

TROPICAL ALPINE ENVIRONMENTS

Plant form and function

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Goldstein, G., Meinzer, F.C., Rada, F.1994. Environmental Biology of a Tropical Treeline Species, *Polylepis sericea*. Capítulo 7. Tropical Alpine Environments: Plant form and function. Rundel, P.W., Smith, A.P, Meinzer, F.C. (Eds). Cambridge University Press, Cambridge, pp. 129-149.

Environmental biology of a tropical treeline species, *Polylepis sericea*

G. GOLDSTEIN, F. C. MEINZER and F. RADA

Introduction

It is likely that *Polylepis* (Rosaceae) occurs naturally at higher elevations than any other arborescent angiosperm genus in the world. The 15 species (Simpson 1979) are confined to the South American Andes where they occur primarily in tropical alpine environments. Some *Polylepis* species tend to form discrete forest stands reaching elevations over 5000 m, well above the upper continuous forest limit (timberline). Throughout their high altitude distribution most members of this genus are exposed to rigorous climatic conditions in which diurnal temperature variations by far exceed seasonal ones and night frosts are frequent.

The genus is exclusively arborescent (trees or shrubs), with individuals ranging in height from 1 m to no more than 30 m. The trees tend to have twisted, crooked stems and branches, particularly in open, exposed habitats. The form and branching pattern of some individuals resembles those of *krummholz* trees found in temperate alpine regions. The bark is deep red in color and consists of several layers of thin, exfoliating sheets. Although the exfoliating bark is particularly thick at the base of the stem or large branches, the insulating effect is by no means comparable to that of the marcescent leaves that surround the stem of the adjacent giant rosette plants (Smith 1979; Goldstein & Meinzer 1983). The leaves are compound and alternate but often appear whorled owing to the compression of internodes at the branch tips. The leaflets are small, dark green above and are covered with dense, silvery trichomes on the underside in several species. An extensive documentation of leaf anatomy and several important species-specific characters of potential adaptive value such as the degree of deciduousness is to be found in Simpson's (1979) revision.

Polylepis trees seldom grow as isolated individuals. They tend to form

small forest 'islands' above the continuous forest limit. Several hypotheses have been proposed to explain the distribution of *Polylepis* and its success at high elevations. Except for a few works suggesting that the patchy type of distribution is the result of past human activities (Ellenberg 1958a, b; Vareschi 1970), most studies attribute the success of *Polylepis* to the special microclimatic conditions associated with the rocky, protected habitats in which it occurs (Rauh 1956; Troll 1959; Walter & Medina 1969). Even though the species growing above 3300–3500 m are usually restricted to microenvironments that produce 'lower elevation' climatic conditions, they are still exposed to below-freezing temperatures at night. Such low temperatures would cause tissue injury and metabolic disturbances such as depressed photosynthesis and decreased stomatal reactivity (e.g. Fahey 1979; Takahashi 1981; Teskey *et al.* 1984) in plants not adapted to these conditions. After a critical review of all the published works up to 1978, Simpson (1979) concluded that the question of the ecological distribution of the genus will remain unsettled until both the physiology of *Polylepis* is better understood and the microclimatic conditions of the areas in which it occurs are more thoroughly documented.

Morphological adaptations in *Polylepis* are not as conspicuous as in the other arborescent growth forms of the high altitude American Tropics. For example, *Polylepis* trees do not possess an insulating layer of dead leaves around the stem, or a pith water reservoir, or a parabolic terminal rosette of leaves with nyctinastic movements as found in giant rosette plants (Meinzer & Goldstein 1986). This poses the question of how *Polylepis* trees prevent frost damage of the stem and leaf tissues and the formation of freezing-induced gas embolisms in the xylem, given that the trees are functionally active throughout the year.

The purpose of this chapter is to summarize and draw together recent studies on microclimatic conditions, frost resistance mechanisms, water relations and carbon economy in *Polylepis sericea* Wedd, the most abundant *Polylepis* species in the Venezuelan Andes. It is our belief that the success of *P. sericea* at high elevations is not solely a consequence of the microclimatic and physical conditions of the areas in which it occurs, but is also dependent on the special features of its carbon economy and frost resistance.

Microclimate and physical characteristics of *P. sericea* forest stands

The altitudinal air temperature lapse rate in the northern part of the Andes chain where *Polylepis sericea* grows is approximately -0.6°C per 100 m

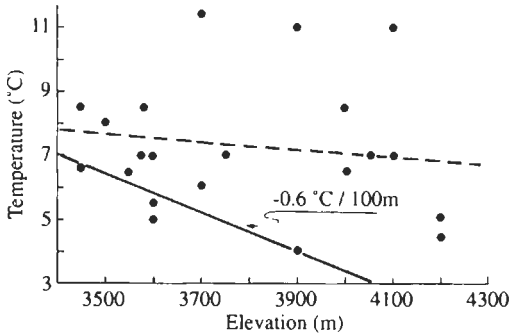


Figure 7.1. Mean air temperature as a function of elevation in *Polylepis sericea* forest stands above 3400 m. The solid line represents the air temperature lapse rate (-0.6°C per 100 m elevation) for the Venezuelan Andes (adapted from Arnal 1983).

elevation. Mean daily air temperatures in *P. sericea* forest islands (above 3000 m), however, do not follow this temperature gradient (Figure 7.1). The lack of correlation between air temperature and elevation in these forest stands suggests that special microclimatic conditions exist there. As expected, air temperature extremes are far less pronounced inside forest islands, than in the adjacent, open páramo (Figure 7.2). Minimum air temperatures inside *P. sericea* stands were usually more than 1.5°C higher and maximum temperatures were more than 3°C lower than in páramo sites dominated by caulescent giant rosette plants. These forest islands of *P. sericea*, which are generally found near massive rock outcroppings and talus slopes, can be considered as true thermal refugia where freezing temperatures are much less frequent than in the open páramo, even at altitudes up to 4500 m. The microclimatic information available suggests that both the shelter and the thermal stability provided by the rocks help to dampen diurnal air temperature variations even more than the presence of the tree canopy cover alone (Rada 1983).

