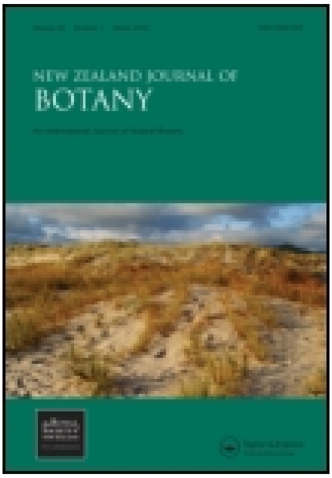

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North Island seral tussock grasslands 1. Origins and land-use history

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North Island seral tussock grasslands 1. Origins and land-use history

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Abstract A review of the history of seral tussock grasslands in the North Island reveals no evidence for their presence below treeline in pre-human times. Tussock grasses were confined to natural non-forest sites, which, below treeline, were dominated not by tussocks, but by low trees, shrubs, and, on oligotrophic bogs, by *Empodisma minus* and *Gleichenia dicarpa*. Non-forest sites below treeline result from cold-air inversion, high water tables, and frequent geomorphic disturbance. Forest clearance by early Maori fires and subsequent recurrent burning of secondary vegetation induced 660 000 ha of seral tussock grassland in three areas of the central North Island: short tussock (*Poa cita* and *Festuca novae-zelandiae*) grasslands on the Volcanic Plateau surrounding Lake Taupo; tall tussock (*Chionochloa rubra*) grasslands on northern and eastern flanks of the Tongariro volcanoes; and tall tussock (*Chionochloa rubra*) on the Moawhango plateaus. The pattern of deforestation and spread of tussock grasses in a region of low economic value to Maori is correlated with extensive undulating topography at montane–subalpine altitudes, summer-dry climates in rain-shadow areas, and free-draining volcanic ash soils. Of the 660 000 ha in grassland in c. 1840, almost half (310 000 ha) had disappeared by c. 1940, and only 10% (64 000 ha) remains today, mostly in Moawhango Ecological District. Conservation status, reserve design, and the renewable resource value of the grasslands are discussed.

Keywords Polynesian; tussock grassland; secondary vegetation; vegetation change; fire; deforestation

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INTRODUCTION

Over the last two millenia, vegetation of the central North Island has been strongly modified by volcanicity and, in the last millenia, by cultural disturbance. The evolution of the seral tussock grasslands of the central uplands reflects this cultural disturbance history.

The pyroclastic flow of Taupo Pumice (1850 yr B.P.) (Froggatt 1981) was the only eruption from the Taupo and Tongariro Volcanic Centres (Froggatt & Lowe 1990) to extensively destroy vegetation in the last 2000 years. Although vegetation within a 50 km radius of Lake Taupo was destroyed by the incandescent ash-cloud, there is abundant evidence that forest rapidly recolonised most, if not all, of the affected region. Evidence for forest recolonisation includes cup-shaped podsol pans developed in Taupo Pumice under individual podocarp trees and distributed throughout the Kaingaroa Basin (Fig. 1) (Henry 1955; Vucetich & Wells 1978), and forest remnants in even the most heavily affected areas (Henry 1954, 1955), for instance, Opepe Bush east of Taupo (Fig. 1) and numerous *Nothofagus* stands within 20 km of the eruption source (Clarkson & Nicholls 1992). Pollen diagrams provide evidence for recovery of forést within c. 400 years of the eruption (Clarkson et al. 1986; Rogers & McGlone 1989; Steel 1989). Nicholls (1978) summarised anecdotal and edaphic evidence of the Waiotapu and Kaingaroa Basins (Fig. 1), concluding that "forest covered most of the region after the Taupo Pumice eruption" and that several hundred years of Maori occupation reduced the forest to its present patchy distribution. Elder (1962) also considered forests of the Kaimanawa Mountains had substantially re-adjusted to climatically determined boundaries. The small plinian eruptions from the Tongariro volcanoes (Topping 1974) would have destroyed vegetation only on the upper slopes of the volcanic cones (Clarkson 1990). There is, therefore, overwhelming evidence in favour of forest below regional treelines in prehuman times (Rogers 1987), and none for extensive tussock grasslands.

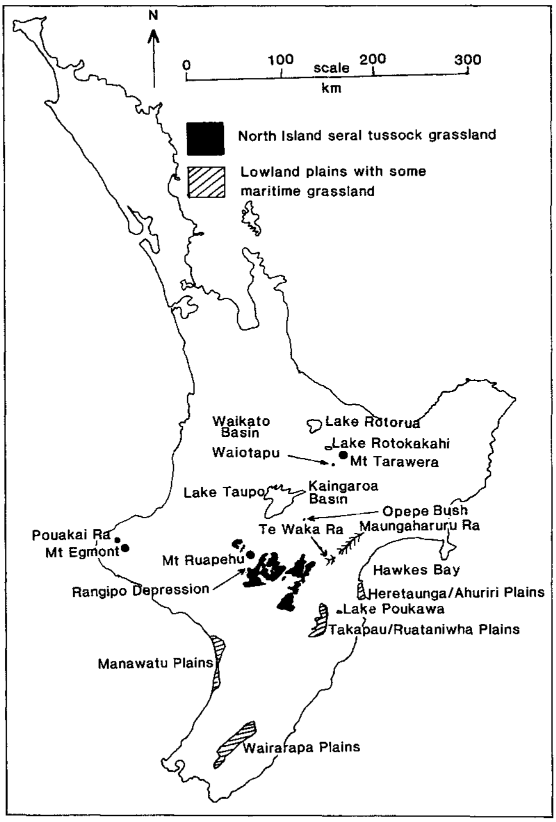


Fig. 1 Distribution of extant seral tussock grasslands of the North Island and lowland plains that originally supported some areas of maritime grasslands in early European times.

The arrival of Polynesian settlers about 1000 yr B.P. initiated long-term deforestation in the central North Island and perpetuation of seral tussock grasslands and shrublands through to the arrival of Europeans in 1839. Short and tall tussock grasslands developed on plateaus, in basins, and on the volcanic ring-plain of the central uplands. Although Maori forest clearance affected extensive areas of the central and eastern North Island (Nicholls 1963; McGlone 1983), seral grasslands developed in only a relatively small part of the total area. In addition to these short and tall tussock grasslands, maritime grasslands of non-tussock species covered summer-dry lowland and coastal plains in Hawke's Bay and Wairarapa (Fig. 1) that were deforested in prehistoric Maori times (Wardle 1991, p. 264).

