Late glacial to Holocene vegetation and climate change in the eastern Takitimu Mountains, western Southland, New Zealand

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Pollen analysis of a core from a raised bog has provided a late glacial and Holocene vegetation record for the Takitimu Mountains in western Southland, New Zealand. The record shows a change from alpine grassland-shrubland at 12 600 yr BP to a low broadleaf bushland by 9800 yr BP. The bushland was succeeded by tall podocarp forest after 9400 yr BP which was replaced by cool montane mixed temperate forest dominated by Nothofagus menziesii after 4000 yr BP. Since 4000 yr BP, the only major changes in vegetation have been a slow increase in the values of Nothofagus fusca type pollen. An increase in Pteridium together with an increase in charcoal within the last 600 years may record Polynesian burning, and the later appearance of Abies and Pinus, together with an increase in grassland, records European influences. Comparison with other pollen profiles from southern New Zealand shows that many of the changes in vegetation associations are broadly synchronous and may be related directly to climate change. Differences in the timing of some floristic changes may reflect the combined effects of local climates and other local environmental factors, including the proximity of vegetation refugia to individual sites. Changes in the pattern of atmospheric circulation of southern New Zealand inferred in earlier published studies are consistent with the results of these findings.

Keywords: palynology, vegetation history, late glacial, Holocene, climate change, vegetation response, western Southland

INTRODUCTION

Southland is the most southerly region of the South Island of New Zealand (Fig. 1), and lies in an area close to the most intense westerly wind circulation of the Southern Ocean (McGlone & Bathgate 1983). The climate of this area is likely to have been sensitive to changes in atmospheric circulation during the Quaternary, particularly to the intensity and frequency of westerly and southerly winds (McGlone & Bathgate 1983).

The earliest studies of post-glacial vegetation in this region divided the late Quaternary into three periods: period 1, characterised by a severe climate at the end of the late Otiran up to 10 000 yr BP; period 2, characterised by uniformly warm and wet conditions between 10 000 and 4000 yr BP; and period 3, characterised by climatic deterioration and establishment of distinct regional climates after 4000 yr BP (Cranwell & von Post 1936; McIntyre & McKellar 1970). Subsequently McGlone & Bathgate (1983) suggested that the utility of Cranwell & von Post’s work is restricted by unreliable pollen identifications and because they did not distinguish between Dacrycarpus dacrydioides (formerly Podocarpus dacrydioides) and Dacrydium cupressinum.

Work by McGlone & Bathgate (1983) in the Longwood Range (Fig. 1) near coastal
Southland showed that grassland-shrubland persisted in the region between 12 000 yr BP and approximately 9400 yr BP. They argued that the Last Glaciation was characterised by extreme climatic variability and increased continentality. After 9400 yr BP a transition into podocarp forest was attributed to a milder, warmer, and drier climate. They interpreted an expansion of *Nothofagus* and *Dacrydium cupressinum* after c. 4000 yr BP as a transition to a cooler, moister climate as the present climatic regime was established. McGlone & Bathgate suggested that during the late glacial, coastal Southland experienced enhanced westerly circulation with more frequent and colder outbreaks of subpolar air. A drier early Holocene climate is related to reduced southwesterly air flow which intensified after 7000 yr BP to
produce the contemporary coastal climatic regime of cool summers, cool winters, and frequent storminess.

Pollen diagrams from Central Otago (McGlone et al. 1995) in the South Island of New Zealand record the persistence of grassland-shrubland with increasing tree ferns during the late glacial-early Holocene between 12 000 yr BP and 7500 yr BP. At 7500 yr BP a podocarp-dominated forest replaced grassland communities in lowland and upland areas, comprising species including *Pruinopitys taxifolia*, *Dacrycarpus dacrydioides*, *Podocarpus Phyllocladus alpinus*, and *Halocarpus bidwilli*. McGlone et al. (1995) suggest that dry late glacial to early Holocene climates resulted in the persistence of grassland-shrubland into the early Holocene and a delay in reafforestation by podocarp-dominated forest, which appears at c. 10 000 yr BP in other South Island pollen diagrams. Expansion of *Nothofagus menziesii* after 6000 yr BP and *N. fusca* type forest after 3000 yr BP in Central Otago is attributed to increasing cooler and wetter conditions occurring throughout the region (McGlone et al. 1995).

This paper reports an investigation of late glacial and post-glacial vegetation change in an inland area of Southland, in the lee of the Fiordland mountains and the Takitimu Mountains (Fig. 1). The primary objective of this study is to examine the applicability of the palaeoclimatic interpretations of Cranwell & von Post (1936), McIntyre & McKellar (1970), McGlone & Bathgate (1983), and McGlone et al. (1995) to the study area. In particular, we ask whether the general periods of vegetation change identified by Cranwell & von Post can be applied to the eastern Takitimu Mountains. Are the climate changes inferred from the coastal site of McGlone & Bathgate (1983) synchronous with changes inferred from this inland site? And can the atmospheric circulation changes inferred by McGlone & Bathgate be confirmed?

