ORIGINAL PAPER

A.K.M.A. Hossain · R.J. Raison · P.K. Khanna

Effects of fertilizer application and fire regime on soil microbial biomass carbon and nitrogen, and nitrogen mineralization in an Australian subalpine eucalypt forest

Received: 23 December 1993

Abstract The effects of a range of fertilizer applications and of repeated low-intensity prescribed fires on microbial biomass C and N, and in situ N mineralization were studied in an acid soil under subalpine Eucalyptus pauciflora forest near Canberra, Australia. Fertilizer treatments (N, P, N+P, lime+P, sucrose+P), and P in particular, tended to lower biomass N. The fertilizer effects were greatest in spring and smaller in summer and late autumn. Low-intensity prescribed fire lowered biomass N at a soil depth of 0-5 cm with the effect being greater in the most frequently burnt soils. No interactions between fire treatments, season, and depth were significant. Only the lime +P and N+P treatments significantly affected soil microbial biomass C contents. The N+P treatment increased biomass C only at 0-2.5 cm in depth, but the soil depth of entire 0-10 cm had much higher (>doubled) biomass C values in the lime + P treatment. Frequent (two or three times a year) burning reduced microbial biomass C, but the reverse was true in soils under forest burn at intervals of 7 years. Soil N mineralization was increased by the addition of N and P (alone or in combination), lime + P, and success + P to the soil. The same was true for the ratio of N mineralization to biomass N. Soil N mineralization was retarded by repeated fire treatments, especially the more frequent fire treatment where rates were only about half those measured in unburnt soils. There was no relationship between microbial biomass N (kg N ha⁻¹) and the field rates of soil N mineralization (kg N ha⁻¹ month⁻¹). The results suggest that although soil microbial biomass N represents

A. K. M. A. Hossain Department of Forestry, The Australian National University, GPO Box 4, Canberra ACT 0200, Australia R. J. Raison (⊠) • P.K. Khanna CSIRO, Division of Forestry,

P.O. Box 4008, Queen Victoria Terrace Canberra, ACT 2600, Australia a distinct pool of N, it is not a useful measure of N turnover.

Key words Microbial biomass · In situ N mineralization · Fertilizer · Prescribed fire · *Eucalyptus* forest

Introduction

The microbial biomass is considered the agent of biochemical change in soil (Jenkinson 1988). It serves as both a sink and a source of plant-available nutrients, especially N, P, and S (Jenkinson and Ladd 1981). The size and activity of the soil microbial biomass is regulated mainly by the availability of organic C, climatic conditions, and other factors such as soil nutrient status. The soil microbial biomass responds much more quickly to changes in management practices (e.g., fertilization) than does soil total organic C or N and may be an indicator of early trends in changes to the soil organic matter pool (Schnürer et al. 1985). Thus measurements of the microbial biomass may make a valuable contribution towards understanding and predicting the long-term effects of changes in soil conditions.

Soil management practices have variable effects on the soil microbial biomass, depending on a multitude of factors with effects that are not sufficiently well understood. For example, the addition of fertilizer-N decreased biomass C in pine forest soils (Nöhrstedt et al. 1989), and biomass N and C in both grassland (Christie and Beattie 1989) and pasture soils (Bristow and Jarvis 1991). In contrast, other studies have showed an increase in biomass C (Hesebe et al. 1985) and N (Shen et al. 1989) in agricultural soils.

Fire removes organic matter and nutrients from a site by volatilization and ash transfer (Raison et al. 1985). Other important short- and long-term changes may also occur in soil conditions (Raison et al. 1990a). Fire-induced changes in soil microbial numbers and activities depend on the severity of the fire, the types of organisms involved, the post-fire environmental conditions, the frequency of fire, the total number (cumulative effect) of fires, and the length of time since the fire. In some studies (Tateishi et al. 1989; Singh et al. 1991; Pietikäinen and Fritze 1993) the effects of low-intensity prescribed or wild fire on soil microbial biomass C and N have been measured. In most cases, a decrease in biomass N and C has been observed. However, Singh et al. (1991) reported that burning increased soil microbial biomass C and N in a dry tropical forest. Too frequent low-intensity burning can lower soil N mineralization in some forest ecosystems (Bell and Binkley 1989; Raison et al. 1990a).

