Microclimate characteristics of alpine bluff ecosystems of New Zealand's South Island, and implications for plant growth

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Abstract: Descriptions of alpine climate in areas of high solar radiation are increasing, but there is a paucity of microclimate data for shaded alpine rock bluff ecosystems. These shaded systems are important because they represent plant habitats that are subject to unique climate drivers within the alpine ecosystem, but which are poorly characterised globally. We describe microclimate characteristics, including photosynthetically active radiation (PAR), atmospheric vapour pressure deficit, and air (T_{air}) and soil temperature (T_{soil}) for three shaded alpine bluff sites at 1370–1800 m altitude on the South Island of New Zealand that support a diverse flora, including obligate shaded-bluff species of *Pachycladon* (Brassicaceae). Maximum instantaneous PAR at all study sites was generally < 100 µmol m^{-2} s^{-1}, or approximately 5% of full sunlight. Monthly mean T_{air} at the lowest altitude site ranged between −1.1°C and +13.7°C and declined to between −4.2°C and +7.6°C at the highest altitude site. T_{soil} covaried with T_{air}, but with less extreme temperatures. The low-incident PAR of these bluff ecosystems suggests leaf temperatures at these sites are primarily regulated by air temperature and not by incident radiation. This study emphasises the need for information on the physiological response of these alpine plants to climate drivers, particularly in relationship to photosynthetic carbon uptake and respiratory carbon loss.

Keywords: alpine microclimate, bluff vegetation, New Zealand, *Pachycladon*, photosynthesis; shade tolerance

Introduction

There is a long-standing interest in alpine climate and its effects on plant life at the highest altitudes (Schimper 1903; Körner 2003), but local measurements are difficult to obtain due to the harsh weather of the alpine zone. Reports describing alpine climate in New Zealand exist in the literature (Morris 1965; McCracken 1980; Körner et al. 1986; Mark et al. 2006, 2008), but these reflect the climate of the open, sunny habitat where much of the alpine flora lives. Despite these efforts, there remains a paucity of climate data for shaded, alpine rock bluff ecosystems with polar aspect (i.e. between 135° and 225° true north). Topographical analysis of areas above treeline in the South Island of New Zealand revealed that of those with slope > 72° – a benchmark for bluff habitat (Speight 1990) – 33.3% have polar exposure (Landcare Research, unpubl. results), and thus represent an important habitat within the New Zealand alpine zone (Fig. 1). Further, this shaded alpine habitat is found in temperate mountain ranges globally, as in North (Kimball et al. 2004) and South America (Ferreyra et al. 1998), but is less common in equatorial alpine systems due to the influence of latitude on solar elevation angles (Barry 1981). Over 800 plant species occur in the New Zealand alpine zone (PBH, unpubl. data), with a considerable number being found on shaded bluffs. These include the obligate shaded-bluff alpine species of *Pachycladon* (e.g. *P. enysii*, *P. fastigiatum*, and *P. stellatum*) (Heenan & Mitchell 2003), as well as other more generalist species such as *Blechnum penna-marina*, *Koeleria cheesemanii*, *Leucogenes grandiceps*, and *Ourisia caespitosa*[1]. A better understanding of the physical environment of the

shaded bluff habitat will aid in understanding the physiological ecology of these plants in the current climate regime and in possible future climate scenarios. This is especially important for the obligate shaded-bluff species of *Pachycladon*, which are part of ongoing evolutionary and genetic studies (Heenan et al. 2002; Joly et al. 2009; Voelckel et al. 2010).

Leaf temperature is a strong regulator of metabolic processes, and is usually determined in alpine plants by solar radiation, slope and exposure, and plant physiognomy (Körner 2003). Leaf energy balance and temperature are maintained in

Figure 1. Alpine areas often comprise steep, shaded and polar-facing bluffs such as on Turks Head, Inland Kaikoura Range, with sunny bluffs of equatorial exposure in the right foreground (Photo Kerry Ford).