**ENVIRONMENT OF WESTERN SOUTHLAND**

The Takitimu Mountains rise to a height of 1650 m and form a major topographic barrier to the westerly and southwesterly airflows that dominate the climate of the area. The mountains are formed mainly of Palaeozoic volcanics dominated by basalt, spilite, olivine, tuff, and agglomerate interbedded with greywacke (McKellar 1973). Soils are mostly moderately leached, infertile yellow-brown earths on the western slopes and moderately infertile yellow-brown sandy clay loams on the eastern slopes (N.Z. Soil Bureau 1968).

The Takitimu Mountains are situated within the rain shadow of the Fiordland mountains, hence they probably supported only small cirque and valley glaciers during the last glaciation. The area to the east of the Takitimu Mountains is influenced predominantly by strong south-westerly air flows carrying cold fronts and associated rain into the region. Westerly air flows are also common, although these can be depleted of moisture by the time they reach inland Southland because of orographically induced rainfall over the Fiordland and Takitimu mountains. Annual precipitation in the area averages 960–1000 mm (N.Z. Met. Service 1983), most of which falls as rain. Although snow caps the peaks for much of the winter there is no permanent snow or ice. Mean annual temperatures in inland Southland range between 8 and 11°C in the lowlands, with moderately warm summers and cool wet winters. Occasional frosts may be recorded over most of the region’s lowlands, while severe inversion frosts are common in the valleys.

The Takitimu Mountains are situated on the border between two main forest types. To the north-west and west in Fiordland, beech (*Nothofagus* sp.) forest dominates the upland areas to the treeline, with *N. menziesii* and *N. solandri* var. *cliffortioides* the most common species. In the south and along the coastal terraces of Fiordland the most common natural vegetation is a mixed forest type consisting of beech, podocarp, and broad-leaved hardwood species (Holloway 1954). *Dacrydium cupressinum* (rimu) tends to be the dominant podocarp, with other important species including *Pruinopitys ferruginea*, *P. taxifolia*, *Podocarpus hallii*, and *Dacrycarpus dacrydioides*. Natural fires, Polynesian burning, and European clearing have restricted most forests to mountain slopes or patches on the lowlands.
Fig. 2 The peat bog at Letham Burn.

**Site location and description**

The pollen core was taken from a raised, ombrotrophic peat bog in a valley on the south-eastern flanks of the Takitimu Mountains (NZMS 260 D44/173810, Fig. 1) at Letham Burn (Fig. 2). The bog lies at an altitude of 460 m a.s.l, and covers an area of approximately 165 m². Probing indicated the peat of greatest depth to lie towards the centre of the bog, from which the core was extracted. The peat bog is dominated by a thick surface mat of *Empodisma minus* with patches of *Sphagnum. Dracophyllum pearsonii, D. longifolium*, and *D. uniflorum* are present in clumped distributions across the bog surface, along with *Halocarpus bidwillii* around the perimeter.

Around Letham Burn, forest vegetation is dominated by *Nothofagus menziesii*, with an understorey of *Coprosma* species, mainly *C. banksii, C. colensoi, C. crassifolia*, and *C. propinqua*. Uncinia sedges, *Sphagnum* moss, and filmy ferns dominate the forest floor, interspaced with scattered *Cyathea smithii* and *Astelia* species. Shrubland-grassland covers the valley floor and is dominated by *Chionochloa rubra and Carmichaelia monroi. Leptospermum scoparium, Discaria toumatou, Coprosma parviflora*, and *C. rugosa* are sparsely distributed.

**METHODS**

A 4.9 m core was recovered using a Russian D-section peat sampler. Pollen samples of 0.5 cm³ were taken at 10 cm intervals throughout the majority of the core and at 5 cm intervals near pollen zone boundaries and near the base of the core. Preparation of pollen slides followed standard treatment (Faegri & Iversen 1989) and included the addition of exotic *Lycopodium* tablets to permit the calculation of concentrations.

Samples were counted until a sum of at least 250 grains of dryland pollen was obtained, after which the remainder of the slide was scanned to identify grains not represented in the sum. These grains were recorded as traces. The pollen sum includes all dryland pollen species. *Pteridium* has also been included in the pollen sum as it forms a major component of
plant cover following vegetation destruction by forest fire or clearing (M.S. McGlone, pers. comm. 1993). Tree ferns (Cyathea and Dicksonia species) have also been included in the sum, as we consider them to be an important component of the forest system in the area. Spores of other ferns and fern allies were excluded from the pollen sum along with pollen from wetland and aquatic species. Charcoal counts were estimated using the point count technique of Clark (1982), to act as an indication of vegetation destruction by burning.

Core samples consisting of 4 vertical cm of peat were taken at 2.6, 4.0, and 4.9 m to radiocarbon date pollen zone boundaries marked by major changes in pollen composition. The samples were air-dried and submitted to the Rafter Radiocarbon Laboratory of the Institute of Geological and Nuclear Sciences (N.Z.).

THE POLLEN DIAGRAM
Radiocarbon dates obtained from the core through the use of conventional and AMS dating yielded dates of 12 599 ± 150 yr BP (NZ–8018) at 4.9 m, 9791 ± 70 yr BP (NZA–3281) at 4.0 m, and 4217 ± 64 yr BP (NZA–3432) at 2.6 m. The pollen diagram has been divided into four zones on the basis of vegetation assemblages, as follows.

