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BURNING IN A NEW ZEALAND SNOW-TUSSOCK GRASSLAND: EFFECTS ON SOIL MICROBIAL BIOMASS AND NITROGEN AND PHOSPHORUS AVAILABILITY

Summary: Fire has been an important management tool in the pastoral use of New Zealand tussock grasslands. The effects of a farm-scale pastoral fire and subsequent grazing by sheep on soil biochemical properties in tussock grasslands dominated by the narrow-leaved snow tussock (*Chionochloa rigida* ssp. *rigida*) were investigated, 1.5 and 2.5 years after the fire event, in 0-2 cm depth mineral soil at a site at 975 m altitude in Central Otago, New Zealand. The nitrogen (N) and phosphorus (P) concentrations of *C. rigida* leaves were also measured. Comparisons were made with soil and tussock leaves from an adjacent unburned site.

At both samplings, values of total soil organic carbon (C), extractable C, microbial biomass C, and basal respiratory activity were, on average, 14%, 18%, 23%, and 40%, respectively, lower at the burned than at the unburned site. In contrast, microbial N values were roughly similar at both sites, while microbial P values were 42% higher at the burned site after 1.5 years. Phosphomonoesterase and phosphodiesterase activities were then also similar at both sites, whereas invertase activity was higher at the burned site. The greater availability of N and P at the burned site was confirmed by the higher concentrations of N and P in *C. rigida* leaves sampled 2 years after the fire. Ratios of microbial C:microbial N and microbial C:microbial P were significantly lower at both samplings at the burned site, and emphasise the importance of the soil microbial biomass in conserving N and P after pastoral burning in a grassland ecosystem.

Keywords: Fire; invertase; microbial biomass; respiration; soil nutrients; tussock grassland.

Introduction

Although fire is a controversial management tool in New Zealand tussock grasslands, it can be an important factor in their pastoral use (Basher, Meurk and Tate, 1990). Its effects on various properties of these ecosystems have, consequently, been widely studied. Most biochemical studies of the effects of burning on grassland soils have concentrated on the availability of nutrient elements, especially N (Raison, 1979; Woodmansee and Wallach, 1981) and P (Harrington, 1974; Singh *et al*., 1991). Investigations of post-fire effects on nutrient availability in New Zealand tussock grasslands include those of Connor, Bailey and O'Connor (1970), Williams and Meurk (1977), McSweeney (1983) and Payton *et al*. (1986) but, as yet, there has been no examination of the impact of fire on their soil microbial nutrient pools.

The importance of the soil microbial biomass as a source of potentially available nutrients, and the essential role of its component microorganisms in nutrient cycling, are now generally accepted (Jenkinson, 1988). Microbial biomass can also respond relatively rapidly to changes in land management (Powlson, Brookes and Christensen, 1987). The effects of fire on soil microbial biomass in other grassland systems have consequently been recently examined (Okano, 1990; Singh *et al*., 1991; Groffmann, Rice and Tiedje, 1993, Ojima *et al*., 1994).

Here we investigate the combined effects of a farm-scale, pastoral fire and subsequent grazing by sheep on soil microbial biomass C, N and P at a tussock-grassland site in Central Otago (Yeates and Lee, 1997). To incorporate the effects of grazing, samples were taken 1.5 and 2.5 years after the fire event. The role of soil organisms in conserving N and P rendered available by the fire was assessed by comparing microbial C, N and P values, and their ratios, with those from an adjacent unburned site. In addition, measurements were made of soil respiratory activity and of phosphatase and invertase enzymes, which can likewise serve as indicators of management-induced changes in soil biochemical properties (Nannipieri, Grego and Ceccanti, 1990; Ross *et al*., 1992). N and P concentrations in tussock leaves two years after the fire event were also determined.

Materials and methods

Site and soil

The area studied was located 975 m above sea level at 45°36' S and 169°16' E on the eastern slopes of Mt Benger at the southern end of the Old Man Range, Central Otago, New Zealand. The sites had been previously unburned for about 25 years and had a dense cover of *Chionochloa rigida* ssp. *rigida* tall-tussock. The site north of a road crossing the study area was burned in spring (October) 1990; the site south of the road remained unburned.

