ECOSYSTEM SERVICES IN NEW ZEALAND'S INDIGENOUS TUSSOCK GRASSLANDS: CONDITIONS AND TRENDS

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ABSTRACT: Indigenous vegetation such as grassland provides a range of services of varying values to humanity, depending on grassland type and degree of intactness. Understanding this complex relationship in a particular ecosystem or related ecosystems is most important and should be an integral component of environmental planning. To set the scene, some historical aspects of the origins, development, management and research in New Zealand's indigenous grasslands are described, and changes in land tenure are outlined to provide a background against which the ecosystem services that grasslands have to offer can be better understood. The ecosystem services that different grassland types are able to provide are described according to the Millennium Ecosystem Assessment categories, especially those of provisioning (biodiversity values); regulating (water production, pollination, biological control); cultural (educational, scientific, recreational and tourism values); and supporting (soil conservation values, carbon storage and sequestration). The threats to these services are then described with emphasis on land use (grazing and intensification, mining), invasive weeds and invertebrates, and climate change. We conclude by pointing out that indigenous grassland ecosystems deliver a wide range of important ecosystem services that provide many tangible benefits to human well-being, which are best protected in public ownership and managed as a critically important public-good resource.

Key words: biodiversity, ecosystem services, grasslands, invasive species, soil, water.

INTRODUCTION

Indigenous vegetation provides a range of services of varying values to humanity. These are associated with the normal functioning of components in integrated ecological systems. The type and level of service inevitably varies among ecosystems but New Zealand's indigenous grasslands can contribute multiple services depending on grassland type and their degree of intactness. As the human population and associated land-use pressures increase in New Zealand, many ecosystem services provided by indigenous ecosystems are reduced and threatened. Understanding this complex relationship in a particular ecosystem or related ecosystems is most important and should be an integral component of environmental planning.

The normal functioning of most ecosystems provides many tangible benefits to human well-being that are usually taken for granted by the general public unless they become obvious by a sudden disruption or threatened failure. Most ecosystem services cannot be privately owned, so are appropriately treated as 'public good', which adds to their risk of being ignored or inadvertently threatened. In addition, disturbing an ecosystem in a particular location often causes effects elsewhere.

The Millennium Ecosystem Assessment (2005) provides a framework for considering ecosystem services derived from indigenous grasslands, categorising ecosystem services as: provisioning (food, fibre, water, fuel, genetic resources); regulating (air quality, climate, water flow, pollination, erosion control, pest and disease control); cultural (spiritual, aesthetic, recreational, educational) and supporting (photosynthesis, soil formation, nutrient cycling). In this chapter we address some of these categories and outline the role of tussock grasslands in the major types of New Zealand's indigenous grasslands.

NEW ZEALAND'S INDIGENOUS GRASSLANDS

Historical aspects

It has been well established that indigenous grasslands probably reached their greatest extent just before European settlement in the 1840s (Holloway 1959; Mark 1993; Mark and McLennan 2005) and this is frequently used as a conservation baseline. Although debated, this baseline is somewhat easier to establish than a prehuman one of for example AD 1100. However, the biota of these grasslands before European settlement essentially comprised only indigenous biota. Moreover, the pattern is consistent with overseas situations where, unlike New Zealand, humans had been present much longer yet had similar impacts on the indigenous vegetation; thus, early human activities generally favoured non-woody, particularly grassland, vegetation because of its generally greater adaptation to fire than the indigenous woody flora (Ogden et al. 1998).

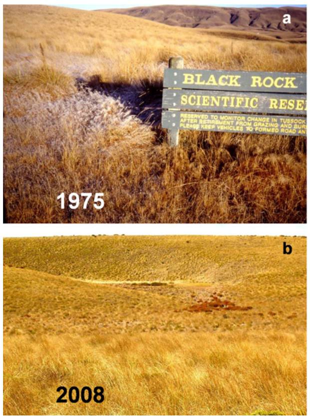
However, the extent of grassland in this rain-shadow region before Polynesian settlement continues to be the subject of debate, much of it based on the Central Otago region. A widely held view considers that areas of low- to mid-altitude tussock grassland, below the climatic treeline in the South Island rain-shadow region, were derived from a woody, mostly forest cover that was removed by not-infrequent burning during the period following Polynesian settlement about 750 years ago (McGlone 2001; Wilmshurst et al. 2008; McWethy et al. 2010). McGlone (2001) considered that in pre-settlement times grassland was 'mostly patchy within the woody ecosystems, occurring in limited areas of droughty or low-nutrient soils and wetlands, or temporarily after infrequent fire or other disturbance'. However, the environmental tolerance of residual populations of a suite of woody taxa led Walker et al. (2003, 2004a, b) to assume forest would have covered the montane and subalpine zones (Figure 1) while 'shrublands may have dominated above the regional treeline'. Walker et al. (2003, p. 58) considered tussock grasses relevant only in the 'alpine tussock-shrubland zone [which] is restricted to the highest elevations in Central Otago … [as on] the summits of the Old Man, Old Woman and Pisa Ranges, and the Garvie Mountains'. They further indicated that 'at low elevations, grassland was probably confined to floodplains and local areas of shallow or permanently moist soils'. Extensive grasslands below

FIGURE 1 A log of thin-barked tōtara, *Podocarpus cunninghamii*, among fescue tussock grassland at 880 metres on the Pisa Range, Lochar Burn, Central Otago. Radiocarbon dating of its outer wood gave a date of AD 1169 ±49 years. This area now has a no-burn covenant associated with its privatisation through tenure review. AFM photo, February 1966.

the treeline would probably have been maintained by fire, but Rogers et al. (2007) found no evidence for this before settlement (after 1000 BP).

Black Rock Scientific Reserve

1972. 144 ha. ~700m. Lammerlaw E.D.



Monitoring results: Mean of 4x1ha. Ht- Frequency method

	1972	1988	2002
Ch. rigida BI	287	690	810
" " *Ht*	*65*	*85*	*100*
He. odora BI	13	8	16
Drac. long.BI	1	2	14
Ozo. lept. BI	2	3	1
Cop. che. BI	13	80	162
Gau. mac.BI	72	106	116
Hyp. cup. BI	8	38	111

Mark & Dickinson. 2004. *N.Z.J. Bot. 41*: 655-68.

FIGURE 2 Biomass index (BI) and height (Ht; cm) over 30 years at Black Rock Scientific Reserve using 4 × 1 hectare plots and the height-frequency method (Mark and Dickinson 2003). **(a)** 1975; **(b)** 2008.

However, Mark et al. (2011) pointed out that there is little evidence for reversion to the historical woody cover predicted by Walker et al. (2003, 2004a, b), at least in two of three long-term (50-year) exclosure plots of long-unburnt (61-year) snow tussock grassland at 1220–1590 metres on the Old Man Range, although a seed source is limited. Similarly, when Mark and Dickinson (2003) studied changes in vegetation over 30 years of non-intervention management on the Black Rock Reserve at 690–770 metres elevation on the Lammerlaw Range (Figure 2), along the eastern margin of the region considered by Walker et al. (2003, 2004a, b), they found that despite predictions to the contrary, only a very sparse woody component accompanied the increased height and dominance of narrow-leaved snow tussock (*Chionochloa rigida*) (Figure 2).

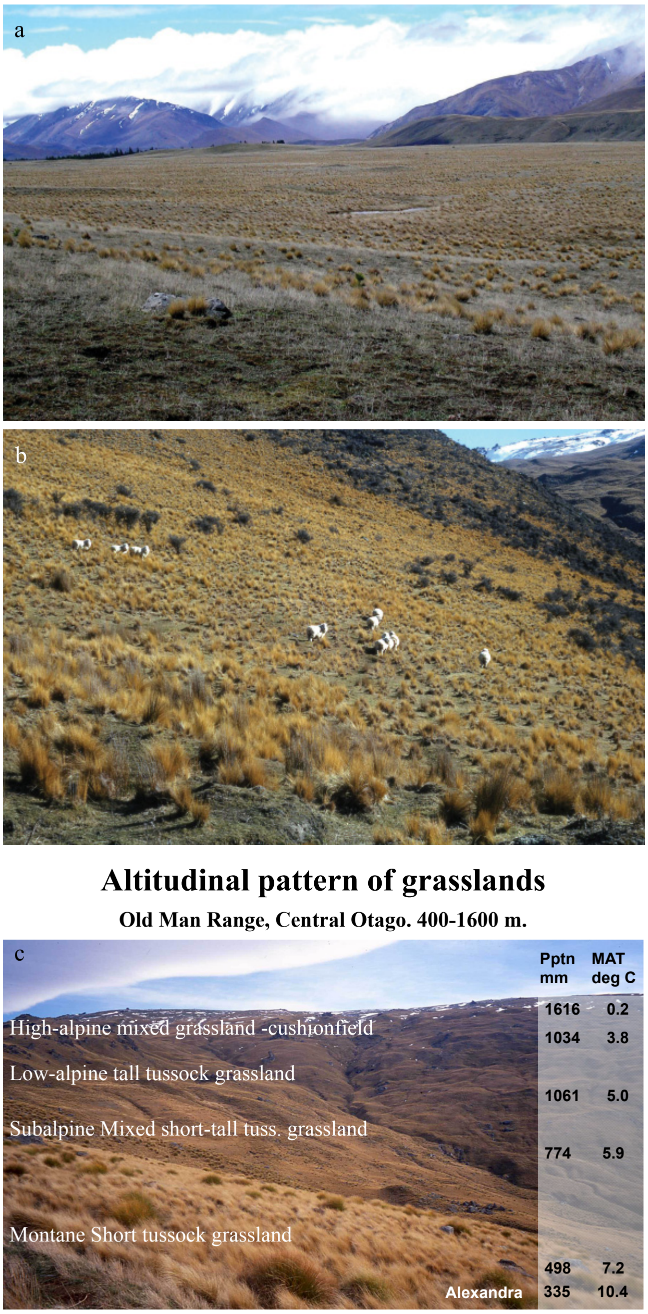


FIGURE 3 Short tussock grasslands: **(a)** Tekapo Scientific Reserve of c. 1000 ha. Short tussock grassland at c. 800 m, Mackenzie Basin, inland South Canterbury, dominated by *Festuca novae-zelandiae*. Protected from grazing for some 20 years. Monitoring has shown a steady improvement in its condition and biodiversity. AFM photo, October 2011.
(b) Montane short tussock (*Festuca novae-zelandiae*) grassland at 460 m, Rock and Pillar Range, Central Otago. Exotic grasses and herbs form the ground cover, with scattered shrubs of the non-leguminous nitrogen-fixing matagouri (*Discaria toumatou*). AFM photo, August 1965.
(c) Altitudinal pattern of grasslands; Old Man Range, Central Otago (400–1600 m). Pptn = precipitation (mm); MAT = mean annual air temperature.

Wardle (1991, pp. 244–245) considered the intermontane basins of Marlborough, South Canterbury and Central Otago in pre-settlement times were probably dominated by short tussock grassland (Figure 3a, b, c), while ‘large *Chionochloa* tussocks were widely dominant on the older, more acid soils of the surrounding slopes, to lower altitudes than to-day’.

Mark et al. (2011) also pointed out that the ecotypic differentiation of *C. rigida* across about 800 metres of altitude on the Old Man Range, in relation to growth rates and patterns (Mark 1965c), and particularly its irregular (mast) flowering (Mark 1965b), was clearly attuned to the associated variation in temperature. Given the extremely slow population turnover of the very-long-lived plants of this species, such genetic differentiation was most unlikely within the c.700-year period of human occupation. Further evidence for the presence of at least localised grassland vegetation on the mid- to lower-mountain slopes comes from the number of specialist Lepidoptera species currently associated with lowland to montane tussock grasslands in the inland South Island (Patrick and Dugdale 2000), and also from the species richness of indigenous moths in the rain-shadow tussock grasslands, from low altitudes to the high-alpine zone (Patrick 2004).

Overall, the evidence is consistent with a natural (i.e. prehuman) grassland component throughout the altitudinal sequence of vegetation on the mountains of the South Island rain-shadow region, most likely as part of a mosaic with woody components, and patterned by physiography and infrequent natural fires. This pattern was described by McGlone et al. (2003) as 'an open mosaic of forest, scrub and grasses', occurring 'between the dense coastal forests of Southland/Otago and the scrub of the interior'; Mark and Dickinson (2003) assumed this pattern was characteristic of the prehuman vegetation of the Lammerlaw Range, eastern Otago uplands.

The difference in pollen size between *Chionochloa* spp. and most of the associated small grasses shows that the non-*Chionochloa* grasses were first to replace the woody vegetation because they reproduced more prolifically, dispersed more effectively, and grew faster than the long-lived and taller species of *Chionochloa* that later prevailed, alone or in mixed shrublands, on the moister upland, low-alpine sites (McGlone 2001). In addition, among the grasses, *Chionochloa* species provide only a modest percentage (10–15%) of the overall pollen rain even when they dominate a site, and even smaller contributions (2–10%) can indicate a substantial presence of snow tussocks. In particular, *Chionochloa* tends to be poorly represented in the pollen rain relative to other grasses for two reasons. First, the characteristic mast flowering in this genus (Kelly et al. 2008, 2013) means pollen is produced in abundance only intermittently, and is low in the many non-masting years, a feature that few other grass genera share; varying flower intensity also has been recorded by Lord (1998) for *Festuca novae-zelandiae*. Second, *Chionochloa* has relatively large pollen grains, so they are less widely dispersed than those of most other grass genera.

Red tussock (*C. rubra*) grassland dominated on the North Island volcanic mountains while broad-leaved snow tussock (*C. flavescens*) and mid-ribbed snow tussock (*C. pallens*) dominated on the other North Island ranges, sometimes together or locally separated by soil factors related to site disturbance. In the South Island's intermontane basins and surrounding areas, the available species was narrow-leaved snow tussock (*C. rigida*), with slim snow tussock (*C. macra*) at higher altitude (Figure 3c), near and above the climatic treeline, while on lower slopes in the moister regions the red or copper tussock (*C. rubra* subsp. *cuprea*) could exploit the displaced woody cover. These species pairs continue to overlap where their specific tolerances merge, as in the Manorburn Ecological District, Central Otago (AFM pers. obs.), Mackenzie Basin (Connor 1964), and mid-Rakaia Valley (Connor 1965). Predictably, all were present and occupying available niches (differentiated mostly by soil moisture status: see Mark et al. 2003, p. 201) in the previous woody-dominated areas. The smaller grasses persisted, at least until European settlement, on the drier, lower elevation and generally less stable areas.

In higher rainfall regions of the country, forest probably persisted up to the time of European settlement. The associated grasslands were mostly low-alpine snow tussock grassland or grass–herbfield throughout upland regions, and mixed tussock grasslands on periodically flooded valley floors below inverted treelines. These grasslands probably remained relatively unmodified up to the time of European settlement.

History of invertebrate research

Our early knowledge of tussock grassland invertebrates has focused mainly on species that have caused damage to plants. Some of the earliest research described damage to tussock plants from Lepidoptera in Canterbury, where scarabaeid larvae were also found to be killing patches of grasses, and where runholders believed that burning tussock in spring reduced the numbers of caterpillars found in tussock plants (Dick 1940). Later, in 1960 the Tussock Grasslands and Mountain Lands Institute (TGMLI) was established to assist sustainable farming of tussock grassland, and an occasional paper on insects was published in its 'Review'. A report of research projects funded by the TGMLI (Anon. 1965) described the research of a student, Graeme White, who had spent 18 months surveying tussock grassland insects in inland Canterbury and eastern Otago. Using a diverse array of trapping methods he collected and identified about 100 000 specimens representing over 1000 species, concluding that the insect fauna of tussock grassland is 'both diverse and extensive'. In a later paper White (1972) emphasised the importance of understanding insect population dynamics if management is to be successful. He also advocated work on plant–insect relationships and on the impacts of insects on plant ecology (White 1970), and researched grasshoppers (White 1975a) and their energetics. He later worked on a whole-system simulation model for a tussock grassland trial area at Tara Hills, North Otago, and carried out long-term light-trapping studies at Cass and other Canterbury sites (White 2002).

Kelsey (1957) listed insects feeding on tussock roots and foliage, and concluded that no one species caused particular damage but all species in combination could reduce vigour and growth. He noted that local infestations of some species inflicted severe damage to tussock plants, and later reported that grass grub and porina, the main pests of lowland pasture, are also the most important pests of tussock grassland (Kelsey 1968), and that aerial application of insecticides was the best solution to the problem.

The concerns of farmers and researchers about insect-related problems in establishing and maintaining exotic pasture species in tussock grassland in Otago prompted research on the ecology and management of the striped chafer (*Odontria striata* White) (Barratt 1982; Barratt and Campbell 1982), and on pests of white clover seedlings oversown into tussock (Barratt and Johnstone 1984). The latter study found that a number of undescribed broad-nosed weevils were responsible for considerable losses of cotyledon-stage white clover seedlings (Barratt et al. 1992).

Knowledge of tussock grassland invertebrate biodiversity and ecology in Otago and Southland was considerably advanced by surveys carried out in the 1980s and '90s. These included the eastern Otago plateau (Barratt and Patrick 1987), Danseys Pass (Patrick 1982), Blue Mountains (Patrick et al. 1985a), Garvie Mountains (Patrick et al. 1985b), Slopedown Range (Patrick et al. 1986), Longwood Range (Patrick et al. 1987), Umbrella Range (Patrick and Barratt 1988), Nokomai Ecological District (Patrick and Barratt 1989), Rastus Burn on The Remarkables (Patrick et al. 1993b), Waipori Ecological District (Patrick et al. 1993a), Hawkdun Ecological District (Patrick 1994), and Waikaia Ecological Region (Dickinson et al. 1998).

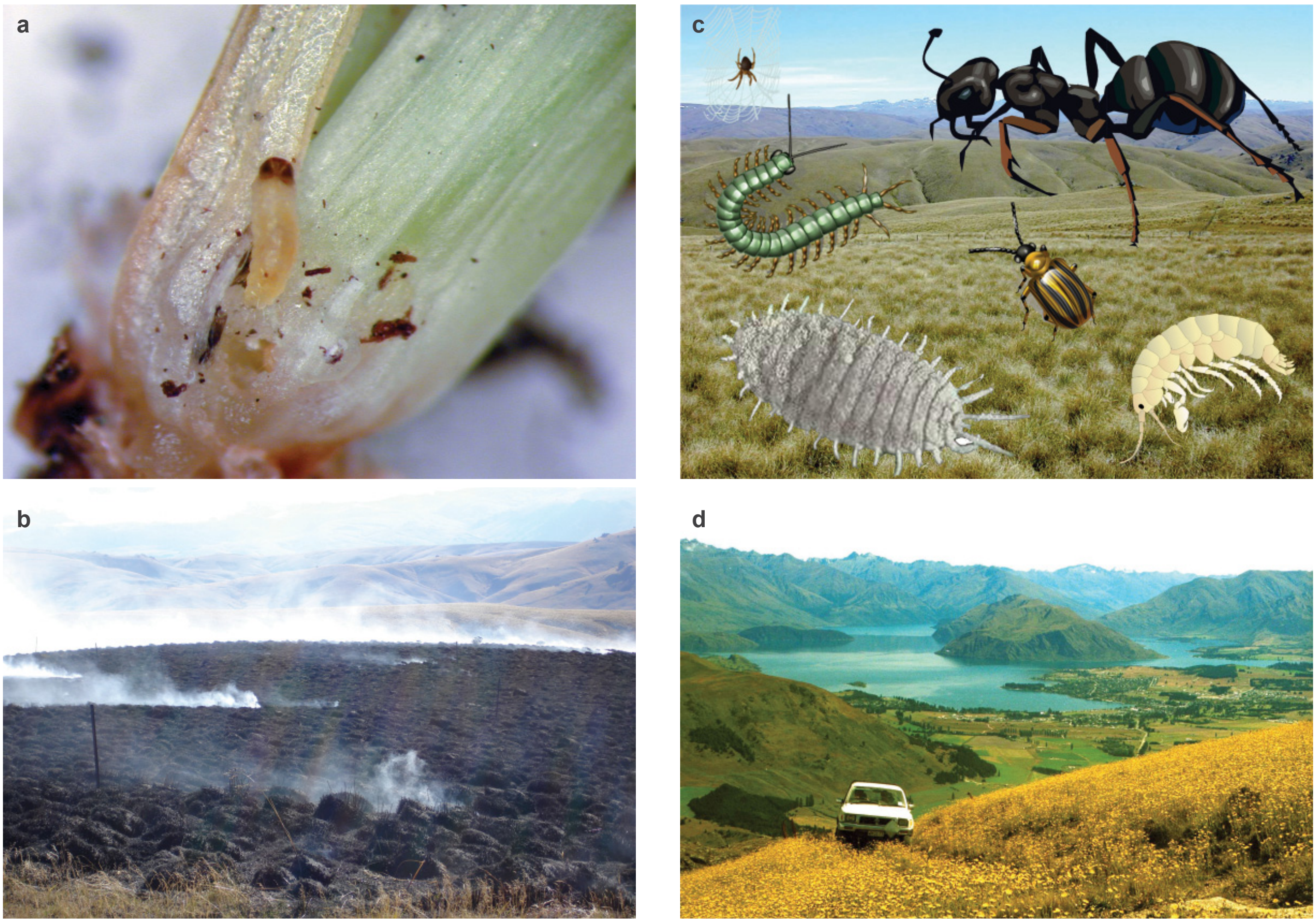


FIGURE 4 Invertebrate studies in Otago: **(a)** Argentine stem weevil (*Listronotus bonariensis*) larva feeding in the tiller of *Poa colensoi*; **(b)** A tussock plot at Mt Benger, Otago, recently burnt as part of a fire study; **(c)** A 'species-scape' for tussock grassland invertebrates where the size of the organism reflects its relative abundance; **(d)** *Hieracium lepidulum* in flower above Lake Wanaka, at an invertebrate survey site. Photos: BIPB.

