Fire-induced changes to the vegetation of tall-tussock (*Chionochloa rigida*) grassland ecosystems

SCIENCE FOR CONSERVATION 290

Department of Conservation
Te Papa Atawhai

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Published by
Publishing Team
Department of Conservation
PO Box 10420, The Terrace
Wellington 6143, New Zealand

Cover: Lighting a summer burn at Mt Benger. *Photo: Marcus Simons.*

Science for Conservation is a scientific monograph series presenting research funded by New Zealand Department of Conservation (DOC). Manuscripts are internally and externally peer-reviewed; resulting publications are considered part of the formal international scientific literature.
Individual copies are printed, and are also available from the departmental website in pdf form. Titles are listed in our catalogue on the website, refer www.doc.govt.nz under *Publications*, then *Science & technical*.

ISSN 1173-2946 (hardcopy)
ISSN 1177-9241 (web PDF)
ISBN 978-0-478-14527-4 (hardcopy)
ISBN 978-0-478-14528-1 (web PDF)

This report was prepared for publication by the Publishing Team; editing by Amanda Todd and layout by Sue Hallas. Publication was approved by the General Manager (Research and Development Group), Department of Conservation, Wellington, New Zealand.

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ABSTRACT

The deliberate use of fire has long been a contentious issue in the South Island high country of New Zealand, being seen by some as damaging to the environment and by others as an essential pastoral management tool. These issues were examined in tall-tussock (*Chionochloa rigida*) grasslands at two sites in Otago, which were burned either in spring, to simulate pastoral management practice, or late summer, to simulate accidental fires. Fire temperatures reached over 1000°C, but were of short duration (4–8 minutes) and had little heating effect on the soil. Biomass, carbon and nutrient losses were lowest when the grasslands were burned under damp conditions, and increased as soil and plant moisture levels declined. The best predictors of biomass loss were the moisture content of the top 5 cm of soil and the base of the tussocks. Spring burns under damp conditions killed c. 35% of the tussock tillers but did not cause the death of tussocks, whereas burns under drier conditions or later in the growing season killed over 75% of tussock tillers and resulted in the death of tussocks. Seedling densities and inflorescence production were also least affected when the grasslands were burned under damp spring conditions; when conditions were drier, both were dramatically reduced and showed little sign of returning to pre-burn levels 4–5 years after the fire. Early season burns under damp conditions posed little threat to the long-term survival of tall-tussock ecosystems, whereas fires later in the season, or when conditions were drier, resulted in substantially greater biomass, carbon and nutrient losses and caused a loss of tussock dominance, at least in the short to medium term. Therefore, minimising their extent should be a priority wherever tussock cover is to be retained.

Keywords: biomass, carbon, nutrients, *Chionochloa rigida*, fire, seedling establishment, tall-tussock grassland, tiller mortality, tussock mortality, tussock flowering.

Payton, I.J.; Pearce, H.G. 2009: Fire-induced changes to the vegetation of tall-tussock (*Chionochloa rigida*) grassland ecosystems. *Science for Conservation 290*. Department of Conservation, Wellington. 42 p.

1. Introduction

Fire and herbivory have been important selective forces in the development, maintenance and, in more recent times, the degradation of New Zealand's indigenous grasslands. Below the climatic timberline, these communities are thought to be largely seral[1] (McGlone 2001; Mark & Dickinson 2003) and, in the absence of periodic disturbance, they will revert to the woody growth forms that characterised montane and lowland landscapes in pre-human times (Molloy et al. 1963; Stevens et al. 1988).

The introduction of pastoralism in the 1850s increased fire frequency, introduced mammalian herbivory and precipitated widespread changes in the stature and composition of these fire-induced grasslands (Connor 1964; O'Connor 1982, 1986). Change has been greatest in areas of lower rainfall, where the displacement of the dominant tall-tussocks by shorter tussock (*Festuca* spp., *Poa* spp.) or mat (*Hieracium* spp., *Raoulia* spp.) growth forms has been exacerbated by a range of alien plant (e.g. *Hieracium* spp., *Rosa* spp.) and animal (e.g. rabbits) pests. As native forage declined, many montane grasslands were oversown with adventive pasture grasses and legumes. Since the introduction of aerial topdressing in the late 1940s, some have also received intermittent applications of phosphate-based fertilisers (O'Connor 1987; O'Connor & Harris 1992). The net result is a mosaic of modified grassland communities that retain varying degrees of native dominance and biodiversity (Mark 1993).

The deliberate use of fire in pastoral management has long been a contentious issue in the South Island high country (Parliamentary Commissioner for the Environment 1995). Environmentalists frequently portray fire as damaging native flora and fauna, increasing the opportunities for the spread of invasive weeds and promoting soil erosion; in contrast, pastoralists see it as a means of improving access for stock, promoting palatable regrowth and reducing or removing so-called 'woody weeds'. There are also increasing concerns over the long-term sustainability of burning and grazing practices, which continue to deplete the nutrient capital of these ecosystems (McIntosh 1997; O'Connor et al. 1999). Furthermore, the retirement of pastoral leasehold land and predictions of reduced rainfall (Hennessy et al. 2007) have raised concerns in rural communities that the increased biomass (fuel load) of grasslands that are no longer intentionally burned or grazed may pose an increased fire risk during the dry summer and autumn months.

Over the last 50 years, a large number of studies have described the impacts of fire and grazing on tall-tussock grassland communities, and have documented the effect of fire on the growth and forage quality of the dominant tussock species (reviewed in Basher et al. 1990; McKendry & O'Connor 1990). Most of these studies have examined only single aspects of the tall-tussock ecosystem, and none have established a pre-burn baseline and characterised the severity of the fires. The present study, which comes at a time when large areas of tall-tussock

[1] A seral community (or sere) is an intermediate stage in an ecological succession, here, from grassland to shrubland or forest.

grassland are shifting from pastoral leases to public conservation land as part of the Tenure Review process (Crown Pastoral Land Act 1998), examined fire-related changes to the vegetation of two *Chionochloa rigida* grasslands in Otago. Parallel studies examined fire behaviour (H.G. Pearce and S.A.J. Anderson, Scion, unpubl. data) and examined fire effects on invertebrate communities (Barratt et al. 2007) in these grasslands.

2. Objectives

The two main objectives of this study were to:

- Document changes associated with early- and late-season burns in tall-tussock grasslands in Otago
- Use these data to address the following questions:
  - —Does fire cause long-term damage to tall-tussock grassland communities?
  - —Are accidental summer–autumn burns more damaging than prescribed burns in late winter–early spring?
  - —Are environmental conditions and fire weather indices good predictors of the severity of a burn?

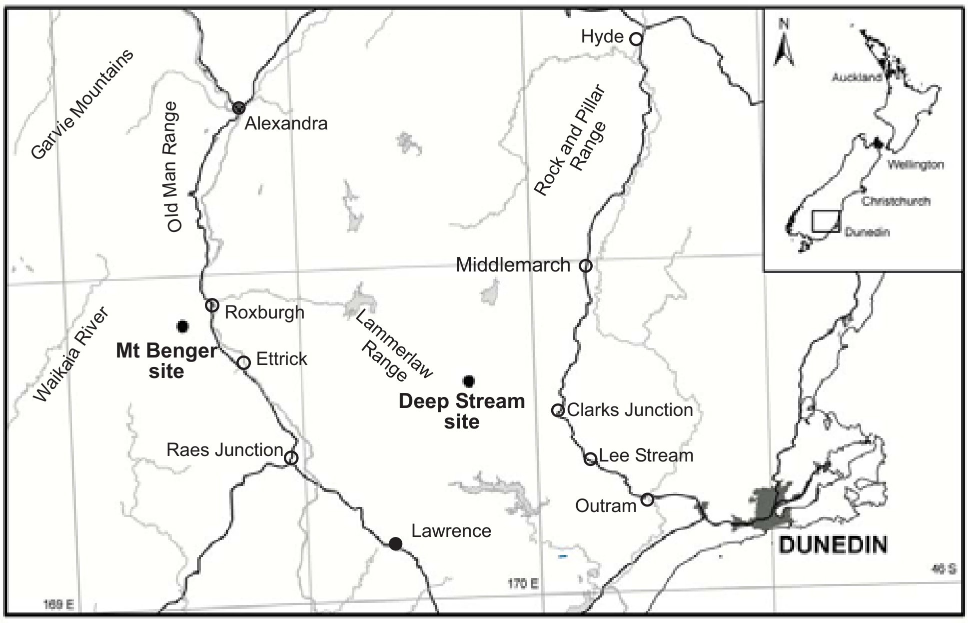
3. Methods

3.1 STUDY SITES

Two experimental sites were used in this study: a coastal range site at Deep Stream (inland from Dunedin), on land owned and managed by the Dunedin City Council, and an inland range site at Mt Benger (near Roxburgh), on pastoral leasehold land (Fig. 1). The Deep Stream site, which is on gently sloping terraces (640–700 m a.s.l.) between Barbours and Clarkes Streams at the eastern end of the Lammerlaw Range, is typical of lower-altitude tall-tussock grasslands that are coming under increasing pressure for pastoral development. The Mt Benger site, situated on a broad ridge crest (1100–1180 m a.s.l.) at the head of Bullock Creek, represents higher-altitude pastoral leasehold land, which is progressively being retired from grazing and incorporated into conservation lands.

Climate profiles for the study sites (Fig. 2) were obtained from climate surfaces developed for the Land Environments of New Zealand (LENZ) programme (Leathwick et al. 2002). These showed that Deep Stream was warmer (mean annual temperature: 6.8°C v. 4.9°C) and drier (rainfall 993 mm v. 1264 mm) than Mt Benger, and on average had a negative water balance (rainfall < potential evapotranspiration) for a larger part of the year (7 months (September–March) v. 4 months (November–February)) than did Mt Benger. At both sites, there was snow during winter and ground frosts could occur in all months of the year.

Figure 1. Map of the study sites at Deep Stream and Mt Benger.



Schist forms the soil parent material at both sites. At Deep Stream, soils are described as silt loams (Wehenga soils), while at Mt Benger, silt loams and stony loams (Carrick soils) predominate. Both soil types are classed as having low to very low natural nutrient status (New Zealand Soil Bureau 1968).

At the outset of the experiment, the vegetation at both sites was intact *Chionochloa rigida* grassland. Both sites had been retired from grazing by farmed stock, and had remained unburned for over a decade prior to the experiment. Brown hares (*Lepus europaeus*) were present at both sites, and there were also low numbers of European rabbits (*Oryctolagus cuniculus*) at Deep Stream.

3.2 EXPERIMENTAL DESIGN

At each site, nine 1-ha (100 × 100-m) plots were subjectively located on gently sloping terrain (Fig. 3), to remove slope-related effects and aid access for heavy machinery. Each plot was surrounded by a mineral-earth firebreak 2–5 m wide. Groups of three adjacent plots were blocked, and treatments (unburned, spring burn, summer–autumn burn) were randomly allocated to plots within blocks. Each plot was subdivided into 25 0.04-ha (20 × 20-m) subplots, and a randomly chosen subplot was allocated to each of the following: destructive harvests (to assess plant biomass, carbon and nutrient pools), non-destructive plant measurements (tussock flowering and seedling establishment) and invertebrate sampling (see Barratt et al. 2007).

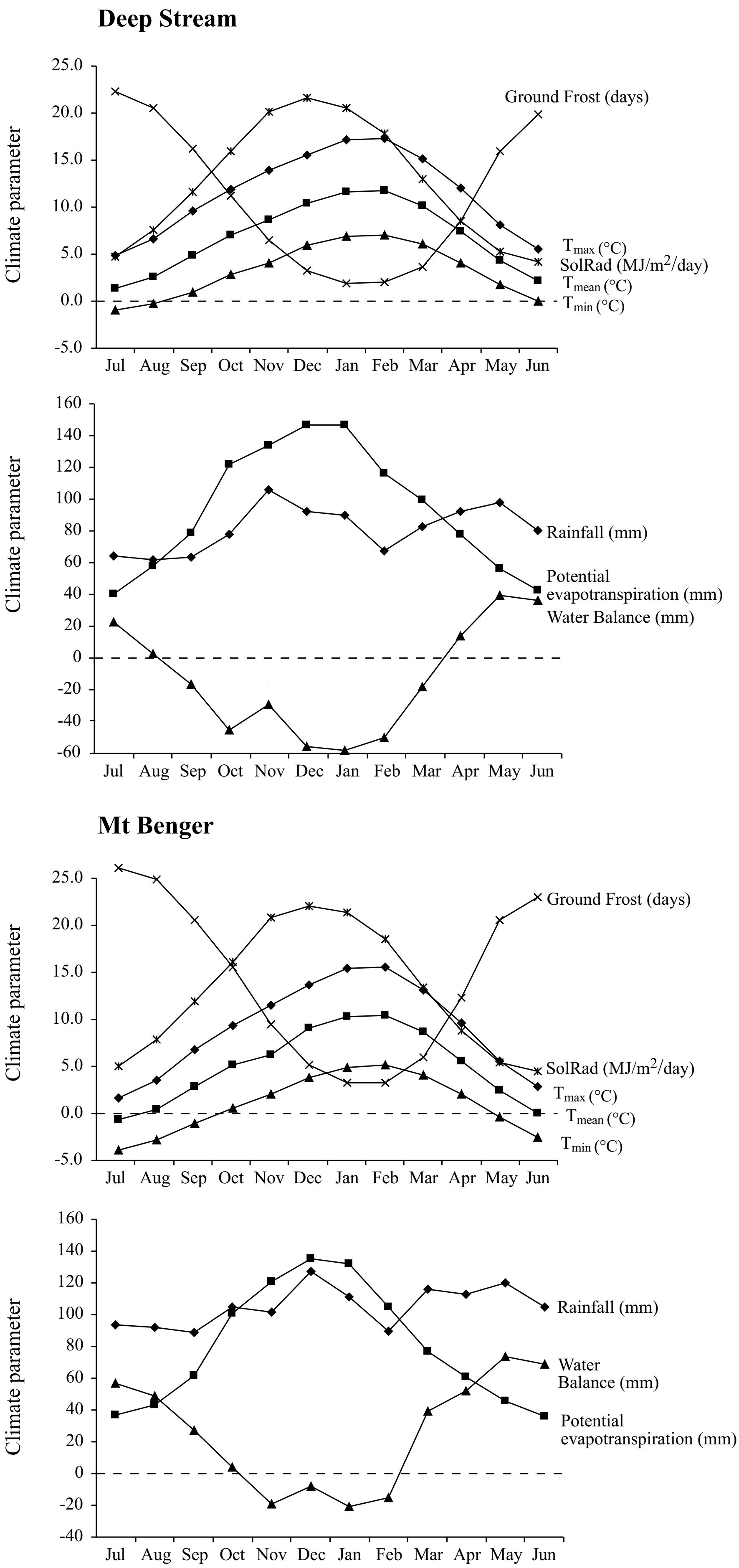


Figure 2. Climate profiles for the Deep Stream and Mt Benger study sites. Monthly temperature (T_{max}, T_{mean}, T_{min}) and solar radiation (SolRad) figures are the mean of daily values.

