns in eucalypts have been clearly shown to alter with age (Table 4.1, 4.2). Across an age series of 4- to 17-year-old *E. regnans* plantations in New Zealand, for example, Frederick *et al.* (1985) found that leaves accounted for 9% of above-ground biomass in the youngest stands but only 2.5% in the oldest. The N content of the leaf fraction ranged from 27-44% of above-ground N. Generally, foliage accounts for the greatest proportion of above-ground biomass and N at early stages of growth and the proportion of N and biomass resources allocated to foliage declines with tree age as branch and stem growth gain in importance (Table 1, 2). In seedlings and young trees, the foliage is the single largest site of N allocation (Wong *et al.* 1992, Cromer *et al.* 1993, Wendler *et al.* 1995, Misra *et al.* 1998). In

*E. camaldulensis*, *E. cypellocarpa*, *E. pauciflora* and *E. pulverenta* seedlings, for example, leaves contained 65-80% of total plant N (Wong *et al.* 1992). The decline in the relative importance of leaves as sites of N allocation can be slow. For example, in *E. grandis* at about 8 months of age and *E. nitens* at 10 months of age the leaves of young plantation-grown trees contained over 80% of above ground N (Cromer *et al.* 1993, Misra *et al.* 1998). At around three years of age, and despite significant branch and stem growth, foliage still contained over half of the above-ground N. Having reached maturity and in the absence of disturbance, the proportional allocation of N and biomass between above-ground organs in eucalypts remains relatively constant (Table 4.1).

#### **4.2.2 Concentration**

Plant nutrient concentrations, particularly N and especially  $N_{\text{leaf}}$ , have long been scrutinised. Apart from the comparative ease with which measurements of concentration can be obtained, a motivation for much of this interest has been the need for reliable indicators of nutritional status and requirements to design and evaluate fertiliser regimes and for predictors of plant vigor and later growth.

Consequently, while the value of foliar and/or fine-twig N analysis for predicting later growth, vigor, evaluating fertiliser regimes and even nutritional status in eucalypts has been contested (see Judd *et al.* 1996a, Bennett *et al.* 1996, 1997), there is a substantial body of data covering a variety of eucalypt species. See for example the cross-species comparisons in Feller (1980) and review by Judd *et al.* (1996a).

Numerous studies have linked the composition of plant communities and the distribution of individual species to soil nutrient availability (Chapin 1980, Aerts *et al.* 1992, Berendse 1994). In eucalypts, comparative studies of tissue nutrient concentration generally show that concentrations, particularly in leaves, vary with nutrient availability in the soil (Kaul *et al.* 1966a,b Cromer *et al.* 1981, Hingston *et al.* 1981, Schonau 1981b, Lambert and Turner 1983, Bell and Ward 1984, Herbert 1991, Herbert and Robertson 1991). Tissue concentrations thus potentially mirror not only the nutritional status of the plant but more broadly indicate the nutritional requirements and aspects of the nutritional physiology of the tree. Species characteristic of poor soils were considered to have inherently lower nutrient requirements and different strategies for acquiring nutrients than those characteristic of, and therefore adapted to, better soils (McColl 1969, Lambert and Turner 1983). The “poor soil” eucalypts, generally considered to encapsulate the Monocalyptus subgenera, are therefore expected to have lower tissue N concentrations than “better soil” species belonging to the subgenera Symphyomyrtus (McColl 1969, Florence 1982, Lambert and Turner 1983, Noble 1989). This assertion was tested by Judd *et al.* (1996a), in a broad reanalysis of the pre-1995 literature. They concluded that in contrast to N content, average  $N_{\text{leaf}}$  in eucalypts are similar across a broad range of species, including species from different taxa. While  $N_{\text{leaf}}$  was responsive to N availability in the soil and fertiliser application, they found no consistent differences in N concentration in the foliage or the bark of smooth-barked species between the sub-genera. Nor did they find evidence of differences in bark N concentrations between species with different types of bark (smooth or fibrous). Across a range of locations, soil types and species, the mean  $N_{\text{leaf}}$  of Monocalyptus eucalypts were around 11.9 mg g<sup>-1</sup>. Those of the Symphyomyrtus and Corymbia were 12.1 and 11.8 mg g<sup>-1</sup> respectively (Judd *et al.* 1996a, their Table 1). There was however, evidence that N concentrations in the twigs (<2 cm diameter) of Monocalyptus species in Victoria were less than those found in the twigs of Symphyomyrtus species (Judd *et al.* 1996a, their Table 5). Overall, dead leaves in the litter of forests dominated by Monocalyptus species had greater N concentrations than in those dominated by Symphyomyrtus eucalypts (Judd *et al.* 1996a, their Table 6.). Such data have been interpreted to indicate that Symphyomyrtus eucalypts retranslocate a greater proportion of N from senescing leaves relative to Monocalyptus species. Thus employing a strategy of highly efficient N recycling, which evolved to compensate for low soil N availability (Lambert and Turner 1983). Judd *et al.* (1996a) found that Symphyomyrtus eucalypts resorb more N than Monocalyptus species. They concluded that forests dominated by Symphyomyrtus species are thus more nutrient efficient than those dominated by Monocalyptus species.

More recently, Hawkins and Polglase (2000) examined the accumulation and resorption of nutrients in 15 eucalypt species across the three sub-genera (two Corymbia, four Monocalyptus and nine Symphyomyrtus species). Comparisons of  $N_{\text{leaf}}$  and resorption are frequently complicated by

environmental differences such as soil type, climate and fertility that influence tree growth rates and canopy N dynamics and thus foliar N concentrations (Pugnaire and Chapin 1993, Judd *et al.* 1996a, Hawkins and Polglase 2000). These factors and the large variation in the ages of trees for which data were obtained are major limitations in the earlier review. Hawkins and Polglase (2000) largely circumvented these problems by sampling even aged trees grown on the same site under identical conditions. The review of Judd *et al.* (1996a) and the Hawkins and Polglase (2000) study are somewhat limited by small data sets for the *Corymbia* eucalypts. In contrast to Judd *et al.* (1996a), Hawkins and Polglase (2000) found that while N concentrations in the mature foliage of *Monocalyptus* and *Symphyomyrtus* species were the same (around 11 mg g<sup>-1</sup>) they were significantly lower in the two *Corymbia* species (about 9 mg g<sup>-1</sup>). Mean N concentrations in senescent foliage did not differ across the sub-genera though there were significant differences within the subgenera.

Variations in concentrations alone are of limited value in comparative studies since they do not allow differences in leaf mass and leaf area to be considered. When Hawkins and Polglase (2000) calculated the amount and proportion of nutrients resorbed, no significant differences were found between the subgenera in terms of N. Trees from each subgenus resorbed around 4-5.5 mg g<sup>-1</sup> N, which amounted to 43-49% of the original N present in mature leaves being withdrawn. This agrees with the estimates of eucalypt N resorption presented by Groves *et al.* (1996). The *Corymbia* species, however, resorbed a greater amount of Phosphorus than the *Monocalyptus* species. Consequently, like Killingbeck (1996), Hawkins and Polglase (2000) concluded that while foliar nutrient status or accumulation may differ between subgenera, phylogeny does not overwhelmingly determine the resorption efficiency of N or other nutrients. Generally there is a greater degree of variation in terms of resorption proficiency within than between subgenera. An unavoidable drawback of this study, which the authors acknowledge, is that a number of the species investigated were growing out of their normal ecological range, which may have influenced their growth. Their conclusions however are valid and supported by previous studies when these are considered individually (for example Killingbeck 1996).

Although the range of N content is similar, several authors have concluded that eucalypts generally have lower average above-ground N concentrations than other forest trees, especially those from northern hemisphere temperate forests (Hingston *et al.* 1979, McColl 1979, Ericsson 1994a,b, Groves *et al.* 1996). Feller (1980) presented a survey of published pre-1980 data on above-ground nutrient content in living tissues of Australian eucalypt forests and temperate forest over 20 years of age. When these data were re-analysed, however, no significant differences were found in mean above-ground N concentrations between Australian eucalypt and temperate zone conifer forests. Above-ground N concentrations in Australian eucalypt forests ranged from between 0.61 and 4.40 mg g<sup>-1</sup>, with a mean of 1.95 mg g<sup>-1</sup>. In comparison, N concentrations in conifers ranged from 0.69 to 4.09 mg g<sup>-1</sup> with a mean of 2.14 mg g<sup>-1</sup> (derived from Feller 1980, Table 13,14). Average above-ground N concentrations were, however, higher ( $P = 0.04$ ) in hardwood forests (mean of 2.89 mg g<sup>-1</sup> and range of 2.13-4.63 mg g<sup>-1</sup>) than in eucalypts. In contrast, comparing  $N_{\text{leaf}}$  in high yielding plantations of species of alders, poplars and willows with eucalypts, Ericsson (1994a) found that eucalypt  $N_{\text{leaf}}$  was lower than other trees. The leaf anatomy of fast growing eucalypts differs significantly from the northern hemisphere species and their lower leaf N concentrations can be largely ascribed to the more highly xeromorphic nature of their leaves (Ericsson 1994b). In that study, concentrations were expressed on a dry matter basis (mg g<sup>-1</sup> dry weight) and as the author points out eucalypt foliage may include juvenile, intermediate and adult leaves. Mature leaves characteristically have lower specific leaf areas (SLA) than other leaves. The retention of juvenile leaves is not a simple function of age and may vary significantly between individuals and stands (Beadle *et al.* 1989). This feature of eucalypt canopies makes comparisons between stands of different ages difficult and potentially complicates across species comparisons unless concentrations are expressed on a leaf area basis (Ericsson 1994a,b).

It is worth noting that in the above studies, the comparisons were made from values published for trees growing in different locations (plantations in Portugal, Australia and South Africa) and under different conditions. Although Judd *et al.* (1996a) report that the foliage and other tissues of plantation eucalypts growing in different countries have comparable nutrient concentrations, there are relatively

few cross-genera nutritional studies where eucalypts can be directly compared with other forest trees growing under the same conditions. Even fewer of these avoid the confounding influence of SLA outlined above by presenting nutritional data on a leaf area basis. Three studies that at least partially satisfy these criteria suggest differing conclusions. In two *E. obliqua* forests with differing soil types, partially cleared and planted with *Pinus radiata*, Baker and Attiwill (1985) found that although soil type influenced foliar N concentrations, eucalypt foliage had significantly lower N concentrations at both sites (8.32 and 10.6 g m<sup>-2</sup> compared with 13.6 and 18.6 g m<sup>-2</sup>, respectively, Table 4.2). These results support the assertion that eucalypts have inherently low foliar N concentrations compared with other forest species. There was, however, a substantial difference in the age of the two species, which may have contributed to these results. The *E. obliqua* trees were around 80-years-old while the two *P. radiata* stands were 20 and 24 years of age. By contrast, a study of a 50-year-old Douglas-fir (*Pseudotsuga menziesii*) plantation growing alongside naturally regenerating stands of *E. dalrympleana* and *E. radiata*, Turner (1980) found that foliar N concentrations were similar or higher in the eucalypts than in the conifer. A little more recently, Hopmans *et al.* (1990) investigated nutrient accumulation in experimental plantations composed of seven species (*Casuarina cunninghamiana*, *E. grandis*, *E. saligna*, *E. camaldulensis*, *P. radiata*, a poplar species *Populus deltoides* and a *P. deltoides* x *P. nigra* hybrid) irrigated with effluent over a period of four years. After 44 months, the above-ground tissues of the eucalypts, poplars and pine had very similar N concentrations, around 24 to 26 g m<sup>-2</sup>. Nitrogen concentrations in the *Casuarina* species, however, were considerably higher at 40.5 g m<sup>-2</sup>. This last study does not provide direct information on foliar concentrations. Like Turner's (1980) investigation, however, it does indicate that given similar growth conditions, eucalypt N<sub>leaf</sub> are not necessarily inherently lower than those of other forest species, including those of the Northern hemisphere.

As shown in Table 3, N concentrations in the various components of eucalypt canopies generally decrease in the order: foliage > twigs ≥ bark ≥ branch ≥ stem (Feller 1908, Cromer and Williams 1982, Bell and Ward 1984, Misra *et al.* 1998). Generally, N concentrations in branch bark are similar to those in stem bark. Summarising the pre-1980 literature on nutrient distribution in Australian eucalypt forests, Feller (1980) established the following broad N concentration ranges in living canopy tissues: in leaves from 5.7 to 17.4 mg g<sup>-1</sup>, branches 1.6-4.0 mg g<sup>-1</sup>, stembark 1.7-9.2 mg g<sup>-1</sup> and stemwood from 0.4 to 2.3 mg g<sup>-1</sup>. Similarly, in young plantation grown *E. globulus*, N concentrations in leaves were approximately three times higher than concentrations in other tissues during the first 2 to 9.5 years of growth. Concentrations in branches and in stembark were similar and these were significantly higher than stemwood N concentrations throughout the experiment (Cromer and Jarvis 1990). For mature trees, Judd *et al.* (1996a) present typical tissue N concentration ranges in the leaves, bark, branches and stem wood of the forest species *E. diversicolor* and *E. obliqua* and two plantation species *E. grandis* and *E. saligna*. These are given as 6.8-31.6 mg g<sup>-1</sup>, 1.6-3.5 mg g<sup>-1</sup>, 1.3-4.8 mg g<sup>-1</sup> and 0.39-1.3 mg g<sup>-1</sup>, respectively.

Variations in N<sub>leaf</sub> with location within the canopy have been extensively recorded in a range of herbaceous and woody species (Field 1983, Field and Mooney 1986, Hirose and Werger 1987a, Anten *et al.* 1995) as well as the canopies of eucalypts (Cromer *et al.* 1975, Lamb 1976, Turner and Lambert 1983, Hingston *et al.* 1990, Leuning *et al.* 1991, Pinkard *et al.* 1998, Henskens *et al.* 2001). Since N is a structural component of amino acids, proteins, etc., N concentrations can generally be expected to be higher in live and actively expanding tissues (Lamb 1976, Bell and Ward 1984). For leaves particularly, concentrations are highly variable within actively expanding tissues because of the changing amount of biomass present, so that the most useful comparisons are between fully expanded leaves (Bell and Ward 1984). In four-year-old *E. globulus* plantations supplied with varying levels of N and P fertiliser, leaf N concentrations increased with height from the lower to the upper section of the crown (Cromer *et al.* 1975). Similarly, Hingston *et al.* (1979) divided the canopies of 80-year-old *E. diversicolor* forest trees into lower, middle and upper thirds. They demonstrated that leaf and branch N concentrations in these older trees also increased with height in the canopy. Nitrogen concentrations increased with height from 10.4 mg g<sup>-1</sup> and 1.9 mg g<sup>-1</sup> at the lowest portion of the canopy to 11.6 mg g<sup>-1</sup> and 2.2 mg g<sup>-1</sup> at the top (Hingston *et al.* 1979). In a laboratory experiment seedlings of *E. grandis*, *E. pilularis* and *E. gummiifera* were grown with two levels of P and full

illumination and six sequential pairs of leaves were sampled from the apex to the base of the seedlings (Mulligan 1989). Vertical gradients of increasing leaf N concentration with proximity to the apex were discernible only in *E. grandis*. In contrast,  $N_{\text{leaf}}$  in *E. gummifera* seedlings grown with no additional nutrients were higher at the base of the seedling than at the apex (Mulligan 1989). This suggests that the development of vertical gradients in  $N_{\text{leaf}}$ , while frequently observed in older and rapidly growing young trees may vary between species, with growth stage and may be influenced by plant or leaf age and environment. For example, Pinkard *et al.* (1998) found clear vertical gradients of foliar N concentration with distance from the apex in one- to two-year-old plantation grown *E. nitens* but not in one-year-old ramets grown in a shadehouse.

In addition to vertical gradients, several studies have also illustrated the existence of horizontal variations in N concentration in eucalypt canopies (Lamb 1976, Leuning *et al.* 1991a, Warren *et al.* 2000, Henskens *et al.* 2001). Generally,  $N_{\text{leaf}}$  increase with proximity to the stem. Lamb (1976) sampled leaves of four-year-old plantation-grown *E. deglupta* trees from the upper, middle and lower strata of crowns. Within each stratum opposite leaf pairs (in groups of three) were collected along a single branch starting with the first fully developed pair at the branch tip. In addition to being higher in leaves from upper than from lower canopy positions,  $N_{\text{leaf}}$  were generally higher in the outer crown positions than in leaves closer to the stem. In a detailed study of the spatial distribution of foliar N in the crowns of young plantation-grown *E. grandis*, Leuning *et al.* (1991a) produced contour maps of N concentrations in the canopies of trees aged 6 and 16 months. Leaving aside the effect of fertiliser and irrigation, distributions of  $N_{\text{leaf}}$  were broadly more homogeneous in the younger trees. Outer leaves contained higher N concentrations than leaves in the middle of branches and greater still than leaves at the innermost, basal portion of the crown. In 16-month-old trees, both the vertical and horizontal gradients were more pronounced. The highest N concentrations occurred only in leaves at the outermost, upper canopy positions. Leaves in this upper and outer portion of these trees contained 25-30 mg N g<sup>-1</sup> dry weight (DW), while concentrations in upper leaves closer to the middle of the branch were 20-25 mg N g<sup>-1</sup>. Leaves in the two innermost positions closest to the stem in the upper and middle canopy had concentrations of 15-20 and 10-15 mg N g<sup>-1</sup>, respectively (Leuning *et al.* 1991a). The lowest foliar N concentrations occurred at the inner portions at the bottom of the crowns of 16-month-old trees. From light response curves, Leuning *et al.* (1991a) concluded that optimal foliar N concentrations depend on mean light levels during growth. When foliar N concentration diagrams were expressed as contour maps in terms of canopy radius and height, the distribution of N concentration was found to differ markedly from the modelled distribution of absorbed light (photosynthetically active radiation, *PAR*), irrespective of tree age. Since *PAR* was modelled rather than directly measured in this study, the validity of conclusions drawn from these results is open to question, as will be examined further in the subsequent chapter.

The spatial distribution of N concentrations within canopy components other than leaves has received relatively little attention. In a few species, gradients in N concentration in twigs have been observed and are generally similar to those observed in branches, higher in the upper and outermost portions of the canopy and lower in the lower and innermost positions. The bark and stemwood of eucalypts show less variation in N concentration with position in the canopy but N concentrations have been found to decrease with distance from the surface (Groves *et al.* 1996, Judd *et al.* 1996a). Thus, N concentrations in the outer layer of branch and stem are greater than of the inner bark. Similarly, N concentrations are generally higher in sapwood than in heartwood (Groves *et al.* 1996).

## 4.3 Components of Canopy Total N

Physiological and ecological investigations of N in eucalypt canopies, particularly in terms of photosynthetic processes and N recycling have primarily been conducted in terms of total N. Broad relationships have been identified between photosynthesis and total foliar N in a number of eucalypt species. The interpretive value of such analyses is, however, limited because C fixation depends on N partitioning within the leaf (see Evans 1989, Warren *et al.* 2000, Close *et al.* 2000, Close and Beadle 2003). Total N analysis fails to distinguish between structural N and physiologically active forms of

N. The chemical separation and analysis of foliar N fractions has been shown to be a suitable tool for investigating physiologically active N in plants during periods of major physiological change and provides a level of physiological detail unattainable from total N data (Polglase *et al.* 1992a,b, Hooda and Weston 1999, Close and Beadle 2003). In general, N partitioning within leaves will be discussed in terms of the major chemical fractions. According to Kedrowski (1983) and subsequently Polglase *et al.* (1992a,b), Hooda and Weston (1999) and Close *et al.* (2000) the physiologically active fractions of total N consist of nucleic acid-N, soluble-N (nitrate, ammonia and amino-acids) and protein-N. Inorganic N is apparently an insignificant portion of total N in eucalypts and *Pinus* species (Polglase *et al.* 1992a, Close and Beadle 2003). The protein N fraction is primarily composed of soluble proteins, of which Rubisco generally predominates (Evans 1989, Wendler *et al.* 1995). Other important components of nonstructural N include pigments and secondary metabolites including cyanogenic glucosides such as prunasin. These have a specialist literature set, consideration of which is beyond the scope of the current review.

In eucalypts, research on N compounds has primarily focussed on the foliage and to a lesser extent xylem sap, though more recently the composition of N in the phloem sap has also been investigated (Muthuchelian 1992, Marsh and Adams 1995, Kupperts 1996, Schmidt and Stewart 1998, Pate *et al.* 1998, Pate and Arthur 2000, Warren *et al.* 2000a,b). The abundance of these N components varies between species, location and the various canopy tissues (Marsh and Adams 1995, Schmidt and Stewart 1998, Pate *et al.* 1998). Protein-N is the largest N fraction and in *E. nitens* and *E. globulus* seedlings consistently accounted for 85-95% of total N (Close and Beadle 2003). More than 85% of protein N is allocated to photosynthetic apparatus, mostly in the thylakoid (Skillman *et al.* 1996). In mature leaves soluble protein concentrations in eucalypts have been recorded ranging from 9.3 mg g<sup>-1</sup> reported in *E. torquata* to 95 mg g<sup>-1</sup> in *E. pauciflora* saplings growing with an *Acacia* (Muthuchelian 1992, Kupperts 1996, Warren *et al.* 2000a,b). The proportion of N<sub>leaf</sub> present as soluble protein similarly varies widely between eucalypt species and can be as little as 15% of leaf N or as much as 78% of total N (Kupperts 1996, Warren *et al.* 2000a,b). Ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) is generally the single most abundant protein and can comprise up to 80% of leaf soluble protein (Evans 1989, Wendler *et al.* 1995).

Rubisco is relatively inefficient, but the relatively low affinity of the enzyme for CO<sub>2</sub> is compensated for by high concentrations and a consequently major proportion of the N of photosynthetic tissues. Tissue Rubisco content has been analysed for relatively few eucalypt species. In other plants, large differences have been found in the proportion of N partitioned to Rubisco (Evans 1989). Similarly, in eucalypts there are considerable differences in the Rubisco contents recorded in different species. In laboratory grown *E. globulus* seedlings, Wendler *et al.* (1995) reported Rubisco concentrations of around 900-2900 mg m<sup>-2</sup>, about 33 to 83% of leaf soluble protein and around 56-78% of total seedling N. Rubisco concentrations and contents reported in other eucalypt species are significantly lower. In natural stands of *E. delegatensis* saplings growing with and without *Acacias*, Rubisco concentrations were around 11-19 mg g<sup>-1</sup> and comprised 18-25% of total leaf N or 34-46% of leaf protein (Kupperts 1996). Similarly, Rubisco levels in *E. pauciflora* saplings growing under the same conditions were between 17 and 30 mg g<sup>-1</sup> and comprised 21-31% of leaf N and 38-41% of leaf protein (Kupperts 1996). Gleadow *et al.* (1998) reported that Rubisco accounted for 20-30% of leaf N in *E. cladocalyx* seedlings. The leaves of three-month-old, laboratory-grown *E. diversicolor* seedlings similarly had Rubisco concentrations of 4.9-7.6 mg g<sup>-1</sup>, which accounted for 17-24% of total foliar N and 27-39% of leaf soluble protein (Warren *et al.* 2000a). From these later data sets, Warren *et al.* (2000a) concluded that the proportion of N that eucalypts allocate to Rubisco is similar to published values for herbaceous species but is consistently higher than most woody species. When the *E. globulus* data (Wendler *et al.* 1992) is included this conclusion apparently becomes more compelling.

If the proportion leaf protein allocated to Rubisco is considered, however, some of these differences disappear. Taking an example cited by Warren *et al.* (2000a) to support their hypothesis, *Salix cv Aquatica gigantea* allocated an average of 13-20% of leaf N to Rubisco (Vapaavuori and Vuorinen 1989). Rubisco, however, comprised up to 30% of total N and 70% of leaf soluble protein during summer. In this species the proportion of N as Rubisco was found to decline during a warm

summer but the proportion of Rubisco as soluble protein remained stable (Vapaavuori and Vuorinen 1989). In a (presumably) subsequent investigation, Warren *et al.* (2000b) demonstrate clearly that eucalypt allocation of N to Rubisco is in fact similar to other woody species. They report that the leaves of field grown *E. torquata*, *E. decipens* and *E. camaldulensis* contained Rubisco concentrations of 4.9-15.5 mg g<sup>-1</sup> or 8.5-24% of leaf N and 32-53% of leaf soluble protein. Rubisco concentrations and N allocation to Rubisco in the leaves of seven other native, woody Australian species fell within similar ranges. The leaves of these species contained Rubisco concentrations of 2.6-22 mg g<sup>-1</sup>, which accounted for 7.1-30.1% of leaf N and 10-75% soluble protein (Warren *et al.* 2000b).

In mature, field-grown *E. tereticornis* trees, amino-compounds dominate the xylem sap and the ethanol-soluble fraction of foliage (Marsh and Adams 1995). In shoots proline, glutamine, glutamate and aspartate made up about two-thirds of the free amino acid fraction. The concentrations of individual amino acids in the sap varied between sites and between immature (epicormic) and adult leaves. In a more detailed analysis of the xylem sap from woody species in the wet/dry tropics of northern Australia, Schmidt and Stewart (1998) found that the composition of sap in *E. alba*, *E. miniata* and *E. tetradonta* changed markedly with season. Arginine comprised 57-93% of the sap of these species during the dry season, but during the wet season the importance of arginine declined and the free amino acid component of *E. miniata* and *E. tetradonta* sap was composed primarily of amide-N. Unlike deciduous and evergreen monsoon forest species nitrate was only a very minor component of eucalypt xylem sap throughout the year (Schmidt and Stewart 1998).

In the phloem sap of young *E. globulus* trees sampled from 29 plantations, amino acid concentrations were 0.7-20.2  $\mu\text{mol ml}^{-1}$  while organic acid concentration were 2.6-9.9  $\mu\text{mol ml}^{-1}$  (Pate *et al.* 1998). Glutamine was the major N-containing solute throughout the year and in all portions of the stem. The concentrations of total amino acid N, however, increased with height and were greatest in the upper portions of the stem (Pate *et al.* 1998).

Chlorophyll is a key physiological component of N in leaves and other CO<sub>2</sub> fixing tissues. The content and concentration of chlorophyll in leaves varies with the canopy, particularly between juvenile and adult leaves (Johnson 1924, James *et al.* 1999). The distribution of chlorophyll within leaves also shows ontogenic variation. In *E. globulus* for example, the chlorophyll a and b content is greatest at the base of a single adaxial palisade layer and declines through the spongy mesophyll (James *et al.* 1999). The chlorophyll a:b ratio declines linearly from the adaxial to abaxial surface. By contrast, the chlorophyll a+b content and chlorophyll a:b ratios of adult leaves has a bimodal distribution, with peak content and ratios occurring in layers beneath the adaxial and abaxial epidermis. Leaves of the transitional type have chlorophyll distributions intermediate between the juvenile and adult forms (James *et al.* 1999). The bark and twigs of eucalypts also contain chlorophyll and indeed as mentioned previously these tissues have the ability to fix CO<sub>2</sub> (Battaglia pers. comm. 2002). Unfortunately, this area of eucalypt physiological research appears to have been almost entirely overlooked and currently no published data appears available. In both eucalypts and tree bark with demonstrable photosynthetic activity, total bark N concentration increases with proximity to the bark surface (Judd *et al.* 1996a, Groves *et al.* 1996). This suggests that pigment concentrations in eucalypt bark may have a similar gradient. Eucalypts produce a range of pigments in addition to chlorophyll, for which there is a growing, specialised literature. Discussion of these pigments, however, is beyond the scope of the current review.

## 4.4 Function

### 4.4.1 Photosynthetic production

As indicated above, N in photosynthetic tissues is allocated primarily to proteins, up to 95% of which is allocated to the photosynthetic apparatus of light gathering and CO<sub>2</sub> fixation complexes of the thylakoid (Evans 1989). This is the basis of the well-established relationship between foliar N and photosynthetic activity and N content and biomass production/growth (whether gross primary production or net primary production). These relationships are also the foundation of the optimality

and co-ordination hypotheses. Numerous authors have indicated limitations of this hypothesis and other hypotheses have failed to find a direct relationship between the distribution of  $N_{\text{leaf}}$  and the distribution of light or photosynthetic activity (Leuning *et al.* 1991b). Pinkard and Beadle (1998) found no relationship between  $N_{\text{leaf}}$  and  $A_{\text{max}}$  in the thinned and unthinned *E. nitens* seedlings and young ramets. Others have reported N concentrations well in excess of the photosynthetic requirements under prevailing light levels (Warren *et al.* 2001). Similarly in *E. nitens* seedlings and saplings, there was no relationship between  $A_{\text{max}}$  and  $N_{\text{leaf}}$  before or after green pruning (Pinkard *et al.* 1998). These and similar findings suggests that some portion of  $N_{\text{leaf}}$  has some other function, generally assumed to be storage. In *E. globulus* and other tree species, N pools in tissues adjacent to rapidly growing apical tissues are used to support apical growth. Maintaining high canopy N concentrations thus allows maximal rates of photosynthesis under prevailing conditions and supports new growth while minimising the supply route (Millard 1988, Pate and Arthur 2000).

Since total N may commonly be present in excess of apparent current photosynthetic requirements, relationships between foliar N and  $A_{\text{max}}$  and irradiance reported in eucalypts are variable. As mentioned previously, Leuning *et al.* (1991b) found little correlation between  $N_{\text{leaf}}$  distribution and photosynthetic activity or between N distribution and the modelled distribution of relative light intensities in young *E. grandis* canopies. In *E. nitens* ramets and saplings, Pinkard *et al.* (1998) reported that although  $N_{\text{leaf}}$  was significantly affected by pruning, the observed increase in photosynthetic activity following pruning was not correlated with or attributable to changed N concentrations. This suggests that in some instances the distribution of N in eucalypt canopies may be more related to N storage and retranslocation to meet growth requirements as much as to light distribution and photosynthesis.

The principal  $\text{CO}_2$  fixing enzyme and foliar protein is Rubisco. Like total N, the high concentrations of Rubisco reported in leaves are only partially explained by its importance in  $\text{CO}_2$  assimilation and relatively low activity (Lawlor *et al.* 1987, Millard 1988, Millard and Thomson 1989). In the herbaceous species *Tritium aestivum*, Lawlor *et al.* (1987) found that Rubisco accumulation in response to increased N supply was not accompanied by any increase in the rate of  $\text{CO}_2$  fixation. They suggested that under conditions of high N supply, up to 50% of the Rubisco was not activated or only half of the catalytic sites were functional. Consequently a number of workers have suggested that Rubisco may also have a function independent of photosynthesis in N storage (Millard 1988, Millard and Thomson 1989, Warren *et al.* 2000a,b). There is evidence of this in apple trees and herbaceous plants, in which a disproportionately high percentage of Rubisco is lost from leaves during senescence (Millard 1988, Millard and Thomson 1989, Crafts-Brander *et al.* 1999). Warren *et al.* (2000a) reported that  $A_{\text{max}}$  of a number of native Australian plants growing in the glasshouse and of *E. camaldulensis*, *E. decipiens* and *E. torquata* growing outside in November showed no relationship to foliar Rubisco concentrations. Unfortunately, Warren *et al.* (2000a) do not present sufficient data for these species to evaluate their claims for eucalypts. Only three leaves per species were sampled, a wide range of growing conditions appear to have been included in their analysis and only a single sampling period was used. Caution may be needed in interpreting their photosynthetic data and the lack of relationship reported between  $A_{\text{max}}$  and internal  $\text{CO}_2$  concentration ( $C_i$ ) and between N, Rubisco and  $A_{\text{max}}$ . From the information given about the conditions when photosynthetic measurements were made in the field (trees growing in the grounds of the University of West Australia), vapour pressure deficit ( $D$ ) may well have been limiting. If so, an absence of a relationship would not be surprising. The  $A_{\text{max}}$  values for *E. camaldulensis*, of  $7.6 \mu\text{mol m}^{-2} \text{s}^{-1}$  presented by Warren *et al.* (2000a) are low for this species (see Sefton *et al.* 2002) while  $C_i$  values are generally somewhat low, around  $180\text{--}200 \mu\text{mol mol}^{-1}$  (see White *et al.* 1999). Leaf temperatures are given as being between  $25$  and  $30^\circ\text{C}$  and relative humidity around 70-75%. From these data, the  $D$  while photosynthetic measurements were being taken would have been at least 0.95-1.30 kbar. Since leaf temperatures are generally at least a few degrees lower than air temperature (Jones 1994), assuming air temperatures of  $2\text{--}5^\circ\text{C}$  higher than the leaf temperatures recorded by the authors,  $D$  was likely to have been between at least 1.0 and 1.7 kbar. This is well within the range of 0.9-1.5 kbar (and above) where

photosynthesis in eucalypts is limited by the partial closure of stomata (White *et al.* 1999). Consequently, further investigation is required particularly at different times of the year and growth stages and before and after canopy closure. In addition, Warren *et al.* (2000a) point out that under differing temperature and water availability regimes the requirement for Rubisco may alter significantly. Muthuchelian (1992) demonstrated that Rubisco activity as well as protein content varies between species. In this study  $A_{\max}$  and biomass production were strongly correlated with Rubisco activity. Nitrogen status influenced the strength and nature of these relationships. If N is not limiting, and N uptake is above the immediate requirements of photosynthesis and stored in canopy tissues then a portion of the major component of leaf total N as Rubisco may not be functionally involved in photosynthesis.

#### **4.4.2 Storage, recirculation and transport**

Nitrogen in plant canopies can be derived from concurrent uptake of soil N and from N stored within canopy tissues. Internal cycling of N has been shown to be a major source of N used for seasonal growth, and in some plant species can provide up to 90% of the N requirement for growth (Millard 1988). Internal cycling allows the seasonal pattern of growth to be independent of N uptake (Proe and Millard 1994). Internal cycling will thus also have an important influence on the long-term response of trees to fertiliser. The processes of internal circulation are generally characterised as comprising seasonal storage followed by remobilisation either during periods of active growth or during leaf senescence (Chapin *et al.* 1990, Millard 1995). In eucalypts, most investigations of N retranslocation have examined N withdrawal from leaves during senescence.

Different authors have variously defined storage. Millard (1988) considered that N is stored if it can be mobilised from one tissue and subsequently reused for the growth or maintenance of another. This capacity for the subsequent reuse of a unit of N must be demonstrated, but not necessarily expressed under all conditions. For example, an N containing compound that accumulates in response to stress, but undergoes no further metabolism and is essentially an inert byproduct once stress has been relieved cannot be considered to be an N store. This distinguishes between storage and accumulation arising from luxury consumption when N supply outstrips growth, which must be considered in relation to the rate of plant growth. Luxury consumption has frequently been defined as storage (for example Pate *et al.* 1983). This definition, however, does not take into account the capacity of N deficient plants to store N while assuming that all N accumulated by luxury consumption is in a form that the plant can reuse (Millard 1988). Chapin *et al.* (1990) refined the Millard (1988) definition to recognise three general types of storage: accumulation as described above, reserve formation, which co-occurs with and directly competes for N with growth, protection and reproductive requirements and finally recycling. In addition, Heilmeyer and Monson (1994) also recognised the process of interim storage, which accounts for short-term accumulation that can have a direct impact on tree growth. These definitions emphasize both the dynamic nature of N storage and that while N status influences the amount of N stored the ability of trees to store N does not depend on N supply (Millard 1995).

Eucalypts like other evergreen species tend to store N in leaves during winter but also during summer (Saur *et al.* 2000). Since the majority of  $N_{\text{leaf}}$  is incorporated into proteins, particularly Rubisco, it has been suggested that Rubisco may function as an N store in a manner equivalent to recycling defined by above (Millard 1988, Chapin *et al.* 1990, Warren *et al.* 2000a,b). This role has been demonstrated in *Pseudotsuga menziesii* (Camm 1993) and suggested in several eucalypts species, primarily on the basis that the levels of Rubisco present greatly exceed photosynthetic requirements (Warren *et al.* 2000a). In contrast, although N is stored in the leaves of *E. globulus* and remobilised to support spring leaf growth (Pereira *et al.* 1989, Carvalho 1993), Wendler *et al.* (1995) found that while leaf soluble protein content declined there was no change in Rubisco and chlorophyll content or in the photosynthetic capacity of old leaves. This suggests that Rubisco may not be universally involved in N storage in all species and that, as yet, the identity of the leaf storage proteins in *E. globulus* are unknown. Unlike conifers (Camm 1993), there is little evidence that chlorophyll or the chlorophyll binding proteins are involved in N storage in eucalypt leaves (Wendler *et al.* 1995).

Many investigations, particularly the earlier studies, of N storage and remobilisation in eucalypts investigated changes to N pools within and between tissues. These have been deduced from changes in tissue N concentrations, from net changes in the N content of plant parts and from  $N^{15}$  tracer or isotope discrimination studies. In eucalypts, most investigations of N retranslocation have examined N withdrawal from leaves during senescence. Mobilisation of stored N has been calculated from the change in N concentrations in green leaves (on the tree) and freshly senescent leaves in litterfall (Baker and Attiwill 1985, O'Connell and Grove 1993, Groves *et al.* 1996, Hawkins and Polglase 2000). The proportion of N estimated in this way to have been remobilised varies between species and with soil fertility (Ashton 1975, Attiwill 1981, Ericsson 1994b, Hawkins and Polglase 2000). Published values for the proportional change in N between green and senescent leaves range from around 25% *E. triflora* (Hawkins and Polglase 2000) to around 80% in *E. regnans* (Ashton 1975). On the basis of studies on nutrient loss from leaves in *E. regnans* forest species and south-western Australian eucalypt forests, Ashton (1975) and Attiwill (1981) suggested that internal recycling is more important under low than abundant nutrient conditions. Supporting this contention Groves *et al.* (1996) compared data from different species and across studies. They showed that greater proportion of N was mobilised from the leaves of *E. marginata* growing on low N soils (64%, source data from O'Connell *et al.* 1978) than from the leaves of *E. diversicolor* growing on more fertile soils and with greater water availability (48%, source data from O'Connell and Menage 1982). Hawkins and Polglase (2000), however, demonstrated that when a range of 15 eucalypt species were grown under the same conditions the proportional loss of N from leaves was similar, around 40-50%. Turner and Lambert (1983) and later Raison *et al.* (1993) used this procedure to measure nutrient redistribution from various plant parts of *E. grandis* plantations and *E. sieberi* forests, respectively. Both studies indicate that little or no N was retranslocated from these tissues prior to litterfall. For example, N concentrations in the bark and twig litterfall of *E. grandis* were 2.6-4.2 mg N g<sup>-1</sup> while live tree branch and bark concentrations were around 2.2-3.2 mg N g<sup>-1</sup> (Turner and Lambert 1983). To be valid this approach requires that the N source tissues have themselves experienced no net increase or decrease in biomass or carbohydrate content as such changes alter N concentrations (Millard 1995). Simply measuring changes in N concentration does not provide a quantitative assessment of either remobilisation or storage since net changes in N content and allocation, whether on a whole plant, above-ground or an individual organ basis are not addressed (Millard 1988, 1995, Saur *et al.* 2000). Estimates based on concentrations also fail to account for increased sclerophylly and thus N dilution as leaves age (Grove *et al.* 1996).

