

¹Manaaki Whenua - Landcare Research, Private Bag 11052, Palmerston North, New Zealand; and

²Manaaki Whenua - Landcare Research, Private Bag 1930, Dunedin, New Zealand.

BURNING IN A NEW ZEALAND SNOW-TUSSOCK GRASSLAND: EFFECTS ON VEGETATION AND SOIL FAUNA

Summary: Soil conditions, vegetation features and soil fauna were recorded in montane tall tussock grassland dominated by narrow-leaved snow tussock *Chionochloa rigida* ssp. *rigida* up to 30 months after a spring fire. Burning reduced the stature of tussocks and the size and density of tillers in the first growing season. After two growing seasons, tussock canopy development and tiller size remained below those found in the unburnt grassland nearby. New tillers and tussocks established following the prolific fire-induced flowering one year after burning. After the fire and sheep grazing, intertussock cover became progressively dominated by introduced grasses and herbs. While soil pH, moisture content, bulk density, surface litter and total nematodes showed significant treatment (burning) effects, these properties also showed significant year-to-year variation. The greatest increase in any nematode group was in *Paratylenchus*, a distinctive genus widespread in tussock grasslands and apparently responsive to environmental fluctuation and root development; its population was 100× and 29× greater in the burned area than in the control area 16 and 30 months after burning. Subject to detailed testing, populations of mites and collembola may provide relatively simple indicators of recovery of ecosystem function of such grasslands after burning.

Keywords: *Chionochloa rigida* ssp. *rigida*; fire; plant community structure; soil fauna; *Paratylenchus*; indicators; Tussock grassland.

Introduction

Although New Zealand has a fire history extending back at least 20 million years, natural fires were rare in the Pleistocene and Holocene and the contemporary vegetation shows few adaptations to burning. A dramatic rise in charcoal occurrence about 1000 years ago, coincident with Polynesian colonization, presaged a widespread phase of deforestation that reduced the area of forest by about 40%. With European settlement in the mid-19th century a further 20-30% of the primary forest, and much of the regenerating lands, were cleared, burned and converted into farmland (Basher *et al.*, 1990; Wardle, 1991). Many areas of New Zealand, especially in the eastern South Island high country, previously supported *Nothofagus* forest which was displaced during Polynesian settlement and later burning of the tall tussock grassland (Tate, 1992; Wardle, 1991).

Fire continues to be used as a cheap and effective but controversial management tool in tussock grassland and scrublands. Fire is widely used to suppress shrub development. Tall tussock grassland is also burnt to improve stock access and induce nutritious regrowth. Studies of post-fire recovery in New Zealand tussock grasslands

demonstrate that after an initial change in species dominance, floristics and structure return to approach the pre-burn condition within two decades (Basher *et al.*, 1990; Allen and Partridge, 1988; Gitay *et al.*, 1992; Payton *et al.*, 1986).

Physical sustainability of agro-ecosystems in the eastern South Island hill and high country of New Zealand, as elsewhere in the world, is dependent on the maintenance of the soil resource as a medium for supplying water and nutrients for plant growth. Objectives in managing the soil resource are to maintain or enhance the physical and chemical characteristics of the soil. Depth of soil, texture, organic matter and structural stability control the ability of the soil to supply water and nutrients for plant growth, and to resist the erosive forces of wind and water. Maintenance of soil fertility is dependent on adequate organic matter levels, a diverse population of soil organisms, and efficient nutrient cycling. Burning without replacement of nutrients by fertiliser, or inputs from the atmosphere and weathering, will ultimately result in soil degradation that will limit plant growth (Basher *et al.*, 1990); the combination of loss of cover and erosion from intense rainfall events could also be important in the context of possible global climate change (Meyer *et al.*, 1992).

The soil fauna plays critical roles in maintaining soil structure and enhancing nutrient cycling (Coleman *et al.*, 1984; James, 1988; McSorley, 1993). Thus the effects of fire on soil properties are also of major importance in determining ecosystem stability.

