Holocene vegetation change at treeline, Cropp Valley, Southern Alps, New Zealand

Matt S. McGlone

Landcare Research, Lincoln, New Zealand
mcglonem@landcareresearch.co.nz

Les Basher

Landcare Research, Nelson, New Zealand

Introduction

New Zealand treelines have been well studied over the past few decades. Peter Wardle carried out extensive observational and experimental studies of their ecology and suggested that the length and warmth of summer was critical in permitting alpine trees to make sufficient growth to survive winter (Wardle 1985a). He also showed that New Zealand treelines were low when compared with global treelines, in particular with those of southern South America, and that exotic *Pinus contorta* could grow up to 300 m above the indigenous treeline (Wardle 1985b, 2008). A later global study demonstrated that warmth of the growing season was the one universal factor controlling position of treeline (Körner and Paulsen 2004). Both Wardle (2008) and Körner and Paulsen (2004) suggested New Zealand alpine trees were incapable of persisting under the cool growing season temperatures typical of treeline sites in most other regions, a possible result of having insufficient time to evolve cool-climate adaptations.

The 20th century trend towards warmer temperatures has intensified interest in treelines, as, being temperature-sensitive, they should be responding to the ca. 1°C increase in mean annual temperatures since 1900 AD. New Zealand investigations have shown there has been little or no response (Wardle and Coleman 1992; Cullen et al. 2001), and a global synthesis (Harsch et al. 2009) indicated that, while many treelines were rising, almost as many were static.

Despite this interest, and the large extent of alpine terrain in New Zealand, relatively little palaeoecological work has been reported from sites above, at, or close to treeline. In contrast, Tasmania and southeastern Australia, in part because of Peter Kershaw's long-standing interest, have many intensively investigated subalpine to alpine sites and a wealth of information on

their treeline history (e.g. Kershaw and Strickland 1988; McKenzie 1997, 2002; Kershaw et al. 2007).

Central western districts of the Southern Alps are of great interest from both ecological and biogeographic perspectives because they lie in the western 'beech' gap of the Southern Alps. This extensive region lacks *Nothofagus*, arguably because of its exclusion by ice during the Last Glacial Maximum (McGlone et al. 1996). As the vast majority of New Zealand treelines are of *Nothofagus*, the history of a non-*Nothofagus* treeline gives a valuable additional perspective. The work presented here consists of several pollen profiles from a west-central Southern Alps alpine site. A summary diagram from this site with a line of accompanying text was included in a review of New Zealand postglacial vegetation history (McGlone 1988). Given the inherent interest in treelines, the renewed importance of understanding them in the context of climate changes, and the paucity of palaeoecological sites at treeline in New Zealand, it was thought appropriate to fully document the site and discuss it in the context of Australasian alpine results.

Environmental setting

Topology and geology

The Cropp River drains an alpine-montane basin of some 28.5 km², centred on 43°05'S, 170°58'E, on the western flanks of the central Southern Alps. This section of the Southern Alps has extremely high annual precipitation and high erosion rates. The basin is 8 km by 3.5 km and has a predominantly east-west orientation, ranging in elevation from 2140 m (Mount Beaumont) to 240 m at the confluence of the Cropp and Whitcombe Rivers (Figure 1).

Figure 1. Location map, Cropp Valley, west-central Southern Alps, New Zealand. Inset: South Island, New Zealand.

The basin is composed of high-grade metamorphic rocks of green schist to amphibolite facies. The rocks are highly fissile and commonly intensely fractured. As it lies 5–8 km southeast of the Alpine Fault, the basin is close to the maximum uplift zone of the central Southern Alps, with an estimated uplift rate of 12 mm a⁻¹ (Little et al. 2005).

Regional glacial chronology indicates that the Cropp Basin was filled with ice until about 16,000 cal BP (calibrated calendar years before 1950 AD; Gellatly et al. 1988). More recent dating of tills on the eastern side of the Southern Alps shows ice retreated after ca. 13,000 cal BP, following a late-glacial cooling during the Antarctic cold reversal between 14,900 and 12,900 cal BP (Kaplan et al. 2010). Till dated at 11,986 ± ca. 12,1000 cal BP from the middle reaches of the basin is interpreted as a subsequent late-glacial readvance (Basher and McSaveney 1989) and gives a maximum age for the postglacial surfaces. U-shaped cirques are present at the head of the Cropp River and its larger tributaries, but most of the glaciated landscape has been modified by postglacial fluvial and mass movement erosion. Slopes are steep (30–60°), valley profiles v-shaped, and stream grades steep and uneven. Regolith is thin (generally ≤2 m). A wide range of soils occurs, including yellow-brown earths, podzols, gley podzols, gley recent soils, gley soils and organic soils. Soils are generally shallow, strongly leached and infertile.

Climate

The western front ranges of the Southern Alps are characterised by frequent, heavy rainfall (>100 mm/day), annual precipitation in excess of 10,000 mm and persistent cloudiness. Mean annual rainfall of the Cropp Basin is estimated at 10,800 mm a⁻¹ (Griffiths and McSaveney 1983). Rainfall is usually well distributed throughout the year. Snow falls are frequent and may occur at any time during the year. Snow cover persists for about three months at treeline. Mean annual air temperature at Cropp Hut (865 m above sea level; 1982–1985; Tonkin and Basher 2001) is estimated at 5.5 ± 0.5°C, with a mean monthly range of 0–10.5°C, and a mean annual soil temperature (at 0.5 m depth) of 6.0 ± 0.5°C. Mean daily temperature ranges from 15°C to –5.5°C, while the absolute range is from 23.4°C to –10.1°C. Frosts may occur at any time of the year but are most common and severe in June and July.