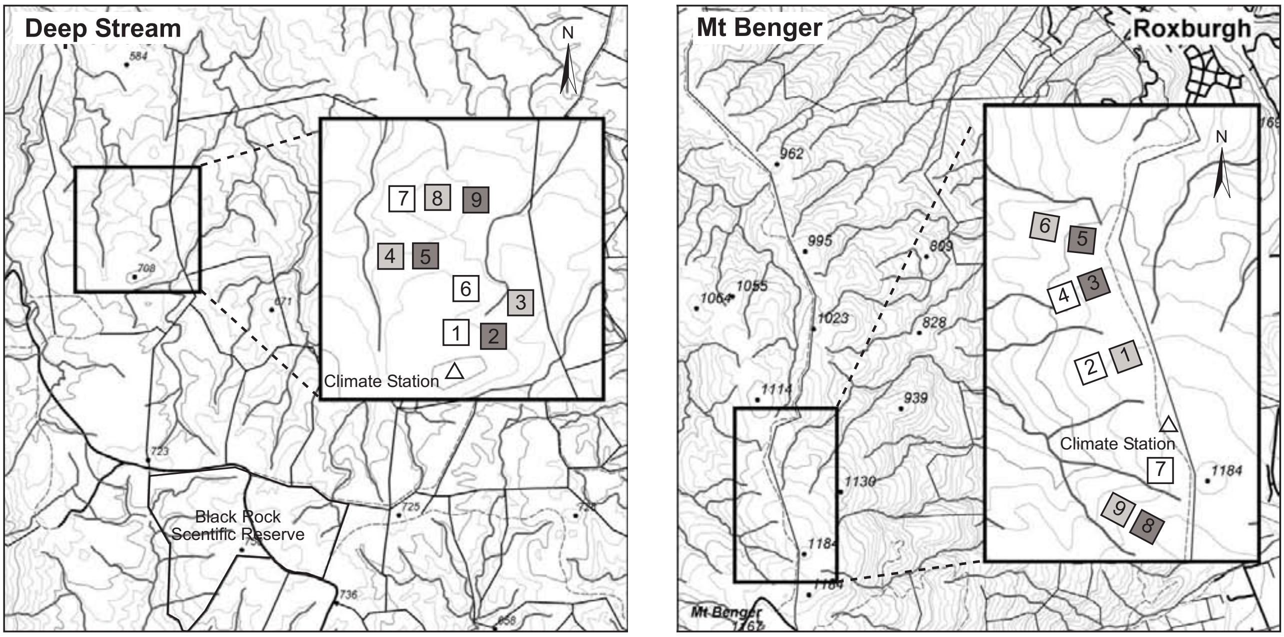


Figure 3. Layout of experimental plots at the Deep Stream and Mt Benger study sites. The colour of the squares denotes the burning treatment – white (unburned), light grey (burned in spring), dark grey (burned in summer).

3.3 BIOMASS, CARBON AND NUTRIENT POOLS

Plant biomass harvest subplots were divided into 400 (1 × 1 m) squares, five of which were randomly chosen for each biomass harvest. The corners of each harvested square were permanently marked with aluminium pegs to ensure that squares were not inadvertently resampled at a later date.

Within each square, a sharp spade was used to remove all above-ground plant material to the level of the mineral soil. All plant material was bagged and returned to the laboratory, where it was separated by species or species-group (e.g. minor forbs, mosses), and into live and dead material. Except for *Chionochloa rigida*, for which live and dead leaves were separated, no attempt was made to partition the live and dead portions of living plant material. Plant samples were dried to a constant weight in a forced-draft oven (70°C).

Below-ground plant biomass was sampled using soil cores. Within each square, four cores (65-mm diameter) were taken to a depth of 20 cm, two from beneath tussocks and two from between them. Roots were washed from the soil cores over a 2-mm sieve, and dried and weighed as described above. At each site, three soil cores were taken to bedrock (35–50 cm) to determine the percentage of roots in the top 20 cm of soil. These figures were then used to scale the 0–20-cm root weights: at Deep Stream, an average of 93.6% of roots below tussocks and 89.8% of roots between tussocks were present in the 0–20-cm cores; at Mt Benger, the figures were 96.8% and 97.9%, respectively.

Below-ground plant biomass was calculated by multiplying soil core root weights by the area of the quadrat beneath or between the tussocks. The area beneath tussocks was determined from a relationship between tiller number and tussock basal area, obtained using a linear mixed effects model with a quadratic term where this was significant:

$$\text{Tussock basal area (cm}^2)_{\text{Deep Stream}} = -1.29 + 1.46\,(\text{tiller no.}) + 0.01\ (\text{tiller no.}^2)$$

$$\text{Tussock basal area (cm}^2)_{\text{Mt Benger}} = -9.70 + 3.92\,(\text{tiller no.})$$

The area between tussocks was obtained by subtracting tussock basal area from the total area of the quadrat. For *Aciphylla aurea,* a fleshy rooted forb that tended to be substantially under- or over-represented in soil cores at Deep Stream, below-ground biomass was estimated from a relationship between root and leaf weight, obtained using a linear regression model:

$$\text{Root weight (g)}_{\textit{Aciphylla aurea}} = 0.1293\,(\text{leaf weight})\,(\text{g})_{\textit{Aciphylla aurea}} + 1.5331$$

Samples of each plant species or species group were ground in a Cyclone Mill to pass through a 40-mesh screen, and held in airtight containers until required for analysis. Phosphorus, potassium, calcium and magnesium (P, K, Ca, Mg) content were determined using a modified semi-micro Kjeldahl method (Blakemore et al. 1987), in which the digestion was carried out in 50-mL calibrated test tubes in a drilled aluminium block on a hotplate. The concentration of orthophosphate in the digest was determined colorimetrically on a flow injection analyser (Method 10-115-01-1-A, Quikchem Methods Manual 1995). Potassium, calcium and magnesium concentrations were determined by atomic absorption spectrometry on a Varian SpectrAA FS-220 spectrophotometer; potassium with an air–acetylene flame, and calcium and magnesium with a nitrous oxide–acetylene flame. Samples analysed for carbon, nitrogen and sulphur were heated in a stream of high-purity oxygen in a Leco furnace to produce CO_2, SO_2, N_2 and NO_x. A subsample of the combustion gases was then passed through a heated copper catalyst to reduce NO_x to N_2, which was measured by thermal conductivity. The CO_2 and SO_2 were measured using infrared detectors.

All plots were initially sampled between November 1997 and April 1998. Where biomass harvest data were more than 12 months old at the time of the experimental burn, plots were resampled immediately before the burn, and these data were used to calculate the pre-burn biomass, carbon and nutrient estimates presented in this report.

Ash deposited by the fires was collected in shallow galvanised iron trays (0.75 m^2) set at ground level (Fig. 4). Trays were located at the centre, and halfway between the centre and each corner, of each plot. After the burn, material deposited in each tray was sieved to extract the ash. Ash samples were dried and weighed, and a composite sample from each plot was analysed for nutrient composition, as described above.

3.4 CLIMATIC CONDITIONS AND FIRE WEATHER INDICES

At each site, weather conditions (temperature, rainfall, humidity, and wind speed and direction) were monitored using an automated climate station that formed part of the National Rural Fire Authority (NRFA) network of fire weather stations. This was supplemented by a portable weather station, which was used to gather more detailed climatic data from individual plots immediately before and during the burns. Data from the fire weather stations, which are used to provide numerical ratings for the New Zealand Fire Weather Index (FWI) System

Figure 4. Galvanised iron tray used to sample ash deposited by the fires.

(Van Wagner 1987; Anderson 2005), enabled changes in fuel moisture codes and fire behaviour indices (see Appendix 1 for details) to be tracked on a daily basis throughout the year. Fuel moisture codes (Fine Fuel Moisture Code—FFMC; Duff Moisture Code—DMC; and Drought Code—DC) provide a measure of the dryness of available fuels and soil organic layers, based on the cumulative effects of temperature, humidity and rainfall. Fire behaviour indices combine these codes with information on wind speed and direction to provide numerical ratings of: the expected rate of fire spread (Initial Spread Index—ISI), fuel availability for combustion (Buildup Index—BUI) and fire intensity (Fire Weather Index—FWI). Target ranges for each of these indices were set to reflect average conditions experienced in the grasslands during spring and summer. For spring burns, these were FFMC 70–90, DMC 0–20, DC 30–200, BUI 10–30, ISI 0.5–12 and FWI 0–19, and for summer burns, they were FFMC 75–90, DMC 10–30, DC > 200, BUI 20–50, ISI 1.0–24 and FWI 1–40.

3.5 FIRE TEMPERATURES

Temperatures during the experimental burns were measured using thermocouple sensors (spring burns at Deep Stream) and heatplates (all burns) marked with temperature-indicating paints (Hobbs et al. 1984; Gill & Knight 1991; Tolhurst 1995). Thermocouple sensors were placed 1 m above the ground and at ground level, at a single point near the centre of the plot. Heatplates were positioned 1 m above the ground, at ground level, and at soil depths of 2.5 cm and 5.0 cm, on a 5 × 5-m grid on the central 20 × 20-m subplot, and on a 20 × 20-m grid over the remainder of the 1-ha plot. Each heatplate consisted of a strip of copper folded back on itself with a row of temperature-indicating paint strips on the inside surface. Paint strips on above-ground heatplates melted at 101°C, 302°C, 500°C, 760°C and 1010°C, while those placed in the soil melted at 69°C and 101°C.

3.6 PLANT AND SOIL MOISTURE

Plant (surface litter, tussock base litter, live tussock tillers) and soil (0–5 cm, 5–10 cm) moisture were determined immediately before each of the experimental burns. Samples were collected from five sites adjacent to the ash collection trays, and placed in sealed plastic containers for return to the laboratory, where they were dried to a constant weight in a forced-draft oven (70°C). Moisture content was expressed as a percentage of the dry weight of the sample.

3.7 TILLER AND TUSSOCK MORTALITY

The percentage of tussocks killed by the spring fires was determined 6–8 weeks after each of the experimental burns, by identifying the nearest tussock at 1-m intervals along a randomly located 50-m tape, and recording whether or not it had resprouted after the fire. At Deep Stream, the post-fire recovery of tussocks was patchy, so tapes were run out through areas of good and poor tussock survival. For summer burns, where winter frosts also affected survival, assessments were delayed until the following spring, at which time tussocks were recorded as either having resprouted, resprouted but died overwinter, or not resprouted.

Ten permanently marked tussocks per plot were used to determine tiller mortality. Tillers were counted immediately before the experimental burns and again 6–10 weeks later to determine the percentage of tillers that had been killed by the fire. For summer burns, where winter frosts also affected tiller survival, the tiller count was repeated the following spring. At Mt Benger, where the tussocks were flowering heavily at the time of the summer burns, flowering tillers were excluded from the tiller mortality estimates, as these would not be expected to resprout after fire.

3.8 TUSSOCK FLOWERING AND SEEDLING ESTABLISHMENT

Flowering and seedling establishment of *Chionochloa rigida* tussocks was recorded annually on each of the plots. Inflorescences and seedlings were counted on ten randomly chosen 1 × 1-m squares in the subplot allocated to non-destructive plant measurements. The same squares were used each year to factor out any spatial variability that may otherwise have masked temporal changes. For the purposes of this study, tussock seedlings were defined as individual plants with between one and five tillers that did not have an observable connection to another group of tillers.

4. Results

4.1 BIOMASS, CARBON AND NUTRIENT POOLS IN THE UNBURNED GRASSLANDS

Pre-burn assessments carried out between November 1997 and April 1998 established that the total plant biomass of intact tall-tussock grasslands at the Deep Stream and Mt Benger study sites was between 37 and 41 tonnes/ha (Table 1, Appendices 2 and 3). The bulk of this biomass was litter (40–51%), followed by roots (25–33%), and the above-ground portions of grasses, rushes and sedges (13–17%), shrubs (2–9%), lower plants (ferns, mosses, lichens and liverworts; 3–4%) and forbs (1–2%). Key differences between the sites were the higher percentage of litter in the Mt Benger grasslands, and the bigger contribution made by shrubs and roots at Deep Stream. Plant nutrient pools were similar at the two sites, with the exception of that for calcium, which was higher in all plant groups at Deep Stream. Between 65% and 80% of the biomass and nutrients (N, P, S) that tend to be limiting for plant growth in high-country environments were present in the above-ground biomass, and therefore directly susceptible to fire.

