

TROPICAL ALPINE ENVIRONMENTS

Plant form and function

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Páramo microclimate and leaf thermal balance of Andean giant rosette plants

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Introduction

General climatic features of tropical alpine regions have been discussed in Chapter 1 of this volume. To reiterate, the nearly complete lack of temperature seasonality in tropical alpine zones is a key feature in distinguishing them from temperate alpine zones. The Andean páramo zone and similar zones in other tropical high mountains are characterized by high inputs of solar radiation in the presence of low inputs of thermal energy. This characteristic might be expected to present special circumstances from the standpoint of regulation of leaf thermal balance, in contrast to temperate alpine and desert habitats where both solar radiation and thermal energy inputs may be seasonally high. It has been suggested that some of the prominent morphological features found in giant rosette plants (see Chapter 1) represent adaptations for regulation of thermal balance under the special microclimatic conditions encountered in tropical mountains (Hedberg 1964; Larcher 1975).

Numerous studies have dealt with the importance of characteristics such as leaf absorptance to solar radiation, leaf angle and rate of transpirational cooling as determinants of leaf temperature under a given set of environmental conditions (Mooney *et al.* 1977; Geller & Smith 1982). However, fewer studies have examined the interaction between spatial and temporal changes in environmental variables and plant features thought to be important for regulation of leaf thermal balance (Smith & Nobel 1977; Ehleringer & Mooney 1978). Ideally, this type of study would be carried out with a single species or several closely related species of similar morphology known to occur over a wide range of environmental conditions (Ehleringer *et al.* 1981; Field *et al.* 1982). The focus of this chapter will be a discussion of certain morphological and behavioral features of Andean giant rosette plants of the genus *Espeletia*

and their influence on leaf thermal balance, under microenvironmental conditions that change both with elevation, and vertically within sites at a given elevation.

Elevational changes in environmental factors

General patterns of decreasing temperature with increasing elevation in the Venezuelan Andes and other tropical and temperate mountains have been described by Rundel in Chapter 2. In addition to temperature, several other factors that influence energy exchange between the leaf and its environment exhibit altitude-dependent changes. These factors affect leaf temperature through their influence on radiation, convection and evaporation, the principal mechanisms of energy exchange. Among the most important of these parameters are solar and longwave radiation, the volumetric heat capacity of the air (ρC_p), radiative resistance (r_r), and the diffusion coefficients for sensible heat (D_H) and water vapor (D_V) in air. The latter two exert a direct influence on resistances to convective and evaporative heat transfer, respectively. An appreciation of how these parameters may ultimately determine leaf temperature can be gained by examining standard energy balance equations (Monteith 1973; Campbell 1977; Jones 1992). Upon examining the equations it should become apparent that the overall effect of elevation on leaf temperature is not entirely predictable unless certain standard weather and microsite conditions are specified. Nevertheless, greater leaf-to-air temperature differences at higher elevations are predicted when simulations are performed using energy balance equations. Observations in temperate (Smith & Geller 1979; Field *et al.* 1982) and tropical mountains (Körner *et al.* 1983; F. Meinzer and G. Goldstein, unpublished observations) seem to confirm this.

The discussion in this section will be restricted to those physical properties of the atmosphere which show 'intrinsic' or consistent changes with elevation regardless of local variations in weather or microsite. Calculated changes in some of these properties along an altitude gradient in the Venezuelan Andes are shown in Fig. 3.1. While it is obvious that these factors vary dramatically between sea level and the upper limit of the páramo zone at 4600 m, it is also apparent that they change significantly within the páramo zone (*c.* 3000–4600 m). This points to the necessity of always including altitude corrections when calculations are to be performed with energy balance equations.

The increases in D_H and D_V with increasing elevation should favor

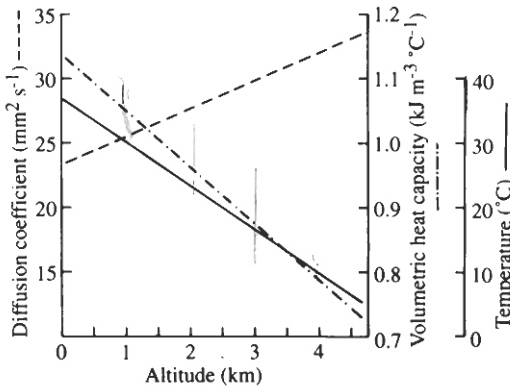


Figure 3.1. Calculated changes in mean maximum air temperature, the diffusion coefficient for sensible heat in air (D_H), and the volumetric heat capacity of the air (ρC_p) with increasing altitude in the Venezuelan Andes. The air temperature lapse rate determined from climatic data for the region, and a function describing decreasing pressure with increasing elevation were used to calculate D_H and ρC_p .

