ORIGINAL ARTICLE

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Carbon and water balance in *Polylepis sericea*, a tropical treeline species

Abstract *Polylepis sericea* trees grow well above the continuous forest line in the Venezuelan Andes. In these environments, extreme daily temperature ranges can occur at any time of the year and trees experience a 4 month dry period. The purpose of this work was to study carbon and water relations of this species in the field during wet and dry seasons in order to understand this species' success at such high altitudes. Leaf gas exchange (portable system in open mode) and leaf water potential (pressure chamber) were measured at 1–2 h intervals during several daily courses at 4000 m elevation in the Páramo de Piedras Blancas. CO_2 assimilation versus leaf temperature curves were also obtained for this species in the laboratory. Clear differences in the measured parameters were observed between seasons. For a wet season day, maximum CO_2 assimilation rate was 7.4 μmol m^{-2} s^{-1} and leaf conductance was relatively constant (approximately 100 mmol m^{-2} s^{-1}). In the dry season day, maximum CO_2 assimilation rate was 5.8 μmolm^{-2}s^{-1} and leaf conductance was close to 60 mmolm^{-2}s^{-1}. Minimum leaf water potentials measured were −1.3 MPa for the wet and −2.2 MPa for the dry season. The CO_2 assimilation-leaf temperature relationship showed a 13.4 °C leaf temperature optimum for photosynthesis with maximum and minimum compensation points of 29.5 and −2.8 °C, respectively. Maximum night-time respiration was relatively high (2.7 μmol m^{-2} s^{-1}). Our results show that *P. sericea* maintains a highly positive carbon balance through all daily courses, even though there is a slight water stress effect during the dry season; this suggests that its carbon assimilation machinery is well adapted to the low temperatures and seasonal water stress found in the high tropical mountains.

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Introduction

The genus *Polylepis* comprises 15 species of tree angiosperms which grow at the highest altitudes in the world (Simpson 1979). *Polylepis sericea*, the only species which grows in the Venezuelan Andes, may reach altitudes of up to 4600 m (Arnal 1983), far above the continuous forest line (3200 m) in this tropical area (Monasterio 1980).

Temperature, and its effects on carbon balance, is one of the most important factors determining the upper altitudinal limit of trees in temperate zone mountains (Tranquillini 1979). Temperature may play an equally important role in the carbon balance of plants in tropical high mountains because daily temperature variations can exceed seasonal variation. Trees in temperate regions, where low temperatures are concentrated in a few months of the year, may become dormant in winter while taking advantage of the rest of the year for growth. *P. sericea*, on the other hand, faces the problem of maintaining continuous growth, even though low temperatures may occur any day of the year and therefore has to adapt its carbon assimilation machinery to these conditions.

Different aspects which help explain *P. sericea*'s unusual ecological distribution have been documented in previous works. The microclimatic conditions of the sites where this species grows are considered as thermal refuges (Azócar and Monasterio 1980), forming small forest 'islands' near massive rock outcroppings (Walter and Medina 1969). Although below zero night temperatures are much less frequent than in the surroundings, night frosts do occur and the large temperature-driven fluctuations in leaf osmotic potential, together with its supercooling capacity are the principal means of avoiding frost damage (Rada et al. 1985).

Due to the extreme daily temperature range which *P. sericea* can experience at any time of the year, its photosynthetic apparatus must be adapted to maintain a positive

carbon balance under extreme conditions. Little is known, however, about the carbon balance of this species. The only information on temperature-net photosynthetic relation is the work of Goldstein et al. (1994), who refer mainly to laboratory conditions. These authors report an optimum temperature of 13 °C for photosynthesis with a rapid fall below and above this optimum. In addition, these trees, as well as other vegetation in this region, experience a 4 month dry period.

The purpose of this work was to study the carbon and water balances of *P. sericea* in the field during both wet and dry seasons in order to improve understanding of this species' success at such high altitudes. Also, by studying gas exchange and water relations of this species during both wet and dry seasons we may explain how water stress affects this species during the dry season.

