

Changes in biomass and soil nutrient pools of tall tussock grasslands in New Zealand

Kevin F. O'Connor¹, Alan H. Nordmeyer², and Kristín Svavarsdóttir³

¹ *Centre for Mountain Studies, Lincoln University, Canterbury, New Zealand*

² *New Zealand Forest Research Institute, Rangiora, Canterbury, New Zealand*

³ *Land Resources Division, Knight Frank Ltd, Christchurch, New Zealand; formerly Hellaby Indigenous Grasslands Trust Research Fellow at Department of Plant Science, Lincoln University, Canterbury, New Zealand*

ABSTRACT

This paper addresses the question whether nutrient loss from ecosystems is a cause of rangeland desertification or an outcome. The history of vegetation changes since humans arrived in New Zealand is summarily reconstructed, emphasising the early effects of fire and grazing in European pastoralism in reducing above-ground biomass of tall tussock grasslands that resulted from Polynesian burning of forest. The paper collates available quantitative information on biomass and nutrient pools in soil and vegetation at different stages of degradation in high country grasslands of South Island. Biomass quantities in different compartments and N, P, K and Ca contents in green shoots of tall tussocks at nine different localities are presented, showing great variation that is not well explained by species or soil differences. From the one comparison possible, reduction in nutrient pools in biomass was largest from mountain beech forest to tall tussock grassland. Comparable data sets of C, N, P, K and Ca in biomass compartments and soil layers are presented from three sequences of ecological degradation in different climatic zones. Reduction in nutrient pools in above-ground biomass with degradation from tall tussock grassland to weedy short grassland is generally significant. Changes in roots were not consistent. When soil nutrients were included, no difference in N and P total ecosystem pools were found between stages of degradation. These results were related to historical phases of vegetation change in the high country with early pastoral fire being credited with major impact on above-ground nutrient pools. Nutrient conservation by soil microbial systems under degraded vegetation is suggested as an explanation for failure to detect change in soils in moister environments, in contrast with nutrient losses from less vegetated soils recorded or inferred in dry and or steep terrains. Nutrient pools in biomass increased with revegetation with both pines and lupins.

Key words: desertification, ecological degradation, New Zealand, nutrient balances, pastoral impact, tussock grasslands.

INTERPRETING CHANGES IN RANGELAND NUTRIENT POOLS: THE OBJECTIVE OF THIS PAPER

A summary account of nutrient pools and fluxes in different plant communities in New Zealand was included with a review of biomass accumulation by Wardle (1991). Principal biomass measurements in mountain grassland communities have been those of Williams (1977), Meurk (1978), and Evans (1980). Williams et al. (1977a, 1977b, 1978a, 1978b,) recorded nutrient concentrations in the principal tall tussock grasses over their geographic range, indicating some of the relationships of nutrient concentrations to selected topsoil properties. The only studies with comprehensive soil chemical data and biomass nutrient pools from the same sites were the records of carbon and nutrients in soils, plant litter and living vegetation, compiled by Forest Research Institute scientists (Kelland 1978, Nordmeyer 1980a, 1980b, Evans 1980). These studies included nutrient comparisons of natural forest and grassland communities with

¹ Corresponding author: Professor Kevin O'Connor, 21 Tuawera Tce., Sumner, Christchurch, New Zealand. Tel./Fax: 64 3 326 6594; E-mail: oconnork@lincoln.ac.nz

planted forests on the Craigieburn Mountains. They were used by Nordmeyer et al. (1987) to examine some aspects of nutrients and reforestation.

Recent studies to model historical changes or measure current rates of change in nutrient balances in South Island tussock grasslands have been summarised by McIntosh (1997). He listed measurements of biomass in different forms of high country vegetation, and from them presented a single, composite account of reduction in biomass nutrient pools, compiled from a wide range of different environments. He also summarised results of studies of changes in nutrient concentrations in topsoils at several sites, including gains under pastoral development as well as losses under traditional use. He concluded that annual rates of nutrient loss calculated from reduction in biomass under pastoral impact, or calculated from estimated losses in grazing systems, were greatly exceeded by losses measured in soil chemical studies, generally in drier zones, of recent changes in unamended topsoils.

To help establish a basis for current and future studies, we have begun to collate from different climates and soils, measurements of element pools in soil and biomass for least-modified mountain vegetation. We also recorded data on levels of element pools at different stages in localised sequences of vegetation change, both ecological degradation under pastoral impact, and with cultural renewal by sown legumes or planted forests. In this paper we report progress results, orienting these to the question: is loss of nutrients from ecosystems a contributor to range deterioration and thereby to desertification, or is it a consequence of desertification?

This question is of considerable interest in New Zealand and in rangeland environments in many parts of the world. The comparatively short history of grazing use of New Zealand grasslands makes it possible to study this issue in a genuinely diachronic perspective, thereby assisting scientific understanding of desertification elsewhere, as well as assisting New Zealand in its own quest for sustainable land management as part of the international movement for sustainable development.

Our approach is first, to summarise the vegetation changes from tall tussock grassland through short tussock grassland to weedy, short grassland that has occurred extensively under pastoral occupation over the last 140 years. The cultural development of legume-rich pastures and plantation forests in place of deteriorated grassland over recent decades is also outlined. Second, we present biomass and nutrient data from studies selected to represent tall tussock grasslands at different altitudes at several high country locations. Third, we demonstrate from particular localities, comparative biomass and soil nutrient pools at different stages of vegetation degradation or cultural development. In discussion, we try to locate in historical time the losses or gains represented by these comparisons, and place our results in a geographic perspective with earlier reported studies.

CHANGES IN TALL TUSSOCK GRASSLANDS UNDER PASTORAL OCCUPATION

Climatic zones and ecological regions of South Island high country used in this paper are outlined in Wardle (1991), generally following the altitudinal zonation of Cockayne (1928). Since the last major glacial recession, tussock grasslands, herbfields and related formations have established and persisted above timberline in the penalpine zone and in the alpine zone above. Below timberline, in the driest zone of sub-

continental lowland and montane central Otago, forests which had developed since the Pleistocene were destroyed before the arrival of man some 1000 years ago, possibly by lightning fire, leading to formation of grasslands (McGlone 1988). Elsewhere in eastern and southern South Island, forest destruction by fire during Polynesian occupation (Molloy et al. 1963) led to tall tussock grasslands, dominated by species of *Chionochloa* (Connor 1964, 1965, Connor and MacRae 1969, Wardle 1991, Mark 1992).

The extent of tall tussock grasslands in the South Island high country at the beginning of pastoral settlement is a matter of some dispute. At the present time, there is general agreement among botanists and ecologists that in the semi-arid interior of Otago where mean annual precipitation is less than 350 mm, grasslands were characterised by abundant *Elymus apricus* and the absence of tall tussock species of *Chionochloa*. Many scientists believe that Intermediate in soil or climate conditions between this semi-arid grassland and the more extensive area of tall tussock grasslands, there was a substantial area of short tussock grassland dominated by *Festuca novae-zelandiae* or *Poa cita*. Others, including ourselves, hold the view that, apart from some specific situations, such short tussock grasslands did not occur naturally but were induced from tall tussock grasslands, shrublands, scrub and forest, by the combined impact of early pastoral fire and sustained grazing. The specific situations which we recognise as exceptions were the semi-arid grasslands of *Elymus apricus*, the coastal grasslands dominated by *Poa cita*, and the often sparse grasslands of stony or recent ground in dry sub-humid sectors of Marlborough or Waitaki where *Elymus solandri*, some forms of *Poa colensoi*, and some species of *Rytidosperma* were prominent.

Outside the semi-arid zone proper, in virtually all areas with annual precipitation greater than 500 mm, grasslands existing prior to the coming of Europeans appear to have been characterised by one or other tall tussock species of the genus *Chionochloa*. Attention in ecological research has been given mostly to the snow-tussock species of existing pastoral lands, *Chionochloa rigida*, *C. macra*, *C. flavescens*, and *C. pallens*. The frequency of remnants of red tussock, *C. rubra*, especially in the montane zone wherever the terrain is well watered in early spring, betrays its former significant extensive role, even in dry sub-humid climate to the borders of the semi-arid, as well as in more humid regions. Most tussock grasses of the genus *Chionochloa* are slow-growing and long-lived. Where they grew in dense stands, they tended to suppress the density and frequency of inter-tussock grasses. These included species of *Festuca*, *Poa*, *Agrostis*, *Deyeuxia*, *Dichelachne*, *Koeleria*, *Lachnagrostis*, and *Elymus*. Other inter-tussock herbs included species of *Luzula*, *Celmisia*, *Ranunculus*, *Geranium*, *Viola*, *Wahlenbergia*, *Gentiana*, *Helichrysum* and *Gingidia*. Many of these inter-tussock plants and possibly some dwarf-shrubs had apparently accompanied the dominant *Chionochloa* species in their migration into former forest lands.