It has been suggested that by allowing warm air to reach considerable depth through the crevices between the rocks, talus slopes provide better soil conditions than those of the surrounding tropical alpine habitats (páramo) (Walter & Medina 1969). Warmer soils should create better conditions for water and nutrient uptake and thereby improve establishment and growth of tree seedlings. Smith (1977) tested this hypothesis by transplanting seedlings of *P. sericea* in open páramo vegetation and sheltered rocky sites. Seedling mortality during the first year was 100% on bare soil. Seven transplanted individuals (14%) in rocky areas were still

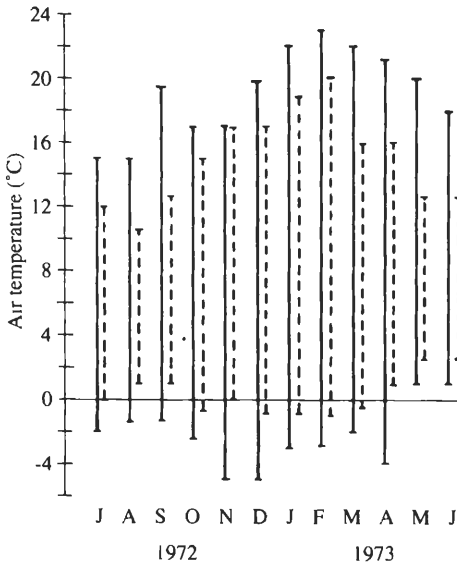


Figure 7.2. Absolute minimum and maximum monthly air temperature ranges in the Mucubaji Páramo at 3550 m (solid lines) and inside adjacent *P. sericea* stands (broken lines) from July 1972 to June 1973 (adapted from Azócar & Monasterio 1980).

alive one year after planting. With few exceptions, mortality was restricted to the dry period of December to April, when soil surface temperatures and soil moisture levels were at their lowest.

The temperature of *P. sericea* leaves also tends to exhibit reduced variation compared with leaves of giant rosette plants growing in the surrounding páramo (Figure 7.3). The leaves of *P. sericea* are small and the upper leaf surface is glabrous. In contrast, leaves of giant rosette plants are typically more than 19 times wider and both leaf surfaces are covered by a 2–3.5 mm thick pubescent layer. Energy balance models and experimental data indicate that leaf pubescence in the giant rosette species *Espeletia timotensis* exerts its principal influence on leaf temperature through increased boundary layer resistance to heat transfer rather than through reduced absorptance to solar radiation (Meinzer & Goldstein 1985). Under clear conditions at 4200 m elevation the temperature of a pubescent leaf would be higher than that of a non-pubescent one during the day. At night, reduced convective heat transfer from air to a pubescent giant rosette leaf would cause it to be cooler than a glabrous leaf. Figure 7.3 also shows that at night, temperatures of *E. timotensis* leaves are indeed

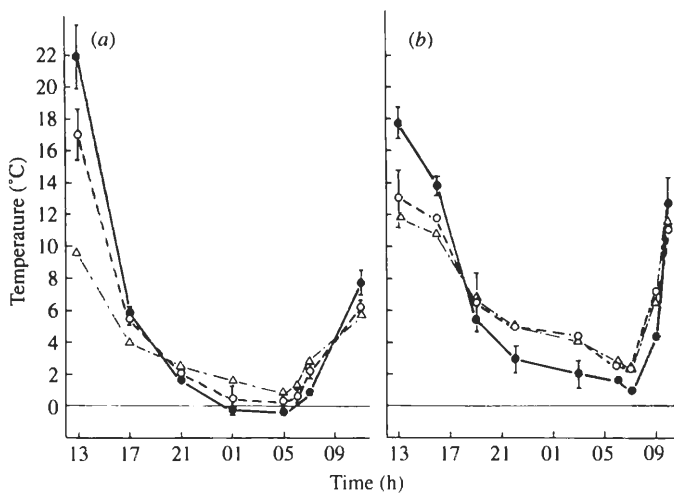


Figure 7.3. Daily courses of air temperature (Δ) and leaf temperature for *P. sericea* (\circ) and the giant rosette plant *Espeletia timotensis* (\bullet), during (a) a dry season day (December 1982) and (b) a wet season day (June 1982). Night-time temperatures were lowest during the dry season due to unimpeded radiational cooling.

consistently more than 1°C lower than those of glabrous *P. sericea* leaves. During the day this temperature pattern is reversed, particularly during periods of high incoming solar radiation.

Arnal (1983) described the physical characteristics of 256 forest islands in previously glaciated areas of the Venezuelan Andes where *P. sericea* occurs. His data failed to show a predominant slope orientation of the *P. sericea* sites (Figure 7.4) as had been suggested earlier by Walter & Medina (1969). More importantly, Arnal (1983) obtained a highly significant multiple linear relationship between tree density and increasing slope angle and number of rocks on the soil surface. This and the results of Smith's (1977) transplant experiment indicate that rocky substrates on relatively steep slopes provide good quality sites for seedling establishment and tree growth. This type of site not only dampens temperature fluctuations on a daily basis, but also reduces water loss from the soil surface, resulting in higher soil moisture levels during the dry season.

Carbon metabolism

Temperature, with its effects on carbon balance, is one of the most important factors determining the upper altitude limit of trees in temperate

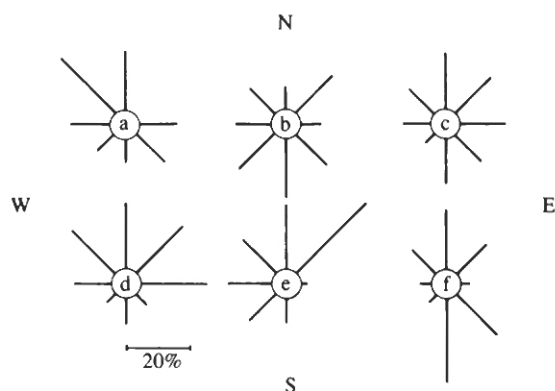


Figure 7.4. Percentage frequencies of slope direction of 256 *P. sericea* forest stands in six different páramo (tropical alpine) regions in the Venezuelan Andes: (a) Páramo de Los Conejos, (b) Páramo de la Culata, (c) Páramo de la Sierra Nevada, (d) Páramo de la Sierra de Santo Domingo, (e) Páramo de Piedras Blancas, and (f) Páramo el Escorial (adapted from Arnal 1983).

zone mountains (Tranquillini 1979). In some respects, high elevation tropical trees are exposed to even harsher environmental conditions than treeline species in cold temperate zones. While temperate trees can become dormant in winter and in a sense escape the most severe portion of the annual environmental regime, tropical treeline species are exposed to changes from summer-like to winter-like conditions in less than 24 hours. These conditions, which require maintenance of a continuously high level of physiological activity, may impose special constraints on the carbon economy of these trees. This section deals with the effects of temperature on photosynthesis and dark respiration in *Polylepis sericea*. Carbon balance data for other higher elevation tree species in the Venezuelan Andes will be cited for comparison.