This paper compares botanical and soil faunal conditions some 18 and 30 months after a routine burn of montane tall tussock grassland dominated by narrow-leaved snow tussock *Chionochloa rigida* ssp. *rigida* and assesses some factors which may be useful as indicators of ecosystem condition. Additional work on soil microbial biomass and nitrogen and phosphorus availability is reported by Ross *et al.* (1997).

Site and methods

Site

The study area, located at 169° 16' E, 45° 36' S, is on the eastern slopes of Mt Bengier (1250 metres), at the southern end of the Old Man Range in Central Otago, South Island, New Zealand. Metamorphic rocks, typically well foliated quartzo-feldspathic schist and lesser chlorite schist-chlorite subzone 4 (Wood, 1962), support soils mapped by N.Z. Soil Bureau (1968) as upland and high country yellow-brown earths of the Carrick Soil Set. The climate and general vegetation patterns in the area are described by Mark (1965a,b).

The study site, at 975 m above sea level, had apparently been unburnt for about 25 years and supported dense *Chionochloa rigida* ssp. *rigida* tall tussock grassland. In spring (October) 1990 the area north of the road through the area was burnt to facilitate continued sheep access and grazing, while the area to the south was unburnt and provided a control for the investigation. Without the ability to carry out an experimental burn on a fully uniform area, involving pre- and post-burn sampling, the investigation was limited to comparing adjacent burnt and unburnt sites. Both sites were accessible for about six months each year for grazing by sheep, at a stocking rate of about 0.2 units ha⁻¹.

Soil and vegetation were sampled in autumn of 1992 (24-25 March) and 1993 (5-6 April).

Vegetation

The vegetation of the control and burnt sites was described and sampled 18 and 30 months (May 1992, April 1993 respectively) after burning. Sampling methods for assessing the stature and structure of the tall tussocks follow Gitay *et al.*

(1992). Cover estimates are qualitative estimates of whole plots and are used to indicate gross differences in the vegetation and its composition. Similarly, presence / absence data refer to whole plots, rather than subplots. Plant nomenclature follows Webb *et al.* (1988) and Connor and Edgar (1987).

Soil fauna

In autumn 1992 and 1993 samples were collected for soil animals; in each of the two areas 5 contiguous plots, each approximately 5 x 15 m, were defined and sampled separately and treated as replicates for statistical purposes. Within each plot, at randomly located points between tussocks, the fauna was sampled as follows- (a) Megascolecoid earthworms and cicadas were recovered by hand-sorting a 0.1 m² pit to 10 cm depth below any detectable macrofauna, and fixed in 10% ethanol before storage in 4% formaldehyde; subsequently they were counted and their wet weight determined. Litter was collected from above the 0.1 m² pit and arthropods extracted into Gault's using simple Tullgren funnels 25 cm Ø; arthropods were subsequently sorted at 25x magnification under a stereo-microscope; the litter was dried at 60°C and weighed. (b) Enchytraeids were extracted from five replicate cores, each 51 mm Ø from 0-2 and 2-5 cm depth, using heated Baermann-type funnels; specimens were counted live at 50x magnification under a stereo-microscope. (c) Nematodes and tardigrades were extracted from soil samples which for each replicate comprised five cores each 51 mm Ø from 0-2 and 2-5 cm depth; the samples were extracted using Whitehead and Hemming trays, total counts made, fixed by addition of boiling double strength F.A. 4:1 (Southey, 1986). Rotifers and microscopic Planaria in these samples were also counted. Subsequently an average of 119 nematodes from each replicate were identified to genus and population estimates converted to a m⁻² basis; nematodes were grouped into feeding types according to Yeates *et al.* (1993).

While the estimates for megascolecids, cicadas, tardigrades, enchytraeids and nematodes are based on standard, quantitative soil zoological methods, data for other groups are less robust and should only be regarded as indicative. Soil moisture, pH and bulk density determinations were also made.

The nature of the site was such that the replicate plots in the control and burned areas were not truly independent. We present results of analyses of variance which test the significance of differences between the two sites. Fisher's LSD tests are used *posteriori* to contrast the means of each season and treatment, with $p < 0.05$ being regarded as significant.

While differences between the sites may be due to the effects of burning, more examples of burnt and unburnt sites are needed before any general conclusions can be drawn.