[1] Plant names follow Allan Herbarium (2002–2010).

plant systems by balancing the interception of solar and reflected radiation, the absorption of some portion of that radiation, and the dissipation of excess energy through sensible and latent heat flux, in air and via transpiration respectively (Jones 1992). Growth habitat dictates the radiation environment, and both slope and exposure can modulate the influence of incident radiation by increasing or decreasing sensible heat flux from plant tissues through exposure to or shelter from wind (Grace 1977). Many, if not most, alpine plants inhabit well-illuminated habitat during snow-free periods, often in sheltered areas that reduce exposure to wind (Bell & Bliss 1979). Plants can also influence their microclimate, and in the alpine zone often exhibit physiognomic characteristics such as prostrate or rosette morphology that enhance the boundary layer and help regulate leaf temperatures (Halloy 1990). In the Southern Hemisphere, plant communities inhabiting steep, polar-exposed, shaded alpine bluffs face unique environmental challenges, but descriptions of the temperature and light gradients in these systems over annual timescales are lacking.

Radiation and temperature co-regulate plant carbon balance through their influence on photosynthetic carbon uptake and respiration. The low stature of herbaceous alpine plants and the common occurrence of snow cover buffer plants from temperature extremes, but can also reduce radiation and, consequently, photosynthesis. In response, high altitude plants exhibit adaptive physiological strategies. For example, the thermal optima of photosynthesis (A_o) in unshaded alpine plants are not different than A_o in low altitude plants (Körner 2003), but are lower in shaded alpine plants (Pisek et al. 1973). This investigation into the interaction between light and temperature on alpine plant carbon dynamics showed an adaptive capacity in *Ranunculus glacialis* where A_o was reduced to 16.5°C when plants were measured under low PAR compared with an A_o of 22.5°C under high light conditions, a pattern repeated in *Geum* and some subalpine conifers (Pisek et al. 1973). Further, photosynthetic capacity is maintained at higher levels in alpine plants when temperature is reduced to half of A_o (Körner & Diemer 1987), a trend frequently observed in cool-grown plants (Silim et al. 2010). These differences among cool-grown plants are due to greater investment in many photosynthetic enzymes and other biochemical shifts (Sage & Kubien 2007), but also influence respiratory processes.

The relationship between leaf mitochondrial respiration (R_d) and temperature is complex, and has important implications for modulating carbon losses over different timescales. R_d increases during short-term (minutes to hours) temperature increases but acclimatises during extended temperature excursions (i.e. days to months) in a manner that largely ameliorates excess carbon losses compared with lower-growth temperature regimes (Atkin & Tjoelker 2003; Atkin et al. 2005; Ow et al. 2008), though some evidence supports a reduced respiratory acclimation response in alpine taxa when compared with congeneric lowland species (Atkin et al. 2006). R_d is generally higher in cool-grown plants, due largely to high investment in photosynthetic enzymes (Atkin & Tjoelker 2003; Silim et al. 2010), and thus carbon losses during winter respiration are not negligible and could consume substantial carbohydrate reserves through extended snow-cover periods where carbon uptake is limited (Körner 2003). Yet despite the harsh climate of the European Alps, studies of the net carbon balance of alpine *Ranunculus* and *Geum* leaves showed that carbon investments during tissue development resulted in multiplicative carbon gains when integrated over the life of the leaf, with populations in sites with high irradiance exhibiting

the most positive carbon budgets (Diemer & Körner 1996).

Because climate drivers are often at the physiological limits in the alpine zone, characterising the physical environment of these shaded, polar-exposed, alpine bluffs is needed to better understand the ecophysiology of some members of the New Zealand alpine flora. In this study, we measured photosynthetically active radiation (PAR), air temperature (T_{air}), soil temperature (T_{soil}), and relative humidity (RH) at three alpine microsites inhabited by *Pachycladon* populations, across one year, to ascertain the range of these key climate drivers of plant growth.