Pollen zone LB1: 12 600–9800 yr BP; 4.9–4.0 m
Poaceae dominate the dryland pollen taxa of this zone (Fig. 3), with levels attaining peaks up to 60%. Plantaginaceae and Hebe pollen is also common early in this zone (at lower levels). Sharp decreases in Poaceae coincide with rises in the pollen levels of small tree-shrub taxa, with Coprosma showing the largest increase of up to 35%. Asteraceae, Myrsine, and Gonocarpus also show marked increases in pollen abundance in relation to decreases in Poaceae, with other taxa such as Hoheria and Muehlenbeckia becoming more common. Herb taxa such as Gentiana and Apiaceae are also common. Forstera also exhibits low levels (<2%) in the early stages of this zone, after which it disappears from the sequence.

Towards the top of this zone, most small tree-shrub taxa that have been well represented in the fossil pollen rain such as Coprosma, Asteraceae, Myrsine, and Hoheria decline markedly, while Poaceae and Gonocarpus pollen fall to very low levels. Exceptions to this are Muehlenbeckia and Apiaceae, which now attain their highest pollen levels recorded, peaking at around 10%, after fluctuating at low levels throughout this zone. Aristotelia, Rubus, and Coriaria pollen also increase through this zone, along with Griselinia, which reaches approximately 25% of the sum at the top of this zone. Of the wetland taxa, Cyperaceae and Centrolepidaceae are abundant at the start and midway through this zone, while Euphrasia, Gunnera, Lobeliaeaceae, and monolete fern spores are recorded at low levels. These taxa give way to Empodisma pollen and Gleichenia spores, which attain high levels towards the top of this zone.

Tree pollen of Nothofagus fusca type, Phyllocladus, Halocarpus, Lepidothamnus, and Dacrydium is consistently encountered at low levels (<2%) throughout this zone.

Pollen zone LB2: 9800–4200 yr BP; 4.0–2.6 m
In the tree pollen assemblages Halocarpus, Prumnopitys taxifolia, and to a less extent Dacrycarpus rise to high levels at the beginning of this zone, and decrease towards the top of the zone. Subsequently the Phyllocladus curve exhibits a similar pattern. Other podocarp taxa such as Dacrydium, Lepidothamnus, Podocarpus, and Prumnopitys ferruginea show low levels of pollen representation, while Metrosideros and Nothofagus fusca type pollen is recorded as traces. Nothofagus menziesii exhibits low but increasing values throughout this zone.

Sharp declines in pollen from tree-shrub and herb taxa such as Asteraceae, Griselinia, Muehlenbeckia, Myrsine, Rubus, and Apiaceae are apparent (Fig. 3). Coprosma pollen also decreases to lower levels for the rest of the sequence, as do Myrsine, Hoheria, Asteraceae, and Apiaceae. Plagianthus, Pseudopanax, Corokia, Tupeia, and Dracophyllum are now represented in low (<2%) or trace amounts, while Geum exhibits a brief peak.
Fig. 3 Letham Burn pollen percentage diagram, including summary diagram and total pollen concentrations plot; (+ symbol) on pollen diagram indicates pollen noted as trace values in the samples. Summary diagram includes only taxa calculated in the pollen sum.
Tree fern spores, *Cyathea* and *Dicksonia*, increase in abundance through this zone, while *Sphagnum* and trilete and monolete fern spores remain at low levels. *Gleichenia* spores rise to a maximum recorded level of 68%.

Among the wetland and aquatic taxa, *Empodisma* pollen declines to levels of around 20%, rises to 30%, and declines again before the end of the zone. Cyperaceae pollen peaks at low levels (10%), after which it declines to fluctuate below 5% for the rest of the zone. Other taxa such as *Euphrasia*, *Gunnera*, Lobeliaceae, and Centrolepidaeae are not represented in the sequence after zone LB2.

**Pollen zone LB3: 4200 – c. 600 yr BP; 2.6–0.35 m**

*Halocarpus* and *Phyllocladus* pollen levels remain high at the beginning of this zone, but then fall to below 10%. Conversely, *Nothofagus menziesii* pollen increases to levels of around 40–45%, rising to a peak of 67% of the pollen sum at the end of the zone. *Dacrydium* pollen increase to levels of around 10%, along with slight increases in *Prumnopitys ferruginea* and *Nothofagus fusca* type. Fluctuations in *Nothofagus menziesii* pollen frequencies alternate with *Prumnopitys taxifolia* pollen, which remains at levels of 15–30%. *Dacrycarpus* and *Podocarpus* pollen are recorded at levels below 5%, along with *Lepidothamnus* and *Metrosideros* taxa. Tree fern spores disappear from the record, with the exception of trace values of *Cyathea smithii* and *Dicksonia squarrosa*.