At least four aspects of its carbon balance distinguish *P. sericea* from its temperate zone treeline counterparts and many other evergreen trees: (i) maximum photosynthetic capacity, (ii) upper temperature limit for net photosynthesis, (iii) temperature span between the upper temperature limit and the optimum and (iv) dark respiration rate. The photosynthetic capacity of *P. sericea* ($9 \mu\text{mol m}^{-2} \text{s}^{-1}$) is roughly twice that of temperate treeline species (Larcher 1969; Pisek *et al.* 1973; Tranquillini 1979). This maximum photosynthetic rate is attained at approximately 13°C (Figure 7.5), with the rate of photosynthesis falling off rapidly above and below this optimum temperature. The upper temperature limit for net photosynthesis in temperate treeline species is typically $35\text{--}45^\circ\text{C}$ with a span

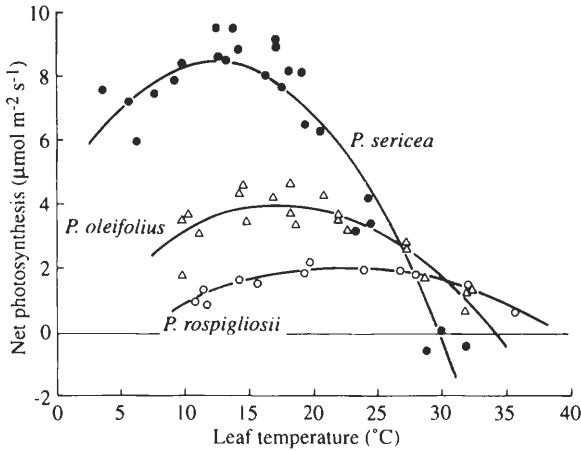


Figure 7.5. Temperature dependence of net photosynthesis in *Polylepis sericea* (●), *Podocarpus oleifolius* (△) and *Podocarpus rospigliosii* (○) as determined in an open gas exchange system. The quantum flux density in all the experiments was maintained at $1100 \mu\text{mol m}^{-2} \text{s}^{-1}$ (adapted from Jaimes 1985).

of 20–25 °C between the upper limit and the optimum (Pisek *et al.* 1973). This contrasts with an upper limit of only 30 °C in *P. sericea* (Figure 7.5) which is one of the lowest reported for any vascular plant species, and a span of only 17 °C between the upper limit and the optimum. Larcher (1975) reports a low temperature limit for net photosynthesis of -5°C for *P. sericea* transported from Venezuela to Austria. If the second degree polynomial regression curve fitted to the points in Fig. 7.5 is extrapolated to zero net assimilation, the corresponding leaf temperature is -5°C . Such cold daytime temperatures are seldom, if ever, observed in *P. sericea* forest islands, even at its absolute altitudinal limit of 4500 m in Venezuela. Thus, if photosynthesis is not inhibited by short night-time periods of subzero temperatures, positive carbon balance could always be maintained when photosynthetically active radiation levels are above the light compensation point.

The temperature dependence of photosynthesis has also been determined for *Podocarpus oleifolius* and *P. rospigliosii* (Figure 7.5), two dominant coniferous species growing in the Venezuelan Andes (Jaimes 1985). The elevational range of *P. oleifolius* is 2200–3300 m, while *P. rospigliosii* occurs at lower altitudes between 1700 and 2500 m. As could be expected, the temperature optimum for photosynthesis increases with decreasing altitudinal range as does the upper temperature compensation point;

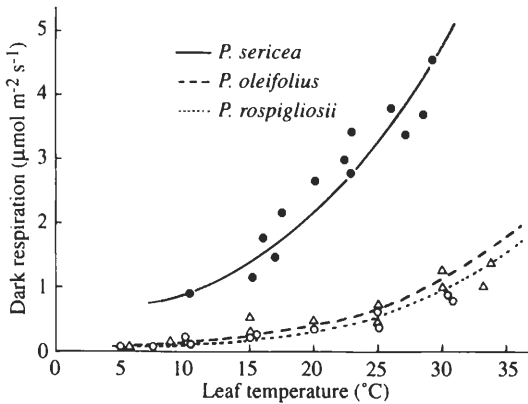


Figure 7.6. Temperature dependence of dark respiration in *Polyilepis sericea*, *Podocarpus oleifolius* and *Podocarpus rospigliosii*. Curves are exponential regressions fitted to the data (obtained from F. C. Meinzer and G. Goldstein, unpublished data, and from Jaimes 1985).

however, the temperature span between the optimum and the upper compensation point remains small. The temperature optima for photosynthesis of the three species tend to coincide with the mean maximum temperatures at the sites where the material was collected, and this gradient follows approximately the same lapse rate as that of air temperature (-0.6°C per 100 m elevation in the Venezuelan Andes).

The temperature dependence of dark respiration in these three species follows a typical positive exponential function over the temperature range in which no thermal injury occurs (Figure 7.6). The respiration rate at 20°C , a standard temperature often used for comparison among species, is $2.3 \mu\text{mol m}^{-2} \text{s}^{-1}$ in *P. sericea*, several times higher than that of the two lower elevation coniferous tree species. Temperate high elevation tree species are noted for having higher dark respiration rates than lowland species. However, dark respiration on a leaf area basis is several times higher in *Polyilepis* than in its temperate high elevation counterparts, even at the low night-time temperatures that prevail in its habitat. These respiration rates resemble those for winter deciduous trees rather than evergreens (Larcher 1969; Pisek *et al.* 1973; Goldstein 1981). The respiration rates of the two *Podocarpus* species are similar to those of temperate montane species.