Results and discussion

Vegetation

Unburnt tall tussock grassland is dominated by *Chionochloa rigida* with scattered *Aciphylla aurea* and sparse intertussock cover of mainly native species (Table 1). Burning removes the tussock canopy and depletes the intertussock vegetation, enabling naturalised grasses and herbs to colonize areas of bare ground in the short-term (Table 1). The presence of more palatable naturalised grasses, together with tussock regrowth, encourage sheep grazing, which was locally intense near the road.

Burning reduced the stature of tussocks and the size and density of tillers in the first growing season (Table 2). After two growing seasons, tussock canopy development was only 25% of that found in the unburnt grassland nearby. New tillers and tussocks established following the prolific fire-induced flowering one year after burning, however, mean tiller size (weight and length) remained markedly depressed (Table 2). The progressive but slow rate of recovery of collective tiller area and tiller weight and length were identified in a previous study as useful parameters for assessing the condition and recovery of tussock grassland after fire (Gitay *et al.*, 1992).

Soils

The soils at both sites were derived from schist colluvium. The control site was on a ridge top, with a slope of *ca.* 8°; the soil was rather shallow (27+ cm to slightly weathered schist), and showed some gley features; horizon depths were: L, 3 cm of tussock litter; A_{hg}, 0-15 cm; B_{w(g)}, 15-27 cm. The burned site was on a debris-mantled side-slope of *ca.* 15°, and had a deeper and more freely draining soil; horizon depths were: A_h, 0-19 cm; B_{w1}, 19-36 cm; B_{w2}, 36-50 cm; C, 50-65+ cm. The soils at the control and burned sites are a Mottled Orthic Brown Soil and a Typic Orthic Brown Soil, respectively, in the New Zealand Soil Classification (Hewitt, 1992) and in Soil Taxonomy (Soil Survey Staff, 1975) they are a Lithic Dystrochrept and a Typic Dystrochrept, respectively.

The soil at the burned site had about twice the depth to the bottom of the B horizon. While this may be reflected in plant vigour and macrofaunal

Table 1: Vascular flora and cover values (on a percentage basis, with values <5% denoted by +) for indigenous and naturalised species(*) at the study sites, Mount Benger, Central Otago, New Zealand.

	Control	Time since last fire	
		18 months	30 months
<i>Aciphylla aurea</i>	10	+	+
<i>Agrostis capillaris</i> *	10	30	40
<i>Anthoxanthum odoratum</i> *		20	35
<i>Bulbinella angustifolia</i>	15	+	+
<i>Carex breviculmis</i>		+	+
<i>Cassinia vauvilliersii</i>	+		
<i>Celmisia gracilentia</i>	+		+
<i>Celmisia prorepens</i>	5		
<i>Cerastium glomeratum</i> *			+
<i>Chionochloa rigida</i>	60	45	50
<i>Coprosma cheesemani</i>	+		
<i>Crepis capillaris</i> *		+	
<i>Festuca novae-zelandiae</i>	+	+	+
<i>Gaultheria crassa</i>	+		
<i>Geranium microphyllum</i>	+	+	+
<i>Gunnera dentata</i>			+
<i>Haloragis erecta</i>			+
<i>Helichrysum bellidioides</i>	+		+
<i>Helichrysum filicaule</i>	+		+
<i>Hieracium pilosella</i> *	+	+	+
<i>Holcus lanatus</i> *		5	5
<i>Hydrocotyle novae-zelandiae</i>			+
<i>Hypochoeris radicata</i> *		+	10
<i>Kelleria dieffenbachii</i>	+		+
<i>Leucopogon fraserii</i>	5	5	5
<i>Luzula rufa</i>	+		+
<i>Muhlenbeckia axillaris</i>		+	
<i>Oreomyrrhis colensoi</i>	+		+
<i>Pernettya macrostigma</i>	5	+	+
<i>Poa cita</i>		+	
<i>Poa colensoi</i>	15	5	5
<i>Rumex acetosella</i> *			+
<i>Rytidosperma setifolium</i>	+		+
<i>Stackhousia minima</i>		+	
<i>Thelymitra longifolia</i>	+		+
<i>Trifolium repens</i> *		+	+
<i>Uncinia rubra</i>	+	+	+
<i>Wahlenbergia albomarginata</i>	+	+	+

populations, most faunal and biochemical analyses were restricted to the upper 0-2 or 0-5 cm soil and are considered to reflect the impact of burning rather than depth of soil development.

