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Effects of temperature on photosynthesis of two morphologically contrasting plant species along an altitudinal gradient in the tropical high Andes

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Abstract The effects of temperature on photosynthesis of a rosette plant growing at ground level, *Acaena cylindrostachya* R. et P., and an herb that grows 20–50 cm above ground level, *Senecio formosus* H.B.K., were studied along an altitudinal gradient in the Venezuelan Andes. These species were chosen in order to determine – in the field and in the laboratory – how differences in leaf temperature, determined by plant form and micro-environmental conditions, affect their photosynthetic capacity. CO₂ assimilation rates (*A*) for both species decreased with increasing altitude. For *Acaena* leaves at 2900 m, *A* reached maximum values above 9 μmol m⁻² s⁻¹, nearly twice as high as maximum *A* found at 3550 m (5.2) or at 4200 m (3.9). For *Senecio* leaves, maximum rates of CO₂ uptake were 7.5, 5.8 and 3.6 μmol m⁻² s⁻¹ for plants at 2900, 3550 and 4200 m, respectively. Net photosynthesis-leaf temperature relations showed differences in optimum temperature for photosynthesis (*A*_{o,t}) for both species along the altitudinal gradient. *Acaena* showed similar *A*_{o,t} for the two lower altitudes, with 19.1°C at 2900 m and 19.6°C at 3550 m, while it increased to 21.7°C at 4200 m. Maximum *A* for this species at each altitude was similar, between 5.5 and 6.0 μmol m⁻² s⁻¹. For the taller *Senecio*, *A*_{o,t} was more closely related to air temperatures and decreased from 21.7°C at 2900 m, to 19.7°C at 3550 m and 15.5°C at 4200 m. In this species, maximum *A* was lower with increasing altitude (from 6.0 at 2900 m to 3.5 μmol m⁻² s⁻¹ at 4200 m). High temperature compensation points for *Acaena* were similar at the three altitudes, c. 35°C, but varied in *Senecio* from 37°C at

2900 m, to 39°C at 3550 m and 28°C at 4200 m. Our results show how photosynthetic characteristics change along the altitudinal gradient for two morphologically contrasting species influenced by soil or air temperatures.

Key words Energy balance · Leaf temperature · Tropical mountain · Plant morphology

Introduction

Plant growth and survival in high mountain habitats is controlled mainly by low temperatures (Sakai and Larcher 1987). However, cold climates are not necessarily cold for plants at all times and the influence of plant growth-form on canopy climate is substantial (Körner and Larcher 1988). Körner and Cochrane (1983) working with different life forms in the Snowy Mountains of Australia found that the smallest differences between day time leaf and air temperatures occur in trees and shrubs, and the greatest differences in low strata plants such as acaulescent rosettes and cushions. In high tropical mountains, leaf temperatures of 15°C above air temperature have been observed in giant rosette plants (Larcher 1975), and 10°C above ambient in *Polylepis sericea*, a small tree (Goldstein et al. 1994), and high temperature differences are also reported for shrubby canopies (Hedberg and Hedberg 1979; Körner et al. 1983.)

Plants growing closer to the ground will be exposed to greater daily leaf temperature changes because there is a temperature gradient along soil-air profiles, with day time temperatures closer to the ground significantly higher – by radiant heating – than those further away from the ground (Azócar and Monasterio 1980). Plant physiognomy, plant density and life-form are the major determinants of plant temperatures in the field (Salisbury and Spomer 1964; Nobel 1988). These microclimatic differences among plant life-forms can lead to divergent metabolic responses to temperature.

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A relationship between temperature limits for net photosynthesis of high tropical mountain species and the temperature regime in their specific habitats has been described (Larcher and Wagner 1976). Rada et al. (1992) studied the relationship between net photosynthesis and leaf temperature in plant species of contrasting sizes belonging to different vegetation strata along an altitudinal gradient in the tropical Andes, and found that the optimum temperature for photosynthesis ($A_{o,t}$) was coupled to air temperature for tall species (arborescent forms), decreasing at higher altitudes. On the other hand, smaller species, like acaulescent rosettes – strongly influenced by radiant warming – showed similar or even increasing $A_{o,t}$ with increasing altitude. Similar results have been reported by Körner and Diemer (1987), describing similar $A_{o,t}$ in herbaceous plants from high or low altitude in the Alps.