TABLE 1. PRE-BURN ASSESSMENT OF BIOMASS, CARBON AND NUTRIENT POOLS (kg/ha) AT THE DEEP STREAM (DECEMBER 1997–FEBRUARY 1998) AND MT BENGER (APRIL 1998) STUDY SITES. VALUES ARE THE MEAN OF FIVE SAMPLES PER PLOT AND NINE PLOTS PER SITE.

	BIOMASS	C	N	P	K	Ca	Mg	S
Deep Stream site								
Grasses, rushes and sedges								
Chionochloa rigida	3771.0	1793.2	23.90	3.36	31.11	2.04	2.52	4.25
Other	1473.7	661.1	11.92	1.27	7.22	1.75	1.36	1.71
Forbs	603.1	276.2	5.09	0.66	8.60	3.62	1.16	0.65
Shrubs	3585.1	1796.8	24.44	2.51	13.80	17.25	5.09	3.06
Lower plants	1467.8	672.3	11.85	1.31	6.22	3.01	1.90	1.17
Litter	15960.8	7167.6	90.53	7.98	44.44	16.15	11.90	13.69
Roots	12932.1	5847.4	77.29	6.88	25.40	2.88	3.37	12.32
Total biomass	39793.7	18214.6	245.02	23.96	136.80	46.71	27.30	36.85
(SEM)	(1175.7)	(538.1)	(7.29)	(0.73)	(4.62)	(2.25)	(0.97)	(1.13)
Mt Benger site								
Grasses, rushes and sedges								
Chionochloa rigida	5536.9	2595.6	36.09	4.97	48.60	2.04	4.13	4.17
Other	1042.5	471.0	9.50	1.03	4.85	0.55	1.11	1.25
Forbs	403.2	179.8	4.05	0.40	2.52	0.51	0.66	0.41
Shrubs	849.0	422.0	7.11	0.78	3.66	2.79	1.61	0.75
Lower plants	1328.9	606.1	9.84	0.89	5.36	0.45	1.40	1.04
Litter	19891.0	9340.4	85.76	7.08	30.48	8.20	11.56	13.45
Roots	9676.4	3867.3	72.37	6.58	39.46	2.27	5.80	10.27
Total biomass	38727.8	17482.1	224.7	21.7	134.9	16.8	26.3	31.3
(SEM)	(1820.6)	(853.5)	(7.8)	(0.7)	(4.7)	(1.0)	(1.1)	(1.1)

4.2 BURN CONDITIONS AND FIRE TEMPERATURES

All of the experimental burns were carried out between 1300 and 1700 hours. Burns were lit on the upwind side of the plot, and the rate and direction of fire spread was determined by the prevailing wind. Where fire safety personnel deemed it necessary, the downwind side of the plot was initially back-burned, to increase the width of the firebreak.

At Deep Stream, the spring burns took place on 2 October 2001, during a 2-week dry spell in what was an otherwise damp end to spring (Fig. 5, Appendix 4). All fire weather indices were in the mid- to upper quartiles of the spring-burn range, with the exception of DC, which was just below the spring-burn threshold. In 2001, the Deep Stream grasslands did not dry out sufficiently for a summer burn until early March; the plots were burned on 7 March, which was the first day that all of the fire weather indices were within the summer-burn range (Fig. 6).

At Mt Benger, the spring burns were lit on 3 November 2000. This is later than pastoral burns are permitted, but weather conditions and fire weather indices (Fig. 7, Appendix 4) were still well within the target range for spring burns (see section 3.4). There was a good crisp frost on the morning of the fires, and snow blanketed the site several days later. The summer burns at Mt Benger were delayed until 31 March 2006, owing to restrictions on burning during a prohibited fire season. After a damp start to summer, conditions exceeded the summer-burn thresholds for only a brief period in late February (Fig. 8). A dry spell during March was not sufficient to enable all fire weather indices to reach the summer-burn thresholds, but did allow the grasslands to dry out sufficiently to carry a fire.

During the spring burns at Deep Stream, thermocouple measurements showed that as the fire front approached, temperatures rose steeply and peaked at approximately 700°C within 30–70 seconds (Fig. 9). The high temperatures were short-lived, however, and both the 1-m and ground-surface sensors were recording near-ambient temperatures 4–8 minutes later. At Deep Stream and Mt Benger, heatplates placed 2.5 cm and 5.0 cm below the soil surface indicated that this short, sharp burst of heat did not raise soil temperatures above 69°C, which is the temperature at which the most heat-sensitive paint changes colour. Above-ground heatplates recorded temperatures of 760°C 1 m above the ground, and 1010°C at the ground surface, during early- and late-season fires at both sites. Rates of fire spread varied from 350 m/h to 1830 m/h, depending on fuel dryness and wind speed (Appendix 4).

Figure 5. Climatic conditions and fire weather indices around the time of the spring burns (indicated by arrow) at Deep Stream.

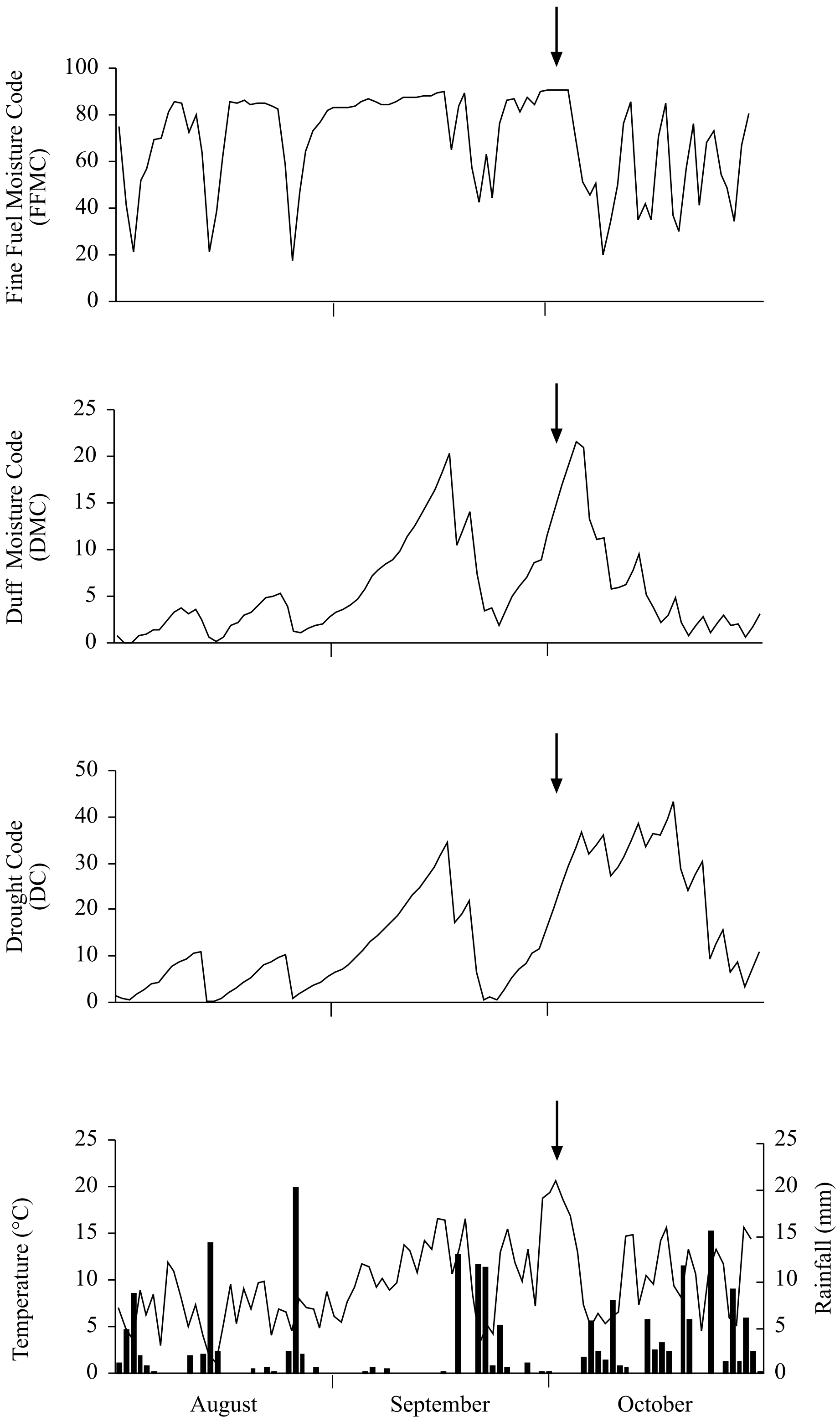


Figure 6. Climatic conditions and fire weather indices around the time of the summer burns (indicated by arrow) at Deep Stream.

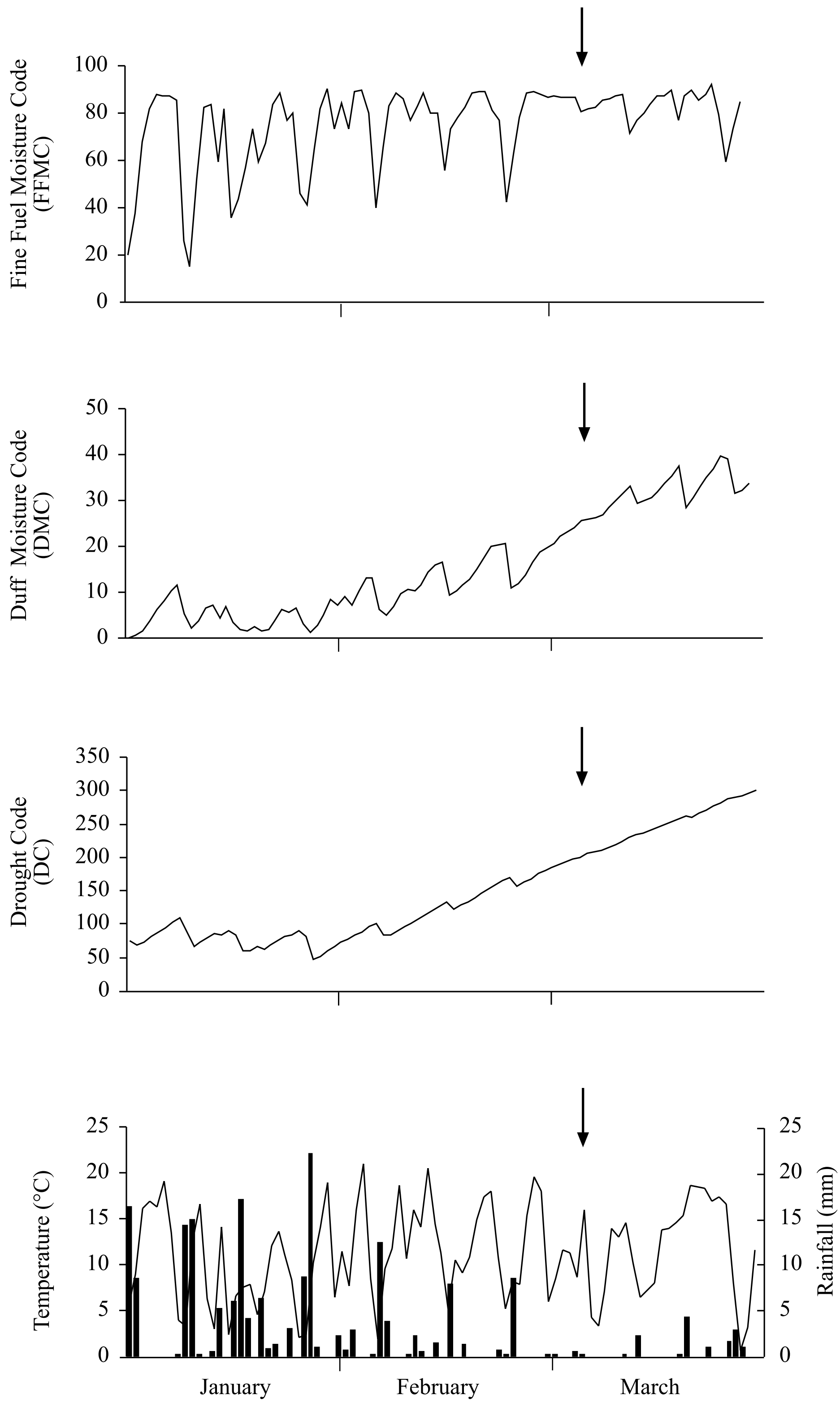


Figure 7. Climatic conditions and fire weather indices around the time of the spring burns (indicated by arrow) at Mt Benger.