Vegetation

Land cover of the basin ranges from permanent snow and ice to dense montane forest, and the high, often torrential, rainfall promotes extensive landslides and soil erosion in the upper reaches. Vegetation descriptions of the valley follow Norton (1983) and our own observations (Basher 1986). Below 350 m to 400 m asl, dense, mixed conifer-angiosperm forests predominate, with tall conifers (*Dacrydium cupressinum*, *Prumnopitys ferruginea* and *Podocarpus hallii*) emergent over an angiosperm canopy dominated by *Weinmannia racemosa*. From 400 m, the tall conifers gradually decline and *Weinmannia racemosa* and *Metrosideros umbellata* low forest extends up to 600 m. A *Metrosideros umbellata* belt with emergent *Libocedrus bidwillii* continues to 800 m, grading into a *Libocedrus bidwillii* forest without *Metrosideros umbellata* that interfingers with a low subalpine forest dominated by tall asterads (*Olearia colensoi*, *O. ilicifolia*, *O. lacunosa*,) and heaths (*Archeria traversii*, *D. longifolium*, *Dracophyllum traversii*) and other angiosperm small trees and shrubs (*Coprosma pseudocuneata*, *Griselinia littoralis*, *Myrsine divaricata*, *Pseudopanax colensoi*). Tall conical emergents of *Libocedrus bidwillii* and lower stature *Podocarpus hallii*, *Phyllocladus alpinus* and *Halocarpus biformis* occur in this association. This subalpine forest grades into alpine shrubland between 900 m and 1000 m asl, with a range of asterad and heath-dominated communities, *Halocarpus biformis* on old, leached soils, and *Hoheria glabrata* on young debris soils. Alpine grasslands replace shrubland at elevations between 900 m and 1400 m asl, depending on aspect, exposure and soil depth and age. *Chionochloa* spp. tussock grasses dominate well-drained sites, and species-rich communities of sedges, reeds, herbs and

prostrate shrubs and cushion plants occur on poorly drained sites. These include the creeping podocarp *Lepidothamnus laxifolium* and low-growing *Podocarpus nivalis*.

There are numerous definitions of treeline in the literature but here we use the definition of Körner and Paulsen (2004): “the connecting line between the uppermost groups of upright trees of at least 3 m in height”. By this criterion, treeline in Cropp Valley lies at about 1000 m asl. The regional treeline in this section of the western Southern Alps lies between 1200 m and 1150 m, with annual average temperatures of 5.8–6.2°C (Ellen Cieraad pers. comm. 2011). The Cropp Valley treeline is therefore somewhat lower and colder than the regional treeline, probably because of cold-air drainage from the high reaches of the basin.

Sites and methods

Site locations are given in Figure 1, site stratigraphies in Figure 2, and radiocarbon date information in Table 1. All sites were sampled from exposed faces in pits or stream exposures.

Table 1. Sample locations and radiocarbon date details. Radiocarbon calibrations were calculated using the software CALIB v 5.0.1 (1) using the Southern Hemisphere Calibration dataset SHCal04 (2) (Stuiver and Reimer 1993; McCormac et al. 2004).

Site	Grid ref. (NZMS1)	Material	Cm below surface	¹⁴ C age BP	Cal BP (median)	¹⁴ C Lab code
Site 1. Cropp Hut: 895 m	J34/439903	Peat	25	1053 ± 87	908	NZ6881
		Peat	55	2851 ± 85	2917	NZ6878
		Peat	88–90	7065 ± 90	7837	NZ6115
Site 2. Tarkus Knob: 950 m	J34/444904	Peat	175	1748 ± 38	1600	NZ5367
	J34/441905	Peat	160–162	7381 ± 70	8134	NZ5369
		Peat	170–180	8390 ± 76	9337	NZ5368
Site 3. Steadman Creek: 820 m	J34/446902	Wood	See text	10295 ± 120	12098	NZ6576

Site 1: Cropp Hut (field sample number: X8404)

A concave basin peat has formed in the distal zone of a prominent high-level alluvial cone of the north bank of Cropp River slightly upstream of the site of the former Cropp Hut (destroyed by a debris flow). The site has an elevation of 895 m and is on a forest-free subalpine valley floor. The plant communities of the general area are grassland (*Chionochloa pallens* and *C. rubra*) or grassland-low shrub on gently sloping surfaces, while steeply sloping surfaces are covered with subalpine scrub (*Coprosma* spp., *Dracophyllum uniflorum*, *Olearia lacunosa*, *Phyllocladus alpinus*, *Podocarpus nivalis*, *Senecio bennettii*) and forest (*Archeria traversii*, *Dracophyllum longifolium*, *Libocedrus bidwillii*, *Halocarpus biformis*). The peat surface is covered with *Chionochloa rubra*, *Carphe alpina*, *Celmisia glandulosa*, *Donatia novae-zelandiae* and *Oreobolus pectinatus*, and with substantial stands of the creeping podocarp, *Lepidothamnus laxifolium*. Ten samples were taken for pollen analysis and pollen results are given in Figures 3a and b.

