

# **An overview of recent nutrition research for the rapidly expanding *Eucalyptus* plantation industry in Australia**

January 2001

C. J. Weston

School of Forestry

University of Melbourne

Creswick, 3363

[weston@unimelb.edu.au](mailto:weston@unimelb.edu.au)

## JOSEPH WILLIAM GOTTSTEIN MEMORIAL TRUST FUND

The Joseph William Gottstein Memorial Trust Fund was established in 1971 as a national educational Trust for the benefit of Australia's forest products industries. The purpose of the fund is *"to create opportunities for selected persons to acquire knowledge which will promote the interests of Australian industries which use forest products for the production of sawn timber, plywood, composite wood, pulp and paper and similar derived products."*

Bill Gottstein was an outstanding forest products research scientist working with the Division of Forest Products of the Commonwealth Scientific Industrial Research Organization (CSIRO) when tragically he was killed in 1971 photographing a tree-felling operation in New Guinea. He was held in such high esteem by the industry that he had assisted for many years that substantial financial support to establish an Educational Trust Fund to perpetuate his name was promptly forthcoming.

The Trust's major forms of activity are,

1. Fellowships - each year applications are invited from eligible candidates to submit a study programme in an area considered of benefit to the Australian forestry and forest industries. Study tours undertaken by Fellows have usually been to overseas countries but several have been within Australia. Fellows are obliged to submit reports on completion of their programme. These are then distributed to industry if appropriate.
2. Seminars - the information gained by Fellows is often best disseminated by seminars as well as through the written reports.
3. Wood Science Courses - at approximately two yearly intervals the Trust organises a week-long intensive course in wood science for executives and consultants in the Australian forest industries.
4. Study Tours - industry group study tours are arranged periodically and have been well supported.

Further information may be obtained by writing to,

The Secretary,  
J.W. Gottstein Memorial Trust Fund,  
Private Bag 10,  
Rosebank M.D.C.,  
Clayton, Victoria, 3169 Australia

The information contained in this report is published for the general information of industry. Although all reasonable endeavour has been made to verify the accuracy of the material, no liability is accepted by the Author for any inaccuracy therein, nor by the Trustees of the Gottstein Memorial Trust Fund. The opinions expressed are those of the author and do not necessarily represent the opinions of the Trustees.

Copyright © Trustees of the J.W. Gottstein Memorial Trust Fund 2000. All rights reserved. No part of this publication may be reproduced, stored in a retrieval system, or transmitted in any form or by any means, electronic, mechanical, photocopying, recording or otherwise without the prior written permission of the Trustees.

# An overview of recent nutrition research for the rapidly expanding *Eucalyptus* plantation industry in Australia

<b>EXECUTIVE SUMMARY .....</b>	<b>4</b>
<b>ACKNOWLEDGEMENTS .....</b>	<b>6</b>
<b><i>EUCALYPTUS</i> PLANTATION DEVELOPMENT IN AUSTRALIA .....</b>	<b>7</b>
<b>PRODUCTIVITY OF <i>EUCALYPTUS</i> PLANTATIONS.....</b>	<b>8</b>
EFFECTS OF ADDED NUTRIENTS ON EUCALYPT PRODUCTIVITY .....	10
<i>Starter fertilizer - application at plantation establishment.....</i>	<i>10</i>
<i>Corrective fertiliser to prevent nutrient deficiency .....</i>	<i>11</i>
<i>Later-age fertiliser or application following canopy development.....</i>	<i>13</i>
<i>Replacement fertiliser for nutrients lost during harvesting and regeneration .....</i>	<i>14</i>
IDENTIFYING RESEARCH NEEDS.....	14
NUTRIENT CYCLING IN <i>EUCALYPTUS</i> PLANTATIONS .....	15
<i>Managing nutrients in plantations .....</i>	<i>16</i>
<b>IMPLICATIONS OF RESEARCH FOR NUTRIENT MANAGEMENT.....</b>	<b>22</b>
<b>REFERENCES .....</b>	<b>25</b>

## Executive summary

The rapid expansion of eucalypt plantations in Australia, now in excess of 50,000 hectares of new plantations annually, is mainly on private land, with areas ranging in size from farm windbreaks and small wood lots to broad-scale plantings. Due to the fragmented nature of plantings, the wide range of planting sites and the proliferation of plantation management companies, there is an emerging need for collaborative research to maintain and improve plantation productivity through nutrient management. With the addition of nitrogen and phosphorus at establishment, the ten-year productivity of *Eucalyptus globulus* can be increased by between 30% and 100%, depending on site characteristics.

Because fertilizer purchase and application is a significant component of establishment costs, the profitability of all plantation enterprises is dependent on the appropriate matching of nutrient prescriptions to site and species characteristics. This involves identifying those sites where nutrient addition will increase productivity and developing appropriate fertilizer regimes.

Nutrition research over the last decade has established the upper bounds for production in only a few of the major plantation development areas. Productivity limits will also change with the planting of superior genotypes, which may require different fertilizer mixtures and rates of application. There is a significant challenge to develop and extend knowledge of nutrient limitation to productivity to the diverse range of planting sites, many of which have received decades of nitrogen and phosphorus enrichment through the use of sub-clover and phosphorus fertilizers. Careful recording of plantation productivity and widespread application of soil and foliage testing will be essential for the successful fostering of Australia's eucalypt plantation enterprise.

New collaborations between the diverse group of plantation establishment companies, research providers, analytical laboratories and funding agencies should be forged to develop effective solutions to managing nutrients in eucalypt plantations. In addition, the refinement and application of novel and effective methods for improving nutrient prescription will be greatly assisted by a cooperative approach. This in turn would speed the development of industry-wide solutions to nutrient management and improve technology transfer to the diverse group of plantation growers.

## **Acknowledgements**

I thank the Gottstein Foundation for providing funds to support study leave in Portugal during 1997 as a component of this study. This report contains some data derived from long-term trials developed originally from a National Afforestation Program (NAP) Grant (Number 49 in 1988) to John Cameron and Phil Whiteman at AP Plantations Pty Ltd, whom I thank for permission to use the data. Since their establishment in 1989, research in these NAP trials has been funded by AP Plantations, the Australian Research Council and the University of Melbourne. Several postgraduate students have developed aspects of the work discussed in this report and in particular I am grateful for many hours of fruitful discussions with Dr Neeta Hooda and Dr Andrew Bussau. I am grateful to two anonymous expert reviewers whose insight and thoroughness improved this report.

## ***Eucalyptus* plantation development in Australia**

Plantations of *Eucalyptus* species are increasing by tens of thousands of hectares annually in Australia, with most activity in Western Australia, New South Wales, Victoria and Tasmania (NFI 1998). For example, about 21,000 hectares of eucalypts were planted in Western Australia in 1998 (NFI 1998). Australia-wide, new areas planted to eucalypts are probably well in excess of 50,000 hectares, with *E. globulus* the dominant species.

Government policy and investment are driving eucalyptus plantation development; key players include international fibre consumers, superannuation fund managers, and established national wood-fibre consumers. Security of wood-fibre supply is a strong motivating force driving plantation expansion in Australia by both national and international wood-fibre consumers.