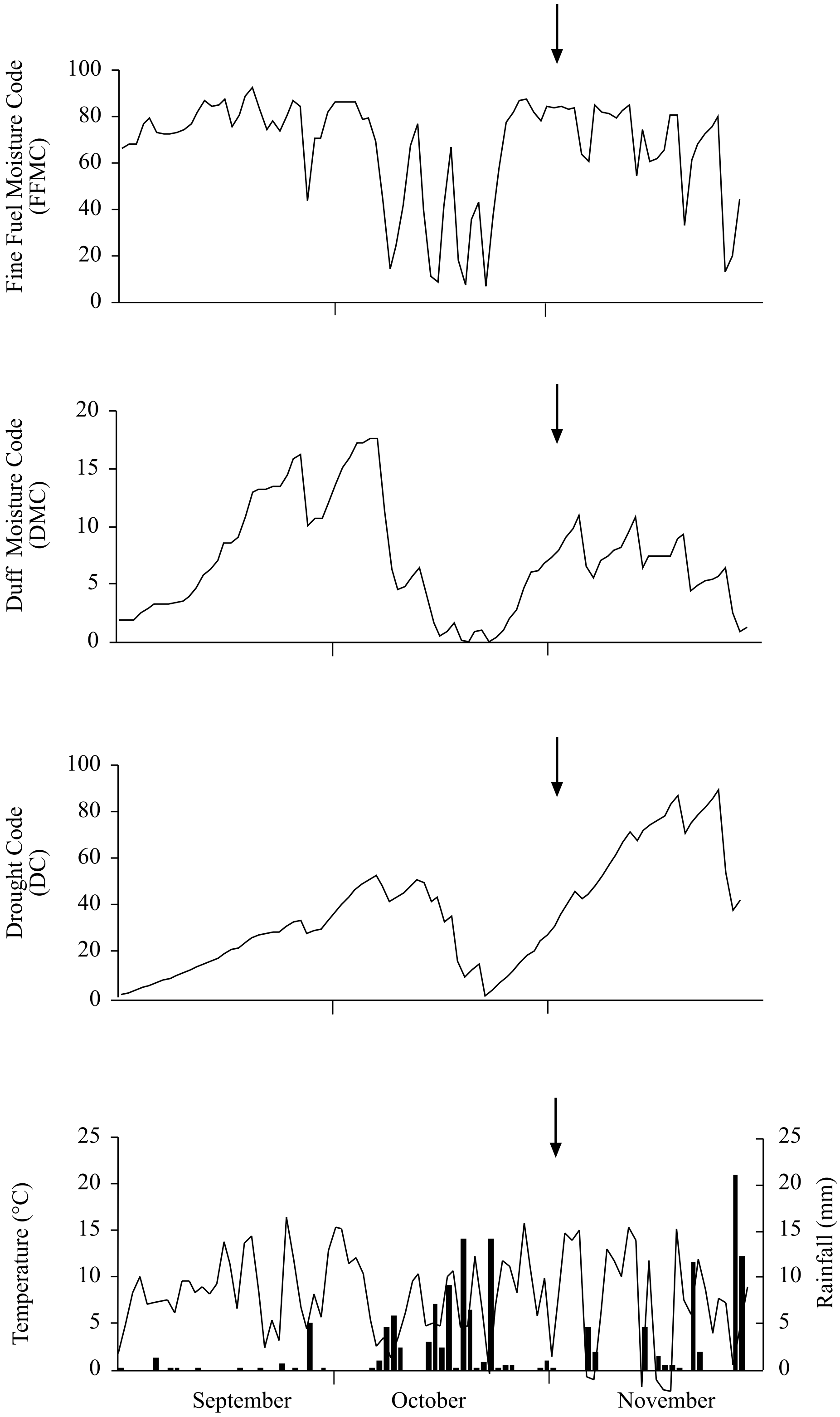
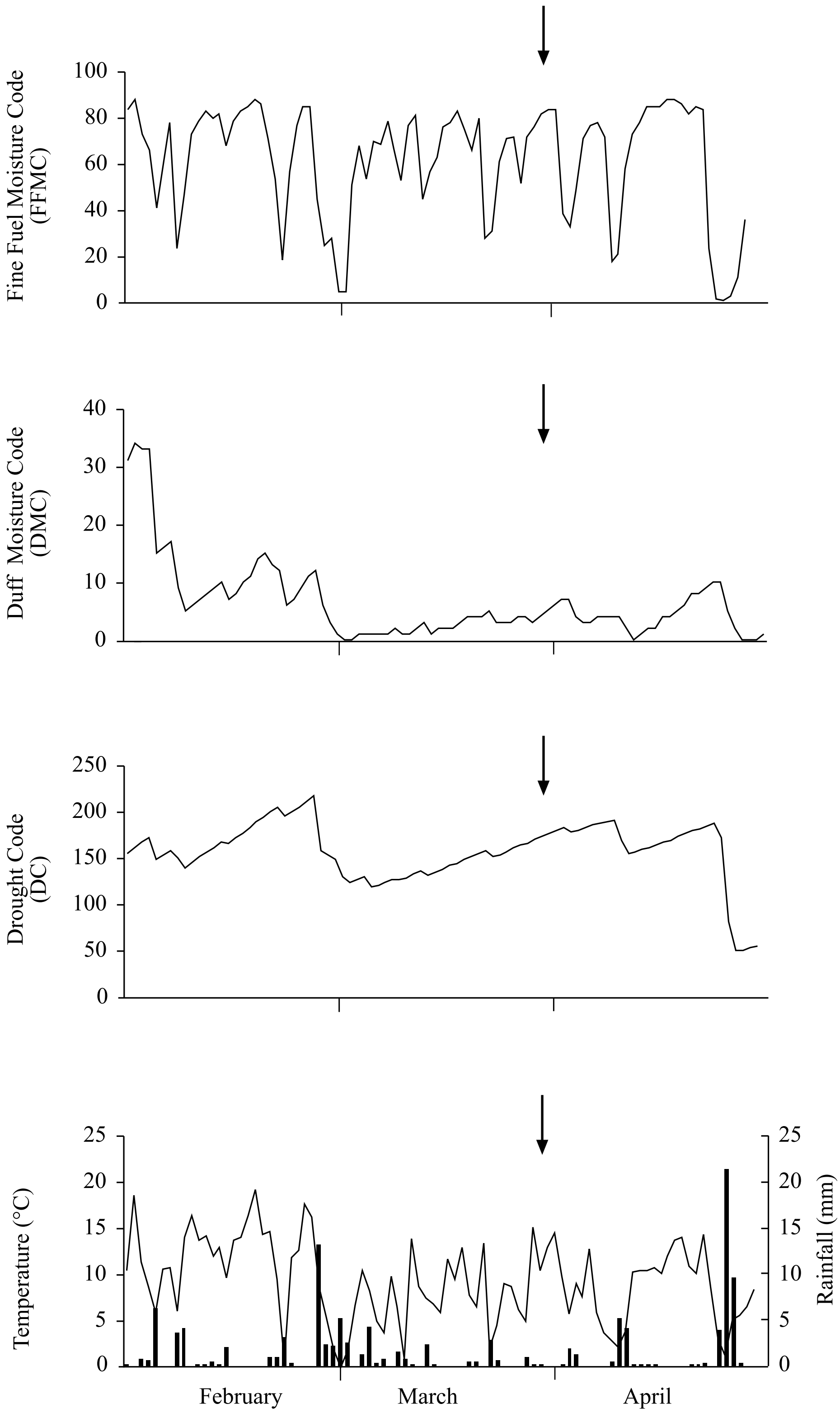


Figure 8. Climatic conditions and fire weather indices around the time of the summer burns (indicated by arrow) at Mt Benger.



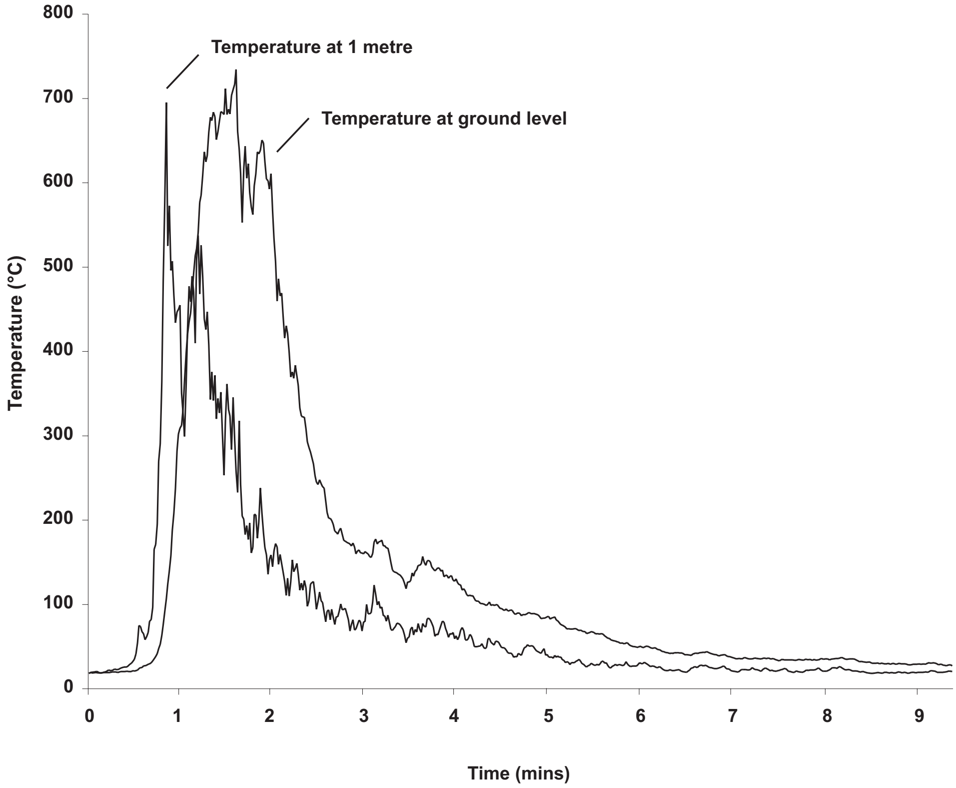


Figure 9. Temperatures reached during a spring burn at Deep Stream. Values on the *x*-axis represent time since the fire front approached the thermocouple sensors.

4.3 BIOMASS, CARBON AND NUTRIENT LOSSES

In all of the plots, above-ground biomass increased between the initial assessment in 1997–98 (Table 1) and the assessment that was carried out within 12 months of the experimental burns (Tables 2 and 3). This was especially noticeable in the summer-burned plots at Mt Benger, where the pre-burn biomass assessment coincided with a mast flowering season for the tussocks.

At Mt Benger, the spring burns consumed an average of 35.6% of the above-ground biomass, and depleted the above-ground nutrient pools by 31–43% (Table 2). The corresponding figures for the summer burns at this site, where plant and soil moisture levels were similar to those at the time of the spring burns (Table 4), were 62.6% and 62–78%, respectively. Both sets of burns at Mt Benger consumed much of the standing plant material, but left almost all of the ground-cover layer intact. At Deep Stream, where the fire weather indices (Appendix 4) and the moisture content data (Table 4) indicated that conditions during both the spring and summer burns were much drier, the biomass loss averaged 75.4% for the spring burns and 74.0% for the summer burns (Table 3). Above-ground nutrient pools were depleted by 70–76% and 68–77%, respectively. Both sets of burns removed not only the majority of the standing plant material, but also most of the ground-cover layer (Fig. 10).

The quantity of ash deposited by the burns ranged from 5.6 to 13.2 kg/ha and was roughly in proportion to the percentage of the above-ground biomass consumed by the fires. Nutrient return in the ash was minimal (Table 5), when compared with the losses resulting from the burns (Tables 2 and 3). Potassium and calcium were the major nutrients present in ash samples, followed by magnesium, phosphorus, and trace amounts of nitrogen and sulphur (Table 5).

TABLE 2. BIOMASS, CARBON AND NUTRIENT LOSSES (kg/ha) RESULTING FROM SPRING AND SUMMER BURNS AT MT BENGER. VALUES ARE THE MEAN OF FIVE SAMPLES PER PLOT AND THREE PLOTS PER TREATMENT.

	BIOMASS	C	N	P	K	Ca	Mg	S
SPRING BURNS								
Pre-burn assessment								
Grasses, rushes and sedges								
Chionochloa rigida	3864.9	1832.0	27.80	4.58	33.81	4.58	5.22	4.06
Other	1471.9	665.3	14.61	1.96	11.03	3.41	2.07	2.08
Forbs	12.2	4.7	0.15	0.02	0.14	0.08	0.03	0.02
Shrubs	604.4	312.5	4.30	0.66	3.95	2.27	1.68	0.53
Lower plants	2170.9	998.6	14.57	1.07	8.37	2.72	1.38	1.84
Litter	30 140.5	13 168.3	187.08	12.04	110.92	37.06	16.12	20.65
Total above-ground	38 264.8	16 981.3	248.51	20.32	168.21	50.13	26.51	29.17
(SEM)	(4034.1)	(1767.4)	(23.76)	(1.27)	(14.43)	(4.61)	(1.61)	(2.55)
Post-burn assessment								
Tussock residue*	13 288.1	6245.4	65.10	4.90	70.49	8.44	5.51	7.59
Non-tussock residue	11 368.2	3928.5	78.77	7.31	62.57	24.93	5.15	9.09
Total above-ground	24 656.3	10 173.9	143.87	12.22	115.39	33.36	17.44	16.68
(SEM)	(2428.2)	(1158.0)	(14.56)	(1.26)	(9.40)	(4.58)	(0.99)	(1.70)
Losses due to fire	13 608.5	6807.4	104.63	8.11	52.82	16.77	9.07	12.49
(SEM)	(2249.5)	(637.8)	(19.54)	(2.03)	(17.92)	(6.92)	(1.32)	(2.24)
%	35.6	40.1	42.1	39.9	31.4	33.5	34.2	42.8
SUMMER BURNS								
Pre-burn assessment								
Grasses, rushes and sedges								
Chionochloa rigida	8641.1	4018.1	66.05	8.81	58.81	10.60	6.89	10.20
Other	684.4	284.8	5.70	0.47	3.35	1.19	0.75	0.91
Forbs	73.1	33.3	0.92	0.13	1.05	0.40	0.24	0.12
Shrubs	451.3	217.1	4.19	0.48	3.12	1.52	1.01	0.46
Lower plants	2233.6	920.5	21.72	2.67	11.43	7.38	5.00	3.46
Litter	32 775.7	14 926.3	182.09	20.59	136.70	36.82	27.68	37.54
Total above-ground	44 823.2	20 400.0	280.67	33.15	214.45	57.92	41.58	52.70
(SEM)	(6523.8)	(3294.3)	(23.50)	(3.45)	(30.88)	(4.66)	(3.54)	(5.40)
Post-burn assessment								
Tussock residue*	9786.3	4619.2	37.89	2.88	25.01	4.77	4.48	5.70
Non-tussock residue	6967.5	3048.3	57.40	5.04	23.27	15.73	11.16	9.20
Total above-ground	16 753.9	7667.5	95.30	7.92	48.29	20.50	15.65	14.89
(SEM)	(1389.5)	(645.7)	(6.40)	(0.56)	(3.99)	(1.84)	(1.19)	(1.10)
Losses due to fire	28 069.3	12 732.5	185.38	25.23	166.16	37.42	25.93	37.81
(SEM)	(5560.0)	(2839.9)	(17.97)	(2.91)	(27.59)	(3.17)	(2.65)	(4.37)
%	62.6	62.4	66.0	76.1	77.5	64.6	62.4	71.7

* Mostly tussock bases.

