Spatial distributions of foliar nitrogen and phosphorus in crowns of *Eucalyptus grandis*

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Summary. *Eucalyptus grandis* trees were grown in plantations with and without added fertiliser to examine the effects of plant nutrition on photosynthesis and growth. Leaves were sampled from known locations within canopies of selected trees and leaf N and P concentrations were measured. Contour maps of N and P distributions were then produced for crowns of trees aged between 6 and 16 months. Gas exchange measurements on sample leaves were used to estimate parameters of a model of C₃ photosynthesis as a function of leaf N and P concentrations. Linear relationships were obtained between model parameters and leaf N concentration, but P appeared to be present in excess, since no correlation was found with P concentration. Photosynthetic light response curves were calculated for model leaves with differing N concentrations. The curves show that optimal concentrations of N in leaves depend on mean levels of irradiance during growth.

Key words: *Eucalyptus grandis* – Canopy – N and P distributions – Photosynthesis-nitrogen response

*Eucalyptus grandis* Hill ex Maiden is native to Australia but has been planted widely in South America, southern Africa and India to provide timber and pulp wood (Burgess 1988). Under favourable conditions, *E. grandis* is capable of reaching 20 m in height in 3 years, and volume growth rates in excess of 50 m³ ha⁻¹ yr⁻¹ have been reported (Campinhos 1980).

Significant growth responses of *E. grandis* to applied nutrients have been reported, and fertilisers are applied routinely during plantation establishment (Schönau and Herbert 1989). However, quite low rates of fertiliser application were recommended by these authors and there has been a lack of research to determine potential growth rates under conditions of high nutrient availability in the field. Studies to examine the response of *E. grandis* to a high rate of fertiliser application, in combination with irrigation have been described by Cromer et al. (1991).

Despite an extensive literature on responses of *E. grandis* and other eucalypts to nutrient supply (Schönau and Herbert 1989), we have only a meagre understanding of the mechanisms responsible for growth as a function of nutrient availability. Productivity in trees is directly linked to the amount of leaf area that intercepts radiation and to the efficiency with which radiation is converted to biomass by photosynthesis (Linder 1985; Turnbull et al. 1988). Clearly, high rates of plant growth are possible only when a large fraction of a plant’s leaf area achieves high rates of net assimilation. Continued growth can only be sustained by production of further leaf area, at least until canopy closure. Analysis of plant response to nutrient supply should thus include an examination of how photosynthesis rates are affected by leaf nutrition, particularly nitrogen (N) and phosphorus (P) contents.

Most of the nitrogen within leaves is used in enzymes involved in photosynthesis and a strong correlation is often observed between photosynthetic capacity and leaf nitrogen concentration. Leaves which receive greater irradiances should thus have relatively higher N concentrations than shaded leaves, if optimum use is to be made of the nitrogen available to the plant (Field 1983; Field and Mooney 1986). Calculations by Field (1983) showed that N distributions within plant species examined were close to optimum for canopy assimilation. Hirose and Werger (1987) extended this concept and postulated that N concentrations should fall exponentially with depth in closed canopies because irradiance decreases exponentially.

This paper examines the effects that leaf N and P levels have on rates of photosynthesis and leaf production in crowns of young *E. grandis* trees grown in plantations subject to either zero or high levels of fertilisation. Information on leaf area index, specific leaf area and
crown biomass is also provided. Leaf gas exchange measurements were used to estimate values of two key parameters \((J_{\text{max}}, V_{\text{cmax}})\) in the model of C\(_3\) photosynthesis developed by Farquhar et al. (1980) and by Farquhar and von Caemmerer (1982). These parameters respectively quantify maximum photosynthetic electron transport rates and the maximum catalytic activity of the enzyme RuBisCO, which incorporates CO\(_2\) into the Calvin cycle. It is shown that parameter values were dependent on leaf N concentrations but were not dependent on P. Mathematical functions are presented in a companion paper (Leuning et al. 1991), to describe spatial distributions of light and leaf N concentrations within tree canopies. The functions are then combined with correlations between \(J_{\text{max}}\) and \(V_{\text{cmax}}\) and leaf N concentration presented in this paper to calculate carbon assimilation distributions within the crowns of several trees. This allows daily assimilation rates calculated for sampled trees to be compared with hypothetical trees with uniform N distributions.

**Materials and methods**

An experimental plantation was grown at Toolara (26°12' S, 152° 45' E), near Gympie in south-east Queensland. Soils at the site are highly weathered and low in plant nutrients, particularly nitrogen, phosphorous, calcium and potassium. Trees were planted on a rectangular grid of 3.4 × 2.65 m, corresponding to a density of 1110 trees ha\(^{-1}\). The plantation included seedlots of E. grandis collected from four locations, but only results from a Coff's Harbour seed orchard (CSIRO seedlot 15641) are reported here. Experimental treatments consisted of zero or high rates of fertiliser application, combined factorially with either no irrigation or with irrigation to maintain soil moisture at field capacity. The treatments are designated - F - I, - F + I, + F - I and + F + I, respectively. Fertiliser maintenance on all plots.