Government policy to encourage the rapid expansion of *Eucalyptus* plantations has targeted a three-fold increase of the 1996 area by 2020 (VPFC 1998). Unlike the rapid expansion of *Pinus* plantations in the 1960s and 1970s —involving extensive clearing of native forests to create the land base — *Eucalyptus* plantations are being established on a wide range of already cleared sites with various past land uses. For example, in south-western Victoria, significant areas of former grazing land are currently being converted to eucalypt plantations: a consequence in part of the decline in the profitability of sheep grazing for wool production.

Many planting sites are in the 500-900 mm annual rainfall zone, with winter dominated rainfall patterns and soil water deficits over the summer and early autumn months. There is limited experience in growing eucalypts on these sites, where water supply inhibits growth for several of the warmest months, as most plantation efforts with eucalypts were restricted to rainfall zones above 900 mm per annum until the late 1970s.

Due to this variety of planting environments, which range from sites which have been improved under pastoral and cropping management to relatively infertile sandy sites, there is an urgent need to develop site specific establishment and fertilizer practices. Working from a poor knowledge base could lead on the one hand to excessive application of nutrients — which is costly and potentially polluting of ground

water — while on the other hand sub-optimal plantation survival and growth may result from poorly formulated fertilizer regimes.

Relationships between productivity and nutrients in soil and foliage are poorly developed in *Eucalyptus* species relative to *Pinus radiata*, where foliage diagnosis has been a routinely applied tool in plantation management for several decades, both in Australia and elsewhere (e.g. Raupach, 1967; Bevege and Richards, 1971; Will, 1985). *Eucalyptus* nutrition research to date has dealt mainly with nitrogen and phosphorus limitation to growth (e.g. Cromer *et al.*, 1981; Bennett *et al.*, 1997); there are few published (i.e. easily accessible) reports detailing growth responses to and deficiencies of other nutrients. The data published on other nutrients (e.g. Dell and Malajczuk, 1994; Shedley *et al.*, 1995; Dell, 1996) suggest the elements most likely to limit growth across the broad range of planting sites in Australia are nitrogen, phosphorus, potassium, boron, zinc and copper.

Reports to date have usually addressed deficiencies at the seedling stage and first two years of growth. The case for further work in mature field-grown trees seems clear, as is the need for the wide dissemination of results in the published literature. The success and profitability of these plantations depends in part on optimizing productivity by identifying and correcting nutrient limitations.

This report reviews the recent national and international literature on nutrition of *Eucalyptus* plantations and identifies implications for management of plantation productivity in Australia. Aspects of nutrient management and productivity are discussed in the light of current knowledge and recommendations outlined for further research to improve nutrient management.

## **Productivity of *Eucalyptus* plantations**

The productivity of eucalypt plantations world-wide varies according to site characteristics and silvicultural inputs, with volume production ranging from as low as 6 m<sup>3</sup> ha<sup>-1</sup> year<sup>-1</sup> on poor sites to over 50 m<sup>3</sup> ha<sup>-1</sup> year<sup>-1</sup> on moist and relatively nutrient rich sites. Where rainfall approaches 2000 mm per year, very high rates of production have been achieved, such as the 60 m<sup>3</sup> ha<sup>-1</sup> year<sup>-1</sup> claimed for the fifteen-year rotations of *E. nitens* in coastal Chile (Prado and Toro, 1996). Relatively high productivity has been reported from good sites in South Africa (25 m<sup>3</sup> ha<sup>-1</sup> yr<sup>-1</sup>; Herbert, 1996) and Argentina (28 m<sup>3</sup> ha<sup>-1</sup> yr<sup>-1</sup>; Dalla-Tea and Marco, 1996), where intensive silviculture has been practiced for several decades. In Australian plantations some of the highest



productivity has been reported in *E. regnans* ( $>30 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$  over twenty to thirty year rotations). *E. globulus* plantations range from about  $10 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$  to  $28 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$  over ten year rotations on a range of sites, with *E. nitens* producing over  $30 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$  (over ten years) on a good site (Weston unpublished data).

A key concern for growers and investors in *E. globulus* plantations on the relatively dry sites in southern Australia is maintaining tree health and productivity in the face of periodic drought (Pate and Arthur, 1998; Aggangan *et al.*, 1999). It is possible that some recently planted sites will be marginal for *E. globulus* growth; similar sites will most likely be established in the future with more drought tolerant species such as *E. botyroides* and *E. cladocalyx*. There is a much stronger emphasis on site selection in western Australia since the occurrence of drought deaths there during the 1990s.

Apart from limited plantings in the 1960s and 1970s, both *E. globulus* and *E. nitens* were not planted widely for wood production in Australia until the mid-1980s. Consequently the industry is currently developing the technology for *Eucalyptus* plantations dominated by these species. In terms of rainfall zone, it is perhaps the plantations in the 500-700 mm per annum rainfall areas where silviculture, including species selection, is most in need of refinement. The productivity of *E. globulus* planted mostly on lowland sites down to 500 mm per annum rainfall is of greatest concern due to the uncertainties associated with both low and seasonally pronounced rainfall (White *et al.*, 1996). This assertion is supported by reports of the productivity of the first ten-year rotations of intensively established *E. globulus* plantations — many of which are below expectation (e.g. Hafner, 2000).

There seem to be fewer potential productivity problems associated with *Eucalyptus* plantations on sites with more than 900 mm per annum rainfall. For example, early experience with *E. nitens* (usually planted on cooler upland sites) has shown up to  $350 \text{ m}^3$  of timber at ten years (Weston unpublished data). In Victoria and Tasmania, these wetter sites are usually associated with well-structured and friable clay-loam soil, and temperature probably limits growth more than available moisture once weed control and nutrition have been addressed.

## Effects of added nutrients on eucalypt productivity

There is no doubt that, on many sites, fertilizers will improve survival and productivity. Research to identify sites requiring nutrient amendment is discussed below according to the four fertilizer practices defined by Flinn (1984), and summarized below:

- *Starter fertilizer* to provide planted seedlings with a competitive advantage;
- *Corrective fertilizer* where one or more applications corrects or prevents the onset of nutrient deficiency;
- *Later-age fertilizer* involving the application of nutrients to stands following full canopy development; and,
- *Replacement fertilizer* where nutrients lost during harvesting and regeneration are subsequently replaced.

With these fertilizer practices in mind, the following observations relate to the recent developments in eucalypt nutrition management.

### Starter fertilizer - application at plantation establishment

Eucalypt productivity has increased in response to establishment applications of phosphorus and/or nitrogen on almost all sites investigated (Cromer *et al.*, 1981; Yost *et al.*, 1987; Schonau and Herbert, 1989; Birk and Turner, 1992; Cromer *et al.*, 1993a; Bennett *et al.*, 1996; Herbert, 1996). There is strong evidence that *E. globulus* and most other commercially important *Eucalyptus* species require nitrogen and phosphorus, and sometimes potassium and micronutrients, for successful establishment and optimum productivity (Cromer *et al.*, 1981; Ritson *et al.*, 1991; Herbert, 1996; Bennett *et al.*, 1997). In Gippsland, productivity of nitrogen and phosphorus fertilized trees is double that of unfertilized trees in ten-year-old stands of *E. globulus* on uniform clay-loam soils (Weston unpublished data). Productivity is further improved by the inclusion of potassium on some sites in Gippsland, but none of the Gippsland sites has responded to basal dressings of boron, zinc, copper and molybdenum (Bennett *et al.*, 1996). There are reports of boron deficiency in eucalypt plantations in north-east Victoria (Hopmans personal communication), but these data have not been widely disseminated in the published literature as yet.

