

REVIEW ARTICLE

The origin of the indigenous grasslands of southeastern South Island in relation to pre-human woody ecosystems

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Abstract: Immediately before human settlement, dense tall podocarp-angiosperm forest dominated the moist Southland and southern coastal Otago districts. Open, discontinuous podocarp-angiosperm forest bordered the central Otago dry interior, extending along the north Otago coast. Grassland was mostly patchy within these woody ecosystems, occurring on limited areas of droughty or low-nutrient soils and wetlands, or temporarily after infrequent fire or other disturbance. *Podocarpus hallii*, *Phyllocladus alpinus* and *Halocarpus bidwillii*, small-leaved and asterad shrubs formed low forest and shrub associations in the semi arid interior, with *Nothofagus menziesii* prominent in the upper montane-subalpine zone. Substantial grasslands were confined to the alpine zone and dry terraces in intermontane basins. The arrival of the first Maori settlers at c. 800 BP led immediately to widespread burning and near-elimination of the fire-sensitive woody vegetation from all but the wettest districts. Non-*Chionochloa* grasses (probably species of *Poa*, *Elymus* and *Festuca*) and, in particular, bracken were the first to spread after fire; later, with continued fire, the more slowly spreading *Chionochloa* tussock grasslands became common. A unique suite of dryland woody ecosystems has thus been replaced with fire-induced grasslands. Recreation of the pre-human vegetation cover from the surviving small remnants is problematical because of the anomalous fire-sensitivity of the indigenous drought-tolerant flora. In the current historically unprecedented fire-prone environment, perhaps the best that can be hoped for is preservation of the *status quo*.

Keywords: *Chionochloa*; fire; grasslands; human settlement; pollen analysis; South Island.

Introduction

At the time of European settlement in the first half of the 19th century, grassland extended across the leeward South Island, from the flanks of the western mountain ranges to the southern and eastern coastlines (Fig. 1). Fernland and scrub were common associates, and patches of forest occurred throughout, with some extensive tracts in coastal districts. It was realised early that fire had destroyed the original forests (Buchanan, 1868), but it was not until the publication of radiocarbon dates from soil charcoal and subfossil wood (Molloy *et al.*, 1963), that it was fully appreciated these fires began at the time of Maori settlement.

These indigenous grasslands – whether pristine or modified – have been the focus of ecological research for many years (see reviews by O'Connor, 1986; Mark, 1992). This interest in the grasslands was at first almost entirely economic, since from the 1850s they had provided the basis for the South Island pastoral industry. Increasingly, however, they are being valued for their

environmental and conservation attributes, and issues such as their conservation, threats from fire, weed invasion and over-grazing, and their role in water supply and preservation of biodiversity are now the focus of scientific attention.

Grasslands below tree line have an unusually problematic status arising in large part because they occupy land that was mostly occupied by forest and scrub before human settlement. Issues therefore arise as to the long-term stability of these grasslands and how that might affect their conservation, and to what extent the woody elements which remain within them should be encouraged.

The ongoing assessment of the status and future prospects of the South Island grasslands requires an historical perspective. There are now sufficient palaeoecological sites and other sources of historical information from the southeastern sector of the South Island to permit an overview of grassland history from the alpine zone to the lowlands. In this paper I first discuss the representation of grasses in the fossil record,



Figure 1. Indigenous grasslands of the southern South Island at the time of European settlement (*c.* 1850 AD). Grassland distribution of physiognomic dominants, after Mark (1992) and Holloway (1959); forest boundaries after New Zealand Forest Service (1983). Localities indicated are pollen sites discussed in the text.

and then review the plant historical literature and present new information concerning the indigenous grasslands of the southeastern South Island, the fernlands that accompanied their fire-induced spread, and the complex pre-fire associations they replaced.

Grasses in the New Zealand fossil record

Grasses are poorly lignified, decay rapidly, and therefore generally leave few identifiable macrofossil remains. However, they are well represented as microfossil

remains, mainly as phytoliths and pollen. Grass phytoliths are distinctive and can be isolated from soils and analysed. In New Zealand they can be divided into nine classes, permitting some separation of genera (Kondo *et al.*, 1994). Initial work has been promising, but as yet only a few sequences have been analysed (e.g., Carter, 2000). Pollen analysis has been the primary technique for charting grassland history both in New Zealand and elsewhere.

Pollen grains are ubiquitous in the environment and their ornamented outer walls preserve well in a range of sediments. They can be extracted by means of simple chemical and physical techniques in large

