Arctic, Antarctic, and Alpine Research, Vol. 48, No. 1, 2016, pp. 61–78
DOI: http://dx.doi.org/10.1657/AAAR0014-084

Temperature microclimates of plants in a tropical alpine environment: How much does growth form matter?

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A B S T R A C T

In the aseasonal tropical alpine environment, plants experience frequent oscillations of air temperature around zero, but little is known about the leaf temperatures of different plant growth forms in dry versus humid climatic conditions. During July–August 2007, we measured air temperature at 100 cm and 20 cm above the ground, soil temperature at 1 cm and 10 cm depth, and temperatures of leaves and stems of tropical alpine plants on the eastern (windward and cloudy) and western (leeward and sunny) sides of the Antisana volcano (Ecuador) between 4100 m and 4600 m, with the aim of examining the effects of climate and growth forms on leaf temperature. The sunnier climate on the western side of the mountain provided a much broader thermal envelope, in which only leaves of low-statured plants showed significant departure from air temperature during the day. In contrast, most plants had warmer leaves than was the air temperature on the eastern side, and except for cushion plants, the difference in temperature was progressively greater in leaves of taller plants. Plants warmed up significantly faster on the western side and at higher elevations, with the fastest warming rates of 13–15 K h^{-1} observed in erect herbs. Night cooling rates did not differ between the opposite mountain sides or between elevations. Erect herbs cooled at the fastest rates (3 K h^{-1}), whereas cushion plants cooled at the slowest rates (about 1 K h^{-1}). Height aboveground along with aspect (west vs. east) were the most significant determinants of the leaf thermal microclimate during the day, with elevation having no effect. Low-statured plants experienced more extreme and more variable microclimates than taller plants in sunnier and drier conditions, but the effect of plant height was almost negligible in humid and cloudy climates. In all climatic conditions, cushion plants performed better than any other growth form by achieving higher temperature during the day and preventing rapid cooling during the night.

Introduction

Temperature affects the rates of metabolic processes and is thus one of the major determinants of plant growth (Larcher, 2003). In the alpine environment, habitat temperature is largely determined by such site attributes as aspect, topography, and substrate, rather than by the macroclimate, and it varies significantly over short distances (Körner, 2003; Scherrer and Körner, 2011; Graham et al., 2012). Moreover, temperatures experienced by alpine plants are influenced by their traits, such as growth form, height, and leaf morphology (Salisbury and Spomer, 1964; Körner, 2003). Many alpine plants,

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particularly low-stature rosette and cushion plants, bear leaves nearly perpendicular to the incoming noon solar radiation. These leaves are heated many degrees above the air temperature, that is, they decouple from the ambient air, which provides the plant with "extra heat" (Salisbury and Spomer, 1964; Körner, 2003; Larcher and Wagner, 2011; Larcher, 2012). In the tropical alpine environment, for instance, the heat accumulated by inflorescences and leaves of some species during the day can help to outbalance rapid cooling after sunset (Miller, 1986, 1994; Beck, 1994). Leaves closely attached to the ground take advantage of the heat capacity of the soil and, moreover, lose heat only unidirectionally toward the sky through long-wave outgoing radiation and sensible heat flux (Jones, 1996). Thus, alpine plants are enabled to inhabit higher elevation than can trees, for which canopy temperature is closely linked to the air temperature. Moreover, tree root growth and functioning are hampered by lower soil temperature due to reduced insolation under the closed canopy (Körner, 1998, 2003; Körner and Paulsen, 2004; Schenker et al., 2014).

The climatic temperature conditions of tropical alpine environments have been well described (Sarmiento, 1986; Rundel, 1994). Because these climatic data mostly come from weather stations, however, they usually depart significantly from particular site microclimates and are of limited value for ecological inference (Scherrer and Körner, 2011; Graae et al., 2012; Graham et al., 2012). The temperature microclimate of tropical alpine plants, in contrast to those of temperate ones (Körner, 2003; Dietrich and Körner, 2014), has been examined only occasionally, by short-term observations (Hedberg and Hedberg, 1979; Young, 1984; Beck, 1994; Diemer, 1996; Ramsay, 2001; Sklenář, 1999, 2007). These studies document the capability of the tropical alpine plants to decouple from the ambient air temperature, but no comparison has been made of microclimates of various tropical alpine growth forms in different climatic conditions. Moreover, measurements, especially long-term records, of leaf temperatures in humid alpine environments are scarce, even from temperate mountains (Körner et al., 1983; Diemer, 1996; Neuner and Hacker, 2012).

In the high-elevation tropics, in contrast to temperate mountains, snow is very ephemeral and unpredictable, and windstorms are generally absent (Sarmiento, 1986). Two important regional co-determinants of alpine plant distribution in temperate mountains (snowpack along with strong winds) thus are absent from the tropics (Körner, 2003). Instead, the tropical alpine plants must continually balance the nighttime risk of freezing injury against the demand for growth during rapidly elevating daytime temperatures (Rundel, 1994; Ramsay, 2001). Analyzing the thermal environment of tropical alpine growth forms may thus help to identify the globally operative driver(s) of the upper distribution limit of plants.

The aim of our research was to examine temperature microclimates of tropical alpine plants of various growth forms. We studied how closely the plants inhabiting contrasting environmental conditions of dry and humid equatorial superpáramo matched the ambient temperature. In particular, we predicted that low-statured plants, in contrast to taller ones, would (1) experience greater and (2) more rapid temperature fluctuations, but would also (3) depart more from the ambient temperature, resulting in (4) more favorable microclimates, in terms of higher mean temperatures.

Methods

Study Site

The study was carried out on the Antisana volcano (5704 m), located in the eastern cordillera of Ecuador. There is a strong climatic gradient between the windward (eastern) and leeward (western) sides of the mountain which determines the major patterns of plant species distributions (Sklenář et al., 2008). Weather on the windward side of Antisana is typically cloudy, with cool days, night air temperatures usually above zero, air humidity close to full saturation, and frequent fog. In contrast, the typical weather on the leeward side of the mountain comprises sunny mornings with frequent hoarfrost, cloudy afternoons, and occasional ephemeral snow (Sklenář et al., 2015).

Data Collection

Microclimates were assessed at two western sites, located at 4280 m (referred to as WL) and 4600 m (WH), and at two northeastern sites located at 4120 m (EL) and 4430 m (EH) (Sklenář et al., 2015); the

lower sites on each side corresponded to shrubby lower superpáramo and the higher sites to open upper superpáramo vegetation. The ~200 m differences in elevation of the corresponding sites on the opposite sides reflected the elevational shift of the relevant vegetation (thermal) belts in the equatorial Andes (Lauer, 1979).

At each site, a simple microclimatic station was established in open areas (i.e., unobstructed by any tall vegetation). The air temperatures at 100 cm and 20 cm aboveground and soil temperature at 1 cm depth were measured with Cu-Co thermocouples encapsulated in thin needles (the air temperature needles were positioned on 50-cm-long arms mounted on a vertical bar and screened by reflective shields), and soil at 10 cm depth with Pt thermometers. Readings were taken every 5 minutes between 17 July and 11 August 2007, and the data were used to construct vertical temperature profiles for each site using absolute maximum/minimum, mean daily maximum/minimum, and mean temperatures. Periods of measurement differed by one or two days between the sites, because they were established consecutively. Needles inserted in the soil were damaged soon after the setup at the eastern sites and so those data were lacking. Measurements continued until July 2009 with a recording interval of 1 hour. These data were used to describe within-day ambient thermal variation using mean hourly values and within-year variation using mean daily maxima and mean daily minima. However, due to damage to sensors and/or dataloggers, data were available for only 720 days for WL, 460 days for WH, 510 days for EL, and 277 days for EH.

Simultaneously with measurements of ambient temperature, we measured temperatures of plants representing various growth forms (Table 1) during July–August 2007. Fine-wire Cu-Co thermocouples were attached to stems and undersides of fully developed and undamaged leaves, and temperatures were recorded by multichannel dataloggers (EMS Brno) every 5 minutes. Because of the daily course of cloudiness and thus temperature variation between the east-facing and west-facing surfaces in the alpine tropics (Young, 1984; Sklenář, 2007), the position of leaves and stems on the plants to be measured was selected to avoid such orientation. In the case of the cushion plants, leaves on the top of the cushion were measured. Due to equipment limitations, we were only able to measure one individual per species and site. We selected plants that were located within 7 m of the dataloggers which was determined by the length of the connecting wires. The functionality of the thermocouples was controlled regularly during this portion of the study; because of sensor damage, the recording periods were shorter by two days for *Azorella pedunculata* (WL) and by seven days for *Loricaria antisanensis* leaf (EH).