Materials and methods

Micrometeorological stations were installed at three field sites in the mountains of the South Island, New Zealand, between November 2008 and January 2009 and data collection commenced immediately following station installation at each site. The alpine *Pachycladon* generally grow in the crevices of rock bluffs that are often oriented vertically (slope > 72°) relative to adjacent scree fields, and plants are found up to 4 m up these bluff habitats. Stations at each site were situated in direct proximity to the plants, and were fixed to rock bluffs adjacent to *Pachycladon* individuals (i.e. between 0.25 and 4 m above the scree surface). The alpine *Pachycladon* are small, herbaceous plants generally < 120 mm high in stature and are frequently covered with snow and/or ice during cool-season months. The Yeo Stream, the lowest altitude site, is located in the Inland Kaikoura Range, Marlborough (42° 9.070S, 173° 15.893E; 1380 m a.s.l.), and is a south-east-facing greywacke bluff, home to a population of *Pachycladon stellatum* plants. At the Yeo Stream site the sensors of the micrometeorological station were situated on a rock bluff between 1 and 1.5 m above the scree surface. Ohau, the intermediate-altitude site, is located in the Barrier Range, Ohau Skifield, South Canterbury (44° 13.276S, 169° 46.832E; 1730 m a.s.l.), and is a south-west-facing greywacke bluff inhabited by a population of *Pachycladon fastigiatum* plants. At the Ohau site the sensors of the micrometeorological station were situated c. 4 m above the scree surface on a rock ledge where *P. fastigiatum* plants live. Mt Hutt, the highest altitude site in this study, is located near the Mt Hutt Skifield, Mt Hutt Range, mid-Canterbury (43° 28.947S, 171° 31.460E; 1800 m a.s.l.), and is a polar-exposed greywacke bluff inhabited by *Pachycladon enysii* plants. At this site the sensors were arrayed on a broad rock escarpment no more than 0.25 m above ground level.
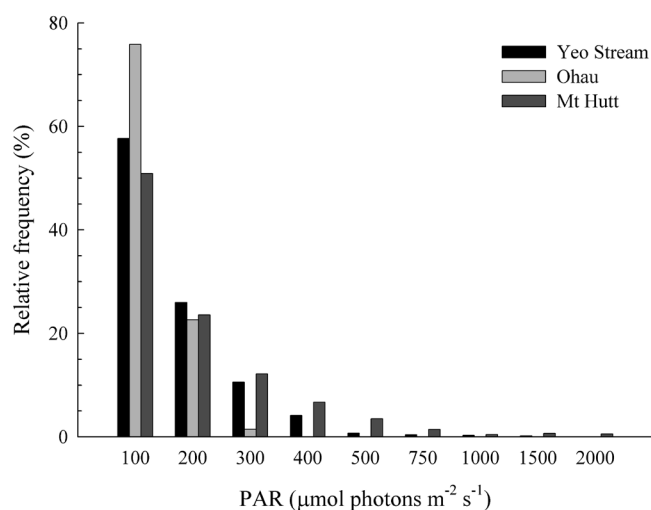
All measurements at each site were collected using a HOBO Micro station logger (H21-002; Onset Computer Corp., MA, USA) coupled to factory-calibrated HOBO Smart sensors. All sensors were situated to mimic the environment immediately surrounding plants, and were located within 1 m of *Pachycladon* plants and fixed to rock walls. T_{air} and RH at each site were measured using a single 12-bit sensor (S-THB-M002) mounted inside a radiation shield (RS3) and installed so that the sensor was c. 110 mm away from the rock wall. T_{air} sensor accuracy is ±0.2°C between 0 and 50°C, but decreases to ±0.28°C at −10°C. RH sensor accuracy is ±2.5% between 10 and 90% humidity, declining to ±3.5% above or below this range. On the alpine bluffs, soils are usually sparse, shallow, highly mineralised, and lacking in horizon profile development, forming on ledges and in crevices and cracks that plants use to establish rooting systems. A single 25-mm solid temperature probe (S-TMB-M002) was fitted into the soil

bank at each site 30–50 mm below the surface to measure soil temperature reflective of plant root zones. Sensor accuracy is reported as ±0.2°C between 0 and 50°C, declining to ±0.25°C at −10°C. PAR (400–700 nm) was measured using a single sensor (S-LIA-M003) mounted adjacent to established plants and at a similar zenith angle to leaves, to mimic leaf light interception at each site. The PAR sensor accuracy is ±5 µmol m^{-2} s^{-1} up to 25°C. The T_{air}/RH and PAR sensors were measured every 2 min and the data averaged and recorded every 30 min. RH was converted to vapour pressure deficit (VPD) following Campbell & Norman (1998). T_{soil} was measured and recorded once every 30 min. Intrasite monthly mean T_{air} and T_{soil} and monthly cumulative PAR were analyzed for the 10-month period where data collection overlapped at all sites, i.e. January–October 2009, using a paired Student's t-test. Mean daylight VPD was calculated using a day period defined as PAR > 0 and between 0530 and 2150 hours. Minimum VPD values reflect lowest values observed throughout the diel cycle.

