



Role of light fraction soil organic matter in the phosphorus nutrition of *Eucalyptus globulus* seedlings

C.P. O'Hara^{1,2,5}, J. Bauhus^{1,3,6} & P.J. Smethurst^{2,4}

¹Forestry Program, School of Resources, Environment and Society, Australian National University, 0200, Canberra, Australia. ²Co-operative Research Centre for Sustainable Production Forestry, Private Bag 12, 7001, Hobart, Tasmania, Australia. ³Institute of Silviculture, Freiburg University, Temnenbacherstr. 4, 79085, Freiburg, Germany. ⁴CSIRO Forestry and Forest Products, GPO Box 252-12, 7001, Hobart, Tasmania, Australia. ⁵Present address: Ministry of Defence, 2600, Russell, ACT, Australia. ⁶Corresponding author*

Received 26 July 2005. Accepted in revised form 31 August 2005

Key words: *Eucalyptus globulus*, light fraction, phosphorus, soil organic matter

Abstract

Different fractions of soil organic matter (SOM) may contribute to varying degrees to phosphorus (P) recycling and supply. This study investigated the potential for light fraction SOM to contribute to plant P nutrition using a bioassay with *Eucalyptus globulus* (Labill.) seedlings. Light fraction SOM, which has been subject to only limited decomposition, was isolated from bulk soil using a density floatation procedure. Seedlings were grown in sand with a P-free nutrient solution and either light fraction SOM from five different native eucalypt forest plots as a source of added P or in sand with no added light SOM (controls). Growth (dry matter accumulation) and P acquisition by seedlings of four of the treatments grown with light fraction organic matter was 2–3 times greater than that of control seedlings. Daily rates of P acquisition ranged from 0.13 $\mu\text{g P day}^{-1}$ (control) to 0.29–0.50 $\mu\text{g P day}^{-1}$ for seedlings grown with added organic matter. Whilst the study indicates that light fraction SOM can contribute to the P nutrition of eucalypt seedlings, accordingly, further research into the nutritional role of light fraction SOM is warranted.

Introduction

In forests, soil organic matter (SOM) constitutes a significant reservoir of carbon (C) and nutrients. The recycling of nutrients such as phosphorus (P) via organic matter is potentially a significant factor contributing to and regulating P supply (Attiwill, 1980, Baker and Attiwill, 1985). However, soil organic matter is not homogenous, but forms a continuum ranging from freshly incorporated plant debris to highly transformed and stable organic complexes (Melillo et al., 1989). Consequently, different fractions of SOM may contribute to different degrees to nutrient supply (Ashton and Kelliher, 1996a;

Hallsby, 1994). The significance of different SOM fractions for P-supply, in particular in forest soils, is largely unknown.

One option to study the dynamics of SOM is through soil physical fractionation approaches in combination with other chemical or biological techniques (e.g., Neff et al., 2002; Six et al., 2002). Physical fractionation can be used to isolate discrete pools of SOM. Ideally, such pools of SOM may relate better to specific functions or processes (Christensen, 1992). Light SOM or sand-sized fractions of SOM (macro-organic matter) are generally regarded as being composed of relatively fresh, uncomplexed organic debris that has undergone only limited transformation (Christensen, 2001; Six et al., 2002). Very few studies have been made of the bioavailability

* E-mail: juergen.bauhus@waldbau.uni-freiburg.de

or potential for P supply from light fraction SOM (Bekunda et al., 1990; Maroko et al., 1999; Phiri et al., 2001; Van Noordwijk et al., 1998). These studies do suggest that P in light SOM, or similar organic matter fractions, may contribute to actively cycling or plant available P pools. However, others (Curtin et al., 2003) have concluded that the organic P in light fraction organic matter would not contribute significantly to pasture nutrition.

The objective of the present study was to determine if P in light fraction SOM recovered from eucalypt forest soil by water floatation can contribute to tree seedling P nutrition in the short-term. A plant bioassay was preferred as it provides an alternative and potentially more direct indication of P availability than P mineralization during incubation. Direct measurement of seedling P content as a measure of P supply (e.g., Ashton and Kelliher, 1996a; Hallsby, 1994) may circumvent technical or methodological difficulties that can arise from the simultaneous, multi-directional nature of transformations between inorganic P, microbial P and organic P pools during incubation (Saggar et al., 1998). Additionally, extraction measures of P 'availability' do not necessarily correlate well with P supply as assessed by plant P content (Giardina and Rhoades, 2001). Consequently, Ashton and Kelliher (1996b) concluded that plant P uptake was a 'better arbiter' of P availability.