The tussock grasslands now occupy intermontane plateaus and plains around Lake Taupo (Volcanic Plateau), the Rangipo Depression, and the Moawhango Ecological District (Simpson 1982) (Fig. 2). These areas experience rainshadow climates with annual rainfall commonly half that of surrounding mountains (New Zealand Meteorological Service 1986; Rogers 1987). The seral and unstable nature of North Island tussock grasslands has been remarked on by Fletcher (1914), Ure (1950), Henry (1955), and Elder (1962, 1965). Their seral nature is shown by community disequilibrium, with invading native shrubs and trees being common in all districts not subject to burning (Rogers & Leathwick 1994). Tussock grasslands have progressively disappeared in European times because of conversion to improved pasture and exotic forests, depletion by overgrazing and burning, and through invasion by weeds, native shrubs, and trees. This depletion and recent shifts in land use have heightened public awareness of tussock landscapes and raised management concerns over their future. Attention is focussed here on the derivation of tussock grassland landscapes of key conservation importance, as input to shaping land-use attitudes and policy on their most appropriate use.

METHODS

Natural non-forest sites to which tussock grasses were confined in pre-human times were mapped from existing indigenous vegetation and an understanding of relationships between present indigenous vegetation, landforms, and soils. The extent of grasslands in c. 1840 and c. 1940 were mapped from historical accounts, aerial photographs, and an interpretation of existing vegetation patterns, and present grasslands were mapped from field reconnaissance. Finally, the degree of representation of the present grasslands in the reserves network was evaluated for each ecological district.

RESULTS

Pre-human extent of tussock grasses

There are no detailed reconstructions of pre-human vegetation patterns of the central North Island. Nevertheless, it is reasonable to assume that, in this humid environment, tussock grasses below treeline occurred only where forest was naturally excluded by edaphic or climatic extremes, or by frequent geomorphic disturbance. The tephrostratigraphic and palynological evidence for the post-glacial for the central North Island shows no long-term clearance

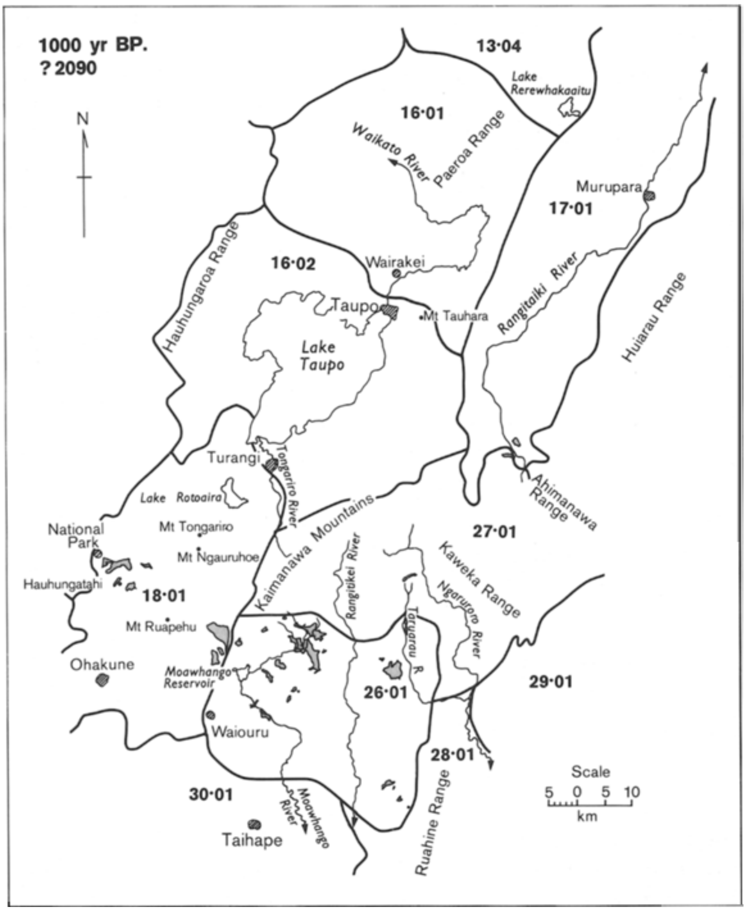


Fig. 2 Distribution of natural, non-forest sites (shaded) of the central North Island uplands in the pre-settlement period. Ecological district (McEwen 1987) numbers are: 13.04, Rotorua; 16.01, Atiamuri; 16.02, Taupo; 17.01, Kaingaroa; 18.01, Tongariro; 26.01, Moawhango; 27.01 Kaimanawa; 28.01, Ruahine; 29.01, Maungaharuru; 30.01, Rangitikei. The possibility that central North Island tussock grasslands will shrink to the area of natural non-forest sites in the next century is high.

of forest, even at a local scale, in pre-human times (Moar 1967; Topping 1973; McGlone & Topping 1977; Clarkson et al. 1986; Newnham et al. 1989; Rogers & McGlone 1989; Steel 1989). Nationally, non-forest sites covered c. 6.4% of the land below treeline in pre-human times (Molloy 1980, p. 64). Non-forest sites in the central North Island were dominated by shrubs and low trees adapted to climatic and edaphic extremes, such as *Dracophyllum subulatum**, *Dracophyllum longifolium*, *Phyllocladus alpinus*, *Hebe* spp., *Halocarpus bidwillii*, and *Olearia virgata*. Mixes of these species dominate the least burnt non-forest sites in several areas, for example, the Te Waiotupuritia valley of the Kaimanawa Mountains, peat bogs between Mts Ruapehu and Hauhungatahi, and clearings south of Ruahine Corner in the northwest Ruahine Range. Since shrubs are taller, tussock grasses were restricted to open understoreys of shrubland and along water courses. Burning caused by lightning-strike on these sites would not have been frequent enough to select tussocks ahead of shrubs (Nicholls 1963; Rogers & McGlone unpubl. data).

Natural non-forest sites within the area of present central North Island tussock grasslands (Fig. 2) are concentrated in the Tongariro and Moawhango Ecological Districts. Less extensive areas exist in the Kaingaroa and Kaimanawa Ecological Districts. Cold air inversion basins infilled with water-sorted Taupo Pumice exclude forest in the northern

*Plant nomenclature follows Cheeseman (1925), Allan (1961), Moore & Edgar (1976), Connor & Edgar (1987), Webb et al. (1988), Brownsey & Smith-Dodsworth (1989), and Connor (1991).

Moawhango Ecological District (Elder 1962). Both blanket and basin bogs (Taylor & Pohlen 1962) exclude forest in the southern Moawhango and northern Tongariro Ecological Districts (Rogers 1987). A combination of high water tables and cold-air inversion on low-fertility Taupo Pumice excludes forest on several small sites in the Kaingaroa Ecological District (Nicholls 1990; Smale 1990) (most do not appear at the mapping scale of Fig. 2). The wide, frost-prone valleys of the Kaimanawa Mountains are also inimical to forest. Forest is also excluded from outwash fans of lahar debris on the south-east flanks of Mt Ruapehu, probably because substrate disturbance by lahars is more frequent than the time needed for forest recolonisation (Purves 1990). The only evidence for perpetuation of open vegetation by frequent volcanic eruptions or eruption-induced fires exists on the flanks of Mt Ngauruhoe, a volcano in existence and active for the last 2500 years (Topping 1974). Ahukawakawa Swamp between Mt Egmont and the Pouakai Range (Fig. 1) is the only *Chionochloa rubra* ssp. *rubra* (hereafter referred to as *Chionochloa rubra*) (red tussock)-dominated clearing below treeline in Egmont Ecological District. The diverse secondary communities that developed with forest clearance were sourced from these scattered non-forest enclaves within extensive montane–subalpine forest (see also Molloy 1969).