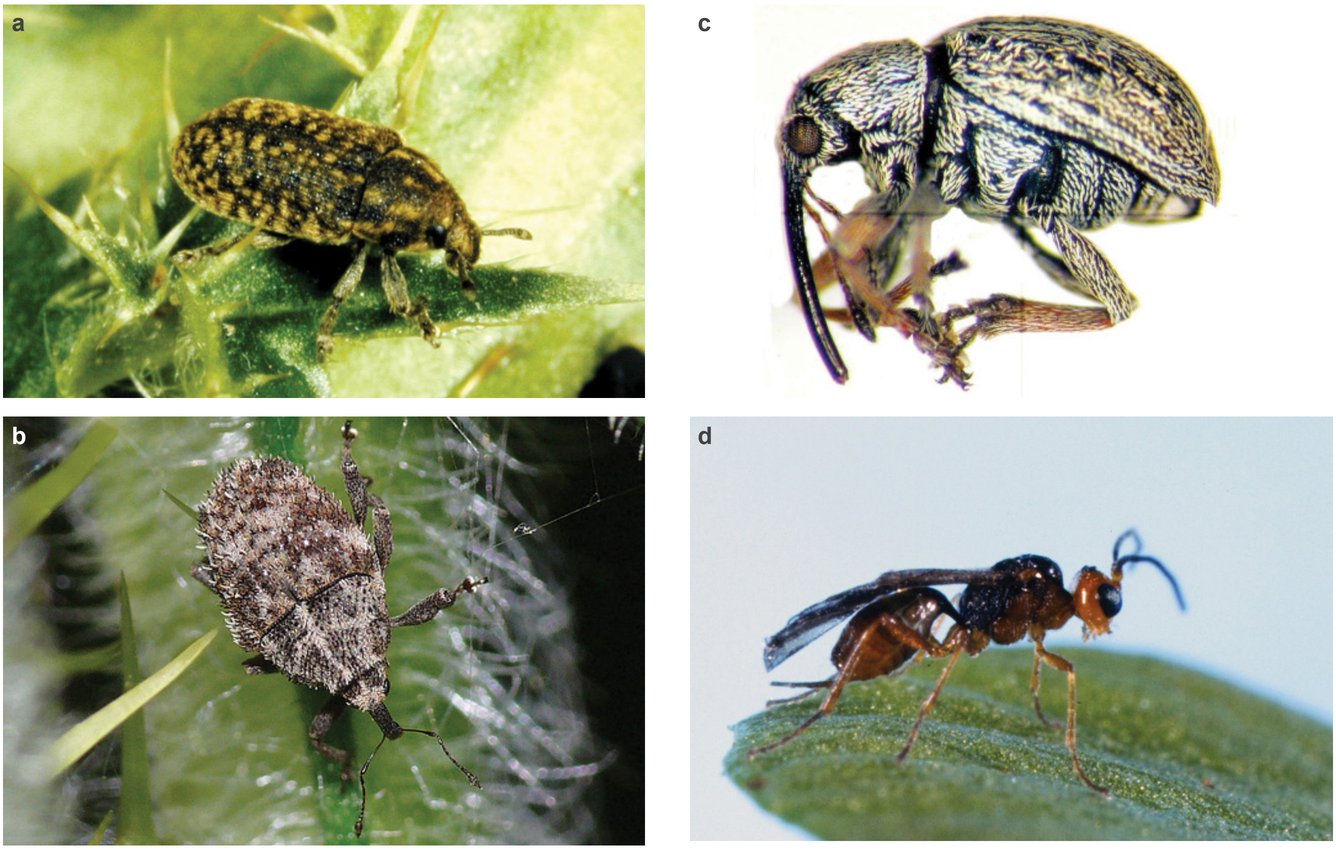


FIGURE 5 Introduced weed and insect pest biological control agents: **(a)** *Rhinocyllus conicus*, introduced for nodding thistle; **(b)** *Trichosirocalus horridus*, also for thistle biocontrol; **(c)** *Exapion ulicis*, introduced to control gorse; **(d)** *Microctonus aethiopoides*, introduced to control lucerne weevil (*Sitona discoideus*).

In the late 1990s, the Department of Conservation initiated a study of the impact of burning in tussock grassland as part of a larger study investigating impacts of fire on the grassland vegetation (Payton and Pearce 2009), and examining the characteristics of fire in tall tussock grassland. This provided an opportunity for more intensive invertebrate sampling, with some baseline information on tussock grassland invertebrate biodiversity (Figure 4) at the two sites selected for this study (Barratt et al. 2005, 2006), and examination of the extent to which introduced biocontrol agents have expanded their range from lower altitude pasture to natural grassland ecosystems (Figure 5). Comparative invertebrate work was carried out at two other native grassland sites, at Cass and near the Tukino Skifield, Mt Ruapehu. These sites were used in conjunction with the Otago sites to investigate impacts on the invertebrate fauna from agricultural development (oversowing with exotic pasture species) and cultivation (Barratt et al. 2012).

Further studies by Otago University students have added to knowledge of tussock grassland invertebrates (Figure 4), such as information on invertebrate biodiversity of tussock shrubland (Derraik et al. 2001, 2002, 2003); biodiversity of insects along a gradient of tussock grassland modification (Dixon 2004), Coleoptera biodiversity (Goodman 2002); Curculionidae and associations with plants (Murray 2001; Murray et al. 2003, 2006); plant–invertebrate relationships (Rate 2005); invertebrates of alpine patterned ground (Scott 2007); and spiders in tussock grassland (Malumbres-Olarte 2010).

THE GRASSLAND PATTERN AT THE TIME OF EUROPEAN SETTLEMENT

Mark and McLennan (2005) attempted to deduce the general pattern of the major indigenous grassland types in immediately pre-European time (1840 baseline); this was a model exercise for the World Conservation Union of IUCN plan to assess the current conservation status of the world's indigenous temperate grasslands.

The New Zealand grassland pattern was assessed on the basis of five major grassland types established in the ecological literature by Cockayne (1928) and Wardle (1991). These patterns are described in Mark (1993), Mark and Dickinson (1997), and Mark and McLennan (2005). Three broad types of wide extent were recognised: lowland to montane short tussock grassland, lowland to montane tall tussock grassland, and subalpine to low-alpine tall tussock grassland. Only the low-alpine grasslands were considered to be strictly natural or primary Figures 3c, 6a, b). In the North Island, the short tussock grassland, generally <50 cm tall, occupied some drier inland areas, and in the South Island, short tussock grassland occupied the lower slopes of the subhumid intermontane basins of Marlborough, inland South Canterbury (Figure 3a), and Central Otago (Figure 3b) below c. 800 metres and where annual rainfall was also less than 700 mm (Figure 3c). The dominant grasses in recent time have been *Festuca novae-zelandiae*, *Poa cita* and locally *Elymus apricus*, but their role in the early post-European grasslands and details of the plant cover at this time remain uncertain, although shrubs and palatable herbs were probably more common (Wardle 1991). *Festuca novae-zelandiae* and *Poa cita* are relatively unpalatable so, as a result of pastoral farming, both have increased and displaced more palatable species (Connor 1964; Mark 1993). Fescue tussock (*F. novae-zelandiae*) is only rarely mentioned in early accounts. Montane to subalpine tall tussock grassland in many areas was dominated by forms of the red tussock, *Chionochloa rubra*, which grows to 1.5 metres tall and has distinctive reddish to copper hues. It was extensive on the North Island volcanic mountains, where limited areas near and above the climatic treeline have persisted as a prominent feature on Mt Egmont (Clarkson 1986) and the central Volcanic Plateau (Atkinson 1981; see Figure 7). Here, in the absence of recent disturbance, indigenous and exotic shrubs have invaded (Rogers and Leathwick 1994).

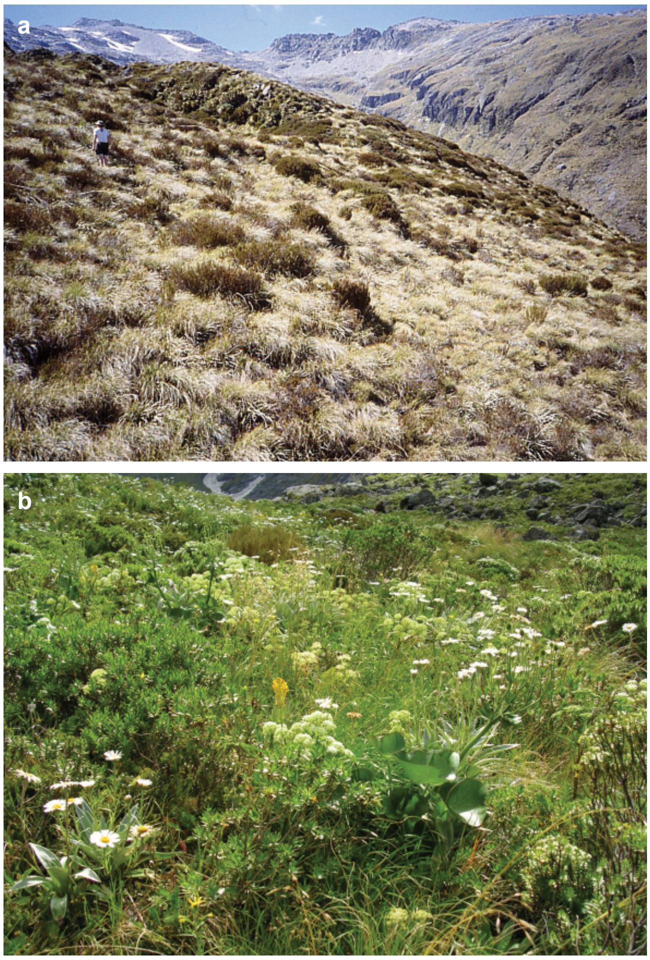


FIGURE 6 Low alpine grasslands: **(a)** Mixed low-alpine shrub (*Dracophyllum rosmarinifolium*) – snow tussock (*Chionochloa rigida* subsp. *amara*) grassland at 1300 metres on Mt Armstrong, South Westland, associated with an eldefulvic soil, described in detail by Molloy and Blakemore (see Mark et al. 2000). AFM photo, January 1996.
(b) Low-alpine snow tussock-herbfield, Gertrude Valley, Fiordland National Park, with large-leaved *Celmisia*, *Bulbinella*, *Ranunculus* and *Anisotome* species among a mixed snow tussock-shrubland. AFM photo, January 2005.

FIGURE 7 Mixed low-alpine red tussock (*Chionochloa rubra*) grass–shrubland, Tongariro National Park, 1450 m. AFM photo, January 1970.

FIGURE 8 Red tussock grass–wetland, Happy Valley, Stockton Plateau, North Westland, where opencast mining by Solid Energy has a requirement to direct transfer some 13 hectares of this 25-hectare grass–wetland. AFM photo, February 2006.

FIGURE 9 Local endemic *Chionochloa juncea*, dominates the bio-rich tussock plateau wetland on the Denniston Plateau, part of the Brunner Coal Measure and now threatened by opencast mining. AFM photo, March 2012.

Red tussock grassland also dominated poorly drained, often peaty soils, particularly depressions below treeline, in both the southern North Island (e.g. Kaiparoro on the northern Tararua Mountains) and northern South Island, while the copper-coloured variant, subsp. *cuprea*, occupied similar habitats from Canterbury–north Westland southwards to Stewart Island. On the infertile, permanently damp Stockton (Figure 8) and Denniston plateaux of the Buller Coal Measures in north Westland, the subsp. *occulta* occupied small fens and the locally endemic *C. juncea* was a more extensive dominant (Figure 9). Both are threatened by current and planned open-cast coal mining. Copper tussock was widespread and dominant over the Southland Plains and locally on valley floors among forest; for example, in eastern Fiordland's Takahe Valley in the Murchison Mountains. It also extended northward on to poorly drained uplands of the Manorburn district of eastern Central Otago where it shared dominance or formed mosaics near its upper limit with narrow-leaved snow tussock close to the original treeline (see Mark et al. 2003; Figs 11, 12). Similar situations occurred along the western fringes of the Canterbury Plains and also further inland (Connor 1964, 1965).

Snow tussock grassland dominated the low-alpine zone on the main axial ranges of the North Island and also above treeline throughout the South Island, descending at least into the subalpine zone on the rain-shadow mountains, where it replaced the destroyed forest. These grasslands included several species of *Chionochloa*, with the overall pattern of species determined by

FIGURE 10 Low-alpine snow tussock grasslands: **(a)** Topography and associated soil factors differentiating low-alpine snow tussock grasslands, Murchison Mountains, Fiordland National Park. Broadleaved snow tussock (*Chionochloa pallens*) codominates with mixed shrubland on the unstable debris slope (centre), with mixed curled (*C. crassiuscula* subsp. *torta*) and narrow-leaved (*C. rigida* subsp. *amara*) snow tussocks dominating the more stable toe, and needle-leaved (*C. acicularis*) and curled snow tussock dominating the poorly drained moraine mound on the left. Takahē (*Porphyrio hochstetteri*) preferentially graze the more nutritious mid-ribbed tussock associated with the more fertile site. AFM photo, February 1973.
(b) Contrasting low-alpine snow tussock dominance related to site disturbance, Denham Ridge, Tararua Range. *Chionochloa pallens* dominates a recent slump with well-drained relatively fertile soils (left) while *C. flavescens* dominates the stable leached and poorly drained stable site (right) each with their distinctive floras (see Williams 1975). AFM photo, November 1968.

elevation, topography, and each species' natural distribution, and local patterns also influenced by soil conditions resulting from the history of site disturbance. Important regional differences in distribution of some of the 14 alpine snow tussock species are assumed to reflect the vagaries of Pleistocene survival (Wardle 1963, 1988, 1991; Burrows 1965) or perhaps tectonic events (McGlone 1985). Altitudinal patterns and more localised ecological patterns among the alpine snow tussock species have been related to variations in topography, particularly as it affects snow-lie (Burrows 1977) or to specific preferences for particular soil and physical factors related to past site disturbances, as in the upper Rakaia Valley (Connor 1965), Tararua Range (Williams 1975), or Fiordland (Williams et al. 1976). In some cases, both topography and specific preferences may influence these patterns, as in south Westland (Mark et al. 2000).

Throughout its wide geographic range (Raukumara Range to Fiordland), *C. pallens* dominated recently disturbed, more fertile and better drained-aerated sites (Figure 10a, b) (see papers cited in previous paragraph). Other snow tussock species associated

FIGURE 11 Low-alpine snow tussock grassland at 860 metres near the summit of Mt Anglem, Stewart Island, dominated by *Chionochloa crassiuscula* subsp. *crassiuscula*, with occasional tussocks of *C. rigida* subsp. *amara* and cushions of *Dracophyllum politum* and *Raoulia goyenii*. AFM photo, February 1973.

FIGURE 12 Snowbank (*Chionochloa oreophila*) grassland (foreground) and curled snow tussock (*C. crassiuscula*) beyond; Pearson Saddle, Mt Aspiring National Park, a permanent monitoring site. AFM photo, March 2007.

FIGURE 13 The upper northern slopes of the Hawkdun Range, North Otago, 1600–1870 m, part of Oteake Conservation Park, on greywacke parent material, showing low-alpine slim snow tussock (*Chionochloa macra*) grassland in good condition (foreground), eroding grassland beyond (mid-distance) and high-alpine fellfield and snowbanks on the highest slopes. AFM photo, January 2007.

with *C. pallens* included *C. flavescens* from the southern North Island to central Westland–Canterbury; *C. australis* (carpet grass), which forms dense low carpets rather than tussocks, in north-west Canterbury and the Tasman district; and three relatively widespread species in the high rainfall western regions: *C. crassiuscula* from north Westland to Stewart Island (Figure 11), *C. rigida* subsp. *amara* from central Westland southwards, and *C. teretifolia* in western Southland and Fiordland.

Tall tussock (*Chionochloa* spp.) grasslands occur in limited areas, including below the treeline in otherwise forested regions; on particularly demanding substrates like the permanent wetlands of the Denniston Plateau in north Westland, where *C. juncea* dominates locally; on peaty coastal benches in Fiordland where *C. acicularis* is a local dominant amongst shrubland, as at West Cape (Wardle et al. 1973); or on ultramafic surfaces in southern Nelson-Marlborough, where *C. defracta* grows among open scrub (Edgar and Connor 2000). The few other alpine species of *Chionochloa* from the high rainfall regions only rarely dominate; the recently described *C. nivifera* is a local dominant mostly at elevations above *C. crassiuscula* grassland in south-eastern Fiordland. Snow-patch grass, *C. oreophila*, is seldom extensive, forming low mats in high-elevation snow-lie areas close to the Alps between Nelson and Fiordland (Mark and Burrell 1966; Burrows 1977; see Figure 12).

In the South Island rangeland region, snow tussock grassland probably spread down-slope from areas above treeline when forest destruction provided a suitable habitat, and merged with the short tussock grassland of the lower slopes and valley floors. South of the Rakaia Valley this involved the narrow-leaved snow tussock, *C. rigida* subsp. *rigida*, which reached an upper limit at 1100–1300 metres (depending on aspect), or somewhat above the climatic treeline at 1000–1100 metres. It was replaced at higher altitudes with the similar slim snow tussock, *C. macra*, which extends to c. 2000 metres, into the high-alpine zone (Figure 13)

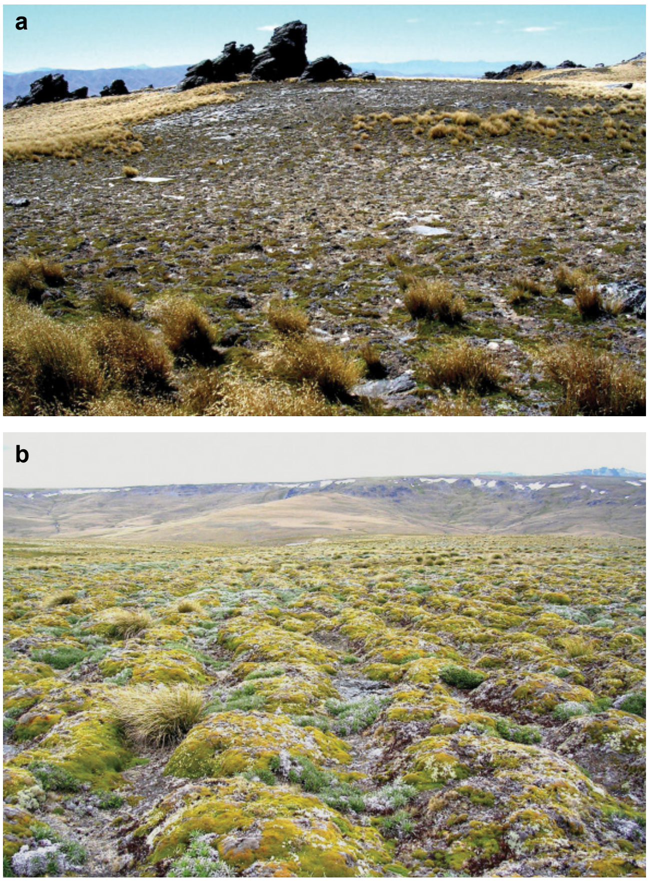


FIGURE 14 Slim snow tussock grassland: **(a)** Crest of the northern Dunstan Mountains, Central Otago, showing an old fire boundary. 1580 m. Cushionfield has been induced from slim snow tussock (*Chionochloa macra*) grassland. AFM photo, January 2006.
(b) Crest of Old Man Range, Central Otago, at 1620 m, showing the ground patterned into soil stripes with some remnant slim snow tussocks, *C. macra*, indicative of an earlier more extensive cover. AFM photo, January 2009.