Soil pH, moisture content, bulk density and surface litter showed marked differences not only between treatments, but also from year-to-year effects; results are given in Ross *et al.* (1997).

Table 2: *Tussock and tiller features.*

	Control	Time since last fire			
		18 months		30 months	
		% control		% control	
Tussock features					
density (No. m ⁻²)	3.3	6.1	184	3.4	103
basal area per tussock (cm ²)	1042	321	31	659	63
canopy area per tussock (cm ²)	7162	1152	15	1747	24
bunched lamina area per tussock (cm ²)	23.7	7.6	32	7.7	33
proportion >30 cm basal diameter (%)	48	11		15	
Tiller features (m⁻²)					
tiller weight (g)	1.6	0.3	19	0.4	25
tiller length (cm)	70.7	28.3	40	35.7	50
number	294	206	70	356	121

Soil fauna

The numbers m⁻² of Tardigrada, Copepoda, Collembola and mites recovered from the litter were consistently lower in the burned area and analysis of variance shows the overall effect to be significant ($p < 0.05$) (Table 3), as was the weight of litter present (data not shown). Overall, the macrofauna recovered from pits (Megascolecidae and Cicadidae) did not differ significantly between control and burned areas. As macrofauna may have a generation time of

several years any response to the fire event may be delayed. Further, the combined A+B horizons were deeper at the burned site and thus may have inherently greater populations than at the control site. According to Lee (1959), native earthworms are able to maintain their populations when the vegetation changed from forest to tussock grassland, while in a North American prairie, James (1988) found earthworm response to burning was dependent on earthworm species, time of burning and subsequent land management regimes. Cicada larvae

Table 3: *Soil faunal populations (number m⁻² in 0-2 cm litter and soil) at control and burned sites 16 and 30 months after the fire event.*

	Time since last fire			
	16 months		30 months	
	Control	Burned	Control	Burned
Total nematodes	189 000 ^c	226 000 ^c	311 000 ^b	407 000 ^a
Rotifers	2 669 ^a	5 439 ^a	4 828 ^a	2 913 ^a
Planaria	1 752 ^a	407 ^a	1 569 ^a	1 894 ^a
Enchytraeidae (n=25)				
0-2 cm	31 804 ^a	24 689 ^a	26 259 ^a	31 128 ^a
2-5 cm	922 ^b	1 242 ^b	4 298 ^a	2 674 ^{ab}
0-5 cm	32 725 ^a	25 932 ^a	30 558 ^a	33 808 ^a
Megascolecidae				
number	42.0 ^a	60.8 ^a	24.0 ^a	52.0 ^a
g wet wt	63.4 ^a	73.2 ^a	46.0 ^a	75.0 ^a
Tardigrada	2 200 ^a	489 ^b	3 096 ^a	428 ^b
Copepoda	19 027 ^a	7 741 ^b	7 277 ^b	1 874 ^b
Collembola	3 142 ^a	1 550 ^c	2 490 ^b	116 ^d
Mites	1 216 ^b	630 ^c	2 420 ^a	166 ^d
Weevils	6 ^a	125 ^a	40 ^a	¹ n.d. ^a
Thysanoptera	141 ^b	202 ^b	446 ^a	14 ^c
Cicadidae				
number	9.6 ^a	35.2 ^a	12.0 ^a	28.0 ^a
g wet wt	2.8 ^b	8.8 ^a	1.7 ^b	4.3 ^{ab}

¹n.d. = not detected

For each group population estimates not marked with the same letter are significantly different ($p < 0.05$)

were also somewhat more numerous in our burned plots and represented a significantly greater biomass than in the control area at 16 months (Table 3).

While this could reflect the presence of more open ground for oviposition (mean weight was lower in the burned area), the life cycle of New Zealand species of cicadas is poorly known and it is not possible to identify larvae to genus (Dugdale, 1971).