Herbaceous pollen is almost absent in this zone; only Apiaceae and Poaceae are present (<5%). Asteraceae, *Griselinia*, *Hoheria*, *Pseudowintera*, and *Myrsine* appear at low levels throughout this zone along with most other small tree-shrub taxa as trace values. *Pteridium*, *Ascarina*, *Quintinia*, and *Neomyrtus* first appear in this zone at low levels. *Dracophyllum* pollen increases to its highest level and fluctuates at values below 10%. *Sphagnum*, *Gleichenia*, and monolete and trilete fern spores are recorded at low values. *Empodisma* pollen remains the dominant wetland taxon, and fluctuates between 30% and 10%.

Composition of the palynoflora zone LB3 is distinctly different from zone LB2. Forest taxa representation becomes more diverse, with an increasing angiosperm component in the pollen rain, notably *Nothofagus* species. Other pollen taxa such as *Phyllocladus* and *Halocarpus* show a marked decline, while most herb and small tree-shrub taxa are represented at low levels.

**Pollen zone LB4: <600 yr BP; 0.35–0.0 m**

This zone is characterised by the first record of charcoal, which increases rapidly as forest pollen declines. *Nothofagus menziesii* pollen remains dominant, although declining from 67% to levels below 40%. This decline in *N. menziesii* pollen coincides with increasing levels of *N. fusca* type, *Prumnopitys taxifolia*, and *Halocarpus* pollen. *Prumnopitys ferruginea*, *Podocarpus*, *Phyllocladus*, *Dacrydium*, and *Dacrycarpus* remain common but at low levels. Pollen of exotic taxa is also present towards the top of this zone, with *Abies* reaching levels up to 20%.

Asteraceae and *Coprosma* pollen show higher levels through this zone than at the end of zone LB3, while *Dracophyllum* and *Myrsine* remain at low levels. *Phymatosorus* and other monolete fern spores occur at low levels throughout this zone. *Sphagnum* peaks to its highest recorded level (7%), and *Empodisma* pollen gradually rises to attain high levels of 67% at the surface sample. Poaceae pollen increases to levels of 7% towards the end of the zone, while *Pteridium* peaks at its highest level recorded and then disappears from the sequence.

**DISCUSSION**

**Interpretation of regional vegetation**

The lower part of zone LB1, which is dated at 12 599 ± 150 yr BP (NZ–8018), suggests that the region was characterised by open grassland-herbfield with scattered low-growing shrubs of *Coprosma* and Asteraceae. Although few of these plants are exclusively alpine or subalpine,
herb communities of *Forstera*, *Apiaceae*, *Geum*, *Plantaginaceae*, and *Gonocarpus*, and dwarf shrubs in the *Scrophulariaceae* (e.g. *Hebe*) and *Asteraceae*, are common at the present treeline (Wilson 1982; Mark & Adams 1986; Poole & Adams 1990).

A transition from grassland-herbfield to a shrubland-grassland phase takes place midway through zone LB1, with an increase in, and dominance of *Coprosma*, *Asteraceae*, *Myrsine*, and *Hoheria* (Fig. 3). Although grassland still remains extensive in the area, most of the higher-altitude herbs present probably became restricted to the more exposed sites during this time. The small shrub-tree species probably extended their distributions in the semi-sheltered gullies or around rocky outcrops (Wardle 1991), while other species in abundance at the time, such as *Gonocarpus* and *Dracophyllum*, may have dominated moist sites towards the snowline or on scree slopes, or may have been abundant on the bog surface (Mark & Adams 1986).

Towards the end of this zone, at 4.2 m depth, a transition in vegetation composition from shrubland-grassland to bushland is apparent (Fig. 3). This bushland was most likely dominated by a low broadleaf forest comprising *Griselinia littoralis* and *Muehlenbeckia*, occupying sites in sheltered gullies and on semi-fertile soils (Wardle 1991; A.F. Mark, pers. comm. 1993). Under these forests *Rubus*, *Aristotelia*, and the tree fern *Dicksonia squarrosa* would probably have dominated the sub-canopy gaps or forest margins (Wardle 1991).

Throughout zone LB1, low but consistent pollen percentages of podocarp trees such as *Dacrydium cupressinum*, *Lepidothamnus*, *Nothofagus fusca* type, *Halocarpus*, and *Phyllocladus* suggest that these trees, although scarce, were present in the region. It is likely that these tree species grew in small groves on the lower leeward flanks of the Takitimu Mountains, generally confined to moist sheltered slopes with a favourable aspect.

At the start of zone LB2 (c. 9800 yr BP) there was a rapid transition from shrubland-bushland to tall podocarp forest. Although dominated by *Prumnopitys taxifolia*, other podocarps including *P. ferruginea* and *Podocarpus* were also common. Together these species probably occupied the warmer, well drained and semi-fertile hill slopes as they do throughout the country today (Wardle 1978, 1991). The less abundant *Dacrydium cupressinum* probably occupied the more restricted wetter sites (Franklin 1968). The occurrence of tree ferns such as *Cyathea dealbata*, *C. smithii*, and *Dicksonia squarrosa* at this time is probably associated with the subcanopy of the dominant tall podocarp forest, and may indicate increasing moisture levels. Surrounding these podocarp forests, and possibly forming the subcanopy, *Griselinia*, *Hoheria*, *Muehlenbeckia*, and *Corokia* persisted, with *Coprosma* and *Myrsine*.