Measuring changes in the canopy N content have been used to derive N budgets to quantify N mobilisation, re-translocation and subsequent reuse (for example, Turner and Lambert 1983, Hooda and Weston 1999). The N budget approach has also been used to quantify the relative contribution of internal recycling and soil uptake. This requires the accurate determination of the components of canopy biomass. Many of these studies in eucalypts are concerned with N cycling at stand or ecosystem scales rather than within individual tree canopies (for example Ashton 1975, Turner and Lambert 1983, Hooda and Weston 1999). Others, like Wendler *et al.* (1995) and Saur *et al.* (2000), have again investigated N retranslocation purely in terms of foliar N. Generally, there appears to be a close, positive relationship between initial N content of a leaf and the amount of N retranslocated (Wendler *et al.* 1995, Hawkins and Polglase 2000, Saur *et al.* 2000). Consequently although a greater proportion of N for new growth is derived from internal reserves in eucalypts grown under low rather than abundant N, plants grown with high N have more leaves which contain more N and thus provide a greater amount of N through retranslocation (Carvalho *et al.* 1993, Wendler *et al.* 1995). In plantation grown *E. globulus*, Saur *et al.* (2000) demonstrated that the greater the maximum leaf N content the greater the amount of N retranslocated. For example, about 2 mg N leaf<sup>-1</sup> was retranslocated from leaves with a maximum N content of 4 mg N leaf<sup>-1</sup> compared with around 6 mg from leaves containing 14 mg N leaf<sup>-1</sup> (Saur *et al.* 2000). Nitrogen content and budget studies may be imprecise where they assume that N remobilisation is equal to the amount of N lost from senescing leaves or older tissues, ignoring N withdrawal prior to senescence. As demonstrated in *E. grandis* and *E. globulus* (Leuning *et al.* 1991a, Carvalho *et al.* 1993, Wendler *et al.* 1995, Saur *et al.* 2000), N may be withdrawn from mature and old leaves and translocated to young leaves prior to senescence.

Although these studies improve upon those simply measuring N concentrations, in the absence of N-tracers or direct measurement of N in-flows (for example Pate *et al.* 1998, Pate and Arthur 2000), the origin of N in new growth can only be inferred and pathways of N movement through the canopy cannot be determined with certainty. A net decline in the N content of old or mature leaves may indeed coincide with increased N content of new and expanding leaves. Whether the N present in this new growth was derived (wholly or partly) from old leaves, concurrent uptake from the soil or other N pools, however, cannot be proved. Both previous approaches also imply a somewhat circular determination of N storage. Storage in a tissue is demonstrated or quantified by the decrease in N concentrations or content generally without assessment of the biological requirements for N of essential processes. Nor does this approach distinguish between storage and accumulation arising from luxury consumption when N supply outstrips growth (Millard 1988). Consequently, accumulation must also be considered in relation to the rate of plant growth. Luxury consumption has frequently been defined as storage (for example Pate *et al.* 1983). This definition, however, does not take into account the capacity of N deficient plants to store N while assuming that all N accumulated by luxury consumption is in a form that the plant can reuse (Millard 1988). In contrast, Millard (1988) argues that N is stored if it can be mobilised from one tissue and subsequently reused for the growth or maintenance of another. This capacity for the subsequent reuse of a unit of N must be demonstrated, but not necessarily expressed under all conditions. An N containing compound that accumulates in response to stress, but undergoes no further metabolism and is essentially an inert byproduct once stress has been relieved cannot be considered to be an N store. In eucalypts these requirements were satisfied by Pate and Arthur's 2000 study of plantation grown *E. globulus*.

Another approach has been to estimate the N requirements of leaf photosynthesis or respiration and to compare these to the quantity of N or N-compounds such as protein or more importantly Rubisco present (de Pury and Farquhar 1997, Warren *et al.* 2000a,b). As indicated by Warren *et al.* (2000a), this requires an accurate measure of enzyme activity and Rubisco content. The latter has generally been deduced from estimates of  $A_{\max}$  (for example De Pury and Farquhar 1997) rather than measured directly as Rubisco is difficult to extract and purify, especially from eucalypt leaves (Warren *et al.* 2000a,b). As demonstrated by Warren *et al.* (2000a) estimates of enzyme concentrations may significantly miscalculate Rubisco content. At least partially because enzyme activity can be variable and difficult to measure, in vivo activity may not correspond to activity in-vitro.

An alternative technique to quantify transport and mobilisation of N, especially within large, field-grown trees has been to directly study N translocation patterns. These have generally been performed in spring in a variety of evergreen and deciduous species. In detailed studies of phloem and xylem sap in young plantation-grown *E. globulus* during early summer, Pate and co-workers have demonstrated the pathways of N transport, partitioning and use between different tissues within the canopy (Pate *et al.* 1998, Pate and Arthur 2000). In these studies, phloem sap was collected during the daytime or through the course of 24 h over two days from a series of incisions to cambium depth (3-5 mm depending on bark thickness). Cuts were made at intervals up a main stem and side branches, commencing close to ground level to a final cut as close as possible to the growing apex. Sets of samples collected in this way were used to study the gradients in the concentrations of phloem solutes (see Pate *et al.* 1998). Xylem sap was collected under vacuum from the same collection sites on branches and stems used for phloem sap collection (Pate and Arthur 2000). In two- to four-year-old *E. globulus*, Pate *et al.* (1998) found that the ratios of amino acids to total sugars and the concentration of total amino acid-N were several times greater at upper sampling positions than those lower down the stem. Amino acids are thus preferentially loaded into upwardly mobile, as opposed to downward, translocation streams. This partitioning of phloem N and C in *E. globulus* is similar to that described for herbaceous species (see Pate and Layzell 1981, Pate 1986, Pate and Jeschke 1995). Empirical models of C and N flows, from earlier work on herbaceous species, and for *E. globulus* (Pate and Arthur 2000), indicate that stems utilise a complex system of xylem-to-xylem and xylem-to-phloem transfers. These occur in transfer cells and restrict the cycling of N through lower leaves and back to the root in the phloem. Amino acids are depleted from this stream while enriching the N in the phloem stream moving to upper leaves and from upper leaves to the shoot apex. Pate *et al.* (1998) note that the marked differences in composition between the upward and downward streams may not

always be evident under all circumstances. This suggests that there is a degree of control over the enrichment process.

The proportional composition of the amino fraction of the sap did not change with stem height (composed primarily of glutamine). Consequently, Pate *et al.* (1998) concluded that the N enrichment of the upward compared to the basipetal phloem stream was due to preferential upwardly directed loading of all major translocated N components. This was accomplished primarily by loading the primary N solute glutamine. The highest concentrations of amino acids in the phloem occurred from September to December (spring to early summer), when mineral N was likely to be readily available from the soil. Other major N-compounds present in the phloem were glutamate, aspartate, phenylalanine, glycine, alanine and serine. Nitrate was present in low concentrations in the xylem but was never detected in the phloem. Similarly, in *E. regnans* and *E. nitens* as well as *E. globulus*, arginine was present in high amounts in the xylem, but not the phloem (Adams 1996, Pate *et al.* 1998). Arginine thus, appears to have a predominant role in xylem N transport and N storage in eucalypts.

Pate and Arthur (2000) used an empirical modelling procedure to follow the uptake, transport and utilisation of soil-derived N in two- year-old *E. globulus* over a 19-day period. Canopies were divided into 4 zones of equal length and an uppermost section comprised entirely of new growth formed during the study period. These trees experienced ongoing N deficiency during the study. Consequently, N from previously established reserves both in the root system and the mature parts of the canopy were mobilised to meet the growth requirements of rapidly growing leaves and stems especially in the upper canopy. The N content of new growth increased in all portions of the canopy. At the base of the canopy (level 1) the N content of the stem also increased, apparently at the expense of substantial N losses from branches and mature leaves. In the second quarter of the crown, the greatest amount of N was lost from the stem but N was also mobilised from existing pools in branches and leaves. In the upper levels of the tree, N accumulated in all tissues but primarily in leaves and new growth.

The profile of N partitioning was dominated by the upward flow of N in the xylem, cycling of this xylem-derived N through the foliage of lower branches, and from the lower branches out into the phloem to various N sinks within the canopy. Under the N limited conditions of this study, mobilisation from established reserves provided more N to new growth and upper canopy organs than uptake from the soil. Growth of new foliage in the upper two thirds of the canopy comprised the largest sink for N followed by apical growth and then by maturing leaves in the upper part of the canopy (level 4). Branches in the lower half of the canopy were older than the upper branches and retained little xylem-derived N. Nitrogen from these branches was mobilised and used elsewhere in the canopy. Upper branches in contrast sequestered N. This differential can be illustrated by the gradient in ratio of N input through the xylem to export via the phloem (Pate and Arthur 2000). In the lower half of the canopy, this ratio was 0.7 for the lowermost branches and 1.2 for those immediately above them. On the two upper levels branches were active N sinks and N input into branches via the xylem greatly outstripped phloem export giving reported ratios of 12.3 and 39.3, respectively. Substantial quantities of N were present in the downward phloem translocation stream were returned to shoots by the xylem.

Pate and Arthur (2000) indicate that in addition to the major cycles of N there appear to be a series of relatively minor transfers of N between the xylem and phloem in stems and branches. Nitrogen from the phloem in branches is apparently fed back into the upwardly moving stem xylem stream. As the authors indicate, this facet of N transport, seasonal influences and how the trees of this and other eucalypt species switch from reliance on uptake from the soil to mobilising existing reserves to maintain shoot growth over summer require further research.

## 4.5 Extrinsic Factors Influencing Distribution

### 4.5.1 N supply

In forestry and agriculture, N availability has traditionally been identified as being an important limitation to plant growth. Strong growth and photosynthetic responses to N are frequently observed and fertiliser is a common tool for eucalypt yield management, particularly in plantations. In *Eucalyptus globulus* seedlings, Sheriff and Nambiar (1991) found a positive linear relationship between  $N_{\text{leaf}}$ , N supply and  $A_{\text{max}}$  but no simple relationship between seedlings N use efficiency (biomass gain/N concentration) and plant N. Like biomass, canopy N content is generally strongly influenced by past or present nutrient supply. Sites that differ significantly in climate, water supply and or nutrients will differ substantially in stand growth and N content and the pattern of these with age (Judd *et al.* 1996b, Binkley *et al.* 1997). Changes in the N content of canopy components generally follow changes in their biomass. This is primarily because increased N supply usually increases above-ground biomass production. The N content of foliage is particularly sensitive to improved N uptake because the primary growth response of eucalypts to N is via increased leaf area and light interception (Pereira *et al.* 1989, 1994, Cromer and Jarvis 1990, Clearwater and Meinzer 2001). As new leaf growth is stimulated by increased N uptake the new and expanding tissues are strong nutrient sinks and the amount of N present in leaves increases. In the field, a combination of N with P frequently has a stronger effect on partitioning and growth than N alone (Shonau and Herbert 1988, Judd *et al.* 1996b). Exceptions, however, have been reported and these include a study of 16-year-old *E. regnans* trees growing in a natural forest in Victoria, Australia (Attiwill and May 2001). In this investigation, 16 years after the first application of fertiliser, trunk basal area and the concentration of N in green leaves were unaffected by the addition of N, P or N and P in combination. The authors did not measure any other growth parameters. Similarly, in a number of Australian plants including *E. camaldulensis*, *E. decipens*, *E. diversicolor*, and *E. torquata*, allocation to Rubisco is insensitive to N supply, changes in total N and leaf age (Warren *et al.* 2000a).

Although canopy N content may change with N availability patterns of allocation may not (see Table 2). The N content of 9.25-year-old *E. grandis* and its canopy components increased markedly with the application of fertiliser alone or in combination with weed and insect control over a six year period. The proportion of above-ground N in leaves increased from around 23% to 30% (Birk and Turner 1992). In glasshouse-grown *E. globulus* seedlings the proportion of N allocated to leaves, and especially to new leaves, increased when the rate of N supply was increased from 0.04 to 0.12 mmol day<sup>-1</sup> (Carvalho *et al.* 1993). In contrast, for six-year-old plantations of *E. globulus* Bennet *et al.* (1997) reported that at Boola (Victoria, Australia), the total amount of N in trees and in above-ground parts were significantly greater in trees supplied with N, P and K than in control plots. The proportional allocation of N to leaves, twigs, branches, bark and stems, however, was largely unaffected. In the same experiment, the N content of trees and above-ground components of trees at other sites did not increase significantly. Such between-site variations in response to N application are common. Initial soil nutrient status and other quality factors are known to influence the response of eucalypts to fertilisers and other silvicultural treatments (for example, Cromer *et al.* 1981, Judd *et al.* 1996b).

Nitrogen concentrations in canopy tissues may or may not respond to changes in soil N availability and the distribution of N concentration in canopies has generally found to be conserved more than N content. This is because there are at least two sets of responses especially to increased N, both of which depend on initial tree and soil nutrient status. Increased N supply generally stimulates increased leaf growth so that despite increased uptake the additional N is diluted by new growth so that tissue and especially foliar N concentrations do not change. If the increase in N availability and N uptake exceeds growth requirements (luxury consumption) more N may be stored and concentrations will increase despite the diluting effect of increased biomass production (Pereira *et al.* 1992, Carvalho *et al.* 1993). As demonstrated by Leuning *et al.* (1991a), within canopy gradients in N concentration can be modified by N availability.

There is little data available for eucalypts on the influence of N supply and N source on the N composition of canopy N. Plants adapted to soils in which ammonium is the principle form of N are

generally more proficient at extracting ammonium than nitrate from the soil. When they are supplied with nitrate they may have lower growth rates and tissue N concentrations than those adapted to nitrate utilisation (Attiwill *et al.* 1996, Warren *et al.* 2000, Close and Beadle 2003). For example, *E. nitens* characteristically grows on ammonium containing soils/ is adapted to utilising ammonium in preference to nitrate. When grown under the same conditions as *E. globulus* seedlings and supplied with N as nitrate, *E. nitens* seedlings had lower growth rates and significantly lower total foliar N and protein concentrations than *E. globulus* (Close and Beadle 2003). In different species, however, N fractions may be less influenced by N supply but are still affected by the N source and vice versa. Gleadow *et al.* (1998) found that the proportion of N allocated to Rubisco in *E. cladocalyx* leaves was independent of N supply. An analysis of soluble protein and Rubisco concentrations in *E. diversicolor* leaves, however found that while total N concentrations were unchanged the balance of canopy N-constituents can be influenced by the N source. Like Gleadow *et al.* (1998), Warren *et al.* (2000a) found that Rubisco concentrations and the proportion of total N present, as Rubisco did not differ consistently between plants grown with ammonium or nitrate at concentrations 0.5 and 4.0 mM. The total concentration of soluble protein, however, increased in trees supplied with ammonium (Warren *et al.* 2000a). In cyanogenic species, the amount of N allocated to defence compounds such as glucosides increases with increasing N supply and leaf N concentration (Gleadow *et al.* 1998).

#### **4.5.2 Age and season**

Nitrogen accumulation like that of biomass is most rapid during early growth stages when leaf area is expanding. Rates of N accumulation decline in older stands. This is due either to a reduced demand for N after full canopy development and thus a static leaf area (where canopy lift compensates for continued height growth) or declining soil nutrient availability (Binkley *et al.* 1997). Initially the greatest accumulation occurs in the foliage. In an *E. grandis* stand growing in the Brazilian cerrado, for example, after about three years the rate of N and biomass accumulation in the stem increases as does the proportion of above-ground N present in stems. This was accompanied by a decline in leaf N content. After about 5 years the N content of the stand did not increase significantly despite continuing stem growth and increasing allocation to stems (Reis *et al.* 1985, 1987, see Table 1 and 2 for further examples). In *E. globulus* seedlings, Wendler *et al.* (1995) reported that although total  $N_{\text{leaf}}$  and soluble protein content declined in old leaves, there was no change in photosynthetic capacity or Rubisco levels. A strong linear relationship was found between  $N_{\text{leaf}}$  and  $A_{\text{max}}$  in *E. dives* and *E. rossii* and  $N_{\text{leaf}}$  and  $A_{\text{max}}$  were greater in the mature than in the expanding leaves (Anderson *et al.* 2000).

Seasonal changes in N content may, but do not necessarily, mirror seasonal patterns of biomass production and availability of water and nutrients in the soil. While much of the N used in a given year or season may have been taken up from the soil recently, a substantial portion, however, may be supplied internally from pools of tissue N. As discussed in detail above, these storage pools are replenished either from uptake from the soil or resorption from tissues. In leaves resorption usually occurs from mature foliage and/or prior to senescence (Saur *et al.* 2000). The storage and internal reallocation of N potentially allows growth to be decoupled from current uptake (Millard 1988). Consequently, growth may proceed when environmental conditions are favourable to net photosynthesis and may precede net N uptake.

#### **4.5.3 Stand density**

Just as stand biomass may increase, decrease or remain the same with increasing numbers of tree per unit area, the effects of density or spacing on N content may also vary (Schonau and Coetzee 1989, Bernardo *et al.* 1998, Harrison *et al.* 2000, Medhurst *et al.* 2001). This is because although generally stand biomass productivity and the amount of N present per unit area increases the greater the density of stems, the individual trees are smaller and contain less N. A number of authors have reported instances where decreased individual tree size results in lower volumes and stand N content despite increased stem density (for example Medhurst *et al.* 2001).

Spacing is known to influence biomass allocation between above-ground plant parts and so may be expected to influence N allocation within the canopy. In three- to four-year-old plantations of *E. globulus* for example, biomass allocation to branches and leaves was greater in trees grown at 10 m

intervals (isolated trees) than those planted with a 2 m x 4 m spacing (block-planted) (Henskens *et al.* 2001). Leaf area and total leaf N content also increased with increased spacing, suggesting that N allocation to leaves and branches may also increase. This issue has received little attention and the results are equivocal. The spacing study of Laclau *et al.* (2000) indicates that in the *Eucalyptus* hybrid grown with a range of densities, stem spacing had little impact on the distribution of N in canopies. This may be partly because the spacings used by Laclau *et al.* (2000) did not differ greatly from one another.

#### **4.5.4 Pruning**

Defoliation whether by herbivores or systematically in the form of pruning may increase photosynthesis, the growth rate, N uptake and thus the rate of N accumulation and N concentrations in the remaining tissues, particularly leaves (Tromp 1980, Cyr and Bewley 1990, Elliott *et al.* 1993). Such compensatory mechanisms have been reported in a wide range of herbaceous and woody plants (Bieleski 1988, Cyr and Bewley 1990, Pinkard *et al.* 1998). The N content of pruned canopies obviously is initially reduced, but in some species compensatory growth may completely restore N lost or overcompensate giving an increased canopy N content. In eucalypts, pruning similarly can have a significant impact on foliar N concentrations. In pot-grown ramets of *E. nitens*, for example, removal of the lower 70% of the green canopy length caused N concentrations in the remaining mature leaves to rise by between 17 and 47% (Pinkard *et al.* 1998). The greatest increase in  $N_{\text{leaf}}$  concentration in the uppermost 10% of the canopy. A vertical gradient in  $N_{\text{leaf}}$  was thus maintained. In four-year-old plantation trees of the same species, pruning also had a significant effect on foliar N concentrations. There was, however, no consistent pattern in responses between trees in which 50% of the green canopy had been removed and those subjected to 70% defoliation (Pinkard *et al.* 1998).

#### **4.5.5 Water**

Water is a major factor determining eucalypt distribution in Australia (Adams 1996). As demonstrated below, soil water availability may directly influence the source of N for growth, especially during summer. Periods of low soil water availability (or potential) reduce the ability of trees to extract N from the soil (where it is held in the soil solution) and so may impose N limitation on plants. During these periods, N for canopy growth is primarily derived from existing internal reserves (Pate and Arthur 2000). Adequate soil water availability (but not water-logging) enables soil N uptake to proceed and assuming sufficient mineral-N is present, soil uptake will be the predominant source of N for growth and or luxury consumption (storage) (Chapin 1980, Millard 1995, Pate and Arthur 2000). Consequently, under conditions of mild drought or water deficit as demonstrated during the onset of summer in *E. globulus* plantations in Western Australia (Pate and Arthur 2000) canopy growth is maintained. The N content and concentration of older tissues, especially of mature and senescing foliage, decline (Millard 1988, Pate and Arthur 2000). In fact severe drought has been observed to trigger leaf senescence in eucalypts. As demonstrated by Pate and Arthur (2000), the N content of older branches may also decline during periods of mild to moderate water limitation. This of course excludes periods of high vapour pressure deficit, during which stomatal closure inhibits photosynthesis.

#### **4.5.6 Temperature and irradiance**

Low temperatures may have a dramatic effect on the N, and especially the pigment, composition of eucalypts, particularly seedlings exposed concurrently to high light levels. In *E. nitens* and *E. globulus* seedlings concentrations of accessory pigments increase in response to low temperatures in combination with high light levels. In keeping with their role in avoiding or minimising light and temperature induced photoinhibition frost tolerance they are degraded and concentrations decline during spring and summer as temperatures rise (Close 2001, Close *et al.* 2000).

In the absence of photoinhibitory temperature conditions, the exposure to high levels of irradiance has been found to extend leaf longevity and increase leaf N concentrations and content. Conversely, the imposition of shade promotes leaf senescence and the withdrawal of N to unshaded portions of the canopy. This appears to be a principle mechanism behind lower canopy leaf senescence and canopy lift (Saur *et al.* 2000).

## 4.6 N Distribution in Growth and Production Models

Leaf nitrogen and its assumed or empirical relationships with photosynthetic carbon assimilation ( $A_{\max}$ ) and intercepted irradiance are important in scaling up from individual leaf measurements to whole canopies and greater scales (Hirose and Werger 1987, Hirose *et al.* 1988, Harley *et al.* 1992, Kirschbaum *et al.* 1994, Anten *et al.* 1995, Kull and Jarvis 1995, Leuning *et al.* 1995, 1998, Aber *et al.* 1996, de Pury and Farquhar 1997). Leaf N has also been used to estimate other photosynthetic parameters important in modelling canopy production. This is because the majority of  $N_{\text{leaf}}$  is located in Calvin cycle proteins and thylakoid membranes (Evans 1989, Wendler *et al.* 1995). Following the Farquhar *et al.* (1980) biochemical model of photosynthesis, the maximum rate of carboxylation ( $V_{\text{cmax}}$ ) is proportional the Rubisco content and light-saturated rate of electron transport ( $J_{\text{max}}$ ) is proportional to the amount of thylakoid protein (Field 1983, Field and Mooney 1986, Evans 1989, Harley *et al.* 1992, de Pury and Farquhar 1997).

These relationships underpin a number of growth and production models used or potentially used in forestry. For simplicity, these can be divided into two broad classes, optimality models and turnover models.

### 4.6.1 Optimality models

In a wide range of plant communities, the  $N_{\text{leaf}}$  of closed canopies declines with depth. This simple observation has given rise to many investigations on how plants allocate canopy N and photosynthetic capacity. Given a fixed amount of N available to leaves, it was proposed that plants allocate resources to maximise C gain over the entire canopy (Field 1983, Field and Mooney 1983, 1986, Hirose and Werger 1987a,b, Hirose *et al.* 1988). Consequently, N is optimally allocated within leaves and canopies when changes in  $A_{\max}$  correspond to alterations in  $N_{\text{leaf}}$ , so that  $\partial A_{\max} / \partial N$  remains constant. This is termed the optimality hypothesis. Following Kull (2002), models based on this hypothesis can be roughly divided into two groups according to scale. The first group of models deals with optimality of photosynthesis on a single leaf scale (Chen *et al.* 1993, Hikosaka and Terashima 1995, 1996, Medlyn 1996). Originally proposed as an alternative to previous optimality models the single leaf approach was named the coordination hypothesis by Chen *et al.* (1993). This approach is based on the biochemical compartmentalisation of the photosynthetic apparatus within leaves. Each portion, the Rubisco-limited ( $W_c$ ) and the electron transport-limited ( $W_j$ ) rates of carboxylation are dependent on  $N_{\text{leaf}}$  and have an associated amount of N (Chen *et al.* 1993, Hikosaka and Terashima 1995, 1996). In addition,  $W_j$  is dependent on photosynthetically active radiation. Consequently, under given total N and light conditions, photosynthesis is maximal at an optimal N distribution between these two processes. Nitrogen allocation is thus driven by the difference between the amount of N required to balance  $W_c$  with  $W_j$  and the current  $N_{\text{leaf}}$ . This follows the Harley *et al.* (1992) parameterisation for cotton of Farquhar *et al.*'s 1980 photosynthetic model, in which  $V_{\text{cmax}}$  and  $J_{\text{max}}$  were linear functions of  $N_{\text{leaf}}$ . In some single leaf approaches, only the parameters of the light response curve are considered and optimal  $N_{\text{leaf}}$  is that which maximises N use efficiency (Hirose and Werger 1987a). Other models define the photosynthetic apparatus in detail (Evans 1993, Hikosaka and Terashima 1995, Medlyn 1996, Larocque 2002). Medlyn (1996) for example, assumed that  $N_{\text{leaf}}$  is distributed among five different pools, four of which are directly involved in photosynthesis. These pools ( $N_p$ ) correspond to component processes of photosynthesis so that  $N_p$  is divided into thylakoid N and soluble protein. In the thylakoids, N is divided between N required for chlorophyll-protein complexes ( $N_c$ ) and components of the electron transport system ( $N_e$ ). Soluble protein is divided between Rubisco ( $N_r$ ) and other soluble protein ( $N_{sp}$ ). The model calculates the distribution of N among components that maximise photosynthesis for a given value of  $N_p$ . A similar approach is used in multi-layer model of Larocque (2002). In this model, the proportion of  $N_{\text{leaf}}$  allocated to electron transport ( $P_{et}$ ), light harvesting systems ( $P_{lh}$ ) and in soluble proteins ( $P_{sp}$ ) are arrived at by assuming after Chapin *et al.* (1987) that 20% of soluble protein is involved electron transport and 80% in light harvesting (Larocque 2002). The dependence of  $V_{\text{cmax}}$  on  $P_{sp}$  is derived from an empirical relationship between leaf soluble protein content per unit leaf area and leaf mass per unit area (specific leaf area, SLA) and the assumption that leaf soluble proteins consist primarily of Rubisco.

The second group of models deals with optimality at the leaf canopy level. In these N is allocated to maximise C gain over the entire canopy (Hirose and Werger 1987b, Hirose *et al.* 1988, Running and Gower 1991, Sellers *et al.* 1992, Schieving *et al.* 1992, Evans 1993, Amthor 1994, Kull and Jarvis 1995, Sands 1995, Hollinger 1996). For a given amount of total N and  $L^*$ , excluding respiratory and other costs, an optimal distribution of  $N_{\text{leaf}}$  and photosynthetic capacity is proportional to the light profile within the canopy (Sands 1995). For a fixed amount of total  $N_{\text{leaf}}$ , maximal canopy photosynthesis is also associated with an optimal value for  $L^*$  (Schieving *et al.* 1992, Anten *et al.* 1995, Sands 1995).

A survey of actual and predicted N distributions from these two groups of optimality models reveals discrepancies between their respective N profiles and canopy photosynthesis (Kull 2002). Measured N profiles are more uniform than optimal and total canopy photosynthesis is 1-20% less than the theoretical maximum (Hirose and Werger 1987b, Chen *et al.* 1993, Schieving *et al.* 1992, Evans 1993, Hollinger 1996, Leuning *et al.* 1998). Optimality models may overestimate photosynthetic capacity at the top of the canopy and contrary to the predictions of simplified canopy models, actual canopy photosynthesis is often higher than that of unshaded upper leaves (Evans 1993, Kull and Jarvis 1995, Sands 1995, Hollinger 1996). Observed  $L^*$  is also greater than optimal  $L^*$  (Schieving *et al.* 1992, Anten *et al.* 1998). Optimality at either scale fails to account for differences in the distribution of C assimilation between species and between dominant and subdominant individuals of the same species within the canopy (Kull and Niinemets 1998, Anten and Werger 1996). According to Schieving and Poorter (1999) competition for resources also result in evolutionary stable allocation patterns, for example higher  $L^*$  and lower photosynthetic capacity which deviate from optimality. These models also fail because the acquisition and redistribution of resources associated with acclimation of the photosynthetic apparatus is a whole plant phenomenon (see Mooney and Gulmon 1979). Kull (2002) concluded that, optimality models have not yet adequately defined the function to be optimised in a natural community and that these models function to describe observed patterns rather than revealing the underlying mechanism.

Given the assumption that a limited or fixed amount of N is available to leaves, the optimality hypothesis of N distribution is generally inapplicable to canopies in which N availability is not limiting. This is especially true of those in which N accumulation (luxury consumption) and or a significant level of storage and internal cycling occurs. Under these conditions, the deposition of a significant portion of N, particularly in the foliage, is not directly involved in meeting the demands of photosynthesis and increased N availability may not increase  $N_{\text{leaf}}$ . The distribution of N in these canopies thus may be more related to meeting the requirements of current or future growth. That is present in forms and in tissues able to be mobilised, translocated and reused elsewhere in the tree. In eucalypts, the predictions of the optimality hypothesis have generally held best for trees growing under N deficient or limited conditions (Pate and Arthur 2000).

The broad class of optimality models encapsulates a number of different modelling approaches. Big-leaf models for example, assume that the integrated characteristics of the whole canopy can be represented as a single leaf for the estimation of photosynthetic rate (Field 1983, Hirose *et al.* 1988, Running and Gower 1991, Sellers *et al.* 1992, Amthor 1994, Kull and Jarvis 1995, Sands 1995). These models assume that. Two-leaf models stratify the canopy into shaded and sunlit portions. They were developed to improve on big-leaf models but contain many of the same assumptions in terms of N. Following Hirose and Werger (1987), Hirose *et al.* (1988) and Anten *et al.* (1995), the sun/shade model of de Pury and Farquhar (1997), assumes that  $N_a$  (corrected for N not associated with photosynthesis declines exponentially with relative leaf area index ( $L^*/L_c$ , where  $L_c$  is cumulative leaf area index) from the top of the canopy in a manner analogous to diffuse light in the Beer-Lambert equation. The N distribution or allocation coefficient ( $k_n$ ) is derived from this relationship. The base level of  $N_{\text{leaf}}$  or N not associated with photosynthesis ( $N_b$ ) is estimated by the regression of  $A_{\text{max}}$  against  $N_a$ . A direct, linear relationship is assumed to exist between  $N_a$  and Rubisco capacity, allowing the ratio of Rubisco activity to foliar N to be determined and subsequently converted to photosynthetic capacity. Similar assumptions are made in the two-leaf canopy model developed by

Leuning *et al.* (1998), Wang and Leuning (1998). This two-leaf model assumes an exponential decline in photosynthetic capacity ( $V_{\text{cmax}}$  and  $J_{\text{max}}$ ) associated decreasing  $N_a$ . Canopy N is estimated from measured means of stem and leaf N within the canopy and used to estimate  $V_{\text{cmax}}$ . The multi-layer process-based model BIOMASS simply assumes a linear relationship between average  $N_{\text{leaf}}$  over the entire canopy and  $A_{\text{max}}$  (McMurtrie *et al.* 1990). In this model estimates of average  $N_{\text{leaf}}$  and its change with time are required as inputs. The net primary production model of Dewar (1996), expresses leaf  $A$  as a saturating function of  $N_{\text{leaf}}$  at low light and a linear function at high light. Like the big-leaf models, the distribution of  $N_{\text{leaf}}$  within a canopy is assumed to maximise canopy  $A$  for a given total amount of canopy N. Consequently, at each level in the canopy  $N_{\text{leaf}}$  is proportional to relative irradiance (the fraction of incident PAR).

In contrast to the above, the three-dimensional canopy model MAESTRO and subsequent modification MAESTRA, makes few assumptions about how  $N_{\text{leaf}}$  is distributed requiring these as input data (Wang and Jarvis 1990, 1991, see Medlyn *et al.* 2001, <http://homepages.edu.ac.uk/bmedlyn/maestra>). Leaf N can be specified over multiple canopy layers and grid points within these layers. The model allows the distribution and physiological parameters for a number of leaf classes to be specified, thus potentially providing a flexible and detailed description of  $N_{\text{leaf}}$  within the canopy. The required input data to run the model include  $A_{\text{max}}$ ,  $J_{\text{max}}$  and  $V_{\text{cmax}}$  and respiration in leaves, branches, roots and stems can also be input. These are, however, also assumed to have a linear relationship to tissue N.

#### 4.6.2 Turnover models

A generally more recent class of mechanistic models, turnover models avoid the subjective “goal-seeking” assumptions of optimality models (see Thornley 1998). Photosynthetic acclimation, be it to irradiance, N availability or temperature and external  $\text{CO}_2$  occur through changes in both the quality (composition) and the quantity of the photosynthetic apparatus (Thornley 1998, Kull 2002). Turnover models are based on the concept that acclimation of the amount of the photosynthetic apparatus occurs via the permanent turnover, that is the synthesis or break down, of this apparatus (Kull 2002). This occurs because the equilibrium amount of photosynthetic apparatus at a given light level is dependent on resource, primarily N and carbohydrate, availability (Kull and Kruijt 1999). Such acclimation is related to the reallocation of resources within the plant and similarly depends on metabolic cues or feedback systems (Anderson *et al.* 1995, Kull 2002). Net changes in irradiance for example result in either the partial breakdown of the existing photosynthetic apparatus or synthesis of new apparatus. According to Kull (2002), this process is usually found to take 5-30 days and occurs as a dynamic equilibrium within processes of protein and chlorophyll regeneration and degradation not just simply switching synthesis or degradation on and off.

Acclimation through the amount of leaf photosynthetic apparatus is a whole plant phenomenon since patterns of N and photosynthetic capacity with respect to irradiance vary with canopy size, position within the canopy and age (Givnish 1988, Anten and Werger 1996, Anten *et al.* 1998). In *E. nitens*, Pinkard and Beadle (1998) found that  $N_{\text{leaf}}$ , but not leaf photosynthetic capacity, rose significantly after green pruning. In the Kull and Kruijt (1999) model, every leaf has its unique local environment to which it acclimates, depending on resource availability. The amount of photosynthetic apparatus in any leaf is thus determined by the balance between the supply of carbohydrates through photosynthesis and the demand for resources by enzyme synthesis, turnover and export to sinks elsewhere in the plant. Leaves export carbohydrates into a common pool and import N from the common N pool. All leaves of one plant are assumed to share these pools.

An important assumption in both the Thornley (1998) and Kull and Kruijt (1999) turnover models is that the relationship between time-averaged leaf photosynthesis and  $N_{\text{leaf}}$  is linear. The intercept of this relationship depends on carbohydrate export from the leaf. If a leaf does not export carbohydrates, then in steady state conditions all of its photosynthetic production is spent on the turnover of its photosynthetic apparatus. Where the cost of this turnover is constant, leaf photosynthetic production and  $N_{\text{leaf}}$  are proportional. When a leaf containing a given quantity of N, exports carbohydrates, photosynthetic activity must increase to meet the demands of both export and

turnover. Consequently, exporting leaves can maintain the same  $N_{\text{leaf}}$  as a non-exporting leaf only under high light conditions.

An important implication of the turnover models is that, contrary to the assumptions of Field (1983) and many subsequent workers (and indeed optimality models), the strong relationship between  $N_{\text{leaf}}$  and photosynthesis does not occur because  $N_{\text{leaf}}$  is mainly in the photosynthetic apparatus. Rather it arises because a certain amount of energy must be captured through photosynthesis to maintain this N within a leaf. Following the results of Warren *et al.* (2000), this is particularly important for eucalypts, since although turn-over models such as that of Thornley (1998) identify the leaf photosynthetic N pool with Rubisco, the Rubisco content of leaves in some species have been clearly shown to be in excess of immediate photosynthetic requirements. In Thornley's (1998) terminology, Rubisco may, therefore, contribute to both the substrate and photosynthetic N pools of these leaves.

The description of import and export of N and carbohydrates between leaves is the weakest part of these models. Thornley (1998), for example, uses a simplified transport resistance approach in which the resistances to substrate transport associated with leaves and roots are dealt with separately and summed to give overall resistances between leaf and root. That used by Dewar *et al.* (1998) is even simpler and deals only with pools and fluxes. Despite this, the turnover models have a much greater explanatory capacity than optimality models and agree more closely with observed data for eucalypts. Turnover models can accommodate the high levels of Rubisco detected by Warren *et al.* (2000a,b) and are compatible with the movement of N through the canopy and canopy elements of *E. globulus* observed by Pate *et al.* (1998) and Pate and Arthur (2000).

