
FUNCTIONAL CHARACTERISTICS OF THE ARBORESCENT GENUS *Polylepis* ALONG A LATITUDINAL GRADIENT IN THE HIGH ANDES

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SUMMARY

Polylepis is a genus restricted to the Andean Mountain Range, naturally occurring above the upper continuous forest limit. The purpose of this work was to integrate and compare functional characteristics in terms of water and carbon relations and low temperature resistance mechanisms in different *Polylepis* species along a latitudinal gradient. The studied species were *P. sericea* in Venezuela, *P. tarapacana* in Bolivia and *P. australis* in Argentina. Seasonal measurements of leaf water and osmotic potentials, stomatal conductance, CO_2 assimilation and respiration rates, and injury and freezing temperatures were compared. There is a gradient, in terms of functional attributes, along the environmental range. *P. tarapacana* is the most tolerant species to water stress, while *P. seri-*

cea avoids the less harsh conditions of its habitat through osmotic adjustments and cell wall elasticity changes. Mean CO_2 assimilation rates were higher in *P. australis* ($9\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) compared to *P. sericea* ($5\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) and *P. tarapacana* ($3\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$). Mean night leaf respiration rates were similar for all species ($1\text{--}2\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$). In terms of low temperature resistance, *P. sericea* shows daily osmotic adjustments and a moderate supercooling capacity (-9°C). The other two species rely on freezing tolerance in order to survive the more extreme low temperature conditions. The functional attributes described in this study for the different species in a wide environmental range may explain some aspects of their success along the latitudinal and altitudinal gradients.

Climate is an important factor for plant growth; it governs distribution and sets limits for survival. One important characteristic of high mountain environments is the low air temperature, which limits plant growth and survival in these habitats (Sakai and Larcher, 1987). On the other hand, tropical high mountain environments present large daily variations and small seasonal changes in temperature, and freezing temperatures occur almost every day of the year (Hedberg, 1961; Azócar and Monasterio, 1980). Temperature and frost occurrence vary with latitude, altitude and topography.

Thus, minimum absolute temperatures become an important variable in order to establish the distribution limits of the major vegetation types (Woodward and Williams, 1987; Prentice *et al.*, 1992). In spite of this, the genus *Polylepis* does not seem to respond in their distribution to this regime of low temperatures, since it presents a unique altitudinal distribution reaching much higher elevations than those of any other angiosperm tree in the world (Lieberman-Cruz, 1986). Additionally, it is an endemic genus in the Andean Mountain Range, found from Venezuela in the north to Central Argentina in the south. Kessler and Schmidt-Leb-

uhn (2006) reported 26 species, with the highest diversity found in Peru (14 species, 3 endemic) and Bolivia (13 species, 4 endemic); only one species was recorded for Venezuela, 3 in Colombia (1 endemic), 7 in Ecuador (2 endemic), 2 in Chile and 4 in Argentina (1 endemic).

Regional forest distribution seems to be related to areas where solar irradiance is controlled by the slope aspect (direction) and inclination (angle), and sun elevation influences local distribution (Braun, 1997). The genus creates a natural treeline well above the timberline (continuous forest line), in some cases forming forest patches

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between 4000 and 5200masl. In general, *Polylepis* forests are restricted to steep slopes in mid to low topographic positions, although some species are also found on flat terrains. *Polylepis* dominates the upper strata of woodlands and shrublands, together with other less abundant woody species of the genera *Berberis*, *Gaultheria*, *Valeriana*, among others. These woody species occasionally form dense stands that cover most of the surface, often called forests, that are usually intermingled with patches of tussock grasslands, ferns or rock outcrops (Kessler, 2006).

Despite their relatively small area cover, these forests represent unique ecological islands of biodiversity that are vanishing rapidly; Fjeldsa and Kessler (1996) indicate that only 2% of the original *Polylepis* forests remain in Perú and 10% in Bolivia, suggesting that human occupation in the Andean highlands has led to considerable destruction of these forests.