Statistical Analysis

For each temperature variable (air, soil, plant) we counted the number of temperature records in intervals of 1 K using the 5-minute data and prepared a frequency table. Additionally, we extracted records of temperature rises during the day and temperature declines during the night that lasted continuously for at least four time periods (corresponding to about 20 min). From these data we assessed the number of the warming and cooling events and their time lengths and prepared a frequency table of these. Finally, we counted the number of freeze/thaw events for which the measured temperature crossed 0 °C. The calculated frequencies were used as response variables in Detrended Correspondence Analysis (DCA) ordination analysis in order to examine relationships among the air, soil, and plant temperatures using CANOCO for Windows 4.5 (ter Braak and Šmilauer, 1998). Data were square-root transformed prior to the analyses. The group boundaries resulting from the first clustering step of a Twinspan procedure were superimposed onto the ordination diagram. Mean rates of subzero cooling during the night and above-zero warming during the day were estimated as the slope of the linear regression between the cooling/warming intensity (i.e., difference between the starting and ending temperature) and cooling/warming length.

To test for differences between the sites, mean plant temperatures from the 5-minute data were regressed onto the log(height), which was the height of the thermocouple relative to the ground. Differences between the sites, i.e., the effects of elevation and aspect, were tested by means of a two-way ANCOVA using log(height) as a covariable in order to partial out its effect. Statistics were calculated in R version 2.15.2.

Results

Temperature Environment (2007–2009)

The daily course of mean air and soil temperatures showed significant environmental variation among the sites (Appendix Figs. A1 and A2). The greatest temperature amplitude appeared in the topsoil (−1 cm) at the western higher site, exceeding 15 K on average and 48 K in absolute values. Mean air temperature varied by 1–2 K more at 20 cm aboveground than at 100 cm, and fluctuation was very mild in the soil at 10 cm depth. Temperature envelopes of the environment were distinctly narrower on the eastern side of the Antisana volcano. For example, the mean air temperature oscillation at 20 cm above ground (5–6 K) was about half of that observed at the western sites (10–11 K) (Fig. 1; Appendix Figs. A1 and A2). Both the absolute minimum (–9.5 °C) and absolute maximum (23.3 °C) air temperatures during the entire period were recorded at 20 cm aboveground at the lower western site. On the eastern side of the mountain, the absolute minimum and absolute maximum air temperatures of –3.1 °C and 20.8 °C, respectively, were also recorded at the lower site at 20 cm height. The uppermost soil layer (−1 cm) occasionally froze at both western sites (minimum temperature of –3.2 °C was observed at the higher site), whereas subzero soil temperatures occurred only at the higher of the eastern sites (minimum of –1.5 °C).

Plant Microclimate (July–August 2007)

Plant temperatures measured during an approximately four-week period generally mirrored the above-described patterns of air and soil temperatures. Plants on the western side experienced the greatest temperature oscillations during the day (Appendix Table A1). The lowest minima, between –7.4 and –7.8 °C, were observed on leaves and stems of erect herbs (*Lasiocephalus ovatus, Gentianella foliosa*) at 6–25 cm aboveground, although some shrubs also experienced minima close to –7 °C. On the eastern side, the lowest minima, between –4.5 and –4.2 °C, were observed on leaves of the shrub *Diplostephium rupestre* (at 45 cm) and the acaulescent herb *Valeriana adscendens* (5 cm), respectively, also at the lower elevation. Maxima between 33.1–35.6 °C and 30.9–33.2 °C on the western and eastern sides, respectively, always occurred among low-statured plants such as cushions of *Azorella* spp. and acaulescent rosettes of *Werneria nubigena* and *Valeriana* spp.

Only low-statured plants (*Azorella pedunculata, Valeriana rigida*) tended to be warmer than the ambient temperature during the day on the western side, whereas leaves of taller plants (shrubs) were even slightly colder (Fig. 1). In contrast, most plants on the eastern side of the Antisana volcano were warmer than the ambient temperature, as both the mean daily maximum and mean daytime plant temperatures exceeded the corresponding air temperatures. Generally, taller plants (shrubs) were warmer than the smaller plants (erect herbs, prostrate subshrubs) and tended to depart more from the ambient temperature; however, *Azorella aretioides* cushions were the exception to this rule, as they were always the warmest. With respect to night temperatures, there was little variation among the growth forms at all study sites. Shrubs and erect herbs were closely coupled with ambient air temperature, whereas low-stature plants were distinctly colder than the upper soil layer and their temperatures were similar to those of the air at 20 cm (Appendix Table A1).

Mean rates of above-zero warming of the plants correlated with their mean maximum temperatures during the day except at the western higher site, whereas mean rates of subzero cooling correlated to the mean night minimum only at the lower western site (Figs. 1–2; Appendix Table A2). Erect herbs on the western side experienced the highest mean warming rates, 10–15 K h^{-1}, whereas shrubs warmed at about 5–9 K h^{-1}. Height aboveground thus significantly affected the rate of warming ($F = 5.1$, $p < 0.05$). On the eastern side, mean warming rates varied much less among the growth forms, that is, about 3–5 K h^{-1} at the lower site and about 5–7 K h^{-1} at the higher site. Warming rates were thus significantly higher on the western side of the mountain ($F = 62.4$, $p < 0.001$) and at the higher sites ($F = 24.9$, $p < 0.001$); both tested by two-way ANCOVA with log(height) above ground as covariable. Night cooling rates were much less variable both among and within the sites (Fig. 2). Erect herbs from the western side cooled most rapidly, at a mean rate of about 3 K h^{-1}, whereas cushion plants tended to cool at the slowest rate, about 1 K h^{-1}. Height aboveground thus had a significant ef-