# 5. Spacing Effects on the Distribution of Nitrogen and Photosynthesis in the Crowns of Plantation Grown Eucalypts

## 5.1 Introduction

Attempts to relate plant growth and photosynthetic activity to nutritional status and light availability gained impetus with the work of Agren, Ingestad (Ingestad 1977, Agren 1985, 1988, Agren and Ingestad 1987), Field, Hirose and their co-workers (Field 1983, Field and Mooney 1983, 1986, Hirose and Werger 1987a,b). These workers drew a connection between the central role of N-compounds in photosynthesis and photosynthetic capacity/activity and growth rate and the light environment. This is because the majority of  $N_{\text{leaf}}$  is located in Calvin cycle proteins (of which Rubisco is a major component) and thylakoid membranes (Evans 1989, Wendler *et al.* 1995). Following the Farquhar *et al.* (1980) biochemical model of photosynthesis, the maximum rate of carboxylation ( $V_{\text{cmax}}$ ) is proportional to the Rubisco content. Similarly, the light-saturated rate of electron transport ( $J_{\text{max}}$ ) is proportional to the amount of thylakoid protein (Field 1983, Field and Mooney 1986, Evans 1989, Harley *et al.* 1992, de Pury and Farquhar 1997). The N productivity concept (Agren and Ingestad 1987) holds that an ideal N content is associated with a given growth rate. Field (1983) and Field and Mooney (1986) proposed that plants allocate resources to maximise C gain. Consequently, N is optimally allocated within canopies when changes in  $A$  correspond to alterations in  $N_{\text{leaf}}$ , so that  $\partial A / \partial N$  is constant. This is termed the optimality hypothesis. Simple radiation models applied to one-dimensional canopies have shown that  $\partial A / \partial N$  is constant when  $N_{\text{leaf}}$  is distributed in proportion to the distribution of photosynthetically active radiation (PAR) (Sellers *et al.* 1992, Anten *et al.* 1995). Chen *et al.* (1993) proposed an alternative theory of canopy N distribution. Their coordination hypothesis holds that plants allocate N to balance the processes, the Rubisco-limited ( $W_c$ ) and the electron transport-limited ( $W_j$ ) rates of carboxylation. Both of these are dependent on  $N_{\text{leaf}}$  and both potentially limit  $A$ . This follows the Harley *et al.* (1992) parameterisation for cotton of Farquhar's photosynthetic model, in which  $V_{\text{cmax}}$  and  $J_{\text{max}}$  were linear functions of  $N_{\text{leaf}}$ . Allocation patterns within the canopy are driven by the difference between  $N_{\text{leaf}}$  required to balance  $W_c$  and  $W_j$  and current  $N_{\text{leaf}}$  (Chen *et al.* 1993). In practise, the  $N_{\text{leaf}}$  distributions obtained from these hypotheses are very similar. Like the  $N_{\text{leaf}}$  profiles observed by Hirose and Werger (1987b) the coordination hypothesis gives more uniform, and therefore, according to Chen *et al.* (1993), a more realistic distribution pattern than the optimality hypothesis (though optimality is still assumed, see Kull 2002).

Many models in current or potential use in forestry assume a simple correspondence among foliar N, light availability and photosynthetic parameters based on these concepts (for details see section 4.7). In eucalypts, however, a variety of relationships have been reported  $N_{\text{leaf}}$ , its distribution through the canopy and patterns of  $A_{\text{max}}$  and irradiance. In *E. globulus* seedlings, Sheriff and Nambiar (1991) found a positive linear relationship between  $N_{\text{leaf}}$ , N supply and  $A_{\text{max}}$  but no simple relationship between seedlings N use efficiency (biomass gain/N concentration) and plant N. Also in *E. globulus* seedlings, Wendler *et al.* (1995), reported that although total  $N_{\text{leaf}}$  and soluble protein content declined in old leaves, there was no change in photosynthetic capacity or Rubisco levels. Anderson *et al.* (2000) found a strong linear relationship between  $N_{\text{leaf}}$  and  $A_{\text{max}}$  in *E. dives* and *E. rossii* and reported that  $N_{\text{leaf}}$  and  $A_{\text{max}}$  were greater in the mature than in the expanding leaves. In contrast, Leuning (1991a,b) demonstrated that for young plantation grown *E. grandis* neither the distribution of light nor photosynthetic activity corresponded to foliar N distribution. In three-year-old trees and one-year-old *E. nitens* ramets, considerable photosynthetic enhancement (175% increase) was observed following pruning, but was not related to changes in  $N_{\text{leaf}}$  (Pinkard *et al.* 1998). More specifically, Warren *et al.* (2000b) reported that leaf total N, soluble protein content and Rubisco contents were only poorly related to  $A_{\text{max}}$  in a variety of Australian species including *E. torquata*, *E. decipens* and *E. camaldulensis*. The amount of  $N_{\text{leaf}}$ , particularly Rubisco, was in excess of photosynthetic

requirements. Allocation to Rubisco was insensitive to N supply, changes in total N and leaf age (Warren *et al.* 2000b). While important, particularly for the improved technique of quantifying Rubisco content, this study is marred by use of only a small number of replicates (three leaves per species), at a single time of year and measuring  $A_{\max}$  under conditions when vapour pressure deficit (around 1 bar) is known to cause partial stomatal closure in eucalypts (White *et al.* 1999). Further, for the purposes of the current investigation, it is not clear how and if these results relate to whole canopies, other eucalypt species growing conditions and longer timeframes.

Many of the former studies were conducted on young, rapidly growing trees and were conducted in the glasshouse or in the field prior to canopy closure, and thus were effectively carried out on isolated tree crowns with little competition for resources. In a variety of plants, canopy N distribution and  $N_{\text{leaf}}$ , are known to change with age, time of year and with canopy closure (Lamb 1976, Field 1983, Hirose and Werger 1987b, Cromer *et al.* 1993, Sadras *et al.* 1993, Millard 1995, Schmidt and Stewart 1998, Anderson *et al.* 2000). Similarly, stem density or spacing may strongly influence light, N and C assimilation profiles in plant canopies (Hirose *et al.* 1988, Schieving *et al.* 1992, Sadras *et al.* 1993, Druet and Bonhomme 1999, Bindraban 1999, Dreccer *et al.* 2000). Relationships between N distribution, irradiance and C assimilation can therefore also be expected to vary with spacing and age. Impacts of stand density are therefore important in predicting and optimising stand production (Grindlay 1997, Papadopoulos and Pararajasingham 1997). The current study addresses this and the apparent conflict between recent findings for eucalypts and assumptions about N distribution and relationships among  $N_{\text{leaf}}$ , light,  $A_{\max}$  and photosynthetic parameters common in the literature, particularly in canopy models. The current study investigates the distribution of foliar N in terms of C assimilation, light and relationships between these and photosynthetic parameters in three- to four-year-old *E. globulus* grown in a plantation with a range of planting layouts over an 18 month period. Major aims was to investigate relationships called into question, either directly or by implication, by recent work on eucalypts and evaluate their significance in older trees grown with a range of spacing.

## 5.2 Materials and Methods

### 5.2.1 Photosynthesis

Photosynthetic measurements were taken from the three measurement trees in each treatment. Light-saturated net photosynthetic rate ( $A_{\max}$ ,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) was measured using a portable infrared gas analysis system (CIRAS-1, PPSystems, Hertshire, UK) fitted with a Parkinson PLC leaf chamber (leaf area  $2.5 \text{ cm}^2$ ) and internal  $\text{CO}_2$  supply. The leaf chamber was illuminated using a PPSystems light unit fitted with a quartz halogen class M projection globe. An electric fan was incorporated into the light source to dissipate heat generated by the globe. Measurements were taken from at least two leaves at each of the 36 sampling locations per tree. Additional measurements were taken from the very top of the canopy. The horizontal distances from the stem (canopy position in the results) roughly corresponded to foliage age classes. At the outer canopy, measurements were made on leaves between the fifth and seventh node from the apex. These leaves were classified as apical. Mid-canopy leaves were mature ( $< 2$  years old but fully expanded). Leaves from the inner portion of the canopy (within 10 cm of main stem) were classified as old ( $> 2$  years of age). Measurements were made in August 1999, November-December 1999 and May 2000. All measurements were made at the widest point of healthy, entire leaves under ambient  $\text{CO}_2$  (ca 350 ppm) with a flow rate of  $200 \text{ ml min}^{-1}$ . The incident photosynthetically active photon flux density ( $PPFD$ ), unless otherwise stated, was  $1520 \mu\text{mol m}^{-2} \text{s}^{-1}$ . All measurements were made between 0900 and 1500 h (Western Standard Time). During November-December 1999 and May 2000, photosynthetic measurements were not taken during known periods of high vapour pressure deficit ( $D$ ) around solar noon. Except for light curves,  $A_{\max}$  data were discarded if stomatal conductance was below around  $150\text{--}200 \text{ mmol m}^{-2} \text{s}^{-1}$ , which under full illumination corresponds to a  $D$  of around 1-1.5 kPa (White *et al.* 1999). The presence or absence of water stress in three replicate trees per treatment, from each of the blocks was measured by predawn water potential in November using a standard pressure bomb technique.

The response of photosynthetic rate ( $A$ ) to varying light intensity was measured in November-December 1999 and May 2000 under ambient  $\text{CO}_2$ . These measurements were made in the block planting, single row and isolated tree treatments. Light response curves were obtained from 13 of the 36 measurement locations (including the top) in the trees in which light was measured. Response curves were started at a  $PPFD$  of  $1740 \mu\text{mol m}^{-2} \text{s}^{-1}$  and reduced in 10 steps to  $0 \mu\text{mol m}^{-2} \text{s}^{-1}$ . At each step leaves were left a few minutes until  $A$  was constant. An adjustable power supply was used to provide light intensities above  $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$ . Neutral density filters were used to produce  $PPFD$ s between 0 and  $840 \mu\text{mol m}^{-2} \text{s}^{-1}$ . The response of  $A_{\text{max}}$  to varying  $\text{CO}_2$  concentration was measured in May 2000 under saturating light. Leaves were first equilibrated with an internal  $\text{CO}_2$  of  $355 \mu\text{bar}$ , after which external  $p(\text{CO}_2)$  was increased  $1700 \mu\text{bar}$  and then decreased in steps to 0. At each step the leaf was left to equilibrate until there was a constant  $\text{CO}_2$  flux and stomatal conductance ( $g_s$ ) had stabilised. A final measurement was made at  $350 \mu\text{bar}$   $\text{CO}_2$  to ensure that leaves were performing similarly at the beginning and end of the measurements.

For photosynthetic measurements, leaf dark respiration ( $r_l$ ), light compensation point ( $PPFD_0$ ),  $A_{\text{max}}$  and the light intensity at which  $A_{\text{max}}$  occurred were determined from light response curves where  $PPFD$  was zero,  $A$  was zero and where  $A$  was saturated, respectively. Carbon dioxide compensation point ( $I$ ) was determined from  $\text{CO}_2$  response curves where  $A$  was zero.

### 5.2.2 Nitrogen

Five leaves were taken from each sampling position of replicate trees of each treatment and weighed, their images recorded using a flatbed scanner for leaf area analysis and air-dried at  $80^\circ \text{C}$  until weight was constant (48 h). The five leaves from each sampling position were bulked together, ground, passed through a 2 mm mesh and kept overnight at  $70^\circ \text{C}$  prior to sub-sampling for N analysis. Subsamples (150 mg) were prepared for analysis according to the acid-hydrogen peroxide technique (after Lowther 1980) and total N was measured using a continuous flow colorimetric autoanalyser (McLeod 1992). The specific leaf area of leaves (single-sided area:weight ratio, SLA) was used to convert weight-based to area-based values and these converted into  $\text{mmol N m}^{-2}$ , which are the units most commonly used in the modelling literature.

### 5.2.3 Data analysis and calculations

Leaf green weights were converted to leaf area using specific leaf area relationships determined from subsamples of leaves (after Medhurst *et al.* 1999). Cumulative leaf area index ( $L_c$ ) was the total of tree leaf areas in the stand or tree divided by canopy basal area as presented previously in Henskens *et al.* (2001). The leaf area index at any position in the canopy ( $L^*$ ) was calculated as the total leaf area above that point divided by basal area. Relative leaf area index,  $L^*/L_c$ , was the ratio of these two measurements. The relative leaf maturity of a leaf sample was estimated as the proportion of juvenile leaves in the five leaves sampled from each measurement position. Leaf maturity was used as a co-variate in the regression analyses. Light extinction coefficients ( $k$ ) were calculated in winter and summer using the Beer-Lambert law:

$$I_N = I_o * e^{(1-kL)} \quad (5.1)$$

where  $I_N$  is the light intensity at the  $N$ th position in the canopy and  $I_o$  is the light intensity incident on the top of the canopy.

A nonrectangular hyperbola was fitted to each light and  $\text{CO}_2$  curve (Battaglia and Sands 1997, Pinkard and Beadle 1998)

$$A = \frac{2 \Phi I_x A_{\text{max}}}{(I_x + A_{\text{max}}) + \sqrt{(\Phi I_x + A_{\text{max}})^2 - 4 \theta I_x A_{\text{max}}}} - r_l \quad (5.2)$$

where in the analysis of light responses ( $\Phi$ ) is the initial slope of the relationship ( $\alpha$ , photosynthetic efficiency at low  $I_x$ ),  $I_x$  is  $I$  (irradiance,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) incident on the leaf;  $r_1$  is leaf dark respiration and  $\theta$  is the shape of the photosynthetic light response curve ( $\theta$ ). In the analysis of response to  $\text{CO}_2$  partial pressure,  $\Phi$  is the initial slope of the relationship (at low internal  $\text{CO}_2$ ) and approximates the photosynthetic utilisation of  $\text{CO}_2$  (carboxylation efficiency),  $I_x$  becomes  $C_i$  and is internal partial pressure of  $\text{CO}_2$ ;  $A_{\text{max}}$  becomes  $V_j$  and approximates the capacity for RuBP-regeneration and  $\theta$  is the shape of the  $\text{CO}_2$  response curve ( $\theta_c$  or coefficient of curvature). From these parameters, the rate of electron transport, ( $J$ ) was determined according to the equation:

$$J = \frac{I_2 + J_{\text{max}} - \sqrt{(I_2 + J_{\text{max}})^2 - 4\theta I_2 J_{\text{max}}}}{2\theta} \quad (5.3)$$

where  $I_2$  is the useful light absorbed by photosystem II,  $J_{\text{max}}$  is the maximum electron transport,  $\theta$  is the empirical curvature factor obtained from the light response curve (Wang 2000). Following von Caemmerer (2000),  $I_2$  is related to incident radiation  $I$  as follows:

$$I_2 = \frac{I_x \text{abs}(1-f)}{2} \quad (5.4),$$

where the absorbance of leaves (abs) is assumed to be 0.85,  $f$  is the correction factor for light spectral quality and is 0.15 (from Evans 1987). The denominator is 2 because each photosystem absorbs half the available light.

The RuBP-saturated or RuBP-limited rate of  $\text{CO}_2$  assimilation is given by:

$$A_c = \frac{(C - \Gamma_*)V_{c\text{max}}}{C + K_c(1 + O/K_o)} - R_d \quad (5.5),$$

where  $C$  and  $O$  are the chloroplastic  $\text{CO}_2$  and  $\text{O}_2$  partial pressures,  $\Gamma_*$  is the  $\text{CO}_2$  compensation point in the absence of mitochondrial respiration, which is a function of the relative specificity of Rubisco for  $\text{CO}_2$  and  $\text{O}_2$  and varies little among  $\text{C}_3$  plants (calculated as the product of the y-intercept, multiplied by  $-1$ , divided by the slope of the linear portion of the  $A/C_i$  curve, after Jones 1994),  $K_c$  and  $K_o$  are the Michaelis-Menten constants for  $\text{CO}_2$  and  $\text{O}_2$  respectively. The RuBP regeneration-limited rate of  $\text{CO}_2$  assimilation is given by:

$$A_j = \frac{(C - \Gamma_*)J}{4C + 8\Gamma_*} - R_d \quad (5.6)$$

Net  $\text{CO}_2$  assimilation proceeds at the minimum of the RuBP-saturated and RuBP regeneration-limited rates:

$$A = \min\{A_c, A_j\} \quad (5.7)$$

Analysis of variance and regression procedures were used to determine differences between spacing treatments and the influence of leaf N on these parameters.

The slope of the exponential relationship between  $N_{\text{leaf}}$  distribution on a leaf area basis ( $N_a$ ) ( $\text{mmol m}^{-2}$ , corrected for N not used in photosynthesis,  $N_b$ ) and relative  $L^*$  ( $L_L/L_c$ ) gave the coefficient of N allocation ( $k_n$ ) (Anten *et al.* 1995 and de Pury and Farquhar 1997). Following Hirose and Werger (1987a,b), and Hirose *et al.* (1988),  $k_n$  was also calculated from the equation:

$$N_L = N_0 \exp^{(-k_n L_L / L_c)} \quad (5.8),$$

where  $N_0$  and  $N_L$  are leaf N per unit area at the top of the canopy and within the canopy at depth  $L_L/L_c$ :  $L_c$  is cumulative  $L^*$ . The predicted  $N_a$  at the top of the canopy without shading,  $N_0$ , was given by the y-intercept of logarithm  $N_a$  on  $L_L/L_c$ . The proportion of leaf N not involved in photosynthesis, or minimum N,  $N_b$  was given by the x-intercept of the relationship between  $N_a$  and  $A_{max}$  (following Anten *et al.* 1995).

The concentration of N required to support observed rates of net photosynthesis were calculated by inserting measured light values (using the maxima and averages over various periods) into the light response equations. The resulting values of  $A$  were inserted into the appropriate equation describing the relationship between  $A_{max}$  and  $N_{leaf}$ . These calculated N values were regressed against measured values.

Nitrogen distribution parameters  $N_b$  and  $N_0$  were obtained using SPLUS linear regressions. Nitrogen, canopy structure ( $L_c$ ,  $L/L_c$ ) and photosynthetic data and relationships among parameters were analysed using SPLUS forward and backward manual selection regression and ANOVA procedures.

## 5.3 Results

### 5.3.1 N distribution

Tree canopies in all layouts had non-uniform N distributions.  $N_{leaf}$  in all canopies was highest at the top of the canopy and lowest at the base (Fig 5.1). The proportion of juvenile to mature leaves (leaf maturity) which influences the SLA of the leaves sampled was only of significance for N concentration on a dry weight basis ( $N_w$ ) (Table 5.1).  $N_w$  increased with greater relative leaf maturity (i.e. an increased proportion of mature leaves). Leaf maturity was primarily related to height in the canopy and tree spacing ( $R^2 = 0.64$ ). In row-planted and in isolated trees there were few or no fully expanded leaves at several sampling positions in the lower or mid canopy. Consequently, the influence of factors describing location within the canopy on  $N_{leaf}$  also differed slightly between mass and area based calculations (Table 5.1).

Leaf N concentrations ( $N_w$  or  $N_a$ ) were significantly influenced by spacing, time of year and height and distance from the stem (position, Table 5.1). There were significant interactions between spacing and time of year, spacing and height, and spacing with position. Concentrations in all treatments were also generally lower on the southern aspects. Whilst  $N_{leaf}$  at the top of the canopy ( $N_0$ ) were much the same in all treatments (around  $3.41 \text{ mmol m}^{-2}$ ), at lower canopy heights and middle and outer canopy positions,  $N_{leaf}$  in isolated trees were significantly greater than in block-planted trees (Fig 5.1, 5.2). Concentrations were generally lower in autumn (May) than in winter (August) or summer (November) irrespective of planting layout (Table 5.1, data not presented). In all leaves, N was primarily associated with photosynthesis as  $N_b$  accounted for only around 0.1-2.0 % of  $N_{leaf}$ .

**Table 5.1.** Analysis of variance of  $N_{leaf}$  distribution in *Eucalyptus globulus* crowns on a leaf area ( $N_a$ ,  $\text{g m}^{-2}$ ) and dry weight ( $N_w$ , %DW) basis.

| Factor           | $N_a$ | $N_w$ |
|------------------|-------|-------|
| Month            | ***   | ***   |
| Spacing          | ***   | ***   |
| Height           | ***   | ***   |
| Position         | **    | ***   |
| Aspect           | NS    | *     |
| Month.Spacing    | ***   | ***   |
| Spacing.Height   | ***   | ***   |
| Spacing.Aspect   | NS    | NS    |
| Spacing.Position | ***   | ***   |
| Leaf maturity    | NS    | ***   |

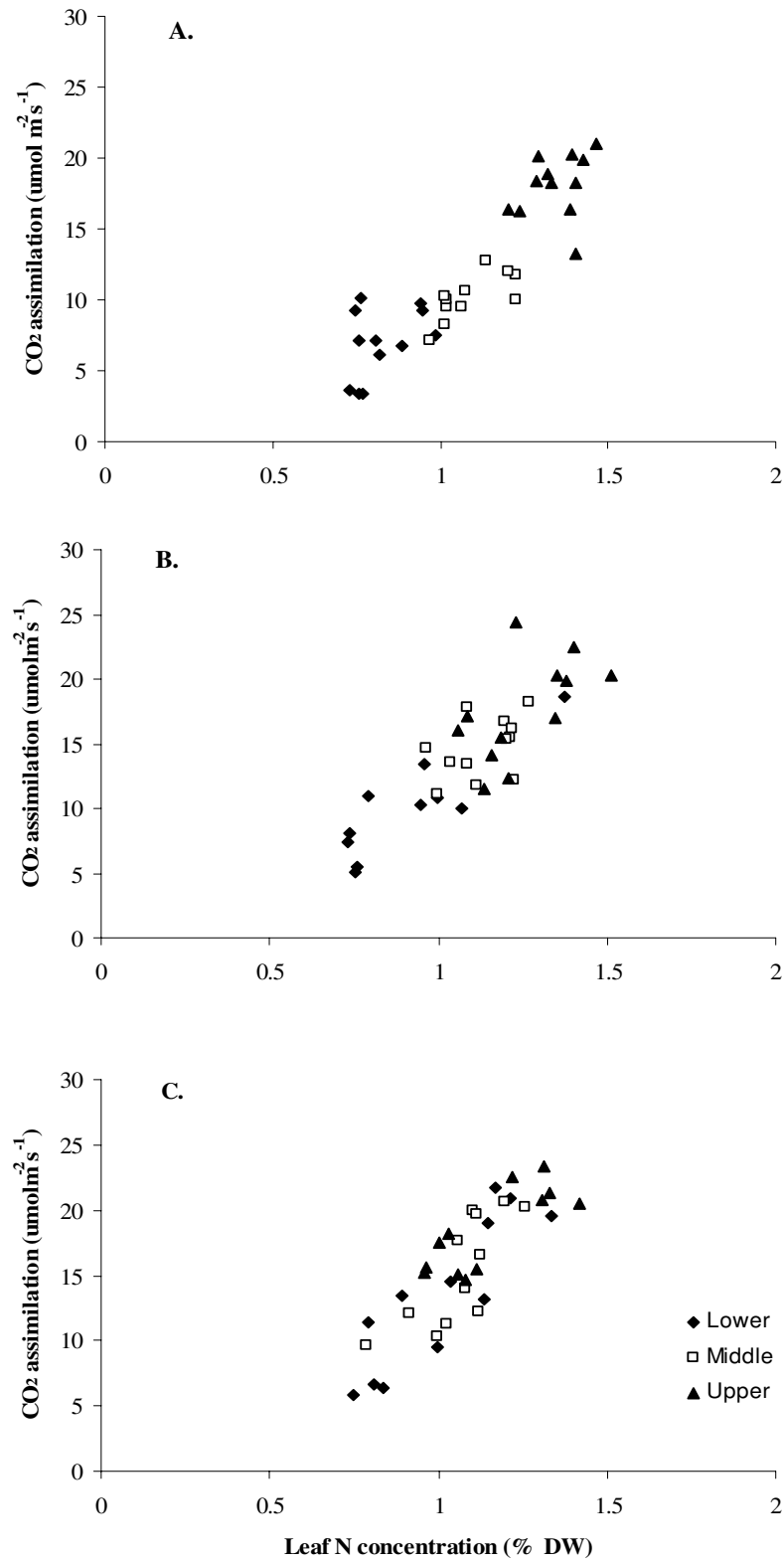


**Figure 5.1.** The vertical distribution of maximum net CO<sub>2</sub> assimilation rate ( $A_{\max}$ ) against foliar N concentration (% DW) through the canopy of **A)** block, **B)** row and **C)** isolated tree plantings in May 2000.

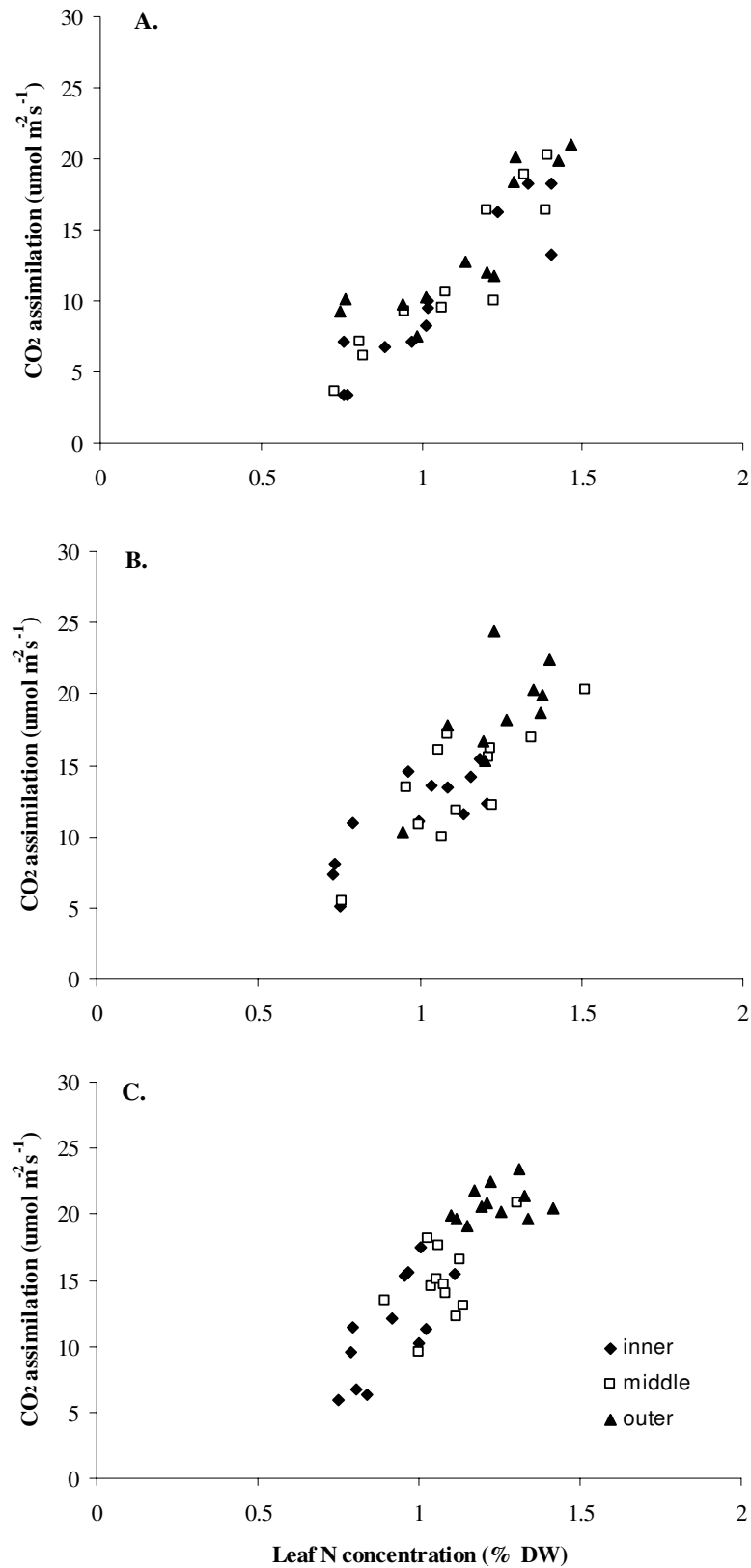


**Figure 5.2.** The horizontal distribution of maximum net CO<sub>2</sub> assimilation rate ( $A_{\max}$ ) against foliar N concentration (% DW) through the canopy of A) block, B) row and C) isolated tree plantings in May 2000.

The vertical distribution of  $N_{\text{leaf}}$  as indicated by the leaf N allocation coefficient ( $k_n$ ) was significantly influenced by spacing ( $P = 0.0008$ ). In isolated trees  $k_n$  also varied with time of year (Table 5.2). The average  $k_n$  over all three observation periods for block-planted trees (1.05) was greater than for row (0.83) and isolated trees (0.68), indicating a stronger vertical  $N_{\text{leaf}}$  gradient and thus less uniform distribution of N in block-planted trees compared with those growing in more widely spaced stands. The lower  $k_n$  of isolated trees was primarily due to the relatively high  $N_{\text{leaf}}$  at all outer portions of the canopy (Fig 5.1c, 5.2c). The presence of horizontal gradients in  $N_{\text{leaf}}$  with increasing distance from the stem meant that a broad range of concentration was observed at each canopy height. These gradients were most evident in isolated trees (Fig 5.2).

**Table 5.2.** The influence of spacing and time of year on the profile of  $N_{\text{leaf}}$  ( $\text{g m}^{-2}$ ) in *E. globulus* canopies in terms of the N distribution coefficient ( $k_n$ ).

| Month    | Block             | Row               | Isolated          |
|----------|-------------------|-------------------|-------------------|
| August   | 1.02 <sup>a</sup> | 0.80 <sup>b</sup> | 0.89 <sup>b</sup> |
| November | 1.06 <sup>a</sup> | 0.89 <sup>b</sup> | 0.70 <sup>c</sup> |
| May      | 1.08 <sup>a</sup> | 0.81 <sup>b</sup> | 0.45 <sup>d</sup> |
| Average  | 1.05 <sup>a</sup> | 0.83 <sup>b</sup> | 0.68 <sup>c</sup> |

Foliar N concentration in both block-planted and isolated trees was strongly related to relative direct beam irradiance around solar noon (Fig 5.3a,b). The relationship between  $N_{\text{leaf}}$  and average, daily relative irradiance was weaker. Foliar N distribution was not exactly in proportion to irradiance, however, since the relationships are curvilinear. Consequently, the occurrence of high  $N_{\text{leaf}}$  only broadly corresponded to positions of high relative light intensity. Similarly,  $A_{\text{max}}$  also did not exactly correspond to noontime or daily relative irradiance (Fig. 5.3c).

### 5.3.2 $N_{\text{leaf}}$ and $\text{CO}_2$ assimilation

The relationship of  $A_{\text{max}}$  against  $N_{\text{leaf}}$  ( $N_a$  and  $N_w$ ) varied between treatments, with time of year, and with canopy height and position (Fig. 5.1, 5.2, Table 5.3, 5.4). The rate of  $\text{CO}_2$  assimilation per unit  $N_{\text{leaf}}$  (given by the slope of the  $A_{\text{max}}-N_{\text{leaf}}$  relationship) however remained constant. In block-planted trees there were strong vertical gradients in which high  $A_{\text{max}}$  and the greatest  $N_{\text{leaf}}$  occurred in the upper canopy. Nitrogen concentrations and  $A_{\text{max}}$  and  $N_{\text{leaf}}$  were least in the lower canopy and intermediate in the middle canopy (Fig 5.2a). In row trees this stratification was less obvious but upper canopy leaves on average had higher rates of  $A_{\text{max}}$  and higher  $N_{\text{leaf}}$  than leaves from lower in the canopy (Fig. 5.1b). In contrast in isolated trees there was no clear vertical  $A_{\text{max}}-N$  gradient and distance from the stem (position) was a much stronger determinant of light availability and thus  $A_{\text{max}}$  and  $N_{\text{leaf}}$  (Fig 5.1c, 5.2c). In isolated trees the highest  $A_{\text{max}}$  and  $N_{\text{leaf}}$  generally occurred in the outer portions of the canopy irrespective of height. There was no similar horizontal  $A_{\text{max}}-N$  gradient in block-planted and row trees (Fig. 5.2a,b).

Light-saturated net photosynthetic rate was curvilinearly related to  $N_{\text{leaf}}$  concentration on a dry weight and on a leaf area basis. Linear regressions of logarithmically transformed  $A_{\text{max}}$  ( $\text{LNA}_{\text{max}}$ ) against the logarithms of  $N_a$  ( $\text{LNN}_a$ ) and  $N_w$  ( $\text{LNN}_w$ ) reveal that a suite of equations is required to describe  $A_{\text{max}}-N_{\text{leaf}}$  relationships in trees growing in different layouts at different times of the year.

These equations must be further modified to account for variation within the canopy and interaction between factors (Table 5.3). The simplest model of  $\text{LNA}_{\text{max}}$  using  $\text{LNN}_a$  required terms for time of year, spacing, height, position and interactions between foliar N and spacing and N and height. When  $\text{LNN}_w$  was used to model  $\text{LNA}_{\text{max}}$ , these N interactions were not significant but leaf age and an interaction between spacing and height had to be included (Table 5.3, 5.4). In both regression models the  $N_{\text{leaf}}$  term was the most important (Table 5.4).

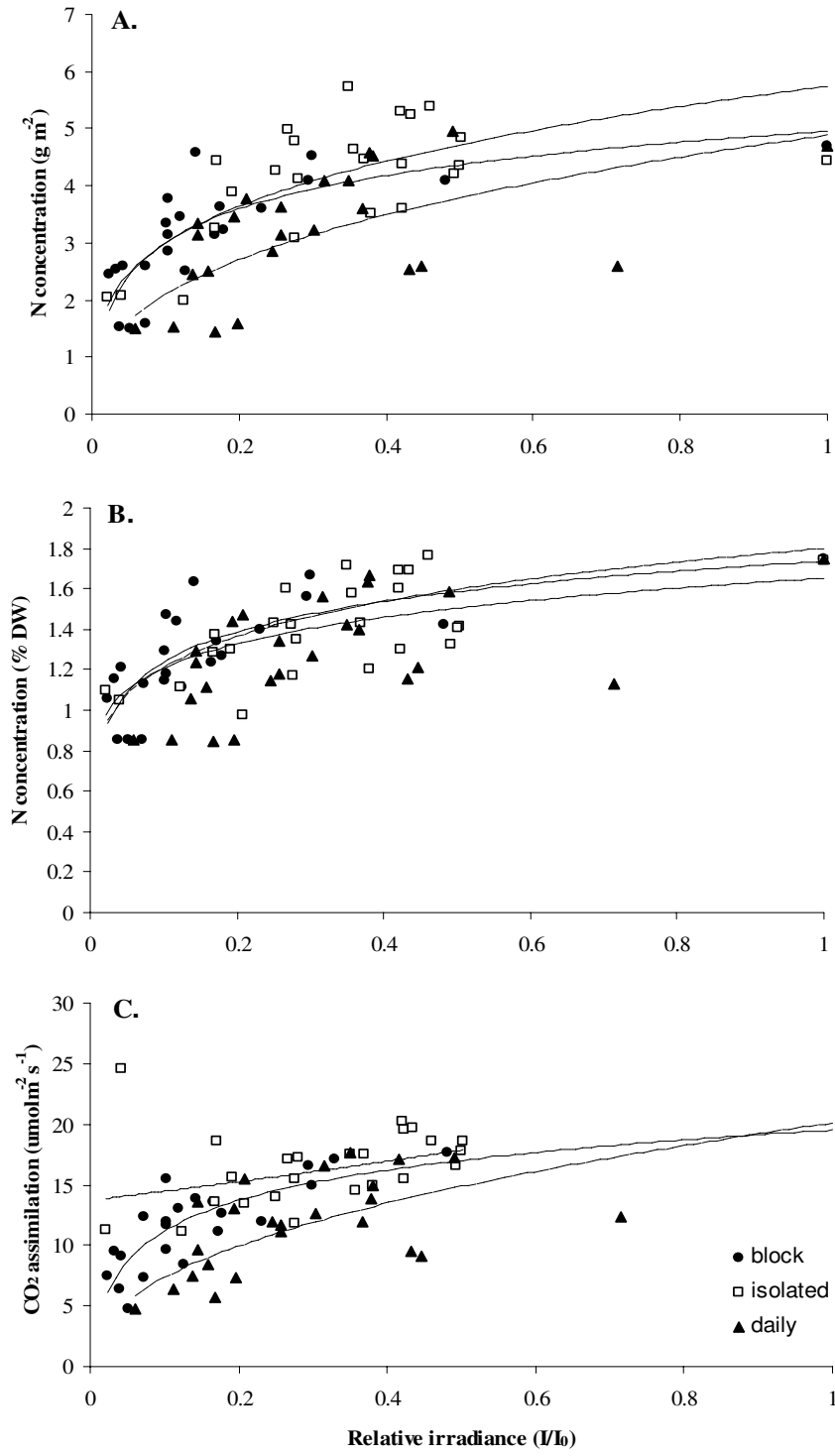


**Figure 5.3.** The relationship between **A)** leaf  $N_a$  ( $\text{g m}^{-2}$ ), **B)** leaf  $N_w$  (% DW) and **C)**  $A_{\max}$  and relative irradiance ( $I/I_0$ ) averaged over one hour around solar noon (noon) and on a daily basis (daily) in block-planted and isolated trees (noon only).