The ecological role of different tussock species on non-forest sites in pre-human landscapes relates particularly to gradients of disturbance, temperature, and soil drainage. *Chionochloa rubra* occupied stable, high water table sites such as basin and blanket bogs, cold air inversion sites in higher altitude wet environments, and the alpine zone in the absence of *Chionochloa pallens* ssp. *pallens* (hereafter referred to as *Chionochloa pallens*), as on Mt Egmont. *Festuca novae-zelandiae* (hard tussock) occupied stable, summer-dry, well-drained, and cold air inversion sites. *Poa cita* (silver tussock) grew at lower altitudes, on sites of frequent disturbance such as braided riverbeds and erosion-prone Taupo Pumice. *Rytidosperma setifolium* (bristle tussock) was a primary coloniser of skeletal soils resulting from mass movement, and of volcanically disturbed terrain. Cultural disturbance has merged and overlapped the ecological and distributional boundaries of these species and has initiated successional trends in mixed-species grasslands.

Timing of deforestation

There is charcoal and palynological evidence in peat bogs of limited pre-human deforestation in the rain-shadow region of the south-western Kaimanawa Mountains. Lightning-strike fires probably caused the forest clearance and led to secondary shrubland but not grassland c. 3000 yr B.P. (Rogers & McGlone 1989). The development of seral grasslands is almost certainly dependent on repeated burning, for taller shrubs rapidly dominate secondary vegetation in the absence of burning (Rogers & Leathwick 1994). The extent of induced shrubland is difficult to estimate from pollen records because of the small number of sites and uncertainties with the source areas of pollen taxa. This forest clearance was the North Island equivalent of the deforestation process underway in south Canterbury and Otago c. 2500 yr B.P. (McGlone 1973, 1983).

The timing and geographical extent of Maori forest clearance is well established for the Moawhango Ecological District (Rogers 1987). A single conflagration deforested the western district in the southern Kaimanawa Mountains c. 570 yr B.P. Another c. 430 yr B.P. deforested the eastern district between the Kaimanawa Mountains and the Ruahine Range. Subsequent repeated burning of the deforested landscapes removed little more forest.

Around Lake Taupo, a period of forest clearance began just before 750 ± 70 yr B.P. (McGlone 1983, fig. 2D), although Grace (1959) suggests human habitation from 600 years ago. The only information for the Tongariro region is for some deforestation of the southern Rangipo c. 500 yr B.P. (Purves 1990) and a period of deforestation on the northern ring-plain commencing 530–700 yr B.P. (Steel 1989, p. 115). Although it is beyond the region of seral tussock grasslands, the rapid deforestation of the Waikato Basin occurred c. 800 yr B.P. (Newnham et al. 1989), as did that at Lake Poukawa in Hawke's Bay (McGlone 1983). Against these dates, the Moawhango Ecological District was burnt comparatively late in the central North Island deforestation phase.

Tussock grasslands in 1840

In 1840, tussock grassland and associated low shrubland dominated three major areas; the central Volcanic Plateau surrounding Lake Taupo, the northern and eastern ring-plain of the Tongariro volcanoes, and the Moawhango plateaus (Fig. 3), all characterised by undulating montane topography surrounded by steep ranges. About 644 000 ha of seral grassland and low shrubland was estimated for 1840 (Table 1), comprising 5.7% of the land area of the North Island. This excludes a small area of the

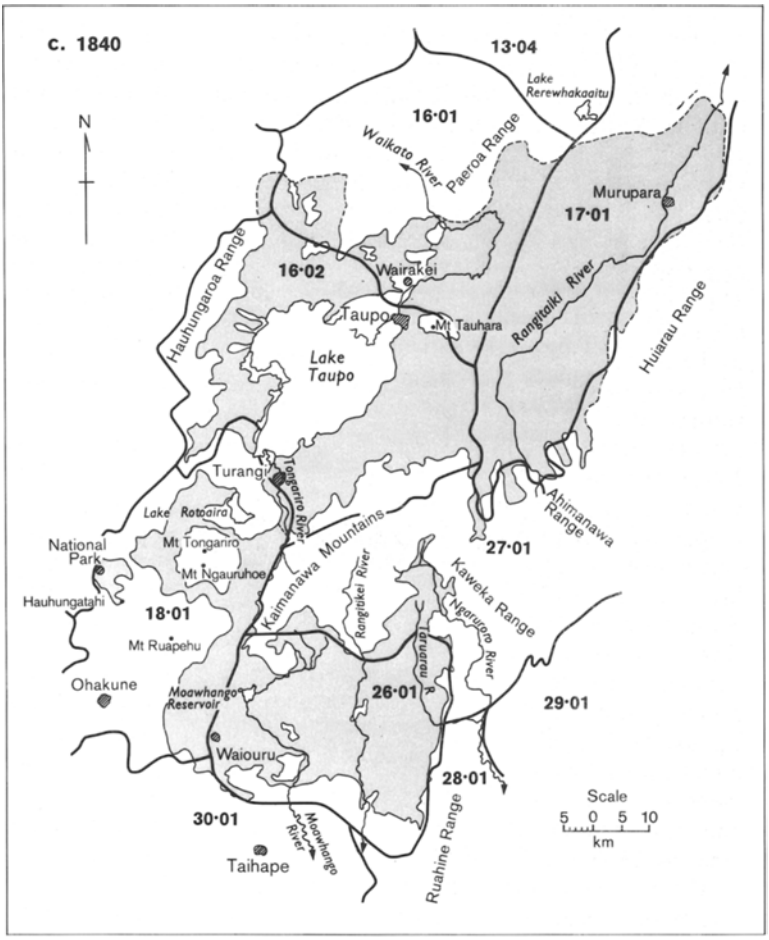


Fig. 3 Estimated distribution of North Island tussock grasslands (shaded) in c. 1840. Dashed boundaries to grasslands indicate approximate limits only. Names of ecological districts are shown in the caption to Fig. 2.

western Hawke's Bay uplands (Maungaharuru and Te Waka Ranges) where there may have been restricted summit grasslands.