enhanced rates of convective and evaporative cooling, respectively. On the other hand, the reduction in ρC_p with increasing elevation would diminish the efficiency of convective cooling because of the reduced capacity of the air as a sink for sensible heat. ‘Resistance’ to radiative heat transfer,

$$r_r = \frac{\rho C_p}{4\epsilon\sigma T^3}$$

where ϵ is the longwave emissivity of the leaf, σ is the Stefan–Boltzmann constant and T is temperature in °K, should decrease with increasing elevation but the rate will depend on the air temperature lapse rate. In giant rosette plants elevational changes in characteristics, such as rosette geometry, leaf boundary layer thickness, absorptance to solar radiation and stomatal opening, interact with intrinsic changes in physical parameters of the external environment to determine patterns of regulation of leaf thermal balance.

Vertical profiles within sites

Typical vertical profiles of air temperature and wind speed for two páramo sites in the Venezuelan Andes are shown in Fig. 3.2. As expected, air temperatures are lower at the higher (4200 m) site. Differences in the

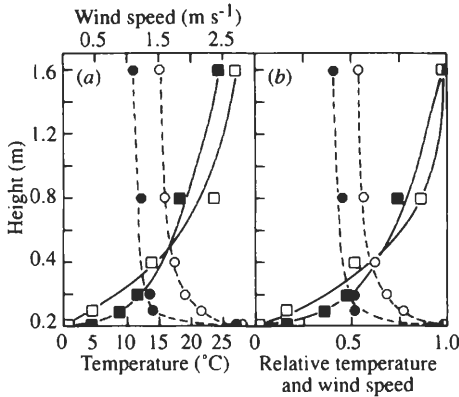


Figure 3.2. Representative vertical profiles (a), (b) of air temperature (○, ●) and wind speed (□, ■) for Piedras Blancas Páramo at 4200 m (closed symbols) and Mucubaji Páramo at 3550 m (open symbols). Data were collected between 1200 and 1300 h local time on clear days during January, 1983.

density and stratification of the vegetation at the two sites (Figure 3.3) may account for the different shapes of the vertical profiles. For example, although wind speeds at 1.6 m are similar for the two sites, the more open high altitude site shows an initial steeper rise in wind speed with increasing height (Figure 3.2b). This is reflected in a steeper decrease in air temperature with increasing height for the 4200 m site (Figure 3.2b). This vertical differentiation within sites could have important implications for regulation of thermal balance in leaves of juveniles and adults of caulescent *Espeletia* species, and in adults of co-occurring acaulescent and caulescent species.

Plant characteristics and leaf thermal balance

At the leaf level *Espeletia* species exhibit significant variation in a number of features that interact to influence leaf temperature. Among the most important of these features are leaf absorptance to solar radiation, boundary layer resistance to convective and latent heat transfer, and stomatal conductance to water vapor. Boundary layer resistance to heat transfer has two components. One of these is a variable aerodynamic component which is a function of leaf dimensions and wind speed. The magnitude of the other component is fixed and determined by the thickness of leaf pubescence. High boundary layer resistance, by impeding heat loss, would tend to raise leaf temperature. On the other hand, the



Figure 3.3. (a) Piedras Blancas Páramo and (b) Mucubaji Páramo near the sites where temperature and wind speed profiles shown in Fig. 3.2 were measured.