Potential PAR was defined as clear-sky potential radiation on an obstruction-free, horizontal surface at the latitude and altitude of each site. The calculation of solar position at 30-min intervals over a year was based on equations by Meeus (1999) and can be found at the NOAA website (http://www.srrb.noaa.gov/highlights/sunrise/azel.html). The solar radiation on a horizontal surface was calculated following Bird & Hulstrom (1981); the effect of pressure reduction with altitude was taken into account, but albedo was kept constant (0.20).
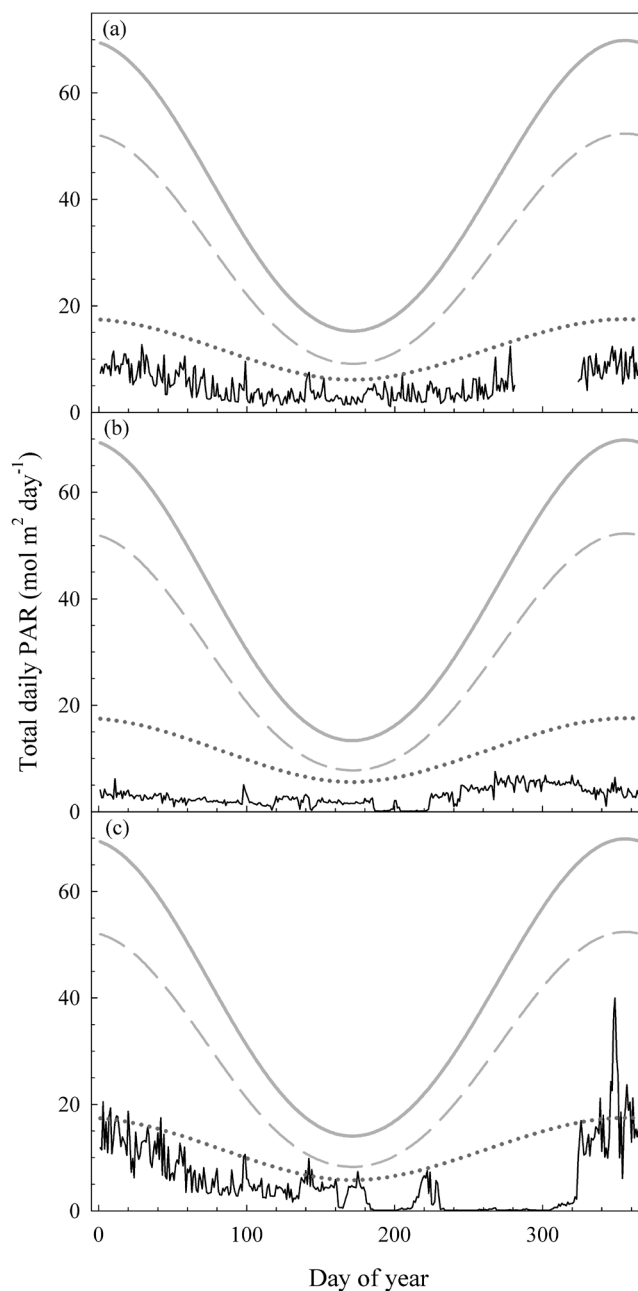
Results

Radiation was low at all sites and was not correlated with altitude (Fig. 2). Instantaneous maximum PAR was observed at the highest altitude site, Mt Hutt, with a photon flux of 1891 µmol m^{-2} s^{-1} (Fig. 2). Maximum PAR values at the