Materials and methods

Polylepis sericea Wedd trees 2–4 m in height were studied at 4000 m elevation in the Páramo de Piedras Blancas in the Venezuelan Andes (8° 37′ N, 70° 12′ W). The mean annual temperature is approximately 3.7 °C with mean monthly temperature differing by only 2.7 °C between the coldest and warmest months. On the other hand, night-day temperature variations range from approximately −2 to 19 °C for the wet and from −4 to 25 °C for the dry season (F. Rada 1983, data not published). The annual precipitation of 800–900 mm falls mainly between April and December. These trees are evergreen, have a twisted stem with layers of thin, exfoliating sheets and compound leaves. Leaflets are less than 1 cm wide with silvery trichomes on the underside.

Daily courses of gas exchange were measured during the wet ($n = 4$) and dry ($n = 4$) seasons. From these different courses, mean values for each of the measured parameters for each season were obtained (Table 1). The daily courses which best approximated to these means were chosen as representative of the wet season (June 1991) and the dry season (January 1992); and a 24-h course in the beginning of the dry season (December 1991) was used to integrate CO_2 exchange rates in order to obtain a daily carbon balance (McCree et al. 1984). Five leaves were chosen from each of three different individuals for these gas exchange measurements.

A fully portable system, consisting of a leaf chamber, an air supply unit, and an infrared gas analyser unit, operating in the open mode was used to measure gas exchange in the field (LCA-2 System, The Analytical Development Co. Ltd., Hoddesdon, England). Gas exchange rates were determined for leaves sealed in the chamber for less than 30 s, using the calculations of von Caemmerer and Farquhar (1981). Leaf temperatures ($n = 3$) were measured with fine-wire copper-constantan thermocouples attached to the lower leaf surface.

Leaf water potentials (Ψ_L, $n = 3$) were measured with a pressure chamber, at approximately 1–2 h intervals during the various daily courses. Air temperatures were measured with copper-constantan thermocouples placed 1 m above the soil surface and relative humidity was measured with a ventilated wet-dry bulb psychrometer. Air temperatures and relative humidities, together with leaf temperatures were used to calculate vapor pressure deficit between leaf and air (VPD).

For net photosynthesis-leaf temperature and dark respiration-leaf temperature curves, several *P. sericea* plants ($n = 4$ and 3, respectively) were excavated with roots and surrounding soil from the study site, transported to the laboratory and placed in a growth chamber equipped with light (12 h photoperiod, 600 µmol m^{-2} s^{-1}) and temperature control simulating field conditions. A detailed description of the methods used for these net photosynthesis and dark respiration-leaf temperature curves is given in Rada et al. (1992).

Table 1 Average values of leaf temperature (T_L, °C), vapor pressure deficit (*VPD*, KPa), leaf water potential (ψ_L, MPa), leaf conductance (K_s, mmol m^{-2} s^{-1}) and CO_2 assimilation rate (A, µmol m^{-2} s^{-1}) for all wet and dry season daily courses carried out during the study ($n = 8$). Values where PPFD was below 700 µmol m^{-2} s^{-1} were not included (mean ± two standard errors, values in parenthesis are maximum with the exception of ψ_L which are minimum measured)

	T_L	VPD	ψ_L	K_s	A
Wet season	15.57 ± 1.2 (21.5)	0.81 ± .18 (1.30)	−0.94 ± .18 (−1.25)	90.6 ± 15.4 (213)	4.60 ± .82 (7.4)
Dry season	18.35 ± 1.4 (24.5)	1.47 ± .30 (2.38)	−1.72 ± .14 (−2.23)	63.3 ± 6.0 (93)	3.60 ± .60 (5.8)

Results

If we consider all the data from the different courses ($n = 8$) carried out, clear differences between seasons were observed (Table 1; *t*-test, $P < 0.05$, for A, $P < 0.054$). Average leaf temperature increased almost 3 °C from wet to dry season. Leaf water potential showed a 2-fold decrease while VPD significantly increased from wet to dry season. As a consequence of these differences between seasons, both leaf conductance and CO_2 assimilation rate varied considerably between seasons.