There is good evidence to show that growth on previous agricultural land is less responsive to fertilizer addition due to higher nutrient availability resulting from years of fertilizer addition (Weston *et al.*, 1991). Furthermore, growth on previous agricultural land is usually more uniform and of higher productivity relative to cleared forest sites (Skinner and Attiwill, 1981; Weston *et al.*, 1991).

Experience to date clearly shows that effective suppression of competing species for at least one year after planting is essential for the survival and rapid early growth of eucalypts. Fertilizer application should accompany first-year weed control to promote rapid early growth, which promotes survival through height growth to resist grazing pressure. Where plantations are remote from native forests and the risk of wallaby browsing of seedlings — or where the plantations are fenced from grazing animals — the risks from grazing pressure can be managed in other ways.

Nutrients have been widely used in the establishment of *P. radiata* plantations since the 1970s and the current practices have resulted from a detailed research effort (e.g. Nambiar and Fife, 1987; Carlyle, 1995). The main elements supplied in fertilizer to *P. radiata* at establishment in Australia are P, K, Cu and Zn; nitrogen has been dropped from most prescriptions as the supply from soil mineralization is apparently adequate over the first few years (Smethurst and Nambiar, 1990a, 1990b). This difference in nitrogen fertilizer requirement between pines and eucalypts is most likely due to the different growth trajectories of eucalypts and pines, well exemplified in the study of Myers *et al.* (1996) on an effluent irrigated site near Wagga Wagga. Eucalypts initially grow faster than pines and place a higher demand on soil nitrogen reserves, as shown by threefold higher stand volume at approximately two years of age (Myers *et al.*, 1996). Therefore, while empirical lessons from *P. radiata* fertilizer practice are not directly transferable to eucalypts, the principals of nutrition management in pines are directly applicable to eucalypts.

### **Corrective fertiliser to prevent nutrient deficiency**

Turnbull *et al.* (1994) reported severe copper deficiency in *E. nitens* growing on a loamy sand in Tasmania. The deficiency was manifest in lack of apical dominance and twisted branches and was corrected with a single application of copper sulphate. Subsequent foliar analysis identified 1.4 ppm as the threshold below which copper deficiency occurred. Published examples of micronutrient deficiency in eucalypts in Australia are few, although there are examples from eucalypt plantations elsewhere (e.g. Dell and Malajczuk, 1994; Dell and Xu, 1995). Work with zinc to date shows that

critical foliage concentrations vary among tropical and temperate eucalypts (Dell and Xu 1995), while copper deficiency impairs wood quality before tree growth is affected (Dell 1994; Gherardi *et al.*, 1999). With the excellent relationships between foliar symptoms and nutrient deficiencies established by Dell and co-workers in Western Australia (for example see Dell, 1996), future occurrences of severe nutrient deficiencies should be rapidly identified and corrected — as most micronutrient deficiencies can be rectified with a single application in each rotation.

## Later-age fertiliser or application following canopy development

While almost all fertilizer applications to Australian eucalypt plantations have been starter fertilizer to increase productivity and survival, nutrient application to older stands could be economically viable. This could include commercial plantations for fibre production as well as mixed product plantations where rotation lengths extend to fifteen or more years, and where site resources allow significant growth response. While most recent plantings have a planned rotation of ten to twelve years, some growers intend to manage eucalypts on 18 to 22 year rotations. Recent studies of later-age (five to seven years of age) weed control and fertilizer effects on productivity in Gippsland have demonstrated significant growth responses on sites with deep, well-drained soils.

To date, later-age fertilizing in *P. radiata* plantations usually follows thinning; by contrast the addition of nutrients to established eucalypt plantations is likely to follow weed control (such as roller-crushing of weeds between planting rows), especially on sites below 1000 mm rainfall. On many sites where plantations will be grown over rotations of 18 to 22 years, there is scope to further increase growth through fertilizer addition, competing species control and thinning. As plantations established over the last decade come to maturity, there will be an increase in the need for research trials to determine which sites will respond to later-age weed suppression.

## **Replacement fertiliser for nutrients lost during harvesting and regeneration**

Maintaining the productivity of eucalypt plantations beyond the first rotation could involve replacement of nutrients removed in one or more harvests, especially where site capital is low in relation to nutrient removal. Nutrient removal in wood is much higher in short rotation plantations due to the high percentage of sapwood relative to heartwood in harvested logs (Birk and Turner, 1992). Harvesting of plantation eucalypts should include on-site bark removal to maximize nutrient retention on site, as between 40% and 60% of above-ground calcium is contained in stem bark (Attiwill *et al.*, 1996). Ideally the bark should be removed at the stump rather than at the landing to ensure even distribution across the site. Therefore, harvesting machinery that fells and debarks at the stump will be critical to the sustainability of eucalypt plantations, especially on low fertility sites.

With current slash retention and chopper-rolling site preparation techniques, the elements most likely to be lost in significant quantities with successive harvests are calcium, potassium and phosphorus (Judd, 1996). Much of the phosphorus removal can be made good if phosphate fertilizers are applied at plantation establishment. Calcium addition is incidental with single superphosphate (Ca 12%) and double superphosphate (6%), but is absent from the commonly used triple superphosphate and di-ammonium phosphate. Therefore, single superphosphate should be selected in preference to other phosphorus fertilizers for sites with low inherent calcium reserves. Alternatively the Ca could be added in the formulation of fertilizers. Similarly, potassium is likely to become an essential component of eucalypt fertilizers, especially on sandy and highly leached soils.

Detailed analyses of site nutrient capital and calculation of nutrient removal in harvests are required to ensure plantation sustainability in many new areas of plantation expansion. Modelling approaches such as those used by Judd (1996) and King (1996) will greatly assist in identifying nutrient depletion over several rotations; these models require site-specific parameters and will rely on growth and nutrition data to be effective.

### **Identifying research needs**

Research has addressed the need for starter fertilizers, but work on other fertilizer practices is not well-developed and in some cases is non-existent. The case for further research, or the need for a review of unpublished information held by the various plantation agencies, seems clear. Questions of immediate concern include:

- What further gains, if any, are possible with fertilizer application after two years of age, and what are the best techniques for identifying sites which will respond to nutrient addition?
- Which nutrients require replacement due to removal in harvested timber? This is one aspect in which the management of eucalypts differs from pines — due to the short rotation period of eucalypts, which can lead to significant cumulative nutrient removal over successive rotations.
- What is the best way to apply foliar diagnosis to identify limiting nutrient availability and what are the elements most likely to become deficient in the major planting areas?
- Can soil testing identify sites with little or no need for fertilizers at establishment?

To identify nutrition research to support eucalypt plantation development in Australia, these questions and others are discussed below in the light of current knowledge and experience drawn from native forests and *Pinus radiata* plantations.