**Table 5.3.** Regression coefficients for the regressions of  $LNA_{max}$  against  $LNN_a$  and  $LNN_w$ .

|            | $N_a$   |           |         |          |           | $N_w$   |           |         |          |
|------------|---------|-----------|---------|----------|-----------|---------|-----------|---------|----------|
|            | Value   | Std error | t-value | Pr(> t ) |           | Value   | Std error | t-value | Pr(> t ) |
| Intercept  | 3.6558  | 0.3409    | 10.7245 | 0.0000   | Intercept | 2.3520  | 0.0441    | 53.3508 | 0.0000   |
| $N_a$      | 0.3085  | 0.0958    | 3.22    | 0.0015   | %N        | 0.82    | 0.1463    | 5.6032  | 0.0000   |
| Month      | 0.0640  | 0.0147    | 4.3647  | 0.0000   | Leaf age  | 0.0335  | 0.0590    | 0.5679  | 0.5708   |
| Spacing1   | -0.2864 | 0.3807    | -0.7522 | 0.4528   | Month     | 0.1173  | 0.0186    | 6.3140  | 0.0000   |
| Spacing2   | 0.2782  | 0.1903    | 1.4614  | 0.1455   | Spacing1  | 0.0664  | 0.0173    | 3.8285  | 0.0002   |
| Height1    | -0.9807 | 0.3539    | -2.7710 | 0.0061   | Spacing2  | 0.0785  | 0.0096    | 8.2093  | 0.0000   |
| Height2    | -0.2659 | 0.2112    | -1.2591 | 0.2095   | Height1   | 0.0979  | 0.0251    | 3.9010  | 0.0001   |
| Depth1     | 0.0855  | 0.0179    | 4.7702  | 0.0000   | Height2   | 0.0884  | 0.0155    | 5.6972  | 0.0000   |
| Depth2     | 0.0941  | 0.0104    | 9.0442  | 0.0000   | Depth1    | 0.0612  | 0.0180    | 3.3945  | 0.0008   |
| N.Spacing1 | -0.0965 | 0.1050    | -0.9188 | 0.3594   | Depth2    | 0.0675  | 0.0114    | 5.9105  | 0.0000   |
| N.Spacing2 | 0.0597  | 0.0540    | 1.1047  | 0.2707   | Spacing1  | -0.0008 | 0.0202    | -0.0394 | 0.9686   |
|            |         |           |         |          | Height1   |         |           |         |          |
| N.Height1  | -0.2910 | 0.0943    | -3.0860 | 0.0023   | Spacing2  | -0.0129 | 0.0119    | -1.0846 | 0.2794   |
|            |         |           |         |          | Height1   |         |           |         |          |
| N.Height2  | -0.1043 | 0.0621    | -1.68   | 0.0946   | Spacing1  | -0.0465 | 0.0118    | -3.9539 | 0.0001   |
|            |         |           |         |          | Height2   |         |           |         |          |
| Spacing1.  | 0.0379  | 0.0291    | 1.3022  | 0.1944   | Spacing2  | -0.0125 | 0.0070    | -1.7865 | 0.0756   |
| Height1    |         |           |         |          | Height2   |         |           |         |          |
| Spacing2.  | -0.0194 | 0.0177    | -1.0953 | 0.2748   |           |         |           |         |          |
| Height1    |         |           |         |          |           |         |           |         |          |
| Spacing1.  | -0.0303 | 0.0208    | -1.4524 | 0.1480   |           |         |           |         |          |
| Height2    |         |           |         |          |           |         |           |         |          |
| Spacing2.  | -0.0246 | 0.0101    | -2.4321 | 0.0159   |           |         |           |         |          |
| Height2    |         |           |         |          |           |         |           |         |          |

### 5.3.3 Light and $CO_2$ response

Photosynthetic responses to light varied with canopy height and position (Fig 5.4). At an external  $p(CO_2)$  of 350  $\mu$ bar only leaf dark respiration ( $r_l$ ) was affected by spacing and month (linear regression  $R^2 = 0.71$ ). Of the light-response curve parameters,  $a_x$  and  $r_l$  had the strongest relationship with  $N_{leaf}$  (only  $N_w$  shown in Fig 5.4,  $R^2 = 0.39, 0.36$ , respectively,  $P = 0.001$  for both).

Photosynthetic efficiency (or apparent quantum yield,  $\Phi$ ) was generally not influenced by  $N_{leaf}$  (Fig 5.5c,  $R^2 = 0.01$ ,  $P = 0.26$ ). The coefficient of curvature ( $\theta_l$ ), however, appeared to be at least weakly influenced by  $N_{leaf}$  (Fig 5d,  $R^2 = 0.18$ ,  $P = 0.025$ ). Relationships between  $N_{leaf}$  and the light-response parameters  $a_x$ ,  $r_l$  and  $\theta_l$  differed significantly between mature and juvenile leaves ( $P = 0.03, 0.03, 0.02$ , respectively). These differences were greater during November ( $P = 0.001$ ). In juvenile leaves,  $r_l$  and  $\theta_l$  were more strongly related to  $N_{leaf}$ , particularly  $N_w$ , than in mature leaves ( $R^2 = 0.98$  and  $0.88$ ,  $P = 0.001, 0.04$ , compared with  $R^2 = 0.30, 0.12$ ,  $P = 0.009, 0.08$ , respectively, Fig 5.5).

The photosynthetic response to external  $p(CO_2)$  also varied with location in the canopy and thus the coefficient of curvature ( $\theta_c$ ) and other response parameters were not constant (Fig 5.6). The capacity for RuBP regeneration ( $V_j$ ), daytime respiration ( $r_d$ ) and carboxylation efficiency ( $C_e$ ) were linearly related to  $N_{leaf}$  ( $R^2 = 0.35, 0.40, 0.35$  and  $P = 0.02, 0.01, 0.02$ , respectively, Fig 5.7a,b). These relationships were stronger with  $N_a$  than with  $N_w$ . Neither  $\theta_c$  nor  $CO_2$  compensation point ( $\Gamma$ , or in the absence of mitochondrial respiration,  $\Gamma^*$ ) were influenced by  $N_{leaf}$  ( $R^2 = 0.05$ , and  $0.01$ , respectively, Fig 5.7b, only  $\theta_c$  presented). The maturity of the sampled leaves significantly influenced their  $N_{leaf}$  ( $R^2 = 0.59$ ,  $P = 0.002$ ) and a number of underlying  $p(CO_2)$  response parameters suggesting enzymatic differences between the two leaf classes (Fig 5.7). Carboxylation efficiency ( $C_e$ ) and  $r_d$  varied strongly between juvenile and mature foliage ( $R^2 = 0.36, 0.41$ ,  $P = 0.02$  and  $0.01$ , respectively). Leaf maturity also appeared to influence  $V_j$  but to a lesser extent ( $R^2 = 0.22$ ,  $P = 0.07$ ). There were strong

linear interrelationships among  $C_e$ ,  $V_j$  and  $r_d$  (Fig 5.8 a,c) but only weak relationships between these and  $\theta_c$  (Fig 5.8b).

**Table 5.4.** Analysis of variance for the regressions of  $LNA_{max}$  against  $LNN_a$  and  $LNN_w$ .

| $N_a$     |     |         |         |          |        | $N_w$    |     |         |         |          |        |
|-----------|-----|---------|---------|----------|--------|----------|-----|---------|---------|----------|--------|
|           | Df  | Sum Sq  | Mean Sq | F-value  | Pr(F)  |          | Df  | Sum Sq  | Mean Sq | F-value  | Pr(F)  |
| $N_a$     | 1   | 21.3253 | 21.3253 | 566.1263 | 0.0000 | $N_w$    | 1   | 17.9380 | 17.9380 | 499.0041 | 0.0000 |
| Month     | 1   | 1.9771  | 1.9771  | 52.4874  | 0.0000 | Leaf age | 1   | 2.6927  | 2.6927  | 74.9063  | 0.0000 |
| Spacing   | 2   | 0.7291  | 0.3646  | 9.6781   | 0.0001 | Month    | 1   | 4.7987  | 4.7987  | 133.4919 | 0.0000 |
| Height    | 2   | 0.2977  | 0.1488  | 3.9515   | 0.0208 | Spacing  | 2   | 2.0155  | 1.0078  | 28.0346  | 0.0000 |
| Depth     | 2   | 3.1148  | 1.5574  | 41.3452  | 0.0000 | Height   | 2   | 0.4059  | 0.2030  | 5.6459   | 0.0041 |
| N.Spacing | 2   | 0.9133  | 0.4566  | 12.1228  | 0.0000 | Depth    | 2   | 1.1667  | 0.5833  | 16.2278  | 0.0000 |
| N.Height  | 2   | 0.5834  | 0.2917  | 7.7435   | 0.0006 | Spacing  | 4   | 0.6641  | 0.1660  | 4.6183   | 0.0007 |
| Spacing   | 4   | 0.5772  | 0.1443  | 3.8311   | 0.0050 | Height   |     |         |         |          |        |
| Height    |     |         |         |          |        | Resid.'s | 198 | 7.1176  | 0.0359  |          |        |
| Resid.'s  | 193 | 7.2701  | 0.0377  |          |        |          |     |         |         |          |        |

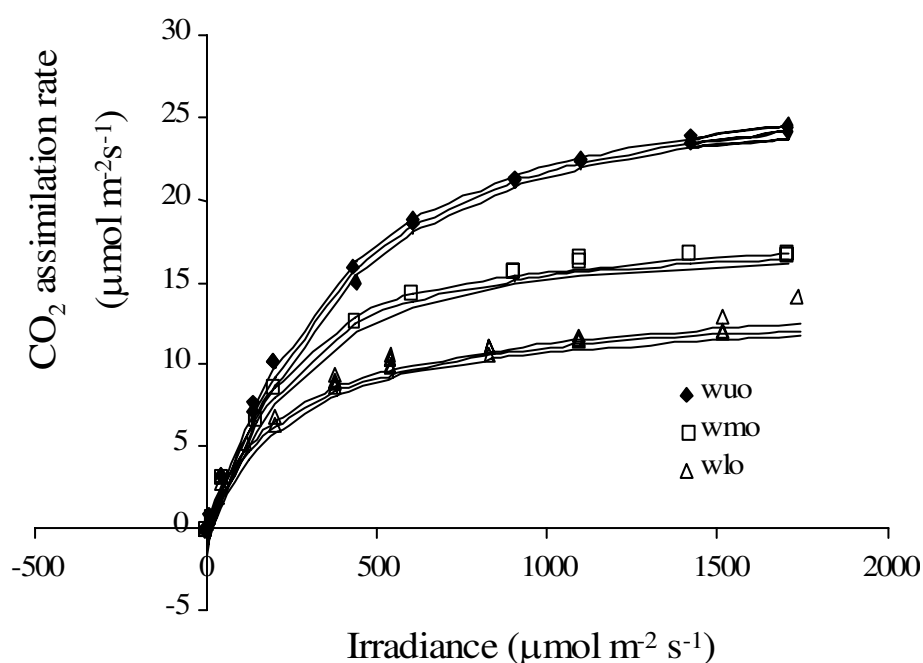


**Figure 5.4.** The response of net  $CO_2$  assimilation rate ( $A_{max}$ ) to irradiance ( $\mu mol m^{-2} s^{-1}$ ) at three different positions along a vertical gradient (west-upper-outer, wuo, west-middle-outer, wmo, and west-lower-outer, wlo) in the canopy of block planted trees. The middle line indicates the fitted values from the regression, the upper and lower lines indicate the 95% confidence interval.

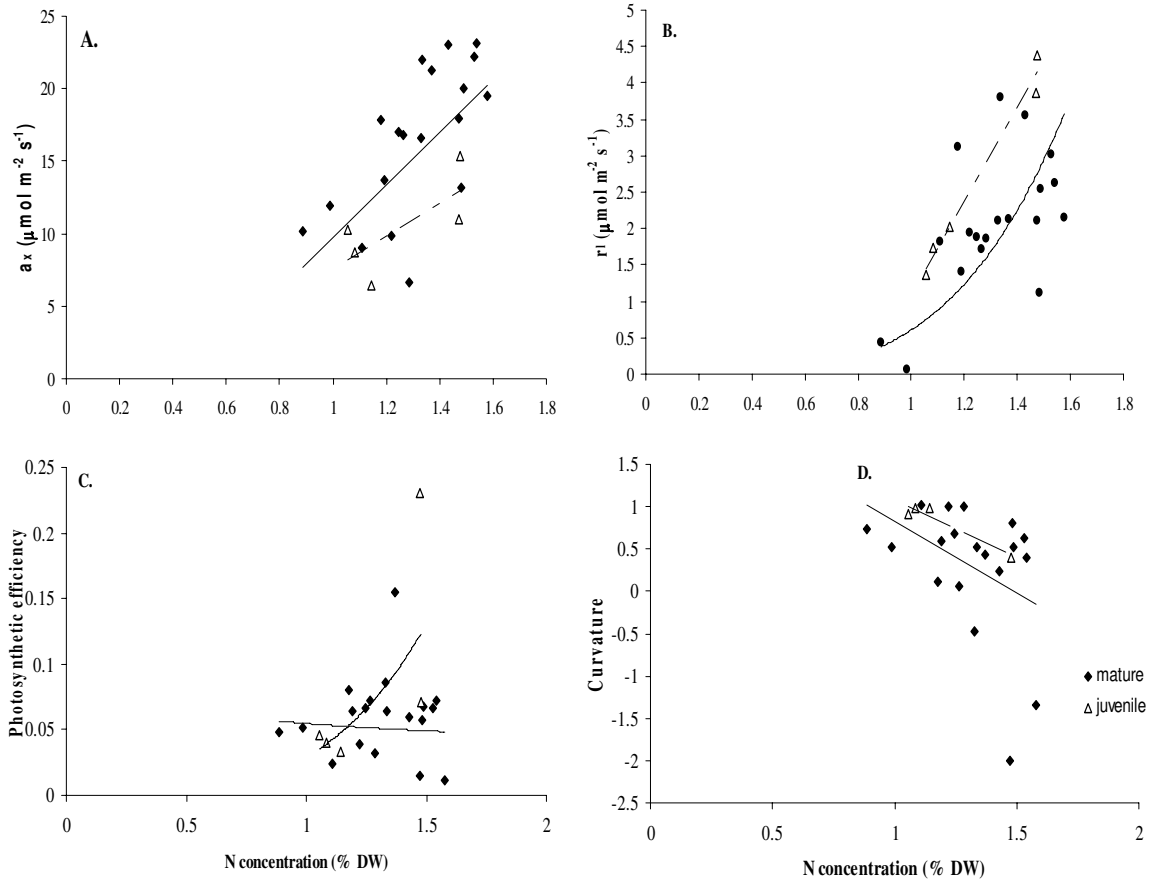


**Figure 5.5.** The effect of  $N_{\text{leaf}}$  (% DW) and leaf maturity (juvenile, mature) on the light response curve parameters **A)**  $a_x$  (overall  $R^2 = 0.41$ , mature  $R^2 = 0.44$ , juvenile  $R^2 = 0.51$ ), **B)**  $r_1$  ( $R^2 = 0.42$ ,  $0.44$ ,  $0.98$ , respectively), **C)**  $\Phi$  (photosynthetic or quantum efficiency,  $R^2 = 0.01$ ,  $0.00$ ,  $0.62$ , respectively) and **D)**  $\theta_1$  (coefficient of curvature,  $R^2 = 0.22$ ,  $0.17$ ,  $0.92$ , respectively) in November 1999. Data from block-planted and isolated trees have been pooled.

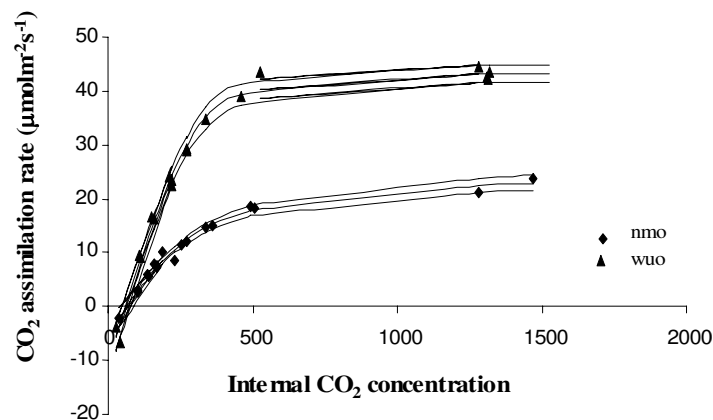


**Figure 5.6.** The effect of internal  $\text{CO}_2$  concentration ( $C_i$ ,  $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ ) on net  $\text{CO}_2$  assimilation ( $A_{\text{max}}$ ) at two different positions (wuo and nmo) in the canopy of block planted trees. A solid line indicates the fitted values from the regression while broken lines represent the upper and lower 95% confidence intervals.

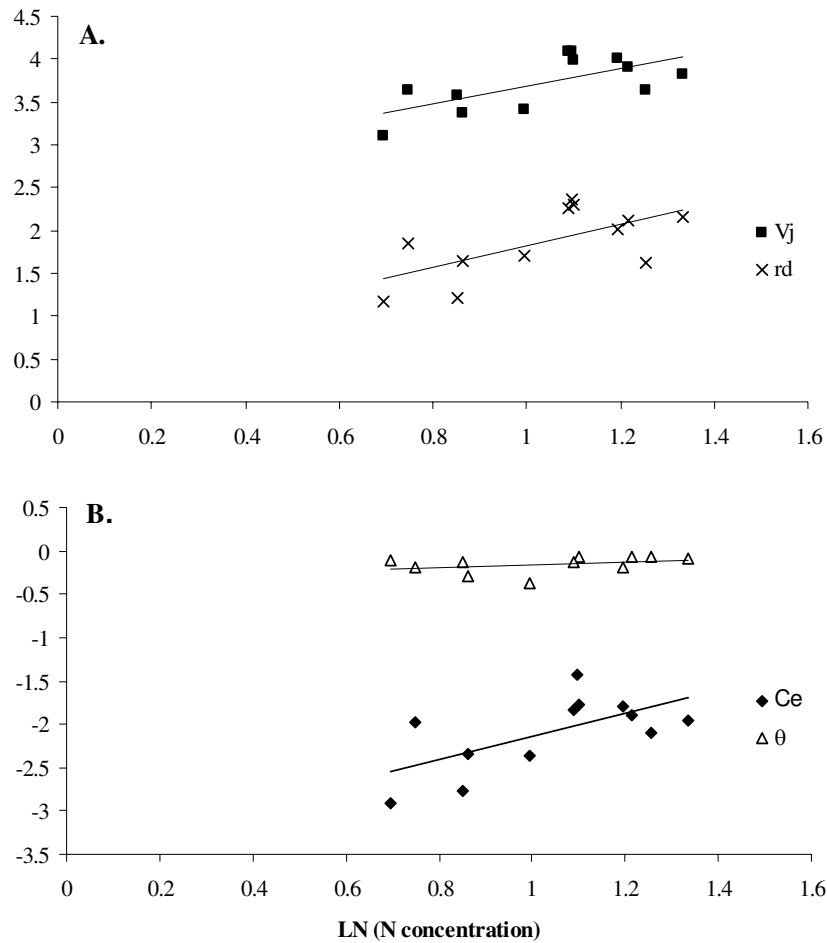


**Figure 5.7.** The effect of leaf  $N_a$  on the  $A/C_i$  response curve parameters **A)**  $V_j$  ( $R^2 = 0.48$ ) and  $r_d$  ( $R^2 = 0.41$ ) and **B)**  $C_e$  ( $R^2 = 0.41$ ) and  $\theta_c$  ( $R^2 = 0.14$ ). All data have been logarithmically transformed.

The maximum rate of Rubisco carboxylation ( $V_{cmax}$ ), the rate of electron transport ( $J$ ) and the maximum rate of electron transport ( $J_{max}$ ) and the electron transport limited rate of  $CO_2$  assimilation ( $A_J$ ) had strong, positive, linear relationships with  $N_{leaf}$  (Fig 5.9a,b). Unlike the light and  $CO_2$  response parameters, the influence of  $N_{leaf}$  on  $V_{cmax}$  did not differ between mature and juvenile leaves ( $R^2$  and  $P$  are not significant). Each of  $A_J$ ,  $J$  and  $J_{max}$  were linearly and strongly related to  $V_{cmax}$  (Fig 5.9c).

#### 5.3.4 N requirement for photosynthesis

During summer, foliar N concentrations at all canopy locations in block-planted and isolated trees significantly exceeded the N requirement for photosynthesis at average levels of irradiance experienced over the 14 h photoperiod or from 0900 to 1500 h WST (Fig. 5.10). In block-planted trees,  $N_w$  in much of the canopy were also greater than required for photosynthesis at the maximum observed levels of irradiance (Fig 5.10a). Only leaves from the outer portions of the east and west middle canopy had lower  $N_w$  than predicted by maximum levels of irradiance. In the canopies of isolated trees, however, observed  $N_w$  at the outer positions of the middle and upper canopy were less than predicted by maximum irradiance (Fig 5.10b). At positions closer to the stem, observed  $N_w$  was similar or greater to the concentrations predicted on the basis of maximum irradiance.

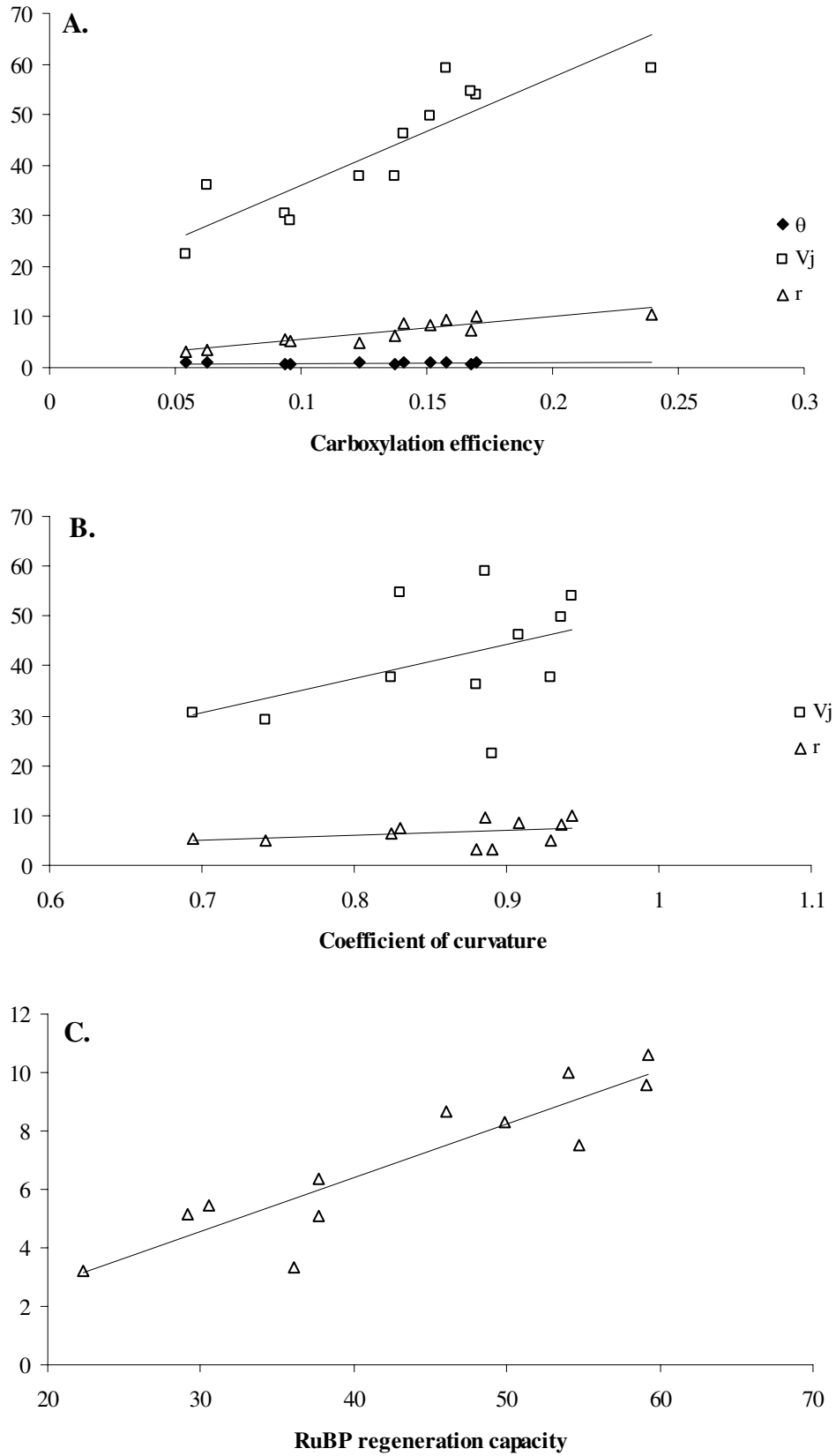


**Figure 5.8.** Inter-relationships among  $A/C_i$  parameters in May 2000 **A)** carboxylation efficiency and coefficient of curvature  $\theta_c$  ( $R^2 = 0.10$ ), RuBP regeneration capacity  $V_j$  ( $R^2 = 0.78$ ) and daytime respiration  $r_d$  ( $R^2 = 0.83$ ), **B)**  $\theta_c$  and  $V_j$  ( $R^2 = 0.21$ ) and  $r_d$  ( $R^2 = 0.12$ ) and **C)** RuBP regeneration and  $r_d$  ( $R^2 = 0.82$ ). (Data for block-planted, row and isolated trees have been pooled.)

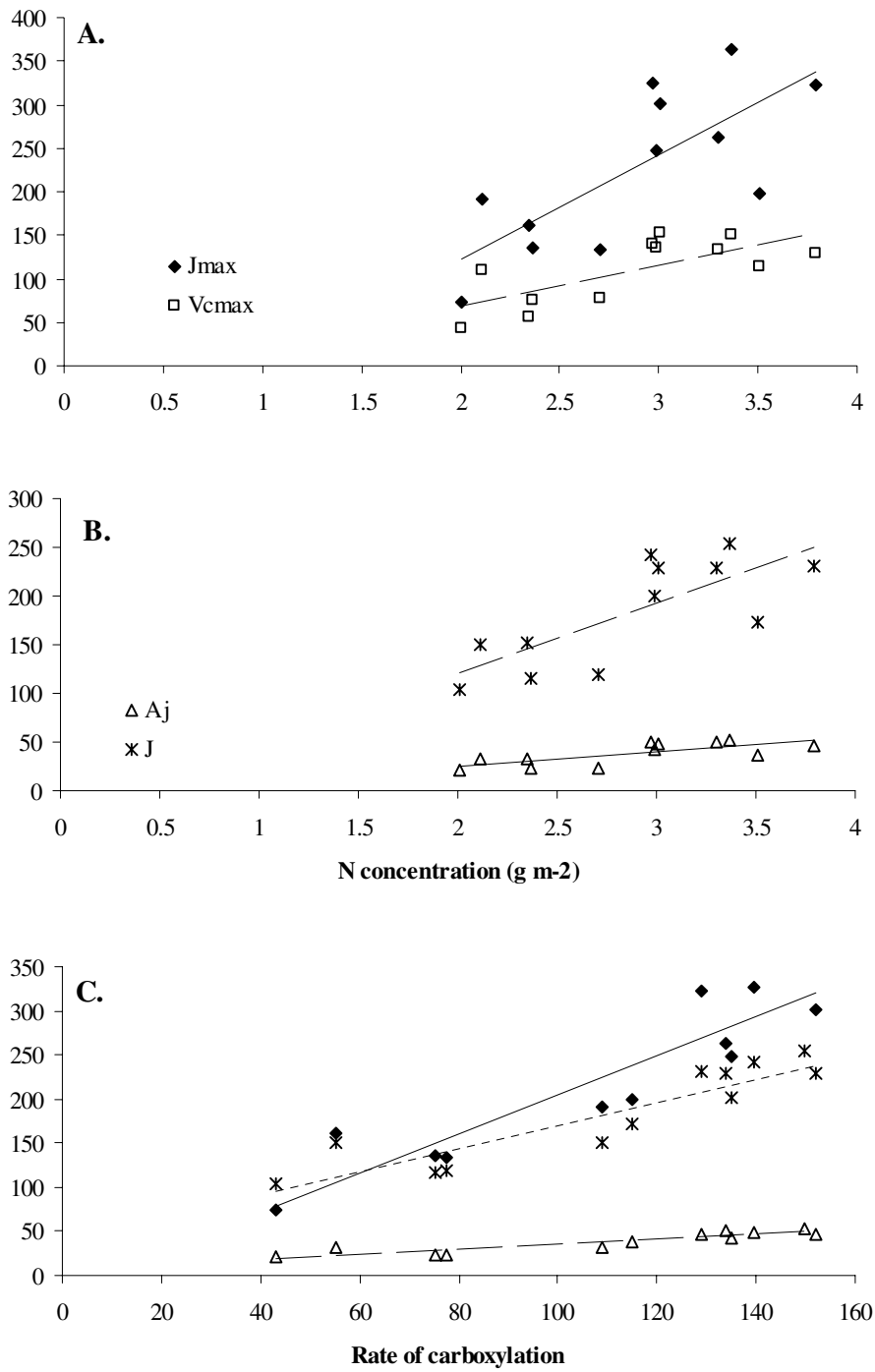


**Figure 5.9.** The N dependence ( $\text{g m}^{-2}$ ) of **A)**  $J_{\max}$  ( $R^2 = 0.50$ ) and  $V_{\max}$  ( $R^2 = 0.48$ ), **B)**  $A_j$  ( $R^2 = 0.50$ ) and  $J$  ( $R^2 = 0.51$ ) and **C)** the relationship between  $V_{\max}$  and  $A_j$  ( $R^2 = 0.82$ ),  $J$  ( $R^2 = 0.84$ ) and  $J_{\max}$  ( $R^2 = 0.84$ ) in May 2000.

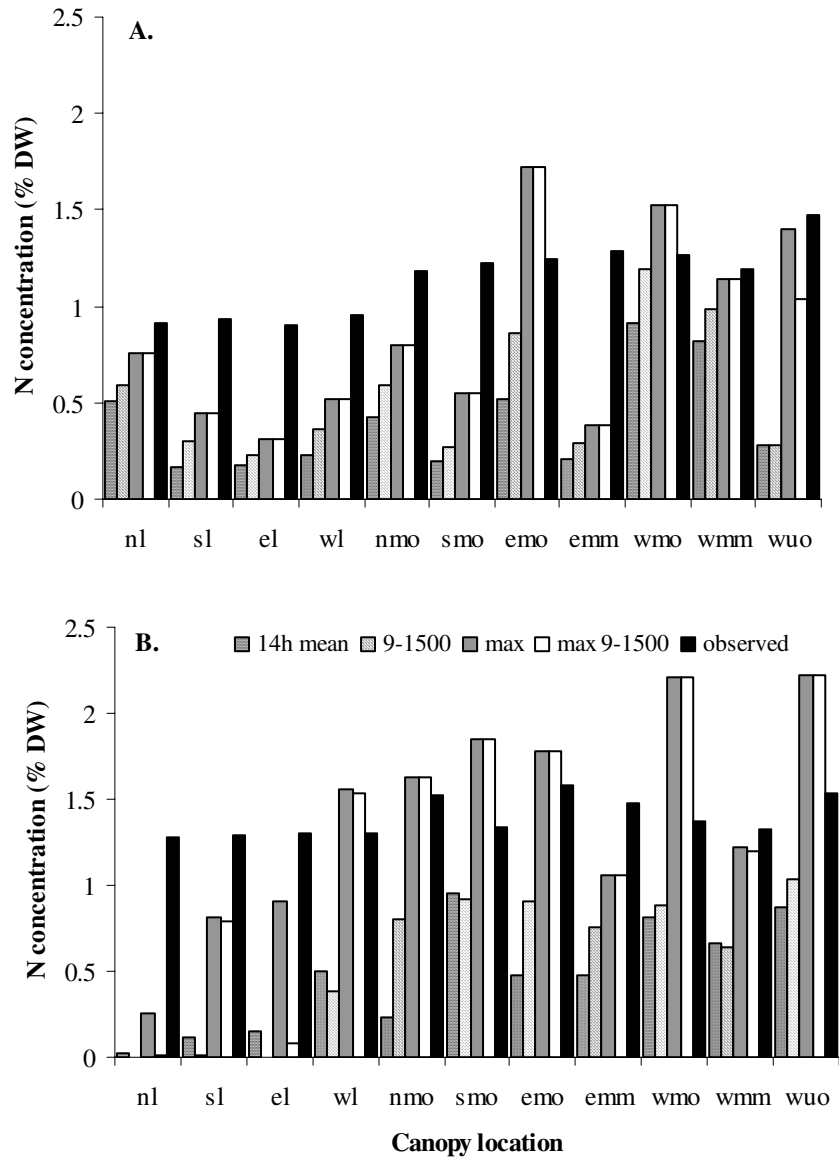


**Figure 5.10.** Leaf N concentrations (% DW) at various positions in the canopy as predicted from mean and maximal irradiance (14 h photoperiod, 9-1500 h WST) in comparison with observed concentrations in **A)** block planted and **B)** isolated trees during November 1999. North = n, south = s, east = e, west = w; lower = l, middle = m, upper = u, outer = o.

## 5.4 Discussion

### 5.4.1 Nitrogen distribution and the N-dependence of photosynthesis

#### 5.4.1.1 N distribution

Consistent with earlier studies in other trees (DeJong and Doyle 1985, Hollinger 1989, Vapaavouri and Vuorinen 1989, Leuning *et al.* 1991a,b, Ellsworth and Reich 1993, Hollinger 1996), the distribution of  $N_{\text{leaf}}$  in *E. globulus* canopies was neither random nor uniform. In addition, planting layout had a marked impact on the distribution of  $N_{\text{leaf}}$  through *E. globulus* canopies (Table 5.1, 5.2, Fig 5.1, 5.2). These impacts were evident across both the horizontal and vertical axes of the canopy. The N distribution coefficient,  $k_N$ , which describes the vertical pattern of  $N_{\text{leaf}}$  distribution with increasing  $L^*$ , was greatest and thus the vertical N gradient steepest in block-planted trees and least in isolated trees (Table 5.2). Agreeing with observations or predictions in earlier studies (Hirose and Werger 1987b, Chen *et al.* 1993), the  $N_{\text{leaf}}$  distribution in the open canopies of isolated trees was more uniform than in block-planted trees. Their  $k_N$ , however, varied less than expected (0.68 compared with 1.05) from the N data in figures 1 and 2. This is at least in part because  $k_N$  addresses only vertical gradients, which were complicated by a strong horizontal heterogeneity component (for example Fig. 5.1c, 5.2c). Consistent with the optimality hypothesis ( $\partial A/\partial N$ ) and previous findings for eucalypts (Leuning *et al.* 1991a), these gradients occur primarily because  $N_{\text{leaf}}$  was highest in exposed, high light environment canopy locations. Variations in  $N_{\text{leaf}}$  and  $A_{\text{max}}N_{\text{leaf}}$  distributions between spacing treatments reflect the impact of planting layout on light distribution within canopies (presented in chapter 3). This needs to be taken into consideration when examining the influence of spacing on N distribution and relationships between foliar N and photosynthesis. While previous studies in eucalypts have reported horizontal and vertical gradients in  $N_{\text{leaf}}$  (Leuning *et al.* 1991a,b), the influence of spacing on these gradients has not been investigated. Leuning *et al.* (1991a) for example, presented contour diagrams of  $N_{\text{leaf}}$  in 6- and 16- month-old plantation grown *E. grandis* showing clear gradients of increasing  $N_{\text{leaf}}$  from the inner to the outer canopy. In 16-month-old trees the highest N concentrations occurred only in the upper portions of the canopy (Leuning *et al.* 1991a). Similarly, in field-grown *E. globulus* seedlings and glasshouse grown *E. nitens*,  $N_{\text{leaf}}$  decreased down the canopy and increased with distance from the stem (N. Davidson pers. comm.). These studies were conducted on young trees prior to canopy closure. The growing conditions of these young trees are therefore closest to the isolated trees in the current study and appear to have  $N_{\text{leaf}}$  distributions similar to isolated trees. In isolated trees in the current study and in *E. grandis* (Leuning *et al.* 1991a) and glasshouse-grown *E. nitens* (N. Davidson pers. comm.) for example, the horizontal  $N_{\text{leaf}}$  gradient is stronger and more evident than the vertical. Harrison *et al.* (2000) did examine the impact of planting density on the N contents of *E. camaldulensis*, *E. pellita* and *E. urophylla* tissues, but only on a coarse scale in terms of the total leaf fraction. In all three species in their study the proportion of above-ground N allocated to leaves did not vary greatly between trees grown 4 x 3 m, 3 x 3 m and 1.5 x 3 m spacings (50-60% of above-ground tree N in all cases, Harrison 2000).

Foliar N distribution also varied with time of year so that the impact of spacing on  $N_{\text{leaf}}$  varied between months, and particularly in isolated trees,  $N_{\text{leaf}}$  gradients within canopies were not constant through out the year (Table 5.1). In isolated trees  $k_N$  and thus the strength of the vertical gradient in  $N_{\text{leaf}}$  declined from 0.89 in August 1999 to 0.45 in May 2000 (Table 5.2). This change in  $k_N$  may indicate the horizontal gradient in  $N_{\text{leaf}}$  was becoming more important as the branches lengthened and leaves in locations closer to the stem became more shaded. These results do indicate that canopy N distributions determined at a given period of time may not reflect or be used to extrapolate distributions at other times of the year and at later stages of growth.

#### 5.4.1.2 Nitrogen and irradiance

The optimality hypothesis and the big-leaf models that are based upon it, assume that  $N_{\text{leaf}}$  is distributed within canopies in proportion to the irradiance profile (Field 1983, Hirose and Werger 1987a, Hollinger 1989, 1996, Ellsworth and Reich 1993). A previous study in *E. grandis* however, reported that  $N_{\text{leaf}}$  distribution patterns do not correspond to those of irradiance (Leuning *et al.* 1991b). The authors concluded that optimal  $N_{\text{leaf}}$  depends on the average light levels during growth (Leuning *et*

al. 1991b). They did not actually measure irradiance and presented data for absorbed PAR generated using the model MAESTRA. The calculated distributions were hourly means for sunny days for one hour around solar noon. While pointing to an over-simplification in big-leaf models, these results are probably not unexpected. As Kull and Kruijt (1999) and Kull (2002), point out leaves do not completely acclimate to irradiance and the process of acclimation is relatively slow (taking a matter of weeks). An exact correspondence between irradiance, particularly spatially or temporally averaged data, and  $N_{\text{leaf}}$  is therefore unlikely. Acclimation to light involves a balance between the breakdown and regeneration of the photosynthetic apparatus. As such, factors other than irradiance, such as N, carbohydrate and water availability and temperature influence acclimation and thus localised  $N_{\text{leaf}}$ . The supply-demand model of photosynthetic acclimation to light (Kull and Kruijt 1999) predicted that in *Corylus avellana* and *Populus tremula* canopies  $N_{\text{leaf}}$  ( $\text{mmol m}^{-2}$ ) has a curvilinear relationship with average diurnal irradiance. Similarly, in the current study (Fig 5.3), both midday and daily relative incident irradiance ( $I_N/I_0$ ) have a curvilinear relationship to  $N_{\text{leaf}}$ . Averaged distributions of irradiance within canopies, however, may differ significantly from instantaneous profiles due to sunflecks, variations in leaf angles, self-shading and gaps in the canopy causing light pools (de Pury and Farquhar 1997, current study chapter 3). Consequently, a direct correspondence between irradiance whether instantaneous or averaged and  $N_{\text{leaf}}$  profiles is unlikely (see de Pury and Farquhar 1997). For example, in the current study, and contrary to Leuning *et al.* (1991b), the photosynthetic N requirement predicted from time averaged irradiance was much less than those predicted from instantaneous maxima (Fig. 5.1a,b). Concentrations predicted using these instantaneous maxima were generally closer to observed  $N_{\text{leaf}}$ , suggesting that  $N_{\text{leaf}}$  in these *E. globulus* leaves was more sensitive to or adapted more to periods of peak irradiance rather than mean light conditions. Hollinger (1996) demonstrated that factors such as wind and herbivory reduce assimilation in high-N foliage to a greater extent than low-N leaves. The results are that  $N_{\text{leaf}}$  and  $A$  in high irradiance locations within the canopy are lower than optimal or in the current study than expected from the  $A_{\text{max}}-N_{\text{leaf}}$  relationship. Just as the use of the  $\partial A/\partial N$  optimality criteria overestimates canopy  $A$  (Hollinger 1996), applying a single light response or  $A_{\text{max}}-N_{\text{leaf}}$  relationship over an entire canopy or using those derived from one planting lay-out to another will not provide an accurate estimate of canopy assimilation.