Atiamuri, Taupo, and Kaingaroa Ecological Districts

Almost all the ignimbrite landforms of the volcanic plateau surrounding Lake Taupo supported short tussock grassland and *Pteridium esculentum* fernland. *Poa cita* tussock grasslands were largely devoid of woody vegetation, and are described in accounts of early journeys by Bidwill in 1839 (Bidwill 1841), Colenso in 1841 (Colenso 1884), and Dieffenbach (1843). These authors recorded "barren" plains with little or no woody plants for camp fires. Nicholls (1978) summarised the late nineteenth century vegetation of the Waiotapu and Kaingaroa Plateaus partly from writings of early observers (Meade 1871; Kirk 1872; Smith 1886; Fletcher 1914; Vaile 1939). Forest was confined to summits and south faces of the highest hills in the flat to undulating topography. Outside the forest, the hills were covered by *Pteridium esculentum*, *Coriaria* spp., *Leptospermum scoparium*, and *Poa cita*. Basin and valley floors supported stunted *P. cita* and *Dracophyllum subulatum*. *Chionochloa rubra* and *Festuca novae-zelandiae*, although present, were comparatively unimportant. Bidwill (1841) also described the replacement of *P. esculentum* by an open tussock cover after frequent burning. Nicholls (1978) noted that Maori "firing the vegetation of the valleys made travel easier, on the hillsides it halted the natural reversion from *Pteridium esculentum* to shrubland (*P. esculentum*-rhizome was a staple food), and it helped to clear the richer forest soils for cultivation at the forest margins".

Tongariro Ecological District

Deforestation affected most of the northern and eastern lahar ring-plain of the Tongariro volcanoes, inducing extensive *Chionochloa rubra – Festuca novae-zelandiae – Poa cita* tussock grassland. Patches of forest remained on the northern slopes of Mt Ruapehu and Mt Tongariro, but deforestation was complete on the eastern or Rangipo Depression side, stretching from Mt Tongariro in the north to Raketapauma and Turangarere (south of Waiouru) in the south. A zone of ablating pavements surrounding the Whangaehu River outwash fan in southern Rangipo is not edaphically or climatically controlled but was induced by forest clearance and subsequent frequent burning of secondary vegetation (Rogers 1987). Once initiated, the unconsolidated Holocene ash sequence erodes to an underlying gravel lag-field (N. Kennedy pers. comm. 1989).

Moawhango Ecological District

The high-altitude, undulating plateaus of the Moawhango Ecological District were mostly deforested by Maori burning, leading to extensive *Chionochloa rubra* tussock grassland. Some forest remained on humid, south-facing valleys or cloud-capped knobs. Forests of the rainshadow-affected southern Kaimanawa Mountains were also substantially removed, but those of the steep peripheral Kaweka and Ruahine Ranges remained intact as fires were deflected by steep topography and higher humidity.

Rotorua Ecological District

Poa cita, along with *Rytidosperma setifolium* and *Microlaena stipoides*, occurred in all the low valleys from Te Ngae (eastern shores of Lake Rotorua) south-west to Whakarewarewa and Lake Rotokakahi (Green Lake) (Kirk 1872). These grasslands resulted from forest clearance and continual burning by Maori of secondary vegetation on edaphically dry Kaharoa Tephra (770 yr B.P.) before it was inundated by Rotomahana Mud in 1886 (B. D. Clarkson pers comm.). Today, *P. cita* occurs on Mt Tarawera in "silver tussock basin" (see Clarkson & Clarkson 1983, fig. 1).

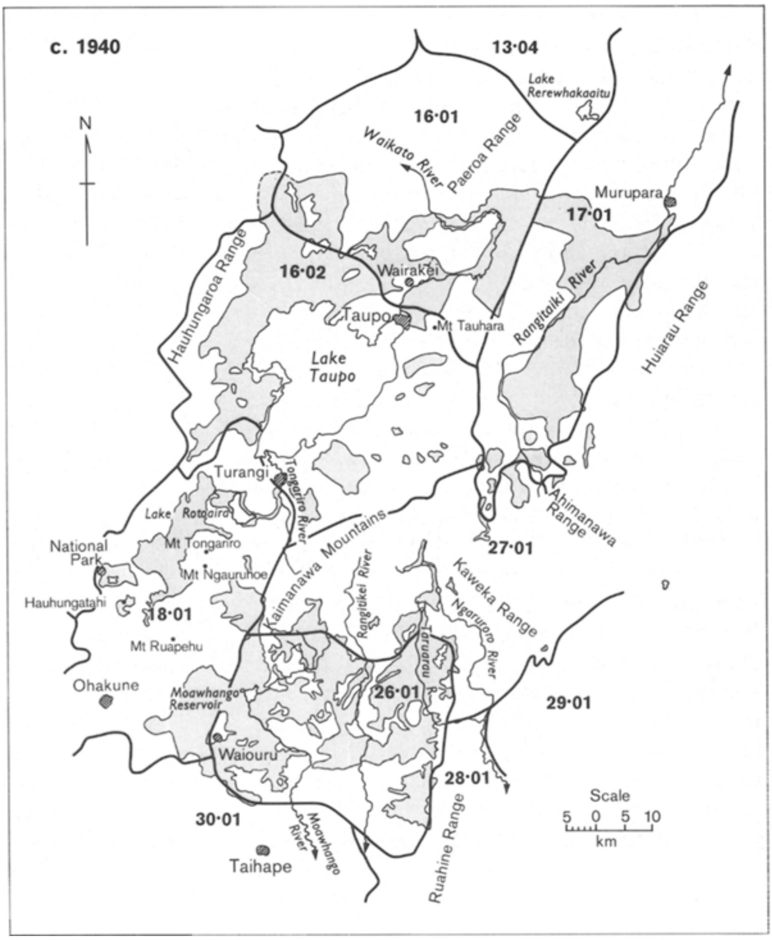
Maungaharuru Ecological District

In the late nineteenth century, small areas of the Maungaharuru Range supported grasslands of *Poa cita* and *Chionochloa rubra*, and *Chionochloa pallens* was present on the Te Waka Range (Wright 1985). Practically all of these grasslands were destroyed before scientific survey. Their occurrence in a potential forest environment points to their seral nature. A 1 ha remnant of *C. rubra* in a pumice-infilled basin is present on the Maungaharuru Range, along with several plants of *P. cita*. Several plants of *C. pallens* remain on the Te Waka Range.

Table 1 Historical extent of North Island tussock grasslands.

			Area (ha)			
Ecological district	Sub-district	Vegetation	c. 1840	c. 1940	1990	Reserved
Atiamuri, Taupo, and Kaingaroa (Volcanic Plateau)	east Taupo	*Poa cita*	301 500	107 500		
	north Taupo		62 900	62 100		
	west Taupo		38 200	28 400		
	south Taupo		34 700			
	subtotal		437 300	198 000		
Tongariro		*Chionochloa rubra*	41 300	22 800	2468	2468
Kaimanawa		*C. rubra*/*Festuca novae-zelandiae*	13 600	5587	5587	1800
Moawhango	north-west	*C. rubra*/*Festuca novae-zelandiae*			44 851	
	north-east				7696	
	south				4073	
	subtotal		165 500	131 900	56 620	1900
Maungaharuru	Maungaharuru Ra.	*Chionochloa rubra*	66	66	1	
	Balls Clearing	*Chionochloa rubra*	4	4		
	Littles Clearing	*Chionochloa rubra*	15	15	15	15
	subtotal		85	85	16	15
	Totals		657 785	358 372	64 691	6183

Fig. 4 Distribution of North Island tussock grasslands (shaded) in c. 1940. Names of ecological districts are shown in the caption to Fig. 2.