### **Nutrient cycling in *Eucalyptus* plantations**

Nutrient cycling has been studied in native eucalypt forests for several decades, with the emphasis shifting from quantification of nutrient pools to include research on processes controlling nutrient availability to trees. The three major cycles of nutrients identified by Attiwill (1979) provide a basis for studying nutrient cycling in forests and plantations and have been useful in determining relationships between nutrient cycling and stand age (Attiwill and Adams, 1993; Attiwill *et al.*, 1996). These nutrient cycles include inputs to and outputs from the ecosystem, nutrient returns from plant to soil, and internal redistribution within plants. The relative importance of each of the above components in total nutrient cycles changes between elements and alters as the stand develops. The relative contribution of internal redistribution and nutrient return to nutrient supply for new growth changes over the life of a forest and can be linked to three stages of forest development as described by (Attiwill, 1979). Nutrient requirement for new growth is derived almost entirely from the soil in the first few years of growth and, as a percentage of total uptake, soil uptake is maximum prior to the commencement of litterfall (Attiwill and Leeper, 1987).

Internal redistribution, nutrient return and decomposition are critical processes supplying nutrients for new growth following canopy development (canopy closure) and

determine productivity in eucalypt plantations. Fertilizer addition can increase rates of both nutrient return and decomposition by increasing the mass and nutrient concentration of litter in particular (Bennett et al., 1996; Judd et al., 1996a; Bennett et al., 1997; Hooda and Weston, 1999). Hooda (1998) identified more rapid decomposition and release of nutrients from decomposing litter in *E. globulus* plantations where nitrogen and phosphorus fertilizer had been applied four years previously. In this way nutrients added at plantation establishment could be expected to benefit growth throughout the rotation, especially where rotations extend beyond ten years.

The emphasis on understanding processes controlling nutrient availability in soil, and nitrogen availability in particular, is shown in the studies of Wang *et al.* (1996) and O'Connell and Rance (1999). Aggangan *et al.* (1998) clearly demonstrated the impact of previous land use — including fertilizer application — on nitrogen mineralization and availability in *E. globulus* plantations in Western Australia. An understanding of how long the benefits of previous nutrient enrichment (fertilizers and nitrogen-fixing plants) will carry over into tree cropping rotations is a key concern for plantation managers. The accumulation of litter and organic matter of high C/N ratio on former pasture sites will have a profound effect on mineralization reactions controlling the availability of nitrogen and, to a lesser extent, sulphur and phosphorus. An understanding of this change in the nature and amount of organic matter on former pastoral sites (Aggangan *et al.*, 1998) will be critical to nutrient management; it is also of great interest in the development of plantations for carbon sequestration.

### **Managing nutrients in plantations**

The recognition of nutrient addition as a necessary component of *Eucalyptus* plantation management, in combination with the wide range of sites currently planted, is the basis for developing and refining nutrient diagnosis techniques. In the case of *Eucalyptus* plantations, although there is a considerable research effort currently under way, relatively little detailed work has been published — leaving the plantation establishment companies with little basis for determining optimum fertilizer regimes. Examples of recent publications specifically dealing with plantation eucalypt nutrition include Cromer et al. (1993b), Judd *et al.* (1996b) and Aggangan *et al.* (1998). To improve the knowledge base of nutrient requirements across a range of sites where new eucalypt plantations are being established requires expansion of the trial base, sustained sampling of trials throughout a rotation, and collaboration among researchers to integrate information from a broad range of sites. Both traditional and novel



approaches to determining nutrient limitation to tree growth will be essential in formulating nutrient management guidelines. A range of approaches is discussed below.

Total nutrients in foliage have been used with some success to diagnose nutrient deficiencies and limitations to growth in coniferous plantation species (e.g. Bevege and Richards, 1971). Indeed, analysis of total nutrients in foliage has been the mainstay of nutrient management for decades. Dell *et al.* (1995) and Dell (1996) have developed "critical" foliage nutrient levels associated with nutrient deficiency in seedling eucalypts grown under controlled conditions in the glasshouse and from juvenile foliage of one- to two-year old field-grown trees. However, these values will most likely need to be varied for application to trees following canopy closure in the field — the stage at which foliage nutrient assessment is most likely to be applied.

Addition of fertilizer nitrogen and phosphorus to recently planted seedlings increases foliage concentrations of nitrogen and phosphorus for up to two years, after which nitrogen concentrations are similar between biomass components of fertilized and unfertilized trees (Bennett *et al.*, 1996; Judd *et al.*, 1996b). In contrast to nitrogen, increases in the phosphorus concentrations in foliage following fertilizer application are more long-lived (Bennett *et al.*, 1997). Given our current knowledge, foliage nitrogen may be useful in indicating nutrient requirements in young trees, soon after fertilizer addition, or in cases of extreme deficiency. However, the general application of foliage nitrogen analysis to the diagnosis of nutrient requirement in eucalypts has not been well-developed in Australian plantations. This is one area where the pooling of data from a wide range of sites will improve our knowledge of critical foliage nitrogen levels.

There is a strong case for the refinement of foliar diagnosis beyond analyses of total element concentrations, to the identification of physiologically active forms of nutrients. In a recent review of the nutritional physiology of eucalypts Grove *et al.* (1996), commented on the need for a greater understanding of the chemical forms in which nutrients are held in plants, the biochemical processes involved in mobilization and transfer of nutrients.

Investigations of physiologically active forms of nutrients are restricted to nitrogen and phosphorus. Progress in identifying physiologically active forms of phosphorus — which may be more useful in determining nutrient status than total phosphorus analysis — has been encouraging. Recent studies with *E. globulus* point to improved diagnosis of nutrient limitation based on a fraction of total phosphorus in foliage (Hooda and Weston, 1999). Unfortunately, the study of nitrogen forms has not identified a nitrogen fraction which is more responsive to N-fertilizer addition than is total nitrogen (Bussau, 1999). These themes are explored further in the following discussion.

### *Nitrogen*

Attempts to refine methods for determining nitrogen requirements in plantation eucalypts will need to carefully consider internal cycling of nitrogen, which is a poorly studied area of eucalypt physiology (see Adams *et al.*, 1995; Wendler *et al.*, 1996). By contrast far more is known about internal nutrient cycling mechanisms in the commercially important coniferous species of North America and Europe (e.g. Millard, 1996; Huhn and Schulz, 1996).

Knowledge of nitrogen metabolism in trees has increased rapidly over the last decade, driven primarily by European studies on the effects of increased nitrogen deposition (N enrichment) on tree nitrogen pools (Edfast *et al.*, 1990; Nasholm *et al.*, 1994). These studies have confirmed the accumulation of glutamine and arginine in *Pinus sylvestris* needles under high nitrogen deposition. Huhn and Schulz (1996) suggest that glutamine and arginine are useful bio-indicators of nitrogen pollution in *Pinus* stands.