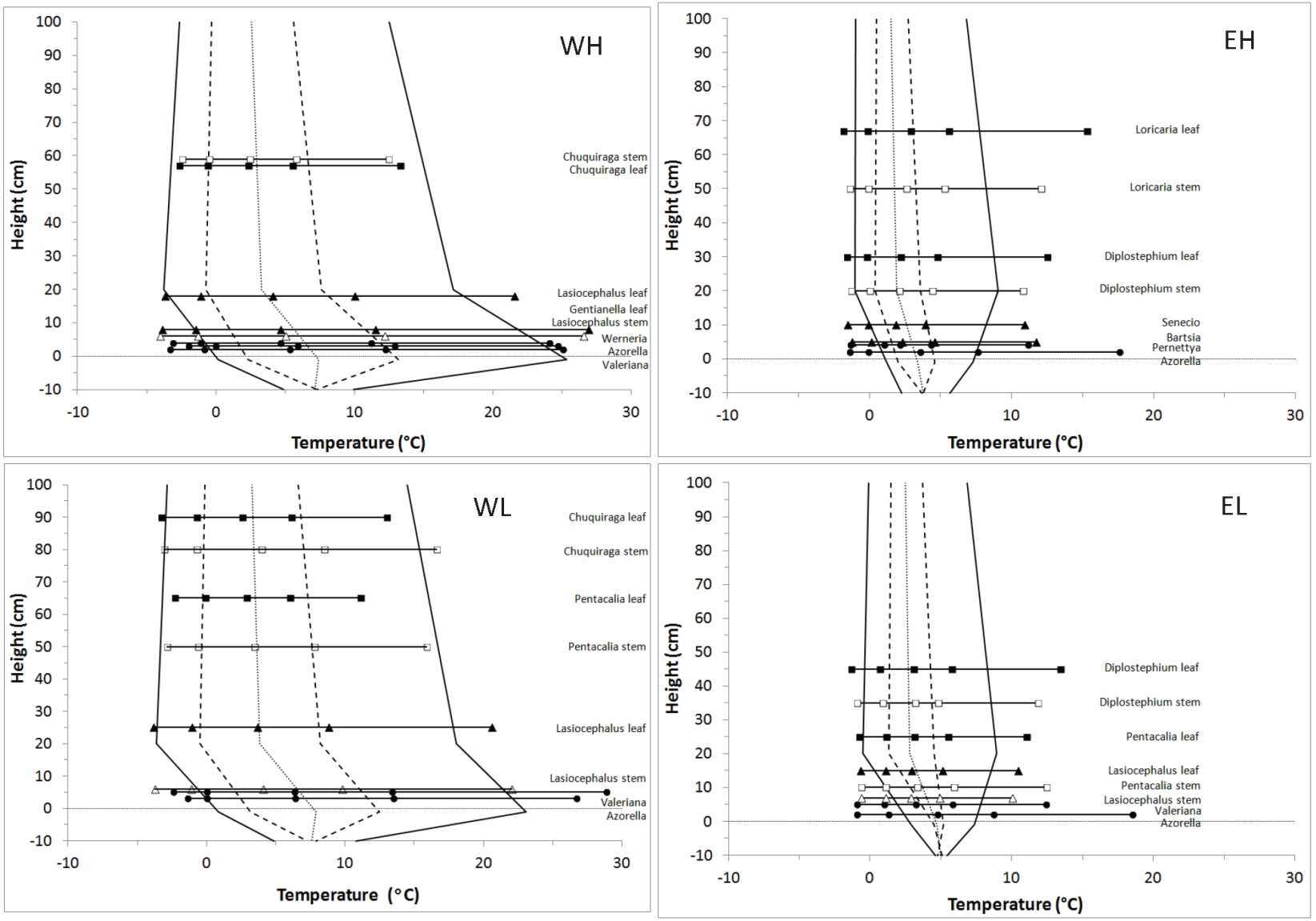


FIGURE 1. Vertical profiles constructed from mean temperature (dotted vertical line), mean day/night temperature (dashed vertical lines), and mean daily minimum/maximum temperature (solid vertical lines) for the period July–August 2007; WH—upper left, WL—lower left, EH—upper right, EL—lower right. Due to damage of soil sensors at EL and EH during July–August 2007, data are presented for the period July–August 2008 for them. Horizontal lines show ranges of temperatures experienced by plants; symbols on each line are, from left to right: absolute minimum, mean daily minimum, mean, mean daily maximum, absolute maximum; squares are shrubs, triangles are erect herbs, circles are cushions, acaulescent plants, and prostrate subshrubs; open symbols are stems, filled symbols are leaves.

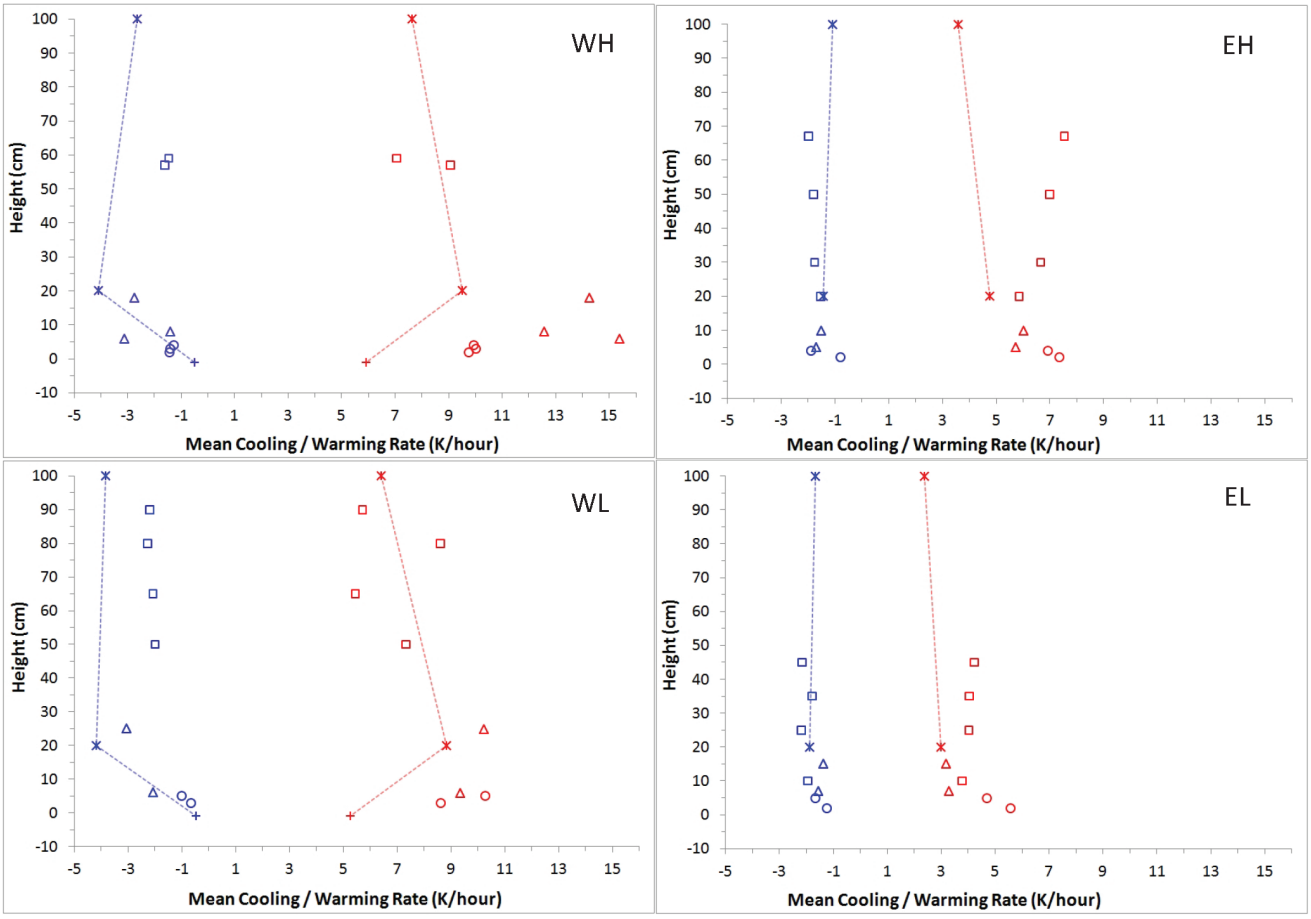


FIGURE 2. Mean cooling rates during the night (blue) and mean warming rates during the day (red) of air (star), soil (cross), and plants at WH (upper left), WL (lower left), EH (upper right), and EL (lower right); squares are shrubs; triangles are erect herbs; circles are cushion plants, acaulescent plants, and prostrate subshrubs.

fect on the mean cooling rate ($F = 7.4$, $p < 0.05$), with cooling being slower near the ground, whereas neither aspect nor elevation had any effect.

The mean period of continuous above-zero warming or subzero cooling was well below 30 minutes (i.e., between 0.4 and 0.45 hours) for the majority of the growth forms. Cushion plants and in some instances also acaulescent and erect herbs or shrubs were exceptions to this pattern since their continuous cooling was, on average, about 10 minutes longer (Appendix Fig. A3). Individual warming or cooling events occasionally exceeded 1 hour, however. At the lower western site, for instance, subzero cooling of *Chuquiraga jussieui* stem, at a mean rate of 3.5 K h^{-1}, lasted for 1.33 h, and subzero cooling of *Pentacalia peruviana* leaf, at 4 K h^{-1}, lasted for 1 hour, whereas above-zero warming of *Valeriana rigida* leaves, at 19.2 K h^{-1}, lasted for 1.25 hours. However, the cooling and warming rates were even higher when temperature changes across zero were considered—for example, *Chuquiragua jussieui* stem cooled continuously at a mean rate of 10.2 K h^{-1} for 1.25 hours starting at 12.7 °C, whereas *Lasiocephalus ovatus* stem warmed at 22.7 K h^{-1} for almost 1 hour starting, from −4.0 °C.