Some properties of the soil, vegetation, and tussock and tiller features at the sites have been given by Yeates and Lee (1997). Tussock density at the unburned site averaged 3.3 m^{-2} with an average basal area and canopy area per tussock of 540 cm^2 and 7160 cm^2, respectively. The density of tussocks at the burned site was at least as high as at the unburned site, although their basal and canopy areas were much smaller. Litter was absent at the burned site, but occurred to an average 3 cm depth at the unburned site. At the burned site, no ash was visible on the soil surface 1.5 years after the fire. Both sites were accessible for about six months each year for grazing by sheep, at a stocking density of about 0.2 units ha^{-1}.

The soil at both sites was a silt loam derived from schist colluvium. At the unburned site it was rather shallow (27+ cm to slightly weathered schist), and less freely draining than the soil at the burned site; the soils are classified, according to Soil Taxonomy (Soil Survey Staff, 1992), as a Lithic Dystrochrept and a Typic Dystrochrept, respectively.

Soil sampling

At each site, five parallel 15-m transects were sampled in autumn, on 24 March 1992 and 5 and 6 April 1993. Ninety cores (2.5 cm dia., 0–2 cm depth) of mineral soil were taken at approximately equal intervals in each transect and pooled to give five replicate samples from each site. The soil was stored at 4°C within 3 days of collection and sieved (< 5.6 mm). Sub-samples of the sieved soil were air-dried and ground (< 250 μm) for total C and N analyses.

Tussock sampling

Tillers of *C. rigida* were collected in spring, on 19 October 1992, from ten separate tussocks in each of five *ca.* 15-m transects. The ten tillers were pooled to give one of the five replicate samples taken at each site. As a result of preferential grazing by sheep, tussock leaves at the burned site were only about 30-40 cm long; at the unburned site they were about 50-80 cm long.

To obtain physiologically similar material, the three youngest leaves (plus sheaths) were dissected out from each of the ten tillers per sample. These leaves were cut 25 cm from the base of the tiller, and the 0–25 cm lengths freeze-dried and ground (< 1 mm) in a Casella (London) E.B.C. mill. Older leaf material (25–40 cm distant from the base of the tillers) was also taken from the samples from the unburned site and was processed similarly.

Analytical methods

Results are expressed on the basis of oven-dry (105°C) weight of material. Soil biochemical analyses commenced within 14 days of sampling and were made in triplicate; four replicates were, however, used for the determination of basal and substrate-induced respiration. Analyses of plant material were made in duplicate.

Soil moisture, pH (in water) and total C and N concentrations were determined according to Blakemore, Searle and Daly (1987); water-holding capacity (WHC) was measured according to Harding and Ross (1964). Plant total C, N and P were also determined according to Blakemore *et al.* (1987).

Extractable C, N and P_i. Extractable C and N were determined by shaking 10 g samples at 60% of WHC (*ca.* –5 kPa) in an end-over-end shaker for 30 min with 25 ml 0.5 M K_2SO_4. Organic C in the filtrates was measured by dichromate oxidation (Jenkinson and Powlson, 1976) and total N by persulphate oxidation (Ross, 1992). Inorganic P (P_i) was extracted with 0.5 M $NaHCO_3$ (pH 8.5) for 2 h and determined according to Brookes, Powlson and Jenkinson (1982).

Microbial C and N. Microbial C and N were determined by fumigation-extraction methods, as described by Ross and Tate (1993a), using specially assessed k_{EC}– and k_{EN}– factors. The suitability of these methods for use with heat-treated soils has been shown by Diaz-Raviña *et al.* (1992). A mean k_{EC}– factor of 0.40 was established initially, with a sample from the burned site and a partly dried sample (Ross, 1988) from the control site, by calibrating the extractable-C flush against microbial C estimated by the fumigation-incubation procedure using a control of fumigated soil incubated for 10–20 days (Ross and Tate, 1993a). A k_{EN}– factor of 0.42 was similarly determined by calibrating the extractable-N flush against microbial N estimated by the fumigation-incubation procedure (Ross and Tate, 1993a), in which a k_N– factor of 0.57 (Jenkinson, 1988) was employed.

Microbial P. The fumigation-extraction method for determining microbial P was based on that of

Brookes *et al.* (1982), but used only 4.0 g (oven-dry equivalent) of field-moist soil and 80 ml 0.5 M $NaHCO_3$ extractant; the extraction time was increased to 2 h. Before filtration, *ca.* 1 ml polyacrylamide solution (0.2% w/v) was added. The dark-coloured extracts were also treated with activated charcoal, as described by Ross *et al.* (1995a), before determining P_i with the reagent of Murphy and Riley (1962). The P_i flush, viz. P_i extracted from fumigated soil *minus* P_i extracted from unfumigated soil, was converted to microbial P by using the k_P– factor of 0.40 and correcting for P_i adsorption from an added P_i spike (Brookes *et al.*, 1982). Recovery of the P_i spike averaged 35% in both the unburned- and burned-site samples.

