

Leaf gas exchange and water relations in *Polylepis tarapacana* at extreme altitudes in the Bolivian Andes

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Abstract

Stress-induced restrictions to carbon balance, growth, and reproduction are the causes of tree-line formation at a global scale. We studied gas exchange and water relations of *Polylepis tarapacana* in the field, considering the possible effects of water stress limitations imposed on net photosynthetic rate (P_N). Daily courses of microclimatic variables, gas exchange, and leaf water potential were measured in both dry-cold and wet-warm seasons at an altitude of 4 300 m. Marked differences in environmental conditions between seasons resulted in differences for the dry-cold and wet-warm seasons in mean leaf water potentials (-1.67 and -1.02 MPa, respectively) and mean leaf conductances (33.5 and 58.9 mmol m⁻² s⁻¹, respectively), while differences in mean P_N (2.5 and 2.8 μmol m⁻² s⁻¹, respectively) were not as evident. This may be related to limitations imposed by water deficit and lower photon flux densities during dry and wet seasons, respectively. Hence *P. tarapacana* has coupled its gas exchange characteristics to the extreme daily and seasonal variations in temperature and water availability of high elevations.

Additional key words: high Andes; leaf water potential; net photosynthetic rate; stomatal conductance; transpiration rate; tree growth limit; water use efficiency.

Introduction

The altitudinal limit of tree growth or tree-line in mountain regions constitutes, at a global scale, a notable ecological ecotone. Different hypotheses suggest that, beyond this limit, the development of tree life forms is limited primarily by thermal restrictions to carbon balance, growth, and reproduction. Damage to vegetative structures due to freezing, wind, and desiccation are also important constraints to tree life forms in high mountain environments which are characterised by harsh climatic conditions (Tranquillini 1979, Stevens and Fox 1991, Körner 1998, 1999, Wang 2003).

At higher latitudes, the adverse climatic conditions are markedly seasonal, therefore the principal strategy of tree-line species to resist low temperatures is to become dormant during winter, while taking advantage of the rest of the year for growth (Tranquillini 1979, Levitt 1980,

Sakai and Larcher 1987). On the other hand, tropical mountain environments are characterised by greater daily temperature variations compared to seasonal ones, with freezing temperatures occurring any night of the year (Rundel 1994). Under these climatic conditions, low temperature resistance mechanisms and the metabolic machinery of trees must cope with wide daily temperature fluctuations and at the same time must be active all year round.

The altitudinal position of tree-lines is a function of latitude and shows wide regional variations depending on local conditions. High altitude tree-lines are found at very similar growing season temperatures (means from 5.5 to 7.5 °C) around the world, considering season length variation between 2.5 and 12 months (Körner 1998). Forest patches beyond what it is normally believed to be the

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climatic tree-line, as in the genus *Polylepis* (Rosaceae), occur at lower temperatures. This genus comprises 20 species of trees restricted to the South American Andes from Venezuela to central Argentina (Kessler 1995). In its northern limit in Venezuela, *Polylepis sericea* may reach altitudes of up to 4 600 m (Goldstein *et al.* 1994) far above the continuous forest line (3 200 m) in this tropical area (Monasterio 1980). Rada *et al.* (1996) found that *P. sericea* in the Cordillera of Mérida, Venezuela (8°37'N), maintains favourable net photosynthetic rates (P_N) all year round, despite a water stress effect during the dry season.

In high mountain semiarid environments found towards the limit of the tropical region in Bolivia

(18°7'S), where thermal and water regimes are markedly seasonal, *Polylepis tarapacana* forms an open forest surrounding the Sajama Volcano, constituting the tree formation at the highest altitudes in the world (up to 5 200 m a.s.l.) (Braun 1997, Liberman-Cruz 1997). Under these environmental conditions we might expect that thermal and stomatal limitations to carbon assimilation be considerable in relation to less extreme environments in the Cordillera of Mérida.

The aim of this work was to characterise gas exchange and water relations of *P. tarapacana* in the field during both wet-warm and dry-cold seasons, considering the possible effects of water stress limitations imposed on P_N .