Materials and methods

Study sites

Soil for physical fractionation and light fraction organic matter recovery was collected from within five 0.1 ha⁻¹ plots located in the Bago-Maragle forest management area of southern New South Wales (N.S.W.), located approximately between 35°35'–35°55' S, and 148°05'–148°20' E. The present day Bago-Maragle forest management area includes about 48,000 ha of native hardwood forest, dominated by *E. delegatensis*, a species of principal commercial interest, and *E. dalrympleana* and *E. radiata*, which are of secondary commercial interest (Ryan et al., 2000). The area lies predominantly between 800 and 1300 m a.s.l., with *E. delegatensis* reaching prime development between 1100 and 1300 m a.s.l. (Turner, 1996). The five sites from which soil was collected for the present study were each dominated by *E. delegatensis* (selected characteristics for each site are presented in Table 1.)

Generally, soils are loams and clay loams over clay, frequently up to 2 m depth, derived principally from sedimentary and igneous parent materials (Ryan et al., 2000). For soil characterization, the fine earth (<2 mm) fraction was used with values expressed on an oven dry (105 °C, 24 h) basis. Total C was determined by dry combustion (Leco CHN 1000), total P and N by

Table 1. Selected stand and soil (0–2.5 cm) characteristics for 5 native forest plots

	BM 4	BM 12	BM 22	CPT 9	ESM 22
<i>Stand</i> ^a					
Stocking (stems ha ⁻¹)	250	310	360	420	1330
Age range (years)	49–72	37–42	31–58	51–54	20–24
Mean height (m)	39.1	32.4	29.4	39.3	23.8
Basal area (m ² ha ⁻¹)	61.0	48.6	43.3	84.6	44.0
<i>Soil</i>					
Bulk density (g cm ⁻³) ^b	0.69	0.74	0.83	0.44	0.51
pH (water)	4.5	5.2	4.7	4.7	4.4
Carbon (%)	8.8	7.8	9.1	14.0	6.3
Nitrogen (mg g ⁻¹)	3.4	3.2	3.8	5.8	2.3
Phosphorus (μg g ⁻¹)	452	508	882	690	257
C:N	26	24	24	24	27
C:P	194	153	103	206	245

^aKhanna, personal communication.

^bBulk density: 0–5 cm, <2 mm fine earth fraction.

autoanalysis (TRAACS 800, Technicon) following a modified Kjeldahl digest (Heffernan, 1985), pH in water (1:5 soil:water) and bulk density was determined on the fine earth fraction (<2 mm) (Table 1).

Soil collection and physical fractionation

Soils were collected in Autumn, 2001, from three small pits located within each plot. After removing overlying litter in order to expose the mineral soil surface, each pit was carefully excavated using small hand tools. Pit size was approximately 20 cm × 15 cm and there were three depth increments, 0–2.5, 2.5–5 and 5–10 cm. Soil samples were bulked by depth to provide a single sample for each depth from each plot. For the present study, due to low quantities of light fraction SOM in the lower depths, only soil from the surface 0–2.5 cm was used.

Physical fractionation was undertaken using field moist soil, which was sieved, firstly over a 4.75 mm sieve and subsequently over a 2 mm sieve to remove coarse material and recover the fine earth (<2 mm) fraction. In field moist condition the soil remained well aggregated and aggregates were gently hand pressed through each sieve. In order to recover sufficient quantities of light fraction organic matter, approximately 1000 g dry weight equivalent of the fine earth fraction was used for physical fractionation.

Water was preferred for the density fractionation as it would recover lighter, and therefore less decomposed SOM, and would minimize the risk of artefacts that could occur with other denser liquids (Magid et al., 1996; Sollins et al., 1984). The soil was suspended in water (ratio 1:7) and the soil–water slurry was continuously and moderately agitated by maintaining a constant inflow of water. Soil material was washed out through the outflow pipe of a bucket onto a 250 µm sieve, enabling the collection of coarse material (>250 µm), whilst allowing for finer material to be washed through the sieve. Soil washing continued until it was visibly evident that no more coarse material was being washed out. Coarse organic matter collected on the 250 µm sieve was subsequently washed under clean running water to remove any adhering fine material. This approach facilitated the fast and easy collection of coarse or macro-organic matter

from a relatively large quantity of soil, whilst finer mineral and organic components were washed through the sieve. Organic material collected on the 250 µm sieve was suspended in water to separate a floating light fraction of organic matter. The light fraction material was dried for 24 h at 65 °C and subsequently ground to provide a more homogenous substrate.