Resolving to what extent the physiology of internal nitrogen cycling in evergreen conifers and deciduous trees is reflected in *Eucalyptus* species will be important in refining foliage nutrient diagnosis in eucalypts. Major findings from the study of coniferous and deciduous trees, which augment nitrogen metabolism knowledge derived from investigation in non-woody plants, includes:

- soluble protein nitrogen can accumulate as a result of luxury nitrogen consumption, usually in vegetative tissues (Millard and Marshall, 1986);

- in some deciduous trees Rubisco serves as an nitrogen storage protein (Huffaker and Miller, 1978; Millard, 1988);
- the ability of a plant to store nitrogen is not dependent on its nitrogen status, which will only influence the amount of nitrogen held in store (Millard, 1988; Millard and Proe, 1993);
- N remobilization in the spring is dependent on the size of the store and is unaffected by current nitrogen supply (Millard and Proe, 1993);
- in the boreal forest, internal cycling provides nitrogen for leaf growth in the spring before rapid root uptake (Millard and Proe, 1991);
- amino acids and amides usually form the bulk of soluble, non-protein nitrogen in foliage; these compounds are usually contained in the vacuole (Pate, 1980; Cyr and Bewley, 1990);
- nitrate accumulation occurs in some species where it may play a role in controlling solute potential (Smirnoff and Stewart, 1985); however, nitrate is unlikely to accumulate in the tissues of forest trees which rely on ammonium as the main form of inorganic nitrogen in soil (Attiwill and Adams, 1993).

As noted by Wendler *et al.* (1996), in contrast to temperate conifers, little is known about processes of nitrogen storage and translocation in eucalypts, and none of the above-mentioned relationships has been demonstrated for eucalypts. Therefore, an understanding of the mechanisms of internal nitrogen cycling and the contribution of remobilization from one tissue for growth or maintenance of another, and the influence of nitrogen, phosphorus and potassium supply on these processes, is required to develop a better understanding of nitrogen requirements in plantation eucalypts. In regard to nitrogen, these queries have in part been addressed in two recent studies of internal nitrogen cycling in *E. globulus* seedlings (Adams *et al.*, 1995; Wendler *et al.*, 1996). These studies are the only detailed attempts to date to elucidate internal nitrogen cycling in eucalypts. Important findings include:

- that nitrogen remobilization occurs from older *Eucalyptus* leaves that do not show any symptoms of senescence (Wendler *et al.*, 1996);
- that nitrogen supply in spring has little effect on either the duration or amount of nitrogen remobilization, and the amount of nitrogen remobilized is therefore dependent on the size of the nitrogen store (Wendler *et al.*, 1996);

- that soluble proteins other than Rubisco seem important in explaining the biochemical basis of nitrogen remobilization from old leaves to new leaves in *E. globulus*. The nature and identity of these soluble proteins is unknown;
- that glutamine is the dominant nitrogenous solute in xylem sap of eucalypt seedlings (Adams *et al.*, 1995);
- that arginine accumulated (40-60% of free amino acid nitrogen) in the lower foliage of seedlings of three eucalypt species cultivated in the glasshouse with contrasting phosphorus supply (Adams *et al.*, 1995).

Several studies have demonstrated that concentrations and relative proportions of soluble non-protein nitrogen (amino acids and amides) increase in relation to total nitrogen in response to fertilization (e.g. Matson and Waring, 1984; Kim *et al.*, 1987; Nasholm and Ericsson, 1990; Huhn and Schulz, 1996; Schneider *et al.*, 1996). Because these foliar chemical characteristics reflect physiological activity and resource limitation, their measurement may be useful in predicting growth response to fertilization.

Attempts to identify a fraction of foliar nitrogen related to growth limitation have not been successful in field-grown trees. There was no change in tri-chloro acetic acid (TCA) extractable nitrogen following urea addition in either *P. taeda* (Polglase *et al.*, 1992) nor *E. globulus* (Hooda and Weston, 1999). Bussau (1999) did not find nitrogen and phosphorus fertilizer-induced changes in the highly labile pool of soluble nitrogen in *E. globulus* foliage on three sites in Gippsland. It seems likely that impacts of fertilizer addition on the concentration and composition of foliage nitrogen are relatively short-lived and must be carefully interpreted in the routine prediction of fertilizer requirement.

### *Phosphorus*

Eucalypt growth is increased by phosphorus application on many sites, usually where phosphorus is applied with nitrogen (Bennett *et al.*, 1997). There is good evidence to show that phosphorus addition exceeding the trees' immediate requirement increases phosphorus concentrations in foliage and wood (Polglase *et al.*, 1992; Hooda and Weston, 1999). While little is known about the precise form in which phosphorus is accumulated in foliage, cold (4°C) tri-chloro acetic acid extracts the accumulated phosphorus from dried and ground foliage (Hooda and Weston, 1999). The accumulated phosphorus is probably highly labile, and may be poly-phosphate granules, as suggested by (Polglase *et al.*, 1992). Where phosphorus accumulates in

foliage, rates of phosphorus cycling are significantly increased due to increased litter phosphorus concentrations, which increases decomposition (Hooda and Weston, 1999). Therefore, both the litter quality and quantity from phosphorus fertilized plantations is altered (O'Connell and Grove, 1993; Scott and Binkley, 1997; Hooda and Weston, 1999). Therefore, phosphorus fertilizer addition increases the rate of release of nutrients bound in litter to the soil (O'Connell, 1994; Hooda, 1998; Hooda and Weston, 1999) so that the benefits of phosphorus addition carry over to the litter decomposition stage and benefit nutrient availability for longer than nitrogen additions.

#### *Potassium and other elements*

Aside from studies of nitrogen and phosphorus, very little is known about relationships between other essential elements and productivity in *Eucalyptus* plantations. On sandy soils and highly leached loams, potassium may limit productivity after growth limitation by nitrogen and phosphorus has been satisfied, as shown by Bennett *et al.* (1996). As mentioned previously, copper deficiency has been reported in two- to four-year-old *E. nitens* plantation on a sandy soil in Tasmania (Turnbull *et al.*, 1994).

Water and nutrient availability are most likely the primary environmental factors limiting productivity on most plantation eucalypt sites in southern Australia. Therefore, plantation eucalypts will only respond to added nutrients where growth is not primarily limited by water availability. Fertilizer management must take into account the seasonal water supply to trees — principally through knowledge of soil properties and the amount and seasonal distribution of rainfall. Promising new techniques for evaluating seasonal water and nutrient status of *E. globulus* involve the analysis of phloem sap  $\delta$  C-13 and solute analyses (principally amino acids), and interpreting these data with the  $\delta$  C-13 signature of foliage and trunk wood (Pate and Arthur, 1998; Pate *et al.*, 1998).

Pate and co-workers in Western Australia have established strong relationships between  $\delta$  C-13 signatures of leaf dry matter carbon and climatic/edaphic conditions (Pate and Arthur, 1998; Pate *et al.*, 1998). Dry matter formed under severe plant water stress has less negative  $\delta$  C-13 values (less C-isotopic discrimination) relative to dry matter formed under conditions of higher water availability. By examining wood at increasing distance from the centre, the  $\delta$  C-13 signature of structural wood could be used to interpret the record of moisture stress experienced by the trees on a site. Furthermore, Pate and Arthur (1998) claim that the ability of *E. globulus* to take up nitrogen is reflected in the relative concentrations of amino acids to sugars in phloem

sap. Low amino acid concentration in phloem sap, relative to sugars, reflects a limited capacity to take up nitrogen relative to photosynthetic fixation of C.