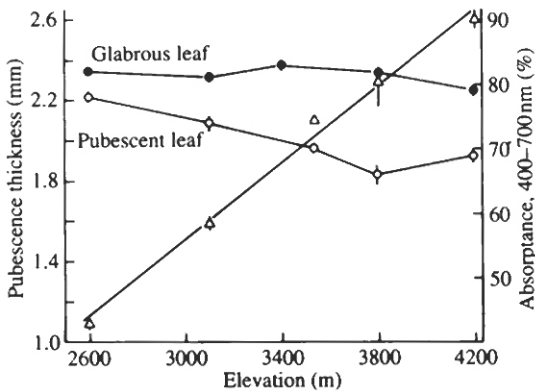


Figure 3.4. Thickness of pubescence covering the upper leaf surface (Δ) and absorbance to solar radiation (400–700 nm) for intact leaves (\circ) and leaves with their hairs artificially removed (\bullet) in five *Espeletia schultzei* populations along an elevation gradient. Bars represent \pm SE; pubescence $n = 80$; absorbance $n = 10$ (From Meinzer *et al.* 1985).

leaf pubescence also reduces leaf absorbance to solar radiation (Meinzer *et al.* 1985), which would tend to lower leaf temperature. In some *Espeletia* species, pubescence effects on boundary layer resistance outweigh those on absorbance to solar radiation, resulting in higher leaf temperatures than would occur in a glabrous leaf at high radiation loads (Meinzer & Goldstein 1985). Attenuation of photosynthetically active radiation by the pubescent layer has been predicted to exact a relatively high cost in terms of reduced carbon dioxide assimilation of *Espeletia* species under some environmental conditions (Goldstein *et al.* 1989).

Pubescence-induced temperature increases have previously been demonstrated for leaves (Wuenschel 1970) and other structures such as inflorescences (Krog 1955). In five populations of *E. schultzei* along an elevation gradient from 2600 to 4200 m, thickness of leaf pubescence increased dramatically while the associated decline in leaf absorbance to solar radiation was relatively small (Figure 3.4). These increases in fixed boundary layer thickness result in potentially higher leaf temperatures relative to air temperature at higher elevations (Meinzer *et al.* 1985). A similar pattern of increasing pubescence thickness and higher plant temperatures relative to air temperature with increasing elevation has been observed for pubescent *Puya* inflorescences in the Ecuadorian Andes (Miller 1986 and Chapter 10).

Some leaf characteristics of several *Espeletia* species are summarized in Table 3.1. Their net effect on leaf temperature is not easily predicted from

Table 3.1 *Summary of leaf characteristics for several Espeletia species*

Species	Elevation (m)	Absorptance 400–700 nm		Pubescence thickness (mm)	Leaf width (cm)	Resistance ratio ^b
		Intact	Glabrous ^a			
<i>E. timotensis</i>	4200	0.70	0.83	2.3	3.7	4.7
<i>E. lutescens</i>	4200	0.61	0.89	1.8	3.4	4.0
<i>E. schultzii</i>	4200	0.69	0.79	2.6	2.7	5.9
<i>E. spicata</i>	4200	0.60	0.79	0.9	1.9	3.0
<i>E. moritziana</i>	4200	0.63	–	1.0	1.4	3.6
<i>E. floccosa</i>	3550	0.61	–	0.4	1.1	2.2
<i>E. lindenii</i>	2800	0.71	–	0.2	2.4	1.4
<i>E. atropurpurea</i>	3100	–	0.87	0	6.0	1

^a Absorptances for glabrous leaves were obtained by plucking the pubescence from the leaf.

^b Resistance ratio is that of sensible heat transfer for intact and glabrous leaves, calculated at a wind speed of 1.5 m s⁻¹.

a simple inspection of the table. It is apparent that, although pubescence invariably decreases absorptance to solar radiation with respect to a glabrous leaf, there is no simple relationship between the thickness of the pubescence and leaf absorptance. The most useful indicators in Table 3.1 for assessing the balance between the effects of pubescence on boundary layer resistance and solar radiation absorption are probably the ratio of sensible heat transfer resistance for pubescent and glabrous leaves, and the difference in absorptance between intact leaves and leaves with their pubescence removed. The possibility that leaf pubescence may have different consequences for thermal balance in different *Espeletia* species will be discussed in the next section.

There is good evidence that the basic rosette geometry of *Espeletia* species strongly influences leaf thermal balance, especially near the apical region. Previous measurements have demonstrated considerable heating in the apical region of *E. schultzii* (Larcher 1975) and this has been attributed to a parabolic heating effect in the rosette, in which the apical bud would form the focus of a paraboloid and the older leaves would form the walls (Smith 1974). When features of rosette geometry in several populations of *E. schultzii* were used to calculate the foci of hypothetical paraboloids formed by the rosettes, it was found that a portion of the apical bud always fell within the focal region (Meinzer *et al.* 1985). It is questionable, however, whether a significant proportion of the warming