Materials and methods

Site characteristics and plant species: The study area comprises the open *Polylepis tarapacana* forest surrounding the Sajama Volcano in Oruro, Bolivia (18°7'S and 68°57'W). This vegetation unit is distributed from 4 200 to 5 200 m. The Sajama Volcano is the highest mountain in Bolivia (6 542 m a.s.l.) as an eastern deviation of the western chain of the Andean range (Liberman-Cruz *et al.* 1997). The study site was located on a lateral moraine of the southern slope of the volcano at 4 300 m. Mean vegetation cover varies between 15–40 % with other dominant species such as *Festuca orthophylla*, *Calamagrostis orbigneana*, *C. curvula*, and *Valeriana nivalis* (Liberman-Cruz 1986). This semiarid tropical high mountain environment is markedly seasonal with respect to temperature and precipitation regimes, with a dry-cold season and a wet-warm season, corresponding to the Austral winter and summer months, respectively. The mean annual precipitation is 347.2 mm with a mean annual temperature of 3.4 °C. Absolute maximum and minimum temperatures registered at 4 200 m were 21 and –19 °C, respectively (Liberman-Cruz 1986).

P. tarapacana, an evergreen tree species, is characterised by twisted trunks and branches, compound leaves with leaflets no greater than 1 cm in width, and silvery trichomes on the lower surface. These trees have a mean height of 3 m whereas exceptional individuals may reach 6 m or more in height (Liberman-Cruz *et al.* 1997). Low temperature resistance in this species is constituted by freezing tolerance during the dry season while during the wet season super-cooling capacity increases significantly so that, for most of the nights, tissue freezing does not occur (Rada *et al.* 2001).

Adult plants ($n = 5$) from 2 to 3 m tall, were chosen

for field and laboratory studies.

Field studies: Three 24-h courses of air temperature, relative humidity, photosynthetic photon flux density (PPFD), leaf conductance (g_s), P_N , transpiration rate (E), and leaf water potentials (Ψ_L) were determined for each the dry-cold (September 1998) and the wet-warm (February 1999) seasons. From these different courses, mean values for each of the measured parameters for each season were obtained.

A portable infrared gas analyser (LCA-4, ADC, Hoddesdon, England) was used for gas exchange measurements. Measurements were carried out on five leaves from five different trees, at 2-h intervals for each daily course. Air temperatures ($n = 3$) were measured with copper-constantan thermocouples connected to a digital thermometer (HH-23, OMEGA, Stamford, Connecticut, USA). Relative humidity was measured with a ventilated dry-wet psychrometer (R. Fuess, Berlin-Steglitz, Germany). PPFD measurements were obtained directly from the analyser leaf chamber. Ψ_L was measured with a pressure bomb (PMS Instruments Co., Corwallis, Oregon, USA) at approximately 2-h intervals in two branches from each of the five different trees.

Laboratory studies: Pressure-volume curves were determined on branches ($n = 6$) during both seasons. Curves were measured 24 h after cutting branches under water and leaving them to saturate covered with polyethylene bags in the dark. Osmotic potentials at full turgor (Ψ_{π}^{100}) and at turgor loss (Ψ_{π}^0), and modulus of elasticity (ϵ) were calculated from these curves (Tyree and Hammel 1972).

Results

Considering plant parameters for the different daily courses during both the dry-cold and the wet-warm seasons, we found marked differences between seasons in microclimatic conditions, water relations, and g_s (Tables 1

and 2). Cloudiness during the dry season was minimal, with daily PPFD values doubling those of the wet season. Mean diurnal air temperature was similar for both seasons (7.5–7.9 °C), however, minimum air temperature