All species of the genus are exposed to very harsh climatic conditions in both their altitudinal and latitudinal distribution, indicating that their survival depends on very special adaptive characteristics that allow them to sustain freezing temperatures and a distinct water stress due to precipitation regimes and drying winds. Normally, these conditions would prevent tree growth; however, the presence of many *Polylepis* species above the timberline, forming forest islands along broad temperature and water availability gradients, suggests a high diversity of functional attributes, which in turn play a fundamental role in their survival.

In this work, some functional attributes of three *Polylepis* species along a wide latitudinal gradient are integrated and compared, in order to establish functional responses that help explain their wide geographical distribution. Functional characteristics are compared in terms of resistance mechanisms to freezing temperatures, leaf gas exchange and water relations. In order to carry out this comparison, a revision and re-interpretation of results obtained throughout the last two decades (Rada *et al.*, 1985, 1996, 2001; García-Núñez *et al.*, 2004) was made, and more recent unpublished results used.

Materials and Methods

Studied species and site characteristics

All species of the *Polylepis* genus have a tree or shrub

TABLE I
ENVIRONMENTAL CHARACTERISTICS AND COORDINATES
OF THE STUDY SITES

| Study site | Species | Coordinates | Altitude (masl) | Mean annual temperature (°C) | Mean annual precipitation (mm) |
|----------------------------|----------------------|--------------|-----------------|------------------------------|--------------------------------|
| Piedras Blancas, Venezuela | <i>P. sericea</i> | 9°N - 70°W | 4200 | 3.7 | 800 |
| Nevado Sajama, Bolivia | <i>P. tarapacana</i> | 18°S - 68°W | 4300 | 3.4 | 347 |
| Los Gigantes, Argentina | <i>P. australis</i> | 32° S - 66°W | 2100 | 8.0 | 854 |

life form (Simpson, 1979), characterized by twisted shapes, a thick, densely laminated and flaky bark with reddish color (Simpson, 1986), and small green-gray leaves. The trees are 1-6m in height and have crown diameters of 3-5m. With respect to their distribution, the species occur in different ecological habitats associated with elevation and humidity.

Three species were compared a latitudinal distribution gradient: *P. sericea* Wedd, in Venezuela, *P. tarapacana* Philippi, in Bolivia and *P. australis* Bitter, in Argentina. Table I shows the environmental characteristics and geographic coordinates for the different study sites.

P. sericea, in the Venezuelan Andes, may reach an altitude of 4600m (Arnal, 1983), well above the treeline (3200masl) in this tropical area (Monasterio, 1980). Its distribution is always associated to more favorable thermal conditions in areas where large boulders accumulate towards the base of glacial cirques (Walter and Medina, 1969; Azócar and Monasterio 1980). This species has the widest latitudinal distribution, from Venezuela to northern Bolivia. Apparently, this species has spread through the Andes in the last million years as a consequence of climatic changes (Simpson, 1986). *P. sericea*'s study site shows a 2.7°C difference between the coldest and the warmest month. Daily temperature fluctuations range from -3° to 15°C during the rainy season and -14° to 18°C in the dry season (Monasterio, 1986).

P. tarapacana forms forests with an amazing altitudinal distribution (4200-5200m) in Bolivia. The lowest altitude represents the maximum elevation for the growth of any shrub or tree life-form, while the high extreme is practically the limit for plant growth in the Andean region (Braun, 1997, Liber-

man-Cruz *et al.*, 1997). The study site is located at Nevado Sajama National Park, where *P. tarapacana* forms the world's highest woody plant forest (Liberman-Cruz, 1986; Braun, 1997) around the Sajama Volcano. Although the study site is considered a semiarid tropical high mountain environment, its latitudinal position determines a marked seasonal pattern in temperature and precipitation regimes, with a cold dry season during the austral winter (May-Oct) and a wet warmer season (Nov-Apr; Liberman-Cruz *et al.*, 1997). Absolute maximum and minimum temperatures registered at 4200m are 21 and -19°C, respectively (Liberman-Cruz, 1986).