observed in apical leaves of Andean giant rosette plants arise from a true parabolic heating effect. Unlike a parabolic mirror which exhibits specular reflectance, the surface of pubescent *Espeletia* leaves exhibits diffuse reflectance. Furthermore, even if the rosette leaves were to form a specular surface, true parabolic heating could take place only when the sun's rays were parallel to the axis of the parabola formed by the rosette. Nevertheless, heat storage in the apical bud of species such as *E. schultzii* is promoted by the basic rosette geometry. Instead of receiving an unobstructed view of the sky and, therefore, the low effective sky temperature, the apical bud is surrounded by a longwave source radiating at a temperature often several degrees above air temperature. The amount of shortwave radiation incident on the apex would also be enhanced by reflection from the pubescent layer of the surrounding leaves.

As suggested earlier, intra- and interspecific differences in rosette height above the ground might be expected to have a significant effect on regulation of leaf temperature. Vertical air temperature profiles in páramo sites are such that temperature gradients of 10 °C between a few centimeters and 1 m above the surface are not uncommon (Figure 3.2). There is some evidence to suggest that within a given páramo site, giant rosette species may exhibit a surprising degree of homeostasis in temperature control regardless of plant height. At 3550 m *E. schultzii* and *E. floccosa* typically exhibit similar average leaf temperatures during periods of moderate to high incident solar radiation (Figure 3.5) despite the different regions of the air temperature profile in which their rosettes are situated. Thus, the nearly sessile rosettes of *E. floccosa* exhibit much smaller leaf-to-air temperature differences than do the taller (up to 1 m) rosettes of *E. schultzii*. Leaf characteristics of these two species probably account for much of the difference in regulation of leaf temperature with respect to air temperature (Table 3.1). While both species have pubescent leaves, the pubescence of *E. floccosa* is more reflective, and represent a less significant contribution to boundary layer resistance to heat transfer than that of *E. schultzii*. Simulations carried out with energy balance equations predict that under most conditions this should result in smaller leaf-to-air temperature differences for *E. floccosa*. It is interesting to note that, unlike the matted, 0.4 mm thick pubescence of its rosette leaves, pubescence of the inflorescence of *E. floccosa* is 2–3 mm thick. These inflorescences occupy a portion of the vertical profile similar to that of *E. schultzii* rosettes. Pubescence on *E. floccosa* inflorescences may have consequences similar to those suggested for Andean *Puya* species (Miller 1986 and Chapter 10).

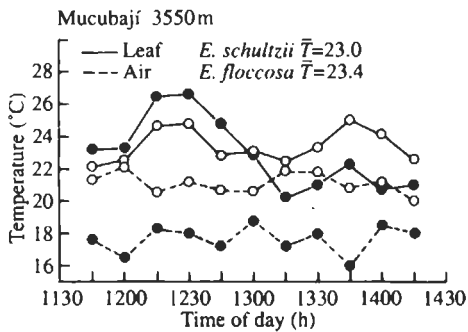


Figure 3.5. Courses of leaf temperature, and air temperature at mid-rosette height, for *Espeletia schultzii* and *E. floccosa* during a clear, warm dry season day in the Mucubají Páramo. Air temperatures were measured at 70 cm for *E. schultzii* and 15 cm for *E. floccosa*. Leaf temperatures for each species are averages of eight leaves at different positions in the rosette.

Significance of plant characteristics and patterns of regulation of plant temperature

It has been suggested that a principal consequence of variation in some of the plant features described above is to decouple plant temperatures and physiological processes from unfavorably low environmental temperatures (Meinzer *et al.* 1985). In high páramo sites environmental temperatures may frequently be suboptimal for translocation and growth. Leaf and apical bud temperatures in many *Espeletia* species are commonly 5–15°C above air temperature (Meinzer & Goldstein 1986). Since a typical Q_{10} for translocation and leaf expansion may be about 2, temperature increases of even a few degrees could be highly significant, especially in an environment lacking temperature seasonality. Some instances in which this hypothesis has been used to interpret and predict pattern of regulation of plant temperature and variation in plant features are discussed below.

The ability of the apical bud core of *Espeletia* species to remain above 0°C during the night is well documented (Smith 1974; Rada 1983). Nocturnal loss of stored heat is retarded by leaf nyctinasty and the presence of pubescence between successive layers of leaves which reduces heat conduction and convection from one leaf layer to the next. The principal adaptive consequence of this diurnal heat storage may be more favorable temperatures for apical growth and leaf expansion rather than protection from freezing, however. Apical bud tissue and young leaves of many *Espeletia* species have the capacity to avoid freezing by supercooling.