#### 5.4.1.3 Nitrogen and $A_{\text{max}}$

Strong  $A_{\text{max}}-N_{\text{leaf}}$  relationships have generally been reported in eucalypts (Mooney *et al.* 1978, Leuning *et al.* 1991b, Sheriff and Nambiar 1991, Pereira *et al.* 1992, Sefton *et al.* 2002). Little, however, has been previously published on changes to or factors that alter the  $A_{\text{max}}-N_{\text{leaf}}$  relationship in eucalypts. Reflecting within canopy gradients in both  $N_{\text{leaf}}$  and  $A_{\text{max}}$ , the  $A_{\text{max}}-N_{\text{leaf}}$  relationship was influenced by location within the canopy, spacing and time of year (Table 5.3). Foliar N however, was the strongest predictor of  $A_{\text{max}}$  (Table 5.4). The relationship between  $N_{\text{leaf}}$  and photosynthesis is crucial to scaling up calculations of  $\text{CO}_2$  assimilation from individual leaves to whole canopies (Leuning *et al.* 1995, DePury and Farquhar 1997, Kull and Kruijt 1999). It underpins a variety of C production/growth models, especially process-models (MAESTRA, big-leaf, sun-shade, multi-layer and supply-demand models). Consequently, factors that influence the  $A_{\text{max}}-N_{\text{leaf}}$  relationship, and the manner in which they influence the relationship, are important in modelling canopy production. The plasticity or complexity of the  $A_{\text{max}}-N_{\text{leaf}}$  relationship in *E. globulus* in the current study indicates that a single relationship may lose accuracy if applied across different planting arrangements, seasons, across entire canopies or even different foliage classes. Leaf maturity, for example, was significant in  $A_{\text{max}}-N_w$ . Distance from the stem or position, which roughly encapsulates leaf age classes (old leaves being closest to the stem, the youngest being apical) was significant in the  $A_{\text{max}}$  relationship with both  $N_a$  and  $N_w$  (Table 5.3, 5.4). Overall,  $N_w$  accounted for 49% of the variation in  $A_{\text{max}}$ , but within this, the relationship was strongest in block-planted trees while the  $A_{\text{max}}-N_{\text{leaf}}$  relationship was much weaker with  $R^2$  values of 34% and 39% for row and isolated trees, respectively. In contrast, the strength ( $R^2$ ) of the overall, row and isolated tree  $A_{\text{max}}-N_{\text{leaf}}$  relationship improved to around 60-70% when months were considered individually. Clearly for these trees, a single  $A_{\text{max}}-N_{\text{leaf}}$  relationship or equation obscures much important variation.

Embedded within a number of C modelling approaches is the idea that the amount of  $N_{\text{leaf}}$  involved in photosynthesis can be calculated and that some portion of  $N_{\text{leaf}}$  is not used in photosynthesis (Hirose *et al.* 1987b, Anten *et al.* 1995, De Pury and Farquhar 1997, Kull and Kruijt 1999). The  $N_{\text{leaf}}$  not involved in photosynthesis ( $N_b$ ) is generally assumed to be structural, small in comparison to the photosynthetic-N portion and is regarded as the minimal  $N_{\text{leaf}}$  concentration (Anten 1995, De Pury and Farquhar 1997). This fraction is calculated from the intercept of the  $A_{\text{max}}-N_{\text{leaf}}$  relationship and used to correct  $N_a$  from which  $k_N$  is calculated. In this context,  $N_a$  is therefore equated with the  $N_{\text{leaf}}$  associated with photosynthesis. While  $N_b$  satisfied these criteria in the current study, this approach may not adequately account for N storage in leaves. Pate and Arthur 2000, for example, demonstrated that N might be stored in the leaves of plantation grown *E. globulus* for subsequent use in other parts of the canopy, particularly younger foliage. The variability of the  $A_{\text{max}}-N_{\text{leaf}}$  relationship, especially with time of year, leaf maturity and spacing may in part reflect N storage in leaves. Warren *et al.* (2000), for example, attributed the poor relationship between  $A_{\text{max}}$  and total  $N_{\text{leaf}}$  ( $\text{mg g}^{-1}$ ), soluble protein and Rubisco contents (in admittedly a very limited sample) of *E. camaldulensis*, *E. decipens* and *E. torquata* leaves to N storage. That is concentrations were beyond the immediate requirements of photosynthesis. Given the range of leaf classes analysed in the current study, N distributions in *E. globulus* may indeed reflect factors such as storage and translocation in addition to C assimilation.

Nitrogen storage in leaves may partially explain the disparity between predicted and observed  $N_{\text{leaf}}$  in leaves from the lower canopy and less exposed regions of the mid-canopy of block-planted trees and leaves from the north, south and eastern aspects of the lower canopy of isolated trees (Fig. 5.10a,b). The observed  $N_{\text{leaf}}$  in these locations substantially exceeded the N required for photosynthesis predicted by average and instantaneous daily maximum irradiance (Fig. 5.10a,b). Consequently, in these leaves, some factor other than  $N_{\text{leaf}}$  appears to determine C assimilation. Contrary to Warren *et al.* (2000b), however, the presence of  $N_{\text{leaf}}$  in excess of photosynthetic requirements did not preclude a significant  $A_{\text{max}}-N_{\text{leaf}}$  relationship. Foliar N concentrations in excess of photosynthetic requirements occurred most commonly in block-planted trees, especially in the old, juvenile lower canopy leaves. While still photosynthetically active (see chapter 3) in November many of these leaves were lost in canopy lift by May. These were thickened (high specific leaf area) and were starting to senesce. The  $A_{\text{max}}-N_{\text{leaf}}$  relationship was, however, uniformly strong with an  $R^2$  of around 0.80 in block-planted trees during both November 1999 and May 2000. These results, with those of Warren *et al.* (2000a,b) and Pate and Arthur (2000), suggest that the assumption underlying the physiological validity of the application of the  $A_{\text{max}}-N_{\text{leaf}}$  relationship: that  $N_{\text{leaf}}$  is primarily involved in photosynthesis and that  $A_{\text{max}}$  is essentially N limited does not always hold in eucalypts. Does this indicate robustness of the relationship or that in eucalypts, under some circumstances the  $A_{\text{max}}-N_{\text{leaf}}$  relationship (when present, Pinkard *et al.* 1998 for example, found no relationship between  $A$  and  $N_{\text{leaf}}$  in *E. nitens* ramets and young trees) represents more of a happy co-incidence rather than being physiologically deterministic, modified by, but also masking other processes?

Leaves from high light environments in the mid- and upper-canopies of block-planted and isolated trees contained lower  $N_{\text{leaf}}$  than predicted by maximal irradiance but more than predicted by average irradiance. Thus in foliage in highly exposed canopy locations some factor other than mean or maximum irradiance appears to determine  $N_{\text{leaf}}$ . Consequently, the distribution of  $N_{\text{leaf}}$  and that of  $A_{\text{max}}-N_{\text{leaf}}$  appear to be the result of a number of interacting processes of which C assimilation is only one. This is consistent with the supply and demand (turn-over) model of Kull (2002) in which common pools of N and carbohydrate modify N distribution. This also implies that the  $A_{\text{max}}-N_{\text{leaf}}$  relationship is better viewed as a whole canopy phenomenon, which at least in eucalypts, may be more or less applicable on a single leaf scale. The relationship may not hold for every leaf in the canopy due to the influence of other N-requiring processes. Data from eucalypts do not support the optimality concept of the dominant role of N in photosynthesis being the basis of the  $A_{\text{max}}-N_{\text{leaf}}$  relationship. They are, however, consistent with the contention that this relationship occurs because a given amount of N in a leaf has a corresponding C or photosynthetic cost (Kull 2002).

#### 5.4.1.4. Nitrogen dependence of biochemical model parameters

The questions raised in the above discussion of the N limitation of  $A_{\max}$  and the underlying validity of the  $A_{\max}$ - $N_{\text{leaf}}$  relationship, have implications not simply for scaling up from leaves to canopies but also for the application of the Farquhar biochemical model of photosynthesis that underpins most C assimilation/growth models. This requires an examination of the N dependence of key light and  $\text{CO}_2$  response parameters and underlying parameters of electron transport and carboxylation regeneration derived from them and the valid use of the biochemical model.

Examining the relationship of the parameters of the light response curve to  $N_{\text{leaf}}$ , the response of *E. globulus* leaves to irradiance in the current study was clearly mediated by  $N_{\text{leaf}}$ . Quantum efficiency (the initial slope of the curve,  $\alpha$ ) was independent of  $N_{\text{leaf}}$  (Fig 5.5c.). The shape or coefficient of curvature ( $\theta$ ) of the light response showed only a very weak dependence on  $N_{\text{leaf}}$  (Fig. 5.5c,d). In contrast, both  $a_x$  and leaf dark respiration ( $r_1$ ) were dependent on  $N_{\text{leaf}}$  (Fig. 5.5a,b). The poor  $N_{\text{leaf}}$ - $\theta$  relationship is a consequence of the high degree of correlation between  $a_x$  and  $\theta$  in the nonrectangular hyperbolic light response model used. The N dependency of  $a_x$ ,  $r_1$  and  $\theta$  of juvenile leaves was different from that of mature leaves (Fig. 5.7 a,b,d; overall  $P = 0.03$ ,  $P = 0.03$ ,  $P = 0.02$ , respectively). Since  $N_{\text{leaf}}$  did not change significantly between mature and juvenile leaves, the different equations of each foliage type presented in Figure 6 reflect physiological differences between mature and juvenile foliage. In addition, there was some evidence that carboxylation efficiency, daytime respiration and to a lesser extent, the capacity for RuBP regeneration differ between mature and juvenile leaves ( $P = 0.02$ ,  $P = 0.01$  and  $P = 0.07$ , respectively). This, however, is based on a dataset in which juvenile leaves dominated at only three canopy locations and further investigation is required to confirm these results. In these leaves, differences in leaf maturity were associated with differing  $N_{\text{leaf}}$ . Both  $V_{\text{cmax}}$  and  $J_{\text{max}}$ , however, did not vary with leaf maturity (Figure 5.9). While the current study included juvenile leaves, they are generally excluded from physiological investigations and thus most models of canopy processes. In wide spaced planting designs (isolated and row-plantings in the current study), which encourage the retention of juvenile foliage, these leaves can form a significant proportion of canopy leaf area and make a substantial contribution to the canopy C balance. Ignoring the presence of juvenile leaves in such situations may consequently reduce the accuracy of canopy production estimates. The array model MAESTRA currently has the ability to include data from different leaf classes. The current study, however, would require two separate layers of leaf classification. Firstly leaf age or position such as apical, expanding and old which could then be assigned some ratio of juvenile to mature leaves at each sampling location within the canopy. Other models could be easily modified to include the distribution of juvenile leaves. This would however increase the complexity of the input data.

Consistent with the Farquhar biochemical model,  $V_{\text{cmax}}$ ,  $J_{\text{max}}$ ,  $A_J$  and  $J$  were strongly related to  $N_{\text{leaf}}$ . This confirms the validity of the  $A_{\max}$ - $N_{\text{leaf}}$  relationship despite the apparent presence of storage N because it demonstrates that the underlying physiological processes of C assimilation in the *E. globulus* canopies were N dependent. The possible presence of storage N as suggested by Figure 5.11, however, does indicate that techniques that infer  $N_{\text{leaf}}$ , Rubisco and other enzyme content from photosynthetic parameters are unlikely to be reliably quantitative (see Warren *et al.* 2000a,b). Foliar N can be used to model canopy  $A_{\max}$  and photosynthetic parameters but not the reverse.

The current study favours models such as MAESTRA, PROMOD, turnover, and multi-layer/sun-shade approaches provided the  $A_{\max}$ - $N_{\text{leaf}}$  relationship is not used to infer foliar N parameters. The assumption of optimality within a number of these models, while convenient is intellectually unhelpful. However, big-leaf models are too simplistic to account for the additional within and between canopy complexity in light,  $N_{\text{leaf}}$  and  $A_{\max}$  caused by spacing. Spacing substantially alters the distribution of  $N_{\text{leaf}}$  through canopies and  $A_{\max}$ - $N_{\text{leaf}}$  but not the underlying biochemical parameters of photosynthesis. These effects are in turn responsive to the time of year and location in the crown. Modelling canopy C requires a substantial amount of data. This data requirement is intensified if spacing is variable and even more so if the model predictions are to be projected over a number of seasons or years.

Big-leaf models are based on the concept that  $N_{\text{leaf}}$  is distributed within canopies to optimise canopy  $\text{CO}_2$  assimilation and use the Farquhar *et al.* (1980) biochemical model of leaf photosynthesis (Field 1983, Sellers *et al.* 1992, Amthor 1994, Lloyd *et al.* 1995, Sands 1995). These models generally treat the canopy as a single unit and distinguish between sunlit and shaded leaves. Sands (1995), presents a proof of Field's (1983) optimality hypothesis, which is demonstrated using a simple big-leaf model. While it improves on most big-leaf models by dividing the canopy into layers, Sands (1995) explicitly states their common underlying assumptions, limitations and structure. Central tenets are: that  $A$  depends on  $N_{\text{leaf}}$ , that  $N$  declines with depth within the canopy, and that consequently, variations in  $N_{\text{leaf}}$  concentration with position within the canopy give rise to variations in the single leaf photosynthetic rate, primarily through a direct effect on  $A_{\text{max}}$ , and that  $A$  is a function of irradiance ( $I$ ). Total canopy photosynthesis ( $A_c$ ) over a period of time is thus a function of total canopy  $N$  content ( $N_c$ ), assuming canopy structure or dimensions do not change over the time interval. Hence  $N_c$  is fixed over time and  $A_c$  will be maximal for  $N_c$  provided that the ratio of  $dA:dN$  is constant. The photosynthetic rate  $A$  depends on location in the canopy both directly through  $I$  and through the dependence of  $A_{\text{max}}$  on  $N$ . Consequently the optimal  $N$  distribution in a canopy is related to the decline in intercepted radiation within the canopy. The (optimal) distribution of  $N$  in a canopy (with fixed  $N_c$ ) thus requires  $N_{\text{leaf}}$  at any point in the canopy to be proportional to the decline in irradiance or relative light intensity at that point. Light is assumed to decline with accumulated leaf area index ( $L^*$ ) through the canopy according to the Beer-Lambert law:  $I(L^*) = I_0 e^{-kL^*}$ , where  $I_0$  is irradiance at the top of the canopy and  $k$  is the light extinction coefficient. Consequently,  $N_{\text{leaf}}$  is also expressed as a function of accumulated  $L^*$ . The theoretical optimum  $N$  distribution therefore occurs when the  $N$  distribution coefficient ( $k_N$ , which describes the decline in  $N$  through the canopy in a manner analogous to  $k$ ) equals  $k$  while a uniform distribution occurs when  $A$  equals zero.

Instantaneous irradiance profiles do not, however, obey the Beer-Lambert law (de Pury and Farquhar 1997) and in *E. globulus*, neither do profiles averaged over hourly or daily time periods (Henskens *et al.* 2002). In studies on eucalypts, other workers have found that the distribution of  $N_{\text{leaf}}$  concentration through the canopy is not correlated with relative light intensity (Leuning *et al.* 1991a, Close *et al.* 2002). Still others report variable degrees of correlation between  $N_{\text{leaf}}$  and  $A_{\text{max}}$  including no relationship at all (Pinkard *et al.* 1998, Warren *et al.* 2000b, Close *et al.* 2002, Henskens *et al.* 2002). As indicated by Sands (1995), the assumptions of big-leaf models do not hold for young or widely spaced canopies.

## 6. Modelling Light Interception in Wide-spaced Stands

### 6.1 Introduction

One of the principal determinants of the rate at which photosynthesis proceeds is the irradiance of foliage. In many models of plant production the representation of this process is a central, and often the most complex element. Where these models are complex it is because they employ numerical integrations or summations over time, position in canopy or leaf classes (e.g. Idso and de Wit 1970, Norman and Welles 1988; Wang and Jarvis 1990a, Leuning *et al.* 1991, Cescatti 1997). Consequently, they require detailed information on the arrangement of plant foliage, its optical properties and require detailed environmental inputs. These models do not readily lend themselves as decision support tools for forest growers.

Relaxing spatial and temporal resolution simplifies calculations. For example it has been observed that annual production of crops at a particular location is linearly related to intercepted solar radiation (Monteith 1977, Linder 1985, Beadle and Turnbull 1992). This was indicated in Chapter 2 for production by the wide-spaced trees at the Kamman study site (see Figure 2.6). When combined with assumptions about the spatial distribution and optical property of foliage elements this leads to models of light interception of acceptable realism in most cases (see for example big-leaf model of Sands 1995, and two-leaf model of Wang *et al.* 1998a and Thornley 2002).

A key component of these big-leaf or two-leaf models is the assumption of horizontal heterogeneity of foliage elements. Verification and validation of these models suggests that such assumptions are reasonable at the canopy-scale (see for example Sands 1995, Leuning *et al.* 1998). However, there application for discontinuous canopies is less successful (see Figure 1.1). The non-linear nature of physiological responses to light suggests that mean irradiance under canopies may not be a reliable variable to assess production (Baldocchi and Hutchinson 1986, Myeni *et al.* 1989). Models for discontinuous canopies have been developed but they have tended to be limited to canopies which can be defined in simple geometrical terms or to require a great deal of detailed information on canopy structure (e.g. Charles-Edwards and Thorpe 1976, Oikawa 1977, Meloni and Sinoquet 1997). Jackson and Palmer (1979) outlined a simple theory of light transmission and interception by discontinuous canopies. In this approach total light transmission to the ground ( $T$ ) was described by:

$$T = T_f + (1 - T_f)e^{-kL'}, \quad (6.1)$$

where  $T_f$  is the light which has passed between trees,  $k$  is the light extinction coefficient and  $L'$  is the effective leaf area per ground area occupied by trees given by:

$$L' = \frac{L}{(1 - T_f)}, \quad (6.2)$$

where  $L$  is leaf area index.

Jackson and Palmer (1979, 1981) were able to show that this approach was reasonable for estimating light interception of hedgerows. It is not clear how well such a model would work for isolated trees, though in principal application would be the same.

Key to the application of this approach for both hedgerows and for isolated trees is calculation of the light that has passed between trees ( $T_f$ ). Because it is so dependent on solar altitude and azimuth the

direct beam component of  $T_f$  is greatly influence by latitude, the time of year, time of day and row orientation.

In this chapter we develop a flexible model structure to estimate  $T_f$  across the range of planting designs likely to be encountered in forestry activities. We then apply this to the model structure of Jackson and Palmer (1979) and validate the predictions against field data and compare the results to predictions from models that are simpler (the application of the big-leaf model) and more complex (the array model MAESTRA).

## 6.2 Model Development

For the purpose of simulation stands are composed of identical trees with the exception that edge trees may have more extensive branches and coarse roots (Fig. 6.1). Each tree has an ellipsoidal crown. Branches extend until they meet an adjacent tree (trees are presumed to be totally crown shy). It is assumed that leaf area is distributed uniformly throughout canopy volume. Leaf area index ( $L^*$ ,  $\text{m}^2$  leaf  $\text{m}^{-2}$  ground), leaf-area density ( $\rho_F$ ,  $\text{m}^2$  leaf  $\text{m}^3$  crown volume) the projected shadow area of trees, the sun's position in the sky and the orientation of tree rows all influence light interception.

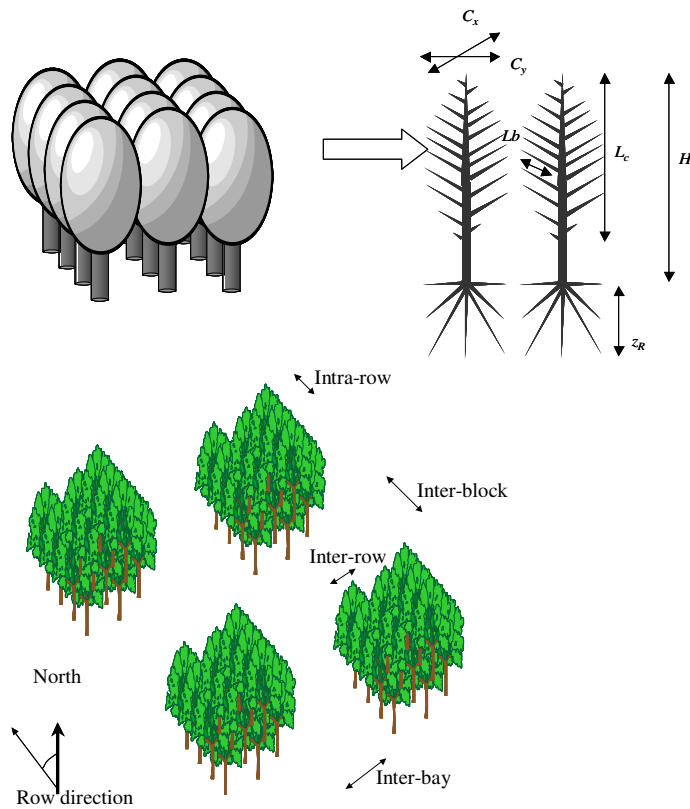


**Figure 6.1.** Representation of tree and stand geometry. Trees have a crown length ( $L_c$ ), height ( $H$ ), root depth ( $z_R$ ) and a crown and root extent in two planes ( $C_x$  and  $C_y$ ). Consequently, branches emerging at a fixed branching angle from the stem have a maximum length of  $L_b$ . Trees spacing is defined by spacing within blocks and spacing between blocks and the orientation of blocks.

In summary radiation interception initially is calculated as that by an array of non-interacting ellipsoids. When trees merge within rows radiation interception is calculated as that for non-interacting hedgerows. Finally when trees merge between rows radiation interception is calculated using the big-leaf model and the Beer-Lambert law. (Fig. 6.2) Calculation of radiation interception by non-interacting ellipsoids and non-interacting hedgerows uses the following procedure.

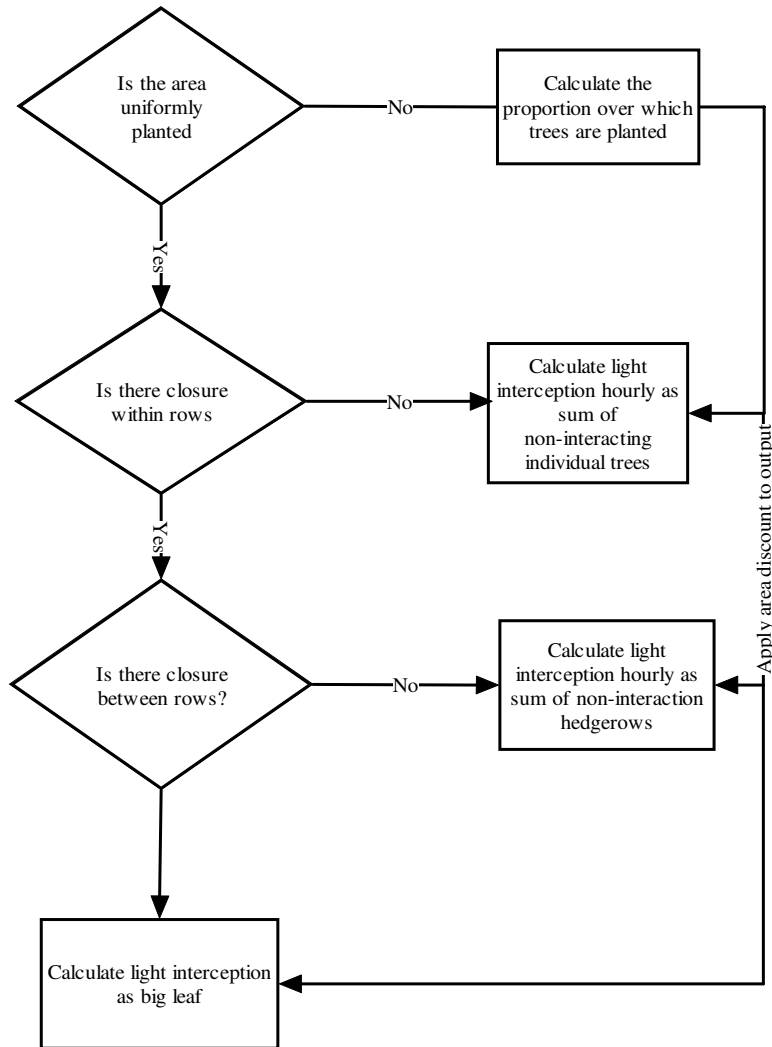


**Figure 6.2.** General approach to calculation of light interception showing the conditions under which different procedures for predicting total stand light interception are employed.

### 6.2.1 Stand geometry and structure

A rectangular co-ordinate system  $Oxyz$  is set up such that the  $z$ -axis is vertical. In the case of the ellipsoid of revolution, the  $x$  (inter-row)- and  $y$  (intra-row)-axes can be oriented arbitrarily because of symmetry. In the case of the hedgerow the  $x$ -axis is normal to the hedgerow, and the  $y$ -axis is along the hedgerow.

The dimensions of the ellipsoidal canopy are specified by its horizontal diameter  $C_y$  and its height  $L_c$  (in the  $z$ -direction). Thus, its horizontal semi-axes are equal and of length  $C_x/2$ , and its vertical semi-axis is of length  $L_c/2$ . The radiation intercepted by the entire ellipsoid is calculated.

The dimensions of the hedgerow are specified by its width  $C_x$  (in the  $x$ -direction) and its height  $L_c$  (in the  $z$ -direction). Thus, its cross-section is an ellipse with horizontal semi-axis of length  $C_x/2$  and vertical semi-axis of length  $L_c/2$ . It is assumed that the hedgerow is of infinite length, but the radiation intercepted by a length ( $l$ , in the  $y$ -direction) of the hedgerow is calculated.

### 6.2.2 Leaf characteristics

The canopy is further characterised by the leaf area density  $\rho_F$  ( $\text{m}^2 \text{m}^{-3}$ ), i.e. the single-sided leaf area per unit volume in the canopy, which is assumed to be constant in the canopy. Leaf area density and canopy leaf area index are related as follows. If a single leaf has area  $\Delta S$  and its normal is inclined at an angle  $\gamma$  to the vertical, its contribution to canopy leaf area index  $L$  is  $\Delta L = \cos(\gamma) \Delta S$ . Assuming constant  $\rho_F$ , it follows that:

$$L = \frac{c_\gamma \rho_F V_C}{S} \quad (6.3)$$

where  $c_\gamma$  is the average of  $\cos(\gamma)$  over all leaves in the canopy,  $V_C$  ( $\text{m}^3$ ) is canopy volume and  $S$  ( $\text{m}^2$  ground) is the projected ground area of the canopy.

### 6.2.3 Calculation of light interception

As a beam of light traverses the canopy some of its energy is absorbed. If  $I$  is the incident intensity ( $\mu\text{mol PAR m}^{-2} \text{s}^{-1}$ ), the intensity after the beam has traversed a distance  $s$  (m) within the canopy is,

$$I_{(s)} = e^{-l(s)} I \quad (6.4)$$

where  $l(s)$  is the accumulated leaf area normal to the beam along the distance  $s$ . If leaf area density  $\rho_F$  is constant and  $\gamma$  is the angle between the normal to a leaf and the beam direction, then  $l(s) = k \rho_F s$  where the extinction coefficient  $k$  is the average of  $\cos(\gamma)$  along the beam. The radiant energy intercepted by the canopy is then

$$E = I \iint (1 - e^{-k \rho_F s}) dx dy \quad (6.5)$$

where the integral is over all beams that pass through the shadow area of the canopy. For use in calculation the fraction of radiation intercepted,  $F_Q$  is:

$$F_Q = \frac{A_P S_E E}{10000 I}, \quad (6.6)$$

where  $S_E$  is the number of elements (individual crowns or hedgerows) per hectare planted (that is the extent to which trees occupy planted blocks) and  $S_P$  is the fraction of each hectare planted (that is the area that is not between planted blocks of trees).

### 6.2.4 Stand growth

The general approach used to implement the light interception model developed above within a stand growth model is documented elsewhere (Battaglia *et al.* in press). The model developed for this work, AGGRO, is a simplified version of the silvicultural decision support CABALA documented by Battaglia *et al.* (in press). The internal logic of the model is identical. AGGRO, however works with a simpler soil-plant systems: the model does not predict soil nitrogen mineralisation and the AGGRO implementation does not allow the user to specify site conditions to the same extent as can be done in CABALA. In addition the range of predicted model outputs is reduced, the model only runs using average weather inputs and only<sup>2</sup> produces outputs on an annual basis.

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<sup>2</sup> AGGRO is designed to give indicative results for farm forestry applications. Users looking at complex silvicultural decision-making will need to be aware of the model limits and perhaps seek access to CABALA through CSIRO Forestry and Forest Products and the Cooperative Research Centre for Sustainable Production Forestry.

## 6.3 Parameterisation and Application of MAESTRA

The array model MAESTRA (Wang and Jarvis 1990, Medlyn 1997) represents a reasonable benchmark against which to compare the performance of simpler or alternative models. This model calculates hourly averages of radiation distribution in an array of trees with given spacing, tree size and crown dimensions. Transfer of beam and diffuse radiation through the canopy is calculated separately for three wavebands, visible (PAR), near-infrared (NIR) and thermal, in the manner of Norman and Welles (1983). MAESTRA allows structurally complex canopies to be described in three dimensions. Radiation fluxes within are well simulated by this model (Grace *et al.* 1987, Wang and Jarvis 1990a, Wang and Jarvis 1990b). Parameterisation of MAESTRA was carried out using data from earlier chapters. To predict radiation absorption by MAESTRA the location, crown dimension, crown length, height, leaf area of each tree is specified along with stand average distribution of specific leaf area and leaf area density throughout tree crowns (Medlyn 1997).

## 6.4 Model Verification

Chapters 2 and 3 document collection of light and canopy data in November 2000 and August 2001 from isolated, single row and block-planted trees at the Kamman experimental site. These data are used in the initial model verification. Two levels of verification were carried out. In the first instance, just the radiation interception model was tested, with the stand average tree dimensions and leaf area density from the MAESTRA implementation used in the prediction. In the second level of verification, the AGGRO model was run from a planted array of seedlings to generate these tree attributes. Further verification of the model using published *E. nitens* data was carried out.

The simple model we have developed predicts similar levels of light interception to MAESTRA across all treatments in both late spring and winter, both on a unit ground area basis and a per tree basis (Fig. 6.3, 6.4). These predictions are both accurate and unbiased. These data suggest that both the interception by individual elements (Fig. 6.4) and the light that falls between elements is well predicted. When AGGRO is run for the Kamman site and initialised with seedlings predictions of light interception are similar at the stand level but poorer on a tree basis (Fig 6.5). The tree level error results from inaccuracies in predicting individual canopy extent and tree leaf area, and is most marked for the isolated trees (10 x 10 m spacing) where intercepted radiation per tree is underestimated by around 40% (Fig. 6.6).

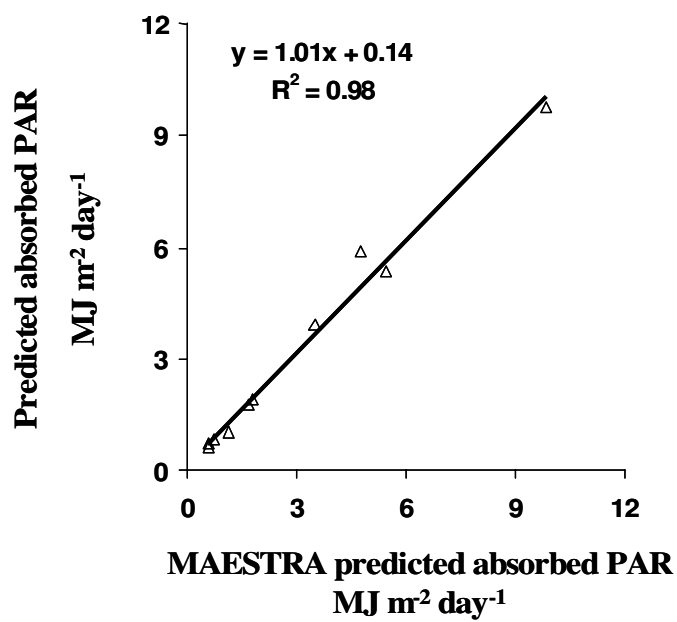


**Figure 6.3.** Comparison of predictions of absorbed PAR per unit ground area made with MAESTRA and the model developed in this work using observed stand attributes as the basis of predictions.

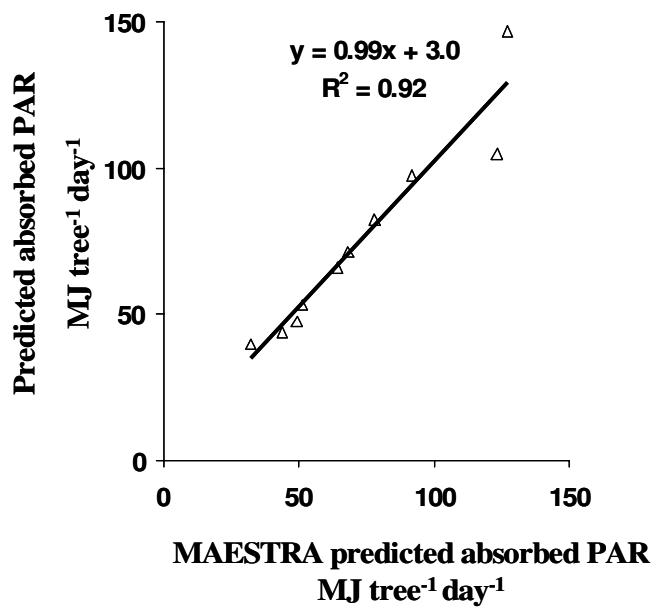


**Figure 6.4.** Comparison of predictions of absorbed PAR per tree per day made with MAESTRA and the model developed in this work using observed stand attributes as the basis of predictions.

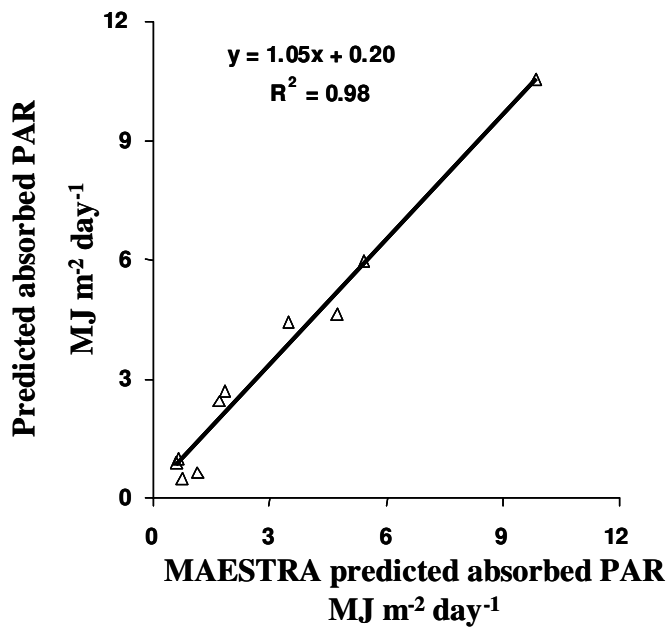


**Figure 6.5.** Comparison of predictions of absorbed PAR per unit ground area made with MAESTRA and the model developed in this work using stand attributes predicted by AGGRO as the basis of predictions.

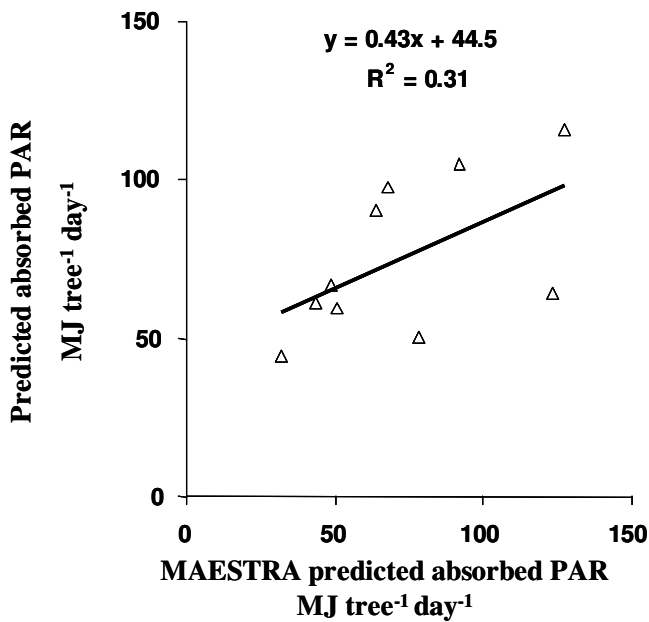


**Figure 6.6.** Comparison of predictions of absorbed PAR per tree per day made with MAESTRA and the model developed in this work using stand attributes predicted by AGGRO as the basis of predictions.

The application of this radiation interception into AGGRO provides good stand level estimates of standing biomass, stem volume increment and individual tree canopy extent for trees at the Kamman experimental site (Fig. 6.7, 6.8, 6.9).