These features of carbon balance in *P. sericea* probably reflect a response to the selective pressures operating in cold tropical environments with frequent freezing temperatures. For example, a high rate of dark

respiration in plants from cold climates has been cited as an adaptation permitting adequate release of chemical energy at low temperatures for repair of cellular damage, particularly membrane damage due to chilling and freezing (Tranquillini 1979; Levitt 1980). Such injury may be cumulative over time and its severity increased if exposure to low temperatures is followed by exposure to high light intensity (Berry & Bjorkman 1980). In the high Venezuelan Andes, frequent subfreezing night temperatures are usually followed by clear skies and, therefore, high irradiance conditions in the morning hours, particularly during the dry season. The especially high respiration rate of *P. sericea* may be in part a response to daily exposure to periods of chilling or freezing temperatures followed by exposure to high light intensities.

P. sericea leaves exhibit large diurnal changes in osmotic potential with maximum osmotic concentrations occurring during the early morning at the time of minimum temperatures (see below, p. 140). This increase in osmotically active solutes at night implies an investment of energy and, therefore, would require an adequate dark respiration rate at low night temperatures. Although one of the species used for comparison (*Podocarpus oleifolius*) occurs at the upper limit of continuous forests (3300 m) its respiration rate is much lower than that of *P. sericea*. The continuous forest limit in Venezuela also coincides with the altitude at which night frosts begin to occur (Monasterio & Reyes 1980). Thus, the seemingly abrupt change in respiration rates with increasing elevation may reflect the rapid increase in risk of night frosts and consequent need for repair of injured tissues. A high respiration rate coupled with a relatively high photosynthetic capacity may be a prerequisite for tree survival at high elevations in the tropics.

It is not known to what extent photosynthesis and respiration in *P. sericea* show temperature acclimation. Temperate treeline and montane species usually show a considerable capacity for photosynthetic and respiratory temperature acclimation (Pisek *et al.* 1973; Berry & Bjorkman 1980; Black & Bliss 1980; Mooney & West 1964). As *P. sericea* trees are exposed only to diurnal and not seasonal temperature fluctuations, there would be little selective advantage in possessing mechanisms for acclimation to long-term temperature changes. The 17 °C difference between the photosynthetic optimum and the upper temperature limit of 30 °C suggests that *P. sericea* may indeed possess little flexibility in this regard. Furthermore, the range of maximum temperatures along the entire altitudinal range of *P. sericea* in Venezuela (11 °C) is much smaller than seasonal fluctuations in maximum temperature at a constant altitude in

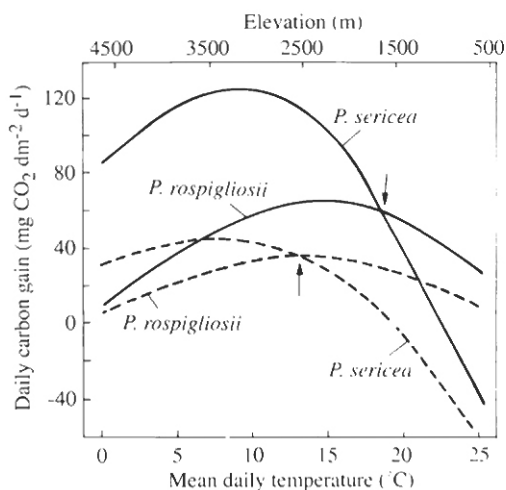


Figure 7.7. Calculated daily carbon balance as a function of mean daily temperature (and elevation) in *Polylepis sericea* and *Podocarpus rospiglosii*. Simulations were obtained for clear days (—), and days with afternoon clouds (---) typical of the Venezuelan Andes. Arrows indicate mean daily temperatures and elevations that produce the same simulated carbon gain in both species under clear and cloudy days.

temperate zone mountains. The two tropical coniferous species used here for comparison, and tropical savanna trees (Sarmiento *et al.* 1985) also have small temperature spans between their temperature optima and upper limits for positive net photosynthesis. Furthermore, preliminary transplant experiments indicate that seedlings of the two coniferous species show almost no short-term photosynthetic temperature acclimation responses (G. Goldstein and F. Meinzer, unpublished data). All of these results suggest that the lack of photosynthetic temperature acclimation potential may be a general phenomenon in trees of tropical mountains.

The lack of seasonal temperature variation and acclimation potential simplify carbon budget calculation. When a mathematical model of carbon balance of *P. sericea* and *Podocarpus oleifolius* is simulated for days with different mean air temperatures and afternoon overcast conditions (Figure 7.7), typical of the high Venezuelan Andes, it is found that below 2600 m *P. oleifolius*, in spite of its lower photosynthetic capacity, has a more positive carbon balance than *P. sericea*. This is approximately the lower altitudinal limit of *P. sericea* and the point in which *Podocarpus*

oleifolius should outcompete *P. sericea* for carbon resource gain. Predicted carbon balance in *P. sericea* deteriorates rapidly with decreasing altitude due to the high dark respiration rate and steep drop in photosynthetic rate above the optimum temperature. On the other hand, net assimilation is still very positive at the upper distribution limit and, therefore, other factors may be limiting *P. sericea* growth above this elevation. Thus, in the absence of significant temperature acclimation as suggested above, some of the features of carbon metabolism that may explain the success of *P. sericea* at high elevations may also partially explain its lower altitude limit.

Frost resistance mechanisms

Plants in high tropical mountains exhibit a wide range of frost resistance mechanisms (Sakai & Larcher 1987; Beck, Chapter 5). For example, leaves of *Draba chionophila*, a small rosette plant found at the highest altitudes reported for vascular plants in the Venezuelan Andes (c. 4700 m), as well as leaves of Afroalpine *Senecio* and *Lobelia* plants, are freezing-tolerant, with freezing injury appearing only at temperatures lower than the temperature at which extracellular ice formation begins (Azócar *et al.* 1988; Beck *et al.* 1982, 1984). In Andean giant rosette plants, on the other hand, leaf, bud and internal stem tissues are protected solely by freezing avoidance mechanisms (Goldstein *et al.* 1985; Rada *et al.* 1985a). In many cases freezing avoidance offers adequate protection against the slight frosts that occur in tropical high mountains throughout the year (Larcher 1982). Of the five possible freezing avoidance mechanisms described by Levitt (1980), (i) freezing point depression through decrease in osmotic potential, and (ii) supercooling are found in *P. sericea*.