In the present study we measured the effects of different fertilizers and of low-intensity prescribed fire on microbial biomass N and C, and in situ N mineralization in an acid forest soil under *Eucalyptus pauciflora* forest. The relationship between soil microbial biomass N and in situ rates of soil N mineralization is examined.

Materials and methods

Site and soil description

The field site, located near Canberra (148° 48' H, 35° 23' S) in the Australian Capital Territory, is a natural subalpine *Eucalyptus pauciflora* (Sieb. ex Spreng) or snow gum forest with a woody leguminous understorey of *Daviesia mimosoides* shrubs (Raison et al. 1985). The elevation is 1220 m and the climate is cool temperate, with warm summers (mean maximum of 24°C and minimum of 10°C in January) and cold winters (4°C and -1°C in July). The long-term mean annual rainfall of 1150 mm shows no marked seasonal pattern.

The soil at the site is a red earth (Stace et al. 1968), derived from highly weathered Ordovician metasediments. The soil is high in total C and N, has a very high P-fixing capacity (Khanna et al. 1986), and is highly acid, well aggregated, and highly permeable. The A horizon (0-40 cm) is an organic loam and the B horizon (40-70 cm) a light clay loam to massive light clay, although the profiles vary in depth, and stone and clay contents. The effective cation exchange capacity is dominated by Al ions, which occupy 81-91% of the exchange sites (Khanna et al. 1986). Selected physical and chemical properties of the surface soil are listed in Table 1.

Field treatments

Fertilizer: Nutrients were applied in a factorial design to triplicate 20×20 m plots in early December, 1986 (Keith 1991). Six treatments were studied, comprising (1) control; (2) Lime+P, with 10 t lime ha⁻¹ and 500 kg P ha⁻¹ as superphosphate; (3) 300 kg N ha⁻¹ as ammonium sulphate; (4) 500 kg P ha⁻¹ as superphosphate; (5) N+P, a combination of the N and P applications in treatments 3 and 4; and (6) sucrose+P, with sucrose equivalent to 2000 kg C ha⁻¹ and 500 kg P ha⁻¹ as superphosphate. Each plot was divided into cells and lime with P was broadcast by hand at a calculated rate.

Fire: A long-term fire ecology study was established at the site in 1975. The site was burnt by low-intensity prescribed fires in 1962 and 1973, and since then a range of frequencies of low-intensity prescribed fires has been imposed on a set of experimental plots. Soil samples were taken from triplicate plots subjected to three fire treatments, (1) unburnt since 1973; (2) regularly burnt at a 7-year frequency (1973, 1980, and 1987); and (3) frequently burnt at 2–3 years' frequency (1973, 1975, 1978, 1981, 1984, and 1987). These fires typically have an intensity of <350 kW m⁻¹, flame heights of <1 m, a forward speed of 1 m min⁻¹, and the mass of litter and understorey combusted is 11-17 t ha⁻¹.

Soil collection

Twenty-four soil cores (54 mm in diameter) were taken from each plot on four occasions (June and September 1988, January and March 1989). The soil cores were sectioned by depth (0-2.5, 2.5-5, and 5-10 cm) and the soil samples were sieved (<2 mm). Six cores were bulked to give composite samples per plot for each depth. Large soil animals, stones, and discrete pieces of undecomposed plant materials were removed by hand. The sieved soils were stored overnight in field-moist conditions at 4 °C before the measurements of soil microbial biomass N and C were undertaken.

Laboratory measurements

Soil microbial biomass N: Microbial biomass N was determined using a fumigation and extraction procedure. This method uses hexanol as a fumigant instead of the chloroform commonly used to kill the microbes, because as a fumigant it is as effective as chloroform, less hazardous, and allows the fumigation of a large number of soil samples at the same time (Hossain 1990). The N rendered extractable with K_2SO_4 after exposure of the soils to hexanol for 24 h showed very good agreement with 5-day chloroform fumigation and extraction in a range of acid forest soils (Hossain 1990).