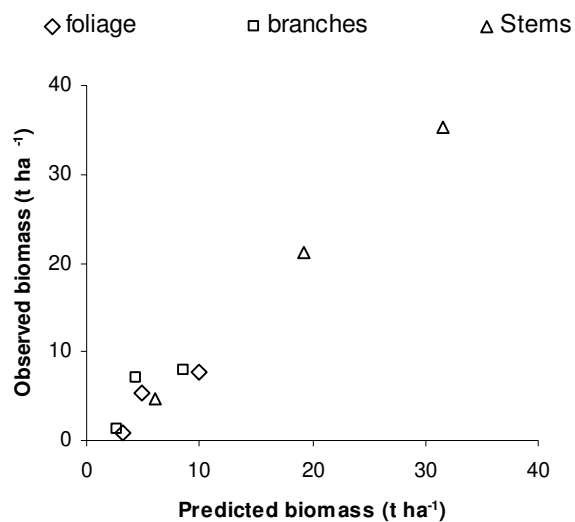


**Figure 6.7.** Predicted and observed above-ground biomass components from the 10 x 10 m spacing, 2 x 10 m spacing and 2 x 4 m spacing treatments at the Kamman experimental site.

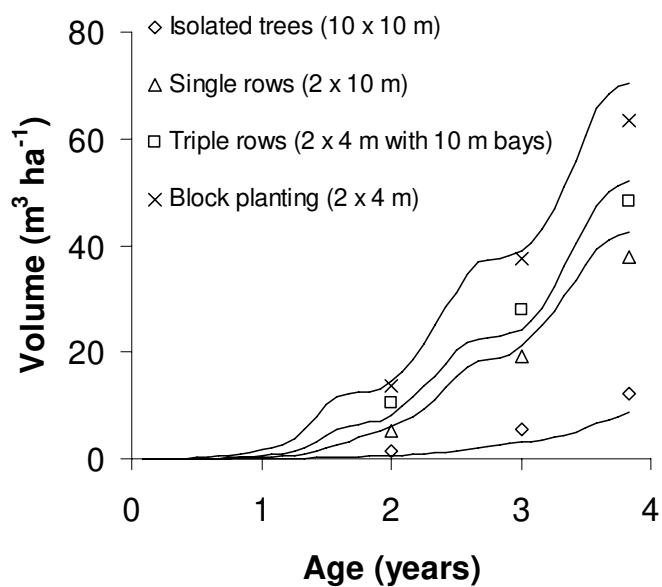


**Figure 6.8.** Predicted and observed volume increment from different spacing treatments at the Kamman experimental site.

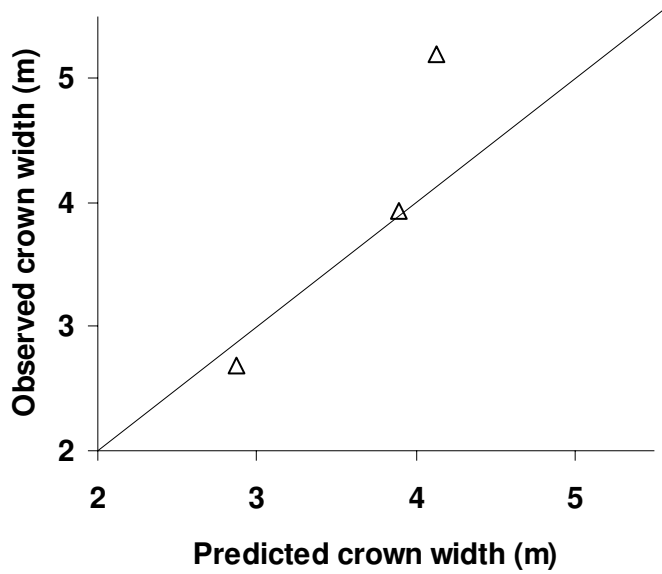


**Figure 6.9.** Observed and predicted average tree crown width at age 3.8 years at the Kamman experimental site.

Application of the model to *E. nitens* stands at planting densities from 500 to 1800 stems per hectare (Neilson and Gerrand 1999) and across a range of nutrition, rainfall and temperature conditions (after Pinkard and Battaglia 2001) also shows predictions sufficiently accurate for scheduling silvicultural operations such as pruning (Figs. 6.10 & 6.11).

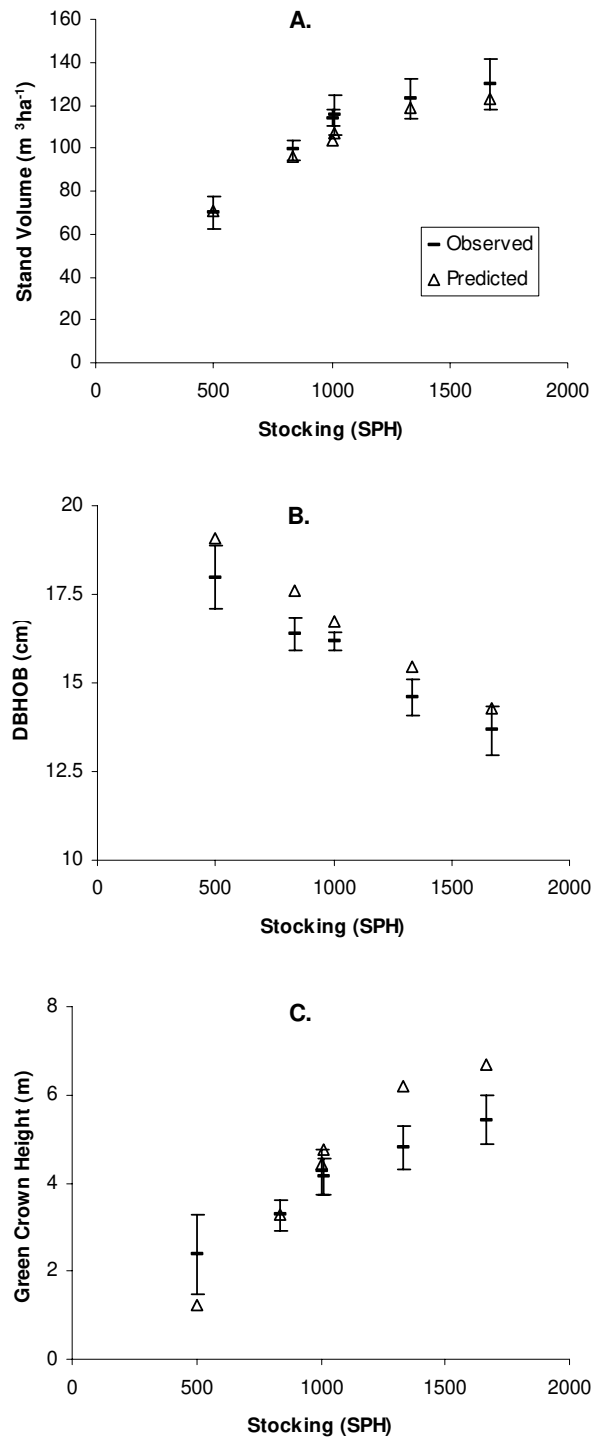


**Figure 6.10.** Observed and predicted **A)** volume, **B)** diameter at breast height (1.3 m) and **C)** green crown height of *E. nitens* planted at varying spacing at Castra, Tasmania (after Neilson and Gerrand 1999).

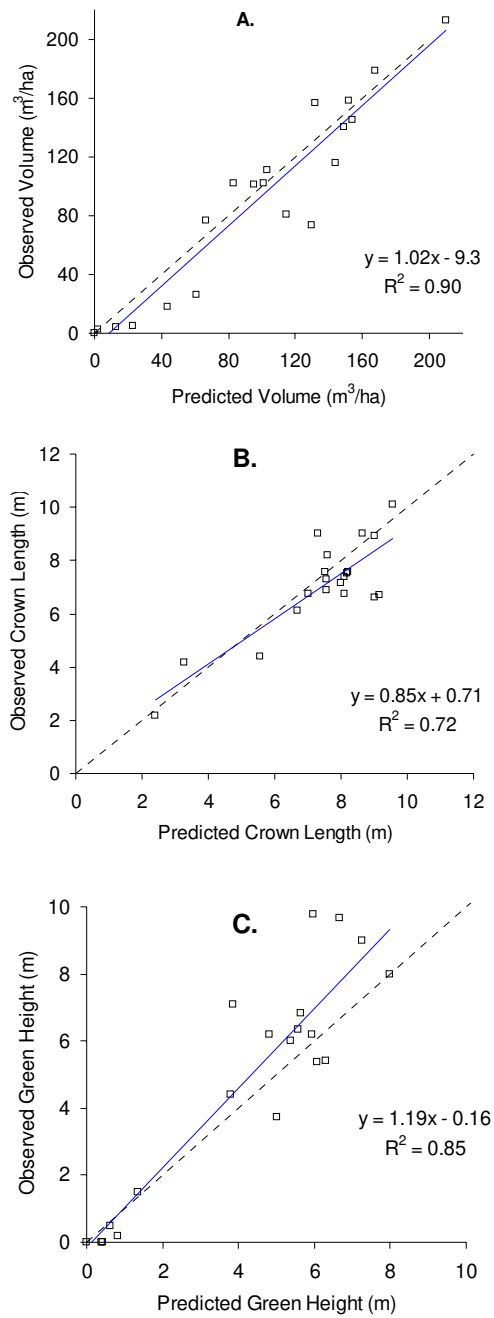


**Figure 6.11.** Prediction of stand structural attributes for a range of *E. nitens* stands in Tasmania: **A)** volume, **B)** crown length and **C)** green crown height (after Pinkard and Battaglia 2001).

# 7. Application of AGGRO in Farm Forestry

## 7.1 Introduction

AGGRO, introduced in Chapter 6, is a simple, easy-to-use forest growth model that has been designed for farm forestry applications. The model takes simple site descriptors and information on spacing, tree layout, irrigation, fertilisation and thinning of plantations and provides stand growth data. In this chapter we will take a look at the inputs and outputs provided by the manager and through a few structured examples demonstrate ways in which the model may be used to manage trees on farms. Although an algorithmic complex model (*sensu* Battaglia and Sands 1998), AGGRO needs only relatively easily obtained inputs and has an easy to use, intuitive interface making it a simple model requiring relatively little introductory training. The model is implemented as VBA code to run behind the familiar Microsoft EXCEL spreadsheet program.

## 7.2 Model Inputs

AGGRO requires three types of input variables from the user. The first set relate to the intrinsic site soil characteristics (Table 7.1). These variables describe the location, fertility, soil water-holding capacity and propensity of waterlogging of the site. The second set of site variables relate to the long term average climate of the site and describe the radiation, temperature and rainfall regime present at the site (Table 7.2). The last set relate to the silvicultural treatments imposed on the stand: the spacing and layout of trees at planting, the time and intensity of any thinning operation carried out, the timing and quantity of nitrogen fertilisation applied and the frequency and amount of irrigation water applied (Table 7.3). A visual representation of the components of spacing and layout are provided in Fig. 7.1.

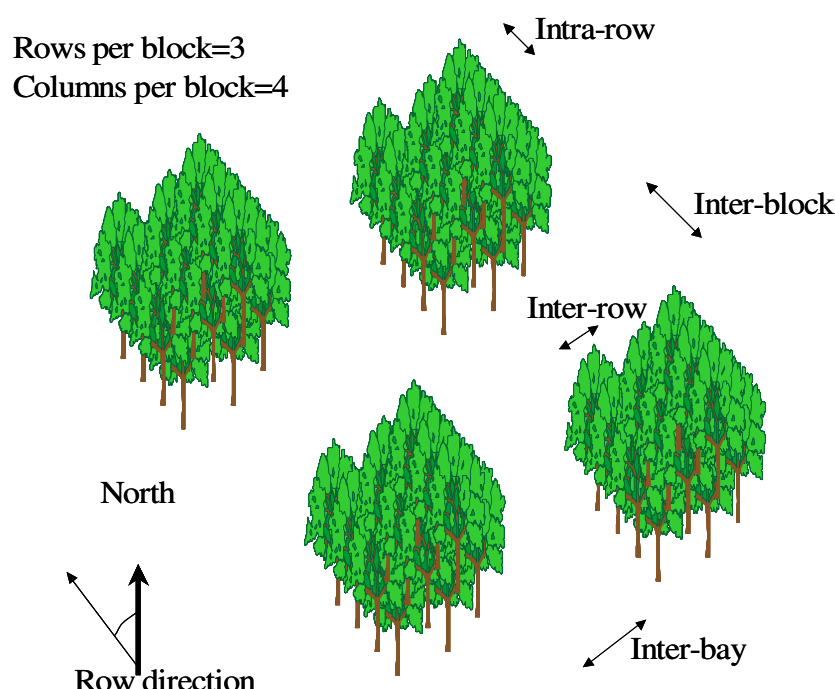


**Figure 7.1.** The components of spacing and layout that can be accommodated by AGGRO. Trees can be arranged in regular arrays of rectangular units.

**Table 7.1.** Site variables used as inputs into AGGRO. Optional variables take a default value of zero.

| Term                                      | Units        | Range               | Explanation                                                                                                                                                         | Status    |
|-------------------------------------------|--------------|---------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------|-----------|
| <b><u>Site description</u></b>            |              |                     |                                                                                                                                                                     |           |
| Site name                                 |              | up to 20 characters | A name for your site                                                                                                                                                | Optional  |
| Latitude                                  | degrees      | 90 to -90           | Latitude of site: negative for southern hemisphere                                                                                                                  | Required  |
| Rotation length                           | years        | >0                  | Rotation length                                                                                                                                                     | Required  |
| <b><u>Spacing</u></b>                     |              |                     |                                                                                                                                                                     |           |
| interrow spacing                          | m            | 0 to 100            | Distance between rows within blocks (x dimension)                                                                                                                   | Required  |
| intrarow spacing                          | m            | 0 to 100            | Distance between trees within rows within blocks (y dimension)                                                                                                      | Required  |
| rows per block                            | m            | 1 to 100/(interrow) | Number of rows per block                                                                                                                                            | Required  |
| columns per block                         | m            | 1 to 100/(intrarow) | Number of trees per row within blocks                                                                                                                               | Required  |
| inter-bay spacing                         | m            | >=0                 | Space between planted blocks in x dimension                                                                                                                         | Optional* |
| inter-block spacing                       | m            | >=0                 | Space between planted blocks in y dimension                                                                                                                         | Optional* |
| row orientation                           | degrees      | 90 to -90           | Direction of rows: degrees from north of row orientation<br>(for details see soil explanation sheet)                                                                | Required  |
| <b><u>Soil description</u></b>            |              |                     |                                                                                                                                                                     |           |
| Site fertility                            | scalar       | 0 to 1              | Site fertility ranking                                                                                                                                              | Required  |
| Waterlogging                              | boolean      | Y or N              | Is the site ever waterlogged?                                                                                                                                       | Required  |
| Depth to fresh watertable                 | cm           | >0                  | Depth to fresh watertable. If no watertable set to deeper than total soil thickness.                                                                                | Required  |
| Soil layer thickness upper horizon        | cm           | >0                  | Thickness of upper soil layer                                                                                                                                       | Required  |
| Proportion stones upper horizon           | proportion   | 0 to 1              | Proportion of upper soil layer composed of stones or gravel                                                                                                         | Required  |
| Plant available soil water upper horizon  | mm per metre | >0 but <300         | Plant available soil water held per metre of soil depth                                                                                                             | Required  |
| Soil layer thickness middle horizon       | cm           | >=0                 | Thickness of middle defined soil layer                                                                                                                              | Optional* |
| Proportion stones middle horizon          | proportion   | 0 to 1              | Proportion of middle soil layer composed of stones or gravel                                                                                                        | Optional* |
| Plant available soil water middle horizon | mm per metre | 0 but <300          | Plant available soil water held per metre of soil depth                                                                                                             | Optional* |
| Soil layer thickness lower horizon        | cm           | >=0                 | Thickness of lower defined soil layer                                                                                                                               | Optional* |
| Proportion stones lower horizon           | proportion   | 0 to 1              | Proportion of lower soil layer composed of stones or gravel                                                                                                         | Optional* |
| Plant available soil water lower horizon  | mm per metre | 0 but <300          | Plant available soil water held per metre of soil depth                                                                                                             | Optional* |
| Hard pan thickness                        | cm           | >=0                 | Thickness of hardpan or impeding layer between upper and middle defined soil layers                                                                                 | Optional* |
| Hard pan hardness                         | scalar       | 0 to 10             | Resistance to root penetration of hardpan: combination of bulk density, porosity and presence of old root channels and fissures. 0= no resistance; 10= impenetrable | Optional* |

**Table 7.2.** AGGRO average climate inputs required for each month of the year.

| Term                                                                  | Units                  | Status   |
|-----------------------------------------------------------------------|------------------------|----------|
| Mean maximum daily temperature for the month                          | °C                     | Required |
| Mean minimum daily temperature for the month                          | °C                     | Required |
| Mean daily radiation incident at ground level                         | MJ/m <sup>2</sup> /day | Required |
| Mean monthly rainfall                                                 | mm                     | Required |
| Mean number of rainy days in the month                                | days                   | Required |
| The lowest daily temperature recorded at the location for that month. | °C                     | Required |

**Table 7.3.** Silvicultural options available in AGGRO.

| Term                                 | Units      | Range                  | Explanation                                                              | Status    |
|--------------------------------------|------------|------------------------|--------------------------------------------------------------------------|-----------|
| <b><u>Planting month</u></b>         | month      | 1-12                   | Month in which trees were planted (first day of month assumed)           | Required  |
| <b><u>Spacing</u></b>                |            |                        |                                                                          |           |
| interrow spacing                     | m          | 0 to 100               | Distance between rows within blocks (x dimension)                        | Required  |
| intrarow spacing                     | m          | 0 to 100               | Distance between trees within rows within blocks (y dimension)           | Required  |
| rows per block                       | m          | 1 to 100/(interrow)    | Number of rows per block                                                 | Required  |
| columns per block                    | m          | 1 to 100/(intrarow)    | Number of trees per row within blocks                                    | Required  |
| inter-bay spacing                    | m          | >=0                    | Space between planted blocks in x dimension                              | Required  |
| inter-block spacing                  | m          | >=0                    | Space between planted blocks in y dimension                              | Required  |
| row orientation                      | degrees    | 90 to -90              | Direction of rows: degrees from north of row orientation                 | Required  |
| <b><u>Irrigation</u></b>             |            |                        |                                                                          |           |
| Quantity                             | mm         | >=0                    | Total irrigation applied in month                                        | Optional* |
| Number of times                      | days       | >=0 but <days in month | Number of days per month over which the total irrigation is applied      | Optional* |
| <b><u>Nitrogen Fertilisation</u></b> |            |                        |                                                                          |           |
| tree age                             | months     | >=0                    | Age in months at which fertiliser applied                                | Optional* |
| elemental N                          | kg/ha      | >=0                    | Quantity of nitrogen fertiliser applied in elemental nitrogen equivalent | Optional* |
| <b><u>Thinning</u></b>               |            |                        |                                                                          |           |
| tree age                             | months     | >=0                    | Age in months at which stand thinned                                     | Optional* |
| Proportion of residual stand removed | proportion | 0 to 1                 | Proportion of residual stand removed. Outrow thinning assumed.           | Optional* |

## 7.3 Model Outputs

The AGGRO model provides average stand mensuration attributes on an annual time step. For the assessment of site productivity, measures of volume, tree height and diameter are provided. For the assessment of stand suitability for silvicultural options, such as pruning and thinning, measures of crown dimension and leaf area are provided.

**Table 7.4** Definition of model outputs provided by AGGRO.

| Output Variable           | Unit                                             | Definition                                                   |
|---------------------------|--------------------------------------------------|--------------------------------------------------------------|
| Volume                    | m <sup>3</sup> ha <sup>-1</sup>                  | Standing entire stem volume under bark per hectare           |
| Thinned Volume            | m <sup>3</sup> ha <sup>-1</sup>                  | Cumulative thinned entire stem volume under bark per hectare |
| Height                    | m                                                | Average tree height                                          |
| Basal Area                | m <sup>2</sup> ha <sup>-1</sup>                  | Stand basal area under bark                                  |
| Diameter at Breast Height | cm                                               | Diameter breast height under bark                            |
| Leaf area index           | m <sup>2</sup> m <sup>-2</sup>                   | Leaf area per unit ground area                               |
| Stocking                  | stems ha <sup>-1</sup>                           | Stems per unit ground area                                   |
| Current annual increment  | m <sup>3</sup> ha <sup>-1</sup> yr <sup>-1</sup> | Accrual rate of wood volume                                  |
| Crown Length              | m                                                | Live crown length                                            |
| Green Height              | m                                                | Height to live crown base                                    |
| Width Crown Between Rows  | m                                                | Width of tree crowns in the inter-row direction              |
| Width Crown Within Rows   | m                                                | Width of tree crowns in the intra-row direction              |
| Length branches           | m                                                | Length of tree branches                                      |

## 7.4 Guidelines for Farm Forestry

### 7.4.1 Demonstration sites

For the purposes of demonstration four study regions are identified. These represent a range of regions in temperate Australia where *E. globulus* (all sites except Castra, Tasmania) or *E. nitens* (demonstrated at Castra, Tasmania) might be planted. The first is Manjimup Western Australia, the second Boyup Brook Western Australia, the third is Castra, Northern Tasmania and the final site is Dergholm, Victoria.

**Table 7.5** Environmental details for the four demonstration sites.

| Site        | Fertility rating | Mean annual rainfall<br>mm | Mean annual temperature<br>°C | Maximum soil water storage<br>mm/m soil depth |
|-------------|------------------|----------------------------|-------------------------------|-----------------------------------------------|
| Manjimup    | 0.66             | 1120                       | 15.6                          | 600                                           |
| Boyup Brook | 0.66             | 620                        | 15.4                          | 1050                                          |
| Castra      | 1                | 1308                       | 10.4                          | 250                                           |
| Dergholm    | 0.66             | 635                        | 13.5                          | 1000                                          |

### 7.4.2. Initial stocking

Increasing planting density up to 1100 stems per hectare is predicted to increase standing volume at age 10 years at all demonstration sites (Fig. 7.2). Marginal gains are realised after this but they are slight except at the highest productivity site at Castra where high rainfall and good soil nutrition enable significant productivity gains up to 2500 stems  $\text{ha}^{-1}$ . The gains in standing volume with increased stocking arise from two processes: firstly higher stocked stands reach crown closure more rapidly and thus occupy the site more rapidly; secondly higher stocked stands have less branch biomass due to shorter branch lengths.

As stocking increases individual tree size gets smaller with the most marked effect being on average tree diameter and a lesser effect on tree height. This highlights the implicit trade-off between producing large trees and maximising site volume production: that is, it is likely that stocking optima for volume production and plantation value will differ. By using AGGRO for particular sites and including wood volume and size specifications into an appropriate economic model the optimum planting density can be determined.

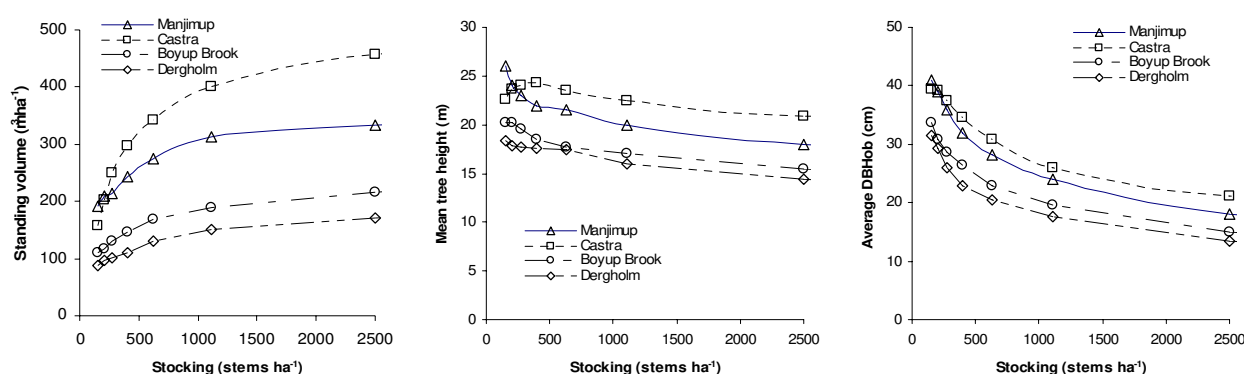


**Figure 7.2.** Simulated effect of stocking on volume at age 10 years, height and diameter at breast height over bark at the four demonstration sites.

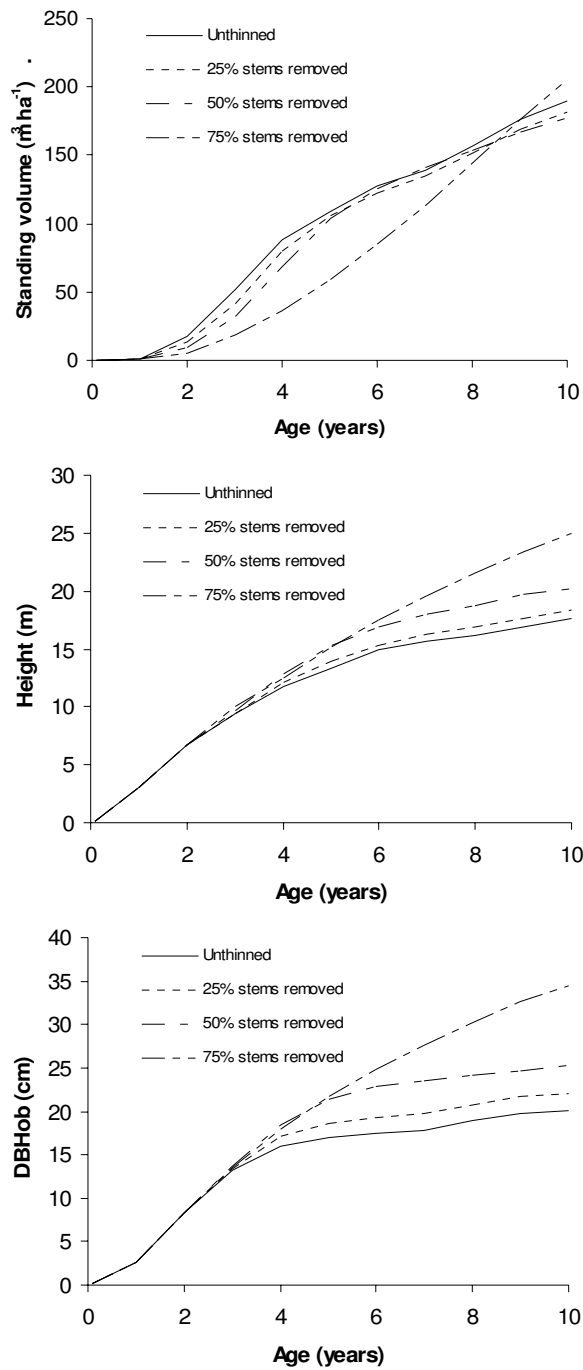
### 7.4.3 Early-aged thinning

Judicious use of early aged thinning on some sites may capture the benefits of increased piece size without the decrease in total stand volume resulting from low initial stocking. In the two examples shown in Fig. 7.3 we can see that on a dry site (Boyup Brook) thinning, even quite severely, does not greatly affect total stand volume, it simply changes the time course of volume accrual. However thinning significantly improves average stem size and thus might be expected to greatly improve tree value (although changes in wood density may influence this to some extent as may adverse effects on tree form – see chapter 2). However on a wetter site (Manjimup) thinning does have a significant impact on final harvest volume.

The effect of thinning depends on timing. Table 7.6 shows how thinning at different ages impacts differently on total stand volume as well as affecting the likelihood that thinnings themselves will be of a commercial size. For example at the Manjimup demonstration site thinning from age 6 years onwards is likely to provide trees of suitable size for pulpwood while still have a beneficial effect on the diameter of retained trees.

These examples demonstrate how AGGRO may be used to tailor thinning regimes for particular site attributes and end product requirements.

## A. Boyup Brook



## B. Manjimup

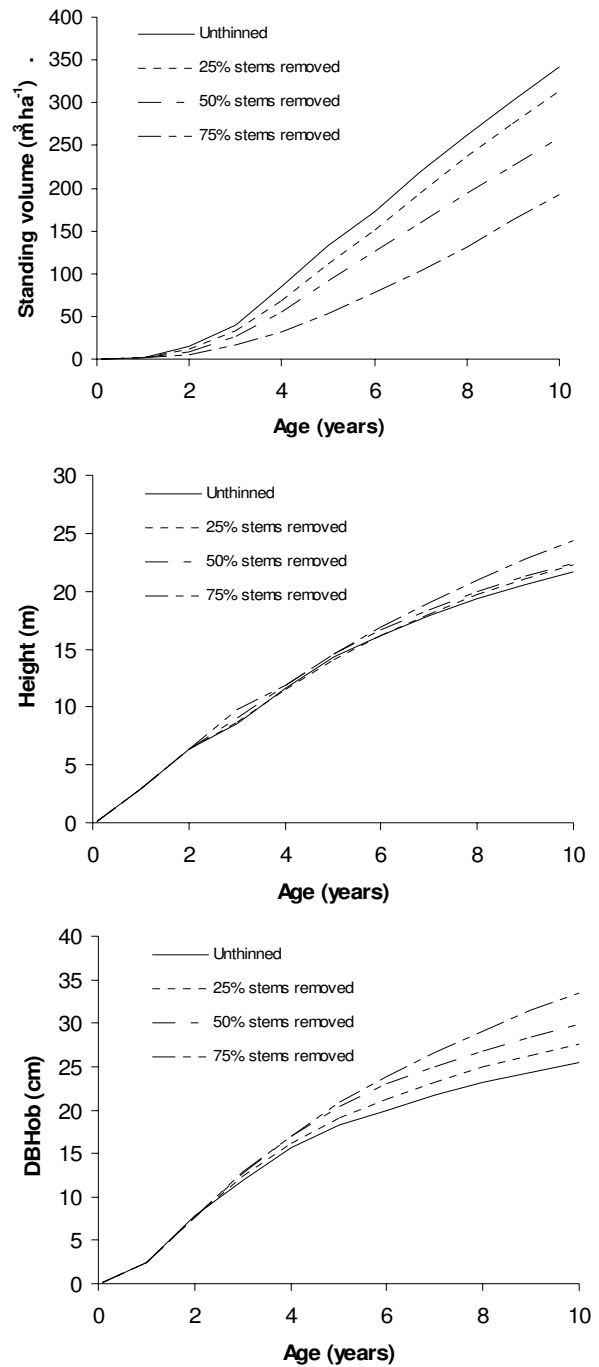


**Figure 7.3.** Simulated effects of thinning on volume and height at: A) Boyup Brook and B) Manjimup.

**Table 7.6** Simulated effect of thinning at different ages at the Manjimup demonstration site.

| Thinning age | Volume at age 10 years          | Volume of thinning              | Total volume (thinned plus harvest) | DBHob at harvest | DBHob thinnings |
|--------------|---------------------------------|---------------------------------|-------------------------------------|------------------|-----------------|
|              | m <sup>3</sup> ha <sup>-1</sup> | m <sup>3</sup> ha <sup>-1</sup> | m <sup>3</sup> ha <sup>-1</sup>     | cm               | cm              |
| 0            | 341                             | 0                               | 341                                 | 25.5             | 0               |
| 2            | 258                             | 7                               | 265                                 | 29.8             | 7.6             |
| 3            | 254                             | 20                              | 274                                 | 29.6             | 11.9            |
| 4            | 250                             | 41                              | 291                                 | 29.2             | 15.6            |
| 5            | 251                             | 65                              | 316                                 | 29.0             | 18.2            |
| 6            | 245                             | 85                              | 330                                 | 28.6             | 19.8            |
| 7            | 240                             | 107                             | 347                                 | 28.4             | 21.6            |
| 8            | 220                             | 129                             | 349                                 | 27.3             | 23.1            |
| 9            | 201                             | 149                             | 350                                 | 26.1             | 24.3            |

#### 7.4.4 Nitrogen fertilisation

The response of stand growth to nitrogen fertilisation depends on the complex interaction of stand demand, constrained by the bioclimatic potential of a site. The interaction is complex because stand demand changes as patterns of biomass, allocation shift and nutrients accumulate in biomass, and retranslocation from senescing biomass pools starts to offset uptake requirements (Fig 7.4). Clearly there is the potential for nitrogen mineralisation in the first year or so of a rotation to lead to increased soil nitrogen levels when demand is low, however if soil supply rates are low (say less than 40-50 kg(N) ha<sup>-1</sup> yr<sup>-1</sup>) demand is likely to exceed supply in the period of rapid crown development around the first 2-4 years of plantation development and a fertiliser response is likely.

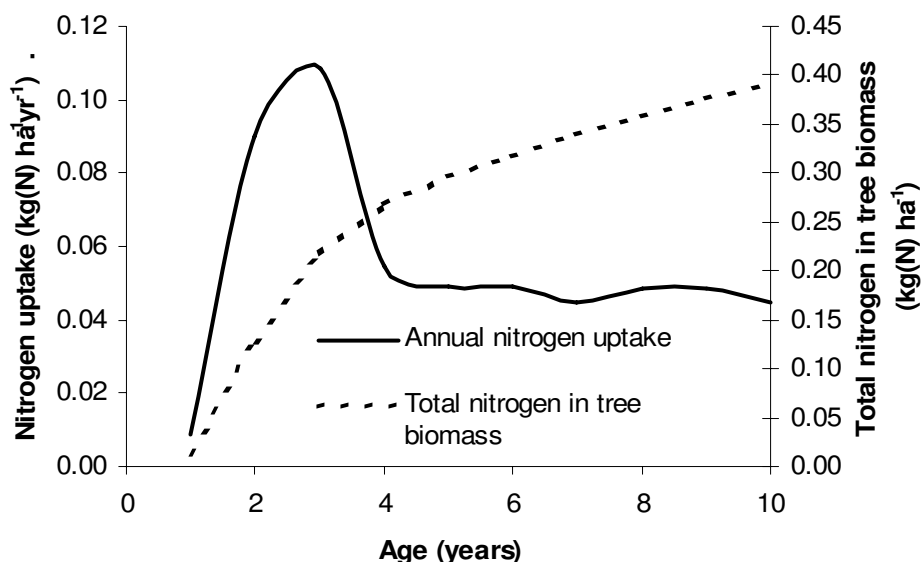


**Figure 7.4.** Simulated annual nitrogen uptake and stand nitrogen accumulation at the Manjimup demonstration site to achieve the bioclimatic upper limit production of 357 m<sup>3</sup> ha<sup>-1</sup> at age 10 years.

In the following examples (Figures 7.5 and 7.6) we show how timing and intensity of fertiliser application affect age 10 plantation yield. On a site of low to moderate inherent fertility (here with a fertility rating of 0.25 or an annual nitrogen supply of around  $35 \text{ kg(N) ha}^{-1} \text{ yr}^{-1}$ ) it can be seen that while there is a continual gain in total volume from repeated fertiliser application (applied as  $200 \text{ kg}$  of nitrogen every 2 years following a  $40 \text{ kg}$  application at planting) the gains become increasingly marginal (Fig 7.5).

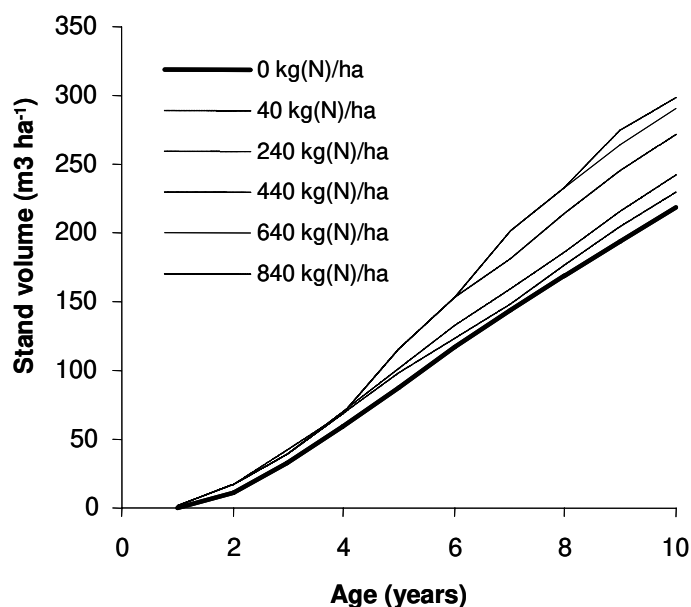


**Figure 7.5.** Simulated effect on plantation volume of total amount of nitrogen applied throughout a rotation. The initial  $40 \text{ kg(N)ha}^{-1}$  is applied at planting with subsequent doses of  $200 \text{ kg kg(N)ha}^{-1}$  applied at 24 month intervals.

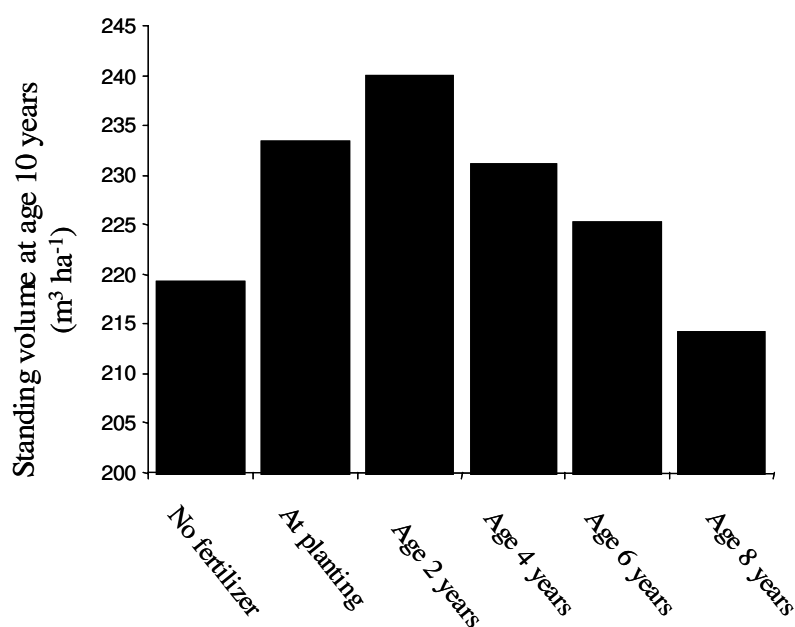


**Figure 7.6.** Simulated effect of adding  $200 \text{ kg(N) ha}^{-1}$  to a low to moderate fertility site (fertility rating 0.25,  $35 \text{ kg(N) ha}^{-1} \text{ yr}^{-1}$  mineralisation rate) in the Manjimup region at different times during the rotation.