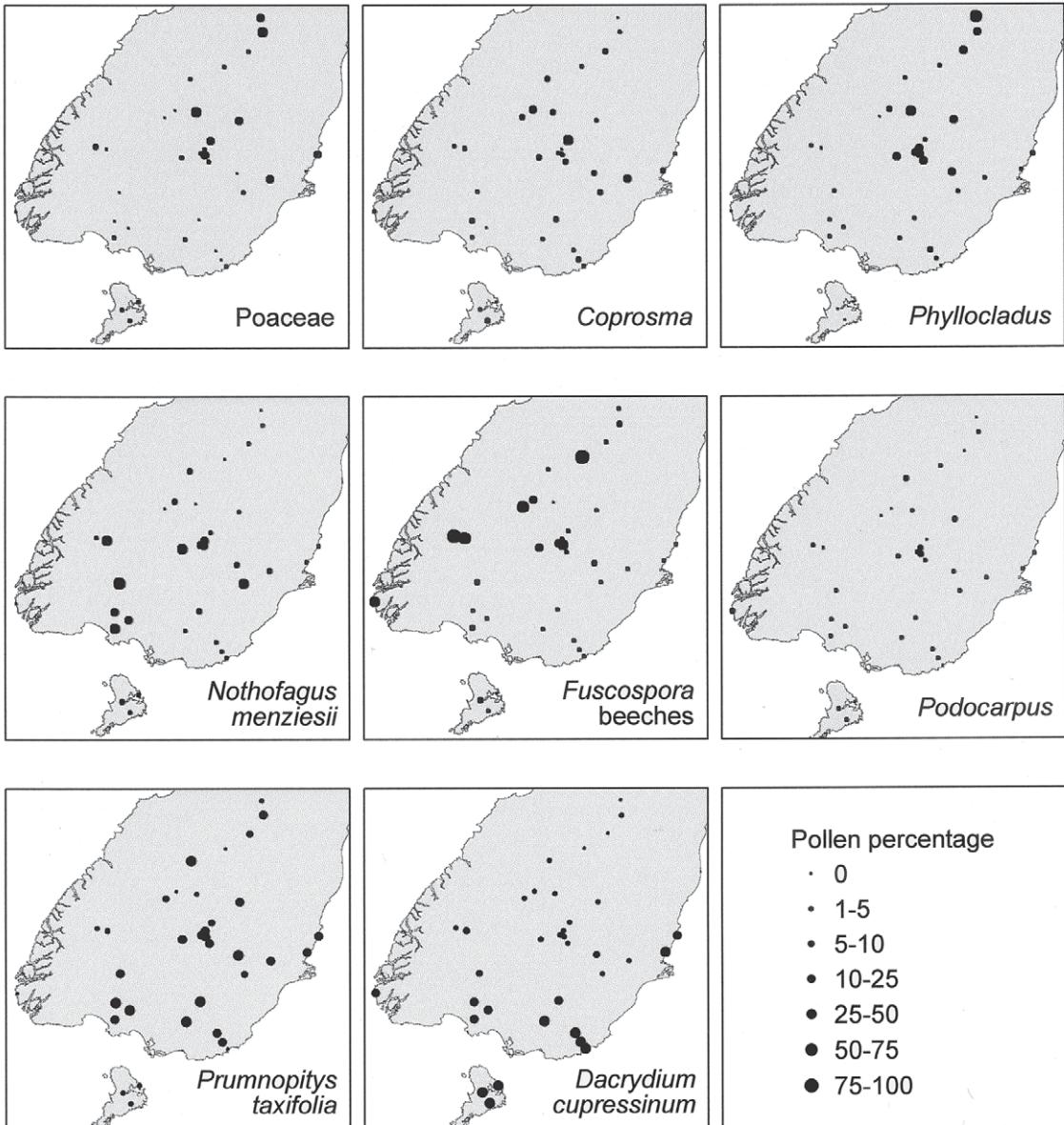


Figure 2. Percentages of major pollen types in southeastern South Island for the period immediately before human impact. Data from published sites and unpublished material in the Landcare pollen data base.

numbers from peats, lake sediments and many soils. Grass pollen is highly distinctive at the family level. Although different grass genera have subtle variations in size, shape and wall structure and ornamentation, they are difficult to determine accurately and consistently during routine fossil pollen analysis. In general, pollen analysts have not attempted to do so. However,

Chionochloa and *Cortaderia* can be distinguished as a group more or less reliably from other New Zealand grasses, by their larger diameter ($>40\ \mu\text{m}$), thin walls relative to their size, and fine, even, wall structural elements (N. T. Moar, Landcare Research, Lincoln, N.Z. *unpubl.*), and are here referred to as the ‘*Chionochloa*’ type. A diameter of $40\ \mu\text{m}$ or greater is

used as a cut-off point that will exclude most pollen grains from other grass genera while encompassing most *Chionochloa* and *Cortaderia*, provided the morphological attributes of the grain are also characteristic. For the purposes of this paper, grass pollen has been reanalysed at selected sites.

Grass pollen is abundantly produced and, being adapted for wind transport, is usually well dispersed. New Zealand modern pollen rain studies have shown that grasses are well represented in the pollen rain (Moar 1970; McGlone 1982, Pocknall, 1982; Macphail and McQueen, 1983; Horrocks and Ogden, 1994; McGlone and Moar, 1997; McGlone and Meurk, 2000). Modern pollen samples from lowland areas dominated by grasses tend to have high percentages of grass pollen (>40%). Above tree line pollen spectra are usually dominated by pollen derived from forests downslope, and thus alpine grasslands have a relatively low pollen representation generally in the range 5-30% (Moar, 1970; Pocknall, 1982; Horrocks and Ogden, 1994). This is largely due to the relatively small pollen source area of the uplands versus the surrounding lowlands, and lower pollen production in cool subalpine and alpine climates.

A recent modern pollen study showed that in surface samples from some inland southeastern South Island grasslands dominated by *Chionochloa*, *Chionochloa* type pollen was usually much less than 10% of the pollen sum, the grass pollen rain being mainly derived from other subsidiary grass species (McGlone *et al.*, 1997; McGlone and Moar, 1998). In a Holocene pollen core from a *Chionochloa*-dominated subalpine basin at 900 m in central Westland, *Chionochloa* type averaged 13% of the pollen sum, but made up over 80% of the grass pollen recorded (M.S. McGlone and L. R. Basher, *unpubl.*). McGlone (1982) noted a correlation between high grass pollen levels (average *c.* 30%) and *Chionochloa* dominance in a subalpine tussock-covered basin on Mt Egmont, and re-examination of the pollen slides shows that roughly half of the pollen is *Chionochloa* type.

Chionochloa therefore provides only modest percentages (10-15%) of the overall pollen rain even when it dominates a site, and even lower levels in the 2-10% range can indicate a substantial presence. It tends to be poorly represented in the pollen rain relative to other grasses. *Chionochloa* species have two attributes that may lead to reduced pollen production and poor dispersal. First, they mast flower, with low pollen production in most years and high pollen production in a few (typically once every 4-5 years at subalpine sites; McKone *et al.*, 1998). However, some other grasses may also have low flowering intensity; for instance, *Festuca novae-zelandiae* (Lord, 1998). Second, pollen sedimentation velocity is proportional to the square of the diameter of the pollen grain (Prentice,

1988); a 60 μm diameter grain falls through air four times as rapidly as one of 30 μm . Therefore, large grains, such as those of *Chionochloa*, should be deposited much closer to the parent plant on average than smaller grains. The exotic agricultural or weed grass species which have now spread throughout many indigenous tussock grasslands produce abundant, mainly small pollen grains that vastly outnumber those of many of the native grasses.

The pattern of pre-human vegetation

Eight hundred years of fire and 150 years of pasture development have obscured the original vegetation patterns of the southeastern South Island. Over large stretches of country no vegetation associations corresponding to those of the pre-human situation remain. Fossil information is therefore essential to gain an insight into the original patterns. In Fig. 2, pollen percentages for major types in the period immediately before human settlement are mapped for all known sites from the southern South Island. Some illustrative pollen diagrams are presented here: in Fig. 3, sites from coastal southeastern districts; in Fig. 4, sites from the interior; and in Fig. 5, high altitude sites from the Old Man and Lammerlaw Ranges.