Table 1. Mean diurnal net photosynthetic rate, P_N [$\mu\text{mol m}^{-2} \text{s}^{-1}$], night respiration rate, R_n [$\mu\text{mol m}^{-2} \text{s}^{-1}$], stomatal conductance, g_s [$\text{mmol m}^{-2} \text{s}^{-1}$], transpiration rate, E [$\text{mmol m}^{-2} \text{s}^{-1}$], intrinsic water use efficiency, IWUE [mmol mol^{-1}], photosynthetic photon flux density, PPFD [$\mu\text{mol m}^{-2} \text{s}^{-1}$], air temperature, T_a [$^{\circ}\text{C}$], and relative humidity, RH [%] for all daily courses carried out during the dry-cold and wet-warm seasons ($n = 3$ daily courses per season). Means $\pm$ one standard error. Maximum values in parenthesis and minimum values in square brackets. Statistical significance (U Mann-Whitney) corresponds to the different parameters between seasons (ns: non-significant differences).

Season	P_N	R_n	g_s	E	IWUE	PPFD	T_a	RH
Dry-cold	2.5 ± 0.4 (4.7)	—	33.5 ± 4.6 (65.0)	1.4 ± 0.2 (3.4)	0.075	$1\,443 \pm 152$ (2\,052)	7.5 ± 1.2 (12.5); [−14.0]	38.6 ± 6.4 (76); [15]
Wet-warm	2.8 ± 0.4 (6.8)	1.3 ± 0.1 (2.6)	58.9 ± 10.4 (127.5)	1.7 ± 0.3 (3.8)	0.047	721 ± 182 (1\,369)	7.9 ± 1.1 (12.5); [4.5]	73.4 ± 6.7 (92); [46]
U test	ns		$p < 0.05$	ns		$p < 0.01$	ns	$p < 0.001$

Table 2. Mean leaf water potential (Ψ_L), minimum leaf water potential ($\Psi_{\min}$), osmotic potential at saturation ($\Psi\pi^{100}$) and at turgor loss ($\Psi\pi^0$), and modulus of elasticity (ϵ) for all daily courses carried out during the dry-cold and wet-warm seasons ($n = 3$ daily courses per season). Means $\pm$ one standard error. Statistical significance (U Mann-Whitney) corresponds to the different parameters between seasons (ns: non significant differences).

Season	Ψ_L	$\Psi_{\min}$	$\Psi\pi^{100}$	$\Psi\pi^0$	ϵ
Dry-cold	-1.67 ± 0.06	-1.98 ± 0.05	-1.38 ± 0.01	-2.25 ± 0.12	7.13 ± 2.44
Wet-warm	-1.02 ± 0.08	-1.54 ± 0.14	-1.46 ± 0.19	-2.23 ± 0.16	18.26 ± 1.92
U test	$p < 0.005$	$p < 0.01$	ns	ns	$p < 0.01$

registered during the dry season was 18°C lower. Clear skies all day, together with strong winds and low relative humidity, determined a higher evaporative demand for plants during the dry season. These differences in environmental conditions between seasons promoted differences in Ψ_L and g_s , however, P_N and E were similar.

Maximum air temperature and minimum relative humidity, together with highest PPFD values, were found around midday (Fig. 1). However, relative humidity during the wet season was high from morning to midday (approximately 80 %). The g_s and E followed a similar trend throughout the day. Maximum g_s and E during the dry season were found during morning hours, decreasing towards midday and remaining relatively constant during the rest of the day. The lower g_s during the dry season determined a slightly lower mean daily C_i/C_a (0.52 ± 0.05) compared to the wet season (0.59 ± 0.05).

P_N followed the PPFD pattern during both seasons (Fig. 2A,B). A decrease in P_N was observed with maximum PPFD during the dry season which may be explained by partial stomata closure towards midday. Linear relationships between P_N and g_s (Fig. 2C,D) were found for both seasons, however, the correlation coefficient was

much higher for the dry season ($r^2 = 0.83$). P_N values throughout the day were slightly higher during the wet period with a mean of $2.8 \mu\text{mol m}^{-2} \text{s}^{-1}$ between 08:00 and 17:00 h. Maximum P_N values were 4.7 and $6.8 \mu\text{mol m}^{-2} \text{s}^{-1}$ for dry and wet seasons, respectively. Intrinsic water use efficiency ($\text{IWUE} = P_N/g_s$) was higher for the dry season compared to the wet season. Mean night respiration rates (R_n) during the wet season were $1.3 \mu\text{mol m}^{-2} \text{s}^{-1}$ with a maximum of $2.6 \mu\text{mol m}^{-2} \text{s}^{-1}$. Even though R_n measurements were supposed to have been carried out during the dry-cold season, extremely low temperatures affected the gas exchange system.