Wet and dry season courses for measured variables are shown for the single representative days in Figs. 1 and 2. Maximum CO_2 assimilation rate for the wet season course was 6.5 µmol m^{-2} s^{-1} obtained at midday with values above 4 µmol m^{-2} s^{-1} the first half of the day when photosynthetic photon flux density (PPFD) was high. Maximum leaf temperature for this day was 19.4 °C at midday. Leaf conductance was relatively constant. Leaf water potential (Ψ_L) reached a minimum value of −1.3 MPa during the early afternoon while leaf to air vapor pressure deficit (VPD) showed its maximum (1.35 KPa) at 1000 hours.

CO_2 assimilation rate during the dry season course was lower than for the wet season (Fig. 2). Maximum CO_2 assimilation was 3.9 µmol m^{-2} s^{-1} at midday, with a positive carbon balance through most of the day and rates above 2.5 µmol m^{-2} s^{-1} from 1000 to 1400 hours. Leaf conductance was constant throughout the day, but with lower values than for the wet season. These lower leaf conductances restrict transpirational losses, even though leaf-air VPD were high compared to the wet season. Minimum Ψ_L was obtained at midday (−2.2 MPa). Leaf temperature is higher during the dry season with a maximum of 24.5 °C at 1400 hours.

The CO_2 assimilation-leaf temperature relationship for *P. sericea* (Fig. 3) shows a 13.4 °C leaf temperature optimum for photosynthesis with a rapid decrease above and below this optimum. Maximum and minimum compensation points were 29.5 and −2.8 °C, respectively. From these curves an average maximum photosynthetic rate of 5.3 µmol m^{-2} s^{-1} was obtained. The dark respiration (dr)-leaf temperature relationship showed minimum dark respiration for this species (0.95 µmol m^{-2} s^{-1}) at 5.3 °C
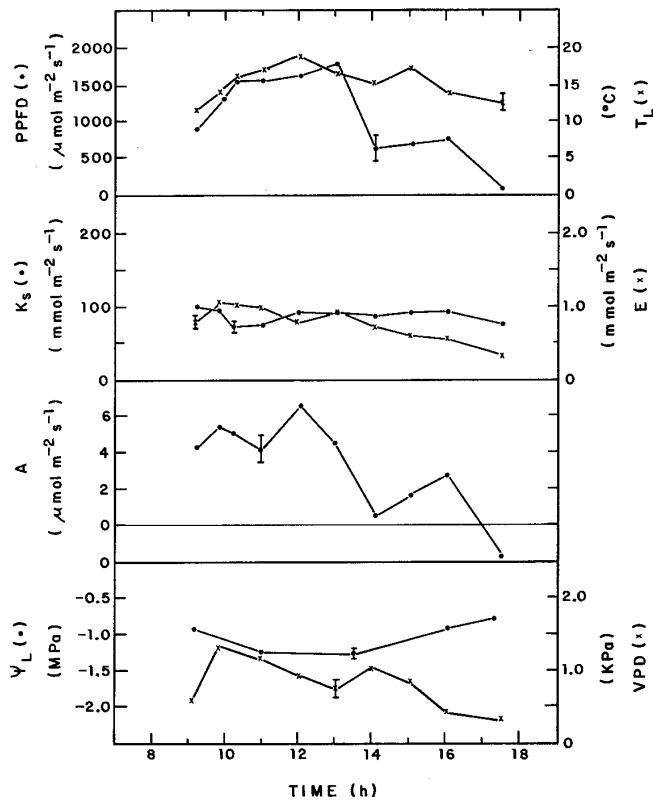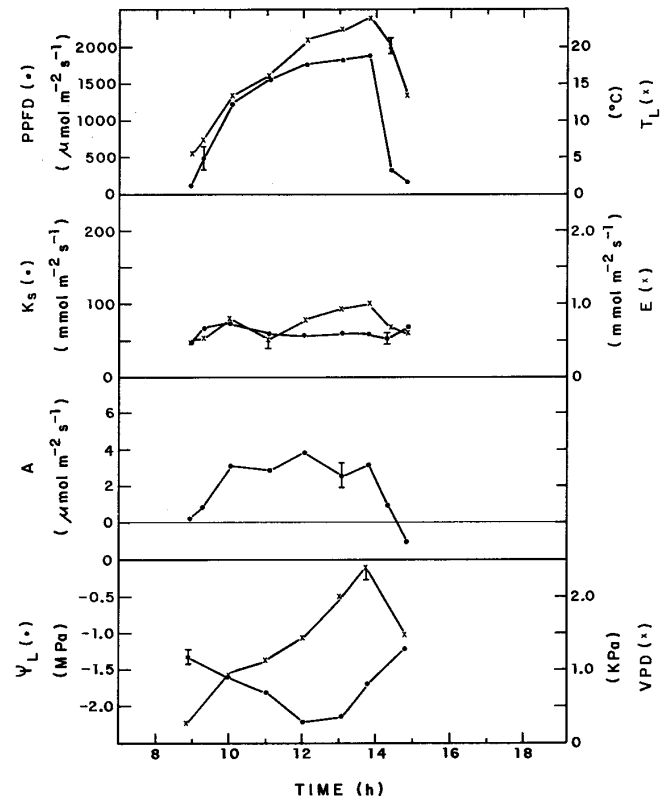
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Fig. 1 Daily course of photosynthetic photon flux density (*PPFD*), average leaf temperature (T_L), leaf conductance (K_s), transpiration rate (*E*), CO_2 assimilation rate (*A*), leaf water potential (Ψ_L) and leaf to air vapor pressure deficit (*VPD*) on a single representative day during the wet season for *Polylepis sericea*. *Bars* represent ± 1 SE of the mean ($n = 5$, for Ψ_L $n = 3$)