The significance of fire

In many situations, such grasslands induced by Polynesian burning of forest also included woody species. Such shrubs and dwarf-shrubs principally belonged to the genera *Olearia*, *Brachyglottis*, *Discaria*, *Podocarpus*, *Phyllocladus*, *Hebe*, *Dracophyllum*, *Coprosma*, *Carmichaelia*, *Cassinia*, *Aciphylla*, *Kunzea* and *Leptospermum*. Dense

shrubby vegetation formed scrub or heath; where it was open, shrubland. Only in situations where topography offered no refuge from recurrent fire for woody plants were grasslands free of shrubs. The varied density and stature of shrubs at the onset of pastoralism may have reflected differences in lapse of time since the last fire. Early European explorers of the interior frequently met conditions which required fire to allow easy passage.

For the high country pastoral settlers of the late 1850s, fire was often essential for access with new flocks of sheep, especially because of scrub and the great mass of vegetation. Following initial depasturing of animals, pastoralists soon learned the usefulness of fire to aid the management of grazing (Butler 1862). Buchanan (1868), fresh from his earlier experience in Marlborough (Buchanan 1867), warned against burning in dry districts of Otago. Thousands of hectares at a time of tall tussock grassland or scrub were burned in the first decade of pastoral occupation. Scrub was often slow to recover, whereas over most of their natural range tall tussocks recovered readily from fire. If, however, grazing pressure after burning was sufficiently sustained, pastoral impact often achieved the transformation of such tall tussock grasslands to short tussock grasslands, usually of *Festuca* and *Poa* communities. *Festuca novae-zelandiae* and *Poa colensoi* became the most abundant tussocks of induced short tussock grasslands in montane and lower subalpine zones of interior subhumid and humid districts from Southland to North Canterbury.

Although this primary conversion of dense tall tussock grasslands to more open, shorter grasslands more suitable as pasturage, was the conscious work of managed pastoral impact, and was recorded by early surveyors (O'Connor 1986), the dramatic nature of this early transformation was not properly appreciated by scientists until relatively recent times. The careful phytosociologic analyses of Connor (1964, 1965) indicated derivation of many short grassland communities from tall tussock *Chionochloa* grasslands, dominated by *C. flavescens*, *C. macra*, *C. rigida*, *C. rubra*, or *C. pallens*. Until that revelation, opinions of resident and visiting scientists generally favoured the interpretation that climate, especially summer droughtiness, controlled the distribution of short grasslands.

For nearly a century, there is little suggestion in the writings of any naturalist or scientist of any awareness of this early vegetation transformation. It is evident from the descriptions of the grasslands in Otago by Petrie (1883, 1912) and by Leonard Cockayne (1899) in Canterbury that any major transformation of tall tussock grasslands to short grasslands must have occurred in the early years of pastoral settlement. Under the combined influence of grazing by rabbits since 1870s and sheep which reached their maximum by late 1880s, unimproved rangeland began to decline in livestock carrying capacity. Analyses of local histories and of statistical records of livestock and land use (O'Connor and Kerr 1978, O'Connor 1980, 1982, 1986, O'Connor and Harris 1992) have established that livestock numbers on unimproved rangeland generally reached their peak within 25 years of its first pastoral occupation, oscillated for a decade or more, and thereafter declined. Such declines were especially large and sustained in drier regions. This feature has been demonstrated (Harris and O'Connor 1998) especially in drier sectors of the Mackenzie Country, even though Mackenzie County as a whole had not shown serious decline.

Following the earlier conversion of tall tussock grasslands to short grasslands, some changes in grassland composition and structure continued under pastoral use. Adventive grasses, especially *Poa pratensis*, *Anthoxanthum odoratum*, *Holcus lanatus* and later, *Agrostis capillaris*, gradually increased with oversowing and grassland disturbance by livestock, especially in the montane and lower subalpine zones, accompanied by forbs such as *Crepis capillaris* and *Hypochaeris radicata*. These adventive herbs have generally improved the pastoral resource, but they have been less successful invaders of open grasslands at higher altitude. In recent years they, along with native inter-tussock herbs, have tended to decline in the face of later-invading species of *Hieracium*, especially *H. pilosella*, *H. lepidulum* and *H. praealtum*. In drier sectors of the high country in particular, an important and continuing vegetation change under continuing pastoral use has been reduction in density of tussock grasses and of inter-tussock vegetation. Although this depletion or reduction in vegetative cover was most dramatically shown in semi-arid central Otago in the *Elymus* grasslands, it has also occurred in sub-humid climatic sectors, and even in humid sectors among *Chionochloa* grasslands and in *Festuca* and *Poa* grasslands derived from them. In some of these grasslands, especially but not exclusively on steep terrains, surface soil erosion has occurred following exposure to erosive agents, especially soil frost and wind.

The influence of animal behaviour and diet selection

In interpreting such changes in botanical composition of tussock grasslands, it is as difficult now as it was for Cockayne (1919, 1920a, 1920b, 1920c) to ignore evidence for the differentially selective grazing pressure of sheep. Differential acceptability to livestock may also affect the physiognomy of tall tussock grasslands. With the exception of *Chionochloa macra*, sometimes grazed, all the tall tussocks are unacceptable to sheep, except as seedlings or as herbage recovering from fire. Cattle have sometimes been used in recent years instead of burning, to open up the canopy of *C. rigida* on shady slopes. Such transformations had not been achieved in a century of fire and sheep grazing, sheep being loath to sustain grazing pressure on shady terrain, even after burning.

When sheep diet has been determined in unimproved grasslands by direct observation or by microscopic analysis of cuticle fragments recovered from faeces, many of the more abundant plant species in the grassland have been found to be uneaten or to contribute very small fractions of the selected diet. For example, *Poa cita* and *Discaria toumatou* have been very rarely recorded in diet, despite their abundance in many communities. This apparently rejected condition likewise belongs to many of the abundant inter-tussock plants. Conversely, in other studies, sheep's diet has been found to have been composed almost exclusively of plant species which occurred only in small areas of naturally or culturally enhanced nutrition. In some other studies in which vegetation has been examined under continued grazing as well as with grazing excluded, differences in seedling abundance in favour of the ungrazed areas indicate that continued grazing may be sometimes serving to arrest vegetation recovery that might otherwise occur.

It is widely accepted that diet selection by sheep may be affected by grazing pressure, the ratio of animal demand to forage supply at a particular time. This has been corroborated in research studies. Research has also shown that sheep diet may be as

much influenced by the nutritional status of the vegetation as by its botanical composition *per se*. In most situations, clovers (*Trifolium* spp.), especially those cultivars which have been bred as forages, are grazed preferentially, but the acceptability to sheep of many of the more abundant grasses in short tussock grassland, such as *Festuca novae-zelandiae*, *Agrostis capillaris*, and *Holcus lanatus* may be greatly affected by the nutritional regime in which they are grown. The great variations in value in which such species are held by farmers may be related to this phenomenon of nutritional effects on palatability. For example, fescue tussock has had a changing reputation with farmers, just as it has with scientists, over more than a century. It was initially highly valued as feed by Buchanan (1880), and by Petrie (1895), less valued by Petrie (1912) as it increased in prominence in short grasslands, progressively devalued as feed by Leonard Cockayne and eventually appreciated by him only for its shelter for other plants. In recent studies, it has been found to be of very low dietary significance in grasslands not receiving fertiliser, but is highly responsive in growth and composition to improved nutrition, and has often been eliminated by preferential grazing after legume oversowing and topdressing.