P. australis is found at the north extreme of Sierra Grande in Córdoba, Argentina, mainly associated with rock outcrops. This species has to cope with altitude conditions in a temperate environment. Most (83%) rainfall occurs in the summer (Renison *et al.*, 2002). Absolute daily maximum and minimum temperatures of 27.1 and -12.8°C were registered during this study.

Field and laboratory studies

Mean air temperature values were measured with copper-constantan thermocouples (n=3) connected to a digital thermometer. Relative humidity was recorded with a digital hygrometer (n=3). Plant response parameters were obtained from daily measurements of three mature leaves of each of three individual trees at the different studied sites. These parameters were CO₂ assimilation (A) and transpiration rates (E), stomatal conductance (Gs), night respiration (R) and minimum leaf water potential (Ψ_{Lmin}) for both dry and wet seasons. Photosynthetically active radiation was obtained from the leaf chamber integrated to the gas exchange systems.

TABLE II
MINIMUM REGISTERED AIR TEMPERATURE, INJURY AND
FREEZING TEMPERATURES AND LOW TEMPERATURE
RESISTANCE MECHANISMS DURING WET AND DRY SEASONS
FOR THE THREE *Polylepis* STUDIED SPECIES

| Species | Dry season temperatures (°C) | | | Wet season temperatures (°C) | | | RM |
|----------------------|------------------------------|--------------|-------------|------------------------------|--------------|-------------|----|
| | T _{min} | Injury | Freezing | T _{min} | Injury | Freezing | |
| <i>P. sericea</i> | -4.5 | -9.0 ±0.5 a | -8.5 ±0.5 a | -2.0 | -8.0 ±0.9 a | -8.0 ±0.3 a | A |
| <i>P. tarapacana</i> | -13.0 | -20.0 ±0.5 a | -3.5 ±0.5 b | -6.0 | -21.0 ±1.2 a | -9.2 ±0.6 b | T |
| <i>P. australis</i> | -13.5 | -24.0 ±1.0 a | -7.0 ±0.2 b | -2.0 | -18.0 ±2.0 a | -6.0 ±0.2 b | T |

Minimum registered air temperature (T_{min}), injury and freezing temperatures and low temperature resistance mechanisms (RM, A = avoidance through supercooling capacity and T = freezing tolerance) during wet and dry seasons for the three *Polylepis* studied species. Different letters represent significant differences (P<0.05) between injury and freezing temperatures for each of the species.

Three 24h courses were carried out for each season and at every site, with 7 measurements during day hours and 3 to 4 at night. Furthermore, water relations parameters such as turgor loss potentials (Ψ_{π} , n=5) obtained from pressure-volume curves and low temperature resistance mechanisms (freezing and injury temperatures) were also obtained in the laboratory for all species. A portable gas exchange system (LCA-2 for *P. sericea* and LCA-4 for *P. tarapacana* and *P. australis*, ADC, Hoddesdon, England) was used for gas exchange measurements comprising leaf conductance, transpiration, CO₂ assimilation and respiration rates. Water relation parameters were measured with a pressure bomb (PMS Instruments Co., Oregon, USA). Daytime CO₂ assimilation and nighttime

respiration rates were used to obtain integrated curves for the assimilation/respiration ratio (A/R) at leaf level. Freezing temperature (initiation of the ice nucleation process) was determined as the appearance of a low temperature exotherm in ten to fifteen samples subjected to thermal analysis in a controlled bath; the system recorded exotherms as plant tissue was cooled at a rate of 9°C·h⁻¹ from 5 to -25°C. Low temperature injury was determined quantitatively with the triphenyl tetrazolium chloride method (TTC) in three different samples; respiring tissues reduce TTC, changing from clear to a red color that was quantified through spectrometry. A full description of the methods used may be found in Rada *et al.*, (1985, 1996, 2001) and García-Núñez *et al.*, (2004).