Site 2: Tarkus Knob (field sample number X8207)

Opposite the former Cropp Hut is a prominent ice-smoothed bedrock promontory informally named Tarkus Knob (elevation at site: 950 m). A hollow along the northern margin of this feature has been in-filled by alluvium which contains two buried peat layers and is capped by a peaty soil. Three radiocarbon-dated samples for pollen analysis have been taken from two exposures along the hollow (Figure 2). The present vegetation is *Chionochloa rubra* grassland-cushion bog (*Carphe alpina*, *Celmisia glandulosa*, *Donatia novae-zelandiae*, *Lepidothamnus*

laxifolium, *Schoenus pauciflorus*). Surrounding vegetation on well-drained slopes is as described for the Cropp Hut site.

Site 3: Terminal moraine, Steadman Creek (field sample X8512)

This site (grid reference NZMS2690 J34/446902; altitude 820 m) is described in Basher and McSaveney (1989). A 30–40 m high terrace of the Cropp River consists of angular to sub-rounded boulders of schist, some with surface striations, in a sandy matrix. Decomposed twigs and logs (up to 20 cm in diameter) were found tightly embedded in a matrix of angular clasts towards the base of the section just above the bed of the river. A piece of wood was dated ($10,295 \pm 120$ BP) and the matrix surrounding the wood sampled for pollen analysis.

Site 4: Surface sample sites (field samples X8621a, b and c)

Surface samples were taken from the surface of the Tarkus and Cropp Hut sites and are included as the upper levels in those pollen diagrams. A further surface sample was taken as far down the valley as could be reached on foot, at the confluence of the Cropp River and Reckless

Figure 2. Site stratigraphies, Cropp Basin. Conventional radiocarbon ages in text boxes. The two Tarkus Knob exposures are less than 100 m apart. Note change of scale between Sites 1 and 2 and Site 3.

Torrent at an altitude of 820 m. The site was a patch of wet *Chionochloa rubra* grassland within subalpine scrub approximately 1.5 km from tall montane forest.

Pollen and spore analysis followed standard extraction procedures (dehumification in 10% KOH, digestion in 40% HF, followed by acetolysis and mounting in glycerine jelly for light microscope examination). A terrestrial pollen sum of >250 grains was used and results are presented as a percentage of the terrestrial pollen sum.

Results and discussion

Modern pollen representation (see Figures 3 and 4)

Alpine and subalpine sites derive a large proportion of their pollen rain from wind-

pollinated trees in lower altitude forests (Moar 1970; McGlone 1982; Pocknall 1982). The two uppermost sites sampled from subalpine grasslands derive ca. 35% of their pollen rain from lowland tree podocarps (*Dacrycarpus dacrydioides*, *Dacrydium cupressinum*, *Prumnopitys ferruginea*, *P. taxifolia*), whereas the lower surface sample site (Site 4, Reckless Torrent), in dense, low subalpine forest, derives only 21% of its pollen from that source. *Metrosideros* and *Weinmannia*, the primary canopy species of the high montane forest in the lower reaches of the basin, make up <5% of the pollen rain. Although virtually absent from the upper altitude forests, two trees, *Ascarina lucida* and *Quintinia serrata*, and a liana, *Ripogonum scandens*, are also registered. Grass and subalpine scrub species (asterads, *Coprosma*, *Dracophyllum*, *Halocarpus*, *Myrsine*, *Phyllocladus*) average ca. 30% for the two upper sites, but ca. 65% for the lower. Although never making up a substantial proportion of the pollen rain, upland herbs, cushion plants and prostrate shrubs are represented. Although *Libocedrus bidwillii* is prominent in the upland low forest of the basin and wind-pollinated, it contributes surprisingly little to the pollen rain, averaging only ca. 1%.

Steadman Creek, till exposure (Figure 4)

The Cropp till at 850 m is attributed to a late-glacial advance at ca. 12,100 cal BP, during which a glacier occupied most of the upper basin (Basher and McSaveney 1989). The wood was incorporated into the advance as the ice moved down valley. The pollen is derived from silt associated with the wood fragments and, as it was reworked by or deposited directly on the ice, is not directly comparable to that from the peat sequences. Exceptionally high levels of *Hoheria* (22%) and abundant *Coprosma*, asterads and grass indicate an open low subalpine forest-shrubland, typical of what might be expected on disturbed sites within the basin at the present day. *Hoheria glabrata* currently does not extend more than about 200 m above the altitude of the till exposure and we conclude that subalpine low forest must have been close to its current limit during the advance. Nevertheless, a number of present-day components of the basin vegetation are missing from the pollen spectrum, including *Dracophyllum*, *Halocarpus* and *Libocedrus*, and lowland conifer forest trees make up only 6% of the pollen rain, rather than the 30% average for the Holocene sites. *Metrosideros* and *Weinmannia* are at trace levels only. Two broad conclusions can be made.