Site Comparison

The first two DCA ordination axes combined gradients of height aboveground and aspect (i.e., west vs. east) (Fig. 3). *Azorella* cushions from all four sites, along with acaulescent rosettes (*Valeriana, Werneria*) and erect herbs (*Gentianella foliosa* and partly also *Lasiocephalus ovatus*) from the western sites, formed a separate, loose group related to soil temperature at −1 cm. Nevertheless, *Lasiocephalus* graded toward shrubs (*Pentacalia*, *Chu-*

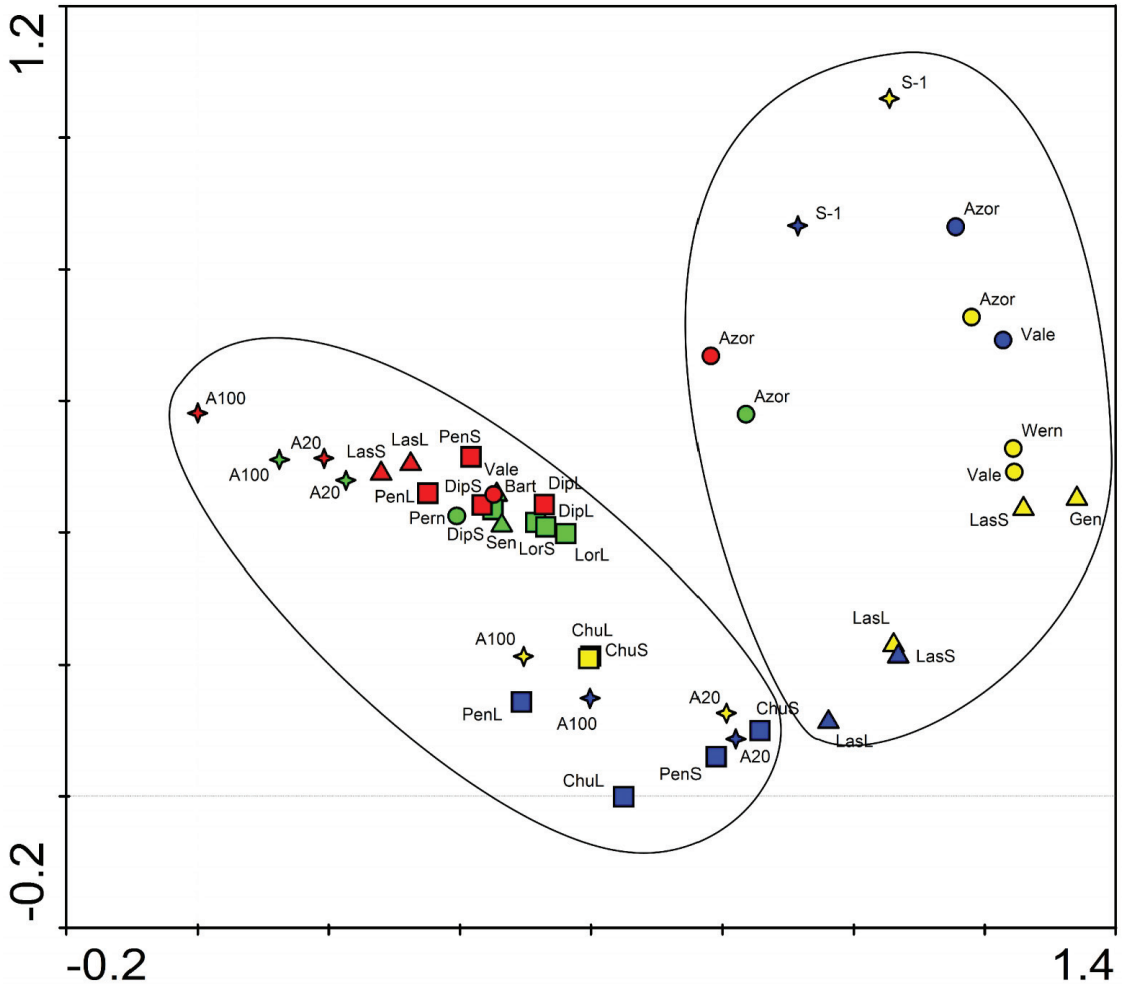


FIGURE 3. Detrended Correspondence Analysis (DCA) ordination diagram based on frequencies of temperature values and temperature changes indicates relationships among air, soil, and plant temperature variables within and between the sites; $\lambda_1 = 0.144$, $\lambda_2 = 0.038$, total inertia = 0.272; the grouping boundaries generated by the first Twinspan clustering step are superimposed on the diagram. Squares are shrubs; triangles are erect herbs; circles are cushion plants, acaulescent plants, and prostrate subshrubs. Blue—WL, yellow—WH, red—EL, green—EH. S and L after plant abbreviations refer to stem and leaf, respectively.

quiraga), which were located on the ordination diagram close to air temperatures at 20 cm and 100 cm. The scatter of variables from the two western sites thus primarily was in concordance with plant height. On the eastern side of the Antisana volcano, the variables, except for those of the *Azorella aretioides* cushions, from each of the two sites formed a distinct cluster. The third axis discriminated between the eastern sites and thus captured, to some degree, the elevational gradient (Appendix Fig. A4). Elevational discrimination was not seen between the western sites and, instead, the third axis tended to order the variables according to height aboveground.

Mean daily temperatures of plants declined with log(height) aboveground at the western sites ($p < 0.01$ for both) (Fig. 4), whereas no relationship was found for the eastern sites ($p = 0.07$ for the lower site and $p = 0.58$ for the higher site). ANCOVA, with mean plant temperature as dependent variable, indicated that height aboveground, along with aspect, had the greatest effect on it during the day ($F = 47.9$ and $F = 117.9$, respectively, $p < 0.001$ for both), whereas elevation had no effect ($p = 0.28$). A significant interaction between aspect and height aboveground ($F = 22.7$, $p < 0.001$) indicated a difference between vertical temperature gradients on the opposite sides of the mountain. During the

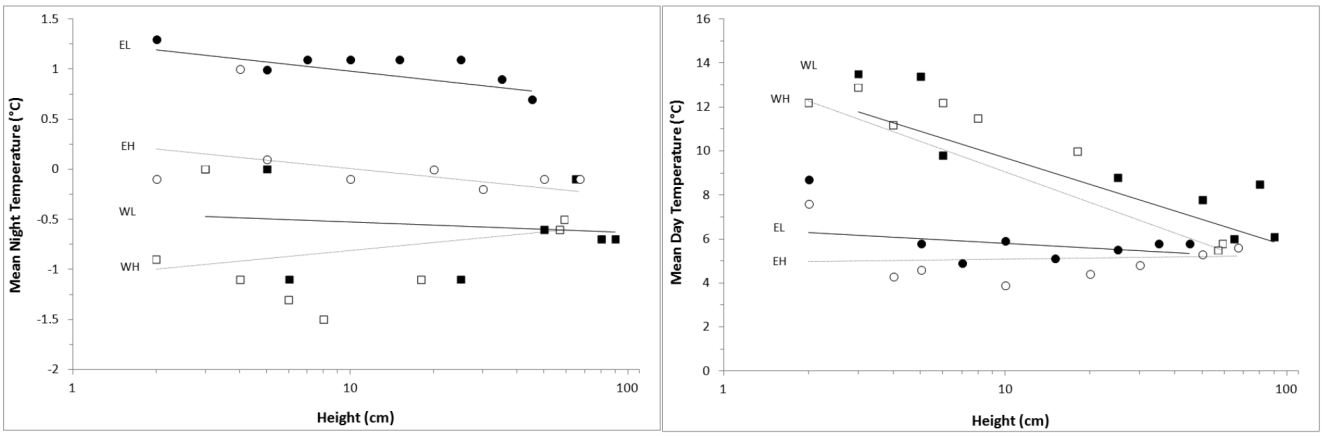


FIGURE 4. Mean plant temperatures plotted against height above ground (*x*-axis in logarithmic scale) demonstrate differences in the vertical temperature profile among the sites during the night (left) and day (right). Squares are western sites, circles are eastern sites, black are low elevation sites, white are high elevation sites. Significance level for the tests of day slopes (Mean Day Temperature) being different from zero are: $p < 0.01$ for WL and WH, $p = 0.07$ for EL, and $p = 0.58$ for EH.

night, no effect of height aboveground on plant mean temperature was detected ($p = 0.16$), whereas the effect of aspect was retained ($F = 76.4$, $p < 0.001$), with the plants on the western side of the Antisana volcano being colder. Moreover, there was a significant difference due to elevation ($F = 22.9$, $p < 0.001$), with lower mean temperatures observed in plants from the higher sites (Fig. 4).

Discussion

In spite of its general thermal aseasonality, the environment at high elevations of the humid tropics varies somewhat during the year (Sarmiento, 1986; Sklenář et al., 2015). However, the July–August 2007 temperature profile is located rather centrally within the 2007–2009 variation (Appendix Fig. A2), which suggests that our observations approximate the average environmental conditions experienced by plants in the high-elevation páramo of the Antisana volcano.