Hexanol fumigation was achieved by incubating 10-g portions of field-moist soils with 4 ml haxenol in an enclosed 100-ml plastic bottle for 24 h, followed by uncapping and evaporation for 16 h in a fume cupboard. Evaporation, however, did not entirely remove the hexanol from the treated soils. The fumigated soils were extracted for 1 h with $0.5 M K_2 SO_4$ (1:5, soil: solution ratio) and filtered through Whatman no. 1 filter paper which had been previously rinsed with K₂SO₄ solution. The extraction was identical for both unfumigated and fumigated samples. The filtered extracts were stored at 4 °C for 2-3 days before analysis. Microbial N was calculated as $F_T - UF_M$, where F_T and UF_M are the total soluble N in the fumigated sample and the mineral N in unfumigated sample, respectively. Microbial N was then converted to biomass N using a correction factor of 1.16 to compensate for the inefficiency of a single K₂SO₄ extraction in removing all microbial N (Hossain 1990).

Soil microbial biomass C: Microbial biomass C was determined on four replicate subsamples on one occasion (March 1989) using the substrate-induced respiration method (Anderson and Domsch 1978) with the modifications suggested by West and Sparling (1986). Respiration was measured as CO_2 release and gas concentrations were determined by injecting 1 ml headspace gas into a por-

Table 1Selected physical and
chemical properties of the red
earth soil (CECe exchangeable
cation capacity)

Soil depth (cm)	Bulk density (kg cm ⁻³)	pH (water) (1:5)	Organic C (%)	Total N (%)	C:N ratio	CECe (mmol ⁽⁺⁾ kg ⁻¹)
0-2.5	0.61	4.1	16.1	0.522	30.8	13.3
2.5 - 5	0.61	4.3	11.5	0.419	27.4	9.8
5 - 10	0.89	4.5	9.6	0.373	25.7	7.4

table CO₂ analyzer (Licor 6200) (Leuning and Sands 1989). The rate of CO₂ evolution was recorded over 2 h after adding 2 ml glucose solution (10 g glucose ml⁻¹) to 1 g field-moist soil. These optimal assay conditions for the soil had been determined previously (Hossain 1990). The respiration rate was converted to microbial biomass C using the following formula suggested by Sparling et al. (1990): Biomass C = 50.4 (μ l CO₂ g⁻¹ h⁻¹).

Measurement of N mineralization under field conditions

Sequential soil coring and in situ exposure (incubation) of intact columns of soil confined within tubes (Raison et al. 1987) were used to estimate N mineralization under field conditions. It has been shown that the in situ soil core technique is effective for estimating temporal changes in soil mineral N fluxes in response to forest treatment and also for tracing the fate of unlabelled N fertilizer (Raison et al. 1992). Rates of N mineralization were calculated as the changes in mineral N content in confined (no N uptake by roots) soils during field exposure (Raison et al. 1990b). The mass of fine earth was used to convert mineral N concentrations on an areal basis and expressed as kg N ha⁻¹ year⁻¹.

Analyses of soil extracts

Inorganic N (NH₄⁺-N and NO₃⁻-N) in the K₂SO₄-soil extracts was analyzed by an automated colorimetric procedure, with NO₃⁻-N reduced to NH₄⁺-N using Ti(SO₄)₂ before analysis (Heffernan 1985). Total N in the K₂SO₄-soil extracts was measured after acid-peroxide (H₂SO₄-H₂O₂) digestion which gives similar results to Kjeldahl digestion for chloroform-fumigated and unfumigated soil extracts (Hossain et al. 1993). Total NH₄⁺-N in the soil extracts was analyzed by the automated indophenol-blue procedure (Heffernan 1985).

Data analysis

The differences between treatment means for microbial biomass N were analyzed by standard analysis of variance using GENSTAT. Significant differences were compared using least significant difference (P < 0.05). Variability among the individual measurements for the substrate-induced respiration biomass C was presented along with the standard error.