Yeo Stream and Ohau sites were 1281 and 328 µmol m^{-2} s^{-1}, respectively. Total daily PAR varied little at Ohau and the Yeo Stream, but was much more dynamic at the Mt Hutt site across the measurement period. Measured PAR was between 0.2% and 76% of potential PAR at the Mt Hutt site, but was only 0.8% to 26% of potential PAR at the Ohau site (Fig. 3). Monthly cumulative PAR was not different between Mt Hutt and other sites ($P \geq 0.13$), but was significantly lower at the Ohau site than at the Yeo Stream site ($P = 0.006$) between January and October 2009. On an annual timescale the highest

Figure 3. Total daily measured photosynthetically active radiation (solid line; PAR) in relationship to calculated potential diffuse PAR radiation (dotted line), calculated potential direct radiation (dashed grey line), and calculated total daily potential PAR (diffuse + direct radiation; solid grey line), at the Yeo Stream (a), Ohau (b), and Mt Hutt (c) sites. Data collection at the Yeo Stream site was for 324 days compared with 365 days at Ohau and Mt Hutt sites; Yeo Stream data for days of year 281–324 are not available.

Figure 2. Distribution of photosynthetically active radiation (PAR) levels at the three study sites (Yeo Stream – 1380 m, Ohau – 1730 m, Mt Hutt – 1800 m). For reference, PAR levels during the summer, under clear conditions and on an obstruction-free, horizontal surface, are approximately 2000 µmol m^{-2} s^{-1}. Each class represents measured PAR between the noted level down to the previous level. Note change in distributional scale of the x-axis with increasing PAR.
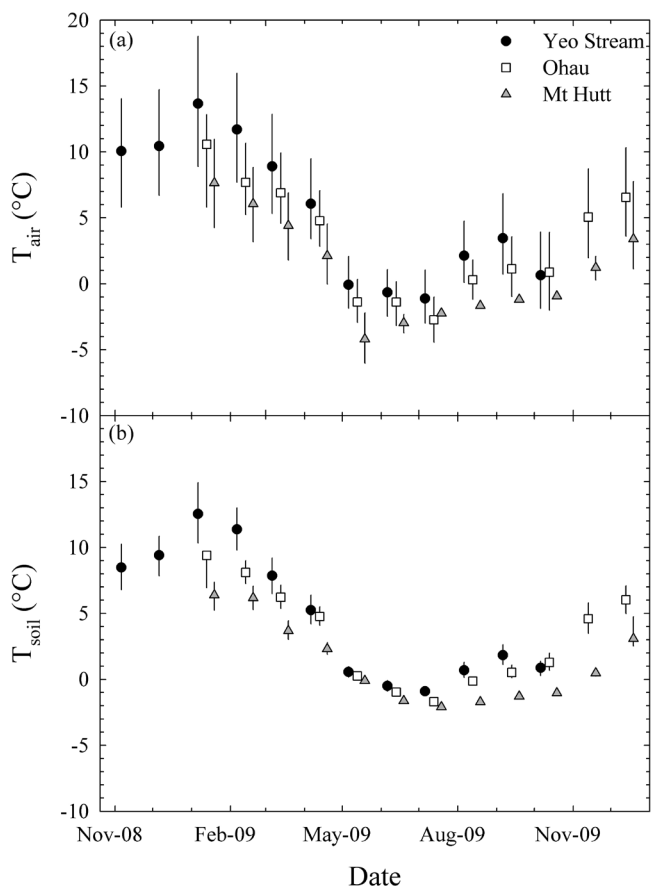
Table 1. Summary statistics for each study site describing the sum of measured annual photosynthetically active radiation (Annual PAR), estimated potential PAR (Pot. PAR), mean annual air temperature (T_{air}), mean annual soil temperature (T_{soil}), and mean annual diurnal vapour pressure deficit (VPD). Ice days are 24-h periods where air temperature was $\leq 0°C$, and are represented as a percent of total measurement days for each site. Across the 10-month period of overlapping measurements at the three sites, intercepted PAR was not different between Mt Hutt and other sites ($P \geq 0.13$) but was higher at Yeo Stream compared with Ohau ($P = 0.006$). During the same period, T_{air} and T_{soil} declined significantly as altitude increased ($P \leq 0.02$).