Some pollen types typically disperse long distances, and can be abundant in percentage terms at sites where the source taxon is absent in the local vegetation, thus complicating interpretation of pollen diagrams. This effect is greatest in sites with low, open vegetation, and especially those near or above tree line. Chief among these well dispersed types are *Nothofagus* subgenus *Fuscospora* and *Prumnopitys taxifolia*. *Nothofagus* subgenus *Fuscospora* pollen is present at most sites, despite the parent taxon being virtually absent from the eastern districts, but generally at levels of <10% which are consistent with long-distance dispersal. The sole site where its pollen abundance is greater than 10% (Potters Bog, western Old Man Range; Fig. 5a), is adjacent to the Waikaia forest which has extensive stands of *Nothofagus fusca* and *N. cliffortioides*.

Prumnopitys taxifolia is more problematical as the pre-human source on the Southland plains and coastal Otago was so large that its pollen is abundant in adjacent areas in central Otago. Its pollen is thus well represented in alpine peats from the Lammerlaw and Old Man Ranges and intermontane basin sites as well (Figs. 2, 4, 5), but at low levels (<5%) in more distant sites in the Kawerau Gorge, and Mackenzie Basin (McGlone *et al.*, 1995; McGlone and Moar, 1998). It seems highly unlikely that *Prumnopitys taxifolia* was present within the semi-arid area, as it is now absent from central districts, and its altitudinal limit of 300-

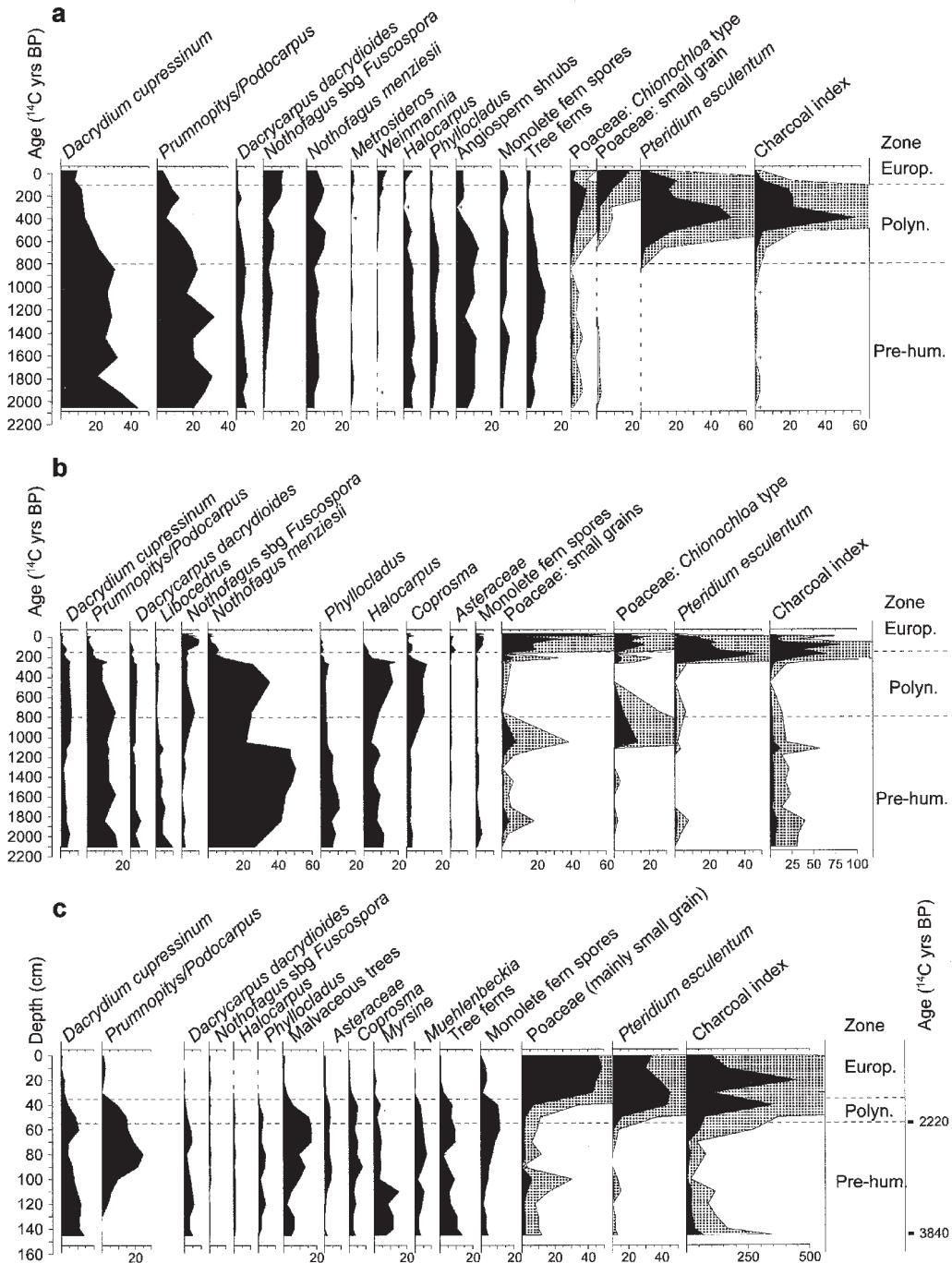


Figure 3. Representative pollen diagrams, coastal southeastern South Island. Selected types only. Values are percentages based on a sum of total terrestrial types. Shaded curves = 5x exaggeration to emphasise low values of significant types. Note y-axis scale may be age or depth. Zones: Europ. = European era, since 1840 AD; Polyn. = Polynesian (Maori) era, c. 800 BP to 1840 AD; Pre-hum. = pre-human era, prior to c. 800 BP. (a) Ajax Hill, alt. 650 m, M. S. McGlone unpubl.; (b) Glendhu, alt. 620 m, McGlone and Wilmsurth (1999a); (c) Pleasant River, alt. 5 m, McGlone, unpubl.