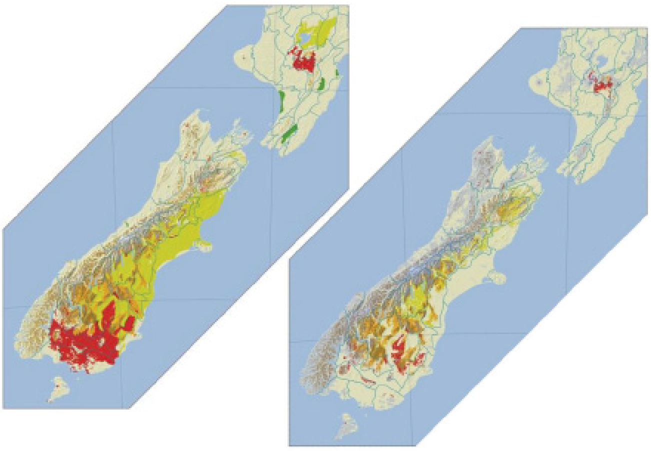


FIGURE 15 Changes in the extent of New Zealand's indigenous grasslands since the arrival of humans. Red is tall red tussock. Light green is short tussock. Brown and orange is tall snow tussock.

where not recently displaced by pastoral farming (Figure 14a, b). North of the Rakaia River this species took the place of *C. rigida*, descending down to c. 500 metres on shaded aspects.

THE GRASSLAND MAPPING EXERCISE

The distribution of five major indigenous grassland types (four of them tussock or bunch grasslands) was reconstructed (minimum scale 1:50 000) on the basis of existing plant cover, interpretation of soils and landforms, available historical accounts, and data from the Land Cover Data base Version One (LCDB 1). Grassland was mapped where grass was assumed to have been at least locally dominant (Figure 15), because grass–woody mosaics were accepted (Mark and McLennan 2005). Information on areas formally protected (as of September 2002) was provided by the Department of Conservation and areas were mapped using ArcGIS with ecological region boundaries. Based on the general pattern of land use and indigenous grassland exploitation, four major geographic regions were identified. Of the baseline area of grassland, 44% remained, and 28% of that – namely, 12.3% of the original baseline area – was formally protected as conservation land. Inevitably, most of this conservation land was modified to varying extents, with the highest portion (87%) in the South Island's western non-rangeland region where much of the steepland, 8.5% of it grassland, had been formally protected from relatively early times. Most grasslands (57.4% of the baseline extent) were located in the rain-shadow uplands of the central and eastern South Island. During European settlement these were quickly allocated for extensive pastoral farming, so by September 2002 only 9.1% of the baseline extent had been formally protected. Grasslands in the South Island's eastern non-rangeland region comprised 23.9% of the baseline area but had been mostly developed for agriculture, so only a

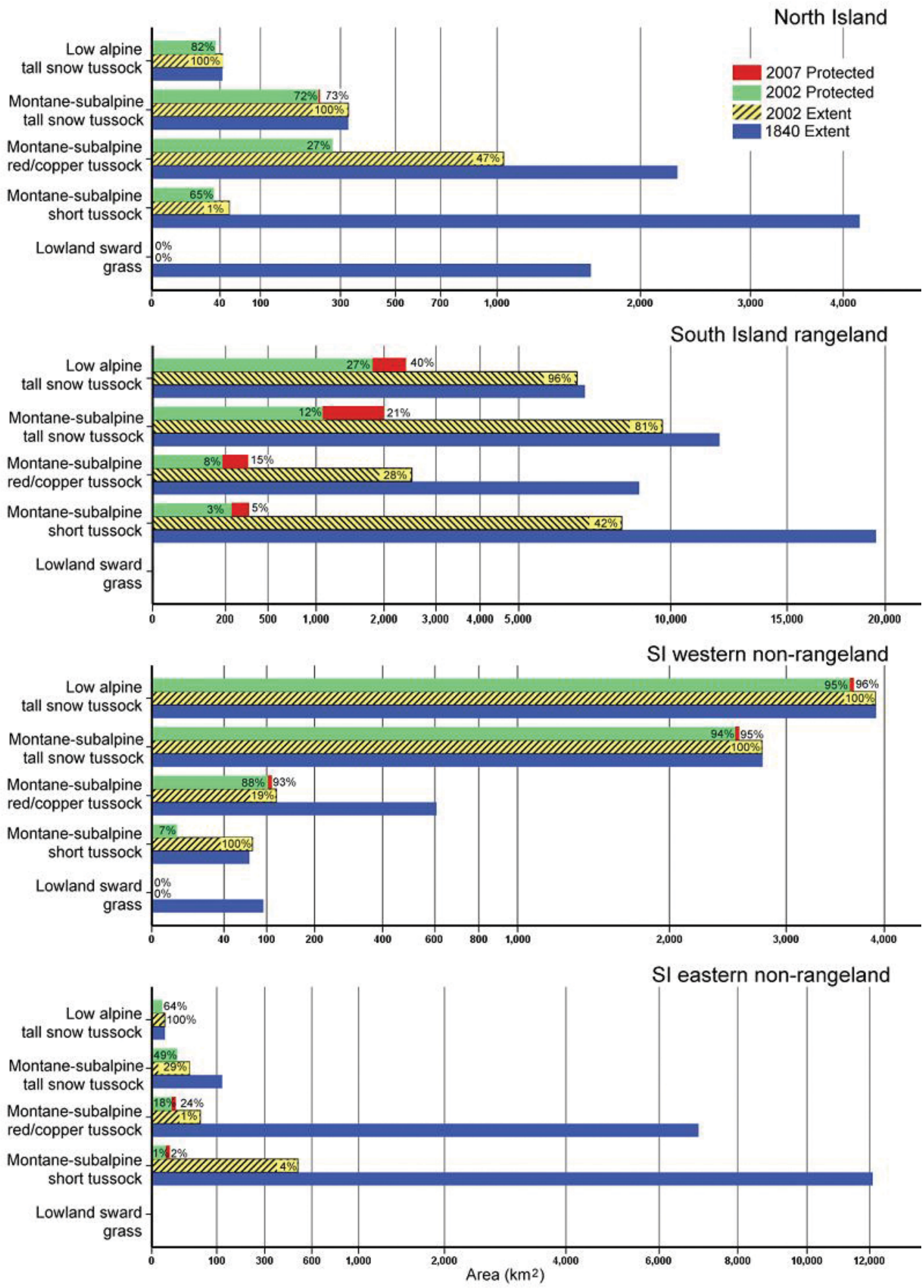


FIGURE 16 Area of each of the five major indigenous grassland types in the four main geographic regions of New Zealand, with values for the baseline (1840) and extent of these types remaining, as well as formally protected in Sep. 2002 and Dec. 2007. The lowland sward grassland no longer exists. Also note the different scales of area in each graph.

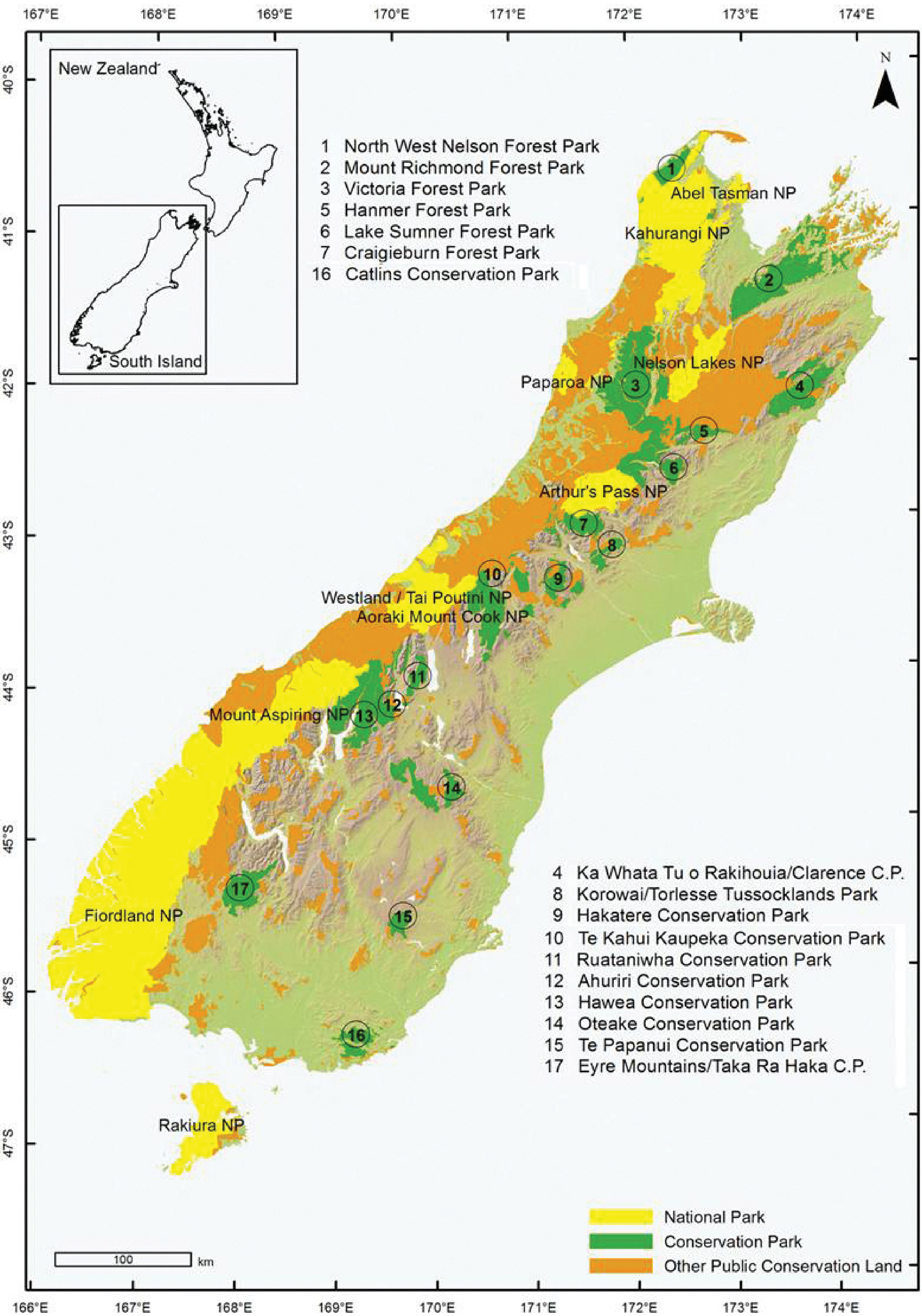


FIGURE 17 Map of South Island conservation parks.

meagre 0.3% was formally protected, while in the North Island in September 2002, grasslands comprised 10.2% of the baseline grassland area and 6.8% was protected (Mark and McLennan 2005).

Grassland types varied with altitude and this was most important in the rangeland region. There, grassland extended over a relatively wide altitude from montane short tussock grassland on the lower slopes, through subalpine mixed short–tall snow tussock grassland to low-alpine snow tussock grassland on the mid- and upper slopes, and mixed tussock–herbfield–cushionfield on the mountain summits (Mark 1993; Mark and Dickinson 1997; see Figure 3c). The level of protection varied substantially with altitude, reflecting the decreasing productivity and increasing environmental severity associated with increasing altitude (Mark 1965a). By September 2002, 96% of the low-alpine snow tussocklands still remained, albeit variously modified through 150 years of pastoral farming, and 27% of this was formally protected. At lower altitudes, about 81% of the montane–subalpine snow tussocklands persisted but only 12% of this was conserved, while just 42% of the short tussocklands remained and a mere 3% of this was formally protected. Red/copper tussocklands fell between the extremes, with 28% remaining and 8% of this protected (Mark and McLennan 2005).

In December 2007 the protection status of these indigenous grassland types was updated (Mark et al. 2009; see Figures 15, 16), primarily to assess effects of tenure review of Crown-owned pastoral leasehold rangelands since September 2002 (Figure 16). Tenure review is a government-introduced process aimed at addressing environmental degradation and other concerns with rangeland management (Mark 1994, 2012; Mark et al. 2009). The process is usually initiated by the farmer who leases the property. The lease is renegotiated to separate the more vulnerable higher altitude areas from the more agriculturally productive, and usually more modified, lower altitude areas of the property, which could be free-holded. The former areas usually retain significant inherent values (e.g. landscape, indigenous biodiversity, soil and water conservation, recreation) and revert to full Crown (i.e. government) control, to be managed in the public interest by the Department of Conservation. Financial aspects of the settlements were initially confidential but were later released as required by the Official Information Act (1982); these and other outcomes have been criticised (Brower 2008). Tenure review is not only the largest reallocation of government-owned land in the country's history, but is also a 'one-off' exercise: a permanent alienation of the free-holded land and all of its remaining inherent values, retrievable only at market prices and only with a willing seller. District councils' district plans, most of which purport to recognise and offer security for inherent values under the Resource Management Act 1991, have in many cases proved ineffective, particularly so with lands free-holded through tenure review. At a planning hearing of the Central Otago District Council, the Otago Conservator decided not to challenge planning decisions on areas recently free-holded through tenure review (refraining from a 'second bite at the cherry'). In 2003 this decision was challenged in the Environment Court by the Forest & Bird Protection Society; however, the challenge was unsuccessful and became enshrined in case law until another case, involving Waitaki District Council in 2012, decided in the Society's favour. This could have important implications for conservation of low - to mid-elevation tussock grasslands following future tenure reviews.

Over the 5-year period to December 2007, areas of formally protected tussock grassland increased from 12.8% to 15.4% of the original baseline (1840) area of 82 432 km^2 or 32% of the land area, reflecting the outcome of additional rangeland tenure reviews during those 5 years (Mark et al. 2009). Protected rangeland actually increased from 9.4% to 15.5% of the remaining 76% of the original baseline area (7.2% to 11.8% of the baseline area). The distorted altitudinal pattern of protection, however, had not altered (Figure 16) and remains a serious downside of the tenure review process in relation to inherent values. Thus, during this period, protection of short tussock grassland at lower altitudes increased only from 3% to 5% of the remaining area but protection of upland, low-alpine snow tussockland increased from 27% to 40%, protection of mid-altitude snow tussockland rose from 12% to 21% and protection of red/copper tussockland rose from 8% to 15% in the rangeland region.

TENURE REVIEW OF HIGH COUNTRY PASTORAL LEASES

The tenure review process was initially promoted by politicians as a 'win-win situation'. Thus, the government would retain ownership and control of the more vulnerable, usually higher elevation, and often more degraded lands with generally higher inherent values; the lessees would be free from bureaucratic constraints on land use apart from those still imposed by the local authorities; and the interested public would also benefit by having a right of access that is inherent in public conservation lands. If necessary, this right of access was to be provided through free-holded land as part of the tenure review process. However, the outcome of tenure has a direct bearing on the grassland's ability to provide ecosystem services because free-holded areas could be heavily modified, whereas protected areas should retain their potential values.

The tenure review process is ongoing. By April 2012, reviews had been completed on 83 of the 303 properties: five had been purchased outright by the government, 42 were in various stages of the formal process, applications had been made for another 68, and 105 were not in the process. The 83 completed reviews represented 441 188 hectares of land; 51% of that area had been taken out under freehold agreements while the remaining 49%, including the whole-property purchases, had reverted to full government ownership to be managed by the Department of Conservation. This is close to the 50% value indicated by the government when the special legislation, the Crown Pastoral Land Act 1998, was publicly debated in the mid-1990s. Beginning in 2000, the largest of the transferred areas – those exceeding 20 000 hectares – have been designated conservation parks, of which there are currently 10, amounting to 581 032 hectares, while smaller areas have been designated as conservation areas (Figure 17). These parks and areas contain a variety of upland, non-forest ecosystems representative of much of their ecological region, but low- to mid-altitude areas remain seriously under-represented (Figure 18). Some, such as Hakatere and Ahuriri conservation parks (Figure 19a, b), include important altitudinal corridors and continuous sequences of ecosystems, and thus are more adequately representative of their ecological region.

Some additional conservation parks have been identified in conservation management strategies for the eastern South Island conservancies, and these may be implemented when future tenure reviews are completed. However, government policies regarding tenure review vary somewhat with the political parties, so the future remains uncertain.

FIGURE 18 Loss of low- to mid-altitude rangelands in the Mackenzie Basin.

FIGURE 19 Conservation parks: **(a)** Copper tussock (*Chionochloa rubra* subsp. *cuprea*) grassland beside Lake Heron, viewed west towards the Main Divide in Hakatere Conservation Park, upper Ashburton catchment, mid-Canterbury. AFM photo, November 2007.
(b) Ahuriri Valley within Ahuriri Conservation Park, south Canterbury, showing the full altitudinal sequence of tussock grassland from valley floor to mountain top, obtained through the whole-property purchase of Birchwood Station. AFM photo, March 2009.

ECOSYSTEM SERVICES OF THE VARIOUS TUSSOCK GRASSLAND TYPES

Among the more obvious ecosystem services provided by the flora and fauna of indigenous grasslands are pollination; contributions to biological control; water production; unique indigenous biodiversity; soil conservation potential; storage and sequestration of carbon; and educational, recreational and ecotourism values. Each of these is discussed below.

Many ecosystem services are hard to appreciate because they cannot be quantified or even evaluated and this is exacerbated by the generally poor knowledge of many ecosystem functions. Inevitably, this means any development likely to affect aspects of an ecosystem function may be difficult to assess; consequently, the precautionary principle should be invoked. This principle states that if an action or policy may harm the environment, then in the absence of adequate scientific knowledge or consensus that the action or policy is harmful, the burden of proof that it is *not* harmful falls on those proposing the action, and it may be advisable to refrain. In some legal systems – for example, that of the European Union – applying the precautionary principle is a statutory requirement, but this is not the case in New Zealand.

Pollination

Over 70% of plant species and 75% of global food crops depend on animals, usually insects, for pollination (Ollerton et al. 2011; Tylianakis 2013). Currently, humans depend enormously on managed populations of the honey bee (*Apis mellifera*) to maximise pollination, but the serious decline of honey bee populations is increasingly threatening successful pollination of many plants in cropping systems. This decline is the result of a combination of an increasing prevalence of colony collapse disorder and spreading infestations of the parasitic *Varroa destructor* mite, as well as the use of chemical pesticides in agriculture. This serious situation now affects many honey bee populations in New Zealand and, as it worsens, is beginning to feature in the general media.

However, it has recently become clear that wild pollinator populations also play a significant role in increasing fruit set of crop plants worldwide (Garibaldi et al. 2013). Unfortunately, habitat loss has led to a global reduction in the abundance and diversity of wild pollinators (Burkle et al. 2013), so the key to maintaining effective populations of wild pollinators lies in maintaining natural habitat, not just in designated conservation areas but also within agricultural landscapes (Tylianakis 2013).