Non-parametric tests for comparison between two samples and between three samples were used. For the comparison of ecophysiological parameters between seasons and for avoidance or tolerance mechanisms the U-Mann-Whitney test was used. For comparison between the three species a Kruskal-Wallis test was used.

Results

Freezing temperature resistance mechanisms

Injury temperatures were similar in *P. tarapacana* for both dry and rainy seasons (Table II), but the temperature at which the freezing process began showed significant differences, with values of -3.5 and -9°C during wet and dry seasons, respectively. *P. australis* showed lower injury temperatures for the dry season but the freezing temperatures were similar in both seasons. Differences between frost formation (i.e. supercooling capacity) and injury temperature for these two species point to freezing tolerance in leaf tissues. In contrast, *P. sericea* showed no significant differences between freezing and injury temperatures during either season, indicating frost avoidance as its resistance mechanism to freezing temperatures.

Water and carbon relations

The three species responded differentially to temperature

TABLE III
MEAN PHOTOSYNTHETICALLY ACTIVE RADIATION, AIR TEMPERATURE,
RELATIVE HUMIDITY AND PLANT RESPONSE PARAMETERS FOR WET AND DRY SEASON DAILY
COURSES IN THREE POLYLEPIS SPECIES

| Species | Season | PAR | Ta | RH | Gs | A | R | A/R |
|----------------------|----------|------------------------------------|---|---------------------------------------|-----------------------------------|-----------------------|-----------------------|-----|
| <i>P. sericea</i> | Wet | 1042 ±168 a ¹ (1700) | 11.6 ±1.2 a ¹ (21.5/-0.7) | 84.2 ±1.4 a ¹ (100-64) | 90.6±15.4 a ¹ (213) | 4.60±0.6 a 1 (7.4) | 2.0 | 2.3 |
| | Dry | 1146 ±256 a ¹ (1900) | 13.4 ±1.7 a ¹ (24.5/-2.7) | 52.2 ±2.1 b ¹ (98-32) | 63.3±6.0 b ¹ (93) | 3.6±0.5 a 1 (5.8) | 1.6 ±0.3 1 (2.7) | 2.3 |
| <i>P. tarapacana</i> | Wet-warm | 721 ±182 a ² (1369) | 7.9 ±1.1 a ² (12.5/-4.5) | 73.4 ±4.0 a ² (92-46) | 58.9±10.4 a ¹ (128) | 2.8±0.4 a 2 (6.8) | 1.3 ±0.1 1 (2.6) | 2.2 |
| | Dry-cold | 1443 ±152 b ¹ (2052) | 7.5 ±1.2 a ² (12.5/-14.0) | 38.6 ±5.2 b ² (76/15) | 33.5±4.6 b ² (65.0) | 2.5±0.4 a 1 (4.7) | - | - |
| <i>P. australis</i> | Wet-warm | 1034 ±126 a ¹ (1943) | 7.7 ±0.8 a ² (15.3/-2.8) | 56.0 ±3.0 a ³ (82/29) | 65.5±10.6 a ¹ (92) | 7.3±0.4 a 3 (14.4) | 1.8 ±0.1 a 2 (2.3) | 4.1 |
| | Dry-cold | 1246 ±133 a ¹ (2231) | 8.5 ±1.4 a ² (15.3/-12.8) | 53.4 ±5.7 a ^{1,2} (89/25) | 43.7±8.5 a ² (75) | 9.0±0.3 b 2 (12.3) | 1.6 ±0.1 a 1 (1.9) | 5.6 |

PAR: mean photosynthetically active radiation, Ta: mean air temperature (°C), RH: relative humidity (%), Gs: stomatal conductance (mmol·m⁻²·s⁻¹), A: CO₂ assimilation rate (μmol·m⁻²·s⁻¹), and R: respiration rate (μmol·m⁻²·s⁻¹). Values in parenthesis are maximum for PAR, maximum and minimum for Ta and RH, and maximum for Gs and A. Different letters correspond to significant differences (P<0.05) for the measured parameters between seasons for each species. Different superscript numbers correspond to significant differences (P<0.05) for measured parameters between species during the same season.