Three temperature gradients determine plant microclimate (bioclimate, sensu Larcher, 2012) on the Antisana volcano. Height aboveground and aspect are of primary importance and during the day they override the effect of the 300 m elevational difference between the lower and higher sites, in agreement with Diemer (1996). The typical daytime vertical temperature profile, with a narrow boundary layer of warm air above heated topsoil and overlaid with cooler air (Geiger, 1965; Meinzer et al., 1994a; Jordan and Smith, 1995; Larcher and Wagner, 2011), was observed only on the leeward, western side. On the windward, eastern side, low radiation input along with very high air humidity due to permanent cloudiness (Sklenář et al., 2015) produced very gentle vertical temperature profiles that lacked the layer of substantially warmer air near the ground. Vertical temperature profiles at night were similar between the two sides of the mountain, as the height above ground had no effect. However, the minimum temperatures were consistently lower and more often below zero on the western side due to frequent clear sky conditions, and there was also a significant effect of elevation. Low-statured plants on the leeward, western side thus inhabit a progressively warmer environment and experience significantly higher temperatures during the day than those on the windward, eastern side, but there is little difference when tall plants (in particular shrubs) are compared (Fig. 4). With respect to the thermal balance, plant height is thus an important trait on the western, sunny side of the mountain. On the eastern, cloudy side, however, except for cushion plants, plants of any height experience similar ambient temperatures most of the time (see also Körner et al., 1983). Our study omitted leaf traits, which are important determinants of leaf thermal balance (Meinzer and Goldstein, 1985; Meinzer et al., 1994a) and may have contributed to

TABLE 1

List of studied species along with their growth form classification (according to Hedberg and Hedberg, 1979; Ramsay, 2001), occurrence at the sites, and measured leaf areas. See text for site abbreviations.

Species	Family	Growth form	Measured organ(s)	Site	Leaf area ± SD (mm^2)
Valeriana adscendens	Valerianaceae	Acaulescent herb	Leaf	EL	1732.4 ± 747.7
Valeriana rigida	Valerianaceae	Acaulescent herb	Leaf	WL, WH	968.8 ± 128
Werneria nubigena	Asteraceae	Acaulescent herb	Leaf	WL, WH	2035.3 ± 411.4
Azorella aretioides	Apiaceae	Cushion plant	Leaf	EL, EH	1628.4 ± 511.9
Azorella pedunculata	Apiaceae	Cushion plant	Leaf	WL, WH	1043 ± 77.4
Bartsia stricta	Orobanchaceae	Erect herb	Leaf	EH	1201.2 ± 212.5
Gentianella foliosa	Gentianaceae	Erect herb	Leaf	WH	—
Lasiocephalus ovatus	Asteraceae	Erect herb	Leaf, stem	WL, WH, EL	985 ± 213.6
Senecio nivalis	Asteraceae	Erect herb/basal rosette	Leaf	EH	1456 ± 192.1
Pernettya prostrata	Ericaceae	Prostrate subshrub	Leaf	EH	716 ± 129.9
Chuquiraga jussieui	Asteraceae	Sclerophyllous shrub	Leaf, stem	WL, WH	1097.2 ± 107.5
Diplostephium rupestre	Asteraceae	Sclerophyllous shrub	Leaf, stem	EL, EH	1699.8 ± 261.5
Loricaria antisanensis	Asteraceae	Sclerophyllous shrub	Leaf, stem	EL, EH	1562.2 ± 237.6
Pentacalia peruviana	Asteraceae	Sclerophyllous shrub	Leaf, stem	WL, EL	670.2 ± 45.4

the patterns observed on the Antisana volcano. Leaf dimensions, shape, and pubescence modify boundary layer resistance to convective heat transfer by which efficient decoupling from air temperature can be achieved (Körner et al., 1983; Meinzer and Goldstein, 1985; Lambers et al., 2008). Because such traits are species-specific, they tend to covary with plant height and thus plant growth form (see Table 1 for leaf size of the species).

The vertical temperature profiles suggest that leaf temperature of most growth forms, and particularly shrubs, matched closely daily air temperature on the leeward, western side, which may result from effective convective heat transfer and/or transpiration cooling under high irradiance and pronounced leaf-to-air vapor pressure deficit. Since the temperature optimum of photosynthesis is usually close to mean growing season temperature (Fryer and Ledig, 1972; Lambers et al., 2008), thermal coupling seems to be a good strategy to maintain optimal conditions for carbon assimilation. Moreover, coupling may prevent overheating during sunny days since initial heat damage in alpine plants can develop within only one hour after the critical temperature threshold of about 30 °C is surpassed (Neuner and Buchner, 2012). Reduced daily air temperature fluctuations on the humid and cooler eastern side provide a distinctly narrower thermal envelope. In such conditions, low leaf-to-air vapor pressure deficits may limit transpiration cooling, and particularly taller plants along with cushion plants tend to be warmer than the ambient temperature (see also Ramsay, 2001). Upright shrubs and erect herbs with both sides of their leaves exposed to the atmosphere can absorb the diffusive radiation (prevailing on the windward, eastern side) more effectively than smaller plants with leaves attached at (or near) the ground (Körner et al., 1983). Moreover, some species, such as the shrub *Diplostephium rupestre*, tend to produce pubescent leaves in humid páramos, which may reduce heat convection. It was also suggested that heat release associated with condensation of water vapor on plant surfaces during the night may be responsible for their higher temperature compared to the air in humid, cloudy páramos (Ramsay, 2001).

Radiative heat loss during clear nights may result in leaf temperature decreases of more than 3 K below the air, occasionally resulting even in subzero values (Larcher and Bauer, 1981; Leuning and Cremer, 1988; Jordan and Smith, 1995; Sanchez et al., 2014). This is important because species distri-

butions in cold environments may be determined by night temperatures, and particularly by the ability to resist freezing events during periods of active growth (Körner, 2003; Scherrer and Körner, 2011). Since tropical alpine plants may experience freezing temperatures anytime during the year, frost survival is a critical issue. Temperature minima during our observations never dropped below (or even approached) temperatures causing 50% injury to leaves measured under laboratory conditions (Sklenář et al., 2010, 2012). Because we did not observe frost injury in the field and have not found any reports of it in the literature, we infer that freezing resistance of the páramo plants is sufficient to protect them from recurrent night frosts, although the situation may be different in woody species from the tree-line ecotone (Cavieres et al., 2000).

However, even without direct injury, frosts may affect plants due to the sensitivity of growth to low temperatures (Körner and Woodward, 1987). Prevention of intensive nighttime cooling by dense pubescence and nyctinastic leaf movement thus appears to be an important trait in some tropical alpine plants (Meinzer et al., 1994a; Miller, 1994; Beck, 1994). Cushion plants lack apparent anatomical features to prevent heat loss, but they experience the slowest rates of night cooling, the least extreme freezing temperatures, and the lowest frost frequency of all growth forms. Growing at the soil surface, the cushion plants gain heat from the soil heat flux during the night and accumulate radiant heat during the day (Robberecht and Junttila, 1992; Ramsay, 2001; Larcher, 2012). This contrasts particularly with tall shrubs, which lose heat from both sides of their leaves through outgoing long-wave radiation during clear nights and are essentially aerodynamically coupled with the air temperature (Jones, 1996). Therefore, shrubs may cool to subzero temperatures at a rate as high as 10 K h^{-1} at sunset, whereas cushion plants usually undergo relatively mild cooling at rates much below 4 K h^{-1}. These findings are in contrast to the short-term measurements of Diemer (1996), who observed that páramo cushion plants experienced lower night minima and higher frost frequencies than most of the other páramo growth forms, particularly shrubs.

Cushion plants were the most efficient growth form at decoupling from ambient temperature and heat accumulation in all climatic conditions on the mountain, which is in conformance with previous findings about alpine cushion plants elsewhere (Körner, 2003; Mark et al., 2008; Larcher, 2012). However, other low-statured herbs, such as *Valeriana* and *Werneria* performed almost as efficiently on the western, sunny side. Whereas efficient heat accumulation may be a useful strategy to deal with nighttime cooling, rapid warming from subzero temperatures under early-morning sunshine might present a problem due to enhanced transpiration demand (Meinzer et al., 1994b; Pfitsch, 1994; see also Sanchez et al., 2014). Short internodes of cushion plants and acaulescent rosettes apparently alleviate this problem by decreasing the length of the route of water transport to the leaves (Hedberg, 1964; Ramsay, 2001). Other tropical alpine plants avoid diurnal drought stress by increased capacitance (Meinzer et al., 1994b; Pfitsch, 1994), which might also be employed by the cushion and acaulescent species.

In terms of growing season mean temperatures, tropical alpine cushion plants seem to survive in colder environments than their temperate alpine counterparts. In our study, the mean temperatures of *Azorella* cushions were 6.3 and 3.6 °C at the upper western (4600 m) and upper eastern (4430 m) sites, respectively, which, due to the thermal aseasonality in the páramo are qualified estimates of their 12-month growing season means. The two sites were about 200 elevational meters below the distributional limit of *Azorella* on the Antisana volcano, which suggests that the uppermost cushion plants might grow at even lower mean temperatures. In contrast, *Saxifraga bryoides*, a cushion plant from a glacier foreland (2880 m) in the Austrian Alps experienced a mean temperature of 8.5 °C during 105 days of the temperate alpine growing season (Larcher and Wagner, 2011; Larcher, 2012). This difference suggests that the growing season mean temperature correlated with the occurrence of alpine treelines worldwide (Körner, 2003; Körner and Paulsen, 2004; Scherrer and Körner, 2011) may not be easily applicable to explain upper distributional limits of alpine plant growth forms, at least in the tropics.