The high values of *Halocarpus* pollen (most likely *H. bidwillii*, as it is found at the site and in the region today) may represent a regional abundance of these species, probably at moist poorly drained sites along with small stands of *Dacrycarpus dacrydioides* and *Lepidothamnus*. Alternatively, over-representation of this pollen is also possible as the tree may have grown at the site as it does today. However, while *H. bidwillii* is abundant around the present site, it is not over-represented in the surface sample. The ability of *Halocarpus* to tolerate temperatures as low as -23°C (Wardle & Campbell 1976; Sakai & Wardle 1978) may have assisted it to dominate areas where cold air drainage or persistent radiation frosts made the site unsuitable for other plant forms. Other cold-tolerant alpine species such as *Dracophyllum*, the herb *Geum*, and *Apiaceae* may also have occupied similar environments on moister sites (Sakai & Wardle 1978; Mark & Adams 1986).

A further change in composition of the podocarp forest is recorded towards the centre of this zone, where a rise in *Phyllocladus* (most likely *P. alpinus*, as it is the only species growing in the area at present) coincides with decreasing levels of *Dacrycarpus*, *Halocarpus*, and *Prumnopitys taxifolia*. Currently *Phyllocladus* occupies boggy, leached sites at lower altitudes (Wardle 1969, 1991) and well drained rocky sites at higher altitudes (Wardle 1969). At the treeline *Phyllocladus* may have replaced previously abundant alpine shrubs such as *Asteraceae* or *Dracophyllum*, while closer to the site *Phyllocladus* may have encroached upon areas previously occupied by *Halocarpus*. As *Phyllocladus* is less tolerant of low
temperatures than *Halocarpus* (Sakai & Wardle 1978), the marked increase in abundance of *Phyllocladus* may indicate a reduction in the frequency of extreme cold temperature events.

A sharp rise in the abundance of *Nothofagus menziesii* and *Dacrydium cupressinum* at the beginning of zone LB3 indicates a major change in forest composition. The increase in *N. menziesii* values at c. 4200 yr BP may be a result of this species expanding its range to occupy moist cool sites similar to those in which it is found today. Increased values of *Dacrydium cupressinum* pollen may also have been in response to increased moisture availability, although this species may have been restricted to less fertile sites (Franklin 1968).

As the taller *Nothofagus* and *Dacrydium* forest spread, values for *Halocarpus* and *Phyllocladus* decline, probably as they became restricted to the frostier, less fertile sites (Wardle 1991). *Dacrycarpus* forest would have remained dominant on the poorly drained soils and swamp sites along with *Lepidothamnus* at open boggy sites. Of the remaining podocarp species, *Prumnopitys taxifolia*, *P. ferruginea*, and *Podocarpus* remain common throughout this zone and probably occupied the well drained, warmer sites. *Griselinia* persists at low levels throughout this zone, probably on dry sites of disturbance in the podocarp forest or forming a subcanopy layer.

Although rare throughout zone LB2, *Dracophyllum* increases early in zone LB3, together with a slight resurgence in Poaceae. These two taxa may have dominated the cooler, moister sites of the subalpine grassland and the lower valley frost pockets, as they do around the area today. However, it is more likely that *Dracophyllum* occupied areas on or around the bog surface. The increasing abundance of *Nothofagus fusca* type pollen probably represents the species *N. solandri* var. *cliffortioides*, because other beeches such as *N. solandri* var. *solandri*, *N. fusca*, and *N. truncata* are either absent from the region (*N. truncata*) or are limited to small pocket distributions. *N. solandri* var. *cliffortioides*, with its wide range of tolerance and its low competitive ability (Wardle 1969, 1991), may have occupied sites at higher altitudes with low soil fertility and poor drainage.

This beech-podocarp association persisted in the area as a dominant forest type up until 600 yr BP. Although there is little change in forest composition in zone LB4, a dramatic decrease in the values for *Prumnopitys taxifolia*, *Nothofagus menziesii*, and *Dacrycarpus dacrydioides* from 0.35 m depth to the surface coincides with the appearance of charcoal, marking the start of widespread forest destruction by Polynesian burning (McGlone 1983). These fires probably cleared large areas of vegetation, which were quickly colonised by opportunist species such as *Pteridium*, which increases in representation over the last 20 cm of the core. In the core examined the increase of *Pteridium* is only minor, and probably records a regional episode of forest clearance further south of Letham Burn. It is unlikely that forest around the site itself was cleared until European times, as *Pteridium* spores would have been recorded in greater abundance after the initial appearance of charcoal. The increase in Poaceae representation at this time may indicate an expansion of more fire-tolerant tussock grassland in the area, or further forest clearance.

Towards the end of zone LB4 a further reduction in beech-podocarp forest in the Takitimu region and an increase in grasslands is indicated by the pollen diagram. These changes are probably the result of clearance of low forest and scrub for the establishment of pastoral farms associated with the arrival of European settlers (McGlone & Bathgate 1983). The appearance of exotic pollen such as *Pinus* and *Abies* in the Letham pollen sequence records the planting of production forests in the Southland district during the last 100 years.