In one of his major efforts to make his understanding of ecology useful to New Zealand grassland management through the Southern Pastoral Lands Commission (1920), Leonard Cockayne distinguished between depletion and deterioration. He recognised that **grassland depletion** was the loss of vegetative cover and increase in bare ground, a process leading to man-made deserts, a stage we now define as desertification. What Cockayne termed **grassland deterioration**, a decline in the pastoral quality of unimproved rangelands by loss of palatable components and increase in unpalatable plants, is discernible in the botanical composition of many unimproved grasslands, just as it is to be found in mountain grasslands under repetitive systems of livestock use in various parts of the world. We can now more easily discern how the processes of vegetation change induced by animal selection in repetitive grazing systems can generate need for further change in management.

Relating such causes and effects in chronological terms is difficult by current vegetation analysis alone. It may be that many of the continuing floristic changes in the grasslands, including some invasions, are part of the adjustment to stresses induced by the major pastoral disturbance of more than a century ago. There are instances where further degradation of vegetation has continued even when current pastoral impact has ceased. There are other instances where cessation of grazing has been accompanied by an arrest of degradation, or even its reversal. In many situations, ecological degradation has been sustained or accelerated under continuing pastoralism (Treskonova 1991, Connor 1992).

Cultural revegetation of degraded rangeland

Deteriorating nutritional regimes for livestock and concern for resource conservation if existing conditions were allowed to continue have together prompted gradual departure from traditional pastoralism. Over the past four decades, substantial efforts have been made by scientists and pastoral managers to revegetate degraded rangeland, especially in the montane zone. For pastoral improvement of sub-humid and humid range, primary emphasis has been given to legume oversowing with the application of sulfur and phosphorus materials as fertiliser. Afforestation with conifers has also been

employed to prevent soil erosion as well as to improve livestock shelter and local timber supplies. The implications of such revegetation to nutrient balances also warrant attention.

QUANTIFYING CARBON AND NUTRIENT POOLS IN SOILS AND BIOMASS

Identification of representative sites and data sources

Reliable data for nutrients in biomass and soil under forest in the high country are at present available only for the Craigieburn Mountains. Several general locations have been identified for which we have substantial collections of comparable data for tall tussock grassland biomass, nutrient concentrations in phytomass, especially above-ground. For many of these we now have data on carbon and nutrient levels in soils, although these are not all complete data sets, nor are soil data or plant nutrient concentration data always derived from the same site as the biomass data.

For the four general locations selected for presentation here, altitude and climate zones are specified for each locality (a, b, c, etc.,) because in some cases, degradation sequences are being studied at more than one altitude. To identify valid examples of stages in such a sequence depends on holding constant other environmental factors. The influence of pastoral animal behaviour on the incidence of vegetation change that has been earlier emphasised, makes it possible to identify examples where there is minimal variation in other factors. Field examples of different stages of a degradation sequence or cultural development sequence are available for some other localities, but many have not yet been sampled adequately and some are not represented with fully processed data.

Location 1. Craigieburn Mountains, Puketeraki Ecological Region, Canterbury

- 1a. Humid, penalpine, Spenser soil, *Chionochloa pallens* grassland.
- 1b. Humid, subalpine, Tekoa soil, (i) *Nothofagus solandri* var. *cliffortioides* forest, (ii) *C. macra* grassland, (iii) induced *Festuca-Agrostis-Hieracium* grassland; (iv) planted *Pinus contorta* afforestation harvested after 13 years.
- 1c. Humid, montane, Cass soil, *C. rubra* grassland.

Data sources: Mountain beech forest biomass, nutrients and soils; Kelland 1978, Nordmeyer 1980a, 1980b. Grassland biomass, nutrients and soils; Kelland 1978, Evans 1980, this paper. Pine forest biomass, nutrients and soils; Nordmeyer 1980a, 1980b, this paper.

Location 2. Hakatere Basin, Heron Ecological Region, Canterbury

- 2a. Moist subhumid, subalpine, Puketeraki soil, *C. macra* grassland.
- 2b. Moist subhumid, montane, Tasman/Pukaki soils, (i) *C. rigida* grassland, (ii) mixed *Festuca-Chionochloa* grassland, (iii) short, sparse *Festuca-Hieracium* grassland, (iv) herbaceous revegetation with legumes, including *Lupinus*.

Data sources: *Chionochloa* biomass and nutrients; Williams 1977, Williams et al. 1977a, 1977b. Soils and all other data; Davis 1991, this paper.

Location 3. Tekapo district, Mackenzie Ecological Region, South Canterbury

3. Dry subhumid, montane, Tekapo/Pukaki soils, (i) *C. rubra* grassland, (ii) derived *Festuca novae-zelandiae* grassland, (iii) short, sparse *Festuca-Hieracium* grassland.

Data sources: (Tekapo soil under derived *F. novae-zelandiae* grassland; Soil Bureau 1968a. All other data; this paper.

Location 4. Old Man Range, Central Otago Ecological Region, Otago

4a. Humid, alpine, Obelisk soil, *C. macra* grassland (Meurk, 1978, 16:O:M).

4b. Humid, penalpine, Carrick soils, (i) *C. macra* / *C. rigida* grassland (13:O:MR), (ii) induced *Poa colensoi* short grassland (13:O:P), (iii) modified mixed tussock herbfield (13:O:PH).

4c. Dry subhumid, subalpine, Tawhiti soil, *C. rigida* / *C. rubra* grassland (9:O:R).

Data sources: Biomass; Meurk 1978. *Chionochloa* nutrients; Williams et al. 1977b. Soils; Molloy and Blakemore 1974. All other data; this paper.

Procedures and conventions adopted for presentation of data

Where sufficient information was available, the following procedures were followed to standardise data for comparison. Biomass data derived from published and unpublished records have been assigned to three compartments: above-ground live plant tissue; above-ground dead plant tissue, including litter; below-ground roots. Roots and rhizomes pedestalled above ground have been here included, as they were in Williams (1977), in above-ground compartments, and discounted from below-ground root mass in data of Evans (1980). Such components are not reported separately in Meurk (1978). Where supplementary estimates were necessary, as for incompletely recovered fine roots in Craigieburn tall tussock samples, or for inter-tussock live shoot material not tabulated in Williams (1977), estimates have been included in data presented here, the presence of such adjustments being identified in the tables. In the case of the *C. pallens* below-ground data of Evans (1980) where fine root recovery was incomplete, measurements were doubled in line with his own estimate. Where inter-tussock above-ground biomass had to be estimated, we followed the modified height frequency data supplied by Williams (1977) to quantify the supplement needed for non-*Chionochloa* components of biomass. Statistical confidence limits are not shown here but are published in the originals to which reference is made. Measurements of biomass reported for the first time in this paper are from destructive sampling, generally of areas of 4 m², supplemented by estimates from height intercept data. Chemical analyses of tall tussock material or of other bulk harvests followed the practices outlined in Williams et al. (1977a).

Nutrient contents in live shoots of *Chionochloa* in Otago have been calculated using nutrient concentration coefficients for whole shoots, derived from the detailed individual locality records of *Chionochloa* species of Williams et al. (1977b). Values used were from the same sites as the biomass determinations of Meurk (1978), calculated for whole live shoots of *C. rigida* and *C. macra* as appropriate. For all live shoot material other than *Chionochloa*, coefficients have been used that were derived from similar analyses in a wide range of Craigieburn, Hakatere, Mackenzie and Otago studies.

We had hoped to include estimates of nutrient contents in Otago dead material and roots, using coefficients derived from the earlier studies at Hakatere and Craigieburn, and weighting these by the deviation of site-specific shoot values from the comparable

Hakatere and Craigieburn values. However, results varied extravagantly, apparently affected by the substantial range between sites in mass of litter. As nutrient concentrations in litter varied greatly from the concentrations in live shoots, even at the sites where both had been measured, we abandoned the estimation procedure as unreliable.

Soils have been named in the list of localities above, according to the soil set to which they correspond in the Soil Bureau (1968b) "General Survey of Soils of the South Island", except for the central Otago localities where soils of the tall tussock sites were named by Molloy and Blakemore (1974). Carbon and nutrient levels reported from such sources have been, where necessary, summed over 0–200 mm and 200–400 mm depth to allow ready comparison with other sites. Methods of analyses for new soil data not previously reported have followed those of Soil Bureau, as used in Forest Research Institute (Kelland 1978). Unless otherwise stated, four replicate samples of soils have been taken from the field at each site and separately analysed.