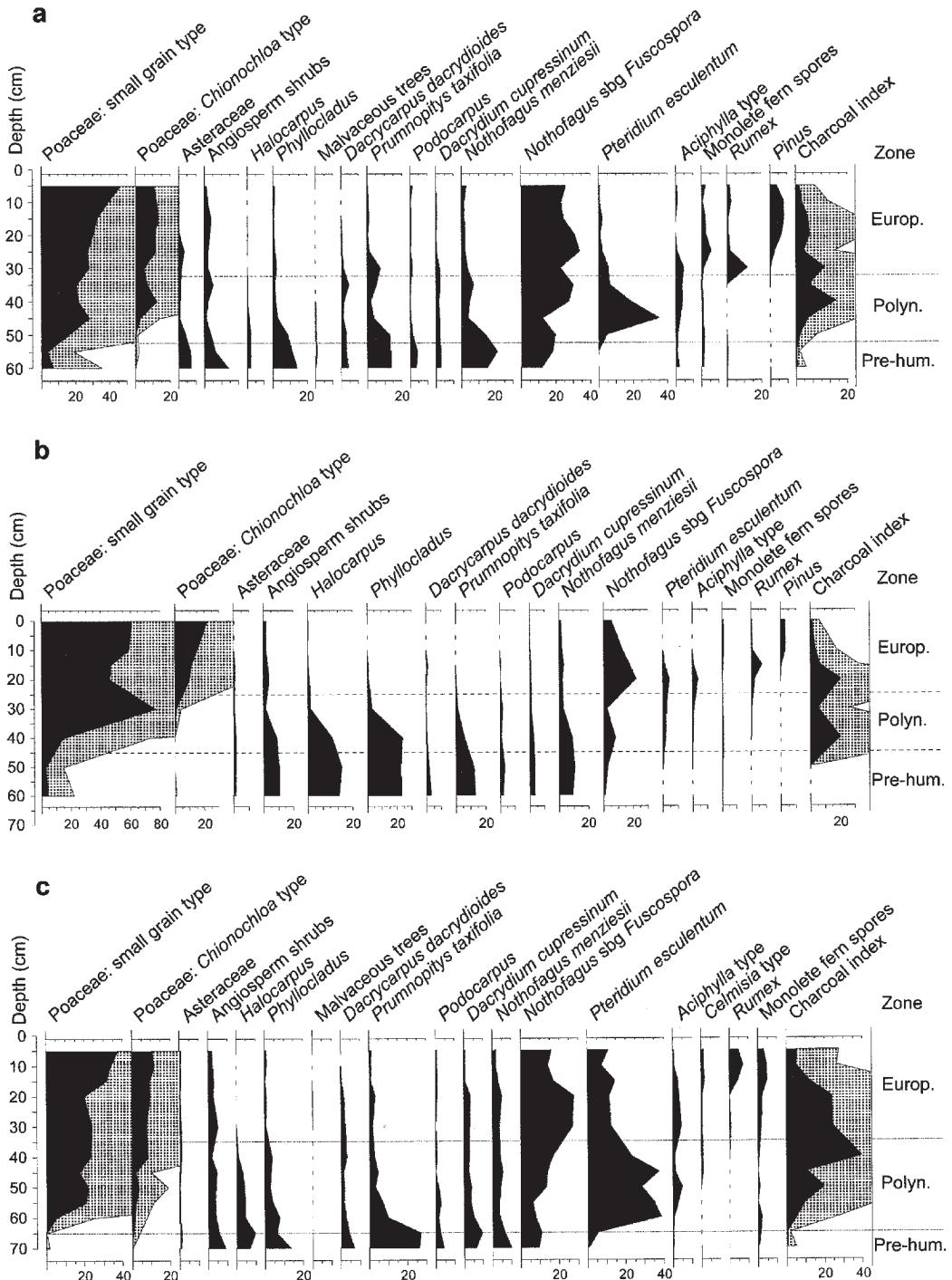


Figure 5. Central Otago, high altitude pollen sites (M. S. McGlone and J. M. Wilmshurst, *unpubl.*). Conventions as in Fig. 3. (a) Potters Bog, western Old Man Range; alt. 1200 m. (b) Pomahaka Rd, eastern Old Man Range, alt. 875 m. (c) Teviot Swamp, Lammerlaw Range; alt. 980 m.

600 m in the southern South Island (Hinds and Reid, 1957) makes it improbable that it could have had a presence in the higher rainfall forest zone on the upper slopes of the interior ranges. There is little corroborating subfossil evidence for its presence. Its wood is not durable in contact with the ground and its charcoal has been identified only infrequently in the central districts, mainly in the high rainfall belt immediately east of the axial mountain ranges (P. Wardle, Landcare Research, Lincoln, N.Z. *pers. comm.*). Other than *Podocarpus hallii*, tall podocarp species were likely to have been almost entirely absent from the drier inland districts of Central Otago and south Canterbury. It is possible that occasional small stands grew in damp gorges, as suggested by Clark *et al.* (1996), but there is no direct evidence that they did so.

On the basis of fossil information, soils and climate, the pre-human vegetation of southeastern South Island can be schematically divided into three broad zones (Fig. 6): (1) A dense moist, *closed forest zone* extended throughout Southland-coastal south Otago; (2) a drier, *open forest-scrub zone* extended inland along the edge of the east Otago upland, reaching the coast north of Dunedin; and (3), a *low forest-scrub-grassland zone* occupied the inland basins and ranges of Central Otago.

1. Closed forest zone.

A dense podocarp-angiosperm forest extended over the Southland downlands and up the lower southern flanks of the flat-topped mountains of Central Otago, and along the Otago coast to just north of the Otago Peninsula (McGlone and Bathgate, 1983; McGlone *et al.*, 1995; Vandergoes *et al.*, 1997; McGlone *et al.*,

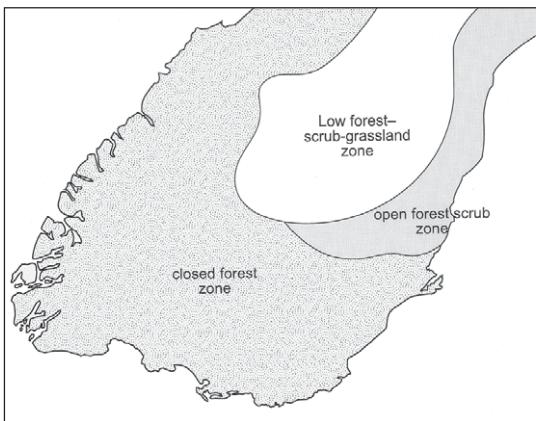


Figure 6. Schematic map of broad vegetation zones during the mid to late Holocene (5000 to 800 BP), southeastern South Island.