**Palaeoclimatic interpretation**

Climatic conditions during the late glacial phase appear to have been too harsh to permit the expansion of tall forest, yet were mild enough to allow some development of woody shrubland. The alpine herbfield-scrub vegetation suggests that the climate was humid and temperatures were considerably lower than at present. By taking an average of 1100 m for the treeline in this area, and an average lapse rate of 0.6°C/100 m, a mean temperature depression...
of at least 3.2°C is suggested. This is consistent with an estimated temperature depression of 4.5–5°C during the last glacial maximum (Porter 1975; Soons 1979). Towards the end of pollen zone LB1 a transition to bushland is marked by increased values and peaking of *Coprosma, Griselinia,* and *Myrsine*. This transition probably marks increasing temperatures and possibly increasing rainfall.

The rapid transition from bushland to podocarp forest at around 9800 yr BP at the beginning of zone LB2 records a major change in climate. The dominant tree species early in zone LB2 are *Halocarpus* and *Pruinopitys taxifolia*, with *Dacrycarpus dacrydioides* and *Dacrydium cupressinum* less common. Currently *P. taxifolia* grows under dry cool conditions, where rainfall seldom reaches 1200 mm/yr and may fall as low as 600 mm/yr (Wardle 1991); *Halocarpus bidwillii* exhibits a tolerance of temperatures as low as −23°C; and *D. cupressinum* is restricted to areas with a rainfall above 1000 mm (Franklin 1968). Although rainfall and temperature probably increased at this time, the change may not have been sufficient to allow any great expansion of some of the more moisture-demanding podocarp species such as *D. cupressinum*. Thus, the rainfall in the early Holocene was probably considerably lower than it is at present. In low-rainfall conditions *D. cupressinum* is often restricted to moister sites (Franklin 1968). Low levels of *D. cupressinum* throughout zone LB2 may therefore suggest that the species grew in moist sites together with *Dacrycarpus dacrydioides*. A subsequent rise in *Phyllocladus* (probably *P. alpinus*) as *Halocarpus* declines through zone LB2 at 3.5 m suggests an amelioration in climate (e.g. a decrease in frost intensity), because *P. alpinus* is less tolerant of very cool temperatures than its predecessor *H. bidwillii*.

In zone LB3 the rapid increase in values for *Nothofagus menziesii* and *Dacrydium cupressinum* by 4000 yr BP signals a major change in forest composition that is probably a response to a change in climate. *N. menziesii* and *D. cupressinum* currently occupy cool, wet montane and lowland habitats (Wardle 1967; Franklin 1968), which strongly suggests that the climate of that time became wetter and possibly cooler than the early Holocene climate. Concurrent expansion of *Dracophyllum*, a genus which often occupies moist alpine or boggy habitats (Mark & Adams 1986), along with the marked increase in peat bog accumulation rates, supports the interpretation of increased rainfall and cooling after 4000 yr BP.

It is possible that this late Holocene forest change is not closely related to climate change. An alternative explanation is that changing soil nutrient conditions by leaching of the soils during the post-glacial period permitted the expansion of species such as *D. cupressinum*, which are tolerant of nutrient deficiencies. However, the apparently synchronous changes in the forest as well as the bog, also evident at other nearby sites as discussed below, suggest that climate is the most important controlling variable, because edaphic changes would be slow and probably not synchronous.

After 4000 yr BP the only major changes in vegetation are the slow increase in the values of *Nothofagus fusca* type pollen, along with signs of Polynesian burning and European forest clearance, including an increase in *Pteridium* and Poaceae, the appearance of *Abies* and *Pinus*, and an increase in the charcoal count. It appears likely that the modern climatic regime of the Takitimu region was fully established at around 4000 yr BP, and has not changed markedly since.

McGlone & Bathgate (1983) suggested that the late glacial vegetation associations of Southland are not explicable solely in terms of lowered annual temperatures. They argued that if the estimated temperature depression calculated by Porter (1975) and Soons (1979) is accepted, the treeline should not have fallen below 300 m a.s.l. Most of Southland is below this altitude, so would have been suitable for forest occupation throughout the last glaciation, yet open grassland is recorded at 60 m above sea level at the Longwood site during the late glacial. They suggested that the late glacial climate was extremely variable, because greater continentality and strengthened westerly circulation brought more frequent and much colder incursions of polar air into the Southland region. While this mechanism of changing circulation is plausible, we cannot substantiate this inference from our interpretation of the Letham Burn
record. An equally plausible interpretation is that the differences in vegetation represent a mosaic of vegetation associations related to local site conditions and microclimate.

McGlone & Bathgate also suggest that during the early Holocene there was a decrease in the extreme climatic ranges of these air masses. They argue that after 7000 yr BP a shift to southwesterly circulation altered the climate towards the present-day regime of persistent cool southwesterly air streams, which favoured the establishment of *Nothofagus menziesii*-dominated forest. A similar trend is detected at the Letham Burn site, which shows that the climate of the early Holocene between 10 000 yr BP and 4200 yr BP is characterised by warmer and probably wetter conditions than the late glacial, and drier than at present. *Nothofagus menziesii*-dominated forest associated with cool montane conditions did not become established until after 4200 yr BP at Letham Burn, a time that coincides with projections made by McGlone & Bathgate for the Longwood sites. A south-westerly shift may have occurred after 7000 yr BP, and could have caused regional change in vegetation structure, which is only moderately expressed in the region until around 4000 yr BP. This and other relationships between vegetation and climate from different southern South Island records are examined below.