Our current understanding of the importance of floral resources and pollinator services supplied by indigenous grassland ecosystems in New Zealand is based on relatively few studies, but both honey bees and bumblebees are known to forage actively on a range of native plant species. Butz-Huryn (1995) compiled a list of 224 native plant taxa utilised by honey bees; this list included many taxa found in tussock grasslands, particularly in plant families Apicaeae, Asteraceae and Ranunculaceae. Recent research in The Remarkables range in Otago indicates widespread reciprocal pollinator relationships, with both exotic and indigenous insects foraging on and pollinating both exotic and indigenous plants (e.g. Figure 20a). Bischoff (2008), working on The Remarkables at 1650–1800 m, recorded honey bees visiting flowers of four native alpine plants (*Celmisia sessiliflora*, *Dolichoglottis lyallii*, *Epilobium porphyrium* and *Gaultheria nubicola*), and captured honey bees were also found to have collected pollen of *Dracophyllum muscoides, Ranunculus gracilipes* and *Ourisia caespitosa*. Bumblebees visited flowers of *E. porphyrium* and *G. nubicola*, as well as *Anaphalioides bellidioides*, *Dracophyllum muscoides* and *Montia sessiliflora*, and were found to be carrying pollen from 13 different native species. In further recent research on The Remarkables, honey bees have been recorded on native *Gentianella* sp. at 1650 metres and bumblebees on a range of native species at about 1500 metres (Christa Miller Otago University, Botany Department pers. comm.). In the same study, native pollinators, mainly bees and hoverflies, were recorded visiting a range of introduced species in the Apiaceae and Asteraceae at altitudes between 700 and 1500 metres. Sawry (2013) and McGimpsey (2013) recorded bumblebees and honey bees foraging on native *Euphrasia dyeri* and *Wahlenbergia albomarginata* respectively,

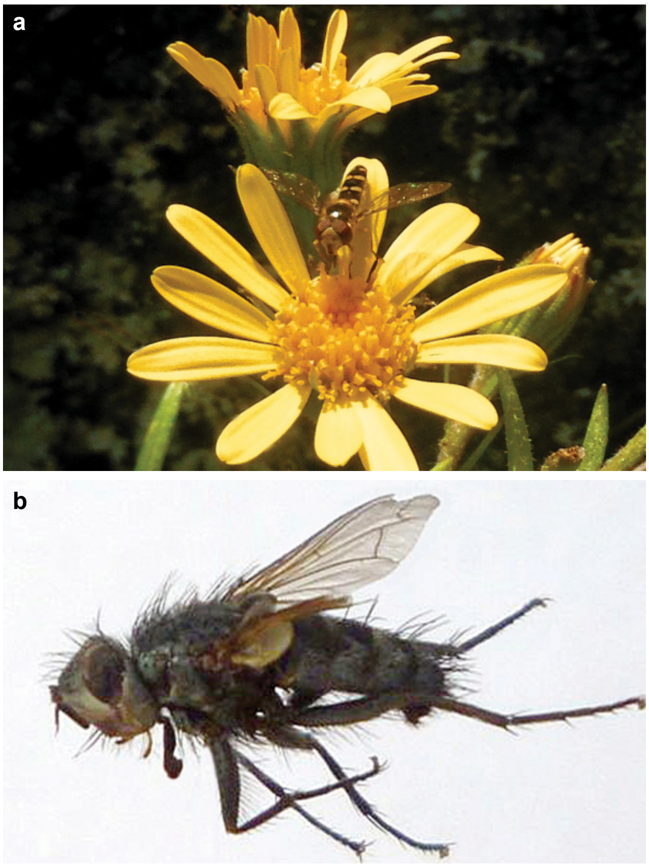


FIGURE 20 Pollinators and biocontrol agents: **(a)** *Allograpta* sp. (exotic species) on *Dolicoglottis lyallii* (native) flower head. Photo: Christa Miller. **(b)** *Procissio cana*, parasitoid of *Costelytra zealandica* (grass grub). Photo: Alan Heath.

at 900–1000 metres on the Blue Mountains, Otago.

Native insects can be abundant visitors to agricultural and horticultural plants. Howlett et al. (2009) used window traps and direct observations to record 51 different insect taxa visiting flowering fields of onions and pak choi. The list included 11 native bee species, 6 native hoverflies and numerous other native flies, with the native bee *Lasioglossum sordidum* second only to managed honey bees as the most abundant visitor to flowering onions. Rader et al. (2009) also studied the importance of native insects as an alternative to honey bees for pollination of crop plants, using a mass-flowering crop of rape, *Brassica rapa* var. *chinensis*, at seven sites in the Canterbury Region before *Varroa* established in the South Island. Over 30 insect species, including 15 native species, visited the crops. The most frequent visitors were managed honey bees, along with the introduced bumblebee (*Bombus terrestris*), two native bees (*Leioproctus* sp. and *Lasioglossum sordidum*), and four hoverflies (*Dilophus nigrostigma*, *Melangyna novaezelandiae*, *Melanostoma fasciatum* and *Eristalis tenax*). Rader et al. (2009) assessed two aspects of pollinator effectiveness: efficiency (pollen deposition per visit) and visit rate (pollinator abundance per available flower and the number of flower visits per minute). While honey bees were more effective pollinators overall because of their greater numbers, bumblebees, one native bee and a hoverfly were as efficient and effective, and if their populations could be increased through land management practices so they visited flowers as frequently as honey bees do, they could potentially replace the services provided by the honey bee.

Native insects are known to visit agricultural crops and may become increasingly important pollinators if honey bee populations decline significantly (McAlpine and Wotton 2009). Situating crops and orchards near semi-natural areas can enhance the abundance and effectiveness of native pollinators. For example, in California, pollination of almond flowers by 'wild' bees and other insects in orchards close to semi-natural vegetation resulted in increased fruit set even when honey bees were present (Klein et al. 2012). While the practical difficulties of this were acknowledged by the authors, they did recommend that orchards located near natural areas could reduce their dependence on honey bees. Similarly, a Swedish study of bumblebees and butterflies as pollinators recommended preserving semi-natural grasslands to help maintain a diversity of pollinators in the agricultural landscape (Öckinger and Smith 2007). However, while these and other studies have shown that close proximity of natural habitats can enhance the abundance and diversity of pollinating insects in agricultural and horticultural systems, very few data are available for New Zealand. One example showed that wild areas near the edges of kiwifruit orchards enhanced the number of hoverflies visiting the kiwifruit flowers (Ricketts et al. 2006); another showed that high floral diversity in the margins of crops can increase the numbers of native hoverflies (Evans 1996).

Biological control

Intensification of agriculture is usually accompanied by loss in biodiversity and an increased likelihood that species that adapt quickly to change will become pests. Two of the most important invertebrate pests of exotic pasture species in New Zealand are grass grub (*Costelytra zealandica*) and porina (*Wiseana* spp.). Both are native insects that have responded positively to the introduction of exotic pasture species. In both cases, natural enemies occurring in native grassland ecosystems contribute to the suppression of these pests. For example, a tachinid parasite (*Procissio cana*; Diptera: Tachinidae) parasitises up to 20% of third-instar *C. zealandica* larvae in the high country (Merton 1982). However, this parasitoid is less common in low-altitude pasture because the adult fly is active during the summer and requires as a host third-instar larvae in a 2-year life cycle, which occurs most frequently in higher altitude grasslands (Jackson 1990). However, the absence of native shrubs may also contribute to the absence of *P. cana* from lowland areas (Merton 1982). Adult *P. cana* (Figure 20b) feed from the flowers of native shrubs, so retaining natural vegetation in proximity of pasture can assist in maintaining these natural enemy populations as useful biocontrol agents, especially in cooler climatic areas where 2-year life-cycle hosts are prevalent.

Other tachinid flies parasitise porina but probably do not reduce populations in pastures. A possible reason for this is that, like grass grub, porina populations have moved away from the preferred habitat of the tachinids, namely, mixed shrub/grassland environments (Eyles 1965).

Naturally occurring entomopathogens such as bacteria, viruses and fungi can also be instrumental in keeping populations in balance in natural ecosystems (Bourner et al. 1996). Porina is susceptible to virus diseases like nuclear polyhedrosis (NPV) and it is thought that when grassland is cultivated, ultraviolet light reduces virus levels, allowing porina pest outbreaks to occur. Thus, virus levels gradually build up and reach epizootic levels, reducing porina populations to sub-damaging densities where they are maintained until another disturbance like cultivation or severe drought reduces the pathogen levels (Fleming et al. 1986).

The value of biological control from natural ecosystems is one of the more readily quantifiable ecosystem services because the value of pesticides or other measures required to compensate for crop loss in the absence of biological control can be easily

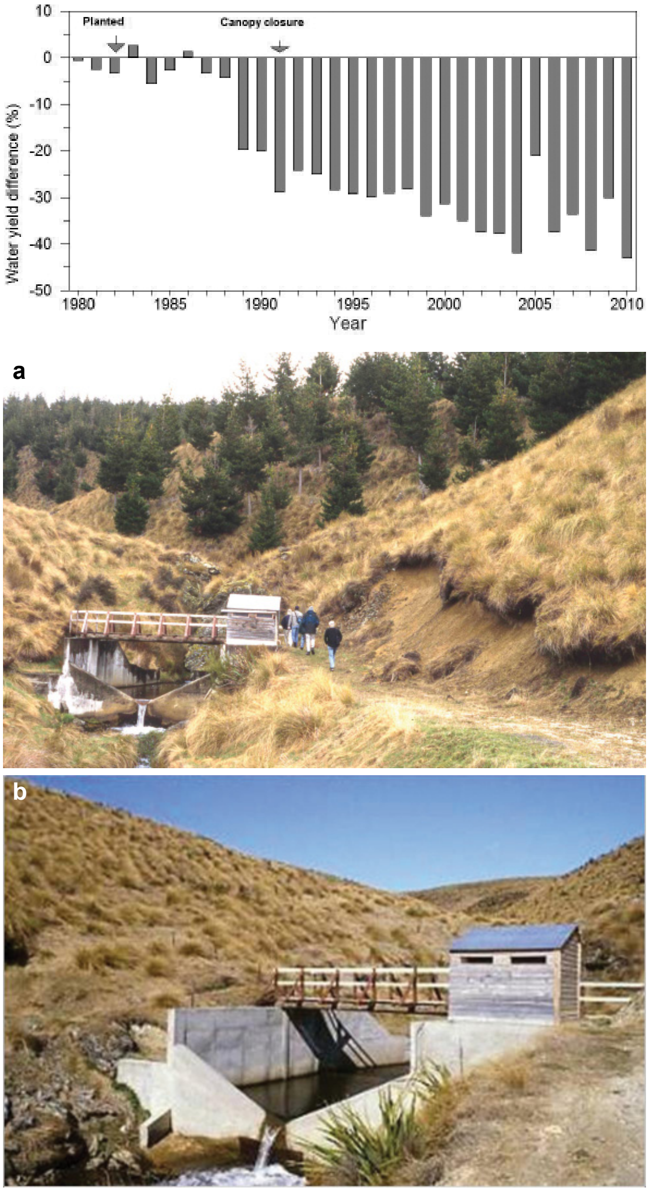


FIGURE 21 Maximising water yield and trade-offs with exotic afforestation. At Glendhu catchment in Otago, pine forest **(a)** reduced water yield by 43% compared with snow tussock **(b)** after 27 years**.** Graph shows water yield in afforested catchment since 1980; pines were planted in 1982 (Mark and Dickinson 2008).

calculated. This has not been quantified in New Zealand, but in the United States the value of pest control services attributed to insect natural enemies has been conservatively estimated at US$4.5 billion per year (Losey and Vaughan 2006).

Like pollination, natural biological control services depend on the mobility of organisms across the landscape, so the spatial structure of natural habitats influences the accessibility of ecological services to agricultural ecosystems (e.g. Tscharntke et al. 2005). In grassland ecosystems in New Zealand, retaining natural tussock grassland vegetation in a matrix with productive pasture might conserve a complex of natural enemies that could assist with general pest management services.

Water production potential

In New Zealand, the first studies of water production associated with indigenous tussock grasslands were made in the mid-1960s. These used non-weighing lysimeters and delivered some unpredictable results (Rowley 1970; Mark and Rowley 1976). Since then, there has been increasing interest and research into this important issue, particularly on the Otago uplands. Later studies have used the more conventional hydrological methodology of paired catchments (Pearce et al. 1984; Duncan and Thomas 2004: see Figure 21), expensive weighing (Campbell 1989; Campbell and Murray 1990) and improved non-weighing lysimeters (Holdsworth and Mark 1990). Controversy over the role of snow tussock foliage in intercepting fog (Fahey et al. 1996; Cameron et al. 1997) led to the use of stable isotopes (Ingraham and Mark 2000), but this also proved controversial (Davie et al. 2006; Ingraham et al. 2008; Fahey et al. 2011). Using the water-balance based WATYIELD model (Fahey et al. 2010), Fahey et al. (2011) rejected the significance of fog. In a subsequent evaluation of several ecosystem services, this data-intensive model was applied to assess water yields in relation to mean annual rainfall for four major vegetation types: exotic forest, scrub, tussock grassland and pasture grassland (Dymond et al. 2012). This confirmed the relatively high yield associated with tussock grasslands with mean annual rainfall <3000 mm, but, surprisingly, when rainfall is higher than this, the yield is assumed to be surpassed only with pasture grassland.

Despite various interpretations of the contribution of fog interception to the water yield of upland snow tussock grasslands, there is general agreement that the particular leaf anatomy and physiology of tall tussocks minimises loss of water by transpiration (Figure 22b, c), and when these tussocks form a healthy stand of upland grassland (Figure 22a) they can yield more clean fresh water (up to 80% of the measured annual precipitation of 1200–1500 mm) than any alternative land use assessed to date (Mark and Dickinson 2008). Bryophytes (mosses and liverworts) also make a significant contribution to sustaining the valued water-holding capacity of these grassland systems (4.3 mm); this contribution is similar to that in New Zealand temperate forests (Michel et al. 2013). In undisturbed upland tall tussock grasslands of the eastern Otago Lammerlaw Range, the dense ground cover of moss cushions (71% ground cover; c. 4% of total above-ground plant biomass) is largely dominated by the 'rough mats/wefts' of *Hypnum cupressiforme*; these have a high water-holding capacity (c. 1400% of dry mass) and contribute 15.5% of the total above-ground water storage capacity, second only to the tussock litter (56.2%). The influence of human-induced disturbance on bryophyte functional composition can have a huge impact on the ability of these tussock grasslands to store water. Thus, the colonist *Polytrichum juniperinum* forms a sparse cover after fire, as do two *Campylopus* spp. after topsoil removal. These three species have much lower water-holding capacity, leading to at least a 76% loss of the total potential water storage associated with bryophytes.

At Glendhu Forest on the Lammerlaw Range, eastern Otago uplands, a 310-hectare catchment of *Pinus radiata* exotic forest at 460–670 metres elevation steadily reduced its yield from year 6 to year 28, by which time its annual yield was 43% less than from an adjacent 218-hectare snow tussock grassland catchment (Mark and Dickinson 2008; see Figure 21). Nearby, in the upper Deep Stream catchment, another similar paired-catchment study compared recently burned (75% of the catchment) with unburned snow tussock grassland (Duncan and Thomas 2004). Summer flows reduced significantly during the early post-fire years, similar to what Mark and Rowley (1976) had shown using non-weighing lysimeters on the adjacent Rock and Pillar Range.

Dymond et al. (2012) analysed trade-offs between soil, water and carbon, on the basis of contemporary New Zealand values, with avoiding soil erosion assessed at NZ$1 per tonne, water at NZ$1 per cubic metre and sequestered carbon at NZ$73 per tonne

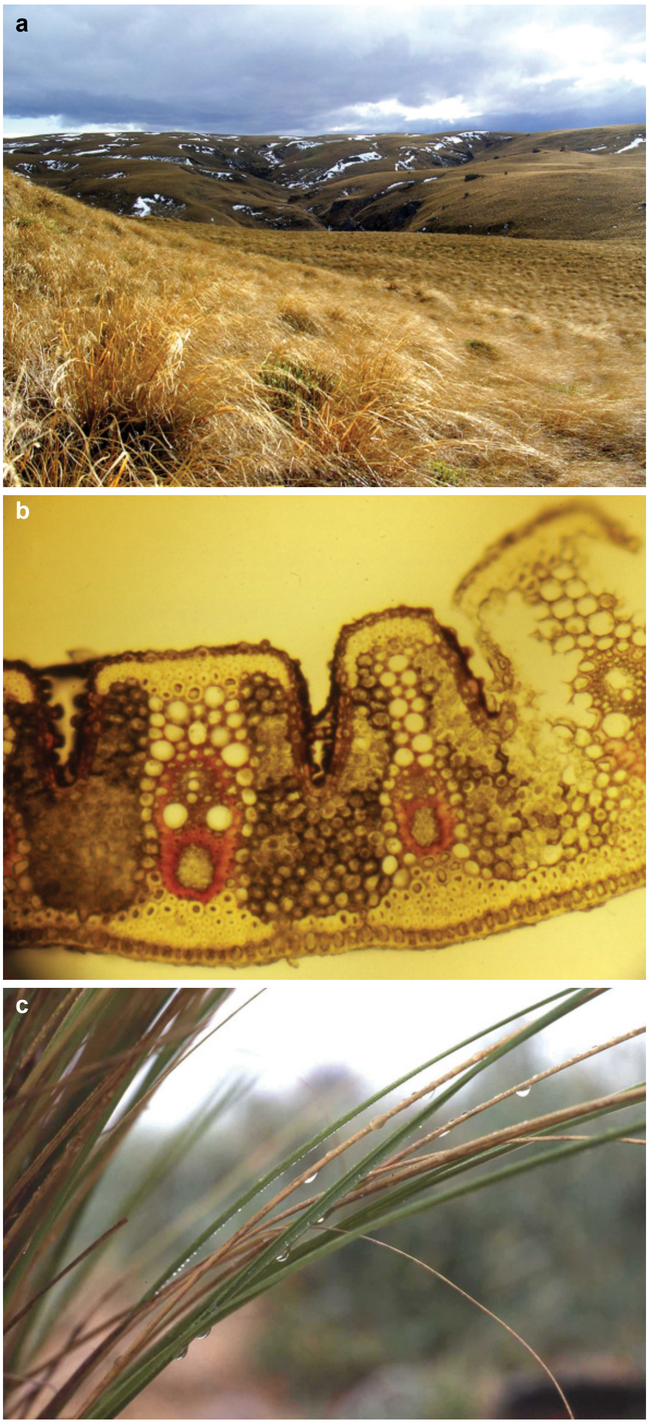


FIGURE 22 Snow tussock features explaining high water yields: **(a)** healthy upland grassland, **(b)** stomata in furrows, **(c)** fog interception.

(i.e. $20 per tonne of CO_2) plus a mean growth rate for *Pinus radiata* forest of 8.5 t C ha^{-1} $year^{-1}$. These generally high growth rates indicated a significant environmental benefit but the reduction in water yield of 30–50% could 'neutralize these benefits in catchments where there is demand for irrigation water, such as … the tussock grasslands of the South Island'. The price per CO_2 unit for the New Zealand Emissions Trading Scheme is now much lower (Treasury are currently using NZ$8.20 per unit; J. Dymond pers. comm. Feb. 2013), so this would further negate any such benefits.

Upland tall tussock grasslands in other regions of the country have not been assessed for water yield but results from the eastern Otago uplands probably extrapolate to most other South Island rangelands. Here, water production is a valuable ecosystem service because in the lowlands it serves various and increasing human demands while maintaining in-stream aquatic ecosystems. Results from Otago indicate that sites below c. 600 metres have relatively low water production potential regardless of the plant cover; this is a consequence of reduced precipitation and increased evapotranspiration (Holdsworth and Mark 1990).

Water production from alpine tall tussock grasslands along and west of the Southern Alps remains largely unstudied but is assumed to be high, with that flowing west being of more limited recreational, aesthetic and in-stream ecological values than that flowing east. The eastward-flowing water is generally valuable for various human uses, particularly if it can be stored in natural or artificial reservoirs and delivered as required throughout the year. Under climate change scenarios rainfall is predicted to increase along the South Island's Main Divide, which would increase flows in rivers flowing from there. However, rainfall is expected to decrease in the rain-shadow regions, which would increase the regional value of their upland tussocklands for water yield. The North Island situation would be more akin to the regions east of the Alps.