		Annual PAR (mol m^{-2})	Pot. PAR (mol m^{-2})	Mean T_{air} (°C)	Mean T_{soil} (°C)	Mean VPD (kPa)	Ice days
Inc.	Yeo Stm	1636	10 916	5.5	4.9	0.48	8.6%
altitude	Ohau	1057	12 715	3.0	3.1	0.34	16.4%
⬇	Mt Hutt	2059	12 919	1.1	1.3	0.20	55.6%

cumulative PAR was at Mt Hutt (2059 mol m^{-2}), while the lowest was at Ohau (1057 mol m^{-2}; Table 1). Cumulative PAR at the Yeo Stream site was 1636 mol m^{-2}, but comparisons with annual PAR at other sites are confounded by a different and abbreviated measurement period at the Yeo Stream site compared with the Ohau and Mt Hutt sites (Fig. 3). These annual PAR values were much lower than annual potential PAR at the Yeo Stream (10 916 mol m^{-2}; measured PAR as a percent of potential PAR: 15%), Ohau (12 715 mol m^{-2}; 8.3%) and Mt Hutt sites (12 919 mol m^{-2}; 16%). Estimates from model calculations of potential global radiation show the majority of intercepted radiation is diffuse, not direct radiation. Direct radiation was greatest at the Mt Hutt site and accounted for 5.6% of the annual radiation budget, with diffuse radiation providing most of the light at this site and the lower study sites (Fig. 3).

Mean and minimum air temperatures declined with increasing altitude. Mean T_{air} declined from 5.5°C at Yeo Stream to 1.1°C at Mt Hutt (Table 1), and mean monthly temperature between January and October 2009 was significantly different between sites and was lower as altitude increased ($P \leq 0.002$; Fig. 4a). Minimum half-hourly T_{air} at the Yeo Stream site was −6.5°C, declining to −9.3°C (Ohau) and −10.7°C (Mt Hutt) as altitude increased. Ice days, defined as 24-h periods over which T_{air} was $\leq 0°C$, were more numerous with increasing altitude (Table 1). At Yeo Stream, 28 of the 324 measurement days (8.6%) were ice days, increasing to 60 days (16.4%) at Ohau and 203 days (55.6%) at Mt Hutt across the 365-day measurement period at those higher sites. Maximum half-hourly air temperature at the Yeo Stream site was 28.2°C, with similar maximum T_{air} values observed at Ohau (24.3°C) and Mt Hutt (24.5°C). Mean annual VPD declined with increasing altitude, from 0.48 kPa (Yeo Stream) to 0.20 kPa (Mt Hutt; Table 1). VPD patterns tracked T_{air}, and thus the highest VPD was observed at Yeo Stream (2.93 kPa), was lower at Ohau (1.94 kPa) and lowest at the Mt Hutt site (1.41 kPa). Mean annual T_{soil} declined from 4.9°C to 1.3°C with increasing altitude (Table 1), and monthly mean T_{soil} declined significantly with increasing altitude across the January–October 2009 period ($P \leq 0.02$; Fig. 4b). Less variation in half-hourly minimum T_{soil} was observed, with all sites exhibiting minimum values of c. −2.4°C. Maximum half-hourly T_{soil} values were lower than those for T_{air}, being within 3°C of maximum half-hourly T_{air} values at the Yeo Stream (maximum half-hourly T_{soil} = 25.5°C) and Ohau (25°C) sites, but more than 13°C lower than maximum T_{air} observed at Mt Hutt (maximum half-hourly T_{soil} = 11.3°C).

Figure 4. Mean monthly air temperature (a) at the Yeo Stream study site (1380 m a.s.l.) between November 2008 and October 2009, and the Ohau (1730 m a.s.l.) and Mt Hutt (1800 m a.s.l.) sites between January and December 2009. Panel (b) shows monthly mean soil temperature, with all symbols as in (a). Bars represent mean daily temperature minima and maxima for each month.