Among the microfauna, only total nematodes showed a significant, positive response to burning (Table 3). However, total nematodes showed significant year-to-year differences which suggests as such they are inappropriate as simple indicators of burning effects (Table 3).

Of 32 nematode 'genera' identified, 18 showed consistent treatment differences in each year and the significance of effects is given in Table 4. Estimates of populations of *Clarkus*, *Dorylaimus* and *Pratylenchus* were consistently lower at the burned site and the differences were significant at 30 months (Table 4). In contrast, *Aphanolaimus*, Rhabditidae, *Cephalobus*, *Tylenchus*, *Ditylenchus*, *Helicotylenchus* and *Paratylenchus* were more abundant at the burned site at each sampling, the difference being significant on at least one sampling occasion.

The greatest increases (100× at 16 months, 29× at 30 months) were in *Paratylenchus*, a root-feeding genus widespread in tussock grasslands (Wood, 1973; Yeates, 1974). While the presence of germinating seedlings may have provided an additional food resource for this plant-feeding genus, its most apparent adaptive characteristic is the presence of a highly resistant subadult stage (Southey, 1978). It is considered that with the soil in the burned area less buffered from diurnal and seasonal temperature fluctuations and having a more variable moisture content [due in part to receiving less moisture input from mist (Rowley, 1970)], *Paratylenchus* is at an advantage in the burned area. *Paratylenchus* did not show significant differences from year to year. *Helicotylenchus* also feeds on plant roots, but lacks the resistant subadult stage. Populations of *Helicotylenchus* were 12× and 4.8× greater at the burned site on the two dates, and there was a significant difference between years (Table 4). Overall there was a significant increase in the root-associated *Tylenchus* which probably reflects greater rhizosphere activity. The overall significant decrease in the root-feeding *Pratylenchus* probably reflects the more variable environment of the exposed ground and the relative competitive advantage of *Paratylenchus* under these conditions. The bacterial feeding taxa *Aphanolaimus*, Rhabditidae and *Cephalobus* also showed significant overall increases in the burned plots; these changes are similar to those in bacterial-feeding nematodes

Table 4: Nematode populations (thousands m⁻² in 0-2 cm litter and soil) at control and burnt sites 16 and 30 months after the fire event.