The P concentration of the light fraction material was determined by digestion in 36 N H₂SO₄ with H₂O₂ additions (Heffernan, 1985) and automated colorimetric determination (TRAACS 800 AutoAnalyzer, Technicon). The C concentration of the light fraction organic matter used for the seedling bioassay was about 45%, and P concentrations for the different sites ranged from 313 µg P g⁻¹ (ESM 22) to 698 µg P g⁻¹ (BM 22) (Table 2). The C concentration of the heavy organic matter was approximately 30–35%. The C concentrations of the organic matter fractions indicated the light fraction material was substantially free of mineral contamination and in a less decomposed state than the heavy organic matter.

Plant growth

Seed material was obtained from the Australian Tree Seed Centre, sourced from the Blue Gum Saddle seedlot, Tasmania (43°12' S, 146°54' E; 250 m a.s.l.) from 15 parent trees of *E. globulus* (subsp. *globulus*). Seeds were not sterilized or pre-treated prior to germination. Germination was in broad, shallow, free draining plastic trays in a sand–perlite mixture (1:1 volume) under prevailing glasshouse conditions. After 3 weeks, seedlings were transferred to small, free draining plastic pots, with one seedling per pot. As far as possible, germinants of similar shoot and root size were chosen for transplanting. Each pot was filled with either a mixture of 110 g coarse sand

Table 2. Selected characteristics for light fraction organic matter from 5 native forest plots

	BM 4	BM 12	BM 22	CPT 9	ESM 22
Carbon (%)	44.3	46.6	45.4	44.8	45.9
Phosphorus (µg g ⁻¹)	454	451	698	534	313
C:P	976	1033	650	839	1466

and 0.5 g light fraction organic matter from the five native forest reference sites (treatments: BM 4, BM 12, BM 22, CPT 9 and ESM 22) or 110 g sand only (control) and watered to field capacity with dilute P-free nutrient solution adjusted to pH 5.2. Measures of extractable inorganic P (Bray and Kurtz, 1945; Olsen et al., 1954) in the sand were equal to or less than $1 \mu\text{g P g}^{-1}$, i.e., P-deficient for eucalypt seedling growth (Mendham et al., 2002). There were 10 replicates of each treatment.

A P-free nutrient solution was prepared by modifying the complete nutrient solution described by Brundrett et al. (1996) for the growth of eucalypt seedlings. Stock (concentrated) macro-nutrient solutions were prepared separately and contained: $132 \text{ g L}^{-1} \text{ NH}_4\text{NO}_3$, $58.9 \text{ g L}^{-1} \text{ Ca}(\text{NO}_3)_2 \cdot 4\text{H}_2\text{O}$, $66.2 \text{ g L}^{-1} \text{ KNO}_3$, $60 \text{ g L}^{-1} \text{ MgSO}_4 \cdot 7\text{H}_2\text{O}$ and $14.8 \text{ g L}^{-1} \text{ K}_2\text{SO}_4$. Additionally, an iron solution was prepared separately containing $1.522 \text{ g L}^{-1} \text{ FeSO}_4$. For micronutrients, a single combined stock solution was prepared, containing: $0.629 \text{ g L}^{-1} \text{ H}_3\text{BO}_3$, $0.573 \text{ g L}^{-1} \text{ ZnSO}_4 \cdot 7\text{H}_2\text{O}$, $0.482 \text{ g L}^{-1} \text{ MnSO}_4 \cdot 5\text{H}_2\text{O}$, $0.219 \text{ g L}^{-1} \text{ CuSO}_4 \cdot 4\text{H}_2\text{O}$ and $0.019 \text{ g L}^{-1} \text{ H}_2\text{MoO}_4 \cdot 4\text{H}_2\text{O}$. For dilution and preparation of the combined working total nutrient solution, 1 mL of each stock was added to water and made to 1 L.