Leaves of *P. sericea* exhibit diurnal osmotic adjustment of the order of 0.4–1.0 MPa, depending on the minimum night temperature. Minimum leaf osmotic potential (Ψ_{π}) and therefore lowest tissue freezing point is generally attained at 0500–0600 h, coinciding with minimum leaf temperatures rather than minimum leaf water potential (Ψ_L , Figure 7.8). Changes in levels of soluble carbohydrates seem to correspond to the pattern of changing Ψ_{π} (Figure 7.8), suggesting that the decline in Ψ_{π} throughout the night results, at least in part, from the accumulation of soluble sugars in the leaves. The diurnal variation in freezing point of the cell sap corresponding to the osmotic fluctuations shown in Figure 7.8 would be 0.5–1.0°C. This small enhancement of freezing avoidance may in itself be important from an ecological standpoint because in the sites where *P.*

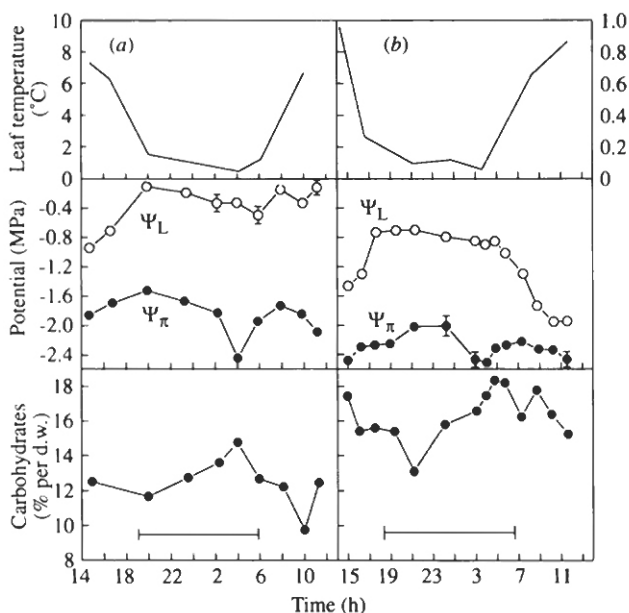


Figure 7.8. Daily courses of leaf temperature, leaf water potential (Ψ_L), leaf osmotic potential (Ψ_π) and soluble carbohydrate levels for *P. sericea* during (a) a wet season day (20 December 1983) and (b) a dry season day (13 February 1984). The horizontal segments in the lower panel indicate the night-time period (from Rada *et al.* 1985b).

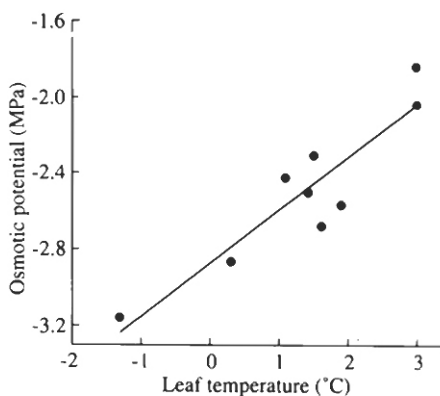


Figure 7.9. Minimum night-time osmotic potential in relation to minimum leaf temperature of *P. sericea*. The solid line represents a linear regression fitted to the data ($r^2 = 0.82$) (from Rada *et al.* 1985b).

sericea grows daily temperature fluctuations are not very pronounced and minimum temperatures do not fall much below 0°C. The magnitude of the nocturnal decline in Ψ_{π} of *P. sericea* leaves appears to be directly related to minimum leaf temperature rather than to changes in Ψ_L (Figure 7.9). This contrasts with water stress-induced osmotic adjustment reported for many other species. Tyree *et al.* (1978) also observed a relationship between Ψ_{π} and temperature in which Ψ_{π} of *Tsuga canadensis* leaves showed a marked seasonal decrease as temperatures fell below 0°C with the onset of winter.

P. sericea leaves do not exhibit freezing tolerance. When leaf temperature is experimentally lowered at a constant rate, the points of 50% tissue injury and release of heat of fusion by freezing of supercooled water approximately coincide (−6.0 to −8.0°C). This poses a question about the adaptive significance of the freezing point depression observed in this species, since supercooling appears to be effective well below the lowest calculated freezing point of the leaf tissue (−3.8°C, corresponding to −3.2 MPa osmotic potential). The transient supercooled state, however, is extremely labile and can seldom be maintained for more than a few hours under natural conditions (Larcher 1982). Thus, the temperature-induced changes in the freezing point of *P. sericea* leaves may serve as a safety valve to prevent tissue freezing and damage when supercooling is no longer effective (Rada *et al.* 1985b). It is interesting to note that leaves of caulescent giant rosette species have a greater supercooling capacity than *P. sericea*, while *Podocarpus oleifolius* growing near the upper continuous forest limit has a much smaller supercooling capacity (Table 7.1). Giant rosette plants are usually exposed to much lower nightly temperatures than *P. sericea* while *Podocarpus oleifolius* is seldom exposed in its habitat to freezing temperatures. Of these species, only *P. sericea* exhibits temperature-induced changes in osmotically active solutes (Rada 1983).

Results from laboratory experiments suggest an alternative interpretation concerning the ecological significance of the variable freezing point depression response described above for *P. sericea*. Plants which were preconditioned at different temperatures showed three clear responses to decreasing temperature (Figure 7.10): (i) a decrease in osmotic potential, (ii) increase in soluble carbohydrates, and (iii) a decrease in supercooling point (increase in supercooling capacity). The approximately 0.5 MPa decrease in Ψ_{π} over the temperature range shown in Fig. 7.10 would result in only a 0.41°C lowering of the freezing point as derived from the van't Hoff and Raoult equations. If the relationship between the lowering of

Table 7.1 Supercooling capacity and freezing injury temperature in several tissues of two tree species (*Podocarpus oleifolius* and *Polylepis sericea*) and two giant rosette species (*Espeletia spicata* and *E. timotensis*) from the Venezuelan Andes