Minimum $\Psi_{\min}$ occurred at midday for both seasons (-1.98 and -1.54 MPa for the dry and the wet season, respectively). Freezing of the stems was observed during the consecutive nights when minimum temperatures were registered (-14°C) in the dry-cold season. Modulus of elasticity (ϵ) showed significant differences between seasons, while none were found in $\Psi\pi^{100}$ and $\Psi\pi^0$ (Table 2). Zero pressure potential during the high evaporative demand midday hours was not found in any of the periods studied.

Discussion

Above the extreme limit of *Polylepis tarapacana* (5 200 m), there is practically bare ground and the beginning of the rock outcrops of the slopes of the glacier of Sajama Volcano. In its upper limit, *P. tarapacana* shares the habitat with graminoids and cushions that are

also close to the altitudinal limit for higher plants (Liberman-Cruz 1986).

Carbon gain at high altitudes is constrained mainly by thermal restrictions due to low temperatures, low CO_2 partial pressures, and low water availability in arid Cor-

dilleras, and in some cases there is a low radiation input (Tranquillini 1979, Körner 1998, Cavieres *et al.* 2000). Nevertheless, remarkably positive photosynthetic rates are reported for different tree species at tree-line (Körner 1999). Rada *et al.* (1996) found positive P_N even at 0 °C ($\cong 1.7 \mu\text{mol m}^{-2} \text{s}^{-1}$) in *Polylepis sericea*, with a low temperature compensation at -2.8 °C.

We found for *P. tarapacana* mean positive P_N along the day without significant difference between seasons (2.5 to $2.8 \mu\text{mol m}^{-2} \text{s}^{-1}$ for both the dry and wet season at 4 300 m, respectively). The P_N of *P. tarapacana* was low and comparable to values measured in giant rosettes of *Espeletia* in the Venezuelan Andes, which ranged between 1.0 – $3.0 \mu\text{mol m}^{-2} \text{s}^{-1}$ for *E. timotensis*, *E. spicata*,

and *E. schultzei* at 4 200 m (Goldstein *et al.* 1989, Rada *et al.* 1998). In the same manner, these low P_N are comparable to those measured for *Podocarpus oleifolius* and *Espeletia neriifolia* (maximum rates between 1.9 and 2.2, respectively, at 3 200 m on a cloudy day), tree species that grow at the timberline in the Venezuelan Andes, in sites characterised by a low quantum input due to cloud cover most of the year (Meinzer *et al.* 1984, Cavieres *et al.* 2000). Relatively higher maximum P_N (8 – $11 \mu\text{mol m}^{-2} \text{s}^{-1}$) were reported for freezing tolerant Afroalpine giant rosettes (Schulze *et al.* 1985). *P. sericea* shows mean and maximum P_N of 5 and $7.4 \mu\text{mol m}^{-2} \text{s}^{-1}$, respectively (Rada *et al.* 1996), under more favourable environmental conditions in terms of temperature and water