Leaves were sampled randomly throughout the canopies of selected trees and the length, width and area of fresh leaves were measured. Harvested leaves were dried at 70 °C, weighed, and ground to pass through a 20-µm sieve, digested in sulfuric acid and hydrogen peroxide and analysed for N and P concentrations using automated spectrometric techniques described by Heffernan (1985).

Spatial coordinates of harvested leaves were calculated from measurements of height to branch base, branch length, branch elevation angle, total number of leaves per first order branch and the insertion number of the sample leaf. It was assumed that leaves were arranged regularly on their respective branches and that they were distributed symmetrically with respect to azimuth. The result calculations allowed construction of two-dimensional contour diagrams for N and P concentrations as a function of tree height and width. Leaf positions and nutrient concentrations were determined for one tree in each treatment at 6, 9, 12 and 16 months after seedling establishment in February 1987. Treatment + F - I was not sampled at 16 months.

Total crown leaf area and biomass was estimated using allometric relationships presented by Cromer et al. (1991).

Gas exchange measurements were made during November 1987 and February 1988 using fully expanded leaves located in the upper portion of the crown. A controlled-environment minicuvette (Bingham Interspace, Hyde Park, Utah) was used for the measurements and Leuning (1990) provided a detailed description of the apparatus and the experimental protocol adopted. Briefly, leaves placed in the cuvette were exposed to high irradiance (1700-2000 µmol quanta m\(^{-2}\) s\(^{-1}\)) and to various external CO\(_2\) mol fractions increasing in steps from ca. 50 to 1110 µmol mol\(^{-1}\). Irradiance was then decreased in steps from ca. 2000 to 0 µmol quanta m\(^{-2}\) s\(^{-1}\) at high external CO\(_2\) (ca. 1000 µmol mol\(^{-1}\)). Leaf temperature was maintained at 25 ± 0.2 °C and relative humidity was maintained at ca. 0.5 for most measurements, except at low irradiances when transpiration was insufficient to maintain humidity levels at minimum air flow rates. Leaves were allowed to equilibrate for at least 20 min at each setting before gas exchange measurements were recorded.

Assimilation rates, stomatal conductances and intercellular CO\(_2\) mol fractions were also determined using a portable photosynthesis apparatus (LI-6200, Li-Cor Inc., Lincoln, Neb.). Raw data were analysed according to theory presented by Leuning and Sands (1989). Two quartz-iodide projector lamps were used to provide steady irradiances and a quantum sensor was used to measure photon flux densities.

**Theory**

Analysis of leaf gas exchange measurements utilized a model of C\(_3\) photosynthesis described by Farquhar et al. (1980) and Farquhar and von Caemmerer (1982). The model may be written as

\[
A = \min(A_c, A_q) - R_d
\]

where \(A_c\) and \(A_q\) are assimilation rates limited by Rubisco activity, and by RuP\(_2\) regeneration, respectively. \(R_d\) is day respiration. The term \(\min(A_c, A_q)\) represents the minimum of \(A_c\) and \(A_q\).

When Rubisco activity is limiting, assimilation is given by

\[
A_c = V_{\text{cmax}} \frac{c_i - \Gamma^*}{c_i + K_c(1 + c_o/K_o)}
\]

in which \(V_{\text{cmax}}\) is the maximum catalytic activity of RuBisCO in the presence of saturating levels of RuP\(_2\) and CO\(_2\). \(c_i\) is intercellular CO\(_2\) mol fraction, \(c_o\) is intercellular oxygen mol fraction, \(\Gamma^*\) is the CO\(_2\) compensation point in the absence of day respiration and \(K_c\) and \(K_o\) are Michaelis constants for CO\(_2\) and O\(_2\), respectively. RuBisCO activity is likely to limit assimilation rates under conditions of high irradiance and low \(c_o\).

When photosynthetic electron transport limits RuP\(_2\) regeneration, assimilation rate is given by

\[
A_q = J \frac{c_i - \Gamma^*}{c_i + 2\Gamma^*}
\]

where \(J\) is the maximum rate of photosynthesis at saturating \(c_i\) for a given absorbed photon irradiance, \(Q\). Farquhar and Wong (1984) used a non-rectangular hyperbolic function to described \(J\) in terms of \(Q\), viz.

\[
\partial J^2 - (\partial Q + J_{\text{max}})J + \alpha QJ_{\text{max}} = 0
\]

where \(\partial\) determines the shape of the non-rectangular hyperbola, \(J_{\text{max}}\) is the potential rate of whole-chain electron transport (expressed here as equivalents of µmol CO\(_2\) m\(^{-2}\) s\(^{-1}\)) and \(\alpha\) is quantum efficiency. RuP\(_2\) re-

\(^1\) Abbreviations used: RuP\(_2\), Ribulose-1,5-bisphosphate; Rubisco, RuP\(_2\) carboxylase-oxygenase