Heretaunga and Wairarapa Plains Ecological Districts

The summer-dry lowland plains of Hawke's Bay and Wairarapa supported grasslands grading into swamps, bracken fernland, and seral scrub in late Maori – early European times. Extensive *Elymus* spp. grasslands occurred on the Takapau and Ruataniwha Plains (Wilson 1939, pp. 11–12), and *Microlaena stipoides* grasslands covered the Heretaunga/Ahuriri Plains of Hawke's Bay (Elder 1949). Lowland grassland covered an estimated 80 000 ha of alluvial plain in central Wairarapa in the mid-nineteenth century (Hill 1963; Wardle 1991, p. 264). A diverse mix of species was recorded, including *Poa*, *Deyeuxia*, *Rytidosperma*, and *Elymus* species.

South-west North Island

Microlaena stipoides, *Rytidosperma* spp., and *Poa anceps* were also prominent on the sand plains of Manawatu in early European times (Esler 1978; Wardle 1991, p. 264). Small *Poa cita* grasslands occurred about the coastal hills of Wellington in early European times.

Tussock grasslands in 1940

By c. 1940, 45% of secondary tussock grassland and associated shrubland had disappeared because of changes in land use (Table 1, Fig. 4). On the Volcanic Plateau, farm development and afforestation in the 1920–30s, along with a cessation of Maori burning and the spread of *Dracophyllum subulatum* and *Leptospermum scoparium*, resulted in a 65% reduction of tussock grassland (Table 1). The solution to boron deficiency in Taupo Pumice soils in the early 1940s intensified conversion of tussock grasslands to improved pasture on the Volcanic Plateau. Grasslands and shrublands of western

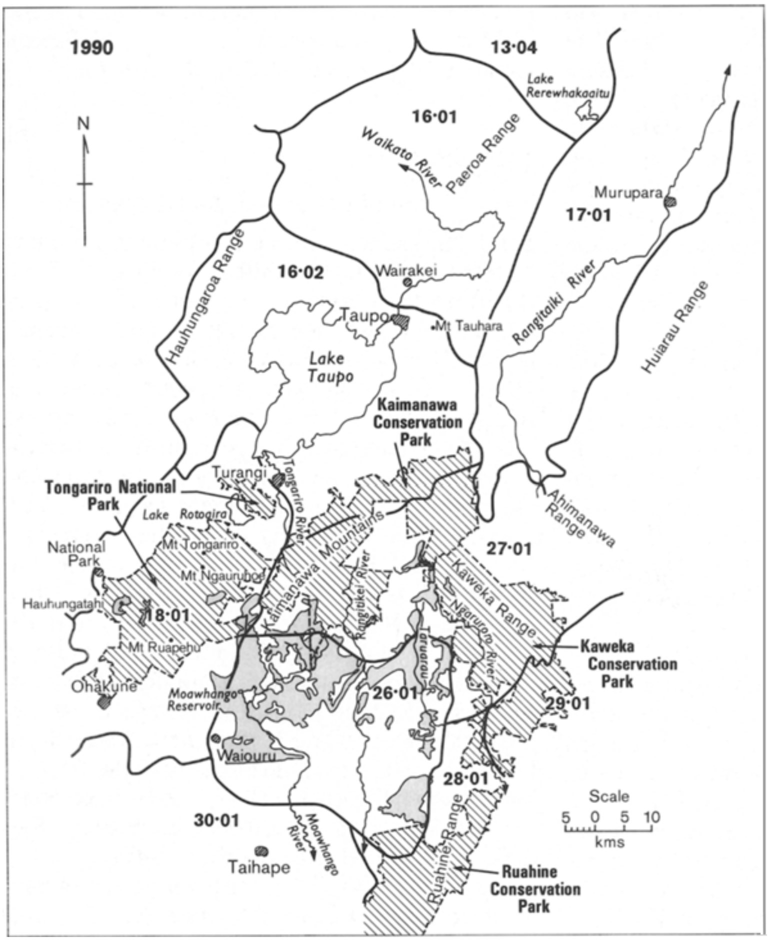


Fig. 5 Distribution of North Island tussock grasslands (shaded) in 1990. Names of ecological districts are shown in the caption to Fig. 2. The reserves network is shown hatched.

Taupo remained as low-productivity rangeland, subject to periodic burning to contain the spread of *L. scoparium*.

Substantial areas of north-east Tongariro and the northern Rangipo Depression from Turangi to Waihohonu on the Desert Road were reverting to *Dracophyllum subulatum* and *Leptospermum scoparium* shrubland after farming was abandoned c. 1917 (Grace 1959). Only small areas of the Moawhango tussock grasslands had disappeared under improved pasture by c. 1940, almost the entire resource being used as rangeland for stock.

Tussock grasslands in 1990

Since 1940, major reductions in tussock grasslands have occurred in Atiamuri, Taupo, Kaingaroa, Tongariro, and Moawhango Ecological Districts (Table 1, Fig. 5). Overall, only 10% of the tussock and shrub-tussock grasslands present in c. 1840 still remains (Table 1). Of these, 70% are in Ministry of Defence tenure at Waiouru, principally in north-western Moawhango Ecological District. On the Volcanic Plateau, afforestation and pasture improvement have destroyed virtually all the remaining *Poa cita* tussock grassland. Only one small catchment of tussock grassland remains at Okoeke in the Rangitaiki River headwaters. Elsewhere on the plateau, only small patches of tussock remain on road margins, waste places, and on shrub-dominated "frost-flats", including Otangimoana, Waimarama, Te Papa, and terraces of the upper Rangitaiki River (Nicholls 1990). Other remaining examples of high water table and cold air-drainage sites in western Taupo are Whenuakura, Pokaiora, and Waipapa. In Tongariro Ecological District, only 10% of the area of grassland in 1840 remains. Tussock grassland has also largely disappeared from the north and north-east Tongariro ring-plain because of invasion by

Calluna vulgaris and *Leptospermum scoparium*, and exotic afforestation in Lake Rotoaira Basin. The Rangipo tussock grasslands from Waihohonu southward are, for the most part, rapidly reverting to shrublands of *Dracophyllum subulatum*, *L. scoparium*, and *Kunzea ericoides* (Rogers & Leathwick 1994). The only exception to early successional grassland is *Phormium* spp. tussockland on more fertile soils at lower altitudes in the Moawhango River catchment east of Waiouru (Rogers 1987), but these rapidly change to *L. scoparium* shrubland.