Fig. 1a-c Main effects of fertilizer treatments (a), seasons (b), and depths (c) on microbial biomass N (mg N kg⁻¹ soil) in a red earth soil under *Eucalyptus pauciflora* forest. Treatments were applied in December 1986. Vertical bars indicate least significant difference (P < 0.05) for determining differences between treatments (T), seasons (S), and depths (D)

Results and discussion

Effects of N, P, lime, and sucrose additions and prescribed fire on soil microbial biomass N

Figure 1 summarizes the main effects of fertilizer treatments, seasons, and depths on the amount of microbial biomass N in the soil. Biomass N was significantly (P < 0.001) lower in the P-only treatment (Fig. 1a). The addition of P has also been shown to depress microbial activity in this soil (Bauhus and Khanna 1994). The addition of P with lime, N, or sucrose also tended to decrease microbial biomass N when compared to the control, but the differences were not statistically significant.

The trend for lower biomass N in N-fertilized soils corresponded with an increased mineralization of soil N (Table 2). Singh et al. (1989) also reported that microbial biomass and nutrient pools declined as N mineralization increased. Christie and Beattie (1989) reported decreased biomass N in N-fertilized soil compared with control soil and attributed this to the acidifying effect of fertilizer N. In our soils, N and P fertilizer applications reduced soil pH (in KCl) for the entire soil depth of 0-10 cm by 0.15-0.32 units compared to the unfertilized control.

The addition of N, lime, or sucrose with P produced more biomass N than treatment with P alone. In a laboratory experiment Bekunda (1987) found that lime+P treatment resulted in a short-term (up to 157 days) reduction in biomass N, which he ascribed to increased microbial activity in this treatment.

Overall microbial biomass N was highest in spring and lower in summer and late autumn (Fig. 1b). The decreased biomass N in summer may have resulted from a low soil moisture content. In these soils, the field moisture content varied between 25 and 30% in summer, and between 40 and 45% in spring and autumn. The moisture content was relatively higher in the top 2.5 cm of soil than at 2.5-5 cm (10-13%) and 5-10 cm (15-18%). In a



Table 2 Mean microbial biomass N and in situ N mineralization (N_{min}) at a depth of 0-10 cm in fertilizer and fire-treated soil under *Eucalyptus pauciflora* forest. Means values for biomass N and N_{min} are based on estimates on three occasions between June 1988 and January 1989

Soil treatment	Biomass N (kg N ha ⁻¹)	Estimated annual N_{min} (kg N ha ⁻¹ year ⁻¹)	Ratio N _{min} /mean biomass N
Fertilizer			
С	41.7	12.1	0,29
Lime + P	46.5	16.7	0.36
P	32.8	17.5	0.53
N	38.7	24.1	0.62
N+P	37.4	18.3	0.49
Sucrose + P	39.1	16.4	0.42
Fire			
Unburnt	43.1	16.1	0.37
Regularly burnt	36.3	10.7	0.30
Frequently burnt	36.6	7.2	0.20

drying-rewetting experiment using field-moist unfertilized soils from different eucalypt forests, air-drying for 3 days decreased biomass N by 54, 48, and 38% at depths of 0-2.5, 2.5-5, and 5-10 cm, respectively (Hossain 1990). Microbial biomass N was significantly (P < 0.001) higher in the surface soil layer and decreased with increasing depths (Fig. 1 c).

The effects of fertilizer treatments averaged across depths varied significantly (P < 0.001) with season and almost the same trend, as in Fig. 1 b, was noticed with all the fertilizer treatments. The average biomass N content was 3.2% of the total soil N, which is within the range (2-5%) reported for a large number of soils from different climatic regions and soil types (Jenkinson and Ladd 1981; Smith and Paul 1990).

Analysis of variance showed that the effect of low-intensity prescribed fire on soil microbial biomass N was significant (P = 0.072), that the other main effects (season and depth) were highly significant (P < 0.001); and that no significant interactions occurred.