1997; McGlone and Wilmshurst, 1999a). *Prumnopitys taxifolia*, *Podocarpus totara* and *Dacrydium dactyloides* were the prevailing lowland podocarp canopy species on fertile soils and under moderately moist climates. In wetter districts, *Dacrydium cupressinum*, *Prumnopitys ferruginea*, *Metrosideros umbellata* and *Weinmannia racemosa* were abundant, the latter two predominating in the upper montane and subalpine zone in the coastal zone in the absence of *Nothofagus menziesii*. *Nothofagus* forest including *N. fusca*, *N. cliffortioides* (members of subgenus *Fuscospora*), and *N. menziesii*, was dominant in the mountains to the west. *Nothofagus menziesii* forest extended out to the east in the montane zone of the Eyre, Garvie, Umbrella and Blue Mountains and the east Otago uplands. More isolated but still extensive tracts occurred on the Longwood Range in western Southland, and the Catlins district in coastal southeastern Southland (Wardle, 1984; McGlone *et al.*, 1996).

Patches of *Chionochloa* grassland occurred in the lowlands in these forest settings, but almost exclusively on wetland sites or on restricted areas of poor soils. Small tracts of non-forested habitat in the uplands supported tussock cover: for instance, tussocks of *Chionochloa rubra* grow on flushes amongst subalpine forest, scrub and bog at Ajax Hill (altitude 700 m) (Johnson *et al.*, 1977); and a small montane (670 m) bog on the Longwood Range (western Southland) in *Nothofagus menziesii* forest has scattered *Chionochloa crassiuscula*. The pollen record from these two sites (Fig. 3a; McGlone and Bathgate, 1983) shows the continuous presence of *Chionochloa* type pollen throughout the Holocene. Glendhu (Fig. 3b), at the inland border of the coastal moist forest zone in east Otago, records several major fires — possibly originating from drier inland areas — which affected the site from the mid-Holocene onwards. After each fire, grassland with *Chionochloa* prominent, temporarily expanded, suggesting that nearby sources persisted throughout the forested period.

2. Open forest-scrub zone.

At Clarks Junction (Fig. 4a), the tall podocarps *Prumnopitys taxifolia*, and *Podocarpus*, the malvaceous trees *Plagianthus regius* and *Hoheria angustifolia*, conifer scrub of *Phyllocladus*, *Halocarpus*, small-leaved scrub of *Coprosma*, *Myrsine* and *Muehlenbeckia*, and *Chionochloa* type and small pollen grasses were all abundant in the pollen rain. This assemblage argues for an open, almost savanna-like vegetation, in which stands of trees co-existed with scrub and grassland. Microscopic charcoal is not particularly abundant at this site, although within a few hundred metres, Leslie and McGlone (1973) recorded a similar pollen flora but found abundant macrocharcoal and small fragments of

charred wood from a fire horizon in a peat and silt section that has been subsequently dated to 1680 BP (NZ 9139A). At Pleasant River (Fig. 3c) in coastal North Otago under a comparable rainfall regime, a similar, but less open podocarp-hardwood forest had a substantial presence of *Hoheria angustifolia* and *Plagianthus regius*, and included abundant shrubs. A consistent although low percentage of small pollen type grasses suggests an open structure prevailed here as well. Microscopic charcoal is more abundant at this north Otago site than inland at Clarks Junction and other sites, but otherwise there is no other evidence of fire being more important here.

These limited pollen results suggest a highly variable vegetation mosaic consisting of forests with widely spaced podocarp dominants over low variable angiosperm canopies. Free-draining, drought-prone soils and occasional fire promoted extensive scrub and occasional grassland patches.

3. Interior low forest-scrub-grassland zone

This zone can be subdivided into three subzones: the semi-arid intermontane basins and lower slopes up to 300-600 m; the moister upper flanks of the broad flat-topped ranges, which become increasingly wetter with altitude; and the broad, wet, alpine tops.

Intermontane basins

There is little fossil information for the dry intermontane basins. Idaburn Valley, the driest lowland area investigated (mean annual rainfall *c.* 400 mm yr⁻¹), was in an open shrubland-grassland, with an unusual amount of local Asteraceae (mainly *Taraxacum magellanicum*, *Raoulia* and small-leaved *Olearia* shrub types), with *Phyllocladus* and *Podocarpus hallii* scrub-forest on the adjacent slopes (Fig. 4c; McGlone and Moar, 1998). At Earnsclough Cave, northern Old Man Range, a *Muehlenbeckia-Coprosma-Myrsine* shrubland with small areas of grassland formed the vegetation cover on the lower slopes at an altitude of 540 m (Fig. 4b; Clark *et al.*, 1996). In the Kawerau Gorge (mean annual rainfall, 500-600 mm yr⁻¹), a low forest of *Phyllocladus*, *Halocarpus* and *Podocarpus hallii*, and *Coprosma* and *Myrsine* scrub co-existed with patches of largely non-*Chionochloa* grassland (McGlone *et al.*, 1995). Duncan Stream, a site near Lake Pukaki under a rainfall of *c.* 900 mm yr⁻¹, but bordering on the semi-arid Mackenzie Basin, was dominated by *Phyllocladus* and *Halocarpus* scrub, with a substantial representation of *Chionochloa* and other grasses (McGlone and Moar, 1998). Ben Dhu, a site within the semi-arid area of the Mackenzie Basin, had a predominately *Halocarpus bidwillii* scrub cover, with 5-10% of small pollen type grasses (McGlone and Moar, 1998).

Closed or tall forest was therefore absent from the lower slopes and valley bottoms of semi-arid central Otago and southern Canterbury. The fossil information is also consistent with the supposition that in pre-human times grasslands occupied the driest sites within this zone. Wardle (1991: pp. 244-245) suggested that these basins with annual rainfalls of less than 500 mm supported the only significant areas of temperate grassland in New Zealand, with *Poa cita*, *Festuca novae-zelandiae* and the now rare *Elymus apricus* common constituents, along with *Chionochloa* spp., shrubs, and forbs.