In the Moawhango Ecological District, 34% of the original tussock grasslands remains. The incentive provided by Land Development Encouragement Loans in the 1970s and early 1980s was responsible for most of the transformation of 75 000 ha to improved pasture. Conversion occurred mainly at lower altitudes, a trend predicted by Scott (1979), and mostly on plateaus east of the Rangitikei River. Conversion ceased in 1985 with the removal of the subsidies.

There are no remnants of the nineteenth century lowland grassland communities of Hawke's Bay on the Takapau and Ruataniwha Plains, on the Heretaunga/Ahuriri Plains, or on the central Wairarapa Plains. Elements of the grassland flora are still present in improved pasture, in riverbeds, and in waste places. Similarly, *Poa cita* tussock grassland on the western Hawke's Bay hill country has disappeared. Only a few plants remain on the summits of the Maungaharuru and Te Waka Ranges. The nineteenth century *Chionochloa rubra* tussock grasslands are now confined to a 1 ha remnant on the Maungaharuru Range at Ahuateatua. Littles Clearing on the Black Birch Range, immediately east of the Kaweka Range, is another small Hawke's Bay outlier of central North Island *C. rubra* tussock grassland. A low-altitude *C. rubra* community within tall podocarp forest at Balls Clearing, Puketitiri, in Hawke's Bay (Elder 1950), was destroyed by land conversion in 1956. Only a few plants of *C. rubra* survive today.

Protection status

Approximately 10% of the surviving tussock grasslands are covered by the reserves network (Table 1). Representative tussock landscapes are included in Tongariro National Park at Hauhungatahi and Waihohonu (Fig. 5). The Kaimanawa Conservation Park spans several tussock-covered montane valley floors. Only 3.4% of Moawhango grasslands are reserved, mainly at the wet end of the rainfall gradient in the north-west Ruahine Range. The 70% of Moawhango grasslands in Ministry of Defence tenure at Waiouru has no formal protection.

DISCUSSION

Environmental patterns of forest clearance

Seral grasslands were concentrated on montane plateaus and undulating hill country surrounded by steep forested mountains. The grasslands only penetrated the mountains to the treeline on Mt Ruapehu and in the southern Kaimanawa Mountains. Steel (1989) indicates an open, fire-prone conifer forest of *Phyllocladus alpinus* and *Halocarpus* spp. was cleared from the northern ring-plain of Mt Ruapehu, and the southern Kaimanawa Mountains experience a marked summer-dry climate (Rogers 1987). Regional conflagrations deforested plateaus of Moawhango Ecological District, rather than piecemeal removal of forest (Rogers 1987). Recurrent Maori burning of fire-promoting secondary vegetation, whether deliberate or accidental, seems to have contributed little to the deforestation process in Moawhango Ecological District, probably because recurrent firing maintained insufficient fuel-loads to carry the fires into bordering forest (Rogers 1987), and because humid healthy forest is fairly difficult to destroy (Sage 1954, p. 58; Cumberland 1961, p. 146).

McGlone (1983) linked the broad pattern of forest clearance in New Zealand to mean annual rainfall. If rainfall was over 1600 mm/a only limited clearance of forest on the most vulnerable sites was possible, whereas in the 800–1600 mm/a rainfall range widespread clearance was possible, depending on secondary factors such as soil, topography, and availability of food resources for humans. For example, in the North Island, areas valued for intensive land use by early Maori, as indicated by a high density of pa sites (Fig. 6A), show broad correlation with areas of seral fernland and shrubland in 1840 (Fig. 6B). However, three areas of extensive deforestation have a low density of pa sites—southern Hawke's Bay, Wairarapa, and the tussock grasslands of the central uplands. Hawke's Bay and Wairarapa share low mean annual rainfall (Fig. 6C), high summer dryness (Fig. 6D), and subdued to undulating topography, all factors predisposing vegetation to burning. In the central uplands of tussock grassland, the most convincing factor explaining deforestation is flat to undulating topography, which offers few barriers to the passage

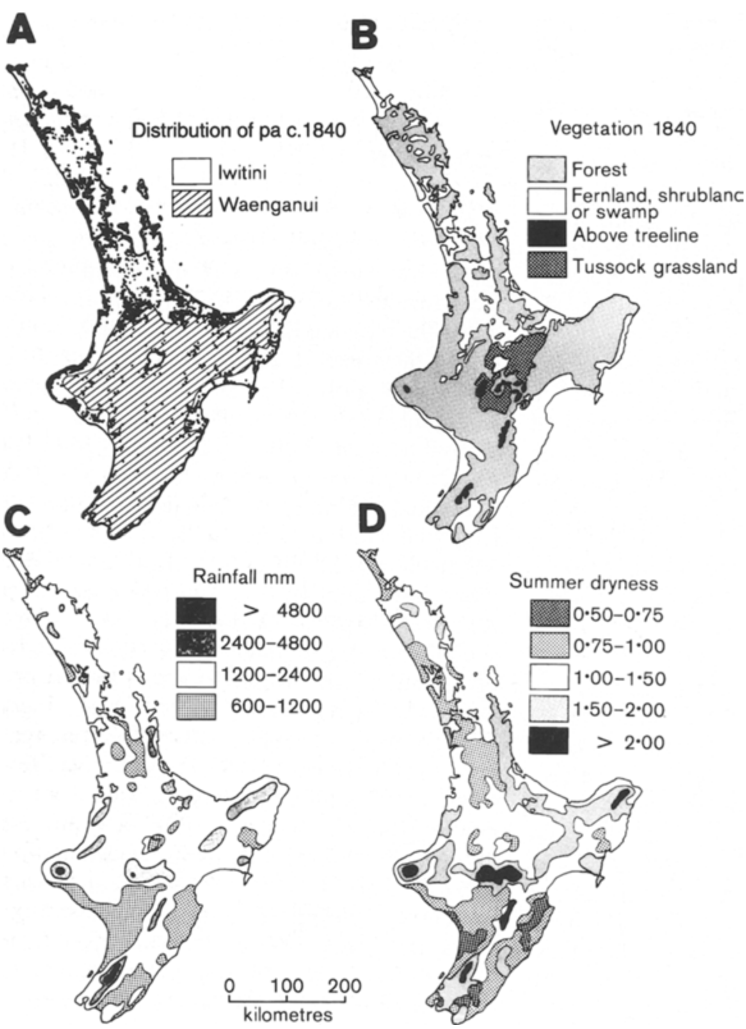


Fig. 6 **A**, Maori population density in the North Island in c. 1840 as indicated by the distribution of pa sites (A. Walton pers. comm. 1991), compared with a classification of New Zealand into the regions of suitability for Maori settlement (Davidson 1984, p. 34). The region "Iwitini" had an estimated 80% of the eighteenth century population, and "Waenganui" 15%. **B**, Extent of major vegetation types at the time of the first European surveys, c. A.D. 1840–60 (modified after McGlone 1983, fig. 1D). **C**, Mean annual rainfall in millimetres (J. Leathwick unpubl. data). **D**, Potential summer dryness as derived from mean seasonal rainfall (Jan–Mar) / potential evapotranspiration (J. Leathwick unpubl. data).