First, the Cropp glacier must have advanced down valley at a time when mean annual temperatures were close to those of the present. *Hoheria glabrata* forest does not extend higher than 1050 m in central Westland (Wardle 1991) and thus the maximum depression in mean annual temperature relative to the present can have only been of the order of 1.2°C. However, as the wood was included within the till and not over-ridden, it is likely the *Hoheria* trees grew up-slope of the site. Given the steep gradient of the river, the *Hoheria* forest is likely to have grown at 900–1000 m altitude, that is, at its current limit.

The second conclusion is that the lowland to montane forest conifer emergents that provide more than 30% of the pollen rain at present must have been very much reduced in extent. This inference is supported by the pollen results from the extensive Okarito Pakihi mire at 70 m asl approximately 63 km to the southwest of the Cropp Basin (Newnham et al. 2007), where emergent conifers made up ca. 30% of the pollen rain at 12,000 cal BP, versus 95% during the Holocene. We therefore have the somewhat paradoxical results that woody vegetation was growing close to or at its present limit, while the upper limit to montane forest appears to have been lower and conifer forest in general much less abundant than now.

Cropp Hut–Tarkus Knob peat sequences (Figures 3, 4 and 5)

Cropp Hut and Tarkus Knob peats are in close proximity and both are currently in grassland vegetation, differing in altitude by 50 m. Their pollen percentages at matched time intervals are

Figure 3a. Cropp Hut (Site 1). Percentage pollen and spore diagram: trees and tree ferns. Pollen sum: dryland trees, shrubs and herbs.

Figure 3b. Cropp Hut (Site 1). Percentage pollen and spore diagram: shrubs, herbs, fern and fern allies. Pollen sum: dryland trees, shrubs and herbs.

Tarkus Knob (Site 1), Steadman Creek (Site 3) & Reckless Torrent surface sample (Site 4)

Figure 4. Surface samples: Reckless Torrent, (820 m); Tarkus Knob (950 m). Three dated peat samples: Tarkus Knob (Site 2) buried peats; Steadman Till (Site 3), silt associated with *Hoheria* wood fragments. Percentage pollen and spore diagram (major types only). Pollen sum: dryland trees, shrubs and herbs.

close, and they can be for most purposes treated as a single record. To get a generalised view of changes, a composite diagram for the arboreal pollen has been constructed from the Cropp Hut, Tarkus Knob and Steadman sequences (Figure 5).

Local vegetation cover appears to have been remarkably uniform throughout the Holocene. Grass pollen, dominated by *Chionochloa*, asterads, *Coprosma Dracophyllum*, *Myrsine*, and sedges and alpine herbs are consistently present at levels suggesting little or no change in the local vegetation structure from the current day (Figures 3 and 4).

The oldest sample (Tarkus Knob site; 9337 cal BP) is ca. 2500 years younger than the till. Independent confirmation of the age of this sample is provided by the trace levels of *Nothofagus* versus the 1–5% levels for those younger than 9000 cal BP. *Nothofagus* became the dominant forest cover between 8200 and 7500 cal BP in the Cass Basin, 70 km to the east (McGlone et al. 2004), and this is the only likely source for this pollen type. The basal sample from the Cropp Hut peat section is younger than 8000 cal BP and has a significant *Nothofagus* representation.

The contribution of lowland conifer pollen rose from 13% to 20–25% by 7500 cal BP and reached present day levels of 30–40% by 6000 cal BP (Figure 5). High-altitude montane

Figure 5. Summary composite percentage pollen diagram (Cropp, Tarkus, Steadman). Lowland pollen types: *Dacrycarpus dacrydioides*, *Dacrydium cupressinum* and *Prumnopitys* spp. Upland pollen types: *Libocedrus*, *Phyllocladus*, *Podocarpus*, *Halocarpus*, *Metrosideros*, *Weinmannia* and *Quintinia*. Note: lowland pollen types are those from emergent wind-pollinated trees that dominate the lowlands; the upland types are those that are known to occur either near the Cropp sites or in the upper montane forest (regardless of whether they also occur further downslope).

forest types expanded from 8% to 12% between 9500 and 4000 cal BP, but did not reach current levels of 18% until 2400 cal BP, which is when *Libocedrus bidwillii* became abundant within the basin. Tree-fern spores are dominated by *Cyathea smithii* type (which includes the short subalpine *C. colensoi*) at levels which suggest wind dispersal from montane forests but its percentage representation does not change in the course of the Holocene.

Quintinia is the last of the montane forest species to be registered at the site (between 1600 and 900 cal BP). This canopy tree, characteristic of infertile soils in central Westland, is confined to scattered patches in the south of the district, and does not occur in south Westland. Wardle (1988) suggested that its distribution reflects a slow movement south from refugia in north Westland at the end of the last glaciation. However, it was present at Bell Hill, north Westland, before 10,400 cal BP (Moar 1971), but even there did not become abundant until ca. 3500 cal BP (Pocknall 1980). A 7000-year migration lag for local spread seems improbable. It is far more likely that *Quintinia* was present throughout its current range at the end of the Last Glacial Maximum, as suggested by its trace occurrences then at Okarito Pakihi (Newnham et al. 2007), but remained uncommon until some aspect of the climate or soils became more favourable for the tree in the course of the late Holocene.