Group	Time since last fire			
	16 months		30 months	
	Control	Burned	Control	Burned
<i>Alaimus</i>	2.2 ^c	9.9 ^b	13.7 ^{ab}	19.3 ^a
<i>Tripyla</i>	2.0 ^b	0.8 ^b	15.7 ^a	3.3 ^b
<i>Clarkus</i>	9.5 ^{ab}	4.0 ^{bc}	11.0 ^a	2.8 ^c
<i>Cobbonchus</i>	1.1 ^a	1.1 ^a	1.0 ^a	1.1 ^a
<i>Dorylaimus</i>	2.0 ^a	0.5 ^a	0.8 ^a	¹ n.d ^b
<i>Eudorylaimus</i>	13.0 ^a	4.5 ^b	13.0 ^a	13.4 ^a
Aporcelaimidae	61.5 ^{bc}	44.9 ^c	76.9 ^b	109.5 ^a
<i>Doryllium</i>	7.6 ^a	9.6 ^a	6.8 ^a	11.2 ^a
<i>Leptonchus</i>	n.d. ^b	2.1 ^a	1.1 ^a	4.5 ^a
<i>Dorylaimellus</i>	1.0 ^a	n.d. ^a	0.7 ^a	0.8 ^a
<i>Nygotaimus</i>	n.d. ^b	2.4 ^a	1.9 ^{ab}	n.d. ^b
<i>Aphanolaimus</i>	0.8 ^b	3.7 ^b	1.7 ^b	8.2 ^a
<i>Plectus</i>	7.0 ^a	5.1 ^{ab}	6.3 ^a	1.5 ^b
<i>Wilsonema</i>	n.d. ^a	0.4 ^a	n.d. ^a	n.d. ^a
Chromadoridae	7.3 ^a	0.8 ^b	3.5 ^{ab}	3.3 ^{ab}
Monhysteridae	1.3 ^b	1.2 ^b	5.8 ^{ab}	9.8 ^a
Rhabditidae	n.d. ^b	0.2 ^b	n.d. ^b	10.6 ^a
<i>Cephalobus</i>	0.6 ^b	7.8 ^{ab}	0.9 ^b	14.8 ^a
<i>Heterocephalobus</i>	0.7 ^a	0.8 ^a	n.d. ^a	n.d. ^a
<i>Cervidellus</i>	0.4 ^a	n.d. ^b	n.d. ^b	n.d. ^b
<i>Panagrolaimus</i>	1.9 ^a	1.7 ^{ab}	n.d. ^b	n.d. ^b
<i>Teratocephalus</i>	0.4 ^b	0.7 ^b	7.0 ^a	1.4 ^b
<i>Euteratocephalus</i>	4.3 ^a	1.6 ^{ab}	1.6 ^{ab}	n.d. ^b
<i>Diplogaster</i>	0.3 ^a	n.d. ^a	n.d. ^a	n.d. ^a
<i>Aphelenchoides</i>	3.2 ^b	1.8 ^b	14.2 ^a	5.3 ^b
<i>Tylenchus</i>	36.2 ^c	50.5 ^c	89.7 ^b	137.7 ^a
<i>Cephalenchus</i>	1.1 ^a	2.0 ^a	4.4 ^a	5.5 ^a
<i>Ditylenchus</i>	1.8 ^b	1.0 ^b	2.3 ^b	18.9 ^a
<i>Helicotylenchus</i>	0.8 ^b	10.3 ^a	0.5 ^b	2.4 ^b
<i>Pratylenchus</i>	4.4 ^b	1.9 ^b	11.0 ^a	1.5 ^b
<i>Criconemoides</i>	17.0 ^a	21.9 ^a	19.3 ^a	2.5 ^b
<i>Paratylenchus</i>	0.3 ^b	30.1 ^a	0.61 ^b	17.4 ^a
Total	189.0 ^c	226.0 ^c	311.2 ^b	406.6 ^a

¹n.d. = not detected

For each group population estimates not marked with the same letter are significantly different (p<0.05)

reported by Christensen *et al.* (1992) following root death. The marked overall decreases (p<0.05) in the abundance of the predatory *Clarkus* and the omnivorous *Dorylaimus* are typical of the loss of large dorylaimid nematodes in perturbed habitats; however, their low abundance is a hurdle to their use as an indicator (Freckman and Ettema, 1993).

At the level of feeding groups, there were increases in the proportion of bacterial-feeding and plant-associated nematodes both 16 and 30 months after burning (Figure 1). At both these times predatory nematodes comprised a lower proportion of the total nematode fauna in the burned than in the control areas. The overall effect of burning on each of these three groups was significant (p<0.05).

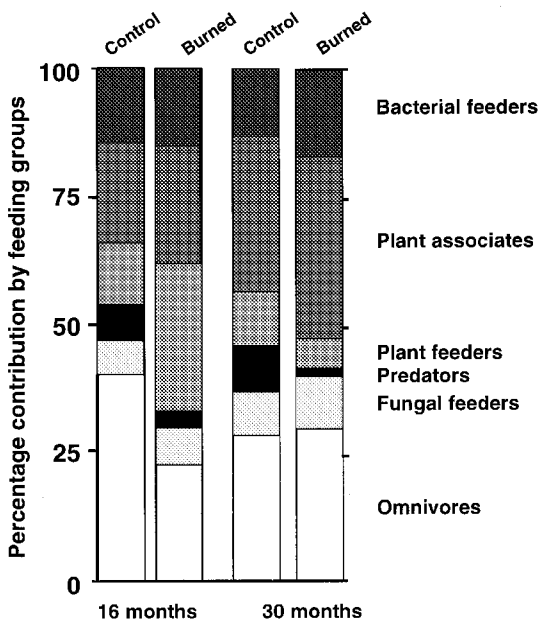


Figure 1: Contribution of six nematode feeding groups to the nematode fauna (in 0-2 cm litter and soil) 16 and 30 months after burning.