Indigenous biodiversity as primary components of ecosystem services

The natural diversity of native plants, animals and other organisms associated with the indigenous grasslands underpins the health of these grassland ecosystems. Although most of this biodiversity remains imperfectly documented, some groups are much better known than others and their interactions provide the essential ingredients of the functional ecosystems. A recent and relatively comprehensive nature guide to alpine New Zealand (Mark et al. 2012) has considerable relevance to the wider grasslands because many species that occur in the alpine zone also extend to lower elevations, particularly in open habitats such as grasslands. This recent guide lists 768 vascular plant taxa (591 dicots, 163 monocots, three conifers, 11 ferns and three club mosses), together with 21 birds, 24 lizards (12 geckos and 12 skinks), as well as some representative, relatively numerous bryophytes and lichens. This represents a not insignificant portion of New Zealand's indigenous flora, including almost one-third (31%) of the country's currently recognised vascular flora of 2415 taxa (de Lange and Rolfe 2010). The pattern of altitudinal distribution of these alpine taxa would be generally similar to that of the 655 taxa (613 species) presented in a previous publication (Mark and Adams 1995) that showed maximum species richness at c. 1250 m, close to the elevation of the climatic treeline. Above this altitude, richness declines rapidly to an upper limit in the nival zone at 2930 m; below it, richness also declines rapidly to sea level where some 50 plants extend (Figure 23).

Although the New Zealand indigenous vertebrate fauna is limited in species diversity compared with larger continental land masses, the indigenous grasslands do include a number of iconic

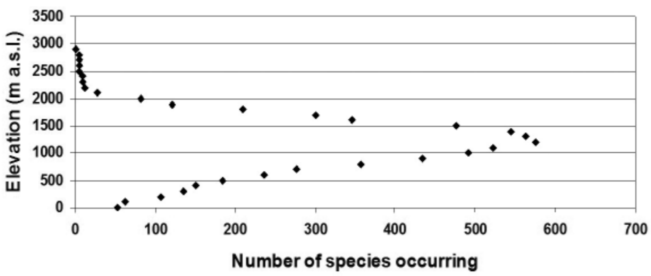


FIGURE 23 Species richness of New Zealand alpine vascular plants in relation to elevation, based on 655 taxa (613 species) and their altitudinal ranges as described in Mark and Adams (1995).

endemic species, highly valued by both Māori and European society in New Zealand. Among these are the tussock-feeding takahē (*Porphyrio hochstetteri*), a flightless bird in the rail family. Takahē were thought to be extinct but were rediscovered in 1948 in Fiordland's Murchison Mountains. Feeding mostly on the more nutritious of the alpine snow tussocks, the midribbed *C. pallens*, it leaves distinctive signs of discarded leaves and faeces (Figure 24). Also inhabiting alpine areas in western South Island is the kea (*Nestor notabilis*), a unique alpine parrot (Figure 25). This species has a wide diet but includes fruits, seeds, leaves and buds of a number of subshrubs common in tussock grassland environments. Among the New Zealand reptile fauna, seven species of skinks occur in indigenous grassland ecosystems, the most spectacular being the 'giant' skinks such as the grand skink (*Oligosoma grande*) and the Otago skink (*O. otagense*) (Figure 26a, b). These species can measure up to 130 millimetres long. Agricultural development has reduced available habitat for these species, which are consequently the subject of a major conservation effort, especially in Otago (Darby et al. 2003).

FIGURE 24 Takahē (*Porphyrio hochstetteri*) nest under an overhang of copper tussock, (*Chionochloa rubra* subsp. *cuprea*), 850 m, Murchison Mountains, Fiordland National Park. Their feeding on the base of tussock tillers results in distinctive signs of the discarded tillers (foreground). AFM photo, December 1976.

FIGURE 25 Kea (*Nestor notabilis*), New Zealand's unique alpine parrot in the low-alpine mixed shrub (*Dracophyllum rosmarinifolium*) – snow tussock (*Chionochloa teretifolia*) grassland, on Mt Burns, Fiordland National Park. AFM photo, April 2013.

Invertebrates are major contributors to species biodiversity in most ecosystems but our knowledge of the New Zealand fauna is comparatively poor, with probably fewer than half the species having been described (Emberson 1998). Consequently, it is not possible to speculate about the proportion of the New Zealand fauna represented in indigenous grassland ecosystems. However, an invertebrate survey of two relatively undisturbed tussock grassland sites in Central and eastern Otago revealed 130–140 species of beetles (Coleoptera) at each site (Barratt 2009). Quantitative invertebrate sampling from four tussock grasslands, two in Otago, one in Canterbury, and one in the central North Island, indicated that ants (Formicidae), beetles (Coleoptera) and mealy bugs (Pseudococcidae) were consistently the most abundant groups (Barratt et al. 2005), although this excludes the microarthropods such as Collembola and mites, which far outnumber the mesoarthropods and macroarthropods (Barratt et al. 2006). Figure 4c shows a 'species-scape' for the Otago grassland sites, where the size of the six most abundant invertebrates represents their relative abundance.

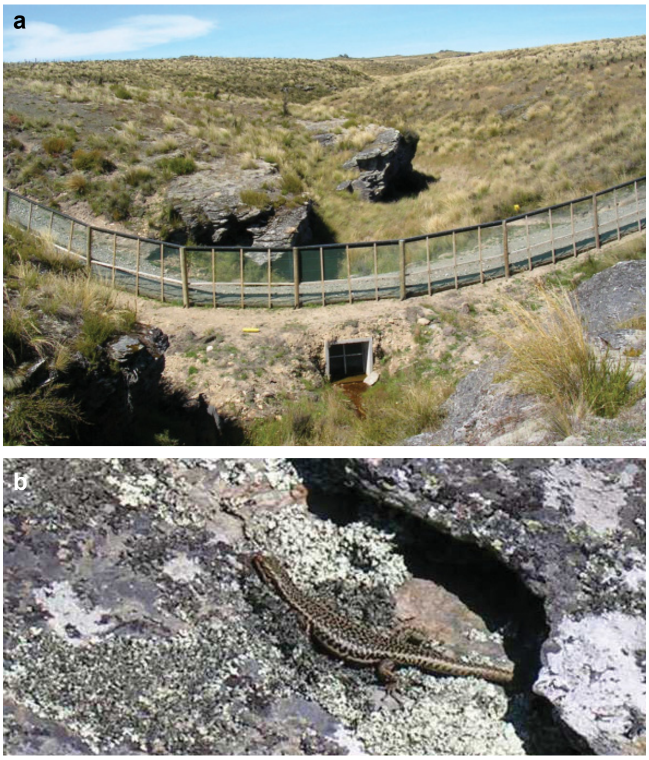


FIGURE 26 Skink conservation within indigenous grasslands: **(a)** Predator-proof fence at Macraes, Central Otago, for conservation management of grand and Otago skinks within mixed snow–copper tussock grassland. AFM photo, May 2006.
(b) Otago skink (*Oligosoma otagense*) on rock outcrop at Macraes Conservation Area, Central Otago. AFM photo, May 2006.

Menta et al. (2011) investigated the potential for permanent indigenous grassland to provide a 'biodiversity reservoir' for soil microarthropods by comparing this environment with woodland and arable land in the Po Valley, northern Italy. Using a combination of indices, they concluded that 'soil biological quality' did not differ significantly between grassland and woodland (although species composition and abundance varied), but the microarthropod community in the arable sites was significantly reduced in species richness and soil biological quality. They concluded that permanent grasslands are important reservoirs for soil biodiversity in agricultural lands.

Invertebrates are generally not highly valued by society, but New Zealand's indigenous grassland fauna includes some spectacular and iconic species. Some, like giant weta (Figure 27), evoke mixed emotions, but others commonly encountered by trampers and recreationists, such as species of large weevils, grasshoppers and cicadas, engender interest and awe.

Many indigenous species of alpine plants, lichens and animals are formally recognised as being under serious threat (Mark et al. 2012). This also applies to some non-alpine grassland plant

FIGURE 27 Female (left) and male low-alpine tussock grassland weta, *Hemideina maori*, northern Dunstan Mountains Conservation Area, Central Otago, at 1430 m. AFM photo, February 2008.

species, though none have yet been rendered extinct (de Lange and Rolfe 2010; de Lange et al. 2010). The most important threat in indigenous grasslands is habitat loss associated with agricultural development, particularly in the low- to mid-altitude grasslands. Another major threat is predation by a broad range of introduced herbivores, including domestic sheep, cattle, goats, and pigs; feral deer, goats, chamois, thar, hares, rabbits and possums; and, to a lesser degree, rats, mice and invertebrates. In particular, predation is a major threat for the most palatable plant species, with each animal having its own preferences as has been well recorded for red deer in the high rainfall alpine regions (Wilson 1976; Mark 1977; Wardle 1979; Clarkson 1986; Mark et al. 2007).

In a review of the importance of ecosystem services delivered by natural vegetation in conservation areas, McAlpine and Wotton (2009) concluded that in general biodiversity and the provision of ecosystem services were positively related, but evidence was highly variable and data were not consistent enough to support the hypothesis that conservation of biodiversity will always ensure the provision of ecosystem services.

Soil conservation values

From the early days of pastoral farming on the South Island rain-shadow tussock grasslands, the frequency of burning greatly increased and, with grossly inadequate fencing to control the relatively very high stocking rates (a government requirement of this time), the plant cover was drastically reduced in both height and cover. Concern by scientists and others throughout this period is well documented, and as this combination of frequent fire and the new phenomenon of mammalian grazing caused a clear degradation of ecosystems, grasslands also began to degrade and the associated soil erosion by both wind and water increased. Botanist and artist John Buchanan (1868) was among the first to express concern, noting for the drier grassland areas that ‘nothing can show greater ignorance of grass conservation than repeated burning which is so frequently practiced’. Grasslands continued to degrade, and in 1910, agriculturist Alfred Cockayne (1910) reported problems associated with grassland burning. In the same year, the Commission on Canterbury Runs Classification (1910) reported that large areas of the Mackenzie Basin were ‘almost depleted of all vegetation save sorrel and scabweed’, and soon after, teacher/botanist Donald Petrie expressed concern about the grass-denuded lands of Central Otago. Then, in 1919, distinguished botanist/ecologist Leonard Cockayne (1919) reported that indiscriminate burning had turned acres of tussock grassland ‘into stony debris’. The following year, the Commission on the Southern Pastoral Runs (1920) reported on the serious depletion of the tussock grasslands as a result of general mismanagement, noting that ‘mountain sheep stations have gone backward, a state of affairs not creditable to the Dominion’. Similar concerns were expressed by general ecologist George Thomson (1922) and by DSIR botanist/ecologist Victor Zotov (1938) for the South Island rangelands in general.

Particular concerns for the serious soil erosion associated with the high country grassland degradation (Figure 28a, b) were outlined by DSIR soil scientists Gibbs and Raeside (1945), Auckland geographer Cumberland (1945), and a Royal Commission that had been established in the same year to report on the New Zealand sheep industry. An ecological study of pastoral leases on South Canterbury’s Hunter Hills by ecologist Philippa Barker (1953) also reported serious land degradation. The consequent government concern prompted establishment of the Tussock Grasslands Research Committee, comprising senior government ecologists, botanists, agriculturalists and soil scientists. The committee concluded that degradation of high country upland tall tussock grasslands was associated with the relict status of the grasslands, being out of phase with the prevailing climate (Tussock Grasslands Research Committee 1954). Some evidence for this came from the relative lack of regenerating juvenile tussocks, as the forest ecologist team member Holloway (1954) had previously claimed for the South Island

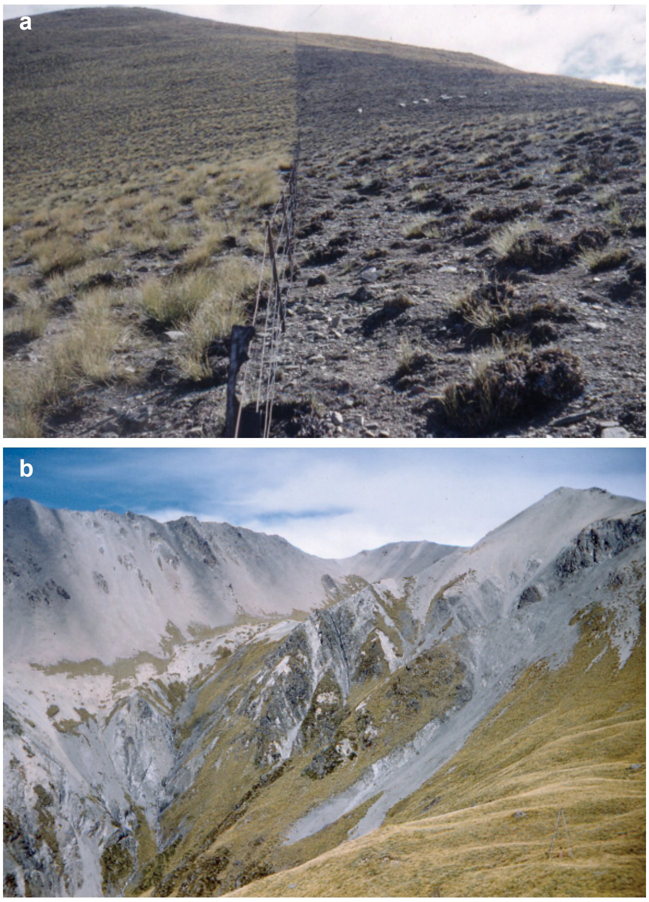


FIGURE 28 Degradation of high country grasslands: **(a)** A fenceline boundary at 900 m, St Bathans Range, North Otago, which has differentiated grazing following a recent fire. Sheep dispersed widely on the large burnt area to the left of the fence but concentrated on the small burnt area on its right and have killed most of the tussocks. AFM photo, February 1959.
(b) Serious induced and natural erosion on greywacke substrate, Craigieburn Range, mid-Canterbury, among low-alpine slim snow tussock (*Chionochloa macra*) grassland at 1430 m. AFM photo, March 1959.

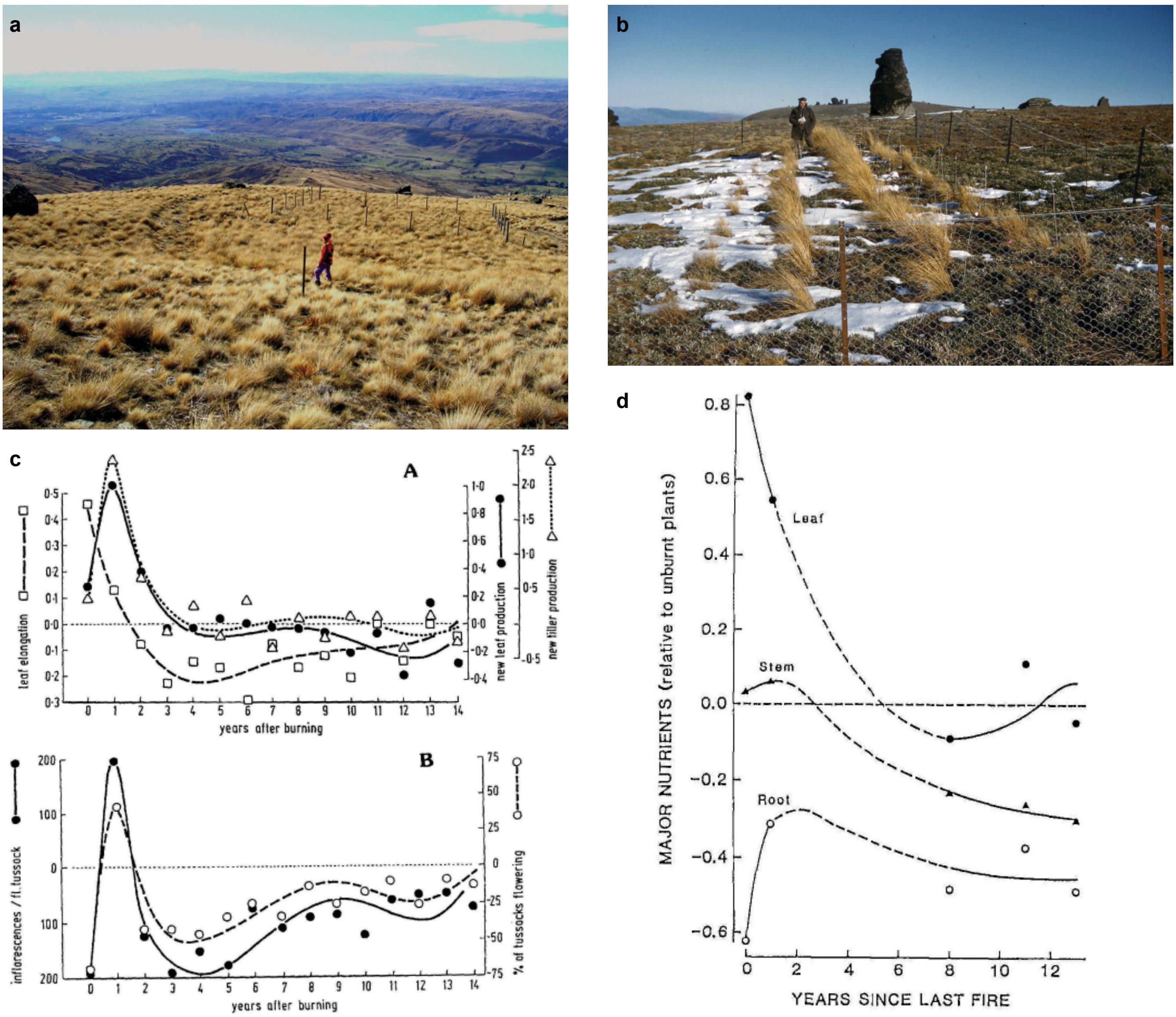


FIGURE 29 Snow tussock autecology, vegetative and flowering responses to burning at 1220 m, Old Man Range, Central Otago: **(a)** study site and transplant garden **(b)**. **(c)** Vegetative growth is shown as leaf elongation, new leaf production and new tiller production [A], and flowering as inflorescence number per tussock and percentage of tussocks flowering [B] up to 14 years post-burn; **(d)** Plant nutrients in leaf, stem and root; and in relation to nearby unburnt plants (zero base; dashed line).

podocarp–broadleaved forests. According to the committee, burning and grazing were merely hastening the natural demise of the dominant tall tussocks. However, the committee recognised that their conclusions were based purely on observation, so they recommended research on the systematics and ecology of the dominant species and their communities, including the roles of introduced plants and animals. One of the committee members, senior DSIR botanist Lucy Moore, stated in a subsequent paper (Moore 1956) that because tussock grassland 'dominants are perennials with very long lives it has many of the characteristics of a forest and few of a short rotation pasture. Like a forest, it is the product of a long slow development, and like a forest it is much easier to destroy than to rebuild'.

Soon thereafter, autecological studies of the dominant tall tussock species of the South Island rangeland, particularly *C. rigida* subsp. *rigida*, were initiated, particularly by O'Connor (1963), Mark (1965a–e, 1968, 1969) and others (Payton and Mark 1979; Payton et al. 1986) (Figure 29). These were followed by comprehensive reviews (O'Connor 1980, 1982; Basher et al. 1990; Mark 1993; Mark and Dickinson 1997), and reports on some vegetation dynamics of recently protected areas (Mark and Dickinson 2003). Importantly, there were no baseline protected areas throughout the South Island rangelands until 1969 (Mark 1985, 2012): the entire 2.6 million hectares had been allocated to pastoral farming. These detailed studies, including reciprocal transplantation of snow tussocks along an elevational (temperature) gradient, indicated that the areas of tussock were not relict but instead were clearly adapted to the environment, even showing genetic or ecotypic/ecoclinal differentiation for both growth and flowering behaviour at particular elevations. Moreover, a subsequent re-reciprocal transplantation study showed this adaptation persisted for 14 years without measurable acclimation effects (Greer 1979). The extreme longevity of snow tussocks was also confirmed; indeed, given their continuous production and replacement of tillers they might even be considered potentially immortal (Mark 2005). Moreover, survival, three aspects of vegetative growth, flowering, and even germination of seed lying dormant on the soil surface show the rangeland dominant narrow-leaved snow tussock, *C. rigida* subsp. *rigida*, can tolerate, and may even be adapted to, fire (Mark 1965b). Similar behaviour was shown by copper tussock, *C. rubra* subsp. *cuprea* (Bycroft 1999). The evolution of fire tolerance/adaptation and the extent of its co-evolution in these and perhaps other species in this genus would be of interest, particularly given the general contrast in these features between biota in Australia (Bowman et al. 2012) and New Zealand.