**Comparison with other pollen diagrams**

In the southern South Island, radiocarbon-dated late glacial pollen sequences have been described from Swampy Hill near Dunedin city (McIntyre & McKellar 1970), the Longwood Range (McGlone & Bathgate 1983), and the Garvie Mountains, Old Man Range, and Kawarau Gorge in Central Otago (McGlone et al. 1995). The Longwood Range sequence comes from two coastal sites in Southland, at 60 m and 670 m, that were remote from permanent snow and ice during the last glaciation. The Central Otago sequences come from peat bogs at 1400 m (Garvie Mountains and Old Man Range) and 800 m (Kawarau Gorge). The Swampy Hill sequence comes from a hilltop mire at 740 m a.s.l. Comparisons between the diagrams from these sites permit reconstruction of the temporal and spatial changes in vegetation during the late glacial and Holocene in the southern part of the South Island (Fig. 4).

At the Longwood Range sites McGlone & Bathgate (1983) identify a late glacial grassland vegetation dominated by Gramineae (Poaceae; up to 75% of the pollen sum) and a variety of other herbs including *Ranunculus*, *Gentiana*, and *Plantago*. Only two woody taxa, *Coprosma* and Compositae (Asteraceae), are represented. This is followed by a shrubland-grassland phase during which *Myrsine* and *Pittosporum* appear together with rare tree pollen. In Central Otago McGlone et al. (1995) identify a late glacial grassland-shrubland vegetation community dominated by Poaceae, *Coprosma*, and Asteraceae along with herbs including *Gentiana* and *Epilobium*, *Plagianthus*, *Myrsine*, *Coprosma*, *Muehlenbekia*, *Halocarpus*, and the tree ferns *Cyathea dealbata*, *C. smithii*, *Dicksonia fibrosa*, and *D. squarrosa*. At Letham Burn the late glacial vegetation is a grassland-shrubland dominated by Poaceae and *Gonocarpus*, but also contains high values of woody shrubs including Asteraceae, *Coprosma*, *Hebe*, *Hoheria*, and *Myrsine*. The grassland-shrubland is followed by the development of a low broadleaf bushland, distinguished from the Longwood and Central Otago sites by the high values attained by the broad-leaved trees *Griselinia* and *Aristotelia*. A similar association is found at Swampy Hill, where McIntyre & McKellar (1970) recorded high concentrations of *Coprosma*, *Myrsine*, and *Muehlenbeckia* together with Poaceae. Thus the dated late glacial pollen records indicate that similar vegetation associations developed in different parts of the South Island, suggesting that most, if not all of the region experienced a much cooler and drier climate than at present.

An abrupt transition from shrubland-grassland to tall podocarp forest at the Longwood site is recorded at approximately 9400 yr BP, and a similar transition from low broadleaf bushland to tall podocarp forest occurs slightly earlier at Letham Burn (c. 9800 yr BP). In comparison with the Swampy Hill site, where podocarp forest was estimated to have expanded at approximately 10 500 yr BP, it appears that forest expansion occurred later in
<table>
<thead>
<tr>
<th>Letham Burn</th>
<th>Longwood Range</th>
<th>Central Otago</th>
<th>Swampy Hill</th>
</tr>
</thead>
<tbody>
<tr>
<td>470 m</td>
<td>Longwood 670 m</td>
<td>Garvie Mtns. 1400 m</td>
<td>739 m</td>
</tr>
<tr>
<td>This paper</td>
<td>Merrivale 60 m</td>
<td>Old Man Range 1400 m</td>
<td></td>
</tr>
<tr>
<td>Expansion of <em>Nothofagus fusca</em></td>
<td>Expansion of <em>Nothofagus fusca</em></td>
<td>Expansion of <em>N. fusca</em> forest</td>
<td></td>
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<tr>
<td>————700 yr BP</td>
<td>————1000 yr BP</td>
<td>————3000 yr BP</td>
<td></td>
</tr>
<tr>
<td>Cool montane mixed temperate rainforest</td>
<td>Cool montane mixed temperate rainforest</td>
<td>Mixed *Nothofagus/Podocarp forest</td>
<td></td>
</tr>
<tr>
<td>dominated by <em>N. menziesii</em></td>
<td>dominated by <em>N. menziesii</em></td>
<td>Appearance of <em>N. menziesii</em></td>
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<tr>
<td>————4000 yr BP</td>
<td>————4000 yr BP</td>
<td>————6000 yr BP</td>
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<tr>
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<td>Tall podocarp forest</td>
<td>Podocarp forest</td>
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<td>Tall podocarp forest</td>
<td>————7000 yr BP</td>
<td>Podocarp forest expansion</td>
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<td>————9800 yr BP</td>
<td>————9400 yr BP</td>
<td>————5900 yr BP</td>
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<td>Low broadleaf bushland</td>
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<td>————c. 11 000 yr BP</td>
<td>————12 000 yr BP</td>
<td>————11 500 yr BP</td>
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<td>Alpine grassland-shrubland</td>
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<tr>
<td>————12 600 yr BP</td>
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* Boundary at 10 500 and 11 500 yr BP is estimated