RESULTS

Tall tussock grassland biomass

Considerable variability in tall tussock grassland biomass is indicated in Table 1. Soil carbon is less variable than phytomass compartments. There is a two-fold difference in magnitude of live shoot biomass between the Canterbury and Otago studies

Table 1. Biomass (tonnes ha⁻¹) of tall tussock (*Chionochloa*) grasslands and soil carbon (tonnes ha⁻¹) in 0–200 mm layer at nine localities in South Island high country. Numbers (1a, 1b, etc.) refer to localities described in text. Superscripts indicate values which include supplementing estimates noted below.

Location	Above-ground		Below-ground Roots	Soil C 0–200 mm
	Live tissue	Dead (incl. litter)		
Craigieburn Mountains				
1a. <i>Chionochloa pallens</i>	7.9	47.1	19.0 ^{a)}	86.7
1b. <i>C. macra</i>	8.9 ^{b)}	33.4	8.5	80.9
1c. <i>C. rubra</i> ^{g)}	14.4	40.6	13.0 ^{d)}	88.1
Hakatere Basin				
2a. <i>C. macra</i>	4.5 ^{c)}	12.2	22.0	61.7
2b. <i>C. rigida</i>	10.3 ^{c)}	30.6	31.4	90.6
Tekapo, Mackenzie Basin				
3. <i>C. rubra</i> ^{g)}	11.4	18.8	16.0 ^{d)}	74.8
Old Man Range, Otago				
4a. <i>C. macra</i>	16.9	25.1	24.2	95.2 ^{e)}
4b. <i>C. macra/C. rigida</i>	16.5	16.5	15.7	52.5 ^{e)}
4c. <i>C. rigida</i>	21.3	44.9	21.0	63.2 ^{e,f)}
CV (%)	42.2	42.4	35.3	19.3

- a) Value includes supplement for incomplete recovery of fine roots.
- b) Value includes supplement for measured amount of pedestalled roots and rhizomes.
- c) Values include supplements for intertussock live biomass, estimated from height intercept data.
- d) Values estimated on the basis of core samples only.
- e) Values calculated from analytical data but with guesstimates of soil bulk density.
- f) Soil reference site some km distant from biomass reference site.
- g) All values from duplicate samples only.

whereas the mean values for dead material and for roots are similar. Differences in technique of measurement, especially of the above-ground live material, between the Canterbury and Otago studies may have affected the relative proportions of the three biomass compartments.

Species differences are not consistent in total biomass or in compartments. Despite smaller stature, *C. macra* grasslands are not consistently lower in above-ground biomass than those of other tall tussocks. Although all these sites had been selected as least-disturbed examples of tall tussock grasslands at these four locations, they show large range in dead above-ground biomass, with variation not closely related to live biomass, suggesting differences in rates of decay or of litter incorporation. Such variations in decomposition rate, including some of the present Otago studies, have been related by Molloy et al (1978ab) to various environmental factors. Differences in lapse of time since a litter-consuming fire might have had some influence on the mass of dead material, but the knowledge that at no site had fire occurred within, at the very least, 15 years does not help resolve the issue, as no information is available on fire severity.

Nitrogen, phosphorus, potassium and calcium in tall tussock biomass

Nitrogen, phosphorus, potassium and calcium have been selected as common from among seven nutrients analysed in different studies, to indicate the range in quantities in live, above-ground biomass among tall tussock grasslands of different species of *Chionochloa*. Table 2 demonstrates the substantial variation in nutrient contents in live above-ground biomass, only K showing lower coefficient of variation than that shown in Table 1 by biomass itself.

Table 2. Weights of N, P, K, Ca (kg ha^{-1}) in above-ground live biomass pools (shoots) in relation to weights of total N and P and of exchangeable K and Ca in 0–200 mm soil layer (kg ha^{-1}), for nine tall tussock grasslands in South Island high country. Pearson correlation coefficients for the relationship between shoot and root of each of the four elements are shown.

Location	N		P		K		Ca	
	Shoot	Soil	Shoot	Soil	Shoot	Soil	Shoot	Soil
Craigieburn Mountains								
1a. <i>Chionochloa pallens</i>	118	4220	12	952	205	211	35	722
1b. <i>C. macra</i>	75	4581	10	1724	88	348	22	353
1c. <i>C. rubra</i> ^{a)}	87	4940	10	1537	137	492	12	1314
Hakatere Basin								
2a. <i>C. macra</i>	29	3765	7	720	39	101	5	176
2b. <i>C. rigida</i>	61	6324	15	1821	107	162	13	486
Tekapo, Mackenzie Basin								
3. <i>C. rubra</i>	63	4842	9	1444	100	696	19	1708
Old Man Range, Otago								
4a. <i>C. macra</i>	128	5477	17	1256	158	301	17	305
4b. <i>C. macra/C. rigida</i>	43	3304	7	1037	160	191	14	103
4c. <i>C. rigida</i>	117	3826	30	1211	177	146	26	264
CV's	43.7	20.4	55.5	28.1	39.4	65.6	48.5	91.8
$r_{\text{shoot, soil}}$	0.21		0.11		-0.11		0.09	

a) Values from duplicate samples only.

Weights of total soil N and P and amounts of exchangeable K and Ca in 0–200 mm soil layers are also shown in Table 2, demonstrating also that above-ground live nutrient pools and surface soil pools are not closely related over all nine localities. Total soil N and total soil P in this 0–200 mm layer show less variation than any other parameter examined. Williams et al. (1978ab) examined the altitudinal distribution of values for topsoil indicators of available nutrients in tall tussock grassland soils and the influence of some such indicators, especially for P, on nutrient weights in live *Chionochloa* shoots. Their larger survey did not reveal any marked relationships, except for the tendency of total shoot P in different species to be more closely related to particular soil P tests or different soil P fractions. It is not surprising, therefore, that soil and live biomass nutrient contents vary independently in the present study over several species. Similarly, there is no clear evidence of influence of live biomass pools on soil pools.

Carbon and nutrient comparisons between stages of ecological degradation

Data for biomass comparisons of degradation stages are at present available from four localities, but nutrient data are incomplete for all of these stages. Table 3 reports C levels (calculated as 50 percent of biomass, inclusive of ash), N, P, K and Ca levels for degradation stages at three of these localities.

Table 3 indicates substantial and consistent reductions in C in above-ground live biomass, from tall tussock grasslands to shorter grasslands and weed communities. These reductions are small in comparison with that in the single example of transformation from forest to tall grassland. Litter C is much lower in forest than is above-ground dead C (including litter) in tall tussock grassland. Reductions in C in above-ground dead associated with transformation of tall tussock grasslands to short grasslands are generally substantial, without being closely parallel to changes in above-ground live material.

When the three localities are considered as replicates and tall tussock grassland compared with weedy short grassland, above-ground C means are highly significantly different ($p=0.001$). Apart from the substantial reduction in C in roots with the change from forest, reductions in root biomass are not consistent. Nevertheless, tall tussock grassland remains significantly greater in total biomass C than weedy short grasslands ($p=0.01$). Differences in weight of soil C in 0–200 mm layer or in combined 0–400 mm layer are not clearly discernible from the three comparable sequences. When the total ecosystem is considered to 400 mm depth, weedy short grassland appears to have less C than tall tussock grassland, but the difference does not reach significance ($p=0.185$).

The Old Man Range three-stage degradation sequence at 1300 metres measured by Meurk (1978) demonstrated similar declines in above-ground live C, an overall decline in above-ground C and total biomass C. It has not been included in the statistical analyses here because the induced vegetation is botanically different from the weedy short grassland of the other three comparisons, and because lack of herbage nutrient data and of soil C and nutrient data for the degradation stages prevents valid system comparisons.

Table 3. Weights of C, N, P, K, and Ca in biomass and soil pools at different stages of ecological degradation for three Canterbury high country localities.