Fig. 2 Daily course of photosynthetic photon flux density (*PPFD*), average leaf temperature (T_L), leaf conductance (K_s), transpiration rate (*E*), CO_2 assimilation rate (*A*), leaf water potential (Ψ_L) and leaf to air vapor pressure deficit (*VPD*) on a single representative day during the dry season for *P. sericea*. *Bars* represent ± 1 SE of the mean ($n = 5$, for Ψ_L $n = 3$)

increasing above and below this value ($dr = 6.864 \times 10^{-3}T_L^2 - 7.292 \times 10^{-2}T_L + 1.1421$, $r^2 = 0.89$).

The results of the 24-h course (Fig. 4) which correspond to the beginning of the dry season, support those presented in Fig. 2 in terms of the daily cycle. Other measured parameters showed patterns similar to Fig. 2. Figure 4 is presented to show this species' response to night-time ambient conditions. Leaf temperature remained below 2 °C throughout the night reaching a minimum of −1.3 °C at 0645 hours and recovering rapidly after 0700 hours. As expected, stomates closed after 1900 hours and remained in this manner until after 0700 hours when leaf conductance began to increase. Leaf water potential became more positive through the night, reaching a maximum of −0.5 MPa. Night-time respiration rate increased after sundown reaching 2.7 μmol m^{-2} s^{-1} at 2200 hours. It is important to note from this figure that although leaf temperatures reached below zero values during the predawn hours, these did not seem to affect in any way the following day's gas exchange behavior, as stomates open and a positive carbon balance was obtained rapidly, even though PPFD values were low.

Discussion

At high altitudes, the zone where the extension of forests is terminated represents the most abrupt change in plant dominance on a large geographical scale (Schulze 1982). The lack of coincidence between the continuous forest line and the treeline in general, suggests that it is strongly determined by the ability of tree species that grow above the forest line to adapt themselves to the increasing severity of natural climatic conditions encountered at higher altitudes.