However, *C. rigida* is vulnerable to grazing. Immediately after burning, macronutrients are transferred to the regrowth foliage from the below-ground system (Payton et al. 1986), and heavy grazing at this time proved highly detrimental to the plant's recovery: severe grazing could kill the plant within one year. Grazing also badly affects *C. macra*, and for both species this would inevitably expose extensive areas of bare soil, making it vulnerable to frost-assisted erosion.

The relevance of these findings was publicised by the New Zealand Mountain Lands Institute (1992) through its 'Guidelines on burning tussock grasslands'; however, the reception among runholders and even some organisations with management oversight was mixed, which largely reflected the depth of traditional high country management.

Further reports on the progressive degradation of high country rangeland followed. These addressed both the drier short tussock and higher-altitude tall tussock grasslands, and pointed to the associated impairment of the soil conservation values that would have otherwise been sustained by a healthy vegetation cover. Prominent among these reports were those by Treskonova (1991) and the Parliamentary Commissioner for the Environment, the latter dealing with both the dry short tussock (1991) and the upland snow tussock (1995) grasslands. Also generally critical was Kerr (1992), working for Lincoln University's Mountain Lands Institute, who described the high country as showing 'a large scale "systems failure" in the management of one of New Zealand's major land resources' and a 'classic' and 'truly ignoble example' by world standards. He attributed this to the 'collective failure' of the overseeing agencies, the land occupiers and their advisors. Adding to the increasing concern was the government-commissioned South Island high-country review, produced by a nine-member group of farmers, professionals and consultants (Martin et al. 1994). They reported deep concern about the 'historic and continuing impact of grazing … on the condition of the soils and vegetation of the pastoral high country', noting that 'burning has caused more rapid change' and 'a decline in soil condition is very likely on the unimproved lands. These comprise about 80% of the land area … and receive no inputs. … Long-term pastoral use of extensive areas of South Island high country is unlikely to be sustainable'. A year later the Parliamentary Commissioner for the Environment (1995) reported that 'the government system for managing tussock grasslands is woefully inadequate' and 'there is limited central government guidance on how the integrated management of the tussock grasslands should be achieved and how the national interest should be protected'. She advised regional councils to take a 'precautionary approach' in granting burning consents. Later, a senior government soil scientist (McIntosh 1997) reported 'compelling evidence that continued grazing and burning of South Island tussock grasslands without nutrient inputs, is unsustainable'.

Concern for the increase in accelerated erosion in the South Island high country and for serious erosion in many other parts of the country, notably much North Island steep hill country, prompted special legislation to establish regional catchment boards (Soil Conservation and Rivers Control Act 1941). The boards comprised appointed members from relevant government departments (Forestry, Lands, Agriculture, Works), as well as elected members, and they employed soil conservators and engineers. Oversight of burning and high country land management was vested in catchment boards, and government subsidies were made available through the lead agency, the Water and Soils Division of the Ministry of Works and Development. Conservation plans for high country runs were developed at the occupier's request and subsidies were offered to encourage uptake of their recommendations, which included retirement of land with a Land Use Capability of Class VIII ('unsuitable for any productive use') or VIIe ('with serious actual or potential soil erosion'). Engineering works were also initiated for flood control in minor and major waterways. Subsidies were provided at varying rates (up to 100%), depending on the relative economic benefit to the occupying farmer, for increased subdivision and retirement fencing as well as improved four-wheel drive access to the uplands (but no provision for maintenance of those lands), particularly for fire control and stock management. Oversight for implementing these run plans was vested in the Ministry of Works but responsibility for implementing the conditional land retirement (destocking and reversion to Crown management) lay with the Lands & Survey Department (its Land Settlement Board had oversight of the pastoral leasehold high country land tenure). However, retirement was seldom enforced even when compensation and full fencing costs had been subsidised by the Crown. Indeed, from the early 1940s some NZ$10.53 million was spent to retire 483 000 hectares on 113 high country properties, but most of this land remained in the leases, and was therefore the responsibility of the lessee. The 1948 amendment to the Land Act provided much increased security of tenure and other rights for high country runholder lessees (occupation, pasturage, trespass), plus several privileges, where permission was required for certain management practices: burning, fencing, cultivation, oversowing–topdressing, tracking, etc., particularly in the expectation that this would induce more sustainable land management.

In a foreshadowing of the Resource Management Act, in 1990 the roles of catchment boards were subsumed by regional councils in relation to water allocation and use and some aspects of land management, including oversight of burning for tussock grassland management, while district councils assumed responsibility for most aspects of land management. However, the distinction of responsibilities was somewhat vague, to the apparent advantage of both types of council.

The government's Land Development Encouragement Loans of 1970–83 promoted much unsustainable land development in the South Island high country. In 1983 the National Parks and Reserves Authority initiated the Protected Natural Areas Programme (Kelly and Park 1986), to survey and protect 'The Best of What Remains' throughout the country. This programme soon concentrated on the South Island high country (Figure 30) when an initial nationwide assessment of the formally protected areas on an ecological district basis (Wassilieff and Timmins 1984) revealed no such areas, at least of any significance, existed in this entire region.

The Rabbit and Land Management Programme of 1986–96 directed NZ$30 million to addressing problems of the South Island semi-arid tussockland regions, while informal Landcare groups based on an Australian model were set up in the early 1990s to promote sustainable management of rural communities through environmental, economic and social reforms. Then in 1997, while the government was engaged in a prolonged evaluation of whether to use rabbit haemorrhagic disease (calicivirus) for rabbit control, particularly in the South Island's semi-arid degraded tussock lands, the disease was introduced illegally.

FIGURE 30 Low-alpine slim snow tussock (*Chionochloa macra*) grassland, southern Old Man Range, Central Otago, showing fenceline differential in tussock height and cover following several years of retirement associated with protection on the left of the fence where *Aciphylla scott-thomsonii* is prominent. AFM photo, January 1991.

FIGURE 31 Narrow-leaved snow tussock (*Chionochloa rigida*) grassland, upper eastern slopes, Rock and Pillar Range, Central Otago, 900–1400 m. Subjected to an initial assessment with the Clayton Committee in 1984, the area above the firebreak-fence (bottom centre to mid-right of picture) at c. 900 metres was formally protected. AFM photo, May 2006.

In response to public concern over free-holding some leases in the Teviot District of Central Otago, the government sponsored the Clayton Committee Report of 1983. This report focused on high country pastoral leasehold lands. It recognised some public-interest values (landscape, recreation, indigenous biodiversity, etc.) in these lands and recommended no further sales without first identifying and providing for such values. This resulted in extensive surveys of the Awatere District in Marlborough, The Mackenzie Ecological Region in Canterbury, and the Rock and Pillar Ecological District in Otago (Figure 31). All surveys confirmed these values. This set the scene for tenure review of high country pastoral leasehold lands, whereby the soil conservation and other values of the upland tall tussock grasslands and associated mountain lands of the South Island high country could be recognised and more adequately provided for.

Carbon storage and sequestration values

Organic carbon stored in New Zealand's ecosystems was estimated by Tate et al. (1997) from updated national databases of vegetation cover and soil carbon, augmented by similar information for Stewart Island and carbon estimates for upland and high country soils of the South Island. Plant biomass estimates from the literature were combined with the vegetation cover map of Newsome (1987) to estimate stocks for vegetation carbon above and below ground, including litter and humus, for 47 vegetation classes, including four tussock grassland types. Of these, snow tussock grassland covered the largest area (1361 × 10^3 ha) and retained the greatest total amount of carbon (37 Mt), followed in extent by short tussock grassland (1116 × 10^3 ha) with about a third as much carbon (12 Mt), and mixed short–snow tussock grassland (710 × 10^3 ha; 14 Mt). Red tussock grassland covered considerably less area (80 × 10^3 ha) and stored far less carbon (1.8 Mt). The areas given for each grassland type vary somewhat from those given by Mark and McLennan (2005), who estimated short tussock grassland as covering 819 × 10^3 ha, snow tussock grassland 1540 × 10^3 ha, and red tussock grassland 247 × 10^3 ha. Total grassland area was estimated at 2605 × 10^3 ha. Tate et al. estimated carbon stored in all tussock grasslands as 64.8 Mt, but this was supplemented by 110 Mt from eight mixed grassland–shrub types, of which all but the category 'Grassland and gorse' would probably include a contribution from indigenous grasses, including tussocks.

According to Tate et al. (1997), New Zealand's ecosystems store about 6660 Mt of natural carbon but tussock grasslands contribute only about 2.7% to that total, with 36% of the total contributed by above-ground vegetation and 64% by roots and soil organic matter. Thus, the indigenous grassland contribution is relatively small considering they occupy some 23.5% of New Zealand's land area.

The upland snow tussock grasslands probably contribute considerably more than the other indigenous and exotic grassland types but cannot compete with exotic forests. Values for upland snow tussock grassland in good condition and adjoining *Pinus radiata* forest at 460–670 metres at Glendhu Forest on the Lammerlaw Range (L. Schweidermann University of Auckland pers. comm. 2011) provide a useful comparison (Figure 32). In a mid-elevation ridge-crest site (at c. 570 m), the snow tussock grassland comprised 14 500 tussocks ha^{-1} (mean height, 1.01 m; mean canopy width, 0.94 m; basal area, 969 cm^2). This grassland contained 33.8 t C ha^{-1} (excluding live roots), with 28.3 t (84%) contributed by the above-ground live and dead material and 5.5 t C ha^{-1} (16%) by the tussock litter. Carbon contributed almost half (46%) the plant's above-ground dry weight. The carbon content of the below-ground organic matter (minus roots) was 153 t C ha^{-1} (82% of the total), similar to values given by Tate et al. (1997) for high country yellow-brown earths. In contrast, the above-ground component of the adjoining 22-year-old *P. radiata* forest stored three times more carbon than did the tussock (110 t C ha^{-1}), although the below-ground value was considerably less (120 t C ha^{-1}) (L. Schweidermann pers. comm.).

These values for snow tussock at Glendhu are similar to those recorded by O'Connor et al. (1997) for the Craigieburn Range, Canterbury. There, snow tussock stored 20 t of organic carbon per

FIGURE 32 A stand of narrow-leaved snow tussock (*Chionochloa rigida*) grassland being sampled at 570 metres on the interfluve of the paired catchments at Glendhu, Lammerlaw Range, eastern Otago uplands, with the *Pinus radiata* stand from the adjacent catchment to the left of the four-wheel drive track separating the two. AFM photo, March 2011.

hectare in above-ground biomass and 112 t ha^{-1} in the soil (0–40 cm; without roots), while values for the adjacent *P. radiata* forest are similar for soil carbon (111 t ha^{-1}) but substantially more (×5.6) for above-ground biomass.

More recently, Burrows et al. (2012) conducted a comprehensive assessment of the carbon pools and sequestration of three different South Island high country grassland ecosystems, including the effects of retirement from sheep grazing for periods of 11–38 years. The study used paired grazed/ungrazed blocks closely matched for soil type and environments, and with a known history of management. Three sites were selected: upper Rakaia Valley (1100–1400 m; short tussock grassland with *Hieracium* and *Celmisia* spp.; 38-year ungrazed block), upper Waitaki valley (800–1200 m, mixed tall–short tussock grassland with matagouri; 20-year ungrazed block) and the upper Clutha Valley: Makarora (300–400 m; valley floor pasture grassland with *Lotus*; 11-year ungrazed block). At each site about 20 stratified random plots (1 m^2) were sampled. Vegetation and litter differed significantly among sites, and retirement increased abundance of litter and the vegetation biomass, but the effects of retirement were small relative to among-site differences in plant biomass, cover or litter mass. Also, longer retirement was not associated with a comparable increase in soil C, including root C, nor with any significant increase in total ecosystem C. Most variation in total ecosystem C and C pools was considered to arise from site differences rather than the 38 years of grazing management. In addition, C sequestration was not considered important in these grasslands, nor was it measurably increased as a result of grazing retirement. The annual increase of C through additional sequestration was estimated to have ranged from c. 0.3 t ha^{-1} at the Waitaki site to c. 0.4 t ha^{-1} at the Clutha site and c. 0.8 t ha^{-1} for the Rakaia site; all relatively small compared with what can apparently be achieved with afforestation (Scott 2007).

Reducing or offsetting high country CO_2 emissions could help mitigate climate change and might provide new business opportunities while improving the sustainable resource use on this c. 10% of New Zealand's land area, but Burrows et al. (2012) concluded there was little justification for modifying grazing management on high country tussocklands for these purposes. Thus, the frequent assumption that above-ground biomass increases significantly when tussocks recover after grazing removal in Canterbury (Rose and Platt 1992) and Otago (Mark and Dickinson 2003) cannot be substantiated on the basis of results from that study. Grassland degradation is associated with a striking decline in plant biomass but perhaps not in carbon storage. McIntosh (1997) summarised the decline in above- and below-ground biomass along a degradation sequence that is considered to have occurred to a varying extent in parts of the South Island rain-shadow region over the 750 years of human occupation. This began with mountain beech forest, transitioned through tall tussock grassland to a short tussock grassland, and ended in a degraded *Hieracium* spp. herbfield. Assuming biomass is c. 50% C, this represents a decline from 173 t ha^{-1} through 32–35 t ha^{-1} and 11 t ha^{-1} to a mere 1–2 t ha^{-1}, respectively.

The Kyoto Protocol explicitly states that if a land-use change is to contribute to carbon sinks and sources in the first commitment period (to December 2012), it must have taken place after 1990. Given that requirement, as well as its current application to only woody cover and the highly variable nature of carbon storage and sequestration of indigenous grasslands globally, it seems highly unlikely that any successor to this commitment will include non-woody cover. Non-inclusion of non-woody cover has been debated with North American prairie ecosystems (DeLuca and Zabinski 2011).

The alternative land use of earning carbon credits and income from afforestation with exotic conifers is a complex issue (Tate et al. 1997; Scott et al. 1999; Kirschbaum et al. 2009), a view shared by Dymond et al (2012), who assessed the trade-offs between soil loss through erosion, water production, and carbon sequestration and storage among four land-cover options. Their assessment of carbon, however, was based on the then current international market value and the 2010 Treasury figure of c. NZ$20 per tonne. Since then the value has fallen to just NZ$2.60 per tonne and continues to be highly unstable because the market has remained open to overseas traders. Despite pleas from forest owners involved with the Emission Trading Scheme (ETS) and/or the Permanent Forest Sink Initiative (PFSI), the government has refused to close this market. Moreover, the ETS Amendment Act of 2012 saw New Zealand withdraw from the Kyoto Second Round and commit to subsidising agricultural emissions of greenhouse gases for the indefinite future. The issue is thus highly confused economically and politically and it is unlikely a credible, stable framework will be attained in the near future.

Educational and scientific values

Indigenous grasslands throughout the country are increasingly valued for a wide range of educational purposes. These activities include short- and long-term scientific studies (Figures 33, 34), and public interpretation through field trips, which attract a wide spectrum of groups from primary, secondary and tertiary institutions, conservation organisations, and national and international conferences.

The wide range of locations and elevations provides a diversity of grassland types. Thus, while indigenous grasslands and their biota complement other ecosystem types available for education, they also offer more extensive and readily apparent landscape and landform features, as well as having unique features worthy of promotion. Moreover, their easy accessibility is important for educational purposes, and groups are easier to supervise in these grasslands than in many alternative ecosystem types.

Recreational and ecotourism values

New Zealand's indigenous grasslands, particularly in hilly and mountain regions, are both readily accessible and remote and are therefore highly attractive for a wide range of outdoor recreational activities (Figure 19a–b). They attract both private (recreational) and commercial (ecotourism) activities, and, as with the educational values, involve lands with the same wide range of tenures and many unique features. These values clearly represent an important ecosystem service. Recreational and ecotourism activities are similar and can range widely: tramping (hiking); mountaineering; rock-climbing; mountain biking; four-wheel driving; horse trekking; cross-country or downhill skiing; various thrill-seeking activities; orienteering; geocaching; multisports like triathlons; botanising, birdwatching and other natural history activities; photography; cultural and historical activities; hunting and shooting; and generally enjoying the outdoors.

Public conservation lands in New Zealand are generally applauded internationally for their inherent right of public access which, with few exceptions ('Special Area' category, where public access could be detrimental to a particular value), has traditionally been free in this country. The type of activity permitted on these lands varies with the land's designation or classification (national park, conservation park, scenic reserve, recreation reserve, etc.) as

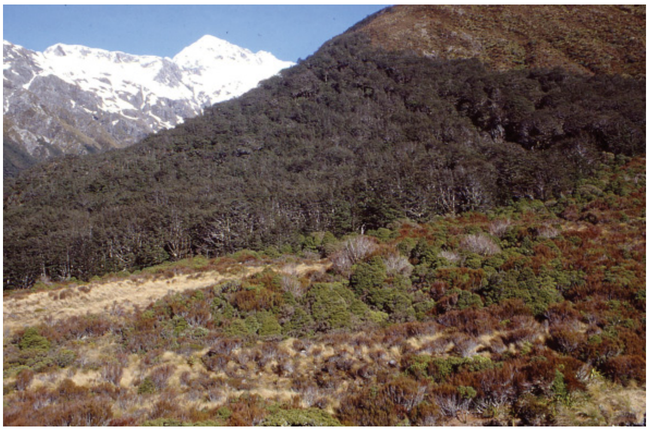


FIGURE 33 Twin Stream, Arthur's Pass National Park, showing a long-term study area where Leonard Cockayne initiated a study of secondary succession after fire in 1898. The succession was later studied by Peter Wardle and was essentially complete by the 1970s. AFM photo, October 2008.

FIGURE 34 Photo-point monitoring of low-alpine curled snow tussock (*C. crassiuscula*) grassland, Joe Valley, Mt Aspiring National Park. Initiated in 1970 along with some 88 other representative sites throughout the park, monitoring will allow for long-term ecological research. AFM photo, March 2007.

FIGURE 35 The Remarkables from Doolans Saddle (2030 m) with Double Cone (2319 m) and Lake Alta, showing upper limit of alpine slim snow tussock (*Chionochloa macra*) grassland at c. 2000 m. AFM photo, February 2009.

detailed in legislation and related policy statements. The General Policy for National Parks (New Zealand Conservation Authority 2005) deals with national parks while the Conservation General Policy (Department of Conservation 2005) covers the remaining conservation lands. The latter policy is more lenient regarding recreation, particularly in relation to the use of both powered and non-powered vehicles. Both policies recognise ecosystem services inherent in public conservation lands, defining them as a 'wide range of conditions and processes through which natural ecosystems, and the species that are part of them, help sustain and fulfil life', but both also require stronger protection for ecosystem services in national parks.

Recreational resources have been assessed with various methods and standards. Detailed assessments of upland and high country recreational resources, based on the Recreational Opportunity Spectrum (ROS) (Molloy 1976), aimed to maximise opportunities while minimising conflicts. This approach was initiated on the South Island West Coast by Molloy (1979) and followed in Otago with a recreation plan based on a conservation plan (Mason 1988). The West Coast and Otago plans both encompassed several biomes but included tussock grasslands as a 'unifying element'. These plans were published by the Federated Mountain Clubs of New Zealand. The ROS approach categorises land according to its recreational significance rather than its condition or commercial opportunities, so an essential step is to evaluate and integrate the detailed field knowledge of many contributors. New Zealand is recognised as having a wide range of outdoor recreational opportunities, particularly on public conservation land. This currently amounts to c. 34% of New Zealand's land area and is relatively well distributed by altitude, geographically, and across ecosystem types. These lands appeal strongly to overseas visitors and immigrants (Lovelock et al. 2011), as well as to local people.