Element	Locality	Ecological stage	Above-ground		Roots	Soil		Total
			Live	Dead		0 to 200 mm	200 to 400 mm	
C (t ha ⁻¹)	Craigieburn	Forest	136.6	6.2	36.9	82.3	44.7	306.7
	Humid	Tall tussock grassland	4.4	16.7	4.2	80.9	34.5	140.7
	Subalpine 1b	Weedy short grassland	1.7	0.8	8.2	72.2	19.8	102.7
	Hakatere	Tall tussock grassland	5.2	15.3	15.7	90.6	56.0	182.8
	Moist sub-humid	Mixed tussock grassland ^{c)}	3.2	4.9	9.5	94.0	50.6	162.2
	Montane 2b	Weedy short grassland	0.4	0.5	5.0	98.3	56.5	160.7
	Tekapo	Tall tussock grassland ^{d)}	5.7	9.4	8.0	74.8	60.0	157.9
	Dry sub-humid	Short tussock grassland ^{c)}	2.3	2.6	6.0	67.2	56.4	134.5
	Montane 3	Weedy short grassland	0.9	0.7	7.1	66.1	40.3	115.1
N (kg ha ⁻¹)	Craigieburn	Forest	884	54	200	2350	1951	5439
	Humid	Tall tussock grassland	75	153	82	4581	2145	7036
	Subalpine 1b	Weedy short grassland	30	8	107	3953	1322	5420
	Hakatere	Tall tussock grassland	61	115	154	6324	5450	12104
	Moist subhumid	Mixed tussock grassland ^{c)}	52	59	76	6327	5242	11756
	Montane 2b	Weedy short grassland	7	4	68	7304	5336	12719
	Tekapo	Tall tussock grassland ^{d)}	63	62	70	4842	3800	8837
	Dry sub-humid	Short tussock grassland ^{c)}	38	31	84	4820	3572	8545
	Montane 3	Weedy short grassland	15	10	93	5705	3887	9710
P (kg ha ⁻¹)	Craigieburn	Forest	141	6	37	500	593	1277
	Humid	Tall tussock grassland	10	23	8	1724	943	2708
	Subalpine 1b	Weedy short grassland	6	1	16	1633	622	2278
	Hakatere	Tall tussock grassland	15	16	19	1821	1290	3161
	Moist sub-humid	Mixed tussock grassland ^{c)}	10	8	15	1735	1301	3069
	Montane 2b	Weedy short grassland	1	1	8	1543	1475	3028
	Tekapo	Tall tussock grassland ^{d)}	9	8	5	1444	1480	2946
	Dry sub-humid	Short tussock grassland ^{c)}	7	4	12	1483	1390	2896
	Montane 3	Weedy short grassland	3	2	14	1439	1341	2799
K (kg ha ⁻¹)	Craigieburn	Forest	591	20	91	65	87	-
	Humid	Tall tussock grassland	88	73	20	348	83	-
	Subalpine 1b	Weedy short grassland	41	3	67	259	87	-
	Hakatere	Tall tussock grassland	107	60	48	162	129	-
	Moist sub-humid	Mixed tussock grassland ^{c)}	78	39	57	190	N.A. ^{a)}	-
	Montane 2b	Weedy short grassland	15	14	58	216	86	-
	Tekapo	Tall tussock grassland ^{d)}	100	34	21	696	94	-
	Dry sub-humid	Short tussock grassland ^{c)}	56	16	36	515	88	-
	Montane 3	Weedy short grassland	18	10	58	200	76	-
Ca ^{b)} (kg ha ⁻¹)	Craigieburn	Forest	697	120	337	550	173	-
	Humid	Tall tussock grassland	22	175	15	353	154	-
	Subalpine 1b	Weedy short grassland	22	5	52	882	243	-
	Hakatere	Tall tussock grassland	13	72	88	486	215	-
	Moist sub-humid	Mixed tussock grassland ^{c)}	20	49	85	690	N.A. ^{a)}	-
	Montane 2b	Weedy short grassland	10	12	97	1044	260	-
	Tekapo	Tall tussock grassland ^{d)}	19	64	54	1708	120	-
	Dry sub-humid	Short tussock grassland ^{c)}	28	21	60	1856	790	-
	Montane 3	Weedy short grassland	10	8	45	1815	515	-

a) Data not available.

b) In soils these are exchangeable values only.

c) Biomass data from one sample only.

d) All data from duplicate samples only.

Comparative nutrient pools for biomass compartments and soil layers have also been compiled for N and P for three degradation sequences in Table 3, as well as comparative biomass compartment pools for K and Ca, and exchangeable K and Ca in soil layers. Reductions in nutrient pools in live biomass compartments, especially in above-ground tissue (including wood), but also in roots, that accompany the transformation of forest to grassland vegetation are far in excess of what is shown for later transformations of the tall tussock grasslands themselves. There is a clear indication, however, that soil pools of N, P and K are higher under grassland than they are under forest.

In respect to N, P and K, degradation of tall tussock grassland to weedy, short grassland has been accompanied by a reduction in above-ground nutrient pools, both live and dead. By use of the three localities as replicates, analysis of variance showed highly significant differences between tall tussock grasslands and weedy short grasslands for above-ground N ($p=0.008$), for above-ground K ($p=0.000$), and almost so for above-ground P ($p=0.013$). These differences in nutrients in above-ground pools are not matched by consistent reductions in N, P and K pools in roots. When roots are included for total biomass nutrients, differences are less significant for N ($p=0.024$), and for P ($p=0.089$), but they are highly significant for K ($p=0.010$). In the case of Ca, evidence for nutrient decline with ecological degradation is much less plain, except in the above-ground dead compartment, where the characteristic persistence of Ca is demonstrated. For difference in above-ground Ca, $p=0.058$, and for total biomass Ca, $p=0.033$.

Soils show no consistent differences in nutrients associated with ecological degradation sequences, apart from the appreciable enhancement of soil N, P, and K, which seems to accompany the conversion of forest to grassland. This is consistent with the substantial difference in favour of forest in all nutrients in biomass. As a consequence of the substantial contribution of soil N and P to the whole system in grasslands, when tall tussock grassland systems as a whole are compared with short grassland systems, differences in total system nutrients are negligible and never approach significance ($p>0.5$ for N and P).

Changes in nutrient pools with cultural renewal of vegetation

Limited opportunities exist to measure nutrient pools in soils and biomass compartments of cultural vegetation, in comparison with reference areas established in sites documented in the earlier tables. An intensive study of soil nutrient pools in Tekapo soil under comparative pastoral cultures over nearly two decades has recently been compiled and will be reported separately (D. Scott, in prep.). Likewise the degraded ecosystem on Pukaki soil in the Tekapo sequence in Table 3 is being used as a reference point for forestry and pastoral development.

At two sites in the Craigieburn subalpine zone, lodgepole pine (*Pinus contorta*) was planted in the early 1960s and biomass and nutrient pools were determined in 1978 (Nordmeyer 1980ab). From one of these sites, live and dead above-ground and below-ground nutrient pools in 13 year old *P. contorta* are presented in Table 4, in comparison with the corresponding values for the *Festuca-Agrostis-Hieracium* community in which trees had been planted.

Table 4. Weight of elements in biomass and soil pools with 13 years afforestation with *Pinus contorta* at Craigieburn and with 13 years revegetation with *Lupinus polyphyllus* at Hakaterere each compared with element pools in weedy short grassland at same sites.

Locality	Element	Ecological stage	Above-ground		Roots	Soil		Total
			Live	Dead		0 to 200 mm	200 to 400 mm	
Craigieburn	C (t ha ⁻¹)	<i>Pinus contorta</i>	67.4	11.4	20.6	52.1	19.4	170.9
		Weedy short grassland	1.7	0.8	8.2	72.2	19.8	102.7
	N (kg ha ⁻¹)	<i>Pinus contorta</i>	550	244	90	2980	1649	5513
		Weedy short grassland	30	8	107	3953	1322	5420
	P (kg ha ⁻¹)	<i>Pinus contorta</i>	106	16	22	788	695	1627
		Weedy short grassland	6	1	16	1633	622	2278
	K (kg ha ⁻¹)	<i>Pinus contorta</i>	454	43	86	125	110	-
		Weedy short grassland	41	3	67	259	87	-
	Ca (kg ha ⁻¹)	<i>Pinus contorta</i>	304	159	66	590	87	-
		Weedy short grassland	22	5	52	882	248	-
Hakaterere	C (t ha ⁻¹)	<i>Lupinus polyphyllus</i>	3.0	3.3	12.9	98.0	53.5	170.7
		Weedy short grassland	0.4	0.5	5.0	98.3	56.5	160.7
	N (kg ha ⁻¹)	<i>Lupinus polyphyllus</i>	138	85	248	7204	5162	12837
		Weedy short grassland	7	4	68	7304	5410	12793
	P (kg ha ⁻¹)	<i>Lupinus polyphyllus</i>	11	6	28	1411	1322	2778
		Weedy short grassland	1	1	8	1543	1475	3028
	K (kg ha ⁻¹)	<i>Lupinus polyphyllus</i>	70	16	162	190	77	-
		Weedy short grassland	25	4	58	216	86	-
	Ca (kg ha ⁻¹)	<i>Lupinus polyphyllus</i>	75	92	124	1267	246	-
		Weedy short grassland	19	2	97	1044	260	-

Table 4 also presents summary comparative data for nutrient pools 16 years after the most degraded grassland site in the Hakaterere montane sequence was revegetated with lupins. At this site, several different legumes had been sown with differential levels of phosphate in 1979 (Davis 1991). Biomass levels and nutrient concentrations were determined after 16 years without grazing or additional fertiliser in *Lupinus polyphyllus* plots with minimal initial P treatment (6.25 kg ha⁻¹).