CO_2 production and substrate-induced respiration (SIR). Basal rates of CO_2 production were measured by gas chromatography with field-moist soil (equivalent to 0.5 g oven-dry weight) incubated at 25°C for 16 h (Orchard and Cook, 1983). Metabolic quotients (qCO_2 values; Anderson and Domsch, 1985) were calculated as the average rate of CO_2-C production (μg g^{-1} soil h^{-1} over this 16-h period) per unit of microbial C (mg g^{-1} soil), estimated by the fumigation-extraction method.

The determination of SIR was based on the procedure of West and Sparling (1986). Water (to a total volume of 2.0 ml) and glucose (30 mg ml^{-1}) were added to the equivalent of 0.5 g oven-dry soil, and the CO_2 produced was measured during 30–150 min after the glucose addition.

Enzyme activities. Invertase activity was measured with 1.0 g soil, 4.0 ml sodium phosphate buffer (0.5 M; pH 5.0), 4.0 ml aqueous sucrose solution (5% w/v) and 0.15 ml toluene according to Ross *et al.* (1995a). Phosphomonoesterase and phosphodiesterase activities were determined according to Sparling, Speir and Whale (1986); the incubation period was, however, reduced to 1 h.

Statistics. The significance of differences between treatments and sampling times was assessed by analysis of variance and Fisher's LSD test (Steel and Torrie, 1980). Matched *t*-tests with log-transformed data were used for estimating errors associated with ratios. Because of limitations in the experimental design (Hurlbert, 1984), we recognise that care is needed in interpreting these statistical results.

Results

Soil chemical and biochemical properties

The pH of these strongly acid soils was slightly higher in samples from the burned site (Table 1).

Table 1: *Chemical and biochemical properties of soil from the control and burned sites ca. 1.5 and 2.5 years after the fire event*

	Time since last fire			
	1.5 years : site		2.5 years: site	
Property	Control	Burned	Control	Burned
pH	4.7^{d}	4.8^{c}	5.1^{b}	5.2^{a}
Moisture (%)	117^{a}	68^{c}	96^{b}	62^{d}
Total C (%)	8.5^{a}	7.3^{c}	8.1^{b}	7.0^{c}
Total N (%)	0.38^{ab}	0.36^{ab}	0.40^{a}	0.36^{b}
C:N	23^{a}	20^{b}	20^{b}	19^{b}
Extractable C (μg g^{-1})	306^{a}	242^{c}	270^{b}	227^{d}
Extractable N (μg g^{-1})	42^{a}	43^{a}	21^{b}	22^{b}
Extractable P_i (μg g^{-1})	11^{b}	21^{a}	11^{b}	12^{b}
Microbial C (μg g^{-1})	2960^{a}	2270^{b}	2910^{a}	2260^{b}
Microbial N (μg g^{-1})	412^{a}	401^{a}	362^{b}	397^{a}
Microbial P (μg g^{-1})	138^{c}	196^{a}	137^{c}	163^{b}
CO_2 production (μl g^{-1} h^{-1}):				
Basal	28^{a}	16^{b}	16^{b}	10^{c}
SIR	56^{a}	43^{b}	38^{c}	38^{c}
Invertase (units)[1]	7.3^{c}	7.9^{b}	7.7^{bc}	9.0^{a}
Phosphomonoesterase (units)[1]	5.2^{a}	5.3^{a}	ND	ND
Phosphodiesterase (units)[1]	1.4^{a}	1.5^{a}	ND	ND

ND, not determined.

[1] Units: invertase, nmol 'glucose' formed g^{-1} s^{-1}; phosphomonoesterase and phosphodiesterase, nmol *p*-nitrophenol formed g^{-1} s^{-1}.

For each property, values not marked with the same letter are significantly different ($P < 0.05$).

Moisture, total C and, to a lesser extent, total N concentrations were lower in soil from the burned site. C:N ratios consequently tended to be slightly lower in the burned-site samples.

Within-site variability was broadly similar at both sites, with coefficients of variation of the five replicate field samples averaging 4% for pH, moisture, total C and N, 7% for extractable and microbial C, N and P, and 10% for CO_2 production and the enzyme activities.

Extractable C was consistently lower in the burned-site samples, whereas total extractable N showed no site differences, although it did differ between samplings (Table 1). In contrast, extractable P_i was significantly higher in the burned-site samples 1.5 years after burning, but was similar at both sites after 2.5 years.