of fire. Mean annual rainfall and summer dryness probably played only a secondary role. Annual rainfall varies widely from moderate to high (1100–2200 mm) and summer rainfall is in balance with, or in deficit to, potential evapotranspiration in some of the region, but is in surplus in other parts (Fig. 6D). Although summer-dry conditions predispose even tall forest to burning, broken topography impedes the spread of fire. The steeply dissected hill country of the Rangitikei Ecological District, south of the Moawhango Ecological District, experiences marked summer dryness (Fig. 6D), yet extensive forest survived into European times, emphasising the role of topography in regulating forest clearance by fire.

In areas of permanent Maori habitation around Lake Taupo, piecemeal forest clearance for habitation and subsistence horticulture (rhizomes of *Pteridium esculentum*) probably contributed to regional deforestation. Forest clearance for horticulture continued in this region through to early European times, when a population of 1100–1500 was resident (Walton 1986). However, the archaeological record and the distribution of Maori settlement sites suggest that clearance for travel or accidental fires seem the only tenable reasons for deforestation of upper montane regions of low economic worth to early Maori. The archaeological record for the North Island shows that the major hunting sites for moa were virtually all at or near the coast, with few or insignificant kill sites in the wet, mountainous, central districts (Davidson 1984). The period of concentrated deforestation of Moawhango Ecological District occurred after the early disappearance of the avian megafauna (McGlone 1989), following loss of the major forest resource.

Spread of tussock grassland

The rate at which tussock grasses dominated deforested landscapes is difficult to judge. *Rytidosperma setifolium* and, to a lesser extent, *Poa cita* are adapted to disturbance, the first as a primary coloniser of fresh pavements, the latter by vegetative spread. The comparatively limited spreading capacity of tussock grasses in general, and the present rapid rates of shrub invasion of tussocks, suggest that in these humid environments recurrent burning of secondary woody vegetation was necessary to select for fire-adapted (basal resprout) tussocks. Central North Island pollen records spanning the post-forest-clearance period (McGlone 1983) show an upsurge in grass pollen late in the sequence after an initial dominance of bracken. McGlone suggested degradation of fernland to grassland as a consequence of frequent burning. Loss of soil nutrients would accompany frequent burning of bracken, advantaging lower nutrient status grasses. Nutrient loss caused by Maori burning was perpetuated by European pastoral practices, and it is likely tussock population growth continued into the early European period. Where bracken and tussocks are now sympatric, the pattern is of bracken fernland on hillslopes and tussock in flat depressions, a topographic separation suggesting increased soil aeration and fertility associated with disturbance on slopes and frost inversion in depressions.

Short tussock grasslands (silver and hard) of the Volcanic Plateau were climatically and edaphically separated from tall (red) tussock grasslands of Tongariro–Moawhango. Edaphically, the short tussocks' drought tolerance was linked to the ignimbrite zone of deep, unconsolidated Taupo Pumice, which is free draining and erosion prone, in a summer-dry climate with mean annual temperatures of 9–12°C (New Zealand Meteorological Service 1984). In Tongariro and Moawhango, andesitic ash from the Tongariro volcanoes moderated the infertility and summer droughtiness of shallower distal Taupo Pumice. Andesitic ash soils are more stable with higher water retention. The climate at these higher altitudes is cooler, mean annual temperatures are 8–9°C, and summer dryness features only in the south-western Kaimanawa Mountains, in the rainshadow of Mt Ruapehu.

Compositional shifts in the European era

The depauperate state and widespread absence of shrubs in North Island grasslands settled by early graziers reflected the practice of frequent burning in Maori times (Bidwill 1841, p. 53; Smith 1871; Colenso 1884; Grace 1959, pp. 524–525). The common appearance of *Leptospermum scoparium* in grasslands accompanying sheep farming in the mid–late nineteenth century probably coincided with Maori forsaking their burning practices (Nicholls 1978), together with animal disturbance fostering the spread of shrubs. The spread of shrubs around the turn of the century was a factor in the abandonment of sheep farming in the Tongariro grasslands in 1917 (Grace 1959). Early shrub invasion of North Island tussock grasslands contrasts with the widespread elimination of shrubs in South Island grasslands as a result of burning by the early European graziers (Buchanan 1868; Burrell 1965; O'Connor 1982, p. 100). Spread of heather, *Dracophyllum* spp., *Leptospermum scoparium*, and *Kunzea ericoides* through Tongariro *Chionochloa rubra* tussock grasslands has nearly eliminated seral tussock grassland from the National Park. Less than 2500 ha of tussock grassland remain in the park centred on Mt Hauhungatahi and the Rangipo Depression. The effective lifespan of undisturbed summer-dry grasslands here is 45 years (Rogers & Leathwick 1994). The process of *Dracophyllum longifolium* and *Phyllocladus alpinus* invasion is slower in the higher altitude, wetter grasslands of southern Moawhango Ecological District, where shrubland results within 65–85 years. In the absence of burning, shrub invasion of all seral North Island grasslands is therefore universal.

The widespread practice of burning alpine areas for pasturing sheep and cattle in the late nineteenth and early twentieth centuries resulted in substantial vegetation changes in the Tongariro, Kaimanawa, and Ruahine uplands. Burning led to expansion of subalpine *Chionochloa rubra* (but not alpine *Chionochloa pallens*) at the expense of subalpine *Nothofagus* and conifer forest and alpine shrubland of *Phyllocladus alpinus*, *Dracophyllum longifolium*, *D. recurvum*, *Halocarpus bidwillii*, *Olearia colensoi*, and *Brachyglottis bidwillii*. Montane–subalpine forests on the northern Tongariro volcanoes, southern Kaimanawa Mountains, and Mokai Patea in the north-west Ruahine Range were fragmented to the point where regional treelines are difficult to reconstruct.

Grazing by farm stock and feral horses has acted continuously, and burning intermittently, in modifying the northern rainshadow grasslands of Moawhango Ecological District since the 1880s. The highly palatable and widespread grass *Elymus* spp. disappeared early from tussock grasslands with the release of stock (see Vaile 1939, p. 178 for the Volcanic Plateau). Rangelands have shifted progressively from tall tussock to short tussock, particularly on sheltered basin floors and warm plateaus favoured by stock. Recurrent burning of tussock in the last 3 decades, for shrub suppression, fodder improvement, and control of *Pinus contorta*, plus feral horse grazing and accidental fires caused by Army artillery practice, have induced adventive grass swards and *Hieracium* herbfield. Overall, the geographic and population expansion of disturbance-adapted weeds has been an inevitable consequence, at least in the short to medium term, of recent burning. Treskonova (1991) showed that the spread of *Hieracium* in the Mackenzie Basin tussock grasslands was a sequence of stages related to disturbance and consequent degradation of the ecosystem.