Range slopes

Pollen evidence suggests that the mixed grassland-shrublands of the intermontane basins and lower slopes gave way with increasing altitude to a more closed low forest-scrub dominated by *Podocarpus hallii*, *Phyllocladus alpinus*, *Halocarpus bidwillii*. On the upper slopes near tree line *Nothofagus menziesii* played an increasingly important role in the vegetation, although *Phyllocladus alpinus* and *Halocarpus bidwillii* were almost certainly still important constituents (Fig. 5). This generalised picture based on pollen is supported to a certain extent by wood and charcoal. Subfossil *Podocarpus* logs dating to early Polynesian times are found on the mid-slopes of many interior mountain ranges, mostly at altitudes between 700 and 1200 m, but are confined to the moister eastern and southern slopes of the driest ranges (Molloy *et al.*, 1963; Wells, 1972). Isolated stands of *Podocarpus hallii* persist on the northern end of the Pisa Range, and stands of *Nothofagus menziesii*, some mixed with *Nothofagus cliffortioides*, are scattered in the district (Wardle, 1984). All of these forest remnants and subfossil remains occur under relatively moist climates (mean annual rainfall > 700 mm).

The structure and composition of these pre-human mid-slope forests and tall scrub communities is open to different interpretations. Burrell (1965) suggested a mixture of *Nothofagus menziesii* forest, *Podocarpus hallii* forest, and *Kunzea ericoides* shrubland, with a savannah-like structure in drier areas. On high rainfall upper slopes, *Podocarpus hallii* and *Nothofagus menziesii* dominated restricting *Kunzea ericoides* to the drier north-facing slopes. On lower slopes, where the climate was too arid for *Podocarpus hallii* forest, a woodland of *Kunzea ericoides* extended downslope to meet lowland tussock grassland at about the 600 mm yr⁻¹ isohyet. Wells (1972) disputed this interpretation, especially the supposition that savannah-like vegetation was widespread, arguing that closed forest was more abundant than Burrell (1965) suggested. Wells noted that the subfossil logs of *Podocarpus hallii* were typically long (3-4 m), straight and unbranched, suggesting they had reached maturity within dense

vegetation. However, she also noted that the density of subfossil logs was insufficient for *Podocarpus hallii* to have formed a closed forest canopy by itself. She deduced that there were other, less durable trees and tall scrub making up the bulk of the forest cover, and suggested that these may have been the present associates in remnant stands — *Nothofagus menziesii*, *Phyllocladus alpinus*, *Halocarpus bidwillii* and *Dracophyllum longifolium*. Wells' observations are supported by pollen analyses from Central Otago ranges: *Podocarpus* pollen rarely makes up more than 10% of the pollen sum (Figs. 2, 5) and, even though it is an under-represented pollen type, this would still be a low representation if it was the dominant forest cover. *Phyllocladus* and *Halocarpus* pollen is abundant, and subfossil charcoal confirms that *Phyllocladus alpinus* was a major component of the mid and upper slope forests. The range of tall woody species involved has to be expanded: *Plagianthus regius*, *Hoheria angustifolia*, *Sophoramicrophylla* played important roles, especially on fertile soils and along river and stream courses. Pollen evidence is silent on whether or not *Kunzea ecricoides* was important before the fires that accompanied human settlement, as it is a very poorly represented pollen type. However, it is represented in pre-human soil charcoal collections in the upper Clutha catchment and, although not forming extensive forests, was present in the low forest and scrub associations, possibly on dry ridges or recent burns (P. Wardle, *pers. comm.*)

Alpine

Interpretation of the alpine pollen records is difficult because of dominance by lower altitude pollen sources. However, there are some hints that the alpine tussock grasslands of the interior zone probably had a very different composition and structure to the fire-affected communities of the present. Small pollen grass types are much better represented than *Chionochloa* type in the pre-human pollen record at sites above tree line (Fig. 5; McGlone *et al.*, 1997). Although *Chionochloa* tussocks were more abundant than their percentage representation in the pollen record suggests, it is unlikely that were as dominant as they now are. Scrub pollen types — mainly *Coprosma*, and *Myrsine* — were more abundant before human impact, and it is possible that a more complex peninsular shrubland-grassland occupied the areas now largely in pure *Chionochloa* tussock, and grasses such as *Festuca* and *Poa* spp. played a more important role (McGlone *et al.*, 1997).

Fire and grassland

Natural fire

Microscopic charcoal fragments are present in most southeastern South Island peat sediments, but seldom in large quantities. The fragments are mainly less than

50 µm in diameter, an indication that they are derived mainly from distant fires (Clark and Royall, 1995), and therefore yield a generalised regional record. Moist coastal sites record very little charcoal. Drier or inland sites, such as those of Pleasant River (Fig. 3c) and Clarks Junction (Fig. 4a) record significant amounts but not in quantities or size classes that necessarily indicate burning of vegetation adjacent to the site. Some sites record local fires. At Manorburn, central Otago, five separate layers of *Phyllocladus alpinus* charcoal range in age from 7500 BP to 1400 BP (B. P. J. Molloy, Landcare Research, *pers. comm.*). Natural fires burnt several times after 6000 BP through *Phyllocladus* scrub at the Duncan Stream site, near the outlet of Lake Pukaki (McGlone and Moar, 1998), at Kawerau Gorge (McGlone *et al.* 1995), in inland Canterbury on the Arrowsmith Range (Burrows and Russell, 1990), and in the conifer scrub and *Nothofagus menziesii* forest of the Glendhu site, east Otago (Fig. 3b). Fires appear to have had a permanent effect on the abundance of *Phyllocladus* at Duncan Stream, Kawerau Gorge, and Arrowsmith Range, grass becoming more common during the period of higher fire frequency. At Glendhu, fire seems to have hastened the spread of *Nothofagus menziesii* into *Prumnopitys taxifolia* and upland conifer communities, but did not favour establishment of permanent grassland. *Phyllocladus* stands may have been both vulnerable to fire, and slow to regain ground afterwards (Wardle, 1969), losing out to *Halocarpus bidwillii* and grassland on dry sites, and to *Nothofagus menziesii* on moist sites.