Discussion

The growing season at the three alpine sites in this study may be limited not only by low air and soil temperature, but also the availability of light and, at times, high VPD. At Mt Hutt, low PAR measurements between July and October suggest the

site was frequently encased in snow or ice (Fig. 3c), and this may have buffered the plants from even lower air temperatures than those recorded in this study (Körner 2003). At Ohau, the highest photoperiod did not coincide with the highest air temperatures (Figs 3b & 4a), and thus when T_{air} was >10°C, a temperature range more conducive to photosynthesis, mean PAR was below 100 µmol m^{-2} s^{-1} and total daily PAR was < 5 mol m^{-2}, or approximately 12% of potential PAR. For comparison, in one New Zealand temperate rainforest system 24% of above-canopy radiation reached the forest floor on an annualised basis (DeLucia et al. 2003), but the PAR measured at the sites in this study was only 8–16% of the potential annual radiation. Further, this radiation environment is generally dominated by diffuse, not direct, radiation (Fig. 3), providing a further challenge for plant photosynthetic carbon gain. Light-flecks have been shown to be important in other light-limited systems (Chazdon & Pearcy 1986; Valladares et al. 1997) and it is possible that short periods (e.g. 15–30 min) of relatively high light intensity, defined here as PAR > 750 µmol m^{-2} s^{-1}, contribute substantially to plant carbon economies at both Yeo and Mt Hutt sites. Mean diurnal VPD was generally low through the study period and across sites (< 0.5 kPa; Table 1), but high VPD (> 2.0 kPa) was observed when T_{air} was elevated, especially at the Yeo Stream site. Low VPD under sunlit and well-watered conditions generally results in high stomatal conductance (Leuning 1995), but the high VPD observed during some periods could result in low leaf gas exchange and, consequently, reduced carbon uptake.

Low PAR and air temperature in these shaded bluff systems create a challenging environment for optimising leaf temperature and photosynthesis. In a study from the European Alps, field-grown *Geum* plants were, at times, subject to shading in their growth microclimate and this negatively impacted their overall leaf carbon budget, reducing their carbon yield by up to 75% compared with high-light species (Diemer & Körner 1996). Importantly, the sensitivity analysis of Diemer and Körner (1996) suggested that growing these shaded *Geum* under high PAR would increase carbon yields nearly 250%.

Additionally, Körner (1982) showed that the photosynthetic response to light varies with leaf temperature in *Carex* and that photosynthetic rate when PAR was 100 µmol m^{-2} s^{-1} was reduced to 40% of maximum at a leaf temperature of 4°C compared with 14°C, the optimal leaf temperature at that PAR flux. Körner (1982) further noted that low light was more limiting to carbon uptake than low temperature in *Carex* and, in subsequent work, that "…low temperatures have surprisingly little effect on alpine plant photosynthesis" (Körner 2003). This may be due in part to rapid recovery of full photosynthetic capacity after exposure to cool temperatures, as observed in alpine *Chionochloa* (Mark 1975). The complex interactions between light, temperature and photosynthesis in cool, dim environments remains unclear, and further studies of *Pachycladon* photosynthetic and respiratory activities under different temperature and light regimes are needed to elucidate their carbon balance dynamics under current and future climate conditions.

The question also remains: how do these alpine *Pachycladon* stay warm in the shade? Radiative warming can increase leaf temperatures up to 20°C above ambient T_{air} during sunlit conditions, and is thought to be an especially important driver of leaf energy balance in alpine systems (Grace 1987; Diemer 1996). The low PAR observed at these sites (Figs 2 & 3), however, suggests the *Pachycladon* and surrounding community must be reliant on T_{air} to a much greater extent to maintain energy and carbon balance. Site characteristics may drive some temperature regulation, as steep scree slopes at the base of the bluffs potentially absorb substantial radiation that may subsequently be emitted back to the environment as sensible heat energy and transferred upslope via convection to these shaded, sheltered sites.

Air temperatures in the bluff sites were comparable with those observed in studies from open alpine habitat, though absolute winter minima in the bluff sites were higher than reported in previous studies (Table 2). Winter mean monthly T_{air} minima were generally similar across studies when comparing sites of similar altitude. Absolute winter minima, however,

Table 2. Summary of historical alpine climate data from the South Island, New Zealand. Mean maximum and minimum monthly air temperatures, winter minimum air temperature, and measurement altitude are summarised for each study location.