Studies combining these new techniques and integrating site characteristics and growth information will hold considerable promise in untangling the complex interactions among nitrogen nutrition, water stress and growth of *Eucalyptus* plantations, and have the potential to inform plantation managers in matching sites to fertilizer regimes.

## **Implications of research for nutrient management**

Eucalypt plantation productivity in south-eastern Australia is strongly limited by the supply of nitrogen and phosphorus from soil (Judd *et al.*, 1996b; Bennett *et al.*, 1996). Therefore nitrogen and phosphorus supply are of prime concern in the maintenance and improvement of productivity. While potassium supply may limit biomass production on soils with very low exchangeable potassium, such as the duplex sandy loams (Dy 2.32; Northcote 1975) of central Gippsland, few trials investigating growth limitation by elements other than nitrogen and P have been reported.

The availability of nitrogen and phosphorus on plantation sites is often strongly influenced by previous land use (Skinner and Attiwill, 1981; Adams and Attiwill, 1986; Wang *et al.*, 1996; Aggangan *et al.* 1998). Compared with previously forested plantation sites, many pasture sites converted to plantations exhibit high nitrogen availability due to legume establishment, which enriches the soil in nitrogen (Aggangan *et al.*, 1998; Weston *et al.*, 1991). Similarly, the sustained application of superphosphate increases both the quantity and intensity of soil phosphorus, especially in heavier textured soils (Skinner and Attiwill, 1981). Clearly, savings in the cost of fertilizers can be made if this legacy of previous land use can be identified through soil testing prior to the implementation of establishment fertilizer practices.

*E. globulus* and *E. nitens* have emerged as the two most commercially important plantation eucalypt species in Australia. For *E. globulus*, the interaction between moisture availability and nutrition limits the response to applied fertilizer on many of the newly planted sites (Bennett *et al.*, 1997). By reducing the competition for moisture it is expected that greater response in growth to nutrient addition can be obtained. Early indications from *E. globulus* trials on 600-800 mm rainfall sites show that response to weed control at five to seven years is greater than to fertilizer application. Conversely, results from *E. nitens* trials show a relatively greater response to fertilizer than to weed control treatments at six to eight years of age — probably due to better soil physical

conditions and moisture-supplying power. While site-specific competition and moisture availability will determine the relative responses to weed control and fertilizer addition on a site, it seems likely that plantations in the 500-700 mm rainfall zone will benefit more from weed control measures than from nutrient addition at later ages.

The larger plantation owners have played the major hand in the development and dissemination of plantation technology for the benefit of all eucalypt growers, of whom many do not have the resources to develop and refine plantation silviculture. A significant challenge for the future is the development of research cooperatives to support the development and maintenance of healthy and productive *Eucalyptus* plantations; many of which are being planted in regions hitherto unplanted with eucalypts.

Although large plantation owners will continue to strongly influence practices throughout the industry, it is inevitable that problems will arise on the wide range of sites represented by smaller holdings. Cooperative research will be essential in identifying and addressing these problems.

Growth rates and productivity gains resulting from silvicultural inputs in well-established eucalypt plantations have not been quantified beyond ten years of age. An understanding of the effects of silvicultural practices on nutrient availability for successive rotations is of key significance for sustainable management of these plantations. Because the major cost and profit driver for the eucalypt plantation industry is the production of more fibre on less land, the early gains in productivity achieved by intensive silvicultural inputs must be maintained throughout rotations of up to twenty years. A key issue for further research is how best to achieve productivity gains through mid-rotation silvicultural inputs, whilst maintaining profitability and sound environmental practices.

On a cautionary note, operational experience to date shows that establishment silviculture of eucalypts requires careful attention in the application of effective weed-control and fertilizer prescriptions; there seems to be less margin for error than for pines. For example, good weed control and careful hand-placement of fertilizer within 20 to 30 cm of seedlings is essential for good survival and growth of eucalypts in Gippsland (Hescock *et al.*, 1999). Therefore, the effective transfer of research-trial knowledge to routine practice is especially important with *Eucalyptus* species, as they appear to be less tolerant than *P. radiata* of below standard establishment practices.



## References

- Adams M.A. and Attiwill P.M. (1986). Nutrient cycling and nitrogen mineralization in eucalypt forests of south-eastern Australia. *Plant and Soil* 92, 319-339.
- Adams, M. A., Attiwill, P. M. and Wang, L. M. (1995). Effects of phosphorus supply on growth and nitrogen fractions in xylem sap and foliage of *Eucalyptus regnans* (F. Muell), *E. nitens* (Maiden) and *E. globulus* (Labill.) seedlings: implications for herbivory. *Trees-Structure & Function* 9, 324-331.
- Aggangan, R. T., O'Connell, A. M., McGrath, J. F. and Dell, B. (1998). Fertilizer and previous land use effects on C and nitrogen mineralization in soils from *Eucalyptus globulus* plantations. *Soil Biology and Biochemistry* 30, 1791-1798.
- Aggangan, R. T., O'Connell, A. M., McGrath, J. F. and Dell, B. (1999). The effects of *Eucalyptus globulus* Labill. leaf litter on C and nitrogen mineralization in soils from pasture and native forest. *Soil Biology and Biochemistry* 31, 1481-1487.
- Attiwill, P. M. (1979). Nutrient cycling in *Eucalyptus obliqua* (L'Herit.) forest. *Australian Journal of Botany* 27, 439-458.
- Attiwill, P. M. and Adams, M. A. (1993). Nutrient cycling in forests. *New Phytologist* 124, 561-582.
- Attiwill, P. M. and Leeper, G. W. (1987). "Forest Soils and Nutrient Cycles". Melbourne University Press, Melbourne.
- Attiwill, P. M., Polglase, P. J., Weston, C. J. and Adams, M. A. (1996). Nutrient cycling in eucalypt forests of south-eastern Australia. In "Nutrition of Eucalypts" (P. M. Attiwill and M. A. Adams, eds.), pp. 191-227. CSIRO, Melbourne.
- Bennett, L. T., Weston, C. J. and Attiwill, P. M. (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, 103-121.
- Bennett, L. T., Weston, C. J., Judd, T. S., Attiwill, P. M. and Whiteman, P. H. (1996). The effects of fertilizers on early growth and foliar nutrient concentrations of three plantation eucalypts on high quality sites in Gippsland, south-eastern Australia. *Forest Ecology and Management* 89, 213-226.
- Bevege, D. I. and Richards, B. N. (1971). Principles and practice of foliar analysis as a basis for crop-logging in pine plantations. II. Determination of critical phosphorus levels. *Plant and Soil* 37.
- Birk, E. M. and Turner, J. (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.
- Bussau, A. J. (1999). Soluble nitrogen containing compounds in *Eucalyptus globulus* (Labill.) foliage: effects of site, season and nutrient addition. Unpublished Ph.D. thesis, University of Melbourne, Creswick.