The transplanted potted seedlings were grown under glasshouse conditions, randomly arranged in a large, shallow plastic tray in which 1–2 cm of tap water was maintained to sustain moisture supply. Additionally, seedlings were watered daily using tap water. Mean P concentration of tap water was $<10 \text{ ng mL}^{-1}$ (Butterfield, personal communication). Seedlings were supplemented by the addition of 5 mL dilute nutrient solution after 1 and 2 weeks, and thereafter at 4, 6, 8 and 10 weeks growth. Approximately every 2 weeks the tray holding the seedlings was rotated 90° .

Seedlings were harvested after 90 days. Whilst still in the pot, seedlings were gently immersed in water and the root-sand matrix carefully removed from the pot. Most sand fell readily away under water and although the root system of eucalypt seedlings is very fine, it was kept substantially intact. Each seedling was washed under running water, over a $63 \mu\text{m}$ sieve, and final adhering sand removed. Seedlings were then dried at 70°C for 72 h, after which root and shoot were separated and dry weights recorded.

Shoot and root material was subjected to concentrated sulphuric acid and hydrogen peroxide digestion and analyzed for P by automatic colorimetric determination. Daily P acquisition by seedlings of light fraction organic matter treatments was estimated by dividing mean total seedling P content, corrected for control seedling P content, by the number of days following transplanting.

Statistics

Differences between treatment means for shoot and root weights were tested by analysis of variance and where a significant difference was indicated, a *post-hoc* least significant difference test ($P = 0.05$) applied. The smallest and largest seedlings were excluded from analysis. The relationship between seedling P content and seedling dry weight was examined by regression analysis following natural logarithmic transformation of both variables. All statistical analyses were performed in JMP (SAS Institute, 1996).

Results

Seedling growth response

Shoot dry matter of seedlings grown on light fraction material from 4 of the 5 sites (BM 12, BM 22, CPT 9 and ESM 22) was significantly higher than that of control seedlings grown without light fraction organic matter (Table 3). A similar pattern was evident in terms of root dry matter weight. Generally, regardless of shoot and root dry weight, shoot dry matter accumulation was about three times that of root dry weight, resulting in a similar root: shoot ratio in dry weight for all treatments.

Root P concentrations were highest for seedlings grown on light fraction material from sites BM 22 and CPT 9, and lowest for seedlings from BM 4 and the control treatment, however, the differences were not significant (Table 3). Root P concentrations were about twice that of shoot P concentrations. The latter were also not significantly different between treatments.

Total seedling P content varied from about $25 \mu\text{g}$ for the control seedlings, to about 60–70 μg for seedlings grown on light fraction mate-

Table 3. Shoot and root dry weights and phosphorus concentrations for *Eucalyptus globulus* seedlings grown in sand with a P-free nutrient solution and either soil light fraction organic matter as a P source or no added P source (control). Within rows, shoot and root values followed by the same letter are not significantly different ($P = 0.05$). Standard error of the mean is in brackets. For BM 4, BM 22, CPT 9 and ESM 22 $n = 8$, for BM 12 and control seedlings $n = 7$

	BM 4	BM 12	BM 22	CPT 9	ESM 22	Control
<i>Dry weight (g)</i>						
Shoot	0.062 ac (0.005)	0.081 ab (0.003)	0.093 ab (0.008)	0.097 b (0.015)	0.103 b (0.005)	0.044 c (0.003)
Root	0.022 ac (0.003)	0.030 ab (0.003)	0.035 ab (0.003)	0.039 b (0.006)	0.034 ab (0.010)	0.016 c (0.002)
<i>Phosphorus concentration ($\mu\text{g P g}^{-1}$)</i>						
Shoot	337 a (34)	342 a (43)	361 a (35)	389 a (26)	374 a (15)	298 a (29)
Root	651 a (107)	743 a (99)	793 a (42)	798 a (38)	715 a (39)	674 a (49)

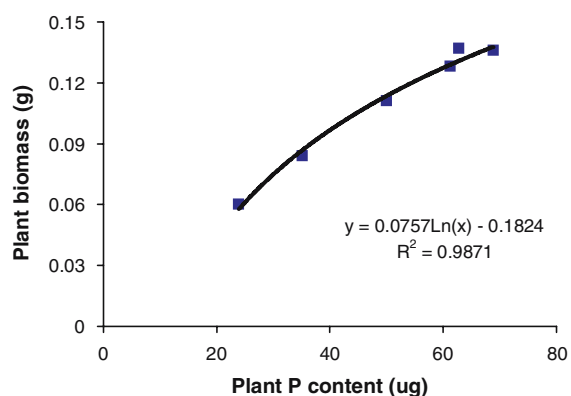


Figure 1. Relationship between seedling P content (μg) and seedling biomass (g) across the six different treatments.

rial from BM 22, CPT 9 and ESM 22 (Figure 1). The root and shoot P content of seedlings from 4 of the 5 sites (BM 12, BM 22, CPT 9 and ESM 22) treatments was significantly greater than that of the control seedlings. Across the six treatments there was a close relationship between seedling P content and biomass.