Species	Organ or tissue	Supercooling capacity (°C)	Freezing injury (°C)	Lowest temperature recorded (°C)
<i>Podocarpus oleifolius</i>	leaf	-4.0	-1.8	3.8
	bud	-2.7		
	stem	-3.8		
<i>Polylepis sericea</i>	leaf	-7.3	-8.2	-0.3
	bud	-11.4		
	stem	-7.6	-8.9	-0.8
<i>Espeletia spicata</i>	leaf	-15.8	-13.8	-2.8
	bud	-5.4	-5.0	2.0
	stem pith	-4.8	-5.0	3.0
	root	-4.1	-4.5	4.0
<i>Espeletia timotensis</i>	leaf	-13.7	-12.8	-1.5
	bud	-6.0	-4.0	2.0
	stem pith	-5.0	-4.8	2.0
	root	-5.4		7.0

the supercooling point and the decrease in the freezing point observed in the laboratory holds under natural conditions, then low temperature preconditioning will produce a larger decrease in the supercooling point than in the freezing point (Figure 7.10). Zachariassen (1982), working with insect hemolymph, found that supercooling point depression was associated with the accumulation of low molecular weight cryoprotective substances, such as glycerol, sorbitol, mannitol and others, but could also be related to sugars such as glucose. The increase in the soluble carbohydrate levels observed at night in *P. sericea* may indicate that these sugars are acting as a cryoprotectant to help decrease the supercooling point or to make supercooling more effective under natural conditions.

In summary, in an environment with frequent, slight frosts, the large temperature-driven fluctuations in osmotic potential observed in *P. sericea* leaves, combined with their relatively high supercooling capacity, appear to be the principal means of avoiding freezing, and therefore tissue injury. At 4500 m, the upper altitudinal limit of *P. sericea*, the minimum

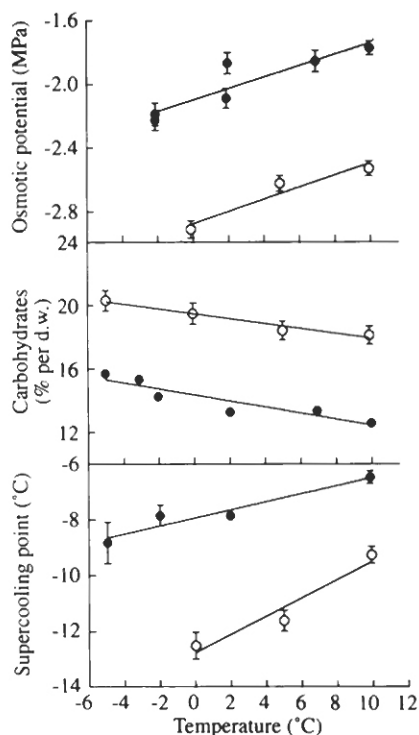


Figure 7.10. Leaf osmotic potential, soluble carbohydrate content and supercooling points obtained for *P. sericea* as preconditioning temperature was decreased in approximately 5 °C steps under controlled conditions. Plant material was obtained 20 February 1984 (●), and 9 April 1984 (○). The latter sampling day coincided with the end of an unusually long dry season (from Rada *et al.* 1985b).

absolute air temperature is approximately -6°C . At this temperature the combined effects of osmotically induced freezing point depression and enhanced supercooling capacity may no longer be effective as a freezing avoidance mechanism under natural conditions, thus allowing leaf tissue injury and metabolic disturbance to occur.

Water relations

Stomatal conductance in *P. sericea* is typically high in the morning hours, sometimes even higher than at midday (Figure 7.11), suggesting that cold night-time temperatures do not reduce stomatal opening capacity during the subsequent day. In temperate zone tree species, on the other hand, exposure to relatively brief periods of chilling or freezing temperatures

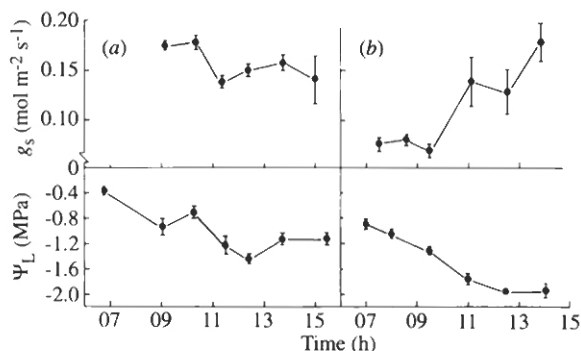


Figure 7.11. Daily courses of stomatal conductance (g_s) and leaf water potential (Ψ_L) of *P. sericea* on two different days during the dry season. Air temperature fell slightly below 0°C in (b) during the previous night.

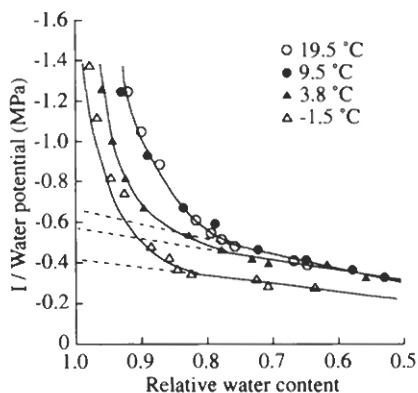


Figure 7.12. Representative pressure–volume curves for *P. sericea* leaves preconditioned at various temperatures during 24 hours. Leaves were kept at their preconditioning temperatures during pressure–volume measurements.

can cause stomatal closure (Teskey *et al.* 1984), and decreased enzymatic activity (Bauer *et al.* 1975). In these species decreased transpiration as winter approaches appears to be a mechanism by which desiccation is avoided during the period when the soil may be frozen, rendering the soil water unavailable. Such a mechanism in tropical treeline species, however, could be detrimental for total annual carbon balance, as prolonged stomatal closure following exposure to night-time chilling or freezing temperatures would not only reduce water vapor loss but also CO_2 uptake.