Growth form is an important trait that determines the ambient temperatures experienced by plants in the equatorial high mountains (Squeo et al., 1991;

Ramsay, 2001), although the strength of its effect is conditioned on the prevailing climate. Predictions that low-statured plants would experience more extreme and more variable microclimates were supported only for the drier and sunnier western side of the Antisana volcano. On the humid and cloudy eastern side of the mountain, the effect of the growth form was much smaller. Under all climatic conditions, cushion plants performed better than any other growth form in terms of temperature decoupling and heat accumulation during the day and prevention of rapid cooling and extreme freezing temperatures during the night.

Acknowledgments

The research was supported by the Grant Agency of the Academy of Sciences, Czech Republic (IAA601110702) and by the Ministry of Education of the Czech Republic (MŠMT 0021620828). The study was part of the long-term research development project no. RVO 67985939. Hugo Navarrete (PUCE, Quito) is thanked for providing research facilities in Ecuador, and Ministerio del Ambiente is acknowledged for the research permit. Petr Macek helped in the field.

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MS submitted 2 November 2014
MS accepted 18 September 2015

APPENDIX

TABLE A1

Summary table of air, soil, and plant temperatures measured in 5 min intervals during July–August 2007; night means and day means were calculated for the periods 7:00 p.m. to 6:00 a.m. and 7:00 a.m. to 6:00 p.m., respectively.

West 4280 m (WL)	*Azorella pedunculata* leaf	*Valeriana rigida* leaf	*Lasiocephalus ovatus* stem	*Lasiocephalus ovatus* leaf	*Pentacalia peruviana* stem	*Pentacalia peruviana* leaf	*Chuquiraga jussieui* stem	*Chuquiraga jussieui* leaf	Soil −10	Soil −1	Air 20	Air 100
	3 cm	5 cm	6 cm	25 cm	50 cm	65 cm	80 cm	90 cm	−10 cm	−1 cm	20 cm	100 cm
	Cushion	Acaulescent herb	Erect herb	Erect herb	Shrub	Shrub	Shrub	Shrub				
Abs min	−2.3	−4.7	−7.4	−7.8	−6.8	−6	−6.6	−6.9	3.2	−0.5	−6.6	−5.9
Mean night min	−1.3	−2.4	−3.7	−3.8	−2.8	−2.3	−3	−3.3	4.9	0.9	−3.6	−2.8
Night mean	0	0	−1.1	−1.1	−0.6	−0.1	−0.7	−0.7	7.3	3.2	−0.5	−0.1
Mean	6.7	6.6	4.3	3.8	3.6	2.9	3.9	2.6	7.6	7.8	3.8	3.2
Day mean	13.5	13.4	9.8	8.8	7.8	6	8.5	6.1	7.9	12.5	8.2	6.6
Mean day max	26.7	28.9	22.1	20.6	15.9	11.1	16.6	13	10.8	23.1	18.1	14.5
Abs max	34.4	33.5	27.5	27	19.2	13.5	21.8	17.0	12.6	30.8	23.0	17.8

West 4600 m (WH)	*Valeriana rigida* leaf	*Azorella pedunculata* leaf	*Werneria nubigena* leaf	*Lasiocephalus ovatus* stem	*Gentianella foliosa* leaf	*Lasiocephalus ovatus* leaf	*Chuquiraga jussieui* leaf	*Chuquiraga jussieui* stem	Soil −10	Soil −1	Air 20	Air 100
	2 cm	3 cm	4 cm	6 cm	8 cm	18 cm	57 cm	59 cm	−10 cm	−1 cm	20 cm	100 cm
	Acaulescent herb	Cushion	Acaulescent herb	Erect herb	Erect herb	Erect herb	Shrub	Shrub				
Abs min	−5.6	−4.1	−5.8	−7.6	−7.7	−6.7	−4.9	−4.8	2.9	−1.3	−6.4	−4.9
Mean night min	−3.3	−2	−3.1	−4	−3.9	−3.7	−2.6	−2.4	4.9	0.1	−3.8	−2.6
Night mean	−0.9	0	−1.1	−1.3	−1.5	−1.1	−0.6	−0.5	7.3	2.3	−0.7	−0.3
Mean	5.5	6.3	4.9	5.3	4.8	4.3	2.4	2.6	7.3	7.6	3.3	2.6
Day mean	12.2	12.9	11.2	12.2	11.5	10	5.5	5.8	7.3	13.2	7.6	5.6
Mean day max	25	24.7	24.1	26.6	26.9	21.5	13.3	12.5	9.9	25.3	17.1	12.5
Abs max	31.7	33.1	34.4	35.6	35.6	30.1	21.3	17.8	12.4	39.4	22.6	16.3

East 4120 m (EL)	*Azorella aretioides* leaf	*Valeriana adscendens* leaf	*Lasiocephalus ovatus* stem	*Pentacalia peruviana* stem	*Lasiocephalus ovatus* leaf	*Pentacalia peruviana* leaf	*Diplostephium rupestre* stem	*Diplostephium rupestre* leaf	Soil −10	Soil −1	Air 20	Air 100
	2 cm	5 cm	7 cm	10 cm	15 cm	25 cm	35 cm	45 cm	−10 cm	−1 cm	20 cm	100 cm
	Cushion	Acaulescent herb	Erect herb	Shrub	Erect herb	Shrub	Shrub	Shrub				
Abs min	−2. 6	−4.2	−3.2	−3.4	−3.3	−3.7	−4	−4.5	3.5	1.1	−3.3	−2.9
Mean night min	−0.9	−0.9	−0.6	−0.6	−0.7	−0.8	−0.9	−1.3	4.6	2.9	−0.5	−0.1
Night mean	1.3	1	1.1	1.1	1.1	1.1	0.9	0.7	5.1	4.5	1.3	1.5
Mean	4.9	3.4	3	3.5	3	3.2	3.3	3.2	4.95	4.7	2.9	2.6
Day mean	8.7	5.8	4.9	5.9	5.1	5.5	5.8	5.8	4.8	5.2	4.5	3.7
Mean day max	18.5	12.4	10	12.4	10.5	11	11.8	13.5	5.4	7.4	8.9	6.9
Abs max	33.2	22.1	17.9	25.2	19.6	19.4	21.2	27.5	6.21	16.6	16.3	12.4

East 4430 m (EH)	*Azorella aretioides* leaf	*Pernettya prostrata* leaf	*Bartsia stricta* leaf	*Senecio nivalis* leaf	*Diplostephium rupestre* stem	*Diplostephium rupestre* leaf	*Loricaria antisanensis* stem	*Loricaria antisanensis* leaf	Soil −10	Soil −1	Air 20	Air 100
	2 cm	4 cm	5 cm	10 cm	20 cm	30 cm	50 cm	67 cm	−10 cm	−1 cm	20 cm	100 cm
	Cushion	Prostrate subshrub	Erect herb	Erect herb	Shrub	Shrub	Shrub	Shrub				
Abs min	−2.9	−3.1	−2.9	−3.4	−3	−3.1	−3.2	−3.3	0.5	−0.4	−3	−3
Mean night min	−1.4	−1.3	−1.2	−1.5	−1.3	−1.6	−1.4	−1.8	2.3	1.2	−1	−1
Night mean	−0.1	1	0.1	−0.1	0	−0.2	−0.1	−0.1	3.7	2	0.4	0.5
Mean	3.6	2.2	2.3	1.8	2.1	2.2	2.6	2.9	3.7	3.4	2	1.6
Day mean	7.6	4.3	4.6	3.9	4.4	4.8	5.3	5.6	3.8	4.6	3.6	2.7
Mean day max	17.6	11.1	11.7	10.9	10.8	12.5	12.1	15.3	5.7	7.3	9.1	6.8
Abs max	30.9	20.9	21.7	22	20.5	23.4	19.9	23.5	10	13.9	17.9	12.9

TABLE A2

Pearson correlation coefficients between plant mean cooling rates and plant mean night minimum temperatures and between their mean warming rates and mean day maximum temperatures. See text for site abbreviations.