TABLE 3. BIOMASS, CARBON AND NUTRIENT LOSSES (kg/ha) RESULTING FROM SPRING AND SUMMER BURNS AT DEEP STREAM. VALUES ARE THE MEAN OF FIVE SAMPLES PER PLOT AND THREE PLOTS PER TREATMENT.

	BIOMASS	C	N	P	K	Ca	Mg	S
SPRING BURNS								
Pre-burn assessment								
Grasses, rushes and sedges								
Chionochloa rigida	2722.2	1287.6	18.22	3.16	19.88	2.76	2.97	2.86
Other	1774.2	817.9	16.47	1.67	14.85	7.10	3.46	2.45
Forbs	1162.3	483.5	13.49	1.27	9.71	10.41	2.56	1.49
Shrubs	3493.0	1725.5	20.68	2.13	10.95	19.05	5.46	2.89
Lower plants	3590.9	1572.8	29.91	3.34	18.02	15.42	4.44	3.91
Litter	21 117.8	7829.7	106.78	10.70	105.12	77.93	22.40	14.87
Total above-ground	33 860.4	13 717.1	205.55	22.27	178.54	132.66	41.28	28.46
(SEM)	(1151.4)	(476.1)	(5.18)	(0.70)	(8.14)	(7.18)	(0.58)	(0.73)
Post-burn assessment								
Tussock residue*	4364.9	2024.0	22.44	2.56	18.20	7.94	6.25	3.40
Non-tussock residue	3957.9	1471.8	30.69	3.58	25.57	23.47	6.12	3.61
Total above-ground	8322.8	3495.8	53.13	6.14	43.77	31.41	12.37	7.01
(SEM)	(1757.6)	(580.7)	(17.07)	(2.17)	(13.76)	(13.75)	(2.89)	(1.92)
Losses due to fire	25 537.7	10 221.3	152.42	16.13	134.77	101.25	28.91	21.45
(SEM)	(1898.1)	(494.3)	(17.60)	(2.21)	(20.55)	(19.03)	(3.04)	(1.75)
%	75.4	74.5	74.2	72.4	75.5	76.3	70.0	75.4
SUMMER BURNS								
Pre-burn assessment								
Grasses, rushes & sedges								
Chionochloa rigida	2909.5	1379.1	18.28	2.77	25.86	4.32	3.23	2.26
Other	760.7	346.9	5.53	0.47	2.57	2.07	0.81	0.76
Forbs	997.2	479.7	4.46	0.66	14.47	7.64	1.72	0.78
Shrubs	4182.8	2129.0	26.64	2.43	11.40	29.31	6.60	3.51
Lower plants	2764.2	1326.8	21.81	2.36	16.04	8.37	2.95	2.53
Litter	23 573.5	9414.7	121.52	14.03	106.72	62.17	14.52	17.68
Total above-ground	35 187.9	15 076.2	198.24	22.74	177.07	113.88	29.83	27.51
(SEM)	(1333.1)	(687.5)	(6.89)	(0.76)	(8.79)	(9.29)	(1.58)	(1.02)
Post-burn assessment								
Tussock residue*	5902.4	2721.0	30.78	3.46	30.89	9.32	4.54	5.27
Non-tussock residue	3230.8	1099.9	21.66	2.87	20.04	17.36	3.45	3.21
Total above-ground	9133.2	3820.9	52.44	6.33	56.93	26.68	7.99	8.48
(SEM)	(87.0)	(77.0)	(0.22)	(0.08)	(0.78)	(1.25)	(0.08)	(0.06)
Losses due to fire	26 054.7	11 255.3	145.80	16.41	120.14	87.20	21.84	19.03
(SEM)	(1403.1)	(723.6)	(6.87)	(0.77)	(8.41)	(8.04)	(1.50)	(1.07)
%	74.0	74.7	73.5	72.2	67.8	76.6	73.2	69.2

* Mostly tussock bases.

TABLE 4. MOISTURE CONTENT (% DRY WEIGHT) OF VEGETATION AND SOIL SAMPLES COLLECTED IMMEDIATELY BEFORE THE EXPERIMENTAL BURNS. FIGURES ARE THE MEAN (± SEM) OF FIVE SAMPLES PER PLOT AND THREE PLOTS PER TREATMENT.

	DEEP STREAM		MT BENGER	
	SPRING	SUMMER	SPRING	SUMMER
Surface litter	9.2 ± 0.7	8.5 ± 0.4	8.1 ± 0.8	16.4 ± 1.8
Tussock base litter	111.5 ± 16.0	100.5 ± 11.6	201.4 ± 19.0	240.3 ± 3.0
Live tussock tillers	115.8 ± 1.2	119.5 ± 0.3	107.5 ± 1.6	109.5 ± 1.6
Soil (0–5 cm)	57.9 ± 5.0	54.2 ± 1.1	99.1 ± 6.5	114.2 ± 14.8
Soil (5–10 cm)	52.7 ± 1.7	50.1 ± 1.5	66.4 ± 1.6	77.4 ± 5.8

TABLE 5. NUTRIENT RETURN (kg/ha) FROM ASH DEPOSITED BY THE EXPERIMENTAL BURNS. FIGURES ARE THE MEAN (± SEM) OF FIVE SAMPLES PER PLOT AND THREE PLOTS PER TREATMENT.

	DEEP STREAM		MT BENGER	
	SPRING	SUMMER	SPRING	SUMMER
Nitrogen	0.06 ± 0.01	0.09 ± 0.01	0.03 ± 0.01	0.04 ± 0.01
Phosphorus	0.14 ± 0.02	0.12 ± 0.01	0.07 ± 0.03	0.09 ± 0.02
Potassium	0.81 ± 0.10	0.65 ± 0.05	0.34 ± 0.15	0.41 ± 0.08
Calcium	0.75 ± 0.14	0.57 ± 0.03	0.19 ± 0.10	0.22 ± 0.04
Magnesium	0.19 ± 0.03	0.13 ± 0.01	0.10 ± 0.05	0.11 ± 0.02
Sulphur	0.02 ± 0.00	0.04 ± 0.00	0.01 ± 0.00	0.01 ± 0.00

Figure 10. Tall-tussock grassland at Deep Stream, 6 weeks after a summer burn. Note the rapid recovery of the spaniard (*Aciphylla aurea*), and the high proportion of exposed soil.

Relationships between biomass loss and measurements of plant and soil moisture were complicated by the fact that the summer burns at Mt Benger occurred during a tussock mast flowering season, which substantially increased the above-ground tussock biomass relative to that present at the time of the spring burns (Table 2). When these data were removed, there was a highly significant relationship between biomass loss and soil moisture$_{(0\text{–}5\ \text{cm})}$ (slope = –0.856, SE_{slope} = 0.144, t = 5.95, df = 7, P < 0.001), and a significant relationship between biomass loss and the moisture content of the tussock bases (slope = –0.351, SE_{slope} = 0.071, t = 4.94, df = 7, P = 0.002) (Fig. 11). Using Spearman rank correlation coefficients, the Fire Weather Index System's FFMC component was the best predictor of biomass loss (r_s = 0.75, n = 9, P = 0.023) followed equally by DMC, ISI, BUI and FWI (r_s = 0.70, n = 9, P = 0.042), and DC (r_s = 0.00, n = 9, P = 0.893).

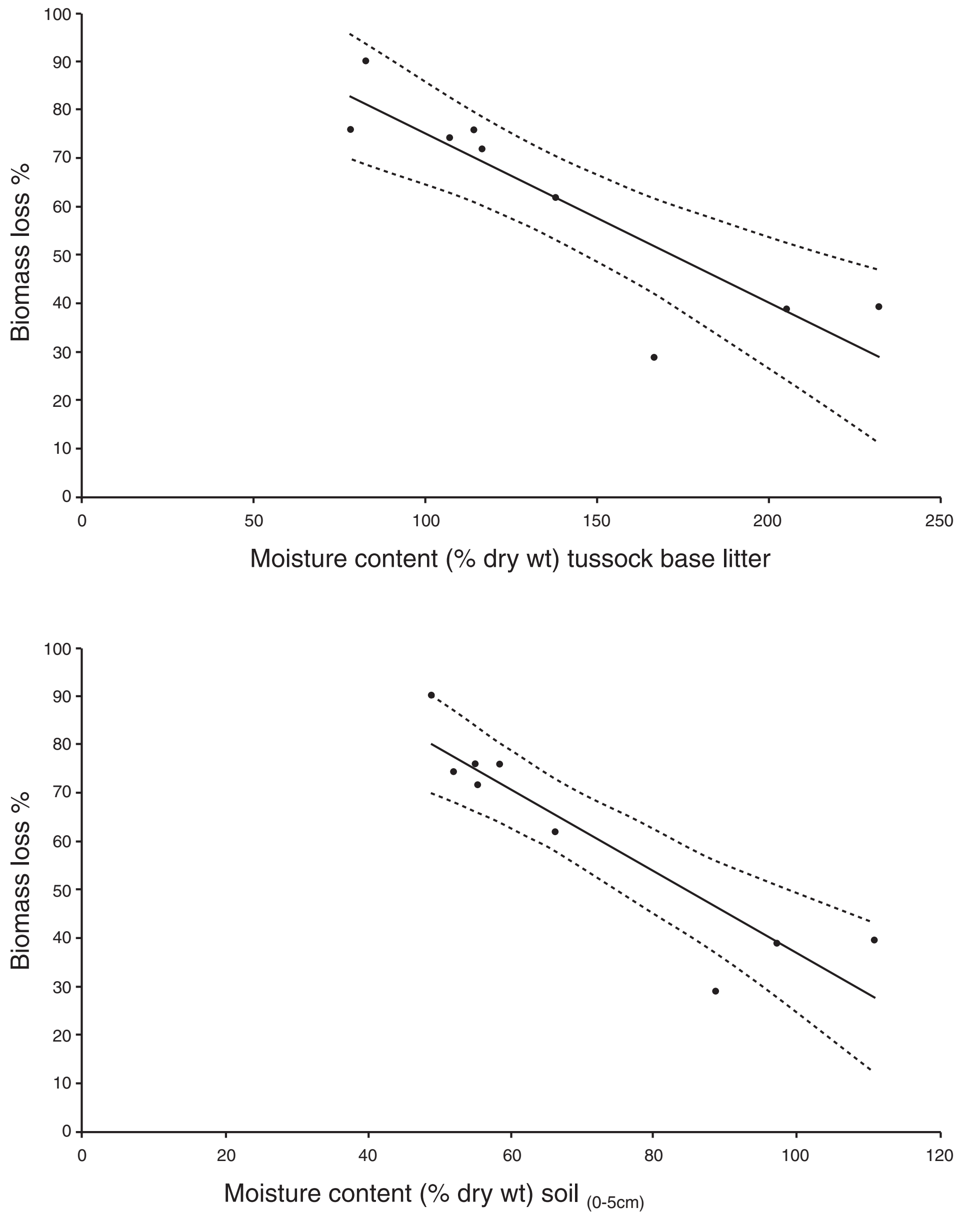


Figure 11. Relationship between above-ground biomass loss and measurements of plant and soil moisture.

4.4 TILLER AND TUSSOCK MORTALITY

Spring burns killed an average of 35% of tussock tillers at Mt Benger (Table 6), but did not cause the death of individual tussocks (Table 7). This is in contrast to the situation at Deep Stream, where spring burns were responsible for the death of nearly 80% of tussock tillers and 21–70% of tussocks. Summer burns killed an average of 83% of tillers at Deep Stream and 87.4% at Mt Benger. They also killed 50.7% of tussocks on the Deep Stream plots, but were not directly responsible for the death of tussocks at Mt Benger. In summer-burned plots, tiller and tussock mortality was exacerbated by the failure of many resprouted tillers to survive the sub-zero winter temperatures. This meant that overall tiller mortality on summer-burn plots rose to 91.6% at Mt Benger and 92.7% at Deep Stream, when the post-burn tiller counts were repeated the following spring. This, in turn, increased tussock mortality from 50.7% to 65.3% at Deep Stream, and from 0% to 27.0% at Mt Benger.