As described earlier, cold air temperatures induce diurnal fluctuations

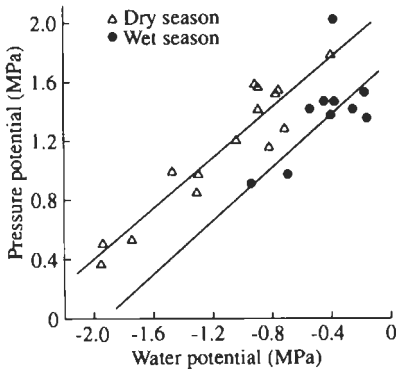


Figure 7.13. Turgor in relation to leaf water potential for a dry season day (13 February 1984), and a wet season day (20 December 1983). Turgor was calculated by subtracting osmotic potential determined psychrometrically from leaf water potential measured with a pressure chamber. The lines are regressions fitted to the data ($r = 0.94$, $p \leq 0.01$ for \triangle ; $r = 0.84$, $p \leq 0.01$ for \bullet) (from Rada *et al.* 1985b).

in osmotic potential of *P. sericea* (Figures 7.8, 7.9). Figure 7.12 shows representative pressure–volume curves determined for leaves from plants preconditioned in the laboratory at one of four different temperature levels for several hours. In plants preconditioned at temperatures above 9°C the osmotic potential at full turgor was -1.5 MPa compared with -2.4 MPa in plants preconditioned at -1.5°C . This 0.9 MPa decrease in osmotic potential after preconditioning at below-zero temperatures provides additional evidence that short-term osmotic changes under field conditions are driven by temperature.

Transient diurnal water stress, on the other hand, does not appear to induce short-term osmotic adjustment and consequent turgor maintenance in *P. sericea* (Figure 7.13). On a seasonal basis, however, maintenance of higher levels of turgor in *P. sericea* via osmotic adjustment does seem to be significant (Figure 7.13). Rada *et al.* (1985b) described a decrease in osmotic potential of almost 1.0 MPa between the end of the wet season in November and middle of the dry season in February (Table 7.2). This adjustment would reduce the likelihood of turgor loss during extraction of water from drying soils. Neither diurnal nor seasonal osmotic adjustment has been found in high elevation *Espeletia* species subjected to similar annual patterns of soil water availability.

The effects of a severe seasonal drought could also be reduced by special characteristics of sites in which *P. sericea* is predominantly found. The

Table 7.2 Parameters obtained from pressure-volume curves of *Polylepis sericea*

	Ppt (mm)	Et (mm)	Ψ_{π}^{100} (MPa)	Ψ_{π}^0 (MPa)	RWC ^c	N_s/D_w
Nov 1982	59.1	71.7	-1.16	-1.40	0.909	0.0575
Dec 1982	19.0	69.7	-1.13	-1.38	0.909	0.0469
Jan 1983	6.4	84.4	-1.55	-1.85	0.851	0.1156
Feb 1983	9.3	108.5	-1.63	-2.13	0.820	0.1123

Ψ_{π}^{100} , osmotic potential at saturation; Ψ_{π}^0 , osmotic potential at turgor loss point, RWC^c, relative water content at turgor loss point; N_s/D_w , number of osmoles/kg dry weight. Climatic information is also included: Ppt, mean monthly precipitation; Et, mean monthly evapotranspiration (for October 1982, Ppt = 80.4 mm and Et = 67.3 mm). From Rada *et al.* 1985b.

presence of talus slopes and large boulders is likely to decrease the rate of water loss from the soil surface. Deep roots have been observed growing through the crevices between the rocks (Arnal 1983). Although seasonal changes in soil water potentials were not monitored, predawn Ψ_L in *P. sericea* was not as negative during the dry season as in other woody plant species growing in the open páramo.

Conclusions

Special microclimatic regimes and physiological features permit *Polylepis sericea* trees to grow at very high elevations in the tropical Andes. The potential for low temperature limitation on water availability, CO₂ uptake and growth appears to have led to a series of physiological adaptations: (i) high photosynthetic capacity and high dark respiration rates to permit an adequate supply of chemical energy for metabolic work such as repair of cellular damage, stomatal opening in the early morning, and production of cryoprotective substances, (ii) daily osmotic adjustment to enhance the supercooling capacity of the leaves and lower the freezing point of the cell sap at night, preventing tissue injury, and (iii) seasonal changes in osmotic potential that may help maintain water uptake and turgor, and thus a positive carbon balance during the dry season. These features allow *P. sericea* a certain degree of homeostasis in the face of an external environment characterized by strong daily fluctuations in temperature and water availability and seasonal shortage of soil water.

To increase our understanding of the ecological distribution of *P. sericea* and the factors responsible for its success in cold tropical climates, further information is required on the mechanisms underlying nocturnal accumulation of osmotically active solutes and on the full adaptive significance of the high dark respiration rates observed under controlled environmental conditions.

Acknowledgements

We are grateful to Noel M. Holbrook for comments on an earlier version of this chapter.

References

- Arnal, H. (1983). Estudio ecologico del Bosque alti-Andino de *Polylepis sericea* Wedd. en la Cordillera de Mérida. Unpubl. Licentiate Dissertation, Universidad Central de Venezuela, Caracas.
- Azócar, A. & Monasterio, M. (1980). Estudio de la variabilidad Meso y Microclimática en el Páramo de Mucubaji. In *Estudios Ecologicos en los Páramos Andinos*, ed. M. Monasterio. Mérida, Venezuela: Ediciones de la Universidad de los Andes.
- Azócar, A., Rada, F. & Goldstein, G. (1988). Freezing tolerance in *Draba chionophila*, a 'miniature' caulescent rosette species. *Oecologia* **75**, 156–60.
- Bauer, H. J., Larcher, W. & Walker, R. B. (1975). Influence of temperature stress on CO₂-gas exchange. In *Photosynthesis and Productivity in Different Environments*, ed. J. P. Cooper. Cambridge: Cambridge University Press.
- Beck, E., Senser, M., Scheibe, R., Steiger, H. M. & Pongratz, P. (1982). Frost avoidance and freezing tolerance in Afroalpine giant rosette plants. *Plant, Cell and Environment* **5**, 215–22.
- Beck, E., Schulze, E.-D., Senser, M. & Scheibe, R. (1984). Equilibrium freezing of leaf water and extracellular ice formation in Afroalpine 'giant rosette' plants. *Planta* **162**, 276–82.
- Berry, J. A. & Bjorkman, O. (1980). Photosynthetic response and adaptation to temperature in higher plants. *Annual Review of Plant Physiology* **31**, 491–543.
- Black, R. A. & Bliss, L. C. (1980). Reproduction ecology of *Picea mariana* (Mill.) Bsp. at treeline near Inuvik, North-west Territories, Canada. *Ecological Monographs* **50**, 331–54.
- Ellenberg, H. (1958a). Wald oder Steppe. Die natürliche Pflanzendecke der Andean Perus. I. *Die Umschau* **21**, 465–8.
- Ellenberg, H. (1958b). Wald oder Steppe. Die natürliche Pflanzendecke der Andean Perus. III. *Die Umschau* **22**, 679–81.
- Fahey, J. H. (1979). The effect of night frost on the transpiration of *Pinus contorta* spp. *latifolia*. *Oecologia Plantarum* **14**, 483–90.
- Goldstein, G. (1981). Ecophysiological and demographic studies of white spruce (*Picea glauca* (Moench) Voss) at treeline in the central Brooks Range of Alaska. PhD dissertation, University of Washington, Seattle.