Microbial biomass N was significantly higher (10-12%) in soils from the long-unburnt site than at the regularly or frequently burnt sites (Fig. 2). The effects of fire were much greater at 0-2.5 cm in depth, less at 2.5-5 cm, and least at 5-10 cm in depth. The effects of burning on microbial biomass N in the surface horizons were probably due to the cumulative losses of C and N from fuels by volatilization (Raison et al. 1985) and perhaps due to the more arid microenvironments generated after the fire (Raison et al. 1986). A decreased in soil microbial biomass N after fire has been observed in other forest soils (Pietikäinen and Fritze 1993), but the effects are not generic (Singh et al. 1991).





Fig. 2 Effects of soil sampling depth on microbial biomass N (mg N kg⁻¹ soil) at the long-unburnt (*UB*) and regularly (*RB*) and frequently (*FB*) burnt sites. The sites were last burnt in autumn 1987 and sampled 18, 22, and 24 months later. Mean values for seasons were used. Vertical bar indicates least significant difference (P < 0.05)

Fig. 3 Effects of season on soil microbial biomass N (mg N kg⁻¹ soil) at the long-unburnt (*UB*) and regularly (*RB*) and frequently (*FB*) burnt sites. Mean values for depths were used. Vertical bars indicate least significant difference (P < 0.05)

The seasonal variation in soil microbial biomass N in the unburnt and burnt sites was similar to that seen on the fertilized plots (Figs. 1 b, 3). The effect of the fire treatments was little affected by the season of measurement.

Effects of fertilization and prescribed fire on soil microbial biomass C

The substrate-induced respiration-microbial biomass C for three depths in the fertilized and fire-treated soils is shown in Fig. 4. Compared with unfertilized control soil, soils treated with lime+P and N+P had more biomass C in the surface horizons, and those treated with lime+P had higher values in the lower depth. Soils treated with N or P alone had lower values at 0-2.5 and 2.5-5 cm, but were not different at 5-10 cm. Sucrose+P had no effect on microbial biomass C, except at 2.5-5 cm where it was significantly lower than in the control soil.



Fig. 4a, b Soil microbial biomass C (mg C kg⁻¹ soil) measured by the substrate-induced respiration method at various depths sampled in March 1989 as influenced by fertilizer (a) and low-intensity prescribed fire (b) treatments. *Error bars* represent the SEM; *UB* unburnt, *RB* regularly burnt, *FB* frequently burnt

The increase in biomass C in the lime+P treatment was possibly a result of solubilization of organic matter. In their modified method, West and Sparling (1986) pointed out that the substrate-induced respiration method will not give reliable biomass C values in near-neutral soil where pH exceeds 6.0, because of retention of evolved CO_2 in the soil solution. In the L+P treatment, soil pH (in KCl) at 0-2.5, 2.5-5, and 5-10 cm was 6.2, 4.1, and 3.8, respectively. Low pH can adversely affect microbial activity. The use of a conversion factor of 50.4, as suggested by Sparling et al. (1990), may not be appropriate for the differently fertilized soils we used. Overall, the effects of fertilizer on soil microbial biomass C cannot be generalized.

Generally, microbial biomass C represents 2-5% of the total soil C over a wide range of locations and soil types (Jenkinson and Ladd 1981; Smith and Paul 1990). Srivastava et al. (1989) reported that biomass C accounted for 2.9% of the soil organic C in a mixed, dry, deciduous-forest soil. In the present study, biomass C accounted for only 0.7% (averaged across treatments and depths, but excluding soils from the lime + P treatment) of the soil organic C.

The microbial biomass C content in the fire-treated soils followed a different pattern to that found for biomass N, especially in the regularly burnt site (Fig. 4b). At all depths the trend in soil biomass C was regularly burnt > unburnt > frequently burnt. The reason why the biomass C concentration increased in the regularly burnt soil and decreased in the frequently burnt soil can only be speculated upon. The frequently burnt site had been subjected to six fires since 1973 applied every 2-3 years, which would have reduced litter C inputs to the soil (Keith 1991) and decreased N mineralization (Table 2). With less frequent fires (regularly burnt), there can be some shortterm increase in fragmentation and incorporation of partly combusted litter residues (Raison et al. 1986). Recently, Pietikäinen and Fritze (1993) showed that prescribed fire reduced microbial biomass C by 41% in a Norway spruce (Picea abies) forest. In contrast, Tateishi et al. (1989) found no significant difference in biomass C between unburnt and burnt treatments in a red pine forest soil. Singh et al. (1991) reported that the higher (18%) biomass C in the burned sites of a dry deciduous forest was associated with increased root turnover and root exudates, which provided extra resources for the associated microbes. Thus, prescribed or forest fire-induced changes in soil microbial biomass C show variable results which depend on a number of factors including severity of fire, post-fire environmental conditions, and frequency and cumulative effects of fire.