- Carlyle, J. C. (1995). Nutrient management in a *Pinus radiata* plantation after thinning: the effect of nitrogen fertilizer on soil nitrogen fluxes and tree growth. *Canadian Journal of Forest Research* 25, 1673-1683.
- Cromer, R. N., Cameron, D. M., Rance, S. J., Ryan, P. J. and Brown, M. (1993a). Response to nutrients in *Eucalyptus grandis*: I. Biomass accumulation. *Forest Ecology and Management* 62, 211-230.
- Cromer, R. N., Cameron, D. M., Rance, S. J., Ryan, P. J. and Brown, M. (1993b). Response to nutrients in *Eucalyptus grandis*. II. Nitrogen accumulation. *Forest Ecology and Management* 62, 231-243.
- Cromer, R. N., Cameron, D., Cameron, J. N., Flinn, D. W., Neilsen, W. A., Raupach, M., Snowdon, P. and Waring, H. D. (1981). Response of eucalypt species to fertiliser applied soon after planting at several sites. *Australian Forestry* 44, 3-13.
- Cyr, D. R. and Bewley, J. D. (1990). Seasonal variation in nitrogen storage reserves in the roots of leafy spurge (*Euphorbia esula*) and responses to decapitation and defoliation. *Physiologia Plantarum* 79, 361-366.
- Dalla-Tea, F. and Marco, M. A. (1996). Fertilizers and eucalypt plantations in Argentina. In "Nutrition of Eucalypts" (P. M. Attiwill and M. A. Adams, eds.), pp. 327-333. CSIRO, Melbourne.
- Dell, B. (1994) Copper nutrition of *Eucalyptus maculata* (Hook) seedlings – requirements for growth, distribution of copper and the diagnosis of copper deficiency. *Plant and Soil* 167, 181-187.
- Dell, B. (1996). Diagnosis of nutrient deficiencies in eucalypts. In "Nutrition of Eucalypts" (P. M. Attiwill and M. A. Adams, eds.), pp. 417-440. CSIRO, Melbourne.
- Dell, B. and Malajczuk, N. (1994). Boron deficiency in eucalypt plantations in China. *Canadian Journal of Forest Research* 24, 2409-2416.
- Dell, B. and Xu, D. P. (1995). Diagnosis of zinc-deficiency in seedlings of a tropical eucalypt (*Eucalyptus urophylla* Blake, S.T.). *Plant and Soil* 176, 329-332.
- Dell, B., Malajczuk, N. and Grove, T. S. (1995). "Nutrient disorders in plantation eucalypts," Australian Centre for International Agricultural Research, c1995, Canberra.
- Edfast, A., Nasholm, T. and Ericsson, A. (1990). Free amino acid concentrations in needles of Norway spruce and Scots pine trees on different sites in areas with two levels of nitrogen deposition. *Canadian Journal of Forest Research* 20, 1132-1136.
- Flinn, D. W. (1984). Practical aspects of the nutrition of exotic conifer plantations and native eucalypt forests in Australia. In "Research for Forest Management" (J. J. Landsberg and W. Parsons, eds.), pp. 73-93. CSIRO, Canberra.
- Gherardi, M.J., Dell, B. and Huang, L. (1999) Functional copper requirement for catechol oxidase activity in plantation *Eucalyptus* species. *Plant and Soil* 210, 75-81.

- Grove, T. S., Thomson, B. D. and Malajczuk, N. (1996). Nutritional physiology of eucalypts: uptake, distribution and utilization. In "Nutrition of Eucalypts" (P. M. Attiwill and M. A. Adams, eds.), pp. 77-108. CSIRO, Melbourne.
- Hafner, S. (2000). Balancing productivity and drought risk in blue gum plantations: a plantation management workshop. In "Climate Change Newsletter", Vol. 12.
- Herbert, M. A. (1996). Fertilizers and eucalypt plantations in South Africa. In "Nutrition of Eucalypts" (P. M. Attiwill and M. A. Adams, eds.), pp. 303-325. CSIRO, Melbourne.
- Hescock, R., Whiteman, P., Wentworth, S., Appleton, R. and Lieshout, H. (1999). Recent developments in silviculture at Australian Paper Plantations. In "Practising Forestry Today. 18th Biennial Conference of the Institute of Foresters of Australia" (R. C. Ellis and P. J. Smethurst, eds.), pp. 176-180. Institute of Foresters of Australia Inc., Hobart, Tasmania.
- Hooda, N. (1998). Nutrient cycling in *Eucalyptus globulus* plantations in Gippsland, south-eastern Australia. Unpublished Ph.D. thesis, University of Melbourne, Creswick.
- Hooda, N. and Weston, C. J. (1999). Influence of site and fertiliser addition on nutrient cycling in *Eucalyptus globulus* plantations in Gippsland, south-eastern Australia. I. Foliage and litter quality. Australian Journal of Botany 47, 189-206.
- Huffaker, R. C. and Miller, B. L. (1978). Re-utilization of ribulose biphosphate carboxylase. In "Photosynthetic Carbon Assimilation" (H. W. Siegelman, ed.), pp. 139-152. Plenum Press, New York.
- Huhn, G. and Schulz, H. (1996). Contents of free amino acids in Scots pine needles from field sites with different levels of nitrogen deposition. New Phytologist 134, 95-101.
- Judd, T. S. (1996). Simulated nutrient loss due to timber harvesting. In "Nutrition of Eucalypts" (P. M. Attiwill and M. A. Adams, eds.), pp. 249-258. CSIRO, Melbourne.
- Judd, T. S., Attiwill, P. M. and Adams, M. A. (1996a). Nutrient concentrations in *Eucalyptus* a synthesis in relation to differences between taxa, sites and components. In "Nutrition of Eucalypts" (P. M. Attiwill and M. A. Adams, eds.), pp. 123-153. CSIRO, Melbourne.
- Judd, T. S., Bennett, L. T., Weston, C. J., Attiwill, P. M. and Whiteman, P. H. (1996b). The response of growth and foliar nutrients to fertilizers in young *Eucalyptus globulus* (Labill.) plantations in Gippsland, south-eastern Australia. Forest Ecology and Management 82, 87-101.
- Kim, Y. T., Glerum, C., Stoddart, J. and Colombo, S. J. (1987). Effect of fertilization on free amino acid concentrations in black spruce and jack pine containerized seedlings. Canadian Journal of Forest Research 17, 27-30.
- King, D.A. (1996) A model to evaluate factors controlling growth in *eucalyptus* plantations of southeastern Australia. Ecological Modelling 87, 181-203.