Climate inferences

As discussed in regard to *Quintinia*, there is no reason to suspect any of the dominant tree species were affected by migration lags: *Weinmannia*, *Metrosideros*, *Quintinia* and *Libocedrus* have small, wind-dispersed seeds and the podocarp trees have bird-dispersed fleshy fruits. While soil requirements may have been a constraint for some species, under the mild, high-rainfall environment of Cropp Basin soils mature and become podzolized extraordinarily quickly, and landslides caused by heavy rain or earthquakes are a constant source of rejuvenated surfaces within the basin (Tonkin and Basher 2001). We therefore argue that the most probable explanation for the Holocene vegetation changes is the direct or indirect consequences of changing climate. Given that the Cropp Basin is directly in the path of the rain-bearing westerlies and has an enormous surplus of well-distributed precipitation far beyond the growth requirements of the vegetation, it further seems unlikely that changes in rainfall would have major effects on the vegetation cover. For that reason, we focus on changes in temperature and seasonality.

A marine-core alkenone sea-surface temperature record 200 km west of the Cropp Basin shows that temperatures peaked in the later late glacial, and were about 1.5°C warmer than present at 12,000 cal BP (Barrows et al. 2007). Pollen-based transfer functions show mean annual temperatures in South Island sites to have been warmer than now from about 12,000 cal BP (Wilmshurst et al. 2007). The occurrence of tree-sized *Hoheria glabrata* high within the Cropp catchment at 12,000 cal BP, close to its upper limit, implies that temperatures during the growing season were within 1°C of those of the present. Warmer than present climates in the Cropp Basin by 12,000 cal BP therefore seem highly probable.

Nevertheless, some observations do not fit a scenario of summer temperatures at or above current values. In the cloudy, high-precipitation, mild climates of the western flank of the Southern Alps, winter cold is not a significant factor except in valley bottoms exposed to cold-air drainage (Leathwick et al. 2003). It follows that regional alpine treelines are controlled by growing-season warmth, as demonstrated by Körner and Paulsen (2004). If summer temperatures were 1.5°C warmer than now, vegetation zones should have been some 250 m higher and the upper limit to closed montane forest at ca. 850–1000 m asl. Forest would have surrounded the Cropp sites. The absence of montane forest trees, and conifers in particular, from the catchment in the early Holocene demonstrates this did not happen. New Zealand glaciers in the central Southern Alps are much more responsive to summer ablation than

winter precipitation (Anderson and Mackintosh 2006). The fact that a glacier advanced beyond Holocene limits to fill the upper Cropp Valley and produce the Cropp till is therefore also incompatible with summer temperatures warmer than those of the present.

Cool summers but higher than present mean annual temperatures necessarily imply much warmer and shorter winters. In temperate latitudes, warm winters are important in the lowlands as they permit frost-sensitive species to flourish. In contrast, at treeline, warm winters are largely irrelevant or even detrimental, as warm temperatures may break dormancy and increase frost. Cool summers and warm winters create an intensely oceanic environment which is understood to further limit tree growth through restricting photosynthesis in summer and increasing metabolic energy expenditure in winter (Stevens and Fox 1991; Crawford 2000). Tall podocarps were less common than now during this intensely oceanic phase in the nearby lowlands at Okarito (Newnham et al. 2007) and it is possible that they were also restricted by cool summers. We conclude that in the late glacial and early Holocene, a warm-winter/cool-summer regime depressed altitudinal forest zones and may have had a disproportionate influence on tall conifer trees.

The Holocene vegetation sequence within the Cropp Valley (Figure 5) is best interpreted as a response to steady increases in summer temperature. By 8200 cal BP, upper montane forests were present in the lower reaches of the valley. By 2500 cal BP, *Libocedrus bidwillii* had occupied the upper part of valley, and lowland-forest pollen rain peaked about the same time, suggesting that upslope movement of forest zones had not reached current altitudes until then.

Other New Zealand sites near treeline or in montane settings support the scenario that summer temperatures have been rising in the course of the Holocene. Pollen and macrofossil evidence from subantarctic Auckland and Campbell Islands indicates that forest did not reach current extent until 6000 cal BP, and may have continued to extend upslope into the late Holocene (McGlone 2002; McGlone et al. 2010). In the Garvie Mountains (Central Otago), high-altitude grassland was abruptly replaced by coniferous forest at 8300 cal BP (McGlone et al. 1995). Pollen sites close to treeline in northwest Nelson suggest late-Holocene spread of subalpine *Nothofagus* forest into low woody vegetation and grassland (Shulmeister et al. 2003). In the North Island, in an altitudinal sequence of organic soil pollen sites across treeline (1140–1470 m asl) on the isolated massif of Mount Hauhungatahi, Tongariro, low conifer forest rose to dominance at ca. 9700 cal BP, but the current tall *Nothofagus-Libocedrus* forest spread only from ca. 8000 cal BP, and was not dominant until several thousand years later (Horrocks and Ogden 2000).

A forest ecosystem process model has been used in inverse mode to explore early Holocene climate scenarios based on pollen and macrofossil data from Cass, an intermontane site 70 km east of the Cropp Valley at 600 m altitude (McGlone et al. 2011). Best fit between early Holocene vegetation and climate was obtained when summers were no warmer than present but winters substantially warmer. If early Holocene summers were set at 0.5°C cooler than present, and compensated for by much warmer winters to achieve an overall warmer climate (+1.5°C), suitable matches could also be made. Annual ocean-surface warmth and terrestrial summer cooling in the early Holocene can thus be reconciled.