Substantial changes occurred in nutrient pools in biomass compartments, both above and below ground, after herbaceous revegetation, without being reflected in any directly discernible change in soil pools. Nutrient pools in lupin roots clearly exceeded corresponding pools in the root mass of degraded grassland, whereas the nutrient pools in pine roots did not always greatly surpass those of the Craigieburn weedy grassland. In above-ground live and dead compartments, the increases in nutrient pools with lupins are considerable, but do not match the dramatic changes in nutrient pools occurring at Craigieburn in above-ground live and dead biomass compartments, following afforestation with *Pinus contorta*.

Soil analyses themselves do not reveal increase in nutrient pools under pine forest or lupins, even though there has been substantial carbon fixation in both cultural development regimes (and under the lupins, substantial N₂-fixation) for more than a decade. We have argued elsewhere (O'Connor and Nordmeyer 1996) that to make such comparisons validly, we would have to survey land surfaces carefully and sample to uniform depth from a fixed benchmark, to take account of soil growth through root

displacement and organic matter accumulation at the surface under any revegetation programme. If we were to make an allowance of only 20 mm soil growth from 16 years revegetation with lupins, an estimate which several features indicate is conservative, we would have to add some 470 kg N, 130 kg P, and small amounts of exchangeable K and Ca to the values reported for soils at Hakatere. These values are calculated for an additional 20 mm of the 300–400 soil layer. In the case of pine forest, we would also have to make a substantial further adjustment due to increased root volume displacing soil upwards. In cultural revegetation as in degradation, soil compartments are slower to change in nutrient contents than are biomass pools.

DISCUSSION AND CONCLUSION

Tall tussock grasslands vary considerably in their biomass and nutrient pool characteristics. Some of these variations arise from the physical environment. Some may arise from differences in past treatment. It is difficult to infer with any confidence either the magnitude or the annual or centennial rate of change in carbon or other elements, by comparison of stages of ecological degradation, except in conditions chosen with some care to avoid influence by some factor other than the degradation itself. The outcomes of our attempts to choose comparable sites encourage us to sustain the work of quantification of nutrient pools in benchmark soil-vegetation systems, chosen to represent both natural and degraded facets in a continuum of ecological history of pastoralism in different terrains.

The present study has so far clearly demonstrated only the self-evident, that weights of above-ground biomass and nutrient pools are substantially lower in transformed and degraded vegetations than they are in the vegetations from which they were derived. Where transformation of tall tussock grassland is involved, we have found only limited evidence that the substantial reduction in carbon and nutrients involved in destruction of above-ground biomass has led to a discernible reduction in carbon or nutrients in the system as a whole. The weedy short grasslands included in this survey were almost certainly transformed from tall grasslands, at least to the stage of short tussock grasslands, early in pastoral occupation. The net losses of nutrients which they suffered in early pastoral fires would have been considerable, especially in volatilised compounds of nitrogen and possibly of sulfur, and in compounds of phosphorus and bases that could have been blown away as ash. The examples of N and P may be used to illustrate.

The mean difference between above-ground biomass of tall tussock grassland and that for weedy short grassland in our study (152 kg N ha^{-1}) is of the same magnitude as the loss likely to ensue from one or two fires in the first years of pastoral occupation, for the above value is approached or exceeded by the above-ground biomass N of most of our nine tall tussock grasslands. The corresponding margin in above-ground P between tall tussock grassland and weedy short grassland (22 kg P ha^{-1}) is also of the same order of magnitude as the above-ground biomass P in our survey. P in ash is less likely to escape completely from the landscape than are gaseous products of fire, but it is subject to transfer by redeposition as windblown ash. Transformation of tall tussock grasslands to short grasslands as a consequence of early fire and grazing induced a vegetation system no longer capable of subtending in its above-ground biomass the weight of nutrients including bases which had previously been there. P and cation re-

ductions in biomass compartments would be reflected in some soil enrichment, which might have persisted for some time, just as we have surmised from the burning of forest in the history of North Island pasture development.

In our current results we can discern no clear evidence of reduction in nutrients in soil pools, associated with the reduction in biomass and nutrient pools above-ground. We do not conclude that nutrients have not been lost from the soil, but we have found no evidence here to support any claim that they have been lost. We accept that there is some evidence of change in soil nutrient regimes following transformation of tall tussock grasslands to short grasslands. McIntosh et al. (1981) in an intensive topsoil survey at two Upper Waitaki localities, Glencairn and Longslip, recorded clear differences in topsoil (0–75 mm) C, N, total P, Olsen P and exchangeable bases in relation to topographic position and precipitation regimes. Many differences were attributed to “soil rejuvenation”, especially on sunny slopes, terrains from which, even at Glencairn with only 500 mm rainfall, tall tussock had probably been destroyed, in our view, by early fire and grazing.

We endorse the suggestion of those authors that the depletion of vegetation cover and consequent higher inorganic P and Olsen P values which they recorded in soils under short tussock grassland are likely outcomes of pastoral culture. We suspect that such effects of fire and grazing in transforming tall tussock grassland to short grassland have persisted since the nineteenth century. In the case of Longslip, the more humid of the two localities, further burning and grazing in this century may have continued or renewed the process. We interpret the demonstrated difference in Olsen P in topsoil between sites under *Chionochloa rigida* and sites in short grassland where soils are otherwise similar, as evidence of increased mineralisation of organic P. We ascribe it to ecological degradation during pastoral occupation.

Likewise, we accept the evidence reviewed by McIntosh (1997), from Glencairn dry sites (500 mm rainfall) revisited after 15 years, of significant changes in nutrient status of 0–75 mm soil layer in unimproved grasslands under grazing. (McIntosh et al. 1996). We agree that such changes in soil N as were measured there are greater than would be explained by grazing transfers alone, and that burning losses were not involved. McIntosh’s suggestions of soil erosion or accelerated mineralisation of soil organic matter and leaching “in areas depleted of tussock cover” point to the likelihood of incipient desertification as a precursor to nutrient loss, rather than as its consequence. McIntosh et al. (1997) have recently demonstrated in the same locality, that desisting from grazing for 15 years and countering the depleting effects of grazing by oversowing weedy short grasslands resulted in increased biomass above and below ground and higher total biomass pools of Ca, Mg, P, S, K and N. This supports their earlier inference that current grazing use was associated with continuing nutrient loss. It is noteworthy that, like our revegetation with legumes at Mt Possession over a similar time span, their oversowing with lucerne without fertiliser did not result in significant differences in total nutrients in the soil compartment, 0–250 mm, above the levels of the grazed or ungrazed-without-oversowing treatments, except in the case of exchangeable K.

How then do we reconcile our present failure to detect differences in soil pools attributable to past ecological changes with this evidence from unimproved grasslands

in North Otago of system losses of nutrients, even affecting topsoil pools? We believe some factors differentiate our situations from those of the North Otago studies. First, in the more moist regimes and less open vegetation which we have examined, there are indications of nutrient conservation in the soil system. This could be, in part at least, an outcome of the phenomenon described and quantified by Robinson and Macdonald (1964) for a weedy short grassland ecosystem of the Craigieburn terraces, where mineralisation of soil organic matter occurred at a very low rate, reflecting the scarcity of available energy substrate for the dominant bacterial flora. Williams et al. (1977a) have already suggested a phenomenon of "pseudo-ageing" as central to nutrient conservation of such short grassland systems, here characterised as suffering from "deterioration", in Cockayne's parlance. In North Otago, in contrast, where grassland "depletion" is more characteristic on sunny slopes of dry sub-humid short tussock grasslands (Glencairn), or even among open tall tussock grasslands, especially on steep slopes (Longslip), soil erosion and mineralisation of residual soil organic matter are likely mechanisms of nutrient loss from soil itself.