In the specific case of the Venezuelan Andes, tree species such as *Vallea stipularis*, *Paragynoxys meridana* and *Espeletia neerifolia* are found up to 3600 m, a few hundred meters above the continuous forest line, but none of these species compares with *P. sericea* in its upper limit of distribution or its size. Recent studies of gas exchange and water relations of *E. neerifolia* and *Alnus jorullensis* growing along an altitudinal gradient (2200–3500 m), show that for the former species, cold resistance mechanisms are sufficient to explain the occurrence at higher altitudes; but a positive carbon balance was not maintained with altitude indicating that this species' capacity to reach higher altitudes decreases abruptly (A. Azócar, unpublished

Fig. 3 Net photosynthesis-leaf temperature curve for *P. sericea*, $y = -0.0197\,x^2 + 0.526\,x + 1.723$, $r^2 = 0.66$

LEAF TEMPERATURE (°C)
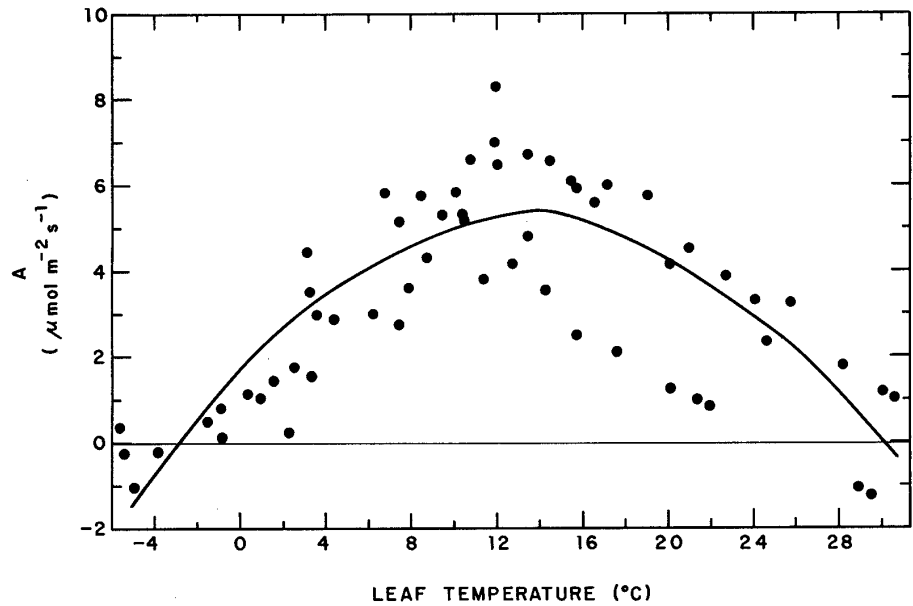
data). According to this author, *A. jorullensis* does not have the cold resistance mechanisms to be capable of having a higher altitudinal distribution.

Our results show that *P. sericea* maintains a highly positive balance throughout all the daily courses carried out during both wet and dry seasons, even though there is a slight water stress effect during the latter season. An average CO_2 assimilation rate of close to 5 μmol m⁻² s⁻¹ during the wet season and maximum rates of 7.4 μmol m⁻² s⁻¹ in the field and 8.2 μmol m⁻² s⁻¹ in the laboratory are high and compare to assimilation rates reported for tropical alpine plants in general (Schulze et al. 1985; Goldstein et al. 1989; Rada et al. 1992) and to trees which reach the limit of continuous forestline (Meinzer et al. 1984; Aylett 1985; Añez 1987). Larcher (1975) and Goldstein et al. (1994) estimate a low temperature limit for net photosynthesis of $-5\,°C$ for *P. sericea*, similar to our measured value of

$-3\,°C$. These low daytime temperatures are never observed in *P. sericea* forest islands, even at its highest altitudinal limit (Azócar and Monasterio 1980).

Even though leaf conductances and CO_2 assimilation rates were significantly lower during the dry season for *P. sericea*, a positive carbon balance was always maintained. This minor effect of the low water availability during the dry season may be explained by an important osmotic adjustment described for this species (Rada et al. 1985). This osmotic adjustment permits *P. sericea* to extract water from a soil with less available water while maintaining turgor. On the other hand, deep roots capable of exploring lower soil horizons between rock fractures have been described by Arnal (1983).