Phosphorus supply

The daily rate of P supply, after correcting for the control treatment as a measure of supply from seed, sand and other background sources, ranged from 0.14 to 0.50 $\mu\text{g P day}^{-1}$ for seedlings grown on light fraction organic matter (Table 4). This equated to an average daily rate of P release from the light fraction ranging from 0.06% for BM 4 to 0.28% for ESM 22. The rate

of supply observed for the BM 4 treatment was similar to that of the control treatment, whereas the rate of supply on the other treatments was about 2–4 times that of the control. After adjusting for (i.e., subtracting) the P content of control seedlings, seedlings grown on light fraction organic matter treatments BM 12 and BM 22 acquired approximately 11–12% of the amount of P added in organic matter, whilst seedlings grown on light fraction material from CPT 9 and ESM 22 acquired 17% and 26% of the amount of P added in organic matter, respectively. On the other hand, seedlings grown on material from BM 4 only acquired 5% of the P added in the light fraction organic matter. A positive correlation ($P < 0.10$) between seedling total P content and total seedling dry weight suggests that seedlings may have been P limited, whereas there was no correlation between seedling N concentration and dry weight (data not shown). However, seedlings did not exhibit visual foliage symptoms of P deficiency (Dell et al., 2001).

Discussion

Seedling growth

A plant bioassay was undertaken to determine whether the P in the light fraction organic matter could contribute to the nutrition of eucalypt seedlings in the short-term. The growth (dry matter) and P acquisition (seedling P content) of *E. globulus* seedlings were strongly related. Four of the five treatments supplied with light fraction

Table 4. Rate of phosphorus supply from light fraction organic matter to *E. globulus* seedlings ($\mu\text{g P day}^{-1}$, % P release)

Supply	BM 4	BM 12	BM 22	CPT 9	ESM 22	Control
$\mu\text{g P day}^{-1}$	0.14	0.29	0.42	0.50	0.45	0.13
% P release day^{-1}	0.06	0.12	0.12	0.18	0.28	n.a.

organic matter accumulated more P than the control seedlings. This indicates clearly that the seedlings were able to acquire P in order to support growth. For comparison, total seedling P content in our study was similar to that found after about 2 months growth of *E. grandis* seedlings (Lacey et al., 1966) and 3 months growth of *E. pilularis* seedlings under conditions of low P supply with P added in inorganic nutrient solution (Mulligan and Sands, 1988). However, it is uncertain to what extent *E. globulus* seedlings would take up P from light fraction organic matter when grown without P limitation.

Seedling biomass and P content were unrelated to total P concentration in the light fraction organic matter and to the C:P ratios of the light fraction organic matter. Phosphorus concentrations for the light fraction organic matter used in the plant bioassay ranged from $313 \mu\text{g g}^{-1}$ at ESM 22 to $698 \mu\text{g g}^{-1}$ at BM 22, and similarly, the C:P ratio was lowest for the light fraction from BM 22, 650, and highest for that from ESM 22, 1466, yet seedling growth and P content was the same. Prescott et al. (1992) also found that the growth and P content of pine, spruce and fir seedlings grown on forest floor (FH) material was inconsistent with the C:P ratio of forest floor and litterfall material. Critical C:P ratios indicating net P mineralization have been estimated to be between 200 to 550 (Blair, 1988, Saggart et al., 1998). On the basis of this critical range, only light fraction organic matter from BM 22 might have been expected to supply P. However, Ribeiro et al. (2002) observed P release from eucalypt litter during field decomposition trials, where the C:P ratio of the litter ranged between 872 and 1234, which is comparable to that for the light fraction organic matter used here.