Relationship between soil microbial biomass N and C

Estimates of microbial biomass N and C in differently treated soils can be compared for samples taken in March 1989. There was a linear relationship between biomass N and C, with the regression accounting for 78.2% of the variance in the data, if soils from lime+P and regularly burnt treatments were excluded from the analysis. The latter had very high biomass C values (Fig. 4). Other studies (Christie and Beattie 1989; Srivastava et al. 1989) have also shown a highly significant correlation between biomass N and C. By contrast, Bristow and Jarvis (1991) found no relationship between these two estimates in grazed and N-fertilized pasture soils.

The microbial C: N ratios were significantly higher at 0-2.5 cm and decreased with increasing depths. This perhaps suggests that more of the biomass is metabolically active in the surface soil and that this declines with increasing depth in the soil (i.e. substrate-induced respiration measures the active biomass component, but the fumigation - extraction procedure measures the pool of microbial biomass N contributed by both active and resting microorganisms). Excluding data for the lime+P treatment which had an abnormally high biomass C content (Fig. 4a), the mean biomass C: N ratio for the fertilized soils was 5.0 (range 3.0-8.1). This is the same as reported for a range of forest soils (Smith and Paul 1990). However, the present microbial C:N ratios were much lower than those found for a dry tropical forest soil (9.0-11.6;Srivastava et al. 1989). Schnürer et al. (1985) reported that the C: N ratio of the soil microbial biomass was almost constant (5.9-6.1), regardless of treatment or sampling time. The ratios of biomass C: N for the unburnt and burnt sites varied between 3.5 and 14.8 (mean 8.3). Overall, the ratios were highest at the regularly burnt site, lower at the unburnt site, and lowest at the frequently burnt site, a similar pattern to that for microbial biomass C (Fig. 4b).

Mineralization of N in fertilizer and fire-affected soils and its relationship with biomass N

Table 2 shows the effects of different fertilizer treatments and low-intensity prescribed fires on in situ N mineralization and the ratio of N mineralization to biomass N. All fertilizer amendments increased soil N mineralization compared to the control. When calculated on an annual basis, the rates of net N mineralization were 100 and 51% greater in the N and N+P treatments, even though the fertilizer had been applied 15 months before measurements of N mineralization commenced. Raison et al. (1990b) also showed that the addition of 400 kg N ha⁻¹ as (NH₄)₂SO₄ increased long-term N mineralization rates in a podzolic soil under a *Pinus radiata* plantation. In the present study, the addition of P increased annual N mineralization rates by 44% (Table 2). Falkiner et al. (1993) concluded that increased N mineralization could persist for at least 2 years after P addition to a range of Australian forest soils. The effects of the lime+P and sucrose + P treatments were smaller, but still significant.

Low-intensity prescribed fire decreased rates of soil N mineralization (Table 2). The annual rate of net N mineralization at the frequently burnt site (3-year frequency) was 7.2 kg N ha^{-1} (45% of the unburnt site), and

10.7 kg N ha⁻¹ (67% that of the unburnt site) at the regularly burnt site (7-year frequency). This result shows that the greater the fire frequency the lower the soil N mineralization; a similar pattern was also observed in soil microbial biomass N (Fig. 3). Repeated frequent fire at the frequently burnt site volatilized significant amounts of N in smoke, reduced the N release from decomposing litter, and lowered the quantity of N held in tree foliage and the rate of leaf fall (an index of stand productivity) and its N content (Raison et al. 1993). In the same soils over a 25-month study period (4 months before and 21 months after the 1987 fire), Raison et al. (1990a) found that the net N mineralization at 0-20 cm was 51% in the frequently burnt sites and 64% in the regularly burnt sites compared to the unburnt sites. Bell and Binkley (1989) have also reported reduced soil N mineralization after repeated low-intensity burning.