The mountain ranges of Tasmania and the southeastern coast between 43°S and 30°S provide the closest comparable sites in Australia to Cropp Valley. Changes in Australian upland regions are complicated by major alterations in rainfall patterns which result in asynchronous vegetation change between sites (Donders et al. 2007). Nevertheless, there is agreement that summer temperatures and forest cover peaked in the mid Holocene, as early recognised by Kershaw (1988). At the northern edge of the temperate forest zone in New South Wales, at high-altitude (1200–1500 m asl) sites on Barrington Top, current forest was established by 10,000 cal BP and vegetation typical of warmer and moister conditions was widespread over

the plateau between 7500 and 4000 years ago (Dodson et al. 1986). In Kosciuszko National Park in New South Wales, sites at treeline had grassy alpine herbfields until ca. 12,500 cal BP and *Eucalyptus* increased to form similar communities to those at current treeline by 7500 cal BP. Subalpine woody communities reached maximum development between 6000 and 3000 cal BP (Martin 1986, 1999). It is possible that drier conditions earlier in the Holocene may have delayed this maximum. In south-central Victoria, forest reached current levels at several high-altitude sites after 11,500 cal BP (McKenzie 1997, 2002; Kershaw et al. 2007), but wet *Eucalyptus* forests and *Nothofagus* did not achieve maximum extent until ca. 7000 cal BP (McKenzie 2002). Changes after ca. 4500 cal BP are complicated by the onset of ENSO and changing precipitation, but the decline in moisture-loving *Nothofagus* may have resulted from the transpiration stress of increasing summer temperatures. In Tasmania, maximum treeline altitude and warmest growing-season temperatures appear to have been achieved by 7000 cal BP (Anker et al. 2001; Fletcher and Thomas 2007).

In summary, Australian results are consistent with those from the Cropp Valley in that they show treelines were lower than now before 11,500 cal BP and current treelines mostly formed only after 7000 cal BP.

Schaefer et al. (2009) note that Holocene glacier advances in the central Southern Alps of New Zealand diminish in volume towards the present. They suggest this is largely due to increased summer ablation, consistent with our claim that treelines have risen and summers warmed in the course of the Holocene. It follows then that ocean-surface temperatures, which fall during the mid-to-late Holocene as treelines rise (Barrows et al. 2007), must reflect substantial winter cooling.

Conclusions

The latter part of the late glacial and early Holocene in New Zealand was characterised by low treelines relative to the present. In the upper Cropp Valley, although shrubs and small trees extended up to current treeline, the current montane-alpine forest was absent, including the conifer *Libocedrus*. Similar patterns of change are seen at near-treeline sites throughout New Zealand, usually involving the late spread of *Nothofagus* forest into early Holocene tall shrubland. We conclude that highly oceanic environments during the late glacial-early Holocene period, characterised by warm winters and cool summers, disproportionately affected trees in the montane to alpine zones. There is a great deal of similarity in timing between the New Zealand montane-alpine vegetation sequences over the late glacial and Holocene, and those of the mountainous areas of Tasmania and southeastern Australia. This probably reflects a common response to a hemispheric temperature trend. Although increasing precipitation after a drier early Holocene is often suggested as a contributory factor to changing treelines at Australian sites, this is far less likely to have been an issue at New Zealand alpine sites.

We suggest that during the latter half of the late glacial and the early Holocene, cool summers, warm winters and generally drier than present conditions prevailed in southeastern Australia and New Zealand. Summers shortened but became warmer, while winters lengthened and cooled in the course of the Holocene. As a consequence, apparently contradictory trends emerged in the mid-to-late Holocene: lowland forests changed character, losing frost-sensitive components as winters became cooler, while alpine trees began to replace previous low-growing shrublands in response to warmer summers. The decline from peak summer warmth in montane-alpine regions noted in Australia after 5000–4000 cal BP is not as obvious in New Zealand records.

Acknowledgements

We thank Neville Moar and Janet Wilmshurst for their comments on a draft of the manuscript, and Rewi Newnham and Geoffrey Hope for their reviews. MSM would also like to record his gratitude to Peter Kershaw for his encouragement and support over many years.