General discussion

Burning of tall tussock grassland resulted in major short-term changes in the composition and structure of the vegetation (Table 1). Depletion of intertussock areas and the removal of much of the tussock canopy during burning facilitate the establishment and spread of naturalised grasses and herbaceous weeds. However, weed invasion may be transient if the full canopy cover of the tussocks is restored. The recovery of burnt tussocks was slow, and after 2.5 years features such as tiller weights and canopy area were only 25% of the values recorded in unburnt grassland (Table 2). If the deeper soil profile development at the burnt site is significant it would have led to relatively better tussock recovery than would be expected on the control area. Full recovery may take between 20-25 years as suggested by Payton *et al.* (1986) and Gitay *et al.* (1992).

Soil pH, moisture content, bulk density and surface litter showed considerable treatment and year-to-year effects. These properties also reflect vegetation development.

Among the soil fauna, only total nematodes in 0-2 cm litter and soil showed a marked positive response to burning. However, total nematodes showed marked year-to-year differences; as minor

climatic variation probably underlies these effects the total populations are probably inappropriate as simple indicators of the effects of burning on soil processes. The greatest increase in any group was in *Paratylenchus* (100× and 29× at 16 and 30 months); as this distinctive root-feeding genus is widespread in tussock grasslands, and apparently showing positive responses to both greater environmental fluctuation and root development, it offers potential as an indicator. The smaller populations of collembola and mites at the burnt site suggest they are worthy of further study as potential, easily assessed indicators.

Using ratios of soil microbial carbon to total soil carbon Ross *et al.* (1997) considered that the post-burn decline in soil microbial biomass was greater than the decline in total soil organic matter. Bacterial grazing by the increased total bacterial-feeding nematodes which we have found may be partly responsible for the decreased soil microbial carbon. Trends in populations of fungal-feeding nematodes are similar, but variance greater. The increase in plant-associated nematodes, such as *Tylenchus*, parallels the plant growth-related increase in soil invertase activity reported by Ross *et al.* (1997).

Soil biochemical properties in 0-2 cm soil offer few prospects of indicators of recovery after burning in this ecosystem (Ross *et al.*, 1997). Given the difficulties of carrying out a fully replicated burning trial on uniform soil greatest progress in understanding the impacts of burning may come from sampling a range of sites of known burning history.

Acknowledgements

Funding was provided by the NZ Foundation for Research, Science and Technology under contract number CO9416. We thank the Miss E.L. Hellaby Indigenous Grassland Research Trust for a grant to W.G.L. Les R. Basher helped with the soil profile descriptions, and referees helped our interpretation of pseudoreplication.

References

- Allen, R. B.; Partridge, T. R. 1988. Effects of spring and autumn fires on the composition of *Chionochloa rigida* tussock grassland, New Zealand. *Vegetatio* 76: 37-44.
- Basher, L.R.; Meurk, C.D.; Tate, K.R. 1990. The effects of burning on soil properties and vegetation: a review of the scientific evidence relating to the sustainability of ecosystems and