There was no relationship $(r^2 = 0.016, n = 27)$ between soil microbial biomass N and the N mineralization rate, and the ratio of N mineralization to biomass N varied significantly with treatment (Table 2). The ratio was much greater in fertilized soils than in unfertilized soil, because the fertilizer additions increased the mineralization rate (Table 2), but not biomass N (Fig. 1a). Among the fire-treated soils, N turnover was higher in the unburnt site and lower in the burnt sites.

Although the microbial biomass has been considered as a pool of readily mineralized N (Jenkinson and Ladd 1981), our findings suggest that attempts to use it as a predictor of soil N availability may not always be productive. In forest soils, N availability depends on many factors, such as temporal changes in organic substrates associated with variation in litterfall, fine root turnover, quality of soil organic matter, and environmental conditions.

Acknowledgements This study was carried out while the senior author was a recipient of an Australian National University Scholarship. In situ N mineralization data were supplied by Dr. H. Keith and Mr. R. A. Falkiner. We thank Mr. J. Hoare and Dr. H. Keith for use of the experimental sites. Mr. P. Snowdon provided advice in statistical analysis.

References

- Anderson JPE, Domsch KH (1978) A physiological method for the quantitative measurement of microbial biomass in soil. Soil Biol Biochem 10:215-221
- Bauhus J, Khanna PK (1994) Carbon and nitrogen turnover in two acid forest soils of southeast Australia as affected by phosphorus addition and drying and rewetting cycles. Biol Fertil Soils 17:212-218
- Bekunda MA (1987) Characterisation and transformation of phosphorus in forest soils. PhD thesis, The Australian National University, Canberra
- Bell RL, Binkley D (1989) Soil nitrogen mineralization and immobilization in response to periodic prescribed fire in a loblolly pine plantation. Can J For Res 19:816-820
- Bristow AW, Jarvis SC (1991) Effects of grazing and nitrogen fertiliser on the soil microbial biomass under permanent pasture. J Sci Food Agric 59:9-21
- Christie P, Beattie JAM (1989) Grassland soil microbial biomass

and accumulation of potentially toxic metals from long-term slurry application. J Apple Ecol 26:597-612

- Falkiner RA, Khanna PK, Raison RJ (1993) Effect of superphosphate addition on N mineralization in some Australian forest soils. Aust J Soil Res 31:285-296
- Heffernan B (1985) A handbook of methods of inorganic chemical analysis for forest soils, foliage and water. Division of Forestry, CSIRO, Canberra
- Hesebe A, Kanazawa S, Takai Y (1985) Microbial biomass in paddy soil. II. Microbial biomass carbon measured by Jenkinson's fumigation method. Soil Sci Plant Nutr 31:349-359
- Hossain AKMA (1990) Estimation of microbial biomass nitrogen in some Australian forest soils. PhD thesis, The Australian National University, Canberra
- Hossain AKMA, Khanna PK, Field JB (1993) Acid-peroxide digestion procedure for determining total nitrogen in chloroform-fumigated and non-fumigated soil extracts. Soil Biol Biochem 25:967-969
- Jenkinson DS (1988) Determination of microbial biomass carbon and nitrogen in soil. In: Wilson JR (ed) Advances in nitrogen cycling in agricultural ecosystems. CAB International, Wallingford, pp 368-386
- Jenkinson DS, Ladd JN (1981) Microbial biomass in soil: Measurement and turnover. Soil Biochem 5:415-471
- Khanna PK, Raison RJ, Falkiner RA (1986) Exchange characteristics of some acid organic-rich forest soils. Aust J Soil Res 24:67-80
- Keith H (1991) Effects of fire and fertilization on nitrogen cycling and tree growth in a subalpine eucalypt forest. PhD thesis, The Australian National University, Canberra
- Leuning R, Sands P (1989) Theory and practice of a portable photosynthesis instrument. Plant Cell Environ 12:669-678
- Nöhrstedt H-Ö, Arnebrant K, Bååth E, Söderström B (1989) Changes in carbon content, respiration rate, ATP content, and microbial biomass in nitrogen-fertilized pine forest soils in Sweden. Can J For Res 19:323-328
- Pietikäinen J, Fritze H (1993) Microbial biomass and activity in the humus layer following burning: short-term effects of two different fires. Can J For Res 23:1275-1285
- Raison RJ, Khanna PK, Woods PV (1985) Transfer of elements to the atmosphere during low-intensity prescribed fires in three Australian sub-alpine eucalypt forests. Can J For Res 15:657-664
- Raison RJ, Woods PV, Khanna PK (1986) Decomposition and accumulation of litter after fire in sub-alpine eucalypt forests. Aust J Ecol 11:9–19
- Raison RJ, Connell MJ, Khanna PK (1987) Methodology for studying fluxes of soil mineral-N in situ. Soil Biol Biochem 19:521-530