McGlone (1988, 1989) suggested that substantial deforestation occurred in Central Otago after 3000 BP but before Maori settlement (c. 800 BP). Evidence for deforestation came from several dated pollen diagrams (Leslie and McGlone, 1973; McGlone *et al.*, 1995), and was supported by *Phyllocladus* charcoal dates from the region. Subsequent work has shown this claim to be a consequence of (1) a misinterpretation of a site in which forest had never been completely dominant during the Holocene [Clarks Junction: Leslie and McGlone (1973)] and; (2) slow growth rate of peats after 3000 BP at certain sites resulting in old dates for what has been later demonstrated to be Maori deforestation [Old Man Range: McGlone *et al.* (1997)]. There is evidence for an increased frequency of fire after 3000 BP in the eastern South Island (Ogden *et al.*, 1998) and some sites suggest a more open vegetation followed these fires (McGlone and Moar, 1998). However, there was no clearance resulting from natural fire that approached the scale of that which accompanied fires associated with human settlement.

As microscopic charcoal is found in all sites in Central Otago and south Canterbury, small, lightning-ignited fires must have been sufficiently common over the whole region to create a background fall-out of

charcoal particles. Peat and lake sediment records have severe limitations in assessing fire: for instance, transport and redistribution of charcoal after a fire often has the effect of smearing charcoal peaks over several decades of sediment even in high resolution cores (Whitlock and Millsbaugh, 1998). We therefore have to consider other sorts of evidence to derive any sense of how frequent fire was.

The only likely source of natural fires in the South Island is lightning strikes. New Zealand has a low frequency of thunderstorms by world standards. Most lightning is associated with mountainous terrain in the west, and low pressure troughs (Tomlinson, 1976; Ogden *et al.*, 1998) and is therefore unlikely to generate extensive fires. However, while lightning is uncommon (2-10 thunder days per annum; 50-60% occurring in summer) in districts to the east of the axial ranges, they have much lower rainfall than western districts, a higher frequency and severity of drought and strong foehn winds. Preconditions for fire are therefore much more favourable than in the more lightning-prone western mountains. Out of *c.* 2000 accidental fires that currently occur each year in rural New Zealand, around 40 (2%) are attributed to lightning (S. M. Timmins, in Ogden *et al.*, 1998). If the nearly 40 000 ha of grassland, scrub and forest burnt in both human and naturally lit wild fires in 1984/5 (Kerr and Hunter, 1986) is typical (and it is unlikely to have had less fires than average, as it was a drier than average year), lightning fires may have contributed as little as 800 ha per annum to the total area burnt. Even making the assumption that this estimate is out by an order of magnitude, for instance by attributing all unknown cause fires to lightning (see Table 2 in Kerr and Hunter, 1986), under present conditions no more than 80 sq km of vegetation are naturally burnt per year in New Zealand, or 0.03% of the landcover. We do not know how vulnerable pre-deforestation vegetation was to fire, and hence how much vegetation is likely to have burnt under natural conditions, but on the basis of these figures it is unlikely to have been substantial. Ogden *et al.* (1998) calculate an average return time for fire of *c.* 2000 years, based on a variety of documented fire histories. Both these estimates therefore suggest a low incidence of fire in pre-human New Zealand. Many areas may have experienced no fire whatsoever.

Natural fires in New Zealand were therefore quite rare, even in dry areas. Multiple fire ignition points were also likely to be uncommon because of the small scale and low frequency of electrical storms, and thus fire breaks such as ridges, streams, moist gullies and rockfalls, would be effective. Woodlands and shrublands where there is a low grass biomass, a great diversity of structural types, and an uneven distribution of fuel, and fallen trunks, tend to experience less intense and more patchy fires than more uniform

vegetation types (Bilbao *et al.*, 1995). As much of the drier eastern South Island was characterised by woodland-shrubland vegetation, we can expect that the natural fires were patchy and predominantly small scale. Small irregular fire clearings where burnt ground is close to seed sources revert quickly to the original vegetation. A scenario where fires were small and infrequent is entirely consistent with the low but consistent input of predominately small-size (<50µm) class charcoal particles to peat and lake sites in eastern districts, and the low, persistent occurrence of grass pollen.

Anthropogenic fire and grassland expansion

Anthropogenic deforestation is registered in southern South Island pollen diagrams by an abrupt fall in the influx of tree and shrub pollen, expansion of grasses, bracken, *Celmisia* spp., and *Aciphylla* spp., and a large increase in charcoal influx (see Figs. 3, 4 and 5 for examples). South Island soil charcoal also records this event, in that the number of dated charcoal deposits after 800 BP increased to a level several times greater than that prevailing before (McSaveney and Whitehouse, 1989; Ogden *et al.*, 1998). The fires that caused these massive environmental changes began sometime between 800 and 550 BP (1150 and 1400 AD) throughout New Zealand (McGlone *et al.*, 1994; McGlone and Wilmshurst, 1999b). Because of uncertainty associated with radiocarbon date-calendar date conversions, contamination by both young and old carbon, variable sediment accumulation rates, and the inherent difficulty of defining when anthropogenic fire as distinct from natural fire began, it is not possible to determine exactly when and how quickly forest and scrub was removed from any given district (McGlone and Wilmshurst, 1999b).

The fires lit by the first Polynesian settlers greatly reduced the amount of woody vegetation in favour of fern and grassland. The impact of fire differed according to district and altitudinal zone. In the high rainfall areas of the western mountain ranges, little forest destruction occurred (Fig. 1). Under the moderate and moist climates of the lowland south and west, forest destruction was only partial, extensive tracts of forest remaining more or less intact, especially in mountainous areas such as the Longwood Ranges, the Blue Mountains, and the Catlins. Fire almost completely eliminated both lowland and montane forest in areas with rainfall <1000 mm yr⁻¹.