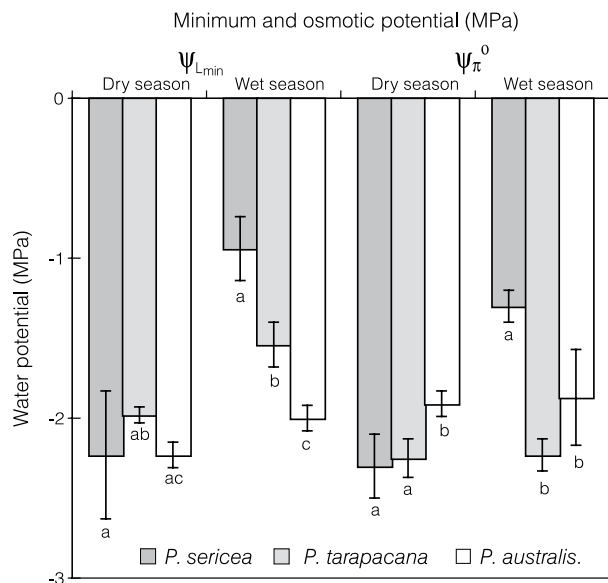


Figure 1. Minimum leaf water potentials (Ψ_{Lmin}) for dry and wet seasons and osmotic potential at turgor loss point (Ψ_{π}^0) during dry and wet seasons for the three *Polylepis* species along a latitudinal gradient. Different letters represent significant differences ($P < 0.05$) between species.

and/or seasonal water availability (Table III). *P. sericea* showed clear differences between seasons; mean air temperature increased by 2°C, while leaf conductance and CO₂ assimilation were lower during the dry season. Air temperatures below zero occurred in both seasons. *P. tarapacana* also showed some differences in gas exchange characteristics between seasons (Table III). Even though a large (43%) drop in leaf conductance was found from the wet to the dry season, only a small (11%) drop in CO₂ assimilation was detected during the latter. Mean air temperatures were similar for both seasons and lower compared to *P. sericea*; however, minimum temperatures were much lower during the dry season. *P. australis* had a substantially different response to the two previous species; means for most of the analyzed parameters showed no significant differences between the two measurement periods. It is interesting to note that the assimilation rate increased towards the dry-cold season, even though leaf conductance tended to decrease (no significant differences).

In general, mean CO₂ assimilation rate (A) was higher in *P. australis* during both seasons, as compared to the other two species. On the other hand, dark respiration rates were lower in *P. tarapacana* during the wet season, as compared to *P. australis* and *P. sericea* (Table III). All three species showed a positive diurnal leaf carbon balance throughout the year, although more favorable in *P. australis*.

In relation to minimum leaf water potentials (Figure 1) *P. sericea* and *P. tarapacana* showed a decrease towards the dry season. *P. australis* showed a tendency to maintain similar potentials between seasons. With respect to turgor loss, both *P. tarapacana* and *P. australis* maintain similar values between seasons. On the other hand, *P. sericea* decreased its turgor loss point during the dry season, indicating a significant capacity for osmotic adjustment.

Discussion

Freezing damage may occur any night of the year in tropical and subtropical high altitude environments, but some authors (Sakai and Larcher, 1987; Goldstein *et al.*, 1994) indicate that it is rather improbable that frost damage plays a decisive role in the survival of trees in these regions. The three studied species respond in contrasting manners to the different thermal conditions of their specific habitats. *P. sericea*, growing in less extreme environments, showed no significant differences between injury and freezing temperatures, indicating that when the freezing process begins, injury will simultaneously occur and, therefore, this species does not resist ice formation in its tissues. However, although freezing takes place at moderate temperatures (-9°C), this supercooling avoidance mechanism seems to be enough to withstand mild, short duration low temperatures present in the Venezuelan Andes throughout the year (Rada *et al.*, 1985). In contrast, *P. tarapacana* and *P. australis* show significant differences between freezing and injury, indicating that once the freezing process occurs, the tissues remain undamaged down to much lower temperatures. This corresponds to a freezing tolerance mechanism, as a response to more extreme temperature conditions of their habitats (Azócar *et al.*, 1988; Squeo *et al.*, 1991).