At both samplings, microbial C content was significantly lower, and microbial P higher, in soil from the burned site (Table 1). Microbial N differed less between sites, although it was significantly higher in the burned-site soil 2.5 years after burning.

Basal CO_2 production was markedly lower in the burned-site soil at each sampling (Table 1). CO_2 production in the presence of glucose (SIR) was also significantly lower in the burned-site samples 1.5 years after burning, but was similar at both sites after 2.5 years.

Phosphomonoesterase and phosphodiesterase activities were similar at both sites 1.5 years after burning. Invertase activity, however, was significantly higher in the burned-site soil, and had increased appreciably 2.5 years after burning (Table 1).

Ratios of microbial C to total C were non-significantly lower at the burned site, whereas ratios of microbial N to total N were at least as high at the burned as at the unburned site (Table 2). In contrast, the ratios of microbial C:microbial N and microbial C:microbial P were significantly lower at the burned site at both samplings.

The metabolic quotient (qCO_2) was consistently lower in the burned-site samples, whereas SIR values per unit of microbial C at the burned site were either similar to, or higher than, those at the unburned site (Table 2).

C, N and P concentrations of *C. rigida* leaves

Total C concentrations in *C. rigida* leaves were not influenced by site or leaf age (Table 3). Total N and P concentrations were, however, higher in leaves from the burned site and, at the unburned site, tended to decline with leaf age.

Discussion

Although our use of a farm-scale burn for studying the effects of fire, and subsequent grazing, on soil biochemical properties would have provided realistic

Table 2: *Ratios of biochemical properties of soil from the control and burned sites ca. 1.5 and 2.5 years after the fire event*

	Time since last fire			
	1.5 years : site		2.5 years : site	
Ratio	Control	Burned	Control	Burned
Microbial C:total C	0.035^{a}	0.031^{a}	0.036^{a}	0.032^{a}
Microbial N:total N	0.108^{a}	0.111^{a}	0.091^{b}	0.110^{a}
Microbial C:microbial N	7.2^{b}	5.7^{c}	8.0^{a}	5.7^{c}
Microbial C:microbial P	21.4^{a}	11.6^{c}	21.2^{a}	13.9^{b}
Microbial N:microbial P	3.0^{a}	2.0^{c}	2.6^{ab}	2.4^{b}
qCO_2 (μg CO_2-C produced mg^{-1} microbial C h^{-1})	4.4^{a}	3.2^{b}	2.6^{c}	2.0^{d}
CO_2-C produced (SIR; μg g^{-1} h^{-1})/Microbial C (mg g^{-1})	10.1^{a}	10.1^{a}	6.8^{b}	8.9^{ab}

For each ratio, values not marked with the same letter are significantly different ($P < 0.05$).

Table 3: *C, N and P contents of C. rigida leaves two years after the fire event*

Site	Length (cm) of leaf segments from tiller base	Total C (%)	Total N (%)	Total P (%)	C:N	C:P	N:P
Control	0-25	46.2^{a}	1.15^{b}	0.133^{b}	40^{a}	$347^{(b)}$	$8.7^{(c)}$
Control	25-40	46.1^{a}	1.10^{b}	0.094^{c}	42^{a}	$490^{(a)}$	$12.7^{(a)}$
Burned	0-25	46.3^{a}	1.65^{a}	0.164^{a}	28^{b}	$282^{(c)}$	$10.1^{(b)}$

For each column, values not marked with the same letter are significantly different ($P < 0.05$; in parentheses < 0.10).

field conditions, it had the disadvantage of being non-replicated. Differences between the burned and control sites cannot, therefore, be attributed unequivocally to the effects of fire but might also be associated with intrinsic inter-site variations. However, in spite of its limitations with respect to treatment replication and overall soil uniformity and depth, this study strongly suggests that several of the properties examined differed with land management treatment, with the differences found being consistent with burning effects. Pre-burn sampling would have assisted data interpretation, but could not be performed.

Although sheep had access to both the unburned and burned areas, grazing effects would be expected to have been greater at the burned site because of their preference for the more palatable herbage from re-growing tussocks. Compared with fire, animal effects on the soil properties examined are likely to have been small. In a low fertility hill pasture, no detectable differences in total C and N, microbial C and P, or invertase activity were observed in 0-5 cm depth soil from rotationally grazed plots and from plots that had been ungrazed for several months (Ross *et al*., 1995b); moreover, in an unfertilized treatment, net N mineralization appeared to be greater in soil from the ungrazed plots at the end of the 'fallow' period. Grazing animals could, however, have a long-term influence on soil biochemical properties. Any enhancement of nutrient cycling through the return of dung and urine is likely to be outweighed by their adverse affect on tussock plant vigour at recently burned sites and the consequent reduction in inputs of plant-derived organic matter and associated nutrients to the mineral soil (Basher *et al.,* 1990).