Virtually all the tussock grasslands and shrublands were feral horse habitat from the late nineteenth to mid twentieth centuries (Morrow 1975). Since the 1950s, land development and recreational and commercial exploitation of horses have confined the population to a 65 000 ha refuge in the south-western Kaimanawa tussock grasslands (Rogers 1991). Horse grazing has contributed to retrogressive successional shifts of tall tussock to adventive grass and *Hieracium* herbfield in preferred habitats such as basin floors and plateaus, around forest margins, and in seepage or flush zones. Elsewhere, *Chionochloa rubra* on undulating hills is lightly grazed, with tussock growth and shrub invasion being largely unaffected by horses.

Feral pigs (*Sus scrofa*) were also abundant in most of the Moawhango tussock grasslands in early European times, but they disappeared with the spread of pastoralism (Smith 1871; Mazey 1979), and their influence on grassland composition is difficult to judge. There is also no reliable information on the effects of red deer (*Cervus elaphus scoticus*) on North Island tussock grasslands, although subalpine tussock grasslands of South Island are showing substantial recovery from recent reductions in deer numbers (Mark 1989). Large herds of deer grazed Moawhango grasslands at the peak of the irruptive phase in the 1930s and 1940s (P. Mahoney pers. comm), but numbers now appear to be low (pers. obs.).

Other feral animals are likely to have markedly altered grassland composition. Rabbit (*Oryctolagus cuniculus*) plagues in the 1920–30s, in combination with burning, were correlated with a significant deterioration in rangeland quality. Rabbits, along with substantial sheep losses to feral dogs (*Canis familiaris*), led to the abandonment of sheep farming on most of the Tongariro and north-western Moawhango grasslands between 1917 and 1939 (Grace 1959; Mazey 1979).

Natural non-forest sites associated with the North Island grasslands support a biogeographically distinct flora of very restricted distribution in central North Island (Rogers 1989). The special non-forest flora indicates a long history of open vegetation at least for the post-glacial if not much longer. Despite clearance of surrounding forest and expansion of their open vegetation habitat, virtually none of the biogeographically special plants have spread out from their restricted sites. For example, the only known inland-upland populations of the spiny shrub *Discaria toumatou* in the North Island are on cliff-tops and basin floors in the Moawhango Ecological District, non-forest sites to which it was probably confined in pre-human times. Most non-forest sites were modified by burning, which favoured tussocks rather than woody species. A general increase of shrubs in the absence of burning reflects recovery toward pre-human, tall scrub vegetation. The few comparatively unmodified examples of non-forest vegetation occur on high water table sites. These lie within old-growth forests between Mt Ruapehu and Hauhungatahi in the northern Tongariro Ecological District and on two sites in the southern Moawhango. No pre-human non-forest vegetation is left on cold air inversion sites.

Contrasts with South Island

There are no xeric environments with YGE (yellow-grey earth) soils supporting tussock grasslands in the North Island, whereas this combination is extensive in the South Island (New Zealand Soil Bureau 1968). In the North Island, YGEs are confined to lowlands of Hawke's Bay and Wairarapa, which previously supported induced maritime grasslands. These *Elymus* spp. and *Microlaena stipoides* grasslands experienced low rainfall (600–800 mm) and mean annual temperatures of 12–14°C. *Elymus* grasslands in the 1840s in the South Island occupied the drier BGEs (brown-grey earths) (McKendry & O'Connor 1990, p. 101) in intermontane basins of Central Otago and the upper Waitaki (New Zealand Soil Bureau 1968).

The majority of North Island tussocks occupy relatively young yellow-brown sands and yellow-brown pumice soils, that are well drained and only lightly to moderately leached (Molloy 1988). Waiouru, with 1083 mm/a (New Zealand Meteorological Service 1983), has the lowest rainfall of the region. Incremental airfall tephra from the Tongariro Volcanic Centre maintains free drainage and counteracts loss of nutrients from soil weathering. In contrast, South Island *Chionochloa rubra* tussock grasslands occupy both YGEs and YBEs and their intergrades, with the extensive YBEs of Southland often developed on loess and characterised by periodic anaerobic soil environments and strong leaching.

In the North Island, tussocks were sourced from within the altitudinal zone of forest clearance. In contrast, some altitudinal migration downward of alpine snow tussocks occurred in South Island, for instance, narrow-leaved snow tussock (*Chionochloa rigida*) in Canterbury (Molloy 1969, p. 357).

Reserve design and management

The conservation value of seral tussock grasslands in North Island is as part of the national heritage, not as an example of original or primeval New Zealand. Their disturbance origin also adds a dynamic dimension to reserve design (O'Connor et al. 1990). Seral communities of deforested regions are transient and, unless artificially manipulated, the values for which they are reserved will disappear.

Deliberate burning of degraded tussock grassland to suppress native shrubs and maintain tussock cover in the North Island is now of questionable merit for nature conservation and rangeland quality. The uncertainties of fire and weed management, and the complexity and inevitability of changes in grassland composition, reinforce the need to target natural non-forest sites in reserve proposals. In this way, reserve design would emphasise the sources of the grasslands below treeline and encompass the grassland flora and fauna linked to these sites. Reserve initiatives for landscape preservation of North Island tussock grasslands will, of necessity, be restricted to the Moawhango Ecological District. Even there, however, shrub invasion is well underway despite local periodic burning. Army training activity at Waiouru unintentionally burns c. 250 ha/a of grassland in the military reserve, representing a return fire period of 250 years for the 65 000 ha. At this rate, and recognising the non-random pattern of burning, shrub invasion is a major land-use dilemma for military training purposes, for maintaining grassland natural biodiversity, and also a significant factor in the contraction of feral horse habitat. In other ecological districts, opportunities exist only for preservation of the grassland flora along roadsides and in non-forest sites, of which some are highly modified and surrounded entirely by cultural landscapes.

If grassland sustainability is desired, management policy for their manipulation needs formulating. Familiarity with the mechanisms controlling disturbance recovery cycles is important in reserve selection and management of the grasslands to maintain their native composition and diversity. Fire is now recognised as a major stimulus for weed invasion of tussock grasslands. Recommendations for burning as a management tool for protected-area managers must be tempered by the realisation that herbaceous and woody weeds, such as adventive grasses, *Hieracium* species, and heather, benefit from gross disturbance of the grassland ecosystem (Williams et al. 1977; McKendry & O'Connor 1990; Rogers & Leathwick 1994). Further, the community dynamics of weed-modified grasslands are not well understood and require further research.

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