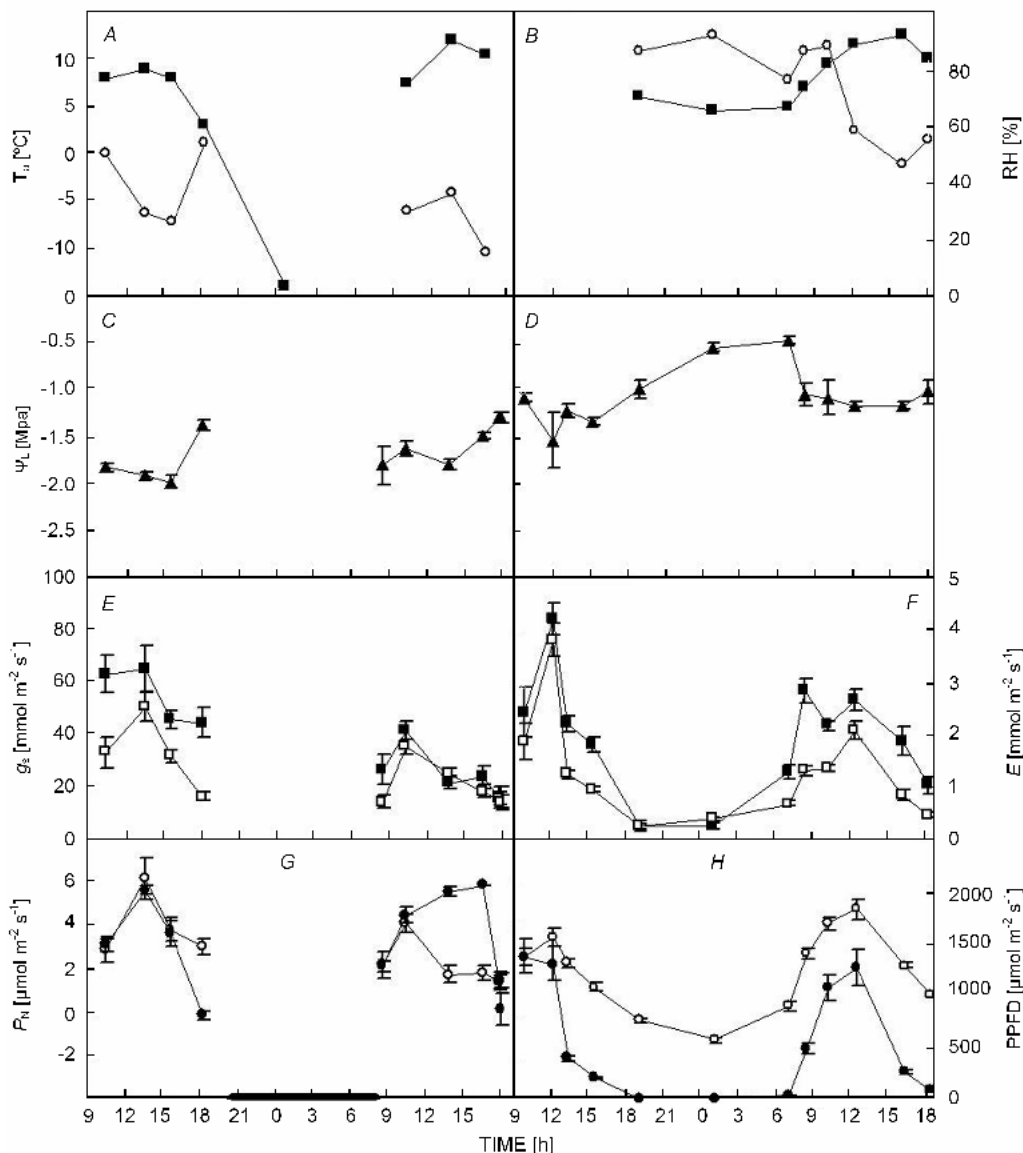


Fig. 1. Daily courses of air temperature (T_a ■), relative humidity (RH ○), leaf water potential (Ψ_L ▲), leaf conductance (g_s ■), transpiration rate (E □), net photosynthetic rate (P_N ○), and photosynthetic photon flux density (PPFD ●), on representative days during (A) the dry-cold season and (B) the wet-warm season for *P. tarapacana*. Bars represent ± 1 SE of the mean ($n = 5$). Dark bar across x-axis represents periods when branches were frozen.

regimes and at lower altitudes (4 000 m), compared to the *P. tarapacana* location.