It was seen in Fig 7.4 that the greatest disparity between plantation nitrogen demand and supply is likely to occur at around 2 years of age when trees are rapidly developing canopies. It is at this time that the response to fertilisation is greatest (Fig. 7.6). The later in the rotation that fertiliser is applied, the lower is the yield gain.

This set of examples for the Manjimup demonstration site shows how AGGRO can be used to develop efficient and cost effective nitrogen fertiliser regimes.

## **7.5 Conclusion**

We have shown in this chapter the types of question that can be easily explored and how silvicultural regimes and planting layouts can be tailored to site characteristics. The detailed physiological and mensurational work in this project has developed a considerable knowledge base on the responses of photosynthetic and morphological traits. This information is inevitably complex. However, it has shown that by embedding this knowledge into a simple-to-use decision support system, the implications of this research can become accessible for end-users.

## 8. Summary and Conclusions

The key results of this research are summarised as follows:

### 1. *Impact of spacing on growth and form*

1. Individual tree growth was maximised by wide spacing but stand production was reduced.
2. Wide-spaced planting had a clear impact on the incidence of thick branches, on branch diameter and on branch angle.
3. Spacing had a major effect on the structure of tree crowns with densely planted trees retaining few branches in the lower third of the crown.
4. Light-utilisation efficiency was unchanged by spacing simplifying modelling of spacing effects.

### 2. *Patterns of light interception by tree crowns*

1. Considerable horizontal and vertical variation in light penetration into tree crowns occurs because of leaf clumping and canopy gaps. A result of this is that light levels, and hence potential carbon fixation, are somewhat higher than might be predicted with the big-leaf model.
2. Light attenuation in the crown is not uniform but appears to follow a two-stage model. In addition there is a marked change in canopy light attenuation in tree crowns, even after the effect of sun angle is removed.
3. At the whole canopy level, a one-dimensional big-leaf approach to modelling carbon fixation in *E. globulus* crowns provides workable estimates of total stand growth.

### 3. *Nitrogen distribution in tree crowns*

1. The largest sink of above-ground nitrogen in eucalypts is in the foliage, typically containing around 40% of the above-ground nitrogen.
2. Tissue nitrogen concentrations typically vary with nutrient availability in the soil.
3. Eucalypts generally retranslocate around 50% of tissue nitrogen prior to litterfall.
4. There is little evidence to support the hypothesis that eucalypts generally have lower average above-ground N concentration than other forest trees.
5. Substantial lateral and vertical gradients in nitrogen exist within trees and are correlated with mean light intensity.
6. Patterns of nitrogen distribution however do not appear to support optimality models but rather support turnover models, the latter being able to accommodate the high levels of Rubisco observed in eucalypt canopies and are compatible with the movement of N through the canopy observed in N-tracing experiments.

### 4. *Spacing effects on nitrogen and photosynthesis*

1. The distribution of leaf nitrogen concentration in the canopies of *E. globulus* was neither random nor uniform and varied with spacing resulting in gradients of concentration both horizontally and vertically in crowns.
2. Steepest gradients of nitrogen were observed in densely packed trees and in part reflected patterns of light distribution though relationships were markedly curvilinear.
3. There was a strong relationship between both the maximum rate of assimilation and leaf respiration and leaf nitrogen concentration. The curvature of the light response curve and the apparent quantum efficiency were largely independent of leaf nitrogen concentration.
4. Consistent with the Farquhar biochemical model, parameters determining the maximum rate of carboxylation were strongly related to leaf nitrogen concentration.

### 5. *Modelling production*

1. A simple radiation interception model based on assumptions of stand structure and geometry was built and verified by comparison with light interception estimates by MAESTRA. The model assumed that light interception initially could be calculated by treating trees as non-interaction ellipsoids, subsequently as non-interacting hedgerows and finally by application of the big-leaf model. Where trees are planted in blocks the Jackson-Palmer method of calculating interception is applied.
2. When the light interception model was combined with a tree growth model it predicted well the effects of tree spacing and stand structural elements such as green height, crown width and crown length.

### 6. *Implications for farm forestry*

1. Using simulations from four demonstration sites that typify the farm forestry environment it is shown how planting density, up to a threshold of around 1100 stem ha<sup>-1</sup>, affects final harvested volume and average tree diameter but has little impact on tree height. Beyond this the planting density effects on volume are slight.
2. Because the effects of planting density on volume are mainly related to time to canopy closure early thinning on some water-limited sites can optimise the balance between volume production and tree size, increasing the value of harvested products and reducing handling costs associated with tree harvesting. However, changes in wood density associated with faster growth and the consequent impact on pulp yield may reduce the extent of these gains if a premium is paid for wood quality.
3. The efficacy of fertiliser application depends on the balance between plantation demand and the inherent capacity of the site to supply the needs of the plantation. Application of AGGRO shows that demand for nitrogen is highest around the time of canopy closure and that therefore fertilisation is most effective at this time. Using AGGRO, the effects and potential gain of fertiliser at different times and rates can be explored.

This project recommended the incorporation of AGGRO into the Farm Forestry Toolbox, which includes an economic evaluation tool. Together, these tools will enable farm foresters to evaluate the economic consequences of plantation project development and management options on their lands with greater confidence. An agreement between JVAP and the Cooperative Research Centre for Sustainable Production Forestry and Private Forests Tasmania was reached at the conclusion of this project, and a cutdown version of AGGRO has now been incorporated in Version 6 of the Farm Forestry Toolbox.

## 9. References

- Aber, J.D., Reich, P.B. and M.L. Goulden (1996). Extrapolating leaf CO<sub>2</sub> exchange to the canopy: a generalized model of forest photosynthesis compared with measurements by eddy correlation. *Oecologia* **106**, 257-65.
- Ackerly, D.D. and F.A. Bazzaz (1995). Seedling crown orientation and interception of diffuse radiation in tropical forest gaps. *Ecology* **76**, 1134-1146.
- Adams M.A. (1996). Distribution of eucalypts in Australian landscapes: landforms, soils, fire and nutrition. In P.M Attiwill and M.A Adams (editors), *Nutrition of Eucalypts*. CSIRO, Canberra, Australia, pp 61-76.
- Aerts, R. (1996). Nutrient resorption from senescing leaves of perennials: are there patterns? *Journal of Ecology* **84**, 597-608.
- Aerts R., DeCaluwe, H. and H. Konings (1992). Seasonal allocation of biomass and nitrogen in for *Carex* species from mesotrophic and eutrophic fens as affected by nitrogen supply. *Journal of Ecology* **80**, 653-64.
- Ågren, G.I. (1985). Theory for growth of plants derived from the nitrogen productivity concept. *Physiologia Plantarum*, pp 17-28.
- Ågren, G.I. (1988). Ideal nutrient productivities and nutrient proportions in plant growth. *Plant, Cell and Environment*, pp 613-20.
- Ågren, G.I and T. Ingstad (1987). Root:shoot ratio as a balance between nitrogen productivity and photosynthesis. *Plant, Cell and the Environment* **10**, 579-86.
- Alban, D.H., Perala, D.A. and B.E. Schlaegel (1978). Biomass and nutrient distribution in aspen, pine, and spruce stands on the same soil type in Minnesota. *Canadian Journal of Forestry Research* **8**, 290-9.
- Amthor, J.S. (1994). Scaling CO<sub>2</sub>- photosynthesis relationships from the leaf to the canopy. *Photosynthesis Research* **39**, 321-50.
- Anderson, J.M. (1986). Photoregulation of the composition, function and structure of thylakoid membranes. *Annual Review of Plant Physiology* **37**, 93-136.
- Anderson, J.E., Kriedemann, P.E., Austin, M.P. and G.D. Farquhar (2000). Eucalypts forming a canopy functional type in dry sclerophyll forests respond differently to environment. *Australian Journal of Plant Physiology* **48**, 759-75.
- Anten, N.P.R., Miyazawa, K., Hikosaka, K., Nagashima, H. and T. Hirose (1998). Leaf nitrogen distribution in relation to leaf age and photon flux density in dominant and subdominant plants in dense stands of a dicotyledonous herb. *Oecologia* **113**, 314-24.
- Anten, N.P.R., Schieving, F. and M.J.A. Werger (1995). Patterns of light and nitrogen distribution in relation to whole canopy carbon gain in C<sub>3</sub> and C<sub>4</sub> mono- and dicotyledonous species. *Oecologia* **101**, 504-13.
- Anten, N.P.R. and M.J.A. Werger (1996). Canopy structure and nitrogen distribution in dominant and subordinate plants in a dense stand of *Amaranthus dubius* L with a size hierarchy of individuals. *Oecologia* **105**, 30-37.
- Aschan G, Wittmann C and H. Pfanz (2001). Age-dependent bark photosynthesis of aspen twigs. *Trees - Structure and Function* **15**, 431-7.
- Ashton, D.H. (1975). Studies of litter in *Eucalyptus regnans* forests. *Australian Journal of Botany* **23**, 413-33.
- Attiwill, P.M. (1981). Energy, nutrient flow and biomass. In: *Australian Forest Nutrition Workshop Productivity in Perpetuity*. CSIRO, Melbourne, pp 131-44.
- Attiwill, P.M. and B.M. May (2001). Does nitrogen limit the growth of native eucalypt forests: some observations for mountain ash (*Eucalyptus regnans*). *Marine and Freshwater Research* **52**, 111-7.
- Attiwill, P.M., Polglase, P.J., Weston, C.J. and M.A. Adams (1996). Nutrient cycling in forests of south-eastern Australia. In: P.M. Attiwill and M.A. Adams (editors) *Nutrition of eucalypts*. CSIRO, Melbourne, pp 191-228.

- Baker, T.G. and P. Attiwill (1985). Above-ground nutrient distribution and cycling in *Pinus radiata* D.Don and *Eucalyptus obliqua* L'Herit. forests in southeastern Australia. *Forest Ecology and Management* **13**, 41-52.
- Baldocchi, D. D., and Hutchinson, B. A. (1986). On estimating canopy photosynthesis and stomatal conductance in a deciduous forest with clumped foliage. *Tree Physiology* **2**, 155-168.
- Ballare, C. L., Scopel, A. L. & Sanchez, R. A. (1997). Foraging for light - photosensory ecology and agricultural implications. *Plant, Cell & Environment* **20**, 820-825.
- Barradas, V.L., H.G. Jones and J.A. Clark (1998). Sunfleck Dynamics and Canopy Structure in a *Phaseolus vulgaris* L. Canopy. *International Journal of Biometeorology* **42**: 34-43.
- Bartelink, H.H. (1998). Radiation interception by forest trees - a simulation study on effects of stand density and foliage clustering on absorption and transmission. *Ecological Modelling* **105**, 213-225.
- Bartelink, H.H. (2000). A growth model for mixed forest stands. *Forest Ecology & Management* **134**, 29-43.
- Battaglia, M. and P.J. Sands (1997). Modelling site productivity of *Eucalyptus globulus* in response to climatic and site factors. *Australian Journal of Plant Physiology* **24**(6), 831-850.
- Battaglia, M., and Sands, P. (1998). Process-based forest productivity models and their application in forest management. *Forest Ecology and Management* **102**, 13-32.
- Battaglia, M., Sands, P. J., White, D.A. and Mummery, D. (in press). A linked carbon, water and nitrogen model of forest growth for silvicultural decision support. *Forest Ecology and Management*.
- Beadle, C. (1997). Dynamics of leaf and canopy development. In: E.K.S. Nambiar, A.G. Brown (editors). *Management of Soil, Nutrients and Water in Tropical Plantation Forests*. ACIAR, Australia, pp 169-212.
- Beadle, C.L., Honeysett, J.L., Turnbull, C.R.A. and D.A. White (1995). Site limits to achieving genetic potential. In: B.M.Potts, N.M.G. Borralho, J.B.Ried, W.N. Tibbits and C.A. Raymond (editors) *Eucalypt Plantations: Improving Fibre Yield and Quality. Proceedings IUFRO Conference*. CRC for Temperate Hardwood Forestry: Hobart, Hobart, 19-24Feb 1995.
- Beadle, C.L., McLeod, D.E., Turnbull, C.R.A., Ratkowsky, D.A and R. McLeod. (1989). Juvenile/total foliage ratios in *Eucalyptus nitens* and the growth of stands and individual trees. *Trees* **3**, 117-24.
- Beadle, C. L., and Turnbull, C. R. A. (1992). Comparative growth rates of eucalyptus in native forest and in plantation monoculture. In: I. R. Calder, R. L. Hall and P. G. Adlard (editors) *Growth and Water use of Forest Plantations*. John Wiley, Chichester, pp 318-331.
- Beadle, C. L., Turnbull, C. R. A. & Dean, G. H. (1996). Environmental effects on growth and kraft pulp yield of *Eucalyptus globulus* and *E.-nitens*. *Appita Journal* **49**, 239-242.
- Bell, A. (1993). *Plant Form*. Oxford University Press, New York.
- Bell, D.T. and S.C. Ward (1984). Foliar and twig micronutrients (N,P,K,Ca and Mg) in selected species of *Eucalyptus* used in rehabilitation: sources of variation. *Plant and Soil* **81**, 363-76.
- Belsky, A.J. (1988). Does herbivory benefit plants? A review of evidence. *American Naturalist* **127**, 870-72.
- Berendse, F. (1994). Competition between plant populations at low and high nutrient supply. *Oikos* **71**, 253-60.
- Bennett, L.T., Weston, C.J. and P.M. Attiwill (1997). Biomass, nutrient content and growth response to fertilisers of six-year-old *Eucalyptus globulus* plantations at three contrasting sites in Gippsland, Victoria. *Australian Journal of Botany* **45**, 103-21.
- Bennett, L.T., Weston, C.J. Judd, T.S., Attiwill, P.M. and Whiteman, P.H. (1996). The effects of fertilisers on early growth and foliar nutrients of three plantation eucalypts on high quality sites in Gippsland, south-eastern Australia. *Forest Ecology and Mangement* **89**, 213-26.
- Bergez, J., Etienne, M., and Balander, P. (1999). ALWAYS: a plot-based silvopastoral system model. *Ecological Modelling* **115**, 1-17.
- Bernardo, A. L., Reis, M. G. F., Reis, G. G., Harrison, R. B. & Firme, D. J. (1998). Effect of spacing on growth and biomass distribution in *Eucalyptus camaldulensis*, *E.pellita* and *E.-urophylla* plantations in southeastern Brazil. *Forest Ecology & Management* **104**, 1-13.

- Berninger, F., Mencuccini, M., Nikinmaa, E., Grace, J. & Hari, P. (1995). Evaporative demand determines branchiness of Scots Pine. *Oecologia* **102**, 164-168.
- Bindabran, P.S. (1999). Impact of canopy nitrogen profile in wheat on growth. *Field Crops Research* **63**, 63-77.
- Binkley, D., O'Connell, A.M. and K.V. Sankaran (1997). Stand development and productivity. In: E.K.S. Nambiar and A.G. Brown (editors). *Management of Soil, Nutrients and Water in Tropical Plantation Forests*. ACIAR Monograph No. 43, pp 419-42.
- Birk, E.M. and J. Turner (1992). Response of flooded gum (*E. grandis*) to intensive cultural treatments: biomass and nutrient content of eucalypt plantations and native forests. *Forest Ecology and Management* **47**, 1-28.
- Brooks, J.R., D.G. Sprugeland and T.M. Hinckley (1996). The effects of light acclimation during and after foliage expansion on photosynthesis of *Abies Amabilis* foliage within the canopy. *Oecologia* **107**, 21-32.
- Brouwer, R. (1963). Nutritive influences on the distribution of dry matter in the plant. *Netherlands Journal of Agricultural Science* **10**, 399-408.
- Buwalda, J.G., J.P. Curtis and G.S. Smith (1993). Use of interactive computer graphics for simulation of radiation interception and photosynthesis for canopies of kiwifruit vines with heterogeneous surface shape and leaf area distribution. *Annals of Botany* **72**(1), 17-26.
- Caldwell, M.H., H.P. Meister, J.D. Tenhunen and O.L. Lange (1986). Canopy structure, light microclimate and leaf gas exchange of *Quercus coccifera* L. in a Portuguese macchia: measurements in different canopy layers and simulations with a canopy model. *Trees-Structure & Function* **1**, 25-41.
- Camm E. (1993). Photosynthetic responses in developing and year-old Douglas-fir needles during new shoot development. *Trees* **8**, 61-6.
- Cannell, M. (1989). Physiological basis of wood production: a review. *Scandinavian Journal of Forest Research* **4**, 459-490.
- Carvalho, P.O., Calderira, M.C., Millard, P. and J.S Pereira (1993). Growth, nitrogen uptake and internal cycling in *Eucalyptus globulus* seedlings in relation to nitrogen supply. In: M.A.C. Fragoso and M.L. van Beusichem (editors). *Optimization of Plant Nutrition*. Kluwer, The Hague, pp 629-34.
- Cernusak, L.A. and J.D. Marshall (2000). Photosynthetic refixation in branches of Western White Pine. *Functional Ecology* **14**, 300-11.
- Cescatti, A. (1997a). Modelling the radiative transfer in discontinuous canopies of asymmetric crowns. I. Model structure and algorithms. *Ecological Modelling* **101**, 263-274.
- Cescatti, A. (1997b). Modelling the radiative transfer in discontinuous canopies of asymmetric crowns. 2. Model testing and application in a Norway spruce stand. *Ecological Modelling* **101**, 275-284.
- Chapin, F.S. III (1980). The mineral nutrition of wild plants. *Annual Review of Ecology and Systematics* **11**, 233-60.
- Chapin, F.S. III, Bloom, A.J., Field, C.B. and R.H. Waring (1987). Plant responses to multiple environmental factors. *BioScience* **38**, 49-57.
- Chapin, F.S. III, Schulze, E.D. and H.A. Mooney (1990). The ecology and economics of storage in plants. *Annual Review of Ecology and Systematics* **21**, 423-47.
- Charles-Edwards, D. A., and Thorpe, M. R. (1976). Interception of diffuse and direct-beam radiation by a hedgerow apple orchard. *Annals of Botany* **40**, 603-613.
- Chazdon, R.L. and R.W. Pearcy (1991). The importance of sunflecks for forest understorey plants. *Bioscience* **41**, 760-766.
- Chen, J-L, Reynolds, J.F., Harley, P.C. and J.D. Tenhunen (1993). Coordination of theory of leaf nitrogen distribution in a canopy. *Oecologia* **93**, 63-9.
- Clearwater, M.J. and F.C. Meinzer (2001). Relationships between hydraulic architecture and leaf photosynthetic capacity in nitrogen-fertilized *Eucalyptus grandis* trees. *Tree Physiology* **21**, 683-90.

- Close, D.G., Beadle, C.L., Brown, P. and G.K. Holz (2000). Cold-induced photoinhibition affects establishment of *Eucalyptus nitens* (Deane and Maiden) Maiden and *Eucalyptus globulus* Labill. *Trees: Structure and Function* **15**, 32-41.
- Close, D.G. (2001). Cold-induced photoinhibition, pigment chemistry, growth and nutrition of *Eucalyptus nitens* and *Eucalyptus globulus* seedlings during establishment. PhD Thesis, University of Tasmania, Australia.
- Close, D.G. and C.L. Beadle (2003). Partitioning of nitrogen and phosphorus chemical fractions in *Eucalyptus* seedlings during early spring and winter and growth chamber trials. *Communications in Soil Science and Plant Analysis*.
- Close, D.G., Battaglia, M., Davidson, N.J. and C.L. Beadle (2003). Within canopy gradients of nitrogen and photosynthetic activity and growth and biomass partitioning of *Eucalyptus nitens* (Deane and Maiden) Maiden and *Eucalyptus globulus* Labill. in response to nitrogen nutrition. *Trees: Structure and Function*.
- Cole, D.W., Gessel, S.P. and S.F. Dice (1967). Distribution and cycling of nitrogen, phosphorus, potassium and calcium in second-growth Douglas-Fir ecosystems. In: *Symposium on Primary Productivity and Mineral Cycling in Natural Ecosystems*. College of Life Sciences and Agriculture, University of Main at Ornon, pp 197-232.
- Crafts-Bandler, S.J., Salvucci, M.E. and D.B. Egli (1990). Changes in the ribulose biphosphate carboxylase/ oxygenase and ribulose 5-phosphate kinase abundance and photosynthetic capacity during leaf senescence. *Photosynthesis Research* **23**, 223-30.
- Cromer, R.N., Cameron, D., Cameron, J.N., Finn, D.W., Neilsrn, W.A., Raupach, M., Snowdeon, P. and H.D. Waring (1981). Response of eucalypt speices to fertiliser applied son after planting at several sites. *Australian Forestry* **44**, 3-13.
- Cromer, R.N., Cameron, D.M., Rance, S.J., Ryan, P.A. and M. Brown (1993). Response to nutrients in *Eucalyptus grandis*. 2. Nitrogen accumulation. *Forest Ecology and Management* **62**, 231-43.
- Cromer, R.N. and P.G. Jarvis (1990). Growth and biomass partitioning in *Eucalyptus grandis* seedlings in response to nitrogen supply. *Australian Journal of Plant Physiology* **17**, 503-15.
- Cromer, R.N. and E. Williams (1982). Biomass and nutrient accumulations in a planted *E. globulus* (Labill.) fertiliser trial. *Australian Journal of Botany* **30**, 265-78.
- Cromer, R.N., Raupach, M., Clark, A.R.P. and J.N. Cameron (1975). Eucalypt plantations in Australia - the potential for intensive production and utilisation. *Appital* **29**, 165-73.
- Cyr, D.R. and J.D. Bewley (1990). Seasonal variation in nitrogen storage reserves in the rots of leafy spurge (*Euphorbia esula*) and responses to decapitation and defoliation. *Physiologia Plantarum* **79**, 361-6.
- de Castro, F. and N. Fetcher (1999). The effect of leaf clustering in the interception of light in vegetal canopies: theoretical considerations. *Ecological Modelling* **116**, 125-134.
- de Jong, T.M. and J.F. Doyle (1985). Seasonal relationships between leaf nitrogen content (Photosynthetic capacity) and leaf canopy light exposure in peach (*Prunus persica*). *Plant, Cell and the Environment* **8**, 701-6.
- de Pury, D.G.G. and G.D. Farquhar (1997). Simple scaling of photosynthesis from leaves to canopies without the errors of Big-Leaf models. *Plant, Cell & Environment* **20**, 537-557.
- Deadman, H. & Hay, A. (1987). Eucalypts -selecting high quality tree crops. In *What's New in Forest research*, pp. 4. Forest Research Institute, Rotorua, New Zealand.
- Deans, J. D. & Milne, R. (1999). Effects of respacing on young Sitka spruce crops. *Forestry* **72**, 47-57.
- Dewar, R.C. (1996). The correlation between plant growth and intercepted radiation: an interpretation in terms of optimal plant nitrogen content. *Annals of Botany* **78**, 125-36.
- Dewar, R.C., B.E. Medlyn and R.E. McMurtrie. (1998). A mechanistic analysis of light and carbon use efficiencies. *Plant, Cell & Environment* **21**, 573-588.
- Dreccer, M.F., Van Oijen, M., Schapendonks, A.H.C.M., Pot, C.S. and R. Rabbinge (2000). Dynamics of vertical leaf nitrogen distribution in a vegetative wheat canopy. Impact on canopy photosynthesis. *Annals of Botany* **86**, 821-31.
- Drouet, J.L. and R. Bonhomme (1999). Do variations in in local leaf irradiance explain changes to leaf nitrogen with in row maize canopies? *Annals of Botany* **84**, 61-9.

- Dutkowski, G.W. (1995). Genetic variation in drought susceptibility of *Eucalyptus globulus* ssp. *globulus* in plantations in Western Australia. In 'Eucalypt Plantations: Improving Fibre Yield and Quality' (Eds. Potts, B.M., Borralho, N.M.G, Reid, J.B., Cromer, R.N., Tibbits, W.N. and Raymond, C.A., pp 199-207. Proc. CRC-IUFRO Conf., Hobart, 19-24 Feb., pp 199-207.
- Egli, P. and B. Schmid (1999). Relationships between leaf nitrogen and limitations of photosynthesis in canopies of *Solidago altissima*. *Acta Oecologica* **20**, 559-570.
- Elliott, H.J., Bashford, R. and A. Greener (1993). Effects of defoliation by the leaf beetle *Chrysophtharta bimaculata* on growth of *Eucalyptus regnans* plantations in Tasmania. *Australian Forestry* **56**, 22-6.
- Ellsworth, D.S. and P.B. Riech (1993). Canopy structure and vertical patterns of photosynthesis and related leaf traits in a deciduous forest. *Oecologia* **96**, 169-78.
- Endler, J. A. (1993). The color of light in forests and its implications. *Ecological Monographs* **63**, 1-27.
- Ennos, A. R. (1997). Wind as an ecological factor [Review]. *Trends in Ecology & Evolution* **12**, 108-111.
- Ericsson, T. (1994). Nutrient requirements of *Eucalyptus globulus* seedlings. In: J.S Pereira and H. Pereira (editors) *Eucalypts for Biomass Production*. Commission of the European Community, pp 224-234.
- Ericsson, T. (1994). Nutrient cycling in energy forest plantations. *Biomass Bioenergetics* **6**, 115-21.
- Evans, J.R. (1987). The relationship between electron transport components and photosynthetic capacity in pea leaves grown at different irradiances. *Australian Journal of Plant Physiology* **14**, 157-70.
- Evans, J.R. (1989). Partitioning nitrogen between and within leaves grown under different irradiances. *Australian Journal of Plant Physiology* **16**: 533-548.
- Evans, J.R (1993). Photosynthetic acclimation and nitrogen partitioning within a lucerne canopy. I. Canopy characteristics. *Australian Journal of Plant Physiology* **20**, 55-67.
- Farquhar, G.D., von Caemmerer, S. and J.A. Berry (1980). A biochemical model of photosynthetic CO<sub>2</sub> assimilation in leaves of C<sub>3</sub> species. *Planta* **149**, 78-90.
- Feller, M.C. (1980). Biomass and nutrient distribution in two eucalypt forest ecosystems. *Australian Journal of Ecology* **5**, 309-33.
- Field, C. (1983). Allocating leaf nitrogen for the maximization of carbon gain: leaf age as a control on the allocation program. *Oecologia* **56**, 341-7.
- Field, C. and H.A. Mooney (1986). The photosynthesis-nitrogen relationship in wild plants. In: T.J. Givnish (editor) *On the Economy of Plant Form and Function*. Cambridge University Press, Cambridge, pp 25-55.
- Florence, R.G. (1982). The Australian Forests. In: G. Jahn (editor). *Application of Vegetation Science to Forestry*. Dr W. Junk Publishers, The Hague, pp 75-95.
- Frederick, D.J, Madgwick, H.A.I, Jurgensen, M.F. and G.R. Oliver (1985). Dry matter content and nutrient distribution in an age series of *Eucalyptus regnans* plantations in New Zealand. *New Zealand Journal of Forestry Science* **15**, 158-79.
- Gerrand, A., Neilsen, W. & Medhurst, J. (1997). Thinning and pruning eucalypt plantations for sawlog production in Tasmanian forests. *Tasforests* **9**, 15-34.
- Givnish, T. (1988). Adaptation to sun and shade: a whole plant perspective. *Australian Journal of Plant Physiology* **15**, 63-92.
- Gleadow, R.M., Foley, W.J. and I.E Woodrow (1998). Enhanced CO<sub>2</sub> alters the relationship between photosynthesis and defence in the cyanogenic glycosides in *Eucalyptus cladocalyx* F. Muell. *Plant, Cell and Environment* **21**, 12-22.
- Gleadow, R.M. and I.E. Woodrow (2000). Polymorphism in cyanogenic glycoside content and cyanogenic  $\beta$ -glucosidase activity in natural populations of *Eucalyptus cladocalyx*. *Australian Journal of Plant Physiology* **27**, 693-9.
- Goudriaan, J. (1977). *Crop Micrometeorology: A Simulation Study*. Wageningen, PUDOC.
- Goudriaan, J. (1986). A simple and fast numerical method for the computation of daily totals of crop photosynthesis. *Agricultural & Forest Meteorology* **38**, 257-262.

- Grace, J.C., P.G. Jarvis and J.M. Norman (1987). Modelling the interception of solar radiant energy in intensively managed stands. *New Zealand Journal of Forest Science* **17**, 193-209.
- Greenwood, D.J., Gastal, F., Lemaire, G., Draycott, A., Millard, P. and J.J. Neeteson (1991). Growth rate and %N of field grown crops: theory and experiments. *Annals of Botany* **66**, 181-96.
- Grindlay, D.J.C. (1997). Towards an explanation of crop nitrogen demand based on the optimization of leaf nitrogen per unit leaf area. *Journal of Agricultural Science* **128**(Part 4), 377-396.
- Grove, T.S. (1990). Twig and foliar nutrient concentrations in relation to nitrogen and phosphorus supply in a eucalypt (*Eucalyptus diversicolor* F. Muell.) and an understorey legume (*Bossiaea laidlawiana* Tovey and Morris). *Plant and Soil* **126**, 265-75.
- Grove, T.S. and N. Malajczuk (1985). Nutrient accumulation by trees and understorey shrubs in an age-series of *Eucalyptus diversicolor* F. Muell. stands. *Forest Ecology and Management* **11**, 75-95.
- Grove, T.S. Thomas, B.D. and N. Malajczuk (1996). Nutritional physiology of eucalypts: uptake, distribution and utilization. IN: P.M. Attiwill and M.A. Adams (Editors). *Nutrition of the Eucalypts*. CSIRO, Melbourne, Victoria, Australia, pp 77-108.
- Hamilton, G. and J. Christie (1974). Influences of spacing on crop characteristics and yield. *Forestry Commission Bulletin, London* **52**, 1-91.
- Harley, P.C., Thomas, R.B., Reynolds, J.F. and B.R. Strain (1992). Modelling photosynthesis of cotton grown in elevated CO<sub>2</sub>. *Plant, Cell and Environment* **15**, 271-82.
- Harrison, R.B., Reis, G.G., Ries, M.D.G.F., Bernardo, A.L. and D.J. Firme (2000). Effect of spacing and age on nitrogen and phosphorus distribution and biomass of *Eucalyptus camaldulensis*, *Eucalyptus pellita* and *Eucalyptus urophylla* plantations in southern Brazil. *Forest Ecology and Management* **133**, 167-77.
- Hawkins, B. and P.J. Polglase (2000). Foliar concentrations and resorption of nitrogen and phosphorus in 15 species of eucalypts grown under non-limited water and nutrient availability. *Australian Journal of Botany*, pp 597-602.
- Heilmeyer, H. and R.K. Monson (1994). Carbon and nitrogen storage in herbaceous plants. In: J. Roy and E. Garnier (editors) *A Whole Plant Perspective on Carbon-Nitrogen Interactions*. SPB Academic Publishing, The Hague, pp 149-71.
- Henskens, F.L., M. Battaglia, M.L. Cherry and C.L. Beadle (2001). Physiological basis of spacing effects on tree growth and form in *Eucalyptus globulus*. *Trees-Structure & Function* **15**, 365-77.
- Herbert M.A. (1991). The influence of site factors on the foliar nutrient content of *Eucalyptus grandis* in Natal. *South African Forestry Journal* **156**, 28-34.
- Herbert, M.A. and M.A. Robertson (1991). Above-ground biomass composition and nutrient content for *Eucalyptus* species in the southeastern Transvaal. In: A.P.G. Schonau (editor) *Symposium on Intensive Forestry: The Role of Eucalypts*, volume 2, 662-74. IUFRO, Durban, South Africa 2-6 September 1991.
- Hikosaka, K. and I. Terashima (1995). A model of acclimation of photosynthesis in the leaves of C3 plants to sun and shade with respect to nitrogen use. *Plant, Cell and Environment* **18**, 605-18.
- Hikosaka, K. and I. Terashima (1996). Nitrogen partitioning among photosynthetic components and its consequence in sun and shade plants. *Functional Ecology* **10**, 335-43.
- Hilbert, D. W. & Messier, C. (1996). Physical simulation of trees to study the effects of forest light environment, branch type and branch spacing on light interception and transmission. *Functional Ecology* **10**, 777-783.
- Hingston, F.J., Galbraith, J.H. and G.M. Dimmock. (1994). Effect of fertilizers on thinned and unthinned jarrah (*Eucalyptus marginata*) stands, on gravelly lateritic soils in the Darling range, Western Australia. (ii) Characteristics of leaves. User Series No. 11, CSIRO, Division of Forestry and Forest Products, Canberra, Australia.
- Hingston, F.J., Turton, A.G. and G.M. Dimmock (1979). Nutrient distribution in karri (*Eucalyptus diversicolor* F. Muell.) ecosystems in southwest Western Australia. *Forest Ecology and Management* **2**, 133-58.
- Hingston, F.J., Dimmock, G.M. and A.G. Turton (1981). Nutrient distribution in a jarrah (*Eucalyptus marginata* Donn. ex Sm.) ecosystem in south-west Western Australia. *Forest Ecology and Management* **3**, 183-207.

- Hingston, F.J., DeBoer, E.S. and M.S. Jones (1990). Distribution of nutrients in component parts of jarrah (*Eucalyptus marginata* three years after application of fertilizer. Division of Forestry and Forest Products User Series **12**, 1-27.
- Hirose, T.; D.D. Ackerly, M.B. Traw, D. Ramseier and F.A. Bazzaz (1997). CO<sub>2</sub> elevation, canopy photosynthesis, and optimal leaf area index. *Ecology* **78**, 2339-2350.
- Hirose, T. and M.J.A. Werger (1987a). Maximising daily canopy photosynthesis with respect to the leaf nitrogen allocation pattern in the canopy. *Oecologia* **75**, 520-526.
- Hirose, T. and M.J.A. Werger (1987b). Maximising daily canopy photosynthesis with respect to the leaf nitrogen allocation pattern in the canopy. *Oecologia* **72**, 520-6.
- Hirose, T., Werger, M.J.A, Pons, T.L. and J.W.A. Rheeunen (1988). Canopy structure and leaf nitrogen distribution in a stand of *Lysimachia vulgaris* L. as influenced by stand density. *Oecologia* **77**, 145-50.
- Hollinger, D.Y. (1989). Canopy organization and foliage photosynthetic capacity in a broad-leaved evergreen montane forest. *Functional Ecology* **3**, 53-62.
- Hollinger, D.Y. (1996). Optimality and nitrogen allocation in a tree canopy. *Tree Physiology* **16**, 627-34.
- Hooda, N. and C.J Weston (1999). Influence of site and fertiliser addition on nutrient cycling in *Eucalyptus globulus* plantations in Gippsland, south-eastern Australia. 1. Foliage and litter quality. *Australian Journal of Botany* **47**, 189-206.
- Hopmans, P., Stewart, H.T.L., Flinn, D.W. and Hillman, T.J. (1990). *Forest Ecology and Management* **30**, 203-11.
- Hopmans, P., Stewart, H.T.L and D.W. Flint (1993). Impacts of harvesting on nutrients in a eucalypt ecosystem in southeastern Australia *Forest Ecology and Management* **59**, 29-51.
- Hunt, M., Beadle, C.L. and M. Cherry (1999). Allometric relationships between stem variables and leaf area in planted *Eucalyptus nitens* and naturally regenerating *Acacia dealbata*. *New Zealand Journal of Forestry Science* **29**, 289-300.
- Idso, S. B., and de Wit, C. T. (1970). Light relations in plant canopies. *Applied Optics* **9**, 177-184.
- Ingestad, G.I. (1977). Nitrogen and plant growth, maximum efficiency of nitrogen fertilisers. *Ambio* **6**, 146-51.
- Iqbal, M. ( 1983). *An Introduction to Solar Radiation*. Academic Press, Toronto.
- Jackson, J.E. and J.W. Palmer (1979). A simple model of light transmission and interception by discontinuous canopies. *Annals of Botany* **44**, 381-383.
- Jackson, J. E., and Palmer, J. W. (1981). Light distribution in discontinuous canopies: calculation of leaf areas and canopy volumes above defined 'irradiance contours' for use in productivity modelling. *Annals of Botany* **47**, 561-565.
- James, S.A. and D.T. Bell (2000). Leaf orientation, light interception and stomatal conductance of *Eucalyptus globulus* ssp. *globulus* leaves. *Tree Physiology* **20**, 815-833.
- James, S.A., Smith, W.K. and T.C. Vogelmann (1999). Ontogenetic differences in mesophyll structure and chlorophyll distribution in *Eucalyptus globulus* ssp. *globulus* (Myrtaceae). *American Journal of Botany* **86**, 198-207.
- Johnson, E.D. (1924) A comparison of the juvenile and adult leaves of *Eucalyptus globulus*. *New Phytologist*, **25**, 202-12.
- Jones, H. (1994). *Plants and microclimate. A quantitative approach to environmental plant physiology*. Second edition. Cambridge University Press, Cambridge United Kingdom. p 425.
- Judd, T.S., Attiwill, P.M. and M.A. Adams (1996a). Nutrient concentrations in *Eucalyptus*: a synthesis in relation to differences between taxa, sites and components. In: P.M. Attiwill and M.A. Adams (Editors), *Nutrition of the Eucalypts*. CSIRO, Melbourne, Victoria, Australia, pp 123-53.
- Judd, T.S., Bennett, L.T., Weston, C.J., Attiwill, P.M. and P.H. Whiteman (1996b). The response of growth and foliar nutrients to fertilizers in young *Eucalyptus globulus* (Labill.) plantations in Gippsland, southeastern Australia. *Forest Ecology and Management* **82**, 87-101.
- Kaul, O.N, Srivastava, P.B.L. and N.K.S Bora (1966). Nutrient studies on Eucalyptus. I. Diagnosis of mineral deficiencies in *Eucalyptus* hybrid seedlings. *Indian Forester* **92**, 264-8.