Each national park has a specific management plan. These are drafted by the regional conservation board in consultation with the general public and the regional conservancy staff; they are formally adopted by the Conservation Authority with the Minister's approval and are scheduled for review every 10 years. A plan specifies the type and conditions of all recreational activities, consistent with the general policy for national parks. Tussock grasslands feature in most of the 14 national parks. Typical is the recently reviewed Mount Aspiring National Park Management Plan, which details the recreational activities permitted, including recreation and tourism concessions and 'competitive sporting events (e.g. the annual 'Routeburn Classic' adventure run) and thrill-seeking activities' (Department of Conservation 2011).

Recreational and ecotourism activities on conservation lands other than national parks are specified for each conservancy in their 'Conservation Management Strategy' (CMS). This presents challenging issues for the sustainable management of indigenous grasslands. As stated in the Otago Conservation Management Strategy (Department of Conservation 1998: under review in 2013), integrated management involves weighing up and combining where practicable, the requirements of management for different purposes. Thus, it states (p. 8):

> A tussock grassland area protected against fire will build up fuel supplies in the tussock bases. Management for the sole purpose of reducing the risk to neighbours' properties of an intense and destructive spreading summer fire might call for periodic burn-offs to control fuel loads. On the other hand, management for the maintenance of biodiversity, ecosystem health and landscape values might require protection from burning, at least for periods approximating the interval between natural fires. … An integrated management solution could call for a combination of fire risk assessment, fire break construction and maintenance of boundaries of low landscape sensitivity or using low impact techniques, some fuel reduction burning in areas of lesser ecological significance or a programme of educating or managing the visitors who may be likely to start fires in summer.

The importance of ecosystem services is not specifically mentioned in this two-volume document but is implied in several sections. For example, it is clearly implied with the objective of protecting the high conservation, landscape, hydrological and historic values of the uplands while allowing and providing for appropriate recreational use for the Lammermoor-Upper Taieri Special Place 10.16 (p. 275). The Otago CMS (Department of Conservation 1998) also contains extensive descriptions of the indigenous species (plants, birds, reptiles, invertebrates and freshwater fisheries) in its 'Functional Objectives' section.

Downhill commercial skiing is permitted over tussocklands and associated mountain lands in Tongariro and Mt Egmont national parks, as is commercial heli-skiing in parts of Mt Cook/Aoraki and Mt Aspiring national parks and commercial downhill skiing on conservation tussocklands at Mt Hutt, Ohau, Mt Dobson, Porter's Pass, Treble Cone, The Remarkables (Figure 35) and Coronet Peak. Commercial cross-country skiing occurs in part on conservation tussocklands at the Waiorau Snow Farm and Snow Park on the Pisa Range. Several private (club) skifields operate on conservation tussocklands at Tukino (Tongariro National Park), Temple Basin (Arthur's Pass National Park) and at Rainbow (Nelson), Amuri, Mt Olympus, Fox Peak, Broken River, and Mt Cheeseman (Canterbury). The Cardrona skifield in Central Otago operates over private tussocklands.

The highly popular Central Otago Rail Trail runs through lowland mixed agricultural and modified short tussock grassland with impressive Central Otago landscapes as a backdrop, on land acquired by the Department of Conservation (Reis and Jellum 2012). This has contributed to a significant rejuvenation of and income for local communities providing supporting facilities.

Recreational and ecotourism values are also recognised and provided for in several locations beyond the conservation areas of indigenous grasslands and associated mountain lands. For example, on Cora Lynn pastoral leasehold land the 'Wilderness Lodge Arthur's Pass' offers a range of activities including a high quality ecotourism facility, and commercial and private horse trekking and four-wheel driving are offered across several contiguous South Island pastoral leasehold properties. However, public access across private land to conservation lands has become contentious in places, particularly because the tenure review exercise is expected to provide public access easements under terms of the relevant Crown Pastoral Land Act. In an attempt to resolve this issue, the government established a Walking Access Consultation Panel. References to this panel's reports are contained within a recent review of the outdoor recreation literature (Booth et al. 2010), in sections 8.1 'Mountains' (p. 45) and 18 'Benefits (positive effects of outdoor recreation)' (p. 176). Currently, cycleways through both conservation and private lands, including tussocklands, are being promoted nationally and developed with government funding in various parts of the country.

CURRENT THREATS TO ECOSYSTEM SERVICES PROVIDED BY TUSSOCK GRASSLANDS

Indigenous grasslands in several regions face several threats. Among these are continued pastoral farming on the South Island pastoral leasehold lands that have not yet proceeded with tenure review, and intensification of land use, often involving conversion to non-indigenous cover, following free-holding of rangelands through tenure review. A range of aggressive exotic plant species, both herbaceous and woody, and several invasive animals threaten many remaining areas of indigenous grasslands. The likelihood of global warming and, more locally, mining, particularly for low- and high-grade coal, also represent serious threats to areas of indigenous grassland of various tenures, with consequent reductions in their provision of ecosystem services.

Continued pastoral use of the South Island rangelands

The impact of pastoral farming, involving periodic burning and extensive grazing of tussockland vegetation still under leasehold tenure, is now generally less damaging than in the past, with less frequent fires and somewhat lower stocking rates. Deer and goats are now used to a limited extent and some cattle are grazed, but sheep continue to predominate on the rangelands.

Payton and Pearce (2001, 2009) reported a large interdisciplinary study of burning and simulated grazing at two sites, both unburned for more than a decade, on the Central and eastern Otago uplands. Information about these sites included detailed pre-burn descriptions. The results for snow tussock responses generally confirmed the earlier results of Payton and Mark (1979) and Payton et al. (1986), including tolerance of snow tussocks and perhaps even their adaptation to early-season (spring) fires, and their vulnerability to heavy grazing in the early post-fire years. Although these authors recorded a greater vulnerability to late-season (summer-autumn) fires than had Mark (1965d), the management recommendations were similar to those from the earlier studies: minimising post-burn grazing for one or preferably two years 'to ensure that the recovery of the post-fire grassland is not impeded'. The invertebrate fauna was also examined as a component of the later study (Figure 4). Most invertebrate groups were initially adversely affected by the burning treatments, with often significant reductions in population density. Some of the groups most severely affected were those dependent upon the litter layer for feeding and for the habitat it provides. Some invertebrate herbivore groups rebounded 2–3 years after the fire in response to tussock regrowth, while other invertebrates recovered gradually over a 3–5 year post-burn period.

Recent intensification of tussock grassland use

Although most of New Zealand's remaining indigenous grasslands have been modified to varying degrees by the indirect or direct effect of human activity, they have continued to support a rich flora characterised by high species diversity (Duncan et al. 1997, 2001; Dickinson et al. 1998; Walker et al. 2008; Mark et al. 2009). However, recent changes in land-use activities have led to further fragmentation and more intensive use. An increasing number of indigenous grassland properties in the South Island are being converted from extensive grazing to intensive agricultural activities or exotic forestry.

Although large areas of indigenous grassland habitat remain in New Zealand, recent losses are continuing (Figure 36). In 1840, 31% of New Zealand was covered by tussock grasslands dominated by endemic tussock grass species, but by 2002 just 44% of this area of indigenous grasslands remained, mostly in the interior areas of the South Island, and only 28% of this was legally protected, with a bias towards the high-altitude areas (Mark and McLennan 2005). By 2008 the remaining indigenous grassland area had been reduced to 40% of the area it had occupied in 1840 (Weeks et al. 2013b). Thus the rate of grassland conversion (ha year^{-1}) has decreased relative to the period between European settlement and 1990. However, the percentage of remaining indigenous grassland converted each year has increased (Weeks 2012). Between 1840 and 1990, 6742 hectares of indigenous grasslands were converted each year on average (0.20% loss of remaining grassland per year) (Figure 37). Between 1990 and 2001, the rate of conversion decreased to 3466 hectares each year on average

FIGURE 36 Recent losses of tussock grassland shown in blue (between 1990–2001) and in red (2001–2008). Yellow shows loss of tussock grassland between 1840–1990.

(0.15% loss of remaining grassland per year), but between 2001 and 2008, the rate of conversion increased to 4734 hectares each year on average (0.21% loss of remaining grassland per year).

Before 1990, this conversion took place in lowland environments well suited for agricultural use. In the last two decades, non-arable land (as defined by Land Use Capability in the New Zealand Land Resource Inventory; Newsome et al. 2000) has been increasingly converted in environments characterised by mid- to low slopes and elevation, summer droughts, extreme winter and summer temperatures, high winds, and limited annual rainfall (Weeks 2012). Many of these grasslands are on relatively infertile or porous, erosion-prone soils where the vegetation cover has been degraded by rabbits and livestock (Hewitt 1998). Since 1990 there has been a trend towards increased production within the South Island indigenous grasslands and particularly towards more productive pasture based on massive ecosystem subsidies of water and nutrients. Two-thirds of the conversion recorded between 1990 and 2008 was to exotic pasture (Weeks et al. 2013b). Methods of conversion usually involve oversowing with legume species, mostly white clover (*Trifolium repens*) and exotic grass forage species, often accompanied by installation of irrigation infrastructure and increased application of fertilisers to attain desired productivity levels. Over the last decade, buoyant commodity prices have driven a noticeable increase in the rate of conversion (expressed as a proportion of remaining grasslands) within these areas, so that between 1990 and 2008 the average rate of conversion increased by 1267 hectares per year (Weeks 2012).

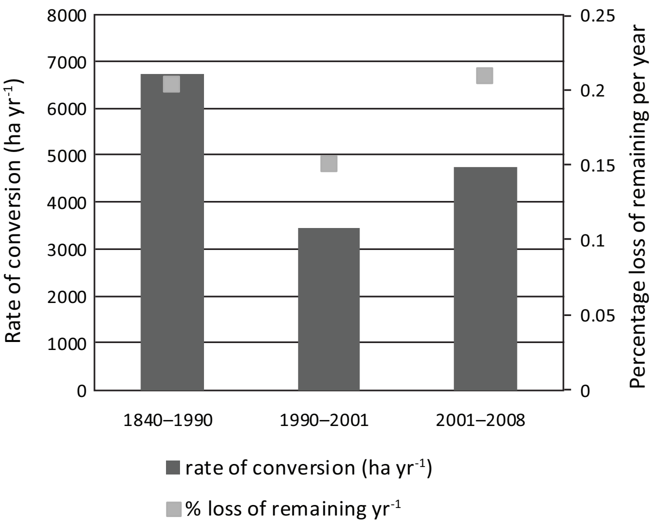


FIGURE 37 A comparison of the rate of conversion (ha year^{-1}, columns with scale on left vertical axis) and the percentage loss (square grey symbols, scale on right vertical axis) of remaining grasslands per year during three periods (1840–1990, 1990–2001, and 2001–2008).

Conversion of indigenous grasslands appears to be most rapid at lower elevations and on private land (Walker et al. 2008; Mark et al. 2009; Weeks et al. 2013a). Here, indigenous tussock grassland communities are most severely modified and invaded by exotic species, and are poorly protected (Mark and McLennan 2005; Mark et al. 2009). Nevertheless, these areas retain important residual indigenous biodiversity, including many threatened plants (Walker et al. 2008; de Lange et al. 2009) and endemic lizards and invertebrates (Patterson 1992; Patrick and Dugdale 2000).

Most land-use conversion in the South Island has been recorded in the Waitaki, Mackenzie, and Central Otago districts. The most noticeable increases were in the Waitaki and Mackenzie districts, where the rate of conversion doubled in the last decade (Weeks et al. 2013). Most individual changes are incremental and of less than 140 hectares, yet over the long term their cumulative effect is significant, particularly when combined with the few larger developments, such as the 2000–5500-hectare changes in the Waitaki district (Weeks 2012).

Recent grassland conversion has been concentrated in poorly protected environments with less than 30% of the total land environment remaining in indigenous cover. A quarter of total indigenous grassland conversion from 1840 to 2008 took place in environments mapped as threatened; that is, with <30% of indigenous cover remaining (Weeks et al. 2013b), and the environments most likely to be converted were those with the least remaining indigenous grasslands. Although the tenure review process has meant the total extent of protected indigenous grasslands has increased in recent decades, most of the new conservation land is at high elevations. Consequently, protection of low- to mid-elevation areas remains inadequate (Walker et al 2008; Mark et al. 2009), yet these low- to mid-elevation, highly modified ecosystems support large numbers of the South Island's threatened plant species (Walker et al. 2008; de Lange et al. 2009). In short, grassland habitats that are most reduced and least protected in New Zealand are also those being most rapidly transformed by intensification.

This consequence of the tenure review process constitutes one of two trends that may be increasing the vulnerability of residual indigenous biodiversity in indigenous grasslands (Weeks et al. 2013a); the second is the recent trend to more intensive use of agricultural land. While extensive pastoral grazing enabled persistence of indigenous biodiversity in some places, more intensive agricultural land use, typically involving cultivation and irrigation, leaves little or no room for indigenous biota. The acceleration of conversion is probably driven by growing international demand for products from New Zealand's high-value, more customised primary industries. In particular, land-based primary industries, particularly dairying, have recently expanded and production has consequently increased (Ministry of Agriculture and Forestry 2007). Dairying has increased most in the South Island, largely through conversions of sheep-and-beef farms in response to low land prices, high per-cow production, and in some cases access to irrigation.

Continued impacts on biodiversity and other ecosystem services are expected over the next century. In grazed areas, plant and invertebrate community compositions will continue to change gradually, depending on stocking rates and variability in climate and disturbance regimes between years. For areas that are completely converted to new land-cover types, changes will be much faster, and these conversions are likely to have significant impacts on the ecosystem structure and provision of ecosystem services.

In a study of impacts of agricultural development of tussock grassland (native cf. oversown and cultivated) on Coleoptera biodiversity, species diversity was higher at native and oversown sites compared with sites cultivated from tussock (Barratt et al. 2012), as might be expected. Only 19 exotic Coleoptera species had established at the four tussock grassland sites included in the study. Densities of most exotic Coleoptera species were also low, although in cultivated pasture the mean density of exotic species was higher than that of native species, unlike native and oversown tussock grasslands. However, there was little evidence to support the hypothesis that modified vegetation provides a source

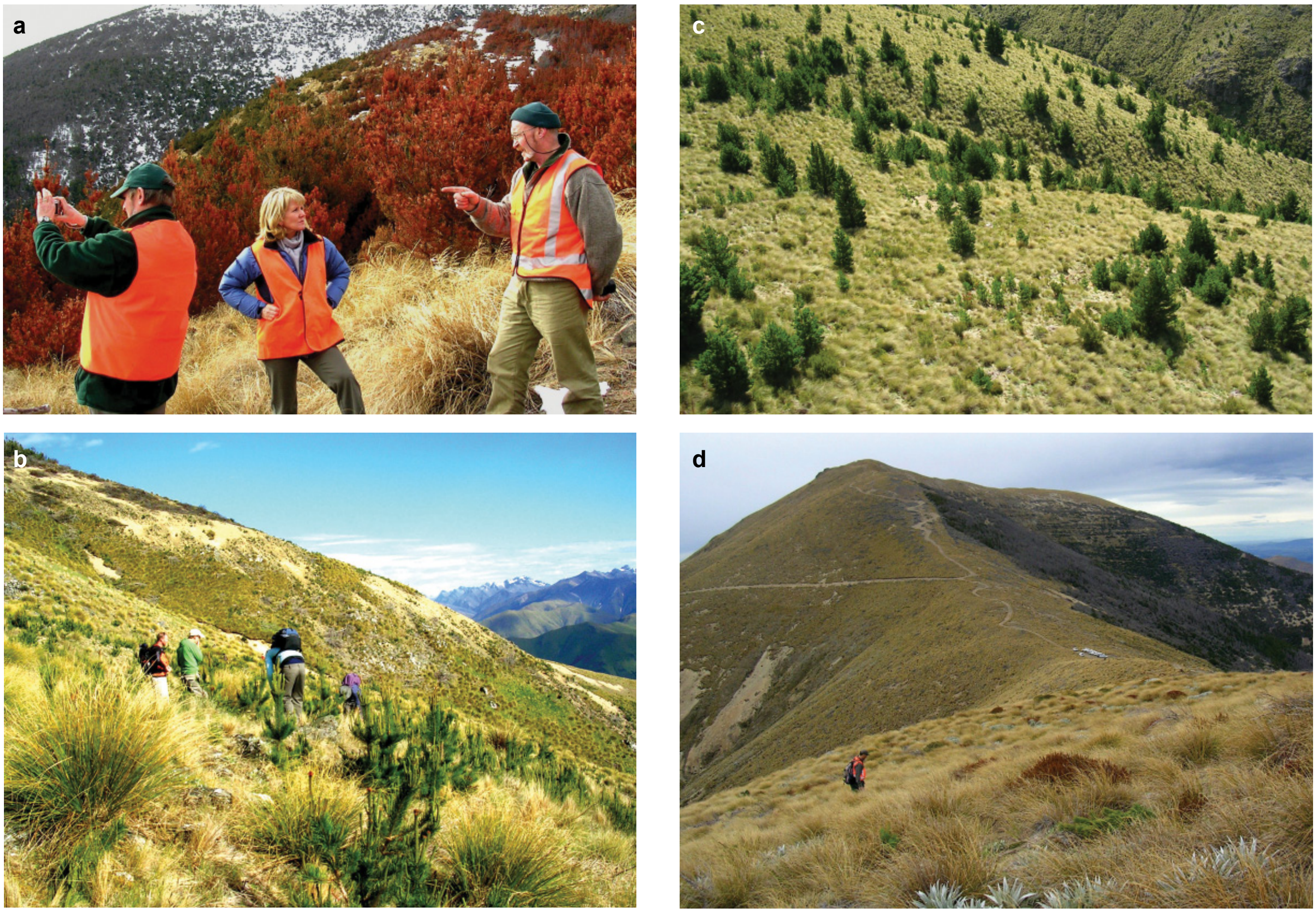


FIGURE 38 Clearance of wilding pines at Mid Dome, northern Southland: **(a)** trees sprayed with diquat herbicide (REGLONE; Syngenta Crop Protection UK), **(b)** volunteers clearing wilding pines, **(c)** before clearance, **(d)** after clearance.

of exotic Coleoptera species to invade native tussock. It was also difficult to demonstrate any pattern either taxonomically, functionally or in area of origin of those species, except that all herbivores were in the family Curculionoidea (weevils).

For other invertebrate groups the situation could be very different. For example, after tussock grassland was burned the number of exotic spiders increased, particularly species in the family Linyphiidae (Malumbres-Olarte 2010). This group includes species which disperse via ballooning.

Weed problems

Indigenous grasslands seem more vulnerable to weed invasion than most ecosystems, perhaps because they are vulnerable to overgrazing, which usually creates open or bare ground; in turn, that open ground can be readily colonised by aggressive, often relatively unpalatable species. New Zealand's tussock grasslands are no exception and have been invaded by a wide range of plant forms including rosette and erect herbs, particularly hawkweeds (*Hieracium* spp.); shrubs such as sweet brier (*Rosa rubiginosa*) and Scotch heather (*Calluna vulgaris*); and trees, particularly several exotic species of conifer. The latter are probably the greatest threat because they can permanently displace grassland and most indigenous woody species.

The wilding conifer threat

New Zealand's indigenous grasslands are threatened by wilding conifers in many regions. These trees pose a serious threat to many areas of tussock grassland, both protected and farmed, from existing stands upwind (Figure 38). Even formally protected areas of tussock grasslands, which should be secure under conservation management, may be threatened from spill-over from adjoining plantation forestry. The consequences of such infestations for ecosystem services could include reduced water production, loss of indigenous biodiversity, and impaired recreational values, among other effects. Action to control wildings has been slow but is currently underway in many regions. However, the threat has increased because recent government policy has encouraged land occupiers to plant additional exotic forests to obtain potentially substantial income from carbon credits. The Emissions Trading Scheme (ETS) under the Climate Change Response Act 2002 allows landowners to obtain carbon credits (NZ units) for certain forest stands, while the Permanent Forests Sink Initiative (PFSI), under the Forests Act 1949 and the Forests (Permanent Forest Sink) Regulations 2007, gains credit for carbon sequestration through the Kyoto Protocol's 'Assigned Amount Units' (AAUs).