- Goldstein, G. & Meinzer, F. (1983). Influence of insulating dead leaves and low temperatures on water balance in an Andean giant rosette species. *Plant, Cell and Environment* **6**, 649–56.
- Goldstein, G., Rada, F. & Azócar, A. (1985). Cold hardiness and supercooling along an altitudinal gradient in Andean giant rosette species. *Oecologia* **68**, 147–52.
- Jaimes, M. (1985). Mecanismos de regulación del intercambio de gases en dos especies de la selva nublada. Unpubl. Licentiate Dissertation, Universidad de los Andes, Mérida, Venezuela.
- Larcher, W. (1969). The effect of environmental and physiological variables on the carbon dioxide gas exchange of trees. *Photosynthetica* **3**, 167–98.
- Larcher, W. (1975). Pflanzenökologische Beobachtungen in der Paramostufe der Venezolanischen Anden. *Anzeiger der mathematisch-naturwissenschaftliche Klasse Österreichischen Akademie der Wissenschaften* **11**, 194–213.
- Larcher, W. (1982). Typology of freezing phenomena among vascular plants and evolutionary trends in frost acclimation. In *Plant Cold Hardiness and Freezing Stress*, ed. P. H. Li and L. Sakai, pp. 417–26. New York: Academic Press.
- Levitt, J. (1980). *Responses of Plants to Environmental Stresses*. Vol. 1. *Chilling, Freezing and High Temperature Stresses*. New York: Academic Press.
- Meinzer, F. & Goldstein, G. (1985). Some consequences of leaf pubescence in the Andean giant rosette plant *Espeletia timotensis*. *Ecology* **66**, 512–20.
- Meinzer, F. C. & Goldstein, G. (1986). Adaptations of water and thermal balance in Andean giant rosette plants. In *On the Economy of Plant Form and Function*, ed. T. J. Givnish, pp. 381–411. New York: Cambridge University Press.
- Monasterio, M. & Reyes, S. (1980). Diversidad ambiental y variación de la vegetación en los Páramos de los Andes Venezolanos. In *Estudios Ecológicos en los Páramos Andinos*, ed. M. Monasterio, pp. 47–91. Mérida, Venezuela: Ediciones de la Universidad de los Andes.
- Mooney, H. A. & West, M. (1964). Photosynthetic acclimation of plants of diverse origin. *American Journal of Botany* **51**, 825–7.
- Pisek, A., Larcher, W., Vegis, A. & Napp-Zinn, K. (1973). The normal temperature range. In *Temperature and Life*, ed. H. Precht, J. Christophersen, H. Hensel and W. Larcher, pp. 102–4. New York: Springer-Verlag.
- Rada, F. (1983). Mecanismos de resistencia a temperaturas congelantes en *Espeletia spicata* y *Polylepis sericea*. Unpublished Masters Dissertation, Universidad de los Andes, Mérida, Venezuela.
- Rada, F., Goldstein, G., Azócar, A. & Meinzer, F. (1985a). Freezing avoidance in Andean giant rosette plants. *Plant, Cell and Environment* **8**, 501–7.
- Rada, F., Goldstein, G., Azócar, A. & Meinzer, F. (1985b). Daily and seasonal osmotic changes in a tropical treeline species. *Journal of Experimental Botany* **36**, 989–1000.
- Rauh, W. (1956). Peruanische Vegetationsbilder, I: Die grossen Gegensätze: Die Küstenwüste und die Wälder des Ostens. *Die Umschau* **56**, 140–3.
- Sakai, A. & Larcher, W. (1987). *Frost Survival of Plants. Responses and Adaptation to Freezing Stress*. Berlin: Springer-Verlag.
- Sarmiento, G., Goldstein, G. & Meinzer, F. (1985). Adaptive strategies of woody species in neotropical savannas. *Biological Reviews* **60**, 315–55.
- Simpson, B. (1979). A review of the genus *Polylepis* (Rosaceae: Sanguisorbeae). *Smithsonian Contributions to Botany* **43**.

- Smith, A. P. (1977). Establishment of seedlings of *Polylepis sericea* in the Paramo (Alpine) zone of the Venezuelan Andes. *Bartonia* **45**, 11-14.
- Smith, A. P. (1979). Function of dead leaves in *Espeletia schultzii* (Compositae), an Andean caulescent rosette plant. *Biotropica* **11**, 43-7.
- Takahashi, K. (1981). Changes in xylem pressure potential in *Abies sachalinensis* Mast. seedlings caused by subfreezing temperature and cold wind. *XVII IUFRO World Congress*.
- Teskey, R. O., Hinckley, T. M. & Grier, C. C. (1984). Temperature induced changes in the water relations of *Abies amabilis* (Dougl.) Forbes. *Plant Physiology* **74**, 77-80.
- Tranquillini, W. (1979). *Physiological Ecology of the Alpine Timberline*. New York: Springer-Verlag.
- Troll, C. (1959). Die tropische Gebirge. *Bonner geographische Abhandlungen* **25**, 1-93.
- Tyree, M. T., Cheung, N. S., MacGregor, M. E. & Talbot, A. J. B. (1978). The characteristics of seasonal and ontogenic changes in the tissue-water relations of *Acer*, *Populus*, *Tsuga* and *Picea*. *Journal of Botany* **56**, 635-47.
- Vareschi, W. (1970). *Flora de los Páramos de Venezuela*. Mérida, Venezuela: Ediciones del Rectorado, Universidad de los Andes.
- Walter, H. & Medina, E. (1969). La temperatura del suelo como factor determinante para la caracterización de los pisos Subalpino y Alpino de los Andes de Venezuela. *Boletín Venezolano de Ciencias Naturales* **115/116**, 201-10.
- Zachariassen, K. E. (1982). Nucleating agents in cold-hardy insects. *Comparative Biochemistry and Physiology* **73**, 557-62.