Although g_s and Ψ_L in *P. tarapacana* during the dry season were significantly lower, there were no differences in P_N between seasons. However, when only values of P_N at saturating PPFD ($>700 \mu\text{mol m}^{-2} \text{s}^{-1}$) were considered, differences would be significant (5.3 ± 0.7 and $2.9 \pm 0.4 \mu\text{mol m}^{-2} \text{s}^{-1}$ for the wet and dry seasons, respectively; $p < 0.002$). This suggests that during the dry season

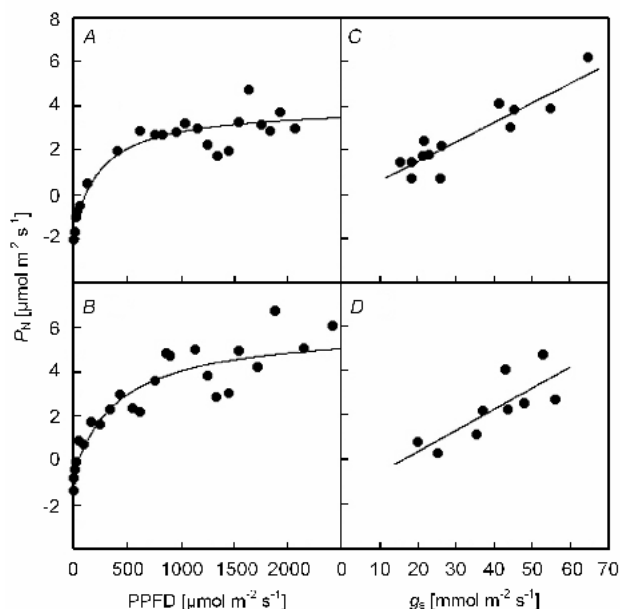


Fig. 2. Net photosynthetic rate (P_N) in relation to photosynthetic photon flux density (PPFD) for (A) dry-cold [$y = 4.0 (-110.8 + x)/(-110.8 + x + 363.4)$; $r^2 = 0.90$] or (B) wet-warm [$y = 6.0 (-44.2 + x)/(-44.2 + x + 421.3)$; $r^2 = 0.86$] seasons, and to stomatal conductance (g_s) for (C) dry-cold ($y = 0.0882x - 0.2851$; $r^2 = 0.83$) or (D) wet-warm ($y = 0.0954x - 1.5586$; $r^2 = 0.62$) seasons in *P. tarapacana*.

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P_N is constrained mainly by water deficit and in the wet season by lower PPFD values.

A linear correlation between P_N and g_s denotes a good coupling between the stomatal apparatus and the capacity to fix CO_2 , which can be translated into relatively constant water use efficiency along the day (Schulze and Hall 1982).

Even though seasonal osmotic adjustment was not found for *P. tarapacana*, an increase in cell wall elasticity occurred during the dry season. This response favours maintenance of pressure potential while less water is available during the dry season. In the case of *P. sericea* in the Venezuelan Andes, a combination of seasonal osmotic adjustments and enhanced cell wall elasticity have been described, permitting this species to maintain positive P_N during the unfavourable season (Rada *et al.* 1985, 1996).

In spite of the occurrence of extra-cellular freezing during the dry-cold season (Rada *et al.* 2001), *P. tarapacana* leaves showed a rapid transition from frozen state to a photosynthetically active state. P_N close to the compensation at low Ψ_L and g_s were registered early in the morning. This rapid recovery of photosynthetic activity is comparable to that reported for freezing tolerant Afroalpine giant rosettes (Schulze *et al.* 1985).

High Andean regions are characterised by extreme environmental conditions where the tree life-form has not been able to succeed, however, the genus *Polylepis* represents a remarkable exception to this rule. Our results show how *P. tarapacana* has coupled its gas exchange characteristics to the extreme daily and seasonal variations in temperature and water availability of high elevations. The results are also in agreement with the view of Körner (1998) in that photosynthetic activity does not constitute the main restriction to the development of tree life forms at the tree-line.

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