References

- Anderson, B. and Mackintosh, A. 2006. Temperature change is the major driver of late-glacial and Holocene glacier fluctuations in New Zealand. *Geology* 34:21-124.
- Anker, S.A., Colhoun, E.A., Barton, C.E., Peterson, M. and Barbetti, M. 2001. Holocene vegetation and paleoclimatic and paleomagnetic history from Lake Johnston, Tasmania. *Quaternary Research* 56:264-274.
- Barrows, T.T., Lehman, S.J., Fifield, L.K. and De Deckker, P. 2007. Absence of cooling in New Zealand and the adjacent ocean during the Younger Dryas Chronozone. *Science* 318:86-89.
- Basher, L.R. 1986. Pedogenesis and erosion history in a high rainfall, mountainous drainage basin – Cropp River, New Zealand. Unpublished doctoral thesis, Department of Soil Science. Lincoln College, University of Canterbury.
- Basher, L.R. and McSaveney, M.J. 1989. An early Aranuiian glacial advance at Cropp River, central Westland, New Zealand. *Journal of the Royal Society of New Zealand* 19:263-268.
- Crawford, R.M.M. 2000. Ecological hazards of oceanic environments. *New Phytologist* 147:257-281.
- Cullen, L.E., Stewart, G.H., Duncan, R.P. and Palmer, J.G. 2001. Disturbance and climate warming influences on New Zealand *Nothofagus* tree-line population dynamics. *Journal of Ecology* 89:1061-1071.
- Dodson, J.R., Greenwood, P.W. and Jones, R.L. 1986. Holocene Forest and Wetland Vegetation Dynamics at Barrington Tops, New South Wales. *Journal of Biogeography* 13:561-585.
- Donders, T.H., Haberle, S.G., Hope, G., Wagner, F. and Visscher, H. 2007. Pollen evidence for the transition of the eastern Australian climate system from the post-glacial to the present-day ENSO mode. *Quaternary Science Reviews* 26:1621-1637.
- Fletcher, M.S. and Thomas, I. 2007. Holocene vegetation and climate change from near Lake Pedder, south-west Tasmania, Australia. *Journal of Biogeography* 34:665-677.
- Gellatly, A.F., Chinn, T.J.H. and Röthlisberger, F. 1988. Holocene glacier variations in New Zealand – a review. *Quaternary Science Reviews* 7:227-242.
- Griffiths, G.A. and McSaveney, M.J. 1983. Hydrology of a basin with extreme rainfalls – Cropp River, New Zealand. *New Zealand Journal of Science* 26:293-306.
- Harsch, M.A., Hulme, P.E., McGlone, M.S. and Duncan, R.P. 2009. Are treelines advancing? A global meta-analysis of treeline response to climate warming. *Ecology Letters* 12:1040-1049.
- Horrocks, M. and Ogden, J. 2000. Evidence for Lateglacial and Holocene tree-line fluctuations from pollen diagrams from the Subalpine zone on Mt Hauhungatahi, Tongariro National Park, New Zealand. *Holocene* 10:61-73.
- Kaplan, M.R., Schaefer, J.M., Denton, G.H., Barrell, D.J.A., Chinn, T.J.H., Putnam, A.E., Andersen, B.G., Finkel, R.C., Schwartz, R. and Doughty, A.M. 2010. Glacier retreat in New Zealand during the Younger Dryas stadial. *Nature* 467:194-197.
- Kershaw, A.P. 1988. Australasia. In: Huntley, B. and Webb III, T. (eds), *Vegetation History*, pp. 237-306. Dordrecht: Kluwer Academic Publishers.
- Kershaw, A.P., McKenzie, G.M., Porch, N., Roberts, R.G., Brown, J., Heijnis, H., Orr, M.L.,

- Jacobsen, G. and Newallt, P.R. 2007. A high-resolution record of vegetation and climate through the last glacial cycle from Caledonia Fen, southeastern highlands of Australia. *Journal of Quaternary Science* 22:481-500.
- Kershaw, A.P. and Strickland, K.M. 1988. The development of alpine vegetation on the Australian mainland. In: Good, R. (ed), *The Scientific Significance of the Australian Alps: the proceedings of the first Fenner Conference on the Environment*, pp. 113-125. Canberra: Australian Alps National Parks Liaison Committee and the Australian Academy of Science.
- Körner, C. and Paulsen, J. 2004. A world-wide study of high altitude treeline temperatures. *Journal of Biogeography* 31:713-732.
- Leathwick, J.R., Wilson, G., Rutledge, D., Wardle, P., Morgan, F., Johnston, K., McLeod, M. and Kirkpatrick, R. 2003. *Land Environments of New Zealand*. Auckland: David Bateman.
- Little, T.A., Cox, S., Vry, J.K. and Batt, G. 2005. Variations in exhumation level and uplift rate along the oblique-slip Alpine fault, central Southern Alps, New Zealand. *Geological Society of America Bulletin* 5-6:707-723.
- Martin, A.R.H. 1986. Late Glacial and Holocene alpine pollen diagrams from the Kosciuszko National Park, New South Wales, Australia. *Review of Palaeobotany and Palynology* 47:367-409.
- Martin, A.R.H. 1999. Pollen analysis of Digger's Creek Bog, Kosciuszko National Park: Vegetation history and tree-line change. *Australian Journal of Botany* 47:725-744.
- McCormac, F.G., Hogg, A.G., Blackwell, P.G., Buck, C.E., Higham, T.F.G. and Reimer, P.J. 2004. SHCal04 Southern Hemisphere calibration, 0-11.0 cal kyr BP. *Radiocarbon* 46:1087-1092.
- McGlone, M.S. 1982. Modern pollen rain, Egmont National Park, New Zealand. *New Zealand Journal of Botany* 20:253-262.
- McGlone, M.S. 1988. New Zealand. In: Huntley, B. and Webb III, T. (eds), *Vegetation History*, pp. 557-599. Dordrecht: Kluwer Academic Publishers.
- McGlone, M.S. 2002. The late Quaternary peat, vegetation and climate history of the southern oceanic islands of New Zealand. *Quaternary Science Reviews* 21:683-707.
- McGlone, M.S., Hall, G.M.J. and Wilmshurst, J.M. 2011. Seasonality in the early Holocene: Extending fossil-based estimates with a forest ecosystem process model. *The Holocene* 21:517-526.
- McGlone, M.S., Mark, A.F. and Bell, D. 1995. Late Pleistocene and Holocene vegetation history, central Otago, South Island, New Zealand. *Journal of the Royal Society of New Zealand* 25:1-22.
- McGlone, M.S., Mildenhall, D.C. and Pole, M.S. 1996. History and palaeoecology of New Zealand *Nothofagus* forests. In: Veblen, T.T., Hill, R.S. and Read, J. (eds), *The Ecology and Biogeography of Nothofagus forest*, pp. 83-130. New Haven: Yale University Press.
- McGlone, M.S., Turney, C.S.M. and Wilmshurst, J.M. 2004. Late-glacial and Holocene vegetation and climatic history of the Cass Basin, central South Island, New Zealand. *Quaternary Research* 62:267-279.
- McGlone, M.S., Turney, C.S.M., Wilmshurst, J.M., Renwick, J. and Pahnke, K. 2010. Divergent land and ocean temperature trends in the Southern Ocean over the past 18,000 years. *Nature Geoscience* 3:622-626.
- McKenzie, G.M. 1997. The late Quaternary vegetation history of the south-central highlands of Victoria, Australia. 1. Sites above 900 m. *Australian Journal of Ecology* 22:19-36.
- McKenzie, G.M. 2002. The late Quaternary vegetation history of the south-central highlands of Victoria, Australia. II. Sites below 900 m. *Austral Ecology* 27:32-54.
- Moar, N.T. 1970. Recent pollen spectra from three localities in the South Island, New Zealand. *New Zealand Journal of Botany* 8:210-221.