- Raison RJ, Keith H, Khanna PK (1990a) Effects of fire on the nutrient-supplying capacity of forest soils. In: Dyck WJ, Mees CA (eds) Impact of intensive harvesting on forest site productivity.
 Forest Research Institute, Rotorua, FRI Bull 159:39-54
- Raison RJ, Khanna PK, Connell MJ, Falkiner RA (1990b) Effects of water availability and fertilization on nitrogen cycling in a stand of *Pinus radiata*. For Ecol Manage 30:31-43
- Raison RJ, Connell MJ, Khanna PK, Falkiner RA (1992) Effects of irrigation and nitrogen-fertilisation on fluxes of soil mineral nitrogen in a stand of *Pinus radiata*. For Ecol Manage 52:43-64
- Raison RJ, O'Connell AM, Khanna PK, Keith H (1993) Effects of repeated fires on nitrogen and phosphorous budgets and cycling processes in forest ecosystems. In: Trabaud L, Prodon R (eds) Fire in Mediterranean ecosystems. EEC Publication, Belgium, pp 347-363
- Schnürer J, Clarholm M, Rosswall T (1985) Microbial biomass and activity in an agricultural soil with different organic matter contents. Soil Biol Biochem 17:611-618
- Shen SM, Hart PBS, Powlson DS, Jenkinson DS (1989) The nitrogen cycle in the Broadbalk wheat experiment: ¹⁵N-labelled fertilizer residues in the soil and in the soil microbial biomass. Soil Biol Biochem 21:529-533
- Singh JS, Raghubanshi AS, Singh RS, Srivastava SC (1989) Microbial biomass acts as a source of plant nutrients in dry tropical forest and savanna. Nature (London) 338:499-500
- Singh RS, Srivastava SC, Raghubanshi AS, Singh JS, Singh SP (1991) Microbial C, N and P in dry tropical savanna: Effects of burning and grazing. J Appl Ecol 28:869-878
- Smith JL, Paul EA (1990) The significance of soil microbial biomass estimations. Soil Biochem 6:357-396
- Sparling GP, Feltham CW, Reynolds J, West AW, Singleton P (1990) Estimation of soil microbial C by a fumigation-extraction method: Use on soils of high organic matter content, and a reassessment of the k_{PC} -factor. Soil Biol Biochem 22:301-307
- Srivastava SC, Jha AK, Singh JS (1989) Changes with time in soil microbial biomass C, N, and P of mine spoils in a dry tropical environment. Can J Soil Sci 69:849-855
- Stace HCT, Hubble GD, Brewet R, Northcote KH, Sleeman JR, Mulchay MJ, Hallsworth EG (1968) A handbook of Australian soils. Rellim Tech Pub, Adelaide, South Australia
- Tateishi T, Horikoshi T, Tsubota H, Takahashi F (1989) Application of the chloroform fumigation-incubation method to the estimation of microbial biomass in burned and unburned Japanese red pine forests. Microb Ecol 62:163-172
- West AW, Sparling GP (1986) Modifications to the substrate-induced respiration method to permit measurements of microbial biomass in soils of differing water contents. J Microb Methods 5:177-189