The degree of burning effects in any ecosystem depends on the intensity of the fire (DeBano, Eberlein and Dunn, 1979; Dunn, DeBano and Eberlein, 1979; Weston and Attiwill, 1990; Marion, Moreno and Oechel, 1991; Saa *et al*., 1993). At this tussock grassland site, temperatures are likely to have declined rapidly with depth (DeBano *et al*., 1979; Tongway and Hodgkinson, 1992) because of the typically moist soil. Sampling was consequently restricted to 0-2 cm depth of mineral soil. Such samples are also unlikely to have been directly affected by the different total depths of soil at the two sites.

Total soil C concentrations were about 14% lower at the burned site than at the unburned site, whereas total N differed by less than 8%. Although volatilization losses of mineral N released after burning (Raison, 1979; Woodmansee and Wallach, 1981) and, to a much lesser extent, leaching losses may have occurred, microbial immobilization of mineral-N (McSweeney, 1983; Weston and Attiwill, 1990) and/or addition of incompletely burned plant residues (Prieto-Fernandez *et al*., 1993) would have contributed to N conservation.

Soil water content differed markedly between sites, with the greater canopy cover and amounts of ground litter at the unburned site being a likely contributing factor. The WHC of the soils also differed, with water contents at 60% of WHC being 127% and 91% in the unburned- and burned-site samples, respectively; differences in the soil organic matter content would have been partly responsible.

The effects of fire on extractable C, N and P would have been modified by the time our first samples were taken. The data nevertheless indicate a loss of extractable C and, as found by Harrington (1974) and Singh *et al*. (1991), an increase in extractable P_i. Extractable N, in contrast, did not differ between sites. The decline in P_i at the burned site between 1.5 and 2.5 years after burning is consistent with plant uptake; it also provides confirmatory evidence that the higher P_i at this site resulted from the fire, and not from any intrinsic site difference.

Variable effects of burning on soil microbial C at grassland sites have been reported, with no change found by Groffman *et al*. (1993) and an increase by Singh *et al*. (1991) and Ojima *et al*. (1994). Results were, to some extent, dependent on burning frequency and sampling time in relation to plant growth recovery. A marked decline in microbial C appears to have occurred in our soil, with values identical 1.5 and 2.5 years after the fire, and about 23% lower than at the unburned site. The somewhat lower ratios of soil microbial C to total C at the burned site than at the unburned site suggests that the post-burn decline in microbial biomass was greater than the decline in total organic matter. Changes in the composition of the soil microflora are also indicated, with the microbial C:microbial N and microbial C:microbial P ratios being different at the burned and unburned sites.

A decline in soil microbial N has been found in some ecosystems as a consequence of fire (Okano, 1990; Bauhaus, Khanna and Raison, 1993), with changes dependent on burning intensity (Pietikäinen and Fritze, 1993). Increases in microbial N and P, as well as microbial C, have also been found after burning (Singh *et al*., 1991) and attributed to increased plant growth. Although organic matter inputs from new plant growth probably increased at our burned site, as the inter-tussock vegetation of grasses and herbs progressively developed (Yeates and Lee, 1997), no change in microbial N concentration was detected between the 1.5 and 2.5 year samplings. However, the microbial N value after 2.5 years was about 10% higher than at the unburned

site. Microbial immobilization of potentially available N released by burning is likely to have resulted in microbial N enrichment and the lower microbial C:microbial N ratios at the burned site.

The greater initial availability of P_i for microbial incorporation at the burned site is reflected in the much higher concentrations of microbial P and lower ratios of microbial C:microbial P than at the unburned site. In the samples taken 1.5 years after the burn, microbial P values were, in fact, 42% higher at the burned than at the unburned site. Again, the extent of these effects would have been influenced by the heat of the fire and sampling time after the burn (Serrasolsas and Khanna, 1995). Our data suggest that microbial P and the microbial C: microbial P ratio at the burned site were slowly returning to pre-burn values, with extractable P_i after 2.5 years being no longer higher than at the unburned site.