**Fig. 4** Comparison of late glacial pollen sequences from the southern South Island, New Zealand.

the Southland region. However, as the Swampy Hill date is the average of two dates (11 850 ± 150 and 9850 ± 120), it is possible that this event took place closer to that of the Southland forest expansion. In Central Otago the transition from shrubland-grassland to tall podocarp forest did not occur until approximately 7500 yr BP (McGlone et al. 1995). The changes in vegetation composition throughout Southland and coastal Otago can be regarded as approximately synchronous, and clearly reflect a substantial climatic amelioration. Amelioration in climate is also considered to be responsible for the reafforestation of Central Otago, where the 2000-year lag is considered to be a result of persisting drier climates (McGlone et al. 1995).
The timing of the establishment of *Nothofagus menziesii* in Holocene forests was different at the Letham Burn and the Longwood sites (Fig. 4). At the Longwood low-altitude site (Merrivale, 60 m) *N. menziesii* became important after about 4000 yr BP and peaks at a pollen value of 15% of the pollen sum. At the higher-altitude site (670 m) *N. menziesii* increases in representation to become dominant at 1000 yr BP, when it reaches 35% of the pollen sum. At Letham Burn *N. menziesii* becomes important at around 4200 yr BP and peaks at a value of about 60% of the pollen sum. The establishment of *N. menziesii* was approximately synchronous at Letham Burn and the Merrivale site. In Central Otago, *N. menziesii* becomes an important component of the pollen rain in higher-altitude sites after 6000 yr BP, although it does not attain the high levels of abundance shown in the Longwood or the Letham sequences. Differences in the timing of vegetation change between the sites may be related to the composition of forest refugia in the region, or the slow expansion of forests into surrounding environments.

The post-glacial establishment of *Nothofagus fusca* in the region appears to have been synchronous (Fig. 3 & 4) in the Southland region. At Letham Burn *N. fusca* type pollen increases rapidly after 700 yr BP, but is consistently represented by lower values before this period. At the Longwood site *N. fusca* type pollen rises after 1000 yr BP and peaks at 20% of the pollen sum. In Central Otago, however, *N. fusca* type pollen values increase rapidly after 3000 yr BP at the higher-altitude sites, suggesting that continuous distributions of *N. fusca* type forest occurred throughout the area in the late Holocene (McGlone et al. 1995). Although the change in forest composition from *N. menziesii* to *N. fusca* forest occurs at different times at the Southland and Central Otago sites, the change in composition occurs in all three pollen sequences and may be related to a change in climate or to natural succession of this species in higher-altitude forests. McGlone & Bathgate (1983) and McGlone et al. (1995) have attributed the rise of *N. fusca* type pollen to the combined effect of cooling climate and increased disturbance of the forests, possibly due to increased storminess, although this suggestion cannot be substantiated from the pollen evidence alone. An alternative explanation is that the rise of *N. fusca* type after 1000 yr BP represents a change in the pollen rain composition coinciding with the decrease in lower-altitude *N. menziesii* forest due to destruction or clearance by human activity.

**CONCLUSIONS**

The transformation of late-glacial vegetation from an open grassland-herbfield at 12 600 yr BP to a shrubland-bushland by 9800 yr BP, and a tall podocarp forest after 9800 yr BP, is floristically similar to other sites in Southland (McGlone & Bathgate 1983), although it is distinguished by the appearance of broadleaved shrubs at around 10 000 yr BP. The timing of the vegetation transformation from grassland to forest appears to have been approximately synchronous throughout Southland and coastal Otago. Although a similar transformation has been recorded in Central Otago (McGlone et al. 1995), forest vegetation was not established until after 7500 yr BP.

The early Holocene tall podocarp forest becomes a mixed beech-podocarp forest after 4200 yr BP as *Nothofagus menziesii* becomes a significant component of the pollen sum (40–60%). This change in forest composition also occurs at other sites in Southland and Otago at 4000 yr BP, although the change occurs earlier, at 6000 yr BP, in Central Otago.

We conclude that the character and timing of the principal vegetation changes reconstructed in this study are consistent with pollen records from the Longwood Range (McGlone & Bathgate 1983), and have some similarities to the pollen record from Swampy Hill (McIntyre & McKellar 1970). Although there are differences in both the timing and structure of late glacial to Holocene vegetation composition and change in Southland and Central Otago (Fig. 4), these can be attributed to different vegetation responses in the drier, continental climate of Central Otago. The synchronicity of the principal vegetation changes in Southland and coastal Otago during the late glacial and Holocene can be attributed to the impact of regional climate change.
ACKNOWLEDGEMENTS

We thank the University of Otago Research Committee and the Department of Conservation for financial support, Dr Matt McGlone and Neville Moar for advice and assistance with pollen identification, and Hugh Kidd and Kath Humphreys for assistance in the field.

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Received 3 December 1995; accepted 14 August 1996