High elevation trees from temperate regions have higher dark respiration rates than those of lowland species. In the case of tropical high mountains, Goldstein et al. (1994)

Fig. 4 Twenty four hour course of photosynthetic photon flux density (*PPFD*), average leaf temperature (*T*ₗ), leaf conductance (*K*ₛ), transpiration rate (*E*), CO_2 assimilation rate (*A*), leaf water potential (Ψₗ) and leaf to air vapor pressure deficit (*VPD*) for P. *sericea* during the early dry season. *Bars* represent ± 1 SE of the mean (*n* = 5, for Ψₗ *n* = 3); *Dark bar* across *x*-axis represents night-time period

TIME (h)
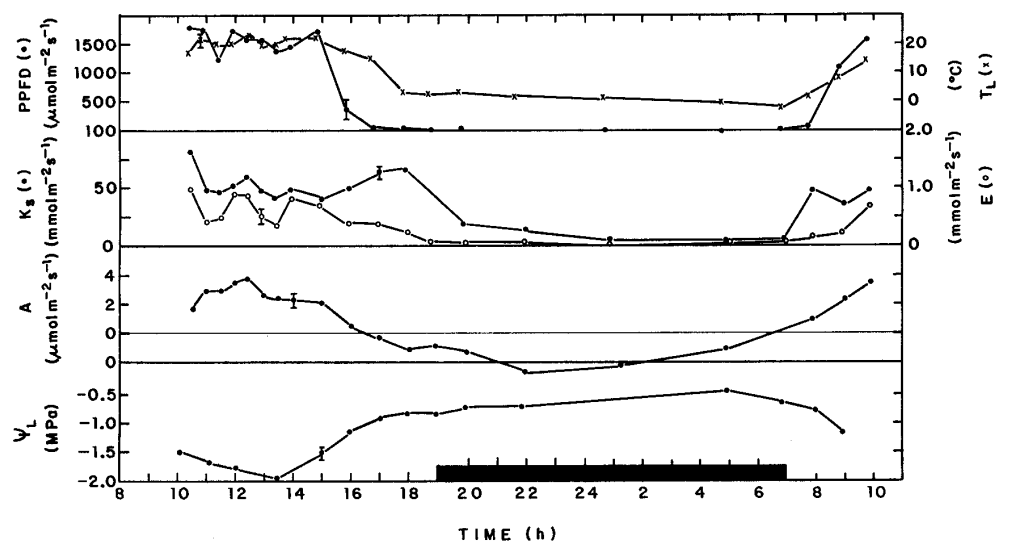
reported even higher respiration rates for *P. sericea* compared to those temperate mountain region species and to tropical cloud forest species such as *Podocarpus rospligliosii* and *P. oleifolius*. In our field studies, night respiration rates were relatively high (2.7 μmol m^{-2} s^{-1}) which support these other results. An increase in respiration induced by low temperatures has been regarded as a physiological adaptation allowing an adequate energy gain under unfavorable temperature conditions (Larcher 1961). In *P. sericea*, this high respiration rate may be needed to increase the osmotically active solutes at night (Rada et al. 1985) or to repair cellular damage produced by low temperatures (Tranquillini 1979; Levitt 1980), both of which imply a significantly greater energy expenditure.

Daytime energy input is relatively low above 3000 m in tropical environments; where this is so, carbon assimilated by plants will be used mainly for maintenance respiration and for the formation of new assimilating organs. Because of this restriction in the quantity of dry matter which may be accumulated by plants, the arborescent forms become poor competitors in these high mountain ecosystems. Goldstein et al. (1994) concluded that "a high respiration rate coupled with a relatively high photosynthetic capacity may be a prerequisite for tree survival at high elevations in the tropics". *P. sericea* has been succesful in reaching such high altitudes by having a positive carbon balance in these year-round low temperature and seasonal water-stressed environments, as has been reported in this work, together with its efficient night-time cold resistance mechanisms reported in previous works (Rada 1983; Rada et al. 1985).

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