- land use in the eastern South Island hill and high country. *New Zealand Department of Scientific and Industrial Research, Land Resources Technical Record 18*.
- Christensen, S.; Griffiths, B.S.; Ekelund, F.; Rønn, R. 1992. Huge increase in bacterivores on freshly killed barley roots. *FEMS Microbial Ecology 86*: 303-310.
- Coleman, D.C.; Anderson, R.V.; Cole, C.V.; McClellan, J.F.; Woods, L.E.; Trofymow, J.A.; Elliott, E.T. 1984. Roles of protozoa and nematodes in nutrient cycling. In: Giddens, J.E.; Todd, R.L. (Editors), *Microbial-plant interactions*. pp. 17-28. American Society Agronomy, Madison, U.S.A. 68 pp.
- Connor, H.E.; Edgar, E. 1987. Name changes in the indigenous New Zealand flora 1960-1986 and Nomina Nova IV, 1983-1986. *New Zealand Journal of Botany 25*: 115-170.
- Dugdale, J.S. 1971. Genera of New Zealand Cicadidae (Homoptera). *New Zealand Journal of Science 14*: 856-882.
- Freckman, D.W.; Ettema, C.H. 1993. Assessing nematode communities in agroecosystems of varying human intervention. *Agriculture, Ecosystems and Environment 45*: 239-261.
- Gitay, H.; Lee, W.G.; Allen, R.B.; Wilson, J.B. 1992. Recovery of *Chionochloa rigida* tussocks from fires in South Island, New Zealand. *Journal of Environmental Management 35*: 249-259.
- Hewitt, A.E. 1992. New Zealand soil classification. *New Zealand Department of Scientific and Industrial Research, Land Resources Scientific Report 19*.
- James, S.W. 1988. The postfire environment and earthworm populations in tallgrass prairie. *Ecology 69*: 476-483.
- Lee, K.E. 1959. The earthworm fauna of New Zealand. *New Zealand Department of Scientific and Industrial Research Bulletin 130*: 1-485.
- Mark, A.F. 1965a. Vegetation and Mountain Climate. In: New Zealand Geographical Society (Editor), *Central Otago*, pp. 69-91. New Zealand Geographical Society, Dunedin, New Zealand. 195 pp.
- Mark, A.F. 1965b. The environment and growth rate of narrow-leaved snow tussock, *Chionochloa rigida*, in Otago. *New Zealand Journal of Botany 3*: 73-103.
- McSorley, R. 1993. Short-term effects of fire on the nematode community in a pine forest. *Pedobiologia 37*: 39-48.
- Meyer, G.A.; Wells, S.G.; Balling, R.C.; Jull, A.J.T. 1992. Response of alluvial systems to fire and climate changes in Yellowstone National Park. *Nature, London 357*: 147-150.
- N.Z. Soil Bureau 1968. General survey of the soils of South Island, New Zealand. *New Zealand Soil Bureau Bulletin 27*.
- Payton, I.J.; Lee, W.G.; Dolby, R.; Mark, A.F. 1986. Nutrient concentrations in narrow-leaved snow tussock (*Chionochloa rigida*) after spring burning. *New Zealand Journal of Botany 24*: 529-537.
- Ross, D.J.; Speir, T.W.; Tate, K.R.; Feltham, C.W. 1997. Burning in a New Zealand snow-tussock grassland: effects on soil microbial biomass and N and P availability. *New Zealand Journal of Ecology 21*: 63-71.
- Rowley, J. 1970. Lysimeter and interception studies in narrow-leaved snow tussock grassland. *New Zealand Journal of Botany 8*: 478-493.
- Soil Survey Staff, 1975. *Soil taxonomy, a basic system of soil classification for making and interpreting soil surveys*. United States Department of Agriculture, Washington, U.S.A. 754 pp.
- Southey J.F. (Editor) 1978. *Plant nematology*. HMSO, London, England. 440 pp.
- Southey J.F. (Editor) 1986. *Laboratory methods for work with plant and soil nematodes*. HMSO, London, England. 202 pp.
- Tate, K.R. 1992. Assessment, based on a climosequence of soils in tussock grassland, of soil carbon storage and release in response to global warming. *Journal of Soil Science 43*: 697-707.
- Wardle, P. 1991. *Vegetation of New Zealand*. CUP, Cambridge, England. 672 pp.
- Webb, C.J.; Sykes, W.R.; Garnock-Jones, P.J. 1988. *Flora of New Zealand, Vol IV*. Botany Division DSIR, Christchurch, New Zealand. 1365 pp.
- Wood, B.L. 1962. *Sheet 22 Wakatipu* (1st Edition) Geological Map of New Zealand 1:250000. DSIR, Wellington, New Zealand.
- Wood, F.H. 1973. Biology and host range of *Paratylenchus projectus* Jenkins, 1956 (Nematoda: Cricematidae) from a sub-alpine tussock grassland. *New Zealand Journal of Agricultural Research 16*: 381-384.
- Yeates, G.W. 1974. Studies on a climosequence of soils in tussock-grasslands. 2. Nematodes. *New Zealand Journal of Zoology 1*: 171-177.
- Yeates, G.W.; Wardle, D.A.; Watson, R.N. 1993. Relationships between nematodes, soil microbial biomass and weed management strategies in maize and asparagus cropping systems. *Soil Biology and Biochemistry 25*: 869-876.