- Kaul, O.N., Srivastava, P.B. and H.M. Mathur (1966). Nutritional studies in *Eucalyptus*. II. N, P, K requirements of *Eucalyptus* hybrid seedlings. *Indian Forester* **92**, 772-8.
- Kaul, O.N., Srivastava, P.B.L. and V.N. Tandon (1968). Nutrient studies on *Eucalyptus*. III. Diagnosis of mineral deficiencies in *Eucalyptus grandis* seedlings. *Indian Forester* **94**, 831-4.
- Kedrowski, R.A. (1983). Extraction and analysis of nitrogen, phosphorus and carbon fractions in plant material. *Journal of Plant Nutrition* **6**, 989-1011.
- Killingbeck, K.T. (1996). Nutrients in senesced leaves: keys to the search for potential resorption and resorption proficiency. *Ecology* **77**, 1716-27.
- King, D. A. (1994). Influence of light level on the growth and morphology of saplings in a Panamanian forest. *American Journal of Botany* **81**, 948-957.
- King, D. A., Leigh, E. G., Condit, R., Foster, R. B. & Hubbell, S. P. (1997). Relationships between branch spacing, growth rate and light in tropical forest saplings. *Functional Ecology* **11**, 627-635.
- Kirschbaum, M.U.F., King, D.A., Comins, H.N., McMurtrie, R.E., Medlyn, B.E., Pongracic, S., Murty, D. Keith, H., Raison, R.J., Khanna, P.K. and D.W. Sheriff (1994). Modelling forest response to increasing CO<sub>2</sub> concentration under nutrient-limited conditions. *Plant, Cell and the Environment* **17**, 1174-82.
- Kriedemann, P.E. and R.N. Cromer (1996). The nutritional physiology of the eucalypts - nutrition and growth. In: P.M. Attiwill and M.A. Adams (Editors), *Nutrition of the Eucalypts*. CSIRO, Melbourne, Victoria, Australia, pp 109-21.
- Kull, O. (2002). Acclimation of photosynthesis in canopies: models and limitations. *Oecologia* **133**, 267-79.
- Kull, O. and P.G. Jarvis (1995) The role of nitrogen in a simple scheme to scale up photosynthesis from leaf to canopy. *Plant, Cell and Environment* **18**, 1174-82.
- Kull, O. and B. Kruijt (1999). Acclimation of photosynthesis to light: a mechanistic approach. *Functional Ecology* **13**, 24-36.
- Kull, O. and Ü. Niinemets (1998). Distribution of leaf photosynthetic properties in tree canopies: comparison of species with different shade tolerance. *Functional Ecology* **12**, 472-9.
- Kuppers, B.I.L. (1996). Nitrogen and Rubisco contents in eucalypt canopies as affected by *Acacia* neighbourhood. *Plant Physiology and Biochemistry* **34**, 753-60.
- Kuppers, M. (1990). Ecological significance of above ground architectural patterns in woody plants. *Trends in Ecology and Evolution* **10**, 1-17.
- Kuppers, M. (1994). Canopy gaps: competitive light interception and economic space filling - a matter of whole plant allocation. In: M. Caldwell and R. Pearcy (editors), *Exploitation of Environmental Heterogeneity by Plants*. Academic Press, San Diego, pp 111-144.
- Kuppers, M. and H. Schneider (1993). Leaf gas exchange of beech (*Fagus sylvatica* L.) seedlings in lightflecks: effects of fleck length and leaf temperature in leaves grown in deep and partial shade. *Trees-Structure & Function* **7**, 160-168.
- Kuppers, M., H. Timm, F. Orth, J. Stegemann, R. Stober, H. Schneider, K. Paliwal, K. Karunaichamy and R. Ortiz (1996). Effects of light environment and successional status on lightfleck use by understory trees of temperate and tropical forests. *Tree Physiology* **16**, 69-80.
- Laclau, J-P. Bouillet, J-P. and J. Ranger (2000). Dynamics of biomass and nutrient accumulation in a clonal plantation of *Eucalyptus* in Congo. *Forest Ecology and Management* **128**, 181-96.
- Lamb, D. (1976). Variations in the foliar concentrations of macro- and micro-elements in a fast-growing tropical eucalypt. *Plant and Soil* **45**, 477-92.
- Lambert, M.J. and J. Turner (1983). Soil nutrient-vegetation relationships in the Eden area, NSW. *Australian Forestry* **46**, 200-9.
- Landsberg, J.J. (1986). *Physiological Ecology of Forest Production*. New York, Academic Press.
- Landsberg, J. J. & Hingston, F. J. (1996). Evaluating a simple radiation/dry matter conversion model using data from *Eucalyptus globulus* plantations in Western Australia. *Tree Physiology* **16**, 801-8.
- Landsberg, J.J. and R.H. Waring (1997). A generalised model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and partitioning. *Forest Ecology and Management* **95**, 209-228.

- Lantinga, E.A., M. Nassiri and M.J. Kropff (1999). Modelling and measuring vertical light absorption within grass-clover mixtures. *Agricultural & Forest Meteorology* **96**, 71-83.
- Larocque, G.R. (2002). Coupling a detailed photosynthetic model with foliage distribution and light attenuation functions to compute daily gross photosynthesis in sugar maple (*Acer saccharum* Marsh.) stands. *Ecological Modelling* **148**, 213-32.
- Larsen, D.R. and J.A. Kershaw (1996). Influence of canopy structure assumptions on predictions from Beers law - a comparison of deterministic and stochastic simulations. *Agricultural & Forest Meteorology* **81**, 61-77.
- Lavigne, M. B., Franklin, S. E. & Hunt, E. R. (1996). Estimating stem maintenance respiration rates of dissimilar balsam fir stands. *Tree Physiology* **16**, 687-695.
- Lawlor, D.W., Boyle, F.A., Young, A.T., Keys, A.J. and A.C. Kendall (1987). Nitrate nutrition and temperature effects on wheat: photosynthesis and photorespiration of leaves. *Journal of Experimental Botany* **38**, 393-408.
- Le Roux, X.S., H. Sinoquet and M. Vandame. (1999). Spatial distribution of leaf dry weight per area and leaf nitrogen concentration in relation to local radiation regime within an isolated tree crown. *Tree Physiology* **19**, 181-188.
- Leuning, R., F.M. Kelliher, D.G.G de Pury and E.D.Schulze (1995). Leaf nitrogen, photosynthesis, conductance and transpiration - scaling from leaves to canopies. *Plant, Cell & Environment* **18**, 1183-1200.
- Leuning, R.W., Y.P. Wang and R.N. Cromer (1991a). Model simulations of spatial distributions and daily totals of photosynthesis in *Eucalyptus grandis* canopies. *Oecologia* **88**, 494-503.
- Leuning, R.W., Cromer, R.N. and S. Rance (1991b). Spatial distributions of foliar nitrogen and phosphorus in the crown of *Eucalyptus gregandis*. *Oecologia* **88**, 504-10.
- Leuning, R., Dunin, F. X., and Wang, Y., -P. (1998). A two-leaf model for canopy conductance, photosynthesis and partitioning of available energy. II. Comparison with measurements. *Agricultural and Forest Entomology* **91**, 113-125.
- Linder, S. (1985). Potential and actual production in Australian forest stands. In: J. J. Landsberg and W. Parsons (editors) *Research for Forest Management*, pp. 11-35. CSIRO, Melbourne, Australia.
- Lloyd, J., Grace, J., Miranda A.C., (1995). A simple calibrated model of Amazon rain-forest productivity based on leaf biochemical-properties. *Plant Cell Environment* **18**, 1129-45.
- Long, J. (1985). A practical approach to density management. *The Forestry Chronicle* **61**, 23-27.
- Long, J. and F. Smith. (1989). Canopy development and leaf area efficiency: links between production ecology and density management. In: R. James and G. Tarlton (editors), *New Approaches to spacing and Thinning in Plantation Forestry*. Forest Research Institute, Rotorua, New Zealand, pp 260-266.
- Lowther, J.R. (1980). Use of a single acid - hydrogenperoxide digest for the analysis of *Pinus radiata* needles. *Communications in Soil and Plant Analysis* **11**, 175-188.
- McColl, J.G. (1969). Soil plant relationships in a *Eucalyptus* forest on the south coast of NSW. *Ecology* **50**, 354-62.
- McColl, J.G. (1979). Comparison of foliar composition of *Eucalyptus globulus* and *Quercus agrifolia* growing together. *Journal of Plant Nutrition* **1**, 65-71.
- McLeod, S. (1992). Determination of total soil and plant nitrogen using a micro-distillation unit in a continuous flow analyser. *Analytica Chimica Acta* **266**, 133-117.
- McMurtrie, R.E., Rook, D.A. and F.M. Kelliher (1990). Modelling the yield of *Pinus radiata* on a site limited by water and nitrogen. *Forest Ecology and Management* **30**, 381-413.
- Mäkelä, A. (1986). Implications of the pipe model theory on dry matter partitioning and height growth in trees. *Journal of Theoretical Biology* **123**, 103-120.
- Marsh N.R. and M.A. Adams (1995). Decline in *Eucalyptus tereticornis* near Bairnsdale, Victoria: insect herbivory and nitrogen fractions in sap and foliage. *Australian Journal of Botany* **43**, 39-50.
- Mattheck, C. (1991). *Trees. The Mechanical Design*. Springer Verlag, New York.
- Medhurst, J.L., M. Battaglia, M.L. Cherry, M.A. Hunt, D.A. White and C.L. Beadle (1999). Allometric relationships for *Eucalyptus nitens* (Deane and Maiden) Maiden plantations. *Trees-Structure & Function* **14**, 91-101.

- Medhurst, J., Beadle, C. & Neilsen, W. (2001). Early-age and later-age thinning affects growth, dominance and intraspecific competition in *Eucalyptus nitens* plantations. *Canadian Journal of Forest Research* **31**, 187-97.
- Medlyn, B.E. (1996) The optimal allocation of nitrogen within the C3 photosynthetic system at elevated CO<sub>2</sub>. *Australian Journal of Plant Physiology* **23**, 593-603.
- Medlyn, B. (1997). The MAESTRA model. Institute of Ecology and Resource Management, University of Edinburgh, Edinburgh.
- Medlyn, B.E. (1998). Physiological basis of the light use efficiency model. *Tree Physiology* **18**, 167-176.
- Meloni, S., and Sinoquet, H. (1997). Assessment of the spatial distribution of light transmitted below young trees in an agroforestry system. *Annals of Science in Forests* **54**, 313-333.
- Millard P. (1988). The accumulation and storage of nitrogen be herbaceous plants. *Plant Cell and Environment* **11**, 1-8.
- Millard P. (1994). Measurement of the remobilization of nitrogen for spring leaf growth under field conditions. *Tree Physiology* **14**, 1049-54.
- Millard P. (1995). Internal cycling of nitrogen in trees. *Acta Horticulturae*. **383**, 3-14.
- Millard P. and C.M. Thomson (1989). The effect of autumn senescence of leaves on the internal cycling of nitrogen for spring growth of apple trees. *Journal of Experimental Botany* **40**, 1285-9.
- Misra, R.K., Turnbull, C.R.A, Cromer, R.N., Gibbons, A.K. and LaSalla, A.V. and L.M. Ballard (1998). Below- and above-ground growth of *Eucalyptus nitens* in a young plantation II. Nitrogen and phosphorus. *Forest Ecology and Management* **106**, 295-306.
- Mobbs, D. C., Cannell, M. G. R., Crout, N. M. J., Lawson, G. J., Friend, A. D., and Arah, J. (1998). Complementarity of light and water use in tropical agroforests. I. Theoretical model outline, performance and sensitivity. *Forest Ecology and Management* **102**, 259-274.
- Mooney, H.A., Ferrar, P.J. and R.O. Slatyer (1978). Photosynthetic capacity and carbon allocation patterns in diverse growth forms of *Eucalyptus*. *Oecologia* **36**, 103-11.
- Mooney, H.A. and S.L. Gulmon (1979). Environmental and evolutionary constraints on the photosynthetic characteristics of higher plants. In: Solbrig, O.T., Jain, S., Johnson, G.B., Raven, P.H. (eds). *Topics in Plant Population Biology*. Columbia University Press, New York, pp 316-37.
- Monteith, J. L. (1977). Climate and efficiency of crop production in Britain. *Phil. Trans. R. Soc. Lond.* **B281**, 277-294.
- Mulligan, D.R. (1989). Leaf phosphorus and nitrogen concentration and net photosynthesis in *Eucalypt* seedlings. *Tree Physiology* **5**, 149-57.
- Muthuchelian, K. (1992). Biomass productivity relative to net photosynthetic rate, ribulose-1,5-biphosphate carboxylase activity, soluble protein and nitrogen contents in ten spruce species. *Photosynthetica* **26**, 333-9.
- Myeni, R. B., Ross, J., and Asrar, G. (1989). A review on the theory of photon transport in leaf canopies. *Agricultural and Forest Meteorology* **45**, 1-153.
- Nambiar, E.K.S. and D.N. Fife (1991). Nutrient translocation in temperate conifers. *Tree Physiology* **9**, 185-207.
- Neilsen, W. A. & Gerrand, A. M. (1999). Growth and branching habit of *Eucalyptus nitens* at different spacing and the effect on final crop selection. *Forest Ecology & Management* **123**, 217-229.
- Noble I.R. (1989). Ecological traits of the *Eucalyptus* L'Herit. subgenera *Monocalyptus* and *Symphyomyrtus*. *Australian Journal of Botany* **37**, 207-24.
- Norman, J. M., and Welles, J. M. (1983). Radiative transfer in an array of canopies. *Agronomy Journal* **75**, 481-488.
- O'Connell, A.M. and T.S. Grove (1993). Influence of nitrogen and phosphorus fertilizers on amount and nutrient content of litterfall in a regrowth eucalypt forest. *New Forests* **7**, 33-47.
- O'Connell, A.M. and P. Menage (1982). Decomposition of litter from three major plant species of jarrah (*Eucalyptus marginata* Donn ex Sm.) forest in relation to site fire history and type. *Australian Journal of Ecology* **8**, 277-86.

- O'Connell, A.M., Grove, T.S. and G.M. Dimmock (1978). Nutrients in the litter of jarrah forest soils. *Australian Journal of Forestry* **3**, 253-60.
- Oikawa, T. (1977). Light regime in relation to plant population geometry. II. Light penetration in a square-planted population. *Botanical Magazine, Tokyo* **90**, 11-22.
- Oker-Blom, P. (1986). Photosynthetic radiation regime and canopy structure in model forest stands. *Acta Forest Fennica* **197**, 1-44.
- Opie, J., Curtin, R.A. and Incoll, W.D. (1984). Stand Management. In: A. B. WE Hillis (editor), *Eucalypts for Wood Production*. Academic Press, London, pp 179-197.
- Ovington, J.D. and H.A.I. Madgwick (1959) The growth and composition of natural stands of birch. *Plant and Soil* **10**, 389-400.
- Palmer J.W. (1977). Diurnal light interception and a computer model of light interception by hedgerow apple orchards. *Journal of Applied Ecology* **14**, 601-614.
- Papadopoulos A.P. and S.Pararajasingham (1997). The influence of plant spacing on light interception and use in greenhouse tomato (*Lycopersicon esculentum* Mill) - a review. *Scientia Horticulturae* **69**(1-2), 1-29.
- Passioura, J. B. (1973). Sense and nonsense in crop simulation. *J. Aust. Inst. Ag. Science* **39**, 181-183.
- Pate, J.S., Lee, J.A., McNeill, S. and H. Rorison (1983). Patterns of nitrogen metabolism in higher plants and their ecological significance. In: J.A. Lee, S. McNeill and H. Rorison (editors), *Nitrogen as an Ecological Factor*. Blackwell Scientific Publications, Oxford, U.K., pp 225-55.
- Pate, J.S. (1986). Xylem to phloem transfer - vital component of the nitrogen-partitioning system of a nodulated legume. In: J. Cronshaw, W.J. Lucas and R.T. Giaquinta (editors) *Phloem Transport*. AR Liss, Inc., New York, pp 445-462.
- Pate, J.S. and D.J. Arthur (2000). Uptake and utilization of carbon and nitrogen in the phloem bleeding tree, Tasmanian blue gum (*Eucalyptus globulus*). *Australian Journal of Plant Physiology* **27**, 869-84.
- Pate, J.S. and W.D. Jeschke (1995). Role of stems in transport, storage and circulation of ions and metabolites by the whole plant. In: B. Gartner (editor), *Stems and Trunks: Their Roles in Plant Form and Function*. Academic Press, New York, pp 177-204.
- Pate, J.S. and D.B. Layzell (1981). Carbon and nitrogen partitioning in the whole plant - a thesis based on empirical modelling. In: J.D. Bewley (editor), *Nitrogen and Carbon Metabolism*. Martinus Nijhoff/Junk, The Hague, pp 94-134.
- Pate, J.S., E. Shedley, D.J. Arthur and M.A. Adams (1998). Spatial and temporal variations in phloem sap composition of plantation-grown *Eucalyptus globulus* *Oecologia* **117**, 312-22.
- Pereira, J.S., Chaves, M.M., Carvalho, P.O., Caldeira, M.C. and J. Tomé (1994). Carbon assimilation, growth and nitrogen supply in *Eucalyptus globulus* plants. In: J. Roy and E. Garner (editors) *A Whole Plant Perspective on Carbon-Nitrogen Interactions*. SPB Publishing, Netherlands, pp 79-89.
- Pereira, J.S., Chaves, M.M., Fonseca, F., Caldeira, M.C. and F. Torres (1992). Photosynthetic capacity of leaves of *Eucalyptus globulus* (Labill.) growing in the field with different nutrient and water supplies. *Tree Physiology* **11**, 381-9.
- Pereira, J.S., Linder, S., Araujo, M.C., Pereira, H., Ericsson, T., Borralho, N. and L. Leal. (1989). Optimization of biomass production in *Eucalyptus globulus* plantations. A case study. In: J.S. Pereira and J.J. Landsberg (editors) *Biomass Production by Fast-Growing Trees*. Kluwer, Dordrecht, pp 101-21.
- Pereira, J.S., J.D. Tenhunen, O.L. Lange, W. Beyschlag, A. Meyer and M.M. David (1986). Seasonal and diurnal patterns in leaf gas exchange of *Eucalyptus globulus* trees growing in Portugal. *Canadian Journal of Forestry* **16**, 177-184.
- Persson, B., Persson, A., Stahl, E. G. & Karlmatz, U. (1995). Wood Quality of *Pinus sylvestris* Progenies At Various Spacings. *Forest Ecology & Management* **76**, 127-138.
- Pfanz, H. (1999). Photosynthetic performance of twigs and stems of trees with and without stress. *Phyton-Annual Review of Botany* **A39**, 29-33.

- Pinkard E.A., Battaglia, M., Beadle, C.L. and P.J. Sands (1999). Modeling the effect of physiological responses to green pruning on net biomass production of *Eucalyptus nitens*. *Tree Physiology* **19**, 1-12.
- Pinkard, E. A., and Battaglia, M. (2001). Using hybrid models to develop silvicultural prescriptions for *Eucalyptus nitens*. *Forest Ecology and Management* **154**, 337-345.
- Pinkard E.A. and C.L. Beadle (1998). Regulation of photosynthesis in *Eucalyptus nitens* (Deane and Maiden) Maiden following green pruning. *Trees-Structure & Function* **12**, 366-376.
- Pinkard E.A., Beadle, C.L., Davidson, N.J. and M. Battaglia (1998). Photosynthetic responses of *Eucalyptus nitens* (Deane and Maiden) Maiden to green pruning. *Trees: Structure and Function* **12**, 119-29.
- Polglase, P.J., Jokela, E.J. and N.D. Comerford (1992a). Phosphorus, nitrogen and carbon fractions in litter and soil of southern pine plantations. *Journal of the Soil Science of America* **56**, 566-72.
- Polglase, P.J., Comerford, N.D., and E.J. Jokela (1992b). Nitrogen and phosphorus release from decomposing needle s of southern pine plantations. *Journal of the Soil Science of America* **56**, 914-20.
- Power, I., Dodd, M. and Thorold, B. (2000). The effects of thinning and pruning on light levels under a *Eucalyptus nitens* canopy. *New Zealand Tree Grower* August, pp 31-33.
- Proe, M.F. and P. Millard (1994). Relationship between nutrient supply, nitrogen partitioning and growth in young Sitka spruce (*Picea sitchensis*). *Canadian Journal of Forest Research* **25**, 1704-9.
- Proe, M.F. and P. Millard (1995). Effect of N supply upon the seasonal partitioning of N and P uptake in young Sitka spruce (*Picea sitchensis* (Bong.) Carr.). *Tree Physiology* **14**, 75-88.
- Pugnaire F.I. and F.S. Chapin (1993). Controls over nutrient resorption from leaves of evergreen Mediterranean species. *Ecology* **74**, 124-9.
- Raison, R.J., O'Connell, A.M., Khanna, P.K. and H. Keith (1993). Effects of repeated fires on nitrogen and phosphorus budgets and cycling processes in forest ecosystems. In: L. Trabaud and R. Prodhon (editors). *Fire in Mediterranean Ecosystems*. Ecosystem Research Report 5. Commission of the European Communities, pp 347-63.
- Raymond, C. & Cotterill, P. (1990). Methods of assessing crown form in *Pinus radiata*. *Silvae Genetica* **39**, 67-71.
- Reis, M.G.F., Barros, N.F. and J.P. Kimmins (1987). Nutrient accumulation over age sequences of *Eucalyptus grandis* W.Hill (ex. Maiden) growing on good and poor cerrado sites. Minas Gerais, Brazil. *Revista Ávore* **11**, 1-15.
- Reis, M.G.F., J.P. Kimmins, J.P. Rezende and N.F. Barros (198). Biomass accumulation over age sequences of *Eucalyptus grandis* W.Hill (ex. Maiden) growing on good and poor cerrado sites. Minas Gerais, Brazil. *Revista Ávore* **9**, 149-62.
- Reynolds J.F., Chen J.L., Harley P.C., Hilbert D.W., Dougherty R.L. and J.D. Tenhunen (1992). Modelling the effects of elevated CO<sub>2</sub> on plants: extrapolating leaf response to a canopy. *Agricultural and Forest Meteorology* **61**, 69-94.
- Richards, G. P., and Evans, D. W. (2000). "CAMFor User Manual v. 3.35." Australia Greenhouse Office, Canberra.
- Rolfe, G.L., Akhtar, M.A. and L.E. Arnold (1978). Nutrient distribution and flux in a mature oak-hickory forest. *Forest Science* **24**, 122-30.
- Running, S.W. and S.T. Gower (1991). FOREST-BCG, a general model for forest ecosystem processes for regional applications. II. Dynamic carbon allocation and nitrogen budgets. *Tree Physiology* **9**, 147-60.
- Ryan, M. (1990). Growth and maintenance respiration in stems in *Picea contorta* and *Picea engelmannii*. *Canadian Journal of Forest Research* **20**, 48-57.
- Ryan, M., Linder, S., Vose, J. & Hubbard, R. (1994). Dark respiration in pines. *Ecological Bulletin* **43**, 50-63.
- Ryan, M. G., Hubbard, R. M., Pongracic, S., Raison, R. J. & McMurtrie, R. E. (1996). Foliage, fine-root, woody-tissue and stand respiration in *Pinus radiata* in relation to nitrogen status. *Tree Physiology* **16**, 333-343.

- Sadras, V.O., A.J. Hall and D.J. Connor (1993). Light-associated nitrogen distribution profile in flowering canopies of sunflower (*Helianthus-annuus* L.) altered during grain growth. *Oecologia* **95**, 488-494.
- Sands, P.J. (1995). Modelling canopy production. II from single-leaf photosynthetic parameters to daily canopy photosynthesis. *Australian Journal of Plant Physiology* **22**, 603-614.
- Sands, P. J. (1996). Modelling canopy production. III. Canopy light-utilisation efficiency and its sensitivity to physiological and environmental variables. *Australian Journal of Plant Physiology* **23**, 103-114.
- Sands, P. J., Battaglia, M., and Mummery, D. (2000). Application of process-based models to forest management: Experience with PROMOD, a simple plantation productivity model. *Tree Physiology* **20**, 383-392.
- Saur, E., Nambiar, E.K.S. and D.N. Fife (2000). Foliar nutrient retranslocation in *Eucalyptus globulus*. *Tree Physiology* **20**, 1105-12.
- Schieving, F., Pons, T.L., Werger, M.J.A. and T. Hirose (1992a). The vertical distribution of nitrogen and photosynthetic activity at different plant densities in *Carex acutiformis*. *Plant and Soil* **14**, 9-17.
- Schieving, F., Pons, T.L., Werger, M.J.A. and T. Hirose (1992b). Canopy structure, nitrogen distribution and whole canopy photosynthetic carbon gain in growing and flowering stands of tall herbs. *Vegetatio* **102**, 173-81.
- Schieving, F. and H. Poorter (1999). Carbon gain in a multispecies canopy: the role of specific leaf area and photosynthetic nitrogen use efficiency in the tragedy of the commons. *New Phytologist* **143**, 201-11.
- Schmidt, S. and G.R. Stewart (1998). Transport, storage and mobilization of nitrogen by trees and shrubs in the wet/dry tropics of northern Australia. *Tree Physiology* **18**, 403-10.
- Schoettle, A.W. and W.K. Smith (1999). Interrelationships among light, photosynthesis and nitrogen in the crown of mature *Pinus contorta* ssp. *latifolia*. *Tree Physiology* **19**, 13-22.
- Schönau, A.P.G. (1981a). Seasonal changes in foliar nutrient content of *E.grandis*. *South African Forestry Journal* **119**, 1-4.
- Schönau, A P.G. (1981b). The effects of fertilizing on several foliar nutrient concentrations in *Eucalyptus grandis*. *Fertilizer Research* **2**, 73-87.
- Schönau, A.P.G. (1984). A factorial thinning experiment in *Eucalyptus grandis*. *Commonwealth Forestry review* **63**, 285-95.
- Schönau, A.P.G. and J. Coetzee (1989). Initial spacing, stand density and thinning in Eucalypt plantations. *Forest Ecology and Management* **29**, 245-66.
- Schönau, A.P.G. and M.A. Herbert (1988). Fertilising eucalypts at plantation establishment. *Forest Ecology and Management* **29**, 221-44.
- Sefton, C.A., Montagu, K.D., Atwell, B.J. and J.P. Conroy (2002). Anatomical variation in juvenile eucalypt leaves accounts for differences in specific leaf area and CO<sub>2</sub> assimilation rates. *Australian Journal of Botany* **50**, 301-10.
- Sellers, P.J., J.A. Berry, G.J. Collatz, C.B. Field and F.G. Hall (1992). Canopy reflectance, photosynthesis, and transpiration. III. A reanalysis using improved leaf models and a new canopy integration scheme. *Remote Sensing and the Environment* **42**, 187-216.
- Sheriff, D.W. and E.K.S. Nambiar (1991). Nitrogen nutrition, growth and gas exchange in *Eucalyptus globulus* Labill. seedlings. *Austrlaian Journal of Physiology* **18**, 37-52.
- Shoulders, E. (1989). An American test of drastic early thinning. In R. James and G. Tarlton (editors), *New Approaches to Spacing and Thinning in Plantation Forestry*. FRI, Rotorua, New Zealand, pp 215-222.
- Sims, D.A. and R.W. Percy (1993). Sunfleck frequency and duration affects growth rate of the understorey plant, *Alocasia Macrorrhiza*. *Functional Ecology* **7**, 683-689.
- Skillman, J.B, Strain, B.R. and C.B. Osmond (1996). Contrasting patterns of photosynthetic acclimation and photoinhibition in two evergreen herbs from a winter deciduous forest. *Oecologia* **107**, 446-455.
- Smith, F.W., D.A. Sampson and J.N. Long (1991). Comparison of leaf area index estimates from tree allometrics and measured light interception. *Forestry Science* **37**, 1682-1688.

- Smith, N.J. (1991). Predicting radiation attenuation in stands of Douglas-fir. *Forestry Science* **37**, 1213-1223.
- Smith, N.J. (1993). Estimating leaf area index and light extinction coefficients in stands of Douglas-fir (*Pseudotsuga menziesii*). *Canadian Journal of Forestry Research* **23**, 317-321.
- Snowdon, P. (1991). A ratio estimator for bias correction in logarithmic regressions. *Canadian Journal of Forest Research* **21**, 720-724.
- Speck, T., Spatz, H. & Voellehner, D. (1990). Contributions to the biomechanics of plants. I. Stabilities of plant stems with strengthening elements of different cross-sections against weight and wind forces. *Botanica Acta* **103**, 111-122.
- Sprugel, D.G., Hinckley T.M., and W. Schaap (1991). The theory and practice of branch autonomy. *Annual Review of Ecology and Systematics* **22**, 309-34.
- Stage, A. (1973). Prognosis model for stand development. USDA Forest Service.
- Stenberg, P. (1998). Implications of shoot structure on the rate of photosynthesis at different levels in a coniferous canopy using a model incorporating grouping and penumbra. *Functional Ecology* **12**, 82-91.
- Takenaka, A. (1994). A simulation model of tree architecture development based on growth response to local light environment. *Journal of Plant Research* **107**, 321-330.
- Takenaka, A. (1997). Structural variation in current-year shoots of broad-leaved evergreen tree saplings under forest canopies in warm temperate Japan. *Tree Physiology* **17**, 205-210.
- Takenaka, A. (2000). Shoot growth responses to light microenvironment and correlative inhibition in tree seedlings under a forest canopy. *Tree Physiology* **20**, 987-991.
- Tang, Y.T., I. Washitani and T. Tsuchiya (1988). Fluctuations of photosynthetic photon flux density within a *Miscanthus sinensis* canopy. *Ecological Research* **3**, 253-266.
- Thornley, J. H. M. (1991). A transport-resistance model of forest growth and partitioning. *Ann. Bot.* **68**, 211-226.
- Thornley, J.H.M. (1998). Dynamic model of leaf photosynthesis with acclimation to light and nitrogen. *Annals of Botany* **81**, 421-30.
- Thornley, J. H. M. (2002). Instantaneous Canopy Photosynthesis: Analytical expressions for sun and shade leaves based on exponential light decay down the canopy and an acclimated non-rectangular hyperbola for leaf photosynthesis. *Annals of Botany* **89**, 451-458.
- Tromp, J. (1983). Nutrient reserves of roots of fruit trees, in particular carbohydrates and nitrogen. *Plant and Soil* **71**, 401-13.
- Turnbull, M. H., Doley, D. & Yates, D. J. (1993). The dynamics of photosynthetic acclimation to changes in light quantity and quality in 3 Australian rainforest tree species. *Oecologia* **94**, 218-228.
- Turner, J. (1980). Nitrogen and phosphorus distribution in naturally regenerated *Eucalyptus* spp. and planted Douglas-fir. *Australian Forestry Research* **10**, 289-94.
- Tuvfer, J. and M.J. Lambert (1983). Nutrient cycling within a 27-year-old *Eucalyptus grandis* plantation in New South Wales. *Forest Ecology and Management* **6**, 155-68.
- Tustin, D. S., Cashmore, W. M. & Bensley, R. B. (1998). The influence of orchard row canopy discontinuity on irradiance and leaf area distribution in apple trees. *The Journal of Horticultural Science & Biotechnology* **73**, 289-297.
- Valladares. (1999). Architecture, ecology and evolution of plant crowns. In: F.V. Pugnaire (editor), *Handbook of Functional Plant Ecology*. Dekker, New York, pp 121-194.
- Vanninen, P., Ylitalo, H., Sievanen, R. & Makela, A. (1996). Effects of age and site quality on the distribution of biomass in scots pine (*Pinus sylvestris* L.). *Trees-Structure & Function* **10**, 231-238.
- Vapaavuori, E.M and A.H. Vuorinen (1989). Seasonal variation in the photosynthetic capacity of a willow (*Salix* cv. *Aquatica gigantea*) canopy. 1 Changes in the activity and amount of ribulose1,5-bisphosphate carboxy;ase-oxygenase and the content of nitrogen and chlorophyll at different levels in the canopy. *Tree Physiology* **5**, 423-44.
- von Caemmerer, S. (2000). *Biochemical models of leaf photosynthesis*. Melbourne, CSIRO publishing.

- Wang, Y.P. (2000). A refinement to the two-leaf model for calculating canopy photosynthesis. *Agricultural and Forest Meteorology* **101**, 143-50.
- Wang, Y.P. and P.G. Jarvis (1990). Description and validation of an array model-MAESTRO. *Agricultural & Forest Meteorology* **51**, 257-280.
- Wang, Y. P., and P.G. Jarvis (1991). Influence of crown structural properties on PAR absorption, photosynthesis and transpiration in Sitka spruce: application of a model (MAESTRO). *Tree Physiology* **7**, 297-316.
- Wang, Y.P. and R.W. Leuning (1998a). A two-leaf model for canopy conductance, photosynthesis and partitioning of available energy I. - Model description and comparison with a multi-layered model. *Agricultural & Forest Meteorology* **91**, 89-111.
- Wang, Y.P., A. Rey and P.G. Jarvis (1997). Carbon balance of young birch trees grown in ambient and elevated atmospheric CO<sub>2</sub> concentrations. *Global Change Biology* **8**, 797-807.
- Warren, C.R. and M.A. Adams (2001). Distribution of N, rubisco and photosynthesis in *Pinus pinaster* and acclimation to light. *Plant, Cell and Environment* **24**, 597-609.
- Warren, C.R., Adams, M.A. and Chen, Z-L. (2000a). Is photosynthesis related to concentrations of nitrogen and Rubisco in leaves of Australian native plants? *Australian Journal of Plant Physiology* **27**, 407-16.
- Warren, C.R., Chen, Z-L. and M.A. Adams (2000b). Effect of N source on concentration of rubisco in *Eucalyptus diversicolor*, as measured by capillary electrophoresis. *Physiologia Plantarum* **110**, 52-8.
- Weinstein, D. A., and Beloin, R. (1990). Evaluating effects of pollutants on integrated tree processes: a model of carbon, water and nutrient balances. In "Process Modelling of Forest Growth Responses to Environmental Stress" (R. K. Dixon, R. S. Meldahl, G. A. Ruark and W. G. Warren, eds.), pp 313-323. Timber Press, Portland, Oregon.
- Wendler, C., Putzer, A. and A. Wild (1992). Effect of glufosinate (phosphinothricin) and inhibitors of photorespiration on photosynthesis and ribulose-1,5-bisphosphate carboxylase activity. *Journal of Plant Physiology* **139**, 666-71.
- Wendler, R. and Carvalho, P.O., Pereira, J.S. and P. Milard (1995). Role of nitrogen remobilization from old leaves for new leaf growth of *Eucalyptus globulus* seedlings. *Tree Physiology* **15**, 679-83.
- White, D.A., C.L. Beadle, P.J. Sands, D. Worledge and J.L. Honeysett (1999). Quantifying the effect of cumulative water stress on stomatal conductance of *Eucalyptus globulus* and *Eucalyptus nitens*: a phenomenological approach. *Australian Journal of Plant Physiology* **26**, 17-27.
- Whitehead, D. (1978). The estimation of foliage area from sap wood basal area in scots pine. *Forestry* **51**, 137-149.
- Whitehead, D.G., J.C. Grace and M.J.S., Godfrey (1990). Architectural distribution of foliage in individual *Pinus radiata* D.Don crowns and the effects of clumping on radiation interception. *Tree Physiology* **7**, 135-155.
- Wilkinson, G. R., and Neilson, W. A. (1995). Implications of early browsing damage on the long term productivity of eucalypt forests. *Forest Ecology and Management* **74**, 117-124.
- Wood, M., Stephens, N., Allison, B., and Howell, C. (2001). "Plantations of Australia - A report from the National Plantation Inventory and National Farm Forest Inventory," Bureau of Rural Sciences, Canberra.
- Wong, S.C., Kriedemann, P.E.m and G.D. Farquhar (1992). CO<sub>2</sub> x nitrogen interaction on seedling growth of four species of Eucalypt. *Australian Journal of Botany* **40**, 457-72.
- Yost, R.S., DeBell, D.S., Whitesell, C.D. and S.C. Miyasaka (1987). Early growth and nutrient status of *Eucalyptus saligna* as affected by nitrogen and phosphorus fertilisation. *Australian Forest Ecology* **17**, 203-14
- Zhang, S., Burkhart, H. E. and Amateis, R. L. (1996). Modeling individual tree growth for juvenile loblolly pine plantations. *Forest Ecology & Management* **89**, 157-172.

# Appendix 1. Industry and Public Liaison

The following leaflets, field days and publicity activities have been undertaken as part of this project.

1. Field day on site with Landowner and WAPRES staff including preliminary presentation of field work, Manjimup November 1999. Attendance, 12 people.
2. Battaglia M, Pinkard EA (2000) Using hybrid models to develop silvicultural prescriptions for cool temperate eucalypts. In 'The future of eucalypts for wood products. Proceedings of IUFRO Conference, Launceston'. Eds L Henderson, G Waugh, G Nolan, and P Bennett. Launceston, Tasmania, 349-356.
3. Henskens FL, Battaglia M, Cherry ML, Beadle CL (2001). How tree form changes with spacing and why: implications for farm foresters. Technical Report No. 51. pp 25 (CRC-SPF, Hobart, Tasmania).
4. Henskens, F., Battaglia, M., and Cherry, M. (2000). Tackling alternative layouts: silvicultural support for farm foresters. In "Opportunities for the New Millennium, Australian Forest Growers Biennial Conference, 4-6 September 2000", Cairns, Queensland.
5. Henskens, F., Battaglia, M., and Cherry, M. (2001). How trees change with spacing and why. In "Biennial Conference of the Institute of Foresters in Australia, 18-25 April 2001", Fremantle Western Australia.
6. Battaglia M (2001) Silvicultural decision support with process-based forest growth models. Beyond the Black Stump 24, CRC-SPF Information Leaflet.
7. Henskens, F. (2003) Turnover models more suitable for predicting N and productivity in eucalypt plantations. Beyond the Black Stump 36, CRC-SPF Information Leaflet.

## Appendix 2. Scientific Publications

- Pinkard, E. A., and Battaglia, M. (2001). Using hybrid models to develop silvicultural prescriptions for *Eucalyptus nitens*. *Forest Ecology and Management* **154**, 337-345.
- Henskens, F., Battaglia, M., Cherry, M., and Beadle, C. L. (2001). Physiological basis of spacing effects on tree growth and form in *Eucalyptus globulus*. *Trees Structure and Function* **15**, 365-377.