4.5 TUSSOCK FLOWERING AND SEEDLING ESTABLISHMENT

At both sites, unburned tussocks flowered heavily (masted) in 1998–99 and 2005–06, and produced a smaller number of inflorescences in 1999–00 and 2002–03 (Fig. 12). As expected, spring-burned tussocks at both sites flowered during the season after fire. At Deep Stream, this coincided with a natural flowering event, but at Mt Benger it was clearly fire-related. Spring-burned tussocks at Mt Benger also flowered during the second and fifth seasons after fire (2002–03 and 2005–06), both of which were natural flowering seasons.

TABLE 6. TILLER MORTALITY (%) IN *Chionochloa rigida* TUSSOCKS AFTER SPRING AND SUMMER FIRES AT DEEP STREAM AND MT BENGER. FIGURES ARE THE MEAN (± SEM) OF TEN TUSSOCKS PER PLOT AND THREE PLOTS PER TREATMENT.

	SPRING FIRES	SUMMER FIRES	
	FIRE	FIRE	FIRE + WINTER FROSTS
Deep Stream	77.9 ± 5.9	83.0 ± 2.7	92.7 ± 2.7
Mt Benger	35.1 ± 3.1	87.4 ± 2.5	91.6 ± 2.1

TABLE 7. TUSSOCK MORTALITY (%) AFTER SPRING AND SUMMER FIRES AT DEEP STREAM AND MT BENGER. FIGURES ARE THE MEAN (± SEM) OF 50 TUSSOCKS PER PLOT AND THREE PLOTS PER TREATMENT.

	SPRING FIRES		SUMMER FIRES	
	AREA OF GOOD SURVIVAL	AREA OF POOR SURVIVAL	FIRE	FIRE + WINTER FROSTS
Deep Stream	21.3 ± 2.4	70.0 ± 5.3	50.7 ± 1.3	65.3 ± 5.5
Mt Benger	0	0	0	27.0 ± 4.6

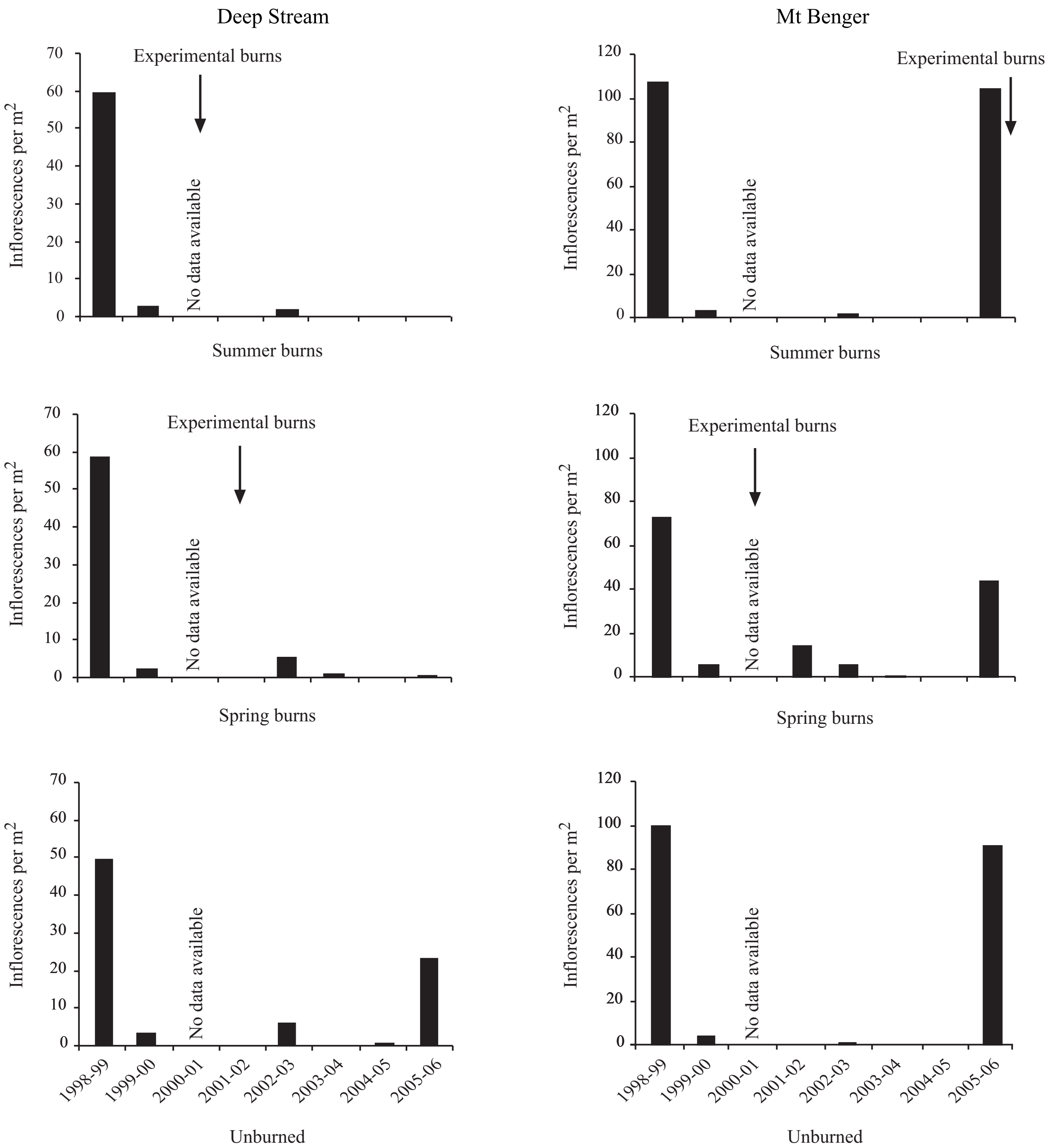


Figure 12. Effect of spring and summer fires on the flowering intensity of *Chionochloa rigida* tussocks at Deep Stream (left column) and Mt Benger (right column). Values are the mean of ten samples per plot and three plots per treatment.

Their flowering intensity 5 years after fire was approximately half that of the unburned plants. At Deep Stream, little or no flowering was observed during the 2005–06 mast year on spring- or summer-burned plots; this was largely due to the dramatic decline in tiller density as a result of the fires. The consequences of fire for autumn-burned tussocks at Mt Benger, where the experimental fires were delayed until March 2006, are yet to be determined.

Over the period of the study, unburned plots at Deep Stream and Mt Benger averaged 5.5 ± 0.6 and 3.9 ± 0.5 tussock seedlings/m^2, respectively (Fig 13).

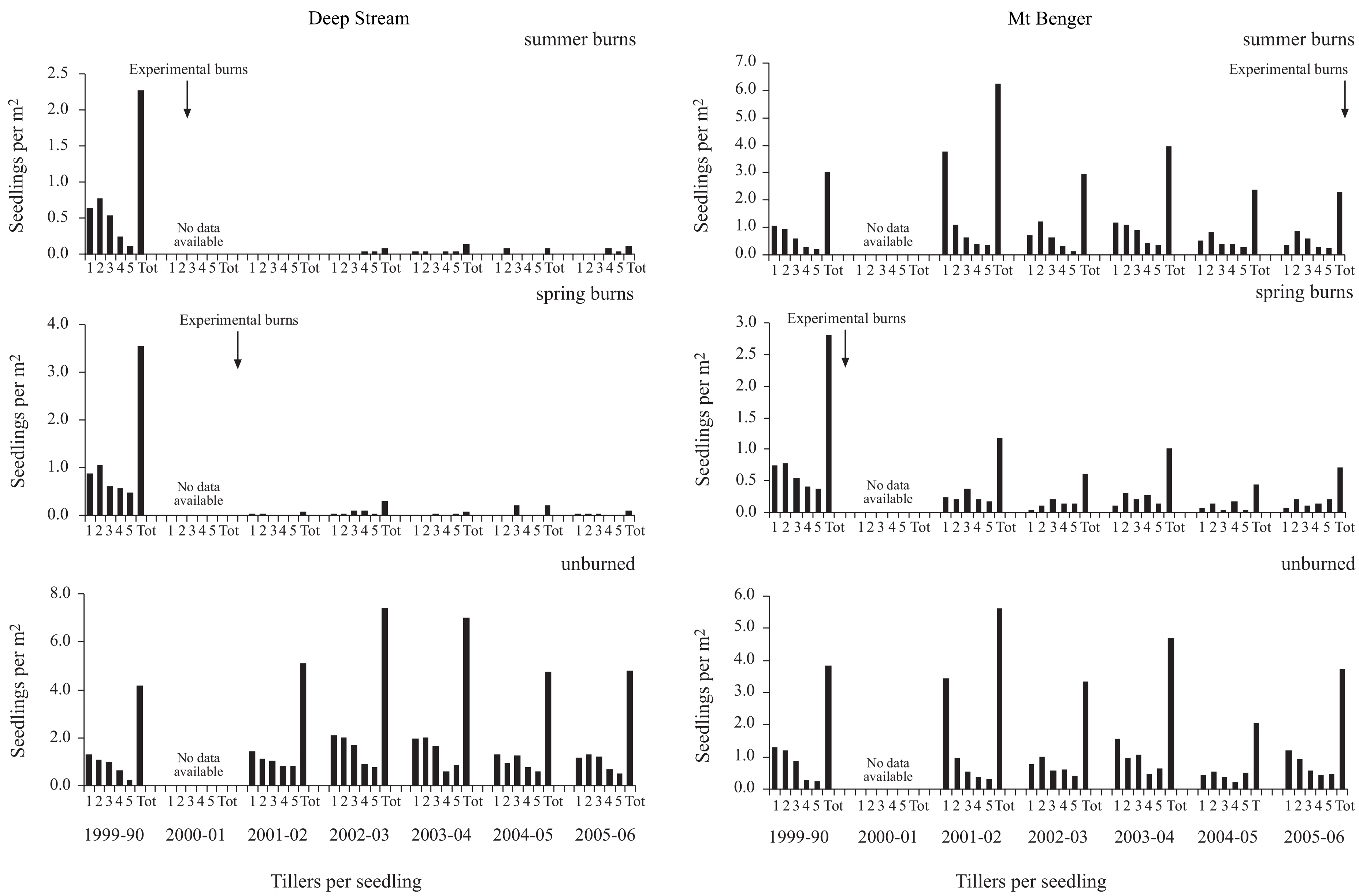


Figure 13. Effect of spring and summer fires on the seedling density of *Chionochloa rigida* tussocks at Deep Stream (left column) and Mt Benger (right column). Labels on the *x*-axis denote the density of individual (1–5) tiller cohorts and total (Tot) seedling density. Values are the mean of ten samples per plot and three plots per treatment.

At Mt Benger, spring burning markedly reduced seedling densities, despite the damp conditions, and 5 years later, there was little sign of a return to pre-burn levels. At Deep Stream, the drier spring and summer burns had an even harsher impact, reducing densities of tussock seedlings by 97.3% and 98.7%, respectively, over the same period.

4.6 CHANGES TO THE STRUCTURE AND COMPOSITION OF THE GRASSLANDS

At Mt Benger, the combination of spring burning under damp conditions and excluding stock from the post-fire grasslands did not substantially alter the structure and composition of the vegetation. Six months after the spring burns, all of the plots showed vigorous regrowth of both tussock and inter-tussock vegetation, and 5 years later there was an intact tall-tussock grassland (Fig. 14), albeit of lower stature than that of the adjacent unburned stands. In contrast, the summer-burned plots at Mt Benger are still in the early stages of post-fire recovery (Fig. 14). High levels of tiller mortality make it unlikely that these grasslands will return to complete tussock cover in the near future, even in the absence of grazing by stock. As with the spring burns at this site, the summer fires had little effect on the ground-cover layer

At Deep Stream, where both the spring and summer burns killed a considerable percentage of the existing tussocks and removed much of the ground-cover layer (Fig. 10), the outlook is very different. Within 12 months of the burns, browntop (*Agrostis capillaris*), which is present throughout the tussock grasslands at Deep Stream, had formed an almost unbroken sward over all of the burned areas; although existing plants of the spaniard *Aciphylla aurea* resprouted vigorously after the burns, these failed to survive. Five years later, browntop remains the

Figure 14. Tussock grassland at Mt Benger, 1 year after a summer burn (foreground) and 5 years after a spring burn (mid-ground). This site has not been grazed since the burns.

dominant cover on all of the burned plots, the surviving tussocks are beginning to re-exert their presence (Fig. 15), and spaniard seedlings are once again common throughout the grasslands.

Figure 15. Spring- (foreground) and summer- (background) burned plots at Deep Stream 5 years after fire, with scattered *Chionochloa rigida* tussocks amidst the browntop (*Agrostis capillaris*).

5. Discussion and conclusions

Studies of fire impacts in New Zealand indigenous grasslands have generally been initiated in response to past fire events (e.g. Wilson 1976; Espie 2002) and have used a space-for-time approach to interpret post-fire responses (e.g. Gitay et al. 1992; Gitay & Wilson 1995). Where experimental treatments have been imposed, these have generally not been at a scale that allowed fire behaviour to be determined, or that replicated the conditions encountered during pastoral burns or wildfire events (e.g. O'Connor & Powell 1963; Payton et al. 1986). This failure to characterise the severity of fire events and to adequately simulate 'real-world' situations has hampered our ability to interpret the short-term response of the grasslands to fire and to predict longer term trends (e.g. Allen & Partridge 1988; Gitay et al. 1991; Calder et al. 1992). The present study, which we believe is the first to incorporate fire behaviour into an ecological study of a New Zealand tall-tussock grassland, sought to rectify these problems by including the measurement of fire parameters in the experimental design and by using larger-scale (1-ha) plots that more closely approximate pastoral burns or wildfire events (Payton & Pearce 2001).