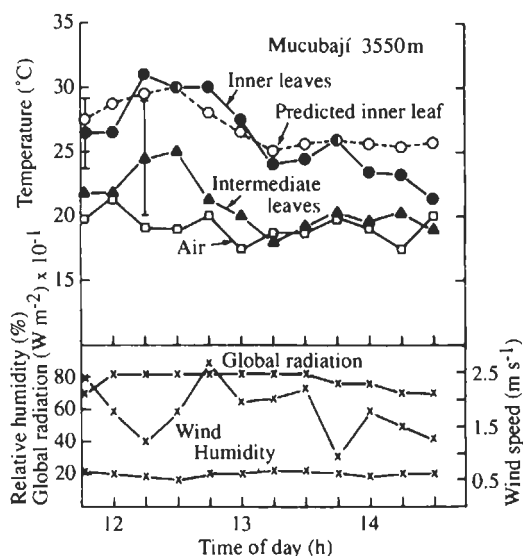


Figure 3.6. The influence of leaf position on temperature in an *E. schultzii* rosette during a portion of a clear warm day in the Mucubaji Páramo. Bars represent the largest $\pm SE$ ($n = 4$). Air temperature, humidity and wind speed were measured at mid-rosette height nearby (from Meinzer *et al.* 1985).

Freezing exotherms occur at temperatures well below minimum air and leaf temperatures commonly measured in the field (Goldstein *et al.* 1985; Rada *et al.* 1985).

On clear days, with their corresponding high levels of incident solar radiation, the temperature of the inner expanding and recently expanded rosette leaves is higher than that of older leaves with an intermediate position (Figure 3.6). Leaf-air temperature differences for individual inner rosette leaves are often as high as 15°C. This heat storage in the apical region may partly explain the observation that leaf production and growth rates in *Espeletia* species from high páramos are relatively rapid considering the low mean air temperature (Estrada 1984). A similar adaptive consequence, promotion of growth, has been proposed to result from northerly orientation and elevated apical temperature in the Atacama Desert cactus *Copiapo* (Ehleringer *et al.* 1980).

Potential increases in leaf temperature caused by high radiation loads in the apical region of *Espeletia* rosettes are further enhanced by variations in two features which exert their influence at the leaf level. Increasing leaf angle in the rosette from nearly horizontal senescent leaves to vertical expanding leaves corresponds to a gradient of increasing

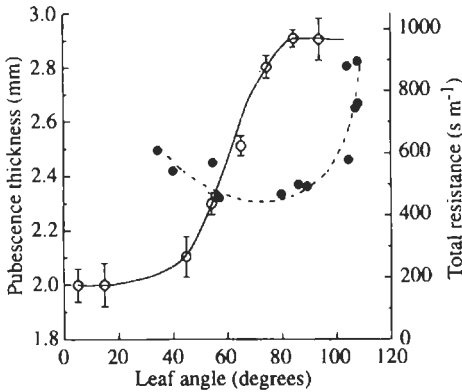


Figure 3.7. Pubescence thickness (○) and total diffusive resistance (●) in relation to leaf angle (inversely related to leaf age) in an *E. timotensis* rosette. Pubescence thicknesses at a given leaf angle are means (\pm SE) for 7–10 leaves. Angle is 0° for a horizontal leaf. Resistance measurements are for individual leaves (from Meinzer & Goldstein 1985).

thickness of pubescence and stomatal resistance (Figure 3.7). Energy balance equations predict that this gradient of increasing boundary layer and total diffusive resistance with decreasing leaf age would promote greater coupling between incident radiation and temperature in young leaves.