While further research along such lines in different climatic regimes may reveal the mechanisms of accelerated nutrient loss as well as those of nutrient conservation in degraded systems, we can indicate the empirical answer for South Island, New Zealand to our earlier question of the relationship of nutrient loss to desertification: Is loss of nutrients from ecosystems a contributor to range deterioration and thereby to desertification, or is it a consequence of desertification?

We conclude that initial fire and grazing achieved most biomass destruction through transformation of tall tussock grasslands and scrub to short grasslands. We conclude that range deterioration and nutrient loss from biomass destruction have been concomitant effects of early pastoral burning and grazing. We infer that continued grazing, sustained for long periods in seasonally repetitive fashion, has allowed animal preferences to reduce the already limited quality of forage available. We interpret this as the primary feature in range deterioration, a deficiency of suitable forage which might have been assuaged for the moment, but could not be permanently counteracted, by periodically resorting to fire.

So long as tall tussock grasslands continued to be burned during the last 100 years, they would lose more nutrients from biomass, especially N and probably S. So long as they recovered from fire, tussock grasses would have to draw on their own reserves, perhaps for some years, drawing also on mineralised nutrients from soil organic matter for themselves and for the adventive plants that were now able to flourish amongst them (O'Connor and Lambrechtsen 1964, Payton et al. 1986, Yeates and Lee 1997, Ross et al. 1997). The fact that induced or modified vegetation recovers from such periodic fire, does not gainsay the evidence that nutrients are lost from the system and the inference that levels of nutrients in soil organic matter pools are lowered. More thorough understanding of this resource-exploiting situation has given rise to more vigorous challenge to its sustainability (Mark 1994). We do not see the evidence of such rates of nutrient loss from biomass destruction leading to desertification, even though we believe that the practice of repeated burning without replacement of nutrients and vegetation cover of soil is unsustainable.

We infer from the earlier model of nutrient balances in tussock grasslands (O'Connor and Harris 1992) and especially from its recent revision by Harris and O'Connor (1998), that animal transfers under extensive grazing practice and periodic rabbit plagues, and not fires, have been the most significant agents of continuing nutrient wastage from unimproved rangeland systems in the past. We recall the especially severe and prolonged declines in livestock numbers in drier regions of the high country (O'Connor 1986). We infer that depletion compounded the problem of deterioration in semi-arid and dry sub-humid regions.

We surmise that sustained depletion of grass cover in semi-arid and dry sub-humid districts that led to incipient desertification, may have thereby led to further loss of nutrients by surface soil erosion or accelerated mineralisation of organic matter and seasonal leaching, in line with recent research by McIntosh et al. (1996). We believe from the evidence of the first Longslip study referred to (McIntosh et al. 1981), that this kind of effect of severe depletion of vegetative cover could be significant, even in humid districts when biomass destruction on steep slopes led to exposure of bare soil or incomplete occupation of soil systems by vegetation.

In review, high country pastoralism accomplished its principal transformations of vegetation very early in pastoral occupation. In the process of that biomass reduction, considerable amounts of nutrients were lost, especially those volatilised in fire. For another 100 years, many tall tussock grasslands persisted despite periodic burning involving further nutrient loss, because grazing pressure after fire was seldom sufficient to prevent vegetation recovery. During all that time, in tall grasslands and in short, extensive pastoralism continued to wear away at nutrient capital, principally through animal grazing and nutrient transfer.

For all this attrition of system nutrients, soil pools may show little net change, except where surface erosion and mineralisation of organic matter has been promoted by depletion of cover. Cultural revegetation with exotic herbaceous or forest cover may have as dramatic effects in rebuilding biomass nutrient pools without having much obvious effect on soil nutrient pools. The apparent ability of less arid high country soils and their organic regimes to buffer ecosystems against dramatic change in nutrients warrants further research attention. This should accompany research into the significance of organic matter maintenance in drier soils. High risks of loss of nutrients from biomass pools may affect forestry and animal husbandry systems in mountain environments, if systems are not well buffered or well managed. Both land uses share with natural vegetation systems the prospect and the need of rebuilding systems with nutrient frugality.

REFERENCES

- Buchanan, J. 1880. *Manual of the Indigenous Grasses of New Zealand*. Colonial Museum and Geological Survey Department, Wellington.
- Buchanan, J. 1867. Botanical notes on the Kaikoura Mountains and Mount Egmont. *New Zealand Geological Survey, Reports of Geological Explorations* 1, 1–16.
- Buchanan, J. 1868. Sketch of the botany of Otago. *Transactions N.Z. Institute* 1 (Part III), 22–53.
- Butler, S. 1862. *A First Year in Canterbury Settlement*. Longman, Roberts and Green, London.

- Cockayne, L. 1899. A sketch of the plant geography of the Waimakariri river basin, considered chiefly from an oecological point of view. *Transactions N.Z. Institute* 32, 95–136.
- Cockayne, L. 1919. An economic investigation of the montane tussock-grassland of New Zealand No. II. Relative palatability for sheep of the various pasture-plants. *N.Z.J. Agric.* 18, 321–331.
- Cockayne, L. 1920a. An economic investigation of the montane tussock-grassland of New Zealand No. VI. Further details regarding the relative palatability for sheep of various pasture-plants. *N.Z.J. Agric.* 20, 209–217.
- Cockayne, L. 1920b. An economic investigation of the montane tussock-grassland of New Zealand No. VIII. An experiment in Central Otago concerning the relative palatability for sheep of various pasture-plants. *N.Z.J. Agric.* 21, 176–188.
- Cockayne, L. 1920c. An economic investigation of the montane tussock-grassland of New Zealand No. IX. Further details regarding the Earnscliffe (Central Otago) palatability experiment. *N.Z.J. Agric.* 21, 324–334.
- Cockayne, L. 1928. *The Vegetation of New Zealand*. 2nd edn. Engelmann Press, Leipzig.
- Connor, H.E. 1964. Tussock grassland communities in the Mackenzie Country, South Canterbury, New Zealand. *N.Z.J. Bot.* 2, 325–351.
- Connor, H.E. 1965. Tussock grasslands in the middle Rakaia Valley, Canterbury, New Zealand. *N.Z.J. Bot.* 3, 261–276.
- Connor, H.E. 1992. The botany of change in tussock grasslands in the Mackenzie Country, South Canterbury, New Zealand. *Review Journal of the New Zealand Mountain Lands Institute* 49, 1–31.
- Connor, H.E. and MacRae, A.H. 1969. Montane and subalpine tussock grasslands in Canterbury. In: *The Natural History of Canterbury* (ed. G.A. Knox). A.H. and A.W. Reed, Wellington, 167–204
- Davis, M.R. 1991. The comparative phosphorus requirements of some temperate perennial legumes. *Plant and Soil* 133, 17–30.
- Evans, G.R. 1980. Phytomass, litter and nutrients in montane and alpine grasslands, Craigieburn Range, New Zealand. In: *Mountain Environments and Subalpine Tree Growth*. Proceedings of IUFRO Workshop November 1979, Christchurch, New Zealand (eds. U. Benecke and M.R. Davis). New Zealand Forest Service, Wellington, pp. 95–109.
- Harris, P. and O'Connor, K.F. 1998. *Effects of Pastoralism on Nutrient Status of Groups of Runs Within the Upper Waitaki Catchment, New Zealand: Historical Study*. Mountain Studies II. Centre for Mountain Studies, Lincoln University.
- Kelland, C.M. 1978. Chemical analyses of some soils from the Craigieburn Range. In: *Revegetation in the Rehabilitation of Mountain Lands*. F.R.I. Symposium No.16, 3–5 December 1974 (ed. J. Orwin). N.Z. Forest Service Forest Research Institute, Wellington, 51–59.
- McGlone, M.S. 1988. New Zealand. In: *Handbook of Vegetation Science 7. Vegetation History* (eds. B. Huntley and T. Webb). Kluwer Academic Publishers, Dordrecht, 557–599.
- McIntosh, P.D. 1997. Nutrient changes in tussock grasslands, South Island, New Zealand. *AMBIO* 26, 147–151.
- McIntosh, P.D., Allen, R.B. and Scott, N. 1997. Effects of exclosure and management on biomass and soil nutrient pools in seasonally dry high country, New Zealand. *J. Environ. Manage.* 51, 169–186.
- McIntosh, P.D., Backholm, G. and Smith, J. 1981. Soil variation related to landscape and vegetation features in North Otago hill country. *N.Z.J. Sci.* 24, 225–244.
- McIntosh, P.D., Ogle, G.I., Patterson, R.G., Aubrey, B., Morris, J. and Giddens, K. 1996. Changes of surface soil nutrients and sustainability of pastoralism on grazed hilly and steep land, South Island, New Zealand. *J. Range Manage.* 49, 361–367.