5.1 EXPERIMENTAL DESIGN

Our study was designed to test the consequences of early- and late-season fires for the long-term sustainability of tall-tussock grassland communities. The experimental design set up a two-way comparison: early- v. late-season fires and damp v. dry burns. At the outset, the expectation was that the damp burns would occur in spring and the dry burns later in the season. As it turned out, however, conditions for both the early- and late-season burns at the more drought-prone Deep Stream site were relatively dry, while at Mt Benger both the early- and late-season burns took place under damper conditions. Thus, despite failing to achieve damp early-season burns at Deep Stream and dry late-season burns at Mt Benger, we were still able to preserve the original two-way comparison, albeit not in the manner originally envisaged.

This raises the question of whether the two sites, which represent opposite ends (higher altitude, damper climate v. lower altitude, drier climate) of the tall-tussock grassland continuum, can be considered as replicates for the purposes of examining fire impacts. The only conclusive way of answering this question would be to repeat the experiment and reverse the treatments (i.e. early- and late-season fires under dry conditions at Mt Benger, and vice versa); however, given the financial and administrative challenges that this would pose, such an experiment is unlikely to happen. What we can say is that, where it is possible to make direct comparisons between the sites, the results are not inconsistent. Examples include the relationship between plant and soil moisture and biomass loss, the post-fire flowering response in the tall-tussocks, and the depression of tussock seedling density.

The other point that needs to be remembered when considering the applicability of our results to 'real-world' situations is that, for reasons of safety, none of the burns were carried out during periods of high fire risk, which regularly occur throughout the eastern South Island high country during late summer and autumn. The data, therefore, do not represent the full range of conditions over which fires in tall-tussock grasslands might be expected to occur.

5.2 BIOMASS, CARBON AND NUTRIENT LOSSES

Detailed breakdowns of the biomass and nutrient composition of natural plant communities are rare, probably because of the time-consuming, and therefore costly, nature of producing them. They are, however, necessary if we are to understand the type and magnitude of the losses sustained as a result of fire, and the shifts in resource allocation in the post-fire vegetation.

In the present study, biomass increased on all plots between the initial assessment in 1997–98 and the assessment carried out within 12 months of the experimental burns, which suggests that both sites were still recovering from past fire events and/or a lengthy history of mammalian grazing. Biomass loss due to fire was least when the grasslands were burned under damp spring conditions, which is the practice used for pastoral management burns (O'Connor 1982), and greatest when soil and vegetation conditions were driest. All of the fires burned the bulk of the loosely compacted plant material. When conditions were damp, as was the case for both the early- and late-season fires at Mt Benger, the tussock bases and ground-cover vegetation (which together constitute a considerable proportion of the above-ground biomass) remained largely unburned. As the grasslands dried out, the fires burned a progressively greater proportion of this more tightly compacted material. Under the driest conditions we encountered (the late-season burns at Deep Stream), most of the ground-cover vegetation was burned and the tussock bases were reduced to stumps no more than 8–10-cm high. The late-season fires at Mt Benger consumed a higher percentage of biomass than was expected due to a spike in the quantity of loosely compacted plant material, which was brought about by a mast flowering season for the tussocks. The best predictors of biomass loss were the moisture content of the top 5 cm of soil and the moisture content of litter at the base of the tussock. For the fire weather indices, those that were more responsive to short-term climatic fluctuations, and which therefore more closely reflected the flammability of the grassland at the time of the burn, were better predictors of biomass loss than those that reflected longer-term trends. Thus, FFMC > DMC, ISI, BUI and FWI, which are > DC (see Appendix 1 for definitions).

Four previous studies have quantified total (above- and below-ground) plant biomass for tall-tussock grasslands, and three of these have included estimates of the nutrient pools (Williams 1977; Williams et al. 1977; Meurk 1978; Evans 1980; O'Connor et al. 1999). However, none presented a breakdown of the non-tussock component of the grassland, although Evans (1980) alluded to the fact that these data were obtained. Results from these studies showed considerable variability in the size of the biomass (39–87 t/ha) and nutrient pools, and no consistent differences between tussock species or between major biomass compartments (live v. dead; above- v. below-ground) (O'Connor et al. 1999). Biomass estimates for *Chionochloa rigida* grasslands, all of which had remained unburned for over a decade, ranged from 62 to 87 t/ha, which is higher than the values reported in the present study. The reason for this is not immediately obvious, but may result from differences in methodology (calculations based on tiller density and weight v. direct harvest). All grasslands showed a high percentage of dead organic matter in the above-ground biomass, a feature which acts to conserve nutrients in an unburned environment but greatly increases their vulnerability to loss by fire (Scott 1999).

There is a widely held view that the repeated use of fire and the limited application of fertiliser in managing indigenous tussock grasslands for livestock production have progressively depleted the biomass and nutrient capital of these ecosystems (Basher et al. 1990; McKendry & O'Connor 1990; Working Party on Sustainable Land Management 1994). It is therefore somewhat surprising to find that this study appears to be the first to have directly measured biomass, carbon and nutrient losses resulting from fire in tall-tussock grasslands.

In our study, carbon and nutrient losses were proportional to biomass losses, indicating that fire temperatures were sufficiently high to volatilise key elements such as nitrogen, phosphorus, potassium and sulphur, which are known to be limiting for plant growth in high-country environments (O'Connor & Harris 1992). We found no evidence of substantial nutrient input from ash deposited by the fires, which confirms earlier findings that nutrient return from tall-tussock grassland fires is minimal and would not be expected to provide a boost to plant growth in the post-fire environment (O'Connor & Powell 1963; Mark 1965a).

5.3 TILLER AND TUSSOCK MORTALITY

In the present study, spring burns under damp conditions killed around a third of tussock tillers, but did not cause the death of tussocks, and clearly had the least disruptive effect of any fire regime on the structure and composition of the grasslands. Where grasslands were burned under drier conditions or later in the growing season, tiller mortality increased dramatically and there was a greater risk of tussocks being killed. Two factors appear to be important in determining the vulnerability of tillers and therefore tussocks to fire: the timing of the burns and the dryness of the grasslands.

Burns in late winter or early spring, before the tussock tillers break their winter dormancy, allow the reallocation of nutrients (principally N and K) from the roots to the new leaf tissue (Payton et al. 1986). Once growth is underway, this option would appear to be reduced or precluded, which we suggest may reduce the chance of tiller survival. The likelihood that tillers will survive also depends on the ability of the tightly compacted plant material at the base of the tussock to shield the apical meristem from the short, sharp burst of heat generated by the fire. Damp tussock bases are little affected by fire, and we suggest they act as an effective heat shield for the majority of the tiller meristems. As the grasslands dry out and progressively greater proportions of the tussock bases are burned, the effectiveness of this heat shield can be expected to diminish, resulting in a greater proportion of the tillers failing to survive. The other damaging influence associated with the timing of the burns is frost. Tillers that resprouted after late-season fires were unable to sufficiently harden off their new foliage before the first autumn frosts, and failed to recover the following season. Thus, although the late-season fires at Mt Benger that occurred when the grasslands were damp did not kill tussocks, the frosts that followed did.

Conventional wisdom is that while fires kill tussock tillers, the combined effects of fire and grazing are required to kill tussocks (O'Connor & Powell 1963). There are, however, few data to support this contention. The only record we have been able to find of the fire-related death of tussock tillers is an illustration in Mark (1965b) showing increased tiller mortality in autumn-burned *Chionochloa rigida* tussocks on Coronet Peak compared with their spring-burned counterparts. Evidence for fire causing the death of tussocks is similarly scarce, and is at times contradictory. O'Connor & Powell (1963: 364) cited anecdotal evidence of 'the fatal effects of extremely severe fires such as occur in midsummer' from Barker (1953) and Raeside (1960), while in the same paper the authors reported their surprise that no tussocks died after a severe fire in early spring in which 'snow tussocks were burnt evenly down to butts of about 2 inches in height' (O'Connor & Powell 1963: 357). Fire during a period of severe drought is reported to have killed *C. rigida* tussocks in the Cardrona Valley, Central Otago (C.D. Meurk, pers. obs., in Basher et al. 1990). Our study showed that both early- and late-season fires can kill tussocks, and that conditions do not have to be extremely dry for this to happen. Our data do not allow us to reconcile the apparent difference between this result and that of O'Connor & Powell (1963).

5.4 SEEDLING ESTABLISHMENT

The recovery of tall-tussock grasslands after fire depends on the ability of the surviving tussocks to regain their former dominance, and of new individuals to establish themselves in the post-fire environment. The latter is especially important where fire has severely depleted tiller populations and killed tussocks. Our study showed reduced numbers of seedlings in the post-fire grasslands. As with other parameters, seedling densities were least affected when grasslands were burned under damp spring conditions, and dramatically reduced when conditions were drier. The other interesting feature of our data is the lack of a move back to pre-burn seedling densities 4–5 years after fire, which does not augur well for the recovery of the grasslands. The reason for the continued low densities of tussock seedlings in the post-burn grasslands is not clear. It may result from the destruction of existing seed banks during the burns, from reduced seed inputs (lack of a mast year) or from changes to the competitive environment after the fire. Which one or combination of these factors is responsible will become apparent only from analysis of a longer-term dataset.

Several studies have investigated regeneration patterns in unburned tall-tussock grasslands (Rose & Platt 1990, 1992; Lee et al. 1993), but only one has examined seedling recruitment and survival in a post-fire environment (Mark 1965b). In this study, Mark (1965a) recorded abundant *Chionochloa rigida* seedlings 8 months after a spring fire on the Old Man Range in Central Otago, and followed their fate under a grazed and an ungrazed treatment for a period of 3 years. The reason for this different response is unclear, but is likely to involve differences in microsites (Rose & Platt 1990) and the severity of the burns.

5.5 GENERAL APPLICABILITY OF RESULTS

In this study, we used intact swards of *Chionochloa rigida* grassland that had remained unburned for at least a decade, and had been retired from grazing, to compare and contrast the effects of early- and late-season fires under damp and dry conditions. Of the four treatments, only the early-season burns carried out under damp conditions appear to have had little lasting effect on the structure of the grasslands. Burning later in the season or when conditions were drier dramatically increased tiller mortality, killed tussocks and resulted in a loss of tall-tussock dominance in the post-fire grassland, at least over the short to medium term. The fact that the treatments produced such different outcomes serves to emphasise the need for careful assessment of the environmental conditions when planning tussock burns, and the importance of considering fire regimes when seeking to understand the trajectory of the post-fire grasslands.

The deterioration of tall-tussock grasslands throughout the South Island high country and their progressive replacement by short-tussock and mat-dominated plant communities is well documented (e.g. Connor 1964, 1965; Mark 1993), and there is ample evidence to implicate the combined influence of fire and grazing by farmed or feral animals (e.g. O'Connor 1982; Mark 1994) in this process. What has not been so clearly articulated is that fire alone can cause the demise of tall-tussocks and their replacement by species better able to establish in the post-fire environment.

6. Management recommendations

The authors make the following recommendations based on the key findings of this study:

- Fires in late winter or early spring, when soil conditions are damp, pose little threat to the long-term survival of tall-tussock grasslands. Because post-fire grasslands attract heavy grazing pressure, priority should be given to minimising the presence of farmed or feral animals for 1 or preferably 2 years after a burn, to ensure that the recovery of the post-fire grassland is not impeded.
- Fires later in the season, or when soil conditions are dry, have the potential to cause significant damage to tall-tussock grassland communities. Minimising their extent should be a priority wherever tussock cover is to be retained.
- The current experiment has the potential to yield a wealth of valuable information on the rates of change in unburned and ungrazed grasslands, as well as those that are recovering from fire. Key to this will be the maintenance of the perimeter fences and the exclosure plots. Provision should also be made for ongoing monitoring and dissemination of the results.
- The current experiment does not consider the consequences of continued grazing, with or without fire, on the long-term sustainability of tall-tussock grassland ecosystems. This would be the next logical step to take.

7. Acknowledgements

A project of this magnitude and complexity would not be possible without the assistance of a wide range of organisations and individuals. We greatly appreciate the support of past and present staff from the Department of Conservation (Otago Conservancy), particularly Brin Barron, Jeff Connell, John Pearce, Tony Perrett, Marcus Simons, Mike Tubbs and Dave White. Nigel Harwood (formerly Dunedin City Council) sought and gained permission for us to use Deep Stream as one of our experimental sites, and Alan Michelle and John Deans allowed us to use land at Mt Benger. Ross Hamilton (formerly Dunedin City Council) and Bob McNeil (Central Otago District Council) provided permits for the burns at Deep Stream and Mt Benger, respectively. We also express our thanks to those who shelved other priorities to help ensure the experimental burns stayed within their allotted bounds, and to the scientific and technical staff from Landcare Research, Scion, AgResearch, SouthTech and the Department of Conservation who helped harvest, sort, dry, weigh and analyse the biomass samples, and collect fire behaviour data. Nutrient analyses were carried out at the Landcare Research analytical laboratory in Palmerston North. James Barringer supplied the climate profiles for the experimental sites; Guy Forrester did the statistical analyses; Anouk Wanrooy and James Barringer drew the figures; Grant Hunter, Bill Lee, Alan Mark, Kevin O'Connor and three anonymous referees reviewed the manuscript; Christine Bezar and Amanda Todd improved its readability; and Wendy Weller completed the final word processing. Funding for the project was provided by the Foundation for Research, Science and Technology, the Department of Conservation, the National Rural Fire Authority, and the Hellaby Indigenous Grasslands Research Trust.