It is apparent that leaf pubescence is one of the key factors involved in regulation of leaf thermal balance of many *Espeletia* species. Leaf pubescence has been shown to be a major determinant of leaf temperature in many desert species where it typically results in reduced absorptance to solar radiation, reduced leaf temperature and thus lower transpirational losses (Smith & Nobel 1977; Ehleringer & Bjorkmann 1978; Ehleringer & Mooney 1978; Ehleringer *et al.* 1981). Thus, in desert plants, the influence of leaf hairs on solar radiation absorption predominates, while in many *Espeletia* species their influence on boundary layer resistance to heat transfer predominates. This suggests that evolution of leaf pubescence in plants of hot, arid habitats and high tropical mountains has occurred in response to dissimilar selective pressures. While both habitats are characterized by high incoming solar radiation, patterns of moisture availability and air temperature are quite different. During most of the year in Andean páramos, low temperatures, rather than lack of precipitation, limit water availability. Air temperatures are consistently low with no distinct favorable season for growth. Typical maximum air temperatures

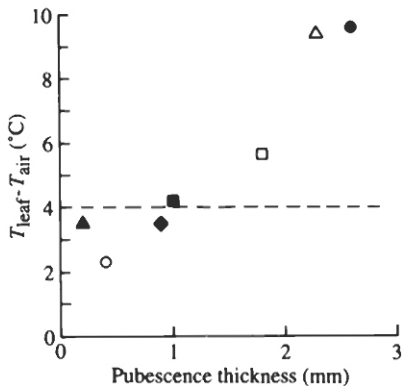


Figure 3.8. Predicted leaf-to-air temperature difference under simulated midday conditions at 3500 m for seven *Espeletia* species with different thicknesses of leaf pubescence. Leaf characteristics from Table 3.1 were used in the simulations. The broken line represents the predicted temperature difference for a completely glabrous *Espeletia* leaf. ●, *E. schultzei* 4200 m; △, *E. timotensis* 4200 m; □, *E. lutescens* 4200 m; ■, *E. moritziana* 4200 m; ◆, *E. spicata* 4200 m; ○, *E. floccosa* 3500 m; ▲, *E. lindenii* (2800 m). Stomatal resistance was held at 200 s m^{-1} , wind speed at 1.5 m s^{-1} , incident solar radiation at 800 W m^{-2} , air temperature at 15°C , and external humidity at 3.5 g m^{-3} for all simulations.

in warm desert habitats may exceed 40°C , at least 30°C above maximum air temperatures in high páramos. While water availability may be limited in both habitats, it is apparent that leaf temperature variations at the higher desert temperatures will have a much greater effect on leaf-to-air vapor pressure gradient and potential rates of transpiration due to the much steeper slope of the saturation vapor pressure curve near 40°C . The consequences of leaf pubescence in some *Espeletia* species and in desert plants are similar in the sense that in both cases, the pubescence represents a mechanism which decouples plant temperature from air temperature.

It is likely that variation in páramo microclimate, and therefore selective pressures, are sufficient to have caused variation in leaf pubescence and its consequences within the genus *Espeletia*. Figure 3.8 shows the results of a simulation in which pubescence thickness and other leaf characteristics of seven *Espeletia* species from several páramo sites were used to predict leaf-air temperature differences under identical clear, midday environmental conditions.

Since stomatal conductance was held constant for the simulation, the predicted temperature differences are due primarily to the opposing influence of pubescence on boundary layer thickness and absorptance to

solar radiation. Leaf dimensions varied among species, but at the wind speed used for the simulation variations in aerodynamic boundary layer did not have a significant effect on leaf temperature. If the leaf air temperature difference for an 'average' glabrous *Espeletia* leaf is used as a reference, it is predicted that for three of the species the presence of leaf pubescence results in lower leaf temperature relative to air temperature under conditions of high incident solar radiation. The species with the smallest predicted leaf-air temperature difference is *E. floccosa* whose leaves are located in the warmer air layers near the soil surface (Figure 3.5). The three species with the highest predicted leaf-air temperature differences are all caulescent, attaining maximum heights of 1.5–3 m and occurring at elevations up to 4200 m.

Conclusions

In the Andean páramo, variations in temperature that occur diurnally, altitudinally, and along vertical profiles within sites are much larger than seasonal temperature fluctuations. Within the páramo zone giant rosette members of the genus *Espeletia* experience a wide range of microclimates, especially with respect to temperature and wind. These conditions have led to a series of plant features that permit a substantial degree of thermoregulation mainly through heat storage and variable coupling between the plant and its temperature and radiation environment. Control of coupling between air temperature, incident radiation and leaf temperature is achieved principally through variations in leaf spectral characteristics and boundary layer resistance to convective heat transfer. This form of thermoregulation contributes to homeostasis of processes such as carbon dioxide assimilation, translocation and growth along environmental gradients.

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