Phosphorus supply from light fraction organic matter

The average daily rate of P supply from light fraction organic matter varied from $0.14 \mu\text{g P day}^{-1}$,

(BM 4), to $0.50 \mu\text{g P day}^{-1}$, (CPT 9). This is similar to the P uptake rate observed for several *Eucalyptus* species (*E. pilularis*, *E. grandis*, *E. regnans*) grown on a range of substrates (e.g., P-deficient sand, burnt soil) for similar periods of time (Launonen et al., 1999; Mulligan and Sands, 1988), but considerably less than that observed for *E. gummifera* ($2.08 \mu\text{g P day}^{-1}$), a species from highly nutrient deficient environments (Mulligan and Sands, 1988). Additionally, the absence of ectomycorrhiza in the present experiment may have limited the P acquisition capacity of *E. globulus* seedlings. Ectomycorrhizal fungi are important symbionts with *Eucalyptus* and are known to increase P acquisition by *E. globulus* when grown in sand with a low P supplement (Burgess et al., 1993; Grove et al., 1996).

Very few studies have attempted to assess the bioavailability of P in soil light fraction organic matter. The rates from the present study, 0.14 – $0.50 \mu\text{g P g light fraction}^{-1} \text{ day}^{-1}$, are considerably lower than those found by Van Noordwijk et al. (1998) for an incubation-mineralization study (2 – $3 \mu\text{g P g light fraction}^{-1} \text{ day}^{-1}$). However, to recover light fraction material by density floatation, Van Noordwijk et al. (1998) employed Ludox colloidal silica, which has been reported to enhance mineralization (Magid et al., 1996). In the present study, water was employed for recovery of light fraction material and may have mitigated against such artefacts. In addition, with the heavier Ludox a different density fraction is being recovered.

To maintain rates of P supply in the field, the rate of turnover of light fraction P must be fast enough and the size of the pool of light fraction P large enough. Hassink (1995) and Magid et al. (1997) estimated turnover rates for light fraction material in pasture and grassland soils to be about 1 year. For the sites investigated, the size of the light fraction pool of P in the top 2.5 cm ranges from about 1 to 4.5 kg P ha^{-1} , representing about 2–4% of total soil P (O'Hara, 2003). If organic matter turnover in eucalypt forests is fast

enough, P release from light fraction organic matter could provide a significant contribution to biological P cycling and supply. However, whilst the turnover rate for some fractions of litter material can be relatively rapid in eucalypt forests (Woods and Raison, 1983), the rate of turnover for light fraction SOM in native eucalypt forest soils is unknown. The origin or source of light fraction material (different aboveground litter components such as leaves or bark, fine root material) could influence its rate of turnover considerably. Presently the origin of light fraction organic matter in eucalypt forest soils remains unknown.

Although the most readily apparent explanation for higher seedling growth relative to control seedlings is P acquisition by seedlings from the light fraction organic matter, additional or alternative factors may also have contributed to the observed response. The grinding of light fraction material which increased the surface area of SOM may have increased P solubility (Friesen and Blair, 1988). In addition, microbial activity may have been stimulated by the added organic matter and in turn stimulated seedling growth due to the production of microbial phytohormones (e.g., Kucey et al., 1989). However, these possible contributing factors are unlikely to invalidate the conclusion that P in light fraction SOM can play a significant role in tree nutrition under P limited conditions.

Conclusion

In forests, the recycling of P through organic matter is important for maintaining and regulating P supply. The present study indicated that light fraction SOM served to increase P acquisition by eucalypt seedlings in the short-term with higher seedling P contents and faster rates of P uptake evident. Light fraction SOM thus represents a pool of biologically active organic matter contributing to P nutrition. Future studies should investigate the contribution of light fraction SOM to P nutrition, the rate of decomposition of and P turnover through light fraction SOM and the physical and chemical relationships between litter material and light fraction SOM.

Acknowledgements

The CRC for Sustainable Production Forestry, CSIRO Forestry and Forest Products and New South Wales State Forests supported this study. Drs C. Beadle and L. Burkitt and two anonymous reviewers provided valuable comments on the manuscript.