- Matson, P. A. and Waring, R. H. (1984). Effects of nutrient and light limitation on mountain hemlock: susceptibility to laminated rot. *Ecology* 65, 1517-1524.
- Millard, P. (1988). The accumulation and storage of nitrogen by herbaceous plants. *Plant, Cell and Environment* 11, 1-8.
- Millard, P. (1996). Ecophysiology of the internal cycling of nitrogen for tree growth. *Journal of Plant Nutrition and Soil Science* 159, 1-10.
- Millard, P. and Marshall, B. (1986). Growth, nitrogen uptake and partitioning within the potato (*Solanum tuberosum* L.) crop, in relation to nitrogen application. *Journal of Agricultural Science, Cambridge* 105, 501-504.
- Millard, P. and Proe, M. F. (1991). Leaf demography and the seasonal internal cycling of nitrogen in sycamore (*Acer pseudoplatanus* L.) seedlings in relation to nitrogen supply. *New Phytologist* 117, 587-596.
- Millard, P. and Proe, M. F. (1993). Nitrogen uptake, partitioning and internal cycling in *Picea sitchensis* (Bong.) Carr. as influenced by nitrogen supply. *New Phytologist* 125, 113-119.
- Myers, B. J., Theiveyanathan, S., O'Brien, N. D. and Bond, W. J. (1996). Growth and water use of *Eucalyptus grandis* and *Pinus radiata* plantations irrigated with effluent. *Tree Physiology* 16, 211-219.
- Nambiar, E. K. S. and Fife, D. N. (1987). Growth and nutrient retranslocation in needles of radiata pine in relation to nitrogen supply. *Annals of Botany* 60, 147-156.
- Nasholm, T. and Ericsson, A. (1990). Seasonal changes in amino acids, protein and total nitrogen in needles of fertilized Scots pine trees. *Tree Physiology* 6, 267-281.
- Nasholm, T., Edfast, A.-B., Ericsson, A. and Norden, L.-G. (1994). Accumulation of amino acids in some boreal forest plants in response to increased nitrogen availability. *New Phytologist* 126, 137-143.
- NFI (1998). "Australia's State of the Forests Report 1998". National Forest Inventory, Bureau of Rural Sciences, Canberra.
- Northcote, KH (1971). "A Factual Key for the Recognition of Australian Soils. " Rellim Technical Publications Pty Ltd, South Australia.
- O'Connell, A. M. (1994). Decomposition and nutrient content of litter in a fertilized eucalypt forest. *Biology and Fertility of Soils* 17, 159-166.
- O'Connell, A. M. and Grove, T. S. (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 Rance, S. J. (1999). Predicting nitrogen supply in plantation eucalypt forests. *Soil Biology and Biochemistry* 31, 1943-1951.
- Pate, J. and Arthur, D. (1998).  $\delta$  C-13 analysis of phloem sap carbon: novel means of evaluating seasonal water stress and interpreting carbon isotope signatures of foliage and trunk wood of *Eucalyptus globulus*. *Oecologia* 117, 301-311.
- Pate, J. S. (1980). Transport and partitioning of nitrogenous solutes. *Annual review of Plant Physiology* 31, 313-340.

- Pate, J., Shedley, E., Arthur, D. and Adams, M. (1998). Spatial and temporal variations in phloem sap composition of plantation-grown *Eucalyptus globulus*. *Oecologia* 117, 312-322.
- Polglase, P. J., Jokela, E. J. and Comerford, N. B. (1992). Phosphorus, nitrogen and carbon fractions in litter and soil of southern pine plantations. *Soil Science Society of America Journal* 56, 566-572.
- Prado, J. A. and Toro, J. A. (1996). Silviculture of eucalypt plantations in Chile. In "Nutrition of Eucalypts" (P. M. Attiwill and M. A. Adams, eds.), pp. 357-369. CSIRO, Melbourne.
- Raupach, M. (1967). Soil and fertilizer requirements for forests of *Pinus radiata*. *Advances in Agronomy* 19, 307-353.
- Ritson, P., Pettit, N. E. and McGrath, J. F. (1991). Fertilising eucalypts at plantation establishment on farmland in south-west Western Australia. *Australian Forestry* 54, 139-147.
- Schneider, S., Gebler, A., Weber, P., von Sengbusch, D., Hanemann, U. and Rennenberg, H. (1996). Soluble nitrogen compounds in trees exposed to high loads of N: a comparison of spruce (*Picea abies*) and beech (*Fagus sylvatica*) grown under field conditions. *New Phytologist* 134, 103-114.
- Schonau, A. P. G. and Herbert, M. A. (1989). Fertilizing eucalypts at plantation establishment. *Forest Ecology and Management* 29, 221-244.
- Scott, N. A. and Binkley, D. (1997). Foliage litter quality and annual net nitrogen mineralization: comparison across North American Forest Sites. *Oecologia* 111, 151-159.
- Shedley, E., Dell, B. and Grove, T. (1995). Diagnosis of nitrogen deficiency and toxicity of *Eucalyptus globulus* seedlings by foliar analysis. *Plant and Soil* 177, 183-189.
- Skinner, M. F. and Attiwill, P. M. (1981). The productivity of pine plantations in relation to previous land use. II. Phosphorus adsorption isotherms and the growth of pine seedlings. *Plant and Soil* 61, 329-339.
- Smethurst, P. J. and Nambiar, E. K. S. (1990a). Distribution of carbon and nutrients and fluxes of mineral nitrogen after clear-felling a *Pinus radiata* plantation. *Canadian Journal of Forest Research* 20, 1490-1497.
- Smethurst, P. J. and Nambiar, E. K. S. (1990b). Effects of slash and litter management on fluxes of nitrogen and tree growth in a young *Pinus radiata* plantation. *Canadian Journal of Forest Research* 20, 1498-1507.
- Smirnoff, N. and Stewart, G. R. (1985). Nitrate assimilation and translocation by higher plants: Comparative physiology and ecological consequences. *Physiologia Plantarum* 64, 133-140.
- Turnbull, C. R. A., Beadle, C. L., West, P. W. and Cromer, R. N. (1994). Copper deficiency a probable cause of stem deformity in fertilised *Eucalyptus nitens*. *Canadian Journal of Forest Research* 24, 1434-1439.

VPFC (1998). "Private Forestry in Victoria: Strategy towards 2020". Victorian Private Forestry Council.

- Wang, X. J., Smethurst, P. J. and Holz, G. K. (1996). Nitrogen mineralisation indices in ferrosols under eucalypt plantations in north-western Tasmania: Association with previous land use. *Australian Journal of Soil Research* 34, 925-935.
- Wendler, R., Carvalho, P. O., Pereira, J. S. and Millard, P. (1996). Role of nitrogen remobilization from old leaves for new leaf growth of *Eucalyptus globulus* seedlings. *Tree Physiology* 15, 679-683.
- Weston, C. J., Attiwill, P. M. and Cameron, J. N. (1991). Growth and nutrition of eucalypt plantations in relation to soil type and former land use in Gippsland, Victoria. In "IUFRO Symposium on Intensive Forestry: The Role of Eucalypts" (A. P. G. Schonau, ed.), Vol. 1, pp. 480-491. Southern African Institute of Forestry, Durban, South Africa.
- White, D. A., Beadle, C. L. and Worledge, D. (1996). Leaf water relations of *Eucalyptus globulus* ssp. *globulus* and *E. nitens*: seasonal, drought and species effects. *Tree Physiology* 16, 469-476.
- Will, G. M. (1985). "Nutrient deficiencies and fertilizer use in New Zealand exotic forests. (with 1986 supplement)," FRI Bulletin No. 97, Forest Research Institute, Rotorua.
- Yost, R. S., De Bell, D. S., Whitesell, C. D. and Miyasaka, S. C. (1987). Early growth and nutrient status of *Eucalyptus saligna* as affected by nitrogen and phosphorus fertilization. *Australian Forest Research* 17, 203-214.