- Mark, A. 1992. Indigenous grasslands of New Zealand. In: *Ecosystems of the World*. Vol. 8B. Grasslands, Eastern Hemisphere (ed. R.T. Coupland). Elsevier, Amsterdam, 361–410.
- Mark, A. 1994. Effects of burning and grazing on sustainable utilisation of upland snow tussock (*Chionochloa* spp.) rangelands for pastoralism in South Island, New Zealand. *Aust. J. of Bot.* 42, 149–161.
- Meurk, C.D. 1978. Alpine phytomass and primary productivity in Central Otago, New Zealand. *N.Z.J. Ecol.* 1, 27–50.
- Molloy, B.P.J., Burrows, C.J., Cox, J.E., Johnston, J.A. and Wardle, P. 1963. Distribution of subfossil forest remains, eastern South Island, New Zealand. *N.Z.J. Bot.* 1, 68–77.
- Molloy, L.F. and Blakemore, L.C. 1974. Studies on a climosequence of soils in tussock grasslands. 1. Introduction, sites and soils. *N.Z.J. Sci.* 17, 233–255.
- Molloy, L.F., Bridger, B.A. and Cairns, A. 1978a. Studies on a climosequence of soils in tussock grassland. 15. Litter decomposition: weight losses and changes in contents of total N and organic constituents. *N.Z.J. Sci.* 21, 265–276.
- Molloy, L.F., Bridger, B.A. and Cairns, A. 1978b. Studies on a climosequence of soils in tussock grassland. 16. Litter decomposition: changes in the contents of some nutrient elements. *N.Z.J. Sci.* 21, 277–283.
- Nordmeyer, A.H. 1980a. Tree nutrient concentrations near timberline, Craigieburn Range, New Zealand. In: *Mountain Environment and Subalpine Tree Growth*. Proceedings of IUFRO Workshop November 1979, Christchurch, New Zealand (eds. U. Benecke and M.R. Davis). New Zealand Forest Service, Wellington, 83–94.
- Nordmeyer, A.H. 1980b. Phytomass in different tree stands near timberline. In: *Mountain Environment and Subalpine Tree Growth*. Proceedings of IUFRO Workshop November 1979, Christchurch, New Zealand (eds. U. Benecke and M.R. Davis). New Zealand Forest Service, Wellington, 111–124.
- Nordmeyer, A.H., Kelland, C.M., Evans, G.R. and Ledgard, N.J. 1987. Nutrients and the restoration of mountain forests in New Zealand. In: *Human Impacts and the Management of Mountain Forests* (eds. T. Fujimori and M. Kimura). Forestry and Forest Products Research Institute, Ibaraki, Japan, 145–154.
- O'Connor, K.F. 1980. The use of mountains: a review of New Zealand experience. In: *The Land our Future: Essays on Land Use and Conservation in New Zealand* (ed. A.G. Anderson). Longman Paul and New Zealand Geographic Society, Auckland, 93–222.
- O'Connor, K.F. 1982. The implications of past exploitation and current developments to the conservation of South Island tussock grasslands. *N.Z.J. Ecol.* 5, 97–107.
- O'Connor, K.F. 1986. The influence of science on the use of tussock grasslands. *Review Journal of the Tussock Grasslands and Mountain Lands Institute* 43, 15–78.
- O'Connor, K.F. and Harris, P.S. 1992. Biophysical and cultural factors affecting the sustainability of high country pastoral land uses. In: *The Proceedings of the International Conference on Sustainable Land Management*, Napier, Hawkes Bay, New Zealand, 17–23 November 1991 (ed. P. Henriques). Hawkes Bay Regional Council, Napier, 304–313.
- O'Connor, K.F. and Kerr, I.G.C. 1978. The history and present pattern of pastoral range production in New Zealand. In: *Proceedings of the First International Rangeland Congress*, Denver, Colorado. American Society of Range Management, Denver, 104–107.
- O'Connor, K.F. and Lambrechtsen, N.C. 1964. Studies on the management of snow-tussock grassland III. The effects of burning, fertilizer, and oversowing on a mid-altitude tall-tussock in South Canterbury, New Zealand. *N.Z.J. Agric. Res.* 7, 264–280.
- O'Connor, K.F. and Nordmeyer, A.H. 1996. Issues and options in high country farming. 4. Cycling nutrients for sustainable management. *Proc. N.Z. Grassld. Assn.* 58, 153–159.

- Payton, I.J., Lee, W.G., Dolby, R. and Mark, A.F. 1986. Nutrient concentrations in narrow-leaved snow tussock (*Chionochloa rigida*) after spring burning. N.Z.J. Bot. 24, 529–537.
- Petrie, D. 1883. Some effects of the rabbit pest. N.Z.J. Sci. 1 (old series), 412–414.
- Petrie, D. 1895. List of the flowering plants indigenous to Otago, with indications of their distribution and range in altitude. Transactions N.Z. Institute 28, 540–591.
- Petrie, D. 1912. Report on the grass-denuded lands of Central Otago. N.Z. Dept. Agric. Ind. Comm. Bulletin 23 (i.e. 28). Wellington, Government Printer.
- Robinson, J.B. and Macdonald, G.M. 1964. Respiration and bacterial growth in a New Zealand grassland soil. N.Z.J. Agric. Res. 7, 569–582.
- Ross, D.J., Speir, T.W., Tate, K.R. and Feltham, C.W. 1997. Burning in a New Zealand snow-tussock grassland: effects on soil microbial biomass and nitrogen phosphorus availability. N.Z.J. Ecol. 21, 63–71.
- Soil Bureau 1968a. Soils of New Zealand. Part 3. NZ Soil Bureau Bulletin 26(3). Department of Scientific and Industrial Research. Wellington, 127 pp.
- Soil Bureau 1968b. General Survey of the soils of South Island, New Zealand. N.Z. Soil Bureau Bulletin 27. Department of Scientific and Industrial Research, Wellington, 404 pp.
- Southern Pastoral Lands Commission 1920. Report of Commission to inquire into and report upon southern pastoral lands. Appendix to the Journal of the House of Representatives NZ 1920 C.15, 24 pp.
- Treskonova, M. 1991. Changes in the structure of tall tussock grasslands and infestation by species of *Hieracium* in the Mackenzie Country, New Zealand. N.Z.J. Ecol. 15, 65–78.
- Wardle, P. 1991. Vegetation of New Zealand. Cambridge University Press, Cambridge.
- Williams, P.A. 1977. Growth, biomass, and net productivity of tall-tussock (*Chionochloa*) grassland, Canterbury, New Zealand. N.Z.J. Bot. 15, 399–442.
- Williams, P.A., Nes, P. and O'Connor, K.F. 1977a. Macro-element pools and fluxes in tall-tussock (*Chionochloa*) grassland, Canterbury, New Zealand. N.Z.J. Bot. 15, 443–476.
- Williams, P.A., Grigg, J.L., Mugambi, S., Nes, P. and O'Connor, K.F. 1977b. Properties of tall tussock (*Chionochloa*) shoots and soils in New Zealand natural grasslands. Tussock Grasslands and Mountain Lands Institute Special Publication 12. Lincoln College, Canterbury.
- Williams, P.A., Mugambi, S., Nes, P. and O'Connor, K.F. 1978a. Macro-element composition of tall-tussocks (*Chionochloa*) in the South Island, New Zealand, and their relationship with soil chemical properties. N.Z.J. Bot. 16, 479–498.
- Williams, P.A., Grigg, J.L., Mugambi, S. and O'Connor, K.F. 1978b. Soil chemical properties beneath tall-tussocks (*Chionochloa*) in South Island, New Zealand. N.Z.J. Sci. 21, 149–156.
- Yeates, G.W. and Lee, W.G. 1997. Burning in a New Zealand snow-tussock grassland: effects on vegetation and soil fauna. N.Z.J. Ecol. 21, 73–79.