	Sub-zero cooling		Above-zero warming	
Site	*r*	*p*	*r*	*p*
WL	0.849	<0.01	0.827	<0.05
WH	0.588	0.12	0.635	0.09
EL	0.323	0.43	0.899	<0.01
EH	0.33	0.43	0.732	<0.05

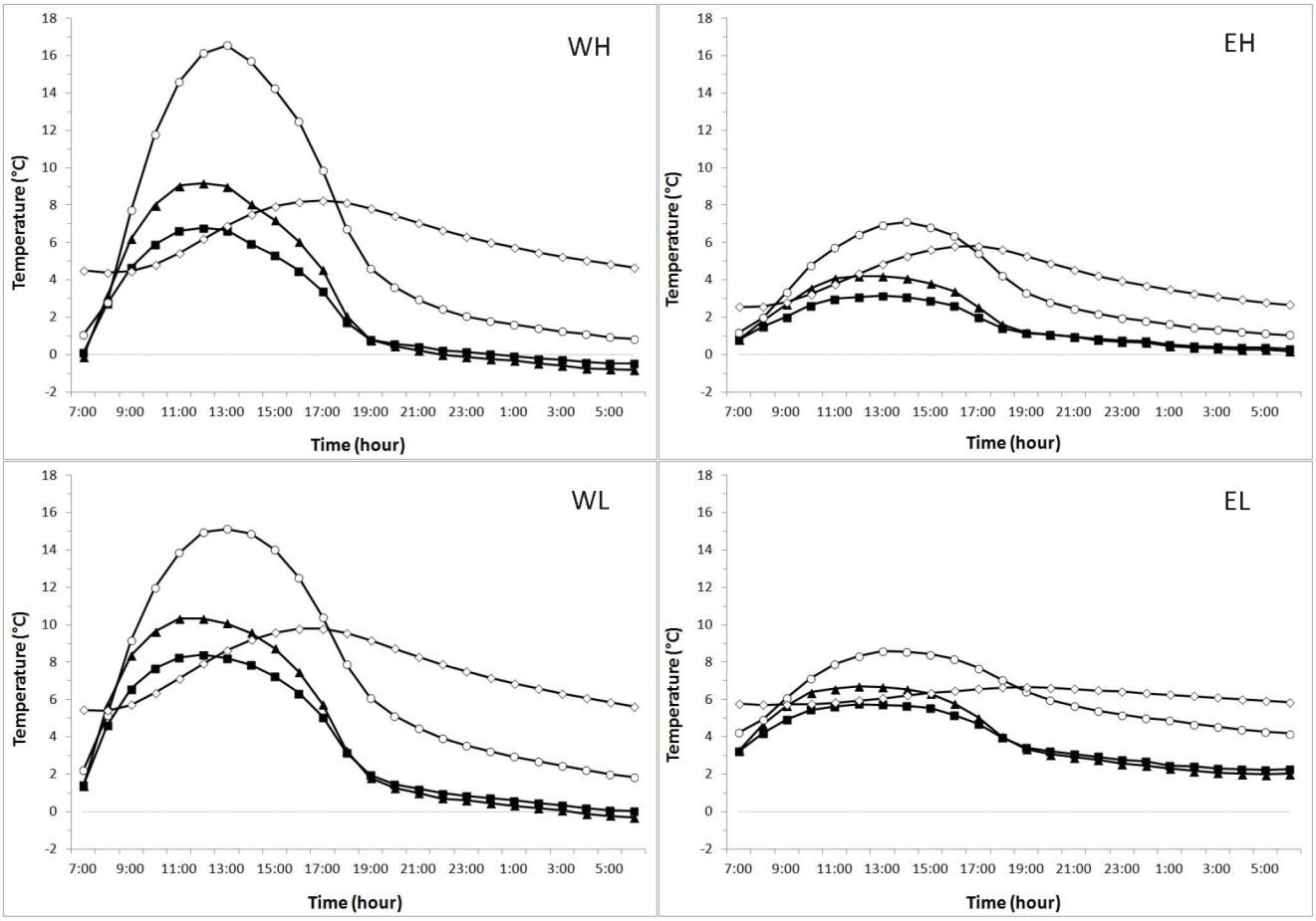


FIGURE A1. Daily course of mean air and mean soil temperatures measured during the period August 2007–July 2009 at WH (n = 460 days), WL (n = 720 days), EH (n = 170 to 277 days), and EL (n = 510 days). Square—air 100 cm, triangle—air 20 cm, circle—soil −1 cm, diamond—soil −10 cm. Presented are hourly means; dotted horizontal lines indicate 0 °C.

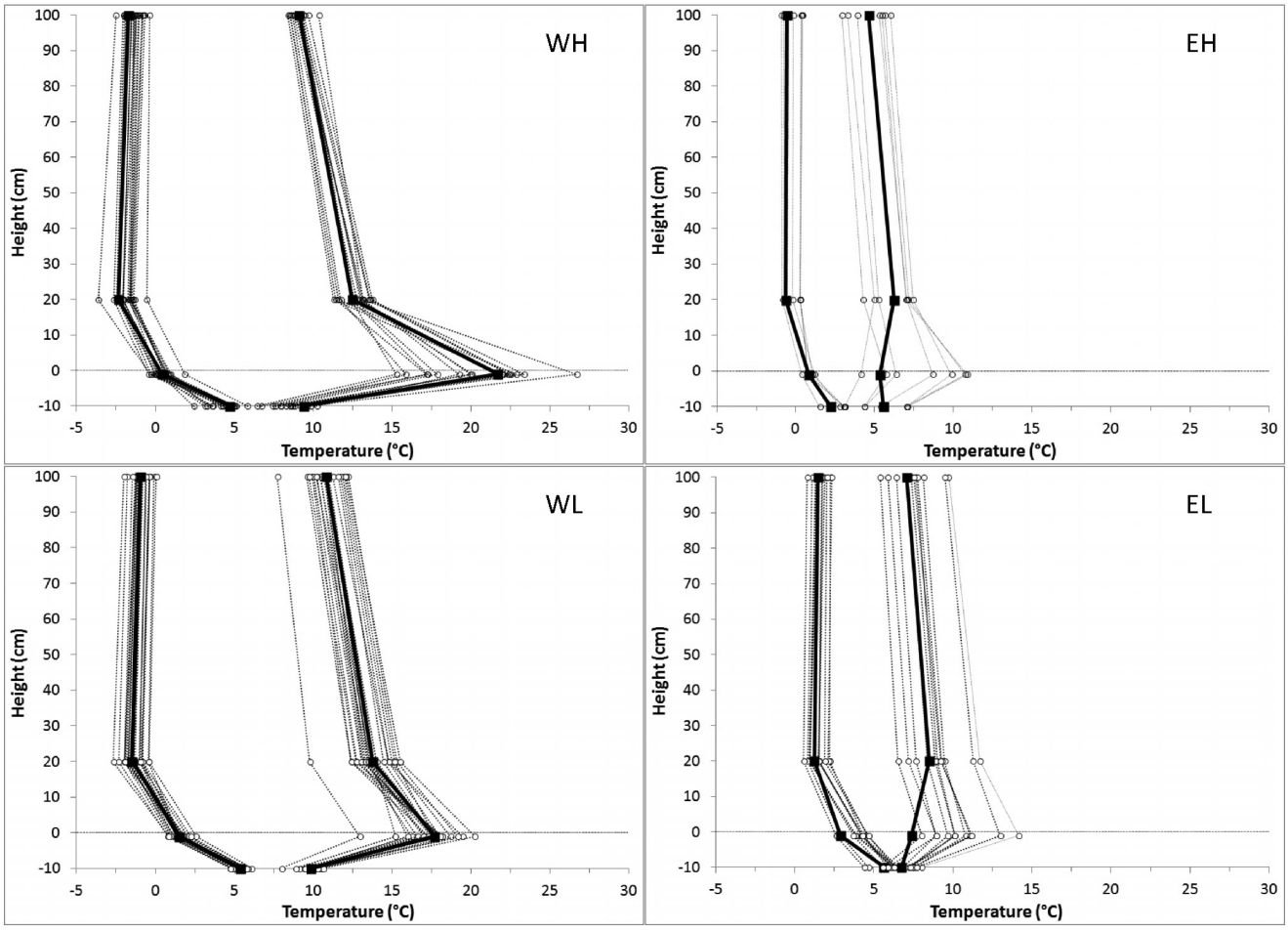


FIGURE A2. Seasonal course of mean daily minimum and mean daily maximum of air and soil temperatures at WH (upper left; n = 17 months between August 2007 and January 2009), WL (lower left; n = 23 months between October 2007 and August 2009), EH (upper right; n = 7 months between November 2007 and February 2008 and between July and October 2008), EL (lower right; n = 11 months between September 2008 and July 2009). Dotted horizontal line indicates 0 °C. The July–August 2007 period is presented in bold as 1-hour means (in contrast to 5-minute data in Fig. 1) to be consistent with the August 2007–July 2009 data. The outlying profile showing lower means for WL daily maxima is that of August 2009, and the two outlying profiles showing higher means for EL daily maxima are those of December 2008 and January 2009.