	Max. mean T_{air} (°C)	Min. mean T_{air} (°C)	Winter minimum (°C)	Altitude (m)	Study
Craigieburn Range	14.4	1.1	−11.1	800	Morris 1965
Craigieburn Range	11.1	−0.5	−8.8	1340	Morris 1965
Craigieburn Range	11.1	−0.5	−9.4	1400	Morris 1965
Craigieburn Range	8.3	−5.6	−14.4	1830	Morris 1965
Craigieburn Range	9.7	−1.4	−14.5	1550	McCracken 1980
Old Man Range	6.5	−6.0	−9.0	1590	Mark & Bliss 1970
Pisa Range	c. 8.5	c. −3.8	c. −12.5	1647	Mark et al. 2006
Pisa Range	c. 6.5	c. −4.5	c. −14.0	1885	Mark et al. 2006
Mt Burns	6.7	−1.3	c. −8.0	1420	Mark et al. 2008
Mt Burns	5.9	−2.4	c. −10.5	1550	Mark et al. 2008
Yeo Stream	13.7	−1.1	−6.5	1380	This study
Ohau	10.6	−2.7	−9.3	1730	This study
Mt Hutt	7.6	−4.2	−10.7	1800	This study

were cooler in earlier studies compared with bluff sites at similar altitude, e.g. the $\geq 3.7°C$ lower T_{air} at sites of similar altitude in the Craigieburn Range (Morris 1965) compared with Mt Hutt. Winter minima were also lower in the historical record at lower altitudes, as T_{air} at 1340 and 1400 m were $-8.8°C$ and $-9.4°C$, respectively (Morris 1965), and cooler than the $-6.5°C$ T_{air} minimum at the Yeo Stream site (1380 m a.s.l.). The maximum summer mean monthly air temperatures at the bluff sites were higher at lower altitude and generally cooler at higher altitude than found in previous studies. At lower altitudes in the alpine zone, mean monthly summer T_{air} was cooler in the Craigieburn Range and at Mt Burns (Morris 1965, Mark et al. 2008) compared with the Yeo Stream site. At higher altitude, summer monthly means at Mt Hutt were cooler than those observed in the Craigieburn Range (Morris 1965) but similar to those observed in the higher latitude Pisa Range (Mark et al. 2006). The lower temperatures in the historical record may be due to variation among sites, such as greater site exposure to wind or a decrease in snow cover that makes them cooler, or they may be due to interannual variability in weather trends. This latter point emphasises the need for long-term monitoring of alpine climate, such as the recently implemented GLORIA network (Mark et al. 2006), to resolve temporal variation in climate trends.

Soil temperatures covaried with T_{air} oscillations and declined with increasing altitude (Fig. 4b), though winter minima were similar at all sites. Comparisons with other climate data are confounded by measurements at different depths, but the mean winter soil temperatures observed at the Yeo Stream, Ohau and Mt Hutt sites at 30–50 mm depth were similar to the c. -3 to $+1°C$ range observed at Mt. Burns and in the Pisa Range when measured at 100 mm (Mark et al. 2006). Low rooting-zone temperatures (i.e. $\leq 0°C$) could reduce nutrient uptake rates, with some evidence that cool winter temperatures (-14.5 to $-6.1°C$) impacted nitrogen uptake during the growing season in several alpine and arctic plants (Bilbrough et al. 2000).

With no obvious dispersal limitations, most species of *Pachycladon* inhabit a limited habitat in the New Zealand alpine zone, being found on polar-facing slopes in relatively wind sheltered rock walls and alcoves but largely absent just metres away in open scree or in bluff habitat that receive more direct sunlight (i.e. slopes with equatorial exposure). These sheltered sites provide protection against the mechanical force of wind that can cool or damage leaves and result in higher tissue costs (Grace 1977). Their restriction to these shaded alpine environments is, however, driven by unknown physiological or ecological constraints, but may be an adaptation to reduce excessive radiation that could induce photoinhibition at cool mountain temperatures (Streb et al. 1998; Germino & Smith 2000). Clearly, the plants inhabiting these shaded bluffs are adapted to the environment they have evolved in, but the microclimates described here emphasise the challenge of maintaining positive carbon balance in this unique habitat of the alpine zone and warrant further study of the relationship between leaf radiation absorption, leaf temperature, light response, respiration and photosynthesis in the *Pachycladon*.

Acknowledgements

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