Dry intermontane basin terraces, and seral, low nutrient or steep cliff face sites throughout the low forests and scrub of the interior acted as a reservoir of grassland species, and it was from these that the fire-induced grassland formed. In the closed tall forest of the moister lowlands, it seems that only *Chionochloa rubra* was consistently present, mainly as a tall tussock

of poorly drained sites, and therefore it became the dominant tussock species over vast areas after fire (Fig. 1). Pollen diagrams show that the small size class grass pollen peaks first in the post-fire successions, the larger grained *Chionochloa* types peaking later (e.g. Figs. 3, 4 and 5). This is interpreted as elimination of woody vegetation from the drier lowland and montane areas encouraging the early spread of non-*Chionochloa* grasses including species of *Poa*, *Festuca*, *Rytidosperma*, and *Elymus*, presumably because of their high reproduction, good dispersal, and fast growth rates. These species persisted until European settlement in semi-arid grasslands, and dry shrublands. On wetter sites (>700 mm yr⁻¹), the long-lived, taller *Chionochloa* spp eventually gained dominance although delayed by slow growth and sporadic seeding. A similar sequence of events has been deduced from ecological analysis of extant grasslands. Connor (1964) and Connor and Macrae (1969) suggested that short tussock species spread first after deforestation, but that *Chionochloa* spp. advanced slowly into these initial grasslands, excluding many species and increasingly confining short-tussock grasslands to unstable sites.

Bracken played and still plays an important role in the fire-induced vegetation of the southeastern South Island, and it was a major beneficiary of fire in the wet western ranges, wetter flanks of mountains of the interior, and the coastal lowlands (Figs. 3, 4 and 5). Its spores are abundant early in most pollen sequences in the coastal and high rainfall areas, but contribute only a minor percentage to the total under the drier or more extreme climate regimes of the interior, where grass and *Aciphylla* spp became the post-fire pollen rain dominants (McGlone and Moar, 1997). Bracken with its vigorous rhizomes, highly inflammable fronds and tendency to accumulate dead fronds and thick litter, is a classic pyrophyte (Page, 1976). Bracken also produces abundant spores which are dispersed by wind over distances of many kilometres. It was thus well placed to take immediate advantage of fire.

Continuing and frequent fire in the Maori era did not increase the dominance of bracken. Bracken, which tended to peak at around 40-80% of the terrestrial pollen sum early in the fire sequence in all but the driest sites, slowly declined to half or less of its original values with continuing fire as first small grass pollen types and then *Chionochloa* type pollen become abundant. Two factors may explain this. First, bracken is favoured by free-draining light soils which permit prolific rhizome growth. Immediately post-burn a combination of an organic, litter-rich upper soil layer inherited from the previous forest soil, plus the addition of ash and charcoal from the fire, may have provided in many areas optimal edaphic conditions for bracken. Repeated fire may have run down this initial soil capital in many areas, leading to shallower profiles (McGlone

and Basher, 1995). Second, spread of grass and other angiosperms may have excluded bracken from sites for which it was ill-suited, but occupied simply because of its superior dispersal ability, or which it had never occupied. For instance, where tussock and bracken are sympatric in the central North Island native grasslands, bracken tends to favour hill slopes rather than the tussock-covered flat depressions, demonstrating its preference for well-aerated soils on less frosty sites over water-logged, frost-prone sites of the depressions (Rogers, 1994).

Conservation and post-fire plant communities

The history of the impact of human settlement on grasslands is an important factor when considering conservation management and goals. The present indigenous lowland and montane grasslands are unparalleled in the historical record. Pre-fire grasslands tended to have abundant *Chionochloa* only above tree line in the wetter western ranges. On the flat topped mountains of the dry interior, a diverse mixture of grass species and low shrubs seems to have been more the rule than pure tussock grassland. Below tree line, the grasses formed intricate mixtures with trees and shrubs. The extensive *Chionochloa rubra*, *C. rigida* and *C. macra* tussock grasslands present in 1840 AD represented a new anthropogenic community that was created by periodic fire that eliminated and repressed the previous woody ecosystems. The ecological behaviour of the *Chionochloa* dominants thus has more in common with species such as *Kunzea ericoides*, *Cordyline australis* and bracken which also played a subsidiary, and perhaps specialist role until massively encouraged by fire.

Despite this clearly anthropogenic origin, the tussock grasslands of the montane and lowland South Island have been regarded as the *de facto* natural vegetation cover. A similar recognition has not been granted to bracken, for instance, despite its historic dominance of Maori and early European landscapes and its major prehistoric economic importance (McGlone, 1983; McGlone *et al.*, 1994). Bracken is conserved in protected landscapes solely for its potential to be eventually replaced by indigenous forest. While it would make sense in terms of ecological logic to take a similar approach to anthropogenically induced grasslands, the considerable economic contribution of these grasslands and their superior visual and recreational potential have dictated otherwise.

Severe conservation problems are presented by the indigenous rain-shadow grasslands of New Zealand (Mark, 1992). Until recently lowland and lower montane grasslands were poorly represented in protected natural

areas, in part because of greater emphasis on forest communities and the conflicting demands of economic (mainly pastoral) uses. As lowland and montane tussock grasslands are increasingly being brought into the national conservation estate, the question of how to manage them has become important. Being seral communities, formed and maintained by fire and modified by grazing, they are unstable. Those adjacent to shrubland and forest, exotic or indigenous, will always be vulnerable to invasion by woody plants. Most are open to fast-spreading weeds and mammalian pests. Ultimately, management designed to maintain them in their current condition, be that continuation of grazing, fire, or other means of woody plant and weed control (for instance, Calder *et al.*, 1992), will have to be undertaken on a large scale.

More importantly, as has been known for a long time, behind nearly every lowland or montane tussock grassland stands the ghost of a destroyed woody ecosystem and, on a national scale, a unique dryland ecological zone has been nearly eliminated. If preservation of the entire span of fully functional New Zealand ecosystems is an aim, it follows that some attempt will have to be made to ensure the existence of self-sustaining examples of the pre-human woody cover of the southeastern South Island. However, there must be some doubt as to how feasible this goal is. New Zealand provided for several millions of years a bioclimatic zone, possibly unique on a global scale, which was dry, drought-prone but free of all but infrequent fire. The anomalous result is that New Zealand possesses a suite of shrubs and trees tolerant of dry, droughty conditions but highly sensitive to fire and slow to recover in its wake. In the current pyrophilic situation, it is difficult to envisage how sustainable indigenous semi-arid woodlands could be recreated. Perhaps the most that can be done is to attempt to preserve small examples as ecosystems-in-waiting while maintaining the ecological health of the magnificent, although thoroughly anthropogenic, successor grasslands.

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