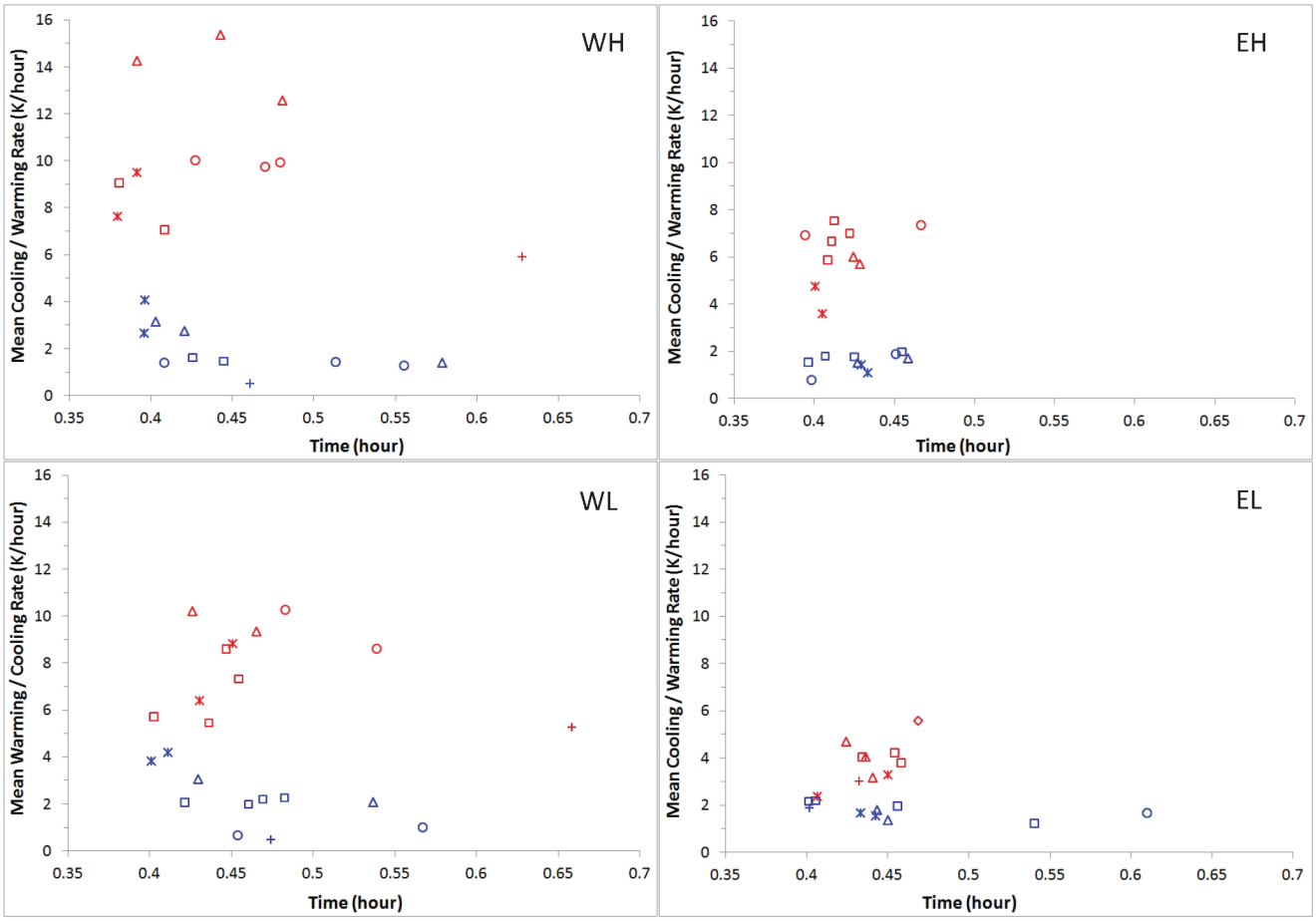


FIGURE A3. Mean cooling (blue) and mean warming (red) rates plotted against mean length of continuous temperature change for WH (upper left), WL (lower left), EH (upper right), and EL (lower right). Square—sclerophyllous shrubs; triangle—erect herbs/subshrubs; circle—cushions, acaulescent rosettes, and prostrate subshrubs. Star—air, cross—soil.

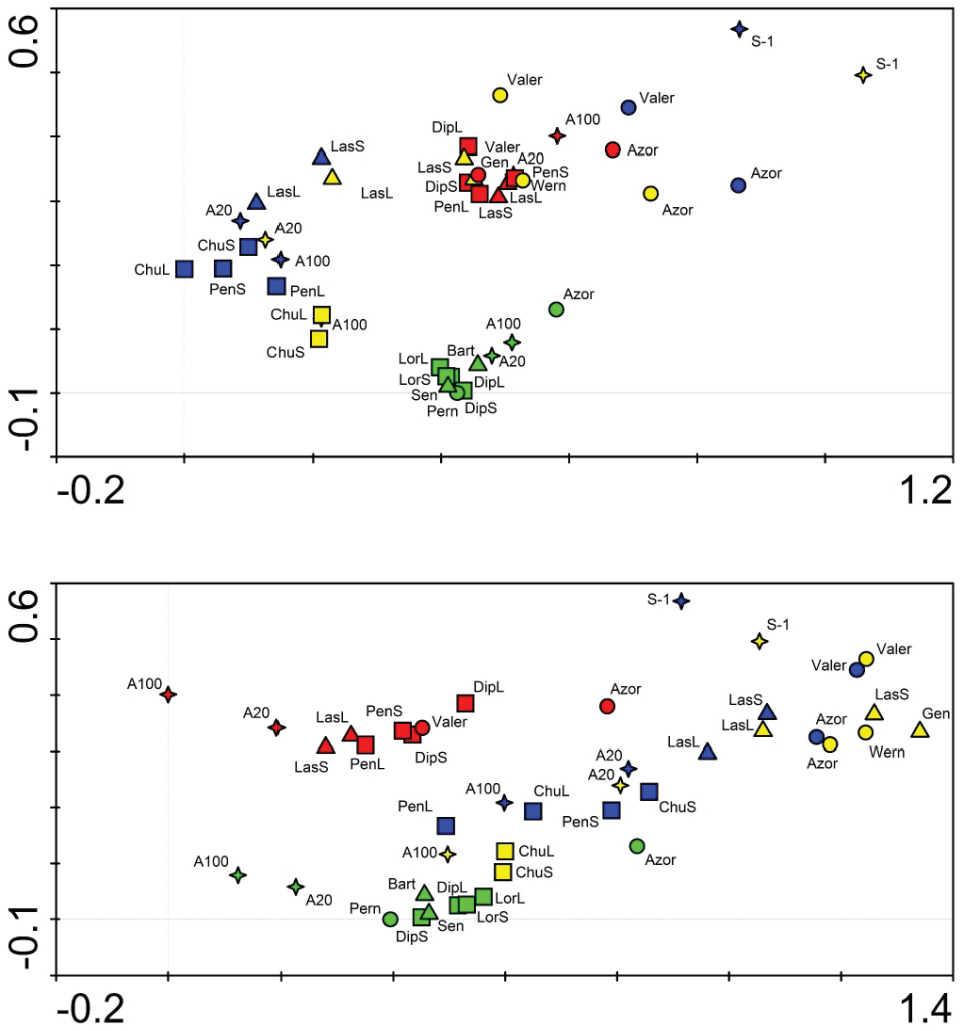


FIGURE A4. DCA ordination diagrams show relationships among temperature variables within and between sites; 2 and 3 DCA axes (above), 1 and 3 DCA axes (below); λ_1 = 0.144, λ_2 = 0.038, λ_3 = 0.01, total inertia = 0.272. Squares are shrubs; triangles are erect herbs; circles are cushion plants, acaulescent plants, and prostrate subshrubs. Blue—WL, yellow—WH, red—EL, green—EH. S and L after plant abbreviations refer to stem and leaf, respectively.