References

- Attiwill P M 1980 Nutrient cycling in a *Eucalyptus obliqua* (L'Hérit.) forest. IV Nutrient uptake and return. *Aust. J. Bot.* 28, 199–222.
- Ashton D H and Kelliher K J 1996a Effects of soil desiccation on the growth of *Eucalyptus regnans* F. Muell. seedlings. *J. Veg. Sci.* 7, 487–496.
- Ashton D H and Kelliher K J 1996b The nutritional effects of soil desiccation on the growth of *Eucalyptus regnans* F. Muell. seedlings. *Plant Soil* 179, 45–56.
- Baker T G and Attiwill P M 1985 Above-ground nutrient distribution and cycling in a *Pinus radiata* D. Don. and *Eucalyptus obliqua* L'Hérit. forests in southeastern Australia. *For. Ecol. Man.* 13, 41–52.
- Bekunda M A, Smethurst P J, Khanna P K and Willet I R 1990 Effects of post-harvest residue management on labile soil phosphorus in a *Pinus radiata* plantation. *For. Ecol. Man.* 38, 13–25.
- Blair J M 1988 Nitrogen, sulfur and phosphorus dynamics in decomposing deciduous leaf litter in the southern Appalachians. *Soil Biol. Biochem.* 20(5), 693–701.
- Bray R H and Kurtz L T 1945 Determination of total, organic and available forms of phosphorus in soil. *Soil Sci.* 59, 39–45.
- Brundrett M C, Bougher N L, Dell B, Grove T S and Malajczuk N 1996 Working with Mycorrhizas in Forestry and Agriculture. ACIAR monograph No. 32, Canberra 374 pp.
- Burgess T I, Malajczuk N and Grove T S 1993 The ability of 16 ectomycorrhizal fungi to increase growth and phosphorus uptake of *Eucalyptus globulus* Labill. and *E. diversicolor* F-Muell. *Plant Soil* 153, 155–164.
- Christensen B T 1992 Physical fractionation of soil and organic matter in primary particle size and density separates. *Adv. Agron.* 20, 1–90.
- Christensen B T 2001 Physical fractionation of soil and structural and functional complexity in organic matter turnover. *Eur. J. Soil Sci.* 52, 345–353.
- Curtin D, McCallum F M and Williams P H 2003 Phosphorus in light fraction organic matter separated from soils receiving long-term applications of superphosphate. *Biol. Fertil. Soil* 37, 280–287.
- Dell B, Malajczuk N, Xu D and Grove T S 2001 Nutrient Disorders in Plantation Eucalypts. Australian Centre for International Agricultural Research monograph 74, Canberra, Australia 188 pp.
- Friesen D K and Blair G J 1988 A dual radiotracer study of transformations of organic, inorganic and plant residue phosphorus in soil in the presence and absence of plants. *Aust. J. Soil Res.* 26, 355–366.