The ETS lets landowners obtain carbon credits (New Zealand units: NZUs) for both post-1989 forests and pre-1990 forests (Froude 2011). Both have implications for privately managed tussock grasslands which, in turn, could affect tussockland conservation areas downwind. Wilding conifers occur as both pre-1990 and post-1989 stands and clear financial inducements exist to plant additional stands of conifers for this purpose. Moreover, landowners can register areas of wilding conifers for NZUs under the ETS, provided this is not contrary to a regional plan (under the Resource Management Act) or to a regional pest management strategy (RPMS) under the Biosecurity Act. In practice, an existing RPMS is unlikely to restrict wilding conifers, except where they are listed as an 'extermination species', as in Otago and Southland. However, there is at least one case where a pre-1990 wilding stand of *Pinus contorta* satisfied the criterion of a forest, because it was established as at 1 January 1990 and still present on 1 January 2008. This has been approved for the ETS in the Mackenzie Basin, where the Canterbury Regional Council (Environment Canterbury) has this species listed as a 'containment species' under its RPMS. Under the Biosecurity Act, 'containment species' can be managed at the discretion of the occupier, in contrast to an 'extermination species', which must be removed. No similar cases are known.

The 'post-1989' provision allows owners of new exotic (or indigenous) forests established after 31 December 1989 to earn NZUs for increases in carbon stock from 1 January 2008. In addition, landowners with wilding conifer stands that meet the criteria of a post-1989 forest can register the stand without any obligation to manage the subsequent spread of wildings – an example of a beneficiary not being required to meet the costs of externalities associated with a financial return from their wildings.

The PFSI scheme is similar but less restrictive: there are no requirements that registration not be contrary to the Resource Management Act or any RPMS (for *P. contorta*, where applicable). Moreover, as with the ETS, there is no requirement under this scheme to manage any subsequent wilding spread. Significantly, both schemes incorporate an important disincentive, in the form of major financial penalties, for removing any registered forest stands. However, this does not appear to be of concern to some Otago high country farmers, including the state-owned enterprise (SOE) Landcorp Farming, who in 2012 planted a 190-hectare stand of Douglas-fir (*Pseudotsuga menziesii*) within upland snow tussockland on the Lammerlaw Range. In addition, the Central Otago District Council approved two applications without public notification on areas zoned 'Outstanding Natural Landscape' in the district plan. These applications were submitted under the Afforestation Grant Scheme administered by the Ministry of Primary Industries. However, in a small concession to the potential impact of these proposed forests (the threat of wilding spread was 'classed as high'), the District Council did attach conditions associated with wilding containment to both applications, consistent with the forestry consultant's proposals for wilding control. The Landcorp application was approved by Clutha District Council (with no provisions for rejection in its district plan) even though it was only 100–250 metres from and almost surrounded by two areas of formally protected snow tussockland, including the 20 590-hectare Te Papanui Conservation Park (which is downwind and therefore at high risk of wilding invasion); moreover, the wilding threat was assessed as 'high' by the forestry consultants. More such plantings, particularly of the relatively invasive Douglas-fir, are likely to follow throughout the tussock grasslands, because the potential income from these forestry incentive schemes appears to be significantly greater (depending on the price of carbon) than current income from pastoral farming on this rangeland.

This seems to be a clear case of two government policies conflicting. At the very least, it represents a new policy with the undesirable consequence of creating a strong incentive for retaining and further promoting wilding conifer infestation in New Zealand's indigenous grasslands and associated mountain lands. This situation arose despite requests from many sectors for a national strategy or policy for managing wilding conifers in these vulnerable lands.

However, some cause for optimism remains. The first two recommendations of the Froude (2011) report state: 'That a non-statutory national strategy be prepared for wilding conifer management' and 'That the Ministry of Primary Industries be the lead agency for preparing this strategy'; these recommendations have been signed off by the Minister of Primary Industries and will be discussed by an informal Wilding Conifer Management Group. Furthermore, in 2008 the government decided to underwrite the Kyoto Protocol-related carbon costs of removing pre-1990 *Pinus contorta* stands that satisfied certain criteria in relation to the wilding threat. This was largely in response to objections by the Mid Dome Wilding Tree (Charitable) Control Trust to an indication from MAF (predecessor organisation to the Ministry of Primary Industries) of a charge of c. NZ$3 million under the Kyoto Protocol for removing c. 245 hectares of *P. contorta*. These stands of pre-1990-planted *P. contorta* were located on the Mid Dome Soil Conservation Reserve in northern Southland, formerly managed by the Ministry of Works and Development Water and Soil Division, but now managed by the Ministry for the Environment. The Mid Dome Trust was already carrying out a 12-year strategic plan, costing NZ$12 million, to remove these stands and exterminate the resultant wildings occupying c. 80 000 hectares downwind on largely inaccessible high country tussocklands.

The effect on soil carbon of grassland afforestation in New Zealand has been assessed on the basis of paired sites for improved (fertilised exotic pasture) and unimproved grasslands. Soil carbon decreased by c. 4.6 t ha^{-1} in the short term in the upper 30 cm, but had not changed after 20 years (Davis and Condron 2002; Baisden et al. 2006). The short-term decline appears to be either site- or species-specific, being greater for *Pinus radiata* than other conifers; for example, soil carbon did not change following afforestation with *P. nigra* on a dryland site in the Mackenzie Basin (Davis et al. 2007). Litter accumulation is likely to exceed any short-term reduction in mineral soil carbon associated with such grassland afforestation.

As previously discussed, the incentive for afforestation of indigenous grasslands is now based not only on timber production but as much or more on income from carbon credits associated with either the ETS or the PFSI. Unfortunately, no such credit system operates for non-woody vegetation, although tall tussock grasslands in good condition and many wetlands with their associated peats and organic soils store considerable amounts of carbon (Tate et al. 1997). Despite this oversight, some upland snow tussock grasslands, e.g. on Ben Avon Station in the Ahuriri Valley, are being researched and promoted for this purpose as an alternative to land uses with adverse landscape effects (Larry Burrows (Landcare Research) and Jim Morris (Lessee, Ben Avon Station), pers. comm. 2012).

Throughout the world, however, indigenous grasslands and other non-woody vegetation vary so highly in their storage of carbon and, apart from deep peat in some wetlands, are so readily reduced by fire or degraded through overgrazing that they are unlikely ever to be considered for carbon credits under the Kyoto Protocol or similar international agreements. Nevertheless, the FAO claims a critical role for global grassland management as a way of adapting to and mitigating climate change, because soils under the world's grasslands contain 20% of its soil carbon stocks. Furthermore, despite the widespread degradation of grasslands, their management is seen as a 'key adaptation and mitigation strategy for addressing climate change and variability' (Conant 2010).

Shrub invaders

The lowland-montane short tussock grasslands have been among the most vulnerable to invasion by exotic shrubs, with sweet briar (*Rosa rubiginosa*) probably the most common and widespread species. Its invasive role in the tussockland of the South Island intermontane basins was studied by Molloy (1964), and an attempt at economic harvesting of their hips in the Mackenzie Basin was relatively short-lived. Spraying has been effective but is used only locally, presumably because the cost would usually outweigh any benefits.

Scotch heather (*Calluna vulgaris*) is another serious but more local invader, particularly on the North Island's volcanic plateau, including Tongariro National Park. Permission to introduce it to the park was refused because of its presumed threat, but in 1912 it was planted immediately outside the park boundary by a ranger, apparently to foster grouse hunting. The grouse failed to establish but the heather thrived, and it is now a major weed problem within the tussock grasslands and shrublands of the park and surrounding regions (Chapman and Bannister 1990, 1994). It is also a potential problem in other locations around the country. A similar aggressive shrub, Spanish heath (*Erica lusitanica*), is present in New Zealand and clearly poses a similar threat where it has escaped, as in the tall tussock grasslands of the eastern Otago uplands (pers. obs.). Both gorse (*Ulex europeaus*) and Scotch broom (*Cytisus scoparius*) are widespread invasive shrubs on lower elevation grasslands in many regions.

Herbaceous invaders

A wide range of aggressive herbs threaten New Zealand's grasslands. Of these, several *Hieracium* species continue to cause most concern throughout extensive areas of farmed and protected indigenous grassland (Hunter 1991; Espie 2001). In many cases, serious infestation of *Hieracium* spp. (Figure 4d) has been associated with degradation of grassland ecosystems through pastoral farming (Treskonova 1991; Kerr 1992; Martin et al. 1994; Duncan et al. 1997; McIntosh 1997). However, there is some conflicting evidence regarding responses of some *Hieracium* species to different management regimes, including the retirement of tussock grasslands for conservation or other purposes (Rose and Frampton 1999; Mark and Dickinson 2003; Mead and Elstob 2005, Norton, et al. 2006; Mark et al. 2011; Day and Buckley 2013 and references therein). This issue remains both complex and controversial, so no firm conclusions can be offered at this time.

Invasive invertebrates

Exotic invertebrates have so far had only a relatively minor impact on New Zealand's natural ecosystems (Brockerhoff et al. 2010). There has been no demonstrated widespread population decline in host or prey populations, or conspicuous impacts resulting from plant defoliation or mortality. However, impacts of exotic invertebrates have received little attention compared to those of exotic mammals and plants, with the exception of a few notable invaders such as the scale insect *Eriococcus orariensis*, which causes 'mānuka blight', and exotic wasps in the genus *Vespula*, neither of which are a threat to tussock grassland ecosystems.

Several exotic weevil species have been collected in the tussock grasslands. These are probably vagrants, as the species have not been recorded feeding on native plants. Deliberately introduced biocontrol agents recorded from tussock grassland include *Rhinocyllus conicus* and *Trichosirocalus horridus*, introduced to control thistles, and *Exapion ulicis*, introduced to control gorse (Dickinson et al. 1998; Murray et al. 2003; Barratt et al. 2009) (Figure 5a–c). *Sitona discoideus*, the lucerne weevil, is a strong flyer and disperses readily; it has been collected above 1000 metres in the Waikaia Ecological Region (Dickinson et al. 1998) and at 2800 metres on the Inland Kaikoura Range (C.B. Phillips pers. comm.). However, it feeds only on introduced legumes (*Medicago* and *Trifolium*), so is highly unlikely to attack New Zealand's native plants.

A flightless European weevil, *Otiorhynchus ovatus*, commonly called the strawberry weevil, is occasionally found in tussock grasslands in Central Otago (Barratt et al. 2009). This species might be sufficiently polyphagous to feed on New Zealand native plants (Brockerhoff and Bain 2000). The weevil species most likely to adopt host plants from New Zealand's native grassland flora is the Argentine stem weevil (*Listronotus bonariensis)*, a South American species with a wide host range within grasses. It is abundant in pasture, is a strong flier, and is the most commonly encountered exotic weevil species found in tussock grassland (Barratt et al. 2007). It has been collected in Otago at altitudes up to 1640 metres on Coronet Peak (Barratt et al. 2007). In the laboratory *L. bonariensis* adults can feed and lay eggs in the stems of several native grasses including *Chionochloa rigida*, *Festuca novae-zelandiae* and *Poa colensoi* (Figure 4a), although not to the same extent as on ryegrass (*Lolium perenne*) (unpubl. data).

White (1975b) examined insect damage to *Chionochloa* seed production in 22 alpine tussock grassland sites in the South Island, but did not record any exotic species as causing damage. However, at least three native insects feed on snow tussock fruits. Mark (1965b) found up to 7% of *C. rigida* florets were infested with a cecidomyiid fly (Diptera: Cecidomyiidae). This was later confirmed and the fly identified as *Eucalyptodiplosis chionochloae* by Kelly et al. (2008), along with another fly, *Diplotoxa similis* (Diptera: Chloropidae), and the moth *Megacrapedus calamogonus* (Lepidoptera: Gelechiidae). Kelly et al. found these three insects in a wide range of *Chionochloa* host species, including *C. macra*, *C. pallens* and *C. rubra*. Each insect species alone can destroy >50% of the florets and collectively >90%, but masting (synchronous, abundant flowering over wide areas at intervals of several years) affects this predation, reducing losses from >70% of florets in low-flowering years to <10% when masting follows a poor flowering year. This is clearly a positive effect of the masting phenomenon.

Various exotic Hymenoptera and other exotic insects visit native flowers. By competing with or displacing native pollinators and pollinating weeds, these exotic species could alter the reproductive success of native plants and potentially affect the native biota (Brockerhoff et al. 2010). Native biodiversity is also potentially threatened by introduced entomophagous parasitoids, which have already been found in native grassland environments. Two species of *Microctonus* (Hymenoptera: Braconidae) have been introduced as biocontrol agents for weevil pests, and one of these, *M. aethiopoides* (Figure 5d*)*, parasitises 14 native and five exotic species of weevils (Barratt 2004). Furthermore, *M. aethiopoides* attacks non-target hosts not just in the target host environment (lucerne) and in developed pasture, but also in native grassland environments (Barratt et al. 2007). Although attack rates are generally low (<10%), up to 24% parasitism of a non-target weevil species has been recorded in modified tussock grassland.

Climate change

Halloy and Mark (2003) attempted to assess the potential impact of climatic warming on the elevational distribution patterns of the indigenous alpine flora. Using the patterns documented by Mark and Adams (1995), and basing their analysis on species–area relationships, they estimated current and projected vascular plant floras and tested the model's sensitivity at different scales, from the whole world to small alpine regions. If temperature rose by 3°C, an approximate prediction for the following century, the New Zealand alpine flora could reach c. 550–685 species while losing 200–300 indigenous species. A lesser (0.6°C) rise could threaten 40–70 indigenous alpine species and result in a significant influx of exotics. Over millennia, fragmentation of alpine areas might favour speciation, but in the shorter term the loss of up to 80% of existing alpine islands would substantially shrink species ranges and significantly increase the risks of extinction. Upward migration of some alpine plant species has already been documented in the European Alps (Grabherr et al. 1994; Gottfried et al. 2012; Pauli et al. 2012) and parts of Asia, but despite earlier claims that treelines in New Zealand were rising (Wardle and Coleman 1992), more recent studies indicate overall stability (Cullen et al. 2001; Harsch et al. 2009, 2012). Impacts of such changes on ecosystem services are difficult to predict.

Species inhabiting alpine regions with a relatively uniform topography, like the plateau summits of the Central Otago mountain ranges, might be particularly vulnerable to climate change because small changes in climate could make the habitat unsuitable over wide areas. In contrast, areas with diverse microtopography offer a diversity of microclimates where species might find at least temporary refuge from changes in climate. Thus, species such as *Myosotis albosericea* and *M. oreophila*, known only from the upper slopes of the southern and northern Dunstan Mountains, respectively, could be among the most vulnerable to global warming (Mark et al. 2012), although a 15-year demographic study of *M. oreophila* indicates an apparently viable and stable population (Dickinson et al. 2007; Mark et al. 2012).

Mark et al. (2012) noted that soil lichens in the alpine zone are considered vulnerable to vegetation change driven by climatic warming, though changes in the distribution and abundance of potential indicator species like *Thamnolia vermicularis* are not yet obvious. They also considered that alpine reptiles would be more vulnerable to climate change indirectly through increased predation by ship rats, which could change their use of alpine habitats. Insects, in contrast, usually move with their communities and host plants in response to most ongoing natural processes. Also, many species are effectively immobile because the females cannot fly, so changes have to be slow enough to maintain a continuous habitat. Therefore, if global warming is gradual enough and there is room to move, then insect communities should survive, perhaps with some redistribution (Mark et al. 2012).

Global warming might also induce increased development of tussock grasslands, but the largely negative consequences of this have been discussed earlier in this chapter.

Mining and other developments

The Ngakawau Ecological District in the North Westland Ecological Region includes two unique upland plateau wetlands dominated by locally endemic tussocks. Unfortunately, these are associated with the Brunner Coal Measures, so they are either already being mined for high quality coal or are threatened with mining. Open-cast mining continues to devastate much of the plateau tussock wetland of the Stockton Plateau (Figure 39), and the mine's operator, Solid Energy, also has a consent to open-cast mine the 25-hectare area of Cypress Swamp/Happy Valley. This is a tall tussock wetland dominated by *Chionochloa rubra* subsp. *occulta* with some *C. juncea*, and it has a rich floral and faunal biodiversity.

The adjoining Denniston Plateau, a roughly circular area (1750 ha) of mostly public conservation land, is also under threat. A resource consent has been granted to open-cast mine some 160 hectares; this, with the associated works, would seriously undermine the unique ecological and biodiversity values that have been identified in this area. It has been described as a unique combination of distinctive physiography, geology, climate, soils, vegetation, and indigenous biota, many formally classified as threatened. The plant cover is dominated by the locally endemic tall tussock grass *Chionochloa juncea* (Figure 9), with many associated wetland species, and has been referred to as a plateau tussock wetland rather than a pakihi. The plateau also contains a wide range of other vegetation types, including biodiverse mixed beech–podocarp forest in the more sheltered depressions.

FIGURE 39 Opencast mining on Stockton Plateau, North Westland, with Denniston Plateau in the distance, showing destruction of indigenous plant cover. Photo: R. Reeves, June 2012.

The plateau has obviously been burned, evidenced in part by the widespread presence of mānuka (*Leptospermum scoparium*), but there is no indication of recent fires. Naturally slow plant succession and an interacting combination of environmental, ecological and biological factors make this a valuable scientific and conservation resource, more so because the impacts of exotic plants or animal predators are negligible, presumably because of the relatively hostile environment. Ecologists presenting evidence to an Environment Court hearing on the mining proposal by Bathurst Resources were in general agreement that the Denniston Plateau constitutes 'an endangered rare ecosystem'. A submission to the Court by one of us (AFM) assessed the Denniston Plateau as 'of outstanding value from the point of view of science and conservation, and too valuable to exploit with open-cast mining'. The case is yet to be completed but any loss of these grasslands would have impacts on the ecosystem services they currently provide.

Wind farms may also impact on grasslands. Given the relatively exposed locations of most upland tussock grasslands, pressure may continue for wind farm development in these areas. However, these developments are often contentious, and in 2012 Meridian Energy abandoned its proposed Project Hayes development on the Lammermoor Range in Central Otago after the Environment Court overturned its resource consent, primarily because of its likely impact on landscape values.

CONCLUDING REMARKS

New Zealand's indigenous grasslands probably reached their maximum extent just before European settlement in the 1840s, because Polynesian fires had replaced a wide range of forest, woodland, shrubland and grass–shrubland mosaic vegetation with more-fire-adapted grasslands. Variation in the use and development of these grasslands over the 170 years of European occupation, however, means that today only about 44% of these grasslands persist. While all are modified to some extent, 15.4% are formally protected – well ahead of the world average of 3.4%. Nevertheless, New Zealand's status as one of the world leaders in temperate grassland protection is not formally recognised by the IUCN because all our protected ecosystems are assigned to just one category: Subtropical/Temperate Rainforests/Woodlands. The Department of Conservation should correct this anomaly.

The higher elevation grasslands mirror the global pattern, predominating in terms of both persistence (98%) and protection (61%), but other grasslands fare less well. In particular there is general concern, recently expressed in the Environment Court (the Waitaki District Council case), with the inadequate protection of the lower elevation grassland ecosystems, the more so because of their unique biodiversity and also because they continue to be most threatened by the tenure review process and subsequent intensification of land use.

Indigenous grassland ecosystems deliver a wide range of important ecosystem services that improve human well-being by providing many tangible benefits. However, most of these benefits cannot be privately owned and are appropriately treated as a 'public good', so they are often ignored or inadvertently threatened – at least until their sudden disruption or threatened failure makes them obvious. Their roles in pollination, biological control, indigenous biodiversity and genetic diversity, water production potential of the upland tall tussocklands, soil conservation, carbon storage and sequestration, education, recreation and ecotourism opportunities deserve close attention and practical, substantial support, because the consequences of not doing so are too important to ignore. We trust this chapter will go some way towards addressing this need.

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