Differences between seasons in supercooling capacity in *P. tarapacana* suggest differences in resistance mechanisms when thermal conditions change (Rada *et al.*, 2001). During the cold-dry period, when air

temperature may be below -10°C, tissue freezing occurs at relatively high temperatures (-3.5°C) determining a freezing tolerance range. During the wet and warmer season, night air temperatures never reach tissue freezing temperatures (-9°C). This seasonal differentiation is a consequence of an increase in total soluble carbohydrates and proline during the wet warm season, determining an increase in supercooling capacity (Rada *et al.*, 2001). Freezing tolerance provides plants a better protection against cold injury and this increase in supercooling capacity may be advantageous to this species since it would permit an earlier start in photosynthetic activity.

In spite of the different degrees of water stress found at the sites, there are no marked effects on carbon gain at the leaf level. In general, mean CO₂ assimilation rates for the three species studied are comparable to or higher than those reported for other tropical alpine plants (Schulze *et al.*, 1985; Goldstein *et al.*, 1994) and timberline species (Meinzer *et al.*, 1984; Aylett, 1985). The studied species showed a coupling of gas exchange characteristics to the extreme daily and seasonal conditions of their respective environments.

In terms of water relations, even though *P. tarapacana* is subjected to the most extreme conditions, minimum leaf water potentials for the dry season are similar to those of *P. australis* and *P. sericea*. This is an indication that under the arid characteristics of its habitat, this species relies on a greater stomatal control. At the other end, *P. sericea* avoids the less harsh water stress conditions of its habitat through osmotic adjustments and wall elasticity changes (Rada *et al.*, 1996).

The results support the statement by Goldstein *et al.* (1994) that high photosynthetic efficiency and frost resistance are the main physiological explanations for the *Polylepis* phenomenon. However, controversy still persists about its restricted distribution, always at altitudes above the natural altitudinal limit of tree growth, associated with rock outcroppings, along streams and, in the case of *P. tarapacana*, around a volcano suggesting the need of special soil conditions. This apparent preference has been explained by the existence of a favorable microclimate at these sites, which permits tree survival in an unfavorable environment (Walter and Medina, 1969; Troll, 1973; Simpson, 1979, 1986; Azó-

car and Monasterio, 1980). It has been suggested that the retraction of *Polylepis* forests in central and south Andean regions is the result of a gradual decrease in temperature and humidity and the setting of a dry-arid climate (Baied, 2000). Pollen spectra from high altitude Andean lake sediments (Lauer, 1988 in Körner, 1999) document that the mean altitude of the treeline was ~200m higher during the warmest post-glacial period than today, and it was formed by *Polylepis*. Van der Hammen (1974) and Baied (2000) indicated that in the Bolivian central high plateau, north of Chile and Argentina, *P. tarapacana* and *P. tomentella* show a reduced distribution in the Holocene; while under fluctuating climates of the Pleistocene, during warm wet periods, *Polylepis* occupied relatively extensive areas and when conditions became colder, low páramo elements became more abundant (van der Hammen, 1974). Taking this last explanation into account, the *Polylepis* treeline represents a living fossil and not the remnant of a potential treeline in current climates (Körner, 1999). Other authors suggest that such forests are remnants in an otherwise deforested landscape, due to centuries of human land use by grazing and fire, which have determined their disappearance from highlands (Ellenberg, 1979; Fjeldsa, 1992; Kessler and Driesch, 1993, Cierjacks *et al.*, 2007). Whichever the explanation for the actual distribution of the *Polylepis* genus, the functional attributes described in this study for the different species in a wide environmental range may explain some aspects of its success along the latitudinal and altitudinal gradients.