- Moar, N.T. 1971. Contributions to the Quaternary history of the New Zealand flora. 6. Aranui pollen diagrams from Canterbury, Nelson, and north Westland, South Island. *New Zealand Journal of Botany* 9:80-145.
- Newnham, R.M., Vandergoes, M.J., Hendy, C.H., Lowe, D.J. and Preusser, F. 2007. A terrestrial palynological record for the last two glacial cycles from southwestern New Zealand. *Quaternary Science Reviews* 26:517-535.
- Norton, D.A. 1983. Population dynamics of subalpine *Libocedrus bidwillii* forests in the Cropp River Valley, Westland, New Zealand. *New Zealand Journal of Botany* 21:127-134.
- Pocknall, D.T. 1980. Modern pollen rain and Aranui vegetation from Lady Lake, North Westland, New Zealand. *New Zealand Journal of Botany* 18:275-284.
- Pocknall, D.T. 1982. Modern pollen spectra from mountain localities, South Island, New Zealand. *New Zealand Journal of Botany* 20:361-371.
- Schaefer, J.M., Denton, G.H., Kaplan, M., Putnam, A., Finkel, R.C., Barrell, D.J.A., Andersen, B.G., Schwartz, R., Mackintosh, A., Chinn, T. and Schluchter, C. 2009. High-Frequency Holocene Glacier Fluctuations in New Zealand Differ from the Northern Signature. *Science* 324:622-625.
- Shulmeister, J., McLea, W.L., Singer, C., McKay, R.M. and Hosie, C. 2003. Late Quaternary pollen records from the Lower Cobb Valley and adjacent areas, North-West Nelson, New Zealand. *New Zealand Journal of Botany* 41:503-533.
- Stevens, G.C. and Fox, J.F. 1991. The causes of tree line. *Annual Review of Ecology and Systematics* 22:177-191.
- Stuiver, M.P. and Reimer, P.J. 1993. Extended 14C data base and revised CALIB 3.0 14C age calibration program. *Radiocarbon* 35:215-230.
- Tonkin, P.J. and Basher, L.R. 2001. Soil chronosequences in subalpine superhumid Cropp Basin, western Southern Alps, New Zealand. *New Zealand Journal of Geology and Geophysics* 44:37-45.
- Wardle, P. 1985a. New Zealand timberlines. 3. A synthesis. *New Zealand Journal of Botany* 23:263-271.
- Wardle, P. 1985b. New Zealand timberlines. 1. Growth and survival of native and introduced tree species in the Craigieburn Range, Canterbury. *New Zealand Journal of Botany* 23:219-234.
- Wardle, P. 1988. Effects of glacial climates on floristic distribution in New Zealand. 1. A review of the evidence. *New Zealand Journal of Botany* 26:541-555.
- Wardle, P. 1991. *Vegetation of New Zealand*. Cambridge: Cambridge University Press.
- Wardle, P. 2008. New Zealand forest to alpine transitions in global context. *Arctic Antarctic and Alpine Research* 40:240-249.
- Wardle, P. and Coleman, M.C. 1992. Evidence for rising upper limits of 4 native New Zealand forest trees. *New Zealand Journal of Botany* 30:303-314.
- Wilmshurst, J.M., McGlone, M.S., Leathwick, J.R. and Newnham, R.M. 2007. A pre-deforestation pollen-climate calibration model for New Zealand and quantitative temperature reconstructions for the past 18 000 years BP. *Journal of Quaternary Science* 22:535-547.