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Appendix 1

NEW ZEALAND FIRE WEATHER INDEX SYSTEM

The Fire Weather Index (FWI) System is the core component of the New Zealand Fire Danger Rating System. It provides the basis for a uniform method of rating fire danger throughout New Zealand (Anderson 2005). It consists of three fuel moisture codes and three fire behaviour indices that are derived from daily observations of weather conditions taken at 1200 hours NZST.

Fuel moisture codes

The following codes are ordered according to length of the response (shorter to longer term).

Fine Fuel Moisture Code (FFMC) Uses temperature, relative humidity, wind speed and daily rainfall to provide a rating of the moisture content of litter and other cured fine fuels. It is an indicator of flammability and hence the relative ease of ignition of fine dead fuels.

Duff Moisture Code (DMC) Rates the moisture content of loosely compacted soil organic layers, based on temperature, relative humidity and daily rainfall. For tussock grasslands, it provides a measure of the dryness of ground-layer vegetation (mosses, forbs, etc.) and decaying plant material.

Drought Code (DC) Uses temperature and daily rainfall to provide a rating of the moisture content of deep, compacted organic soil layers. It is a good indicator of general soil dryness and, for tussock grasslands, and would be expected to be a useful indicator of the dryness of the base of tussock clumps and hence overall tussock fuel consumption.

Fire behaviour indices

Initial Spread Index (ISI) Provides a rating of the expected rate of fire spread, and is determined using Fine Fuel Moisture Code (FFMC) and wind speed data.

Buildup Index (BUI) Combines the Duff Moisture Code (DMC) and Drought Code (DC) to provide a rating of the total amount of fuel available for combustion, and would be expected to correlate with the amount of fuel that is actually consumed by the fires.

Fire Weather Index (FWI) Uses ISI and BUI to provide a rating of potential fire intensity, and would be expected to be a useful indicator of flame length. It also serves as a general index of fire danger.

Appendix 2

PRE-BURN ASSESSMENT OF BIOMASS, CARBON AND NUTRIENT POOLS (kg/ha) AT THE DEEP STREAM STUDY SITE (DECEMBER 1997–FEBRUARY 1998)

Values are the mean of five samples per plot and nine plots per site.

	BIOMASS	C	N	P	K	Ca	Mg	S
Grasses, rushes and sedges								
Adventive grasses[a]	1338.1	601.1	10.76	1.13	6.57	1.62	1.27	1.54
Chionochloa rigida	3771.0	1793.2	23.90	3.36	31.11	2.04	2.52	4.25
Poa colensoi	123.2	54.6	1.05	0.13	0.59	0.11	0.08	0.15
Rushes and sedges	12.4	5.4	0.12	0.01	0.06	0.01	0.01	0.01
Forbs								
Aciphylla aurea	272.7	127.6	1.54	0.27	5.21	1.96	0.38	0.23
Celmisia gracilenta	108.4	49.9	1.23	0.13	1.08	0.57	0.24	0.14
Hieracium spp.[b]	7.5	3.3	0.07	0.01	0.14	0.05	0.02	0.01
Oreobolus pectinatus	77.2	34.5	0.60	0.06	0.33	0.08	0.09	0.07
Raoulia subsericea	0.8	0.4	0.01	0.00	0.01	0.01	0.00	0.00
Minor forbs	136.6	60.4	1.64	0.18	1.83	0.96	0.43	0.20
Shrubs								
Coprosma cheesemanii	30.1	14.4	0.29	0.03	0.22	0.19	0.10	0.02
Acrothamnus colensoi	419.8	210.1	2.60	0.31	1.75	2.14	0.49	0.26
Leucopogon fraseri	36.6	18.2	0.31	0.03	0.08	0.30	0.06	0.03
Muehlenbeckia axillaris	31.4	16.3	0.20	0.02	0.08	0.19	0.04	0.03
Pentachondra pumila	871.7	450.9	5.67	0.47	2.28	5.19	1.21	0.61
Pernettya macrostigma	2194.2	1086.2	15.36	1.65	9.38	9.23	3.19	2.11
Minor shrubs	1.3	0.7	0.01	0.00	0.01	0.01	0.00	0.00
Lower plants								
Lycopodium spp.[c]	373.5	177.7	3.16	0.36	1.75	0.29	0.35	0.30
Coarse mosses[d]	43.1	19.4	0.30	0.03	0.20	0.08	0.07	0.03
Fine mosses	946.7	430.2	7.84	0.85	3.97	2.56	1.41	0.79
Lichen	104.4	44.9	0.55	0.06	0.30	0.09	0.08	0.05
Litter								
Aciphylla aurea	488.0	239.1	1.75	0.16	1.22	3.02	0.56	0.33
Chionochloa rigida	8470.3	4092.6	28.21	2.48	8.20	3.36	3.17	6.51
Other	7002.5	2835.8	60.57	5.34	35.03	9.77	8.17	6.85
Total above-ground	26861.6	12367.2	167.7	17.1	111.4	43.8	23.9	24.5
(SEM)	(1200.1)	(560.3)	(7.2)	(0.9)	(5.3)	(2.3)	(1.1)	(1.1)
Roots								
Aciphylla aurea	45.5	19.8	0.26	0.08	0.72	0.17	0.13	0.03
Beneath tussocks	8242.0	3699.3	50.90	4.23	16.17	1.54	1.97	7.88
Between tussocks	4644.7	2128.3	26.13	2.57	8.51	1.17	1.27	4.40
Total below-ground	12932.1	5847.4	77.3	6.9	25.4	2.9	3.4	12.3
(SEM)	(817.3)	(367.7)	(5.0)	(0.4)	(1.5)	(0.2)	(0.2)	(0.8)
Total above- and below-ground	39793.7	18214.6	245.0	24.0	136.8	46.7	27.3	36.9
(SEM)	(1175.7)	(538.1)	(7.3)	(0.7)	(4.6)	(2.3)	(1.0)	(1.1)

[a] Mostly *Agrostis capillaris* and *Anthoxanthum odoratum*.

[b] *Hieracium pilosella* and *H. lepidulum*.

[c] *Lycopodium fastigiatum* and *L. scariosum*.

[d] Mostly *Polytrichadelphus magellanicus*.

Appendix 3

PRE-BURN ASSESSMENT OF BIOMASS, CARBON AND NUTRIENT POOLS (kg/ha) AT THE MT BENGER STUDY SITE (APRIL 1998)

Values are the mean of five samples per plot and nine plots per site.

	BIOMASS	C	N	P	K	Ca	Mg	S
Grasses, rushes and sedges								
Adventive grasses[a]	722.7	326.3	6.51	0.71	3.38	0.40	0.76	0.80
Chionochloa rigida	5536.9	2595.6	36.09	4.97	48.60	2.04	4.13	4.17
Poa colensoi	278.5	125.7	2.54	0.27	1.17	0.13	0.29	0.38
Rushes and sedges[b]	41.3	19.0	0.44	0.05	0.30	0.03	0.06	0.06
Forbs								
Aciphylla hectori	11.6	5.3	0.15	0.02	0.25	0.09	0.05	0.01
Celmisia gracilenta	22.6	10.3	0.31	0.03	0.18	0.08	0.07	0.03
Hieracium spp.[c]	1.8	0.7	0.02	0.00	0.02	0.00	0.01	0.00
Isolepis aucklandica	66.2	28.2	0.75	0.06	0.37	0.03	0.08	0.08
Oreobolus pectinatus	190.5	86.8	1.58	0.17	1.02	0.08	0.23	0.14
Raoulia subsericea	34.8	16.4	0.34	0.04	0.21	0.15	0.09	0.05
Minor forbs	75.7	32.1	0.90	0.08	0.47	0.08	0.14	0.10
Shrubs								
Coprosma cheesemanii	12.2	6.2	0.10	0.01	0.04	0.05	0.01	0.01
Gaultheria depressa	31.0	14.9	0.25	0.03	0.14	0.10	0.06	0.03
Hebe odora	243.9	124.9	1.56	0.29	1.66	0.47	0.52	0.21
Acrothamnus colensoi	110.2	53.7	1.25	0.12	0.36	0.44	0.17	0.12
Leucopogon fraseri	93.6	45.6	1.06	0.10	0.30	0.37	0.15	0.10
Pentachondra pumila	268.1	134.9	2.09	0.16	0.70	1.02	0.37	0.20
Pernettya macrostigma	2.9	1.4	0.02	0.00	0.01	0.01	0.01	0.00
Minor shrubs	87.2	40.3	0.79	0.07	0.44	0.33	0.31	0.07
Lower plants								
Hymenophyllum sp.	27.8	10.0	0.30	0.03	0.29	0.02	0.05	0.03
Lycopodium spp.[d]	112.5	51.5	1.31	0.19	0.86	0.05	0.13	0.13
Coarse mosses[e]	1069.3	492.7	7.17	0.59	3.68	0.32	1.07	0.77
Fine mosses[f]	77.8	33.9	0.71	0.07	0.40	0.06	0.12	0.08
Lichen	41.5	17.9	0.34	0.03	0.14	0.01	0.03	0.03
Litter								
Aciphylla hectorii	3.4	1.6	0.02	0.00	0.02	0.02	0.02	0.00
Chionochloa rigida	16032.0	7671.3	52.98	3.90	14.44	6.66	8.19	8.79
Other	3855.7	1667.4	32.76	3.18	16.01	1.52	3.36	4.66
Total above-ground	9051.5	13614.8	152.4	15.2	95.5	14.6	20.5	21.1
(SEM)	(1550.5)	(751.1)	(5.8)	(0.6)	(4.2)	(1.0)	(0.9)	(0.9)
Roots								
Beneath tussocks	3291.5	1441.0	19.00	1.66	8.29	0.25	0.83	3.24
Between tussocks	6384.9	2426.3	53.38	4.92	31.17	2.02	4.97	7.02
Total below-ground	9676.4	3867.3	72.4	6.6	39.5	2.3	5.8	10.3
(SEM)	(694.7)	(271.9)	(5.5)	(0.5)	(3.1)	(0.2)	(0.5)	(0.8)
Total above- and below-ground	38727.8	17482.1	224.7	21.7	134.9	16.8	26.3	31.3
(SEM)	(1820.6)	(853.5)	(7.9)	(0.7)	(4.7)	(1.0)	(1.1)	(1.1)

[a] Mostly *Agrostis capillaris* and *Anthoxanthum odoratum*.
[b] Mostly *Carex wakatipu*.
[c] *Hieracium pilosella* and *H. lepidulum*.
[d] *Lycopodium fastigiatum* and *L. scariosum*.
[e] Mostly *Polytrichadelphus magellanicus*.
[f] Mostly *Leptotheca gaudichaudii*.

Appendix 4

WEATHER CONDITIONS, FIRE WEATHER INDICES AND FIRE BEHAVIOUR FOR TUSSOCK GRASSLAND FIRES AT DEEP STREAM AND MT BENGER

Plots are listed in the order in which they were burned.

	DEEP STREAM						MT BENGER					
	SPRING BURNS			SUMMER BURNS			SPRING BURNS			SUMMER BURNS		
	PLOT 3	PLOT 8	PLOT 4	PLOT 2	PLOT 5	PLOT 9	PLOT 9	PLOT 1	PLOT 6	PLOT 3	PLOT 5	PLOT 8
Weather conditions												
Temperature (°C)	19.3	21.4	18.3	18.0	18.2	18.7	7.8	9.5	10.8	11.2	12.1	11.9
Relative humidity (%)	41	43	51	59	59	60	70	65	57	73	68	70
Wind speed at 10 m (km/h)	17.4	23.2	25.3	24.8	26.6	21.8	11.1	16.7	18.1	8.1	12.4	11.0
Days since rainfall > 6 mm	4	4	4	10	10	10	2	2	2	2	2	2
Fire weather indices												
Fine Fuel Moisture Code (FFMC)	89.9	89.9	88.7	86.6	86.6	86.6	78.7	79.9	81.4	74.6	75.3	75.9
Duff Moisture Code (DMC)	14	14	14	26	26	26	6	6	6	5	5	5
Drought Code (DC)	20	20	20	204	204	204	33	33	33	178	178	178
Initial Spread Index (ISI)	10.1	13.6	12.6	9.2	10	7.9	1.7	2.6	3.3	1.1	1.5	1.4
Buildup Index (BUI)	14	14	14	39	39	39	9	9	9	9	9	9
Fire Weather Index (FWI)	11.8	14.9	13.8	18.4	19.6	16.4	1.0	2.3	3.2	0.6	0.8	0.8
Fire behaviour												
Flame length (m)	2.5	2.5	3.0	2.0	2.5	3.0	2.0	2.0	2.5	2.5	2.5	2.0
Rate of spread (m/h)	1100	1190	1830	350	460	1300	510	420	1040	1280	1540	800

What effect does fire have on tall-tussock grasslands?

The effects of early- and late-season fires on tall-tussock grasslands were examined at two sites in Otago. Fires reached high temperatures (>1000°C), but were of short duration (4–8 minutes) and had little heating effect on the soil. Fires under damp spring conditions posed little threat to the long-term survival of the tall-tussock ecosystem. However, fires later in the season or under drier conditions resulted in higher plant biomass, carbon and nutrient losses, and much greater tiller and tussock mortality. Therefore, minimising the extent of fires under these conditions should be a priority wherever tussock cover is to be retained.

Payton, I.J.; Pearce, H.G. 2009: Fire-induced changes to the vegetation of tall-tussock (*Chionochloa rigida*) grassland ecosystems. *Science for Conservation 290*. 42 p.

New Zealand Government