Although soil water content has a marked effect on respiratory activity (Orchard and Cook, 1983; Fritze *et al*., 1994), differences in field-moisture content would not have been primarily responsible for the lower CO_2 production in soil from the burned site. Even when samples were adjusted from field-moisture content to the same WHC, CO_2 production by soil from the unburned site was still 1.6 times higher than that by soil from the burned site (D.J. Ross and C.W. Feltham, unpublished data). Basal rates of CO_2 production may here have been influenced by the decline in extractable C in the burned-site samples. Although there is not always a close relationship between CO_2 production and extractable-C content in other ecosystems (Wolters and Joergensen, 1991; Ross and Tate, 1993b; Fritze *et al*., 1994), a shortage of readily metabolized substrates in the burned-site soil is strongly suggested by the qCO_2 values and SIR results.

In unamended soil, qCO_2 values were consistently lower in samples from the burned than from the unburned site. In the presence of added glucose (SIR), however, CO_2-C production per unit of microbial C did not differ significantly between the soil from either site. When interpreting these respiratory results, it is again essential to take into account the time elapsed between the fire and the first sampling. Generally, qCO_2 values can be expected to increase with different forms of ecosystem stress (Anderson and Gray, 1991; Anderson and Domsch, 1993). The results of Pietikäinen and Fritze (1993) and Fritze *et al*. (1994) are in accord with this concept, with the qCO_2 values of forest humus initially increasing after a fire. Their qCO_2 values did, however, decline with time and, as in our study, tended to be lower than those from the unburned sites one year after burning (Pietekäinen and Fritze, 1993). Our results, overall, suggest that no long-term change in the potential respiratory activity of the soil microbial population had occurred as a result of the burning.

Soil invertase activity appears to have increased with time after burning, probably because of the post-burn development of inter-tussock plants (Yeates and Lee, 1997). An association between plant growth and soil invertase activity has been demonstrated in other grassland ecosystems (e.g., Ross *et al*., 1992). A decrease (Binkley *et al*., 1992; Saa *et al*., 1993; Serrasolsas and Khanna, 1995), or no change (Saa *et al*., 1993), in soil phosphatase activity has been observed in forest ecosystems after burning. Again, time after burning influenced these results (Serrasolsas and Khanna, 1995). Neither phosphomonoesterase nor phosphodiesterase activity differed between our grassland sites 1.5 years after the burn. Although inorganic phosphate can act as a suppressor of phosphatase activity (Speir and Ross, 1978), the increase in extractable P_i at the burned site appears to have had no observable effect.

The greater availability of N and P at the burned site than at the unburned site is strongly suggested by the N and P concentrations in the young *C. rigida* leaves sampled 2 years after the fire. Comparisons with nutrient-element values at other tussock-grassland sites are dependent on the age of leaves sampled, as well as site fertility (Williams *et al*., 1978) and time after any burning event (Williams and Meurk, 1977). Generally, the N and P concentrations in our present samples fall within the ranges previously reported (Connor *et al*., 1970; Williams and Meurk, 1977; Williams *et al*., 1978; Payton *et al*., 1986).

When calculated on an area basis, using the tiller weights and numbers of tussocks at each site (Yeates and Lee, 1997), the N and P contents of these tussock leaves from the burned site would have been roughly 30% of those at the unburned site. The actual contents per unit area cannot be determined accurately from our data because only young tussock leaves were analysed. However, contents would not have exceeded 5.3 and 1.7 g N m^{-2} and 0.53 and 0.17 g P m^{-2} at the control and burned sites, respectively. Although some N and P would have been incorporated into inter-tussock vegetation, an appreciable decline in above-ground nutrient pools at the burned site is indicated.

Conclusions

The experimental approach used in this study does not allow unequivocal conclusions to be drawn about the effects of a pastoral fire, and associated

grazing, on soil biochemical properties at this tussock grassland site. A decline in organic matter content, and especially microbial biomass C, in 0-2 cm depth mineral soil 1.5 and 2.5 years after the fire is, nevertheless, strongly suggested. The importance of soil microorganisms, as well as tussock vegetation, in immobilizing N and P released by the fire is indicated. No deleterious effects on the metabolic potential of the microbial populations, or on enzyme activities, at the burned site were apparent 1.5 years after the fire.

Further work is now required under replicated field conditions to confirm the generality of these results, and establish in more detail the effects of burning on these key biochemical properties. Measurements of post-fire changes at different soil depths would also enable a better assessment to be made of the quantitative importance of our present results to the overall functioning of tussock-grassland ecosystems.

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