- Giardina C P and Rhoades C C 2001 Clear cutting and burning affect nitrogen supply, phosphorus fractions and seedling growth in soils from a Wyoming lodgepole pine forest. *For. Ecol. Man.* 140, 19–28.
- Grove T S, Malajczuk N and Hardy G E S 1996 The effect of soil pH on the ability of ectomycorrhizal fungi to increase the growth of *Eucalyptus globulus* Labill. *Plant Soil* 178, 209–214.
- Hallsby G 1994 The influence of different forest organic matter on the growth of one-year-old planted Norway spruce seedlings in a greenhouse experiment. *New For.* 8, 43–60.
- Hassink J 1995 Decomposition rate constants of size and density fractions of soil organic matter. *Soil Sci. Soc. Am. J.* 59, 1631–1635.
- Heffernan B 1985 A Handbook of Methods of Inorganic Chemical Analysis for Forest Soils Foliage and Water. CSIRO Forest Research.
- Kucey R M N, Janzen H H and Leggett M E 1989 Microbially mediated increases in plant-available phosphorus. *Adv. Agron.* 42, 199–228.
- Lacey C J, Leaf A L and Talli A R 1966 Growth and nutrient uptake by flooded gum seedlings subjected to various phosphorus supplies. *Aust. For.* 30, 212–222.
- Launonen T M, Ashton D H and Keane P J 1999 The effect of regeneration burns on the growth, nutrient acquisition and mycorrhizae of *Eucalyptus regnans* F. Muell. (Mountain Ash) seedlings. *Plant Soil* 210, 273–283.
- Magid J, Gorrissen A and Giller K E 1996 In search of the elusive “active” fraction of soil organic matter: three size-density fractionation methods for tracing the fate of homogeneously ¹⁴C-labelled plant materials. *Soil Biol. Biochem.* 28, 89–99.
- Magid J, Jensen L S, Mueller T and Nielsen N E 1997 Size-density fractionation for *in situ* measurements of rape straw decomposition-an alternative to the litterbag approach? *Soil Biol. Biochem.* 29, 1125–1133.
- Maroko J B, Buresh R J and Smithson P C 1999 Soil phosphorus fractions in unfertilized fallow–maize systems on two tropical soils. *Soil Sci. Soc. Am. J.* 63, 320–326.
- Melillo J M, Aber J D, Linkens A E, Ricca A, Fry B and Nadelhoffer K J 1989 Carbon and nitrogen dynamics along a decay continuum: plant litter to soil organic matter. *Plant Soil* 115, 189–198.
- Mendham D, Smethurst P, Holz G, Menary R, Grove T, Weston C and Baker T 2002 Soil analyses as indicators of P status in young *Eucalyptus nitens* and *E. globulus* plantations. *Soil Sci. Soc. Am. J.* 66, 959–968.
- Mulligan D R and Sands R 1988 Dry matter, phosphorus and nitrogen partitioning in three *Eucalyptus* species grown under a nutrient deficit. *New Phytol.* 109, 21–28.
- Neff J C, Townsend A R, Gleixner G, Lehman S J, Turnball J and Bowman W D 2002 Variable effects of nitrogen additions on the stability and turnover of soil carbon. *Nature* 419, 915–917.
- O’Hara C P 2003 The significance of soil physical fractions for the cycling of phosphorus, carbon and nitrogen in forests of south-east Australia. PhD Thesis, Australian National University, 287 pp.
- Olsen S R, Cole C V, Watanabe F S and Dean L A 1954 Estimation of Available Phosphorus in Soils by Extraction with Sodium Bicarbonate. United States Department of Agriculture circular No. 939.
- Phiri S, Barrios I M and Singh B R 2001 Changes in soil organic matter and phosphorus fractions under planted fallows and a crop rotation system on a Colombian volcanic-ash soil. *Plant Soil* 231, 211–223.
- Prescott C E, Corbin J P and Parkinson D 1992 Availability of nitrogen and phosphorus in the forest floors of Rocky Mountain coniferous forests. *Can. J. For. Res.* 22, 593–600.
- Ribeiro C, Madeira M and Araújo M C 2002 Decomposition and nutrient release from leaf litter of *Eucalyptus globulus* grown under different water and nutrient regimes. *For. Ecol. Man.* 171, 31–41.
- Ryan P J, McKenzie N J, O’Connell D, Loughhead A N, Leppert P M, Jacquier D and Ashton L 2000 Integrating forest soils information across scales: spatial prediction of soil properties under Australian forests. *For. Ecol. Man.* 138, 139–157.
- Saggar S, Parfitt R L, Salt G and Skinner M F 1998 Carbon and phosphorus transformations during decomposition of pine forest floor with different phosphorus status. *Biol. Fert. Soil* 27, 197–204.
- SAS Institute 1996 JMP Start Statistics – A Guide to Statistics and Data Analysis using JMP and JMP IN Software. Duxbury Press, Belmont 521 pp.
- Six J, Conant R T, Paul E A and Paustian K 2002 Stabilization mechanisms of soil organic matter: implications for C-saturation of soils. *Plant Soil* 241, 155–176.
- Sollins P, Spycher G and Glassman C A 1984 Net nitrogen mineralization from light- and heavy-fraction forest soil organic matter. *Soil Biol. Biochem.* 16, 31–37.
- Turner J (1996) Evaluation of Santiago (Montreal) Declaration Indicators of Sustainability for Australian Commercial Forests. A New South Wales Alpine Ash Forest as a Case Study. Vol. 3, Forest and Wood Products Research and Development Corporation, Tech Pub 3, 113 pp.
- Van Noordwijk M, Hairiah K, Woomer P L and Murdiyarso D 1998 Criteria and indicators of forest soils used for slash-and-burn agriculture and alternative land uses in Indonesia. *In* The Contribution of Soil Science to the Development of and Implementation of Criteria and Indicators of Sustainable Forest Management Eds M B Adams, K Ramakrishna and E A Davidson pp. 137–154. Soil Science Society of America Special publication No. 53. Soil Science Society of America, Wisconsin.
- Woods P V and Raison R J 1983 Decomposition of litter in sub-alpine forests of *Eucalyptus delegatensis*, *E. pauciflora* and *E. dives*. *Aust. J. Ecol.* 8, 287–299.