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CARACTERÍSTICAS FUNCIONALES DEL GÉNERO ARBORESCENTE *Polylepis* EN UN GRADIENTE LATITUDINAL EN LOS ALTOS ANDES

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RESUMEN

Polylepis es un género restringido a la Cordillera de los Andes, encontrándose de forma natural por encima del límite superior de bosque continuo. El propósito de este trabajo fue integrar y comparar las características funcionales, en términos de relaciones hídricas y de carbono y mecanismos de resistencia a bajas temperaturas, en diferentes especies de *Polylepis* a lo largo de un gradiente latitudinal. Las especies estudiadas fueron *P. sericea* en Venezuela, *P. tarapacana* en Bolivia y *P. australis* en Argentina. Se compararon medidas estacionales de potencial hídrico y osmótico foliares, conductancia estomática, asimilación de CO₂ y respiración, y temperatura de congelamiento y daño. Se evidencia un gradiente de atributos funcionales a lo largo del rango ambiental. *P. tarapacana* es la especie más resistente al estrés hídrico, mientras que *P. sericea*

evade condiciones menos severas de su habitat a través de ajuste osmótico y cambios en la elasticidad de las paredes celulares. Las tasas promedios de asimilación de CO₂ fueron mayores en *P. australis* (9 μmol·m⁻²·s⁻¹) que en *P. sericea* (5 μmol·m⁻²·s⁻¹) y *P. tarapacana* (3 μmol·m⁻²·s⁻¹). La tasa promedio de respiración foliar nocturna fue similar para todas las especies (1-2 μmol·m⁻²·s⁻¹). En términos de resistencia a bajas temperaturas, *P. sericea* muestra ajuste osmótico diario y capacidad moderada de sobreenfriamiento (-9°C). Las otras dos especies dependen de la tolerancia al congelamiento para soportar las temperaturas bajas más extremas. Los atributos funcionales descritos para las diferentes especies en un amplio rango ambiental pueden explicar algunos aspectos de su éxito en los gradientes latitudinales y altitudinales.

CARACTERÍSTICAS FUNCIONAIS DO GÊNERO ARBORESCENTE *Polylepis* EM UM GRADIENTE LATITUDINAL NOS ALTOS ANDES

Aura Azócar, Fermín Rada e Carlos García-Núñez

RESUMO

Polylepis é um gênero restringido a Cordilheira dos Andes, encontrando-se de forma natural por encima do limite superior de bosque contínuo. O propósito deste trabalho foi integrar e comparar as características funcionais, em termos de relações hídricas e de carbono e mecanismos de resistência a baixas temperaturas, em diferentes espécies de *Polylepis* ao longo de um gradiente latitudinal. As espécies estudadas foram *P. sericea* na Venezuela, *P. tarapacana* na Bolívia e *P. australis* na Argentina. Compararam-se medidas estacionais de potencial hídrico e osmótico foliares, condutância estomática, assimilação de CO₂ e respiração, e temperatura de congelamento e dano. Evidencia-se um gradiente de atributos funcionais ao longo da faixa ambiental. *P. tarapacana* é a espécie mais resistente al estresse hídrico, enquanto que *P. sericea* evade condições menos seve-

ras de seu habitat a través de ajuste osmótico e mudanças na elasticidade das paredes celulares. As taxas médias de assimilação de CO₂ foram maiores em *P. australis* (9 μmol·m⁻²·s⁻¹) que em *P. sericea* (5 μmol·m⁻²·s⁻¹) e *P. tarapacana* (3 μmol·m⁻²·s⁻¹). A taxa média de respiração foliar noturna foi similar para todas as espécies (1-2 μmol·m⁻²·s⁻¹). Em termos de resistência a baixas temperaturas, *P. sericea* mostra ajuste osmótico diário e capacidade moderada de super-resfriamento (-9°C). As outras duas espécies dependem da tolerância ao congelamento para suportar as temperaturas baixas mais extremas. Os atributos funcionais descritos para as diferentes espécies em uma ampla faixa ambiental podem explicar alguns aspectos de seu sucesso nos gradientes latitudinais e altitudinais.