Microenvironmental conditions determine the gas exchange characteristics needed by plants to adapt to these extreme environments. On the other hand, different plant features tend to uncouple plant temperatures and physiological processes from unfavourable environmental temperatures (Nobel 1991). The main objective of this work was to study the relationship between leaf temperature and CO_2 assimilation in two morphologically contrasting plants along an altitudinal gradient in the tropical high Andes. Two species belonging to the lower vegetation stratum were chosen to determine in the field and in the laboratory – how differences in leaf temperature, determined by plant form and microenvironmental conditions, affect the photosynthetic capacity of both species.

Materials and methods

Site characteristics and plant species

A perennial acaulescent rosette, *Acaena cylindrostachya* R. et P. (Rosaceae), which grows at ground level (<5 cm) with pinnate, postrate and horizontal leaves, and a perennial herb, *Senecio formosus* H.B.K. (Asteraceae), growing 20–50 cm in height and with vertically oriented leaves, were selected for our study. Three sites were selected along an altitudinal gradient in the Cordillera de Mérida, Estado Mérida, Venezuela (c. 8°52'N, 70°45'W): Los Plantios at 2900 m, Mucubaji at 3550 m and Las Cruces at 4200 m. Las Cruces has a “desert páramo” vegetation (total plant cover ranging from 5 to 30%) contrasting with the more mesic and humid Mucubaji and Los Plantios, with ground cover between 75 and 100% by natural páramo vegetation. This 2900–4200 m altitudinal gradient corresponds to a seasonal climatic gradient of decreasing temperature and precipitation with increasing altitude (Table 1) with a dry period, between December and March. This gradient comprises the entire altitudinal range of both species (Sarmiento 1986; Vareschi 1970). The studies were carried out with adult individuals during the middle of the wet season.

Gas exchange and water relations in the field

A portable system (LCA-2, ADC Ltd., Hoddesdon, England), calibrated at each of the study sites, was used to determine gas exchange rates in six leaves of four different individuals. Leaf water

Table 1 Climate data from selected high Andean localities along the altitudinal gradient

Site	Altitude (m)	Rainfall (mm)	Mean Temperature (°C)	Mean max warmest month	Mean min coldest month
Los Plantios	2900	1005	8.1	13.4	2.2
Mucubaji	3550	969	5.4	11.5	-0.4
Las Cruces	4200	798	2.8	7.8	-1.0

potential (Ψ_L) was measured with a pressure chamber (PMS Instrument Co., Corvallis, USA) approximately at 2- to 3-h intervals, four to six times a day during the daily courses, in four adult leaves of different individuals of each species. Leaf temperature ($n = 3$ for each species) was measured, at 1- to 2-h intervals, with copper-constantan thermocouples in contact with the lower leaf surface and connected to a digital multimeter (Data Precision, Model 258), and air temperature ($n = 4$) was measured at 30 cm above and at ground level. At the same time, relative humidity was measured with an Assmann ventilated wet-dry bulb psychrometer installed 40 cm above ground. Leaf and air temperatures and relative humidity were used to calculate vapor pressure difference between leaf and air (VPD). Total radiation was measured at 1-h intervals with a pyranometer connected to a LI-COR (LI-170) radiometer.

Net photosynthesis-leaf temperature relations measured in the laboratory

Several plants ($n \geq 5$) for each species and at each site were excavated with roots and surrounding soil, taken to the laboratory, and placed in a growth chamber equipped with light (12 h photoperiod, $500 \mu\text{mol m}^{-2} \text{s}^{-1}$) and temperature control simulating field conditions (15°C light period, 5°C dark period at 2900 m; 12°C light period, 3°C dark period at 3550 m; 7°C light period, 1°C dark period at 4200 m). Net photosynthesis-leaf temperature curves were determined in the laboratory using an infrared gas analyser (LCA-2, ADC Ltd) connected to a whole plant chamber (0.14 m^3). The chamber was equipped with a fan and a radiator with hose connections to a refrigerated bath, through which temperature was modified; and fine-wire copper-constantan thermocouples, two attached to the lower leaf surfaces and one for chamber temperature. Light was maintained constant at c. $900 \mu\text{mol m}^{-2} \text{s}^{-1}$ within the chamber, with minimal shading of leaves. A tray with circulating water was placed between the light source and the chamber to filter long wave radiation. CO_2 concentration was kept at 350 ± 25 ppm and relative humidity c. 80–90%. Measurements were started after the plants were brought to the laboratory and completed in a period no longer than 48 h for each species. CO_2 assimilation rates were measured through CO_2 depletion from the chamber making sure only photosynthetic tissue was exposed to the chamber environment. Temperature inside the chamber was increased from -2°C to 40°C, plants were left c. 10 min at each set temperature. Assimilation rates were measured at 1 minute intervals for 5 min at each of the chosen temperatures (approximately 3°C intervals at extremes and 0.5–1°C at temperatures near the optimum). Net photosynthesis (A , $\mu\text{mol m}^{-2} \text{s}^{-1}$) was calculated as:

$$A = V \times \Delta CO_2 / L \times \Delta \text{time}$$

where V is the chamber volume (m^3), L is the leaf area (m^2) and ΔCO_2 are changes in CO_2 concentrations ($\mu\text{mol m}^{-3}$) per time in seconds (Field et al. 1989).

Relationships between leaf and air or soil temperature in the field were obtained with linear regressions (Statgraphics 5.0). Optimum temperature for photosynthesis ($A_{o,t}$) for each species from each altitude was calculated as the first derivative of the net

photosynthesis-leaf temperature polynomial curves fitted to the data obtained in the laboratory.

Results

Diurnal courses of gas exchange in the field

CO₂ assimilation rates for *Acaena* at 2900 m (Fig. 1) reached a maximum above 9 $\mu\text{mol m}^{-2} \text{s}^{-1}$, about twice as high as the rates found at 3550 and 4200 m, 5.2 and 3.9 $\mu\text{mol m}^{-2} \text{s}^{-1}$, respectively. Maximum rates were measured, for the three altitudes, with photosynthetically active radiation (PAR) above 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and with leaf temperatures of 16–18°C, 17–24°C and 20–21°C from the lowest to the highest altitude, respectively. However, the lowest site is characterized by a rainy and humid climate, and the complete diurnal course shown corresponds to an exceptional day for this site with PAR levels greater than the normal for the wet season. When overcast conditions prevailed at Los Plantios with PAR below 500 $\mu\text{mol m}^{-2} \text{s}^{-1}$, maximum *A* rates were 4.7 $\mu\text{mol m}^{-2} \text{s}^{-1}$, similar to the rates obtained for this species at the other sites. For the three altitudes, patterns of CO₂ assimilation in *Acaena* closely followed the PAR curve, and the highest rates were

obtained during midmorning and decreased after noon. This decrease in assimilation may be attributed to progressively lower leaf conductances after midday. Ψ_L for this species at 3550 and 4200 m were relatively constant during the daily courses with the lowest values at noon (more than –0.5 MPa). Even though minimum Ψ_L was –1.1 MPa at 2900 m, normal overcast days also showed Ψ_L above –0.5 MPa.

CO₂ exchange rates for *Senecio* decreased with increasing altitude (Fig. 2). Maximum rates of CO₂ uptake in leaves was approximately 7.5, 5.8 and 3.6 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for plants at 2900, 3550 and 4200 m, respectively. Highest rates were reached between midmorning and early afternoon with PAR levels of 1000–1500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and leaf temperatures between 16/22°C at 2900 m, 15/18°C at 3550 m and 15°C at 4200 m. Patterns of CO₂ assimilation for this species closely followed the PAR curve, and the decrease in assimilation rate after midday may be explained by lower leaf conductances. It is important to note that for *Senecio* at 2900 m, when mean PAR values were 500 $\mu\text{mol m}^{-2} \text{s}^{-1}$, mean CO₂ assimilation was 6.6 $\mu\text{mol m}^{-2} \text{s}^{-1}$, close to the maximum value obtained in the exceptional day with higher PAR. In terms of Ψ_L , *Senecio* plants behaved similarly to *Acaena* along the gradient. Low values in Ψ_L at noon of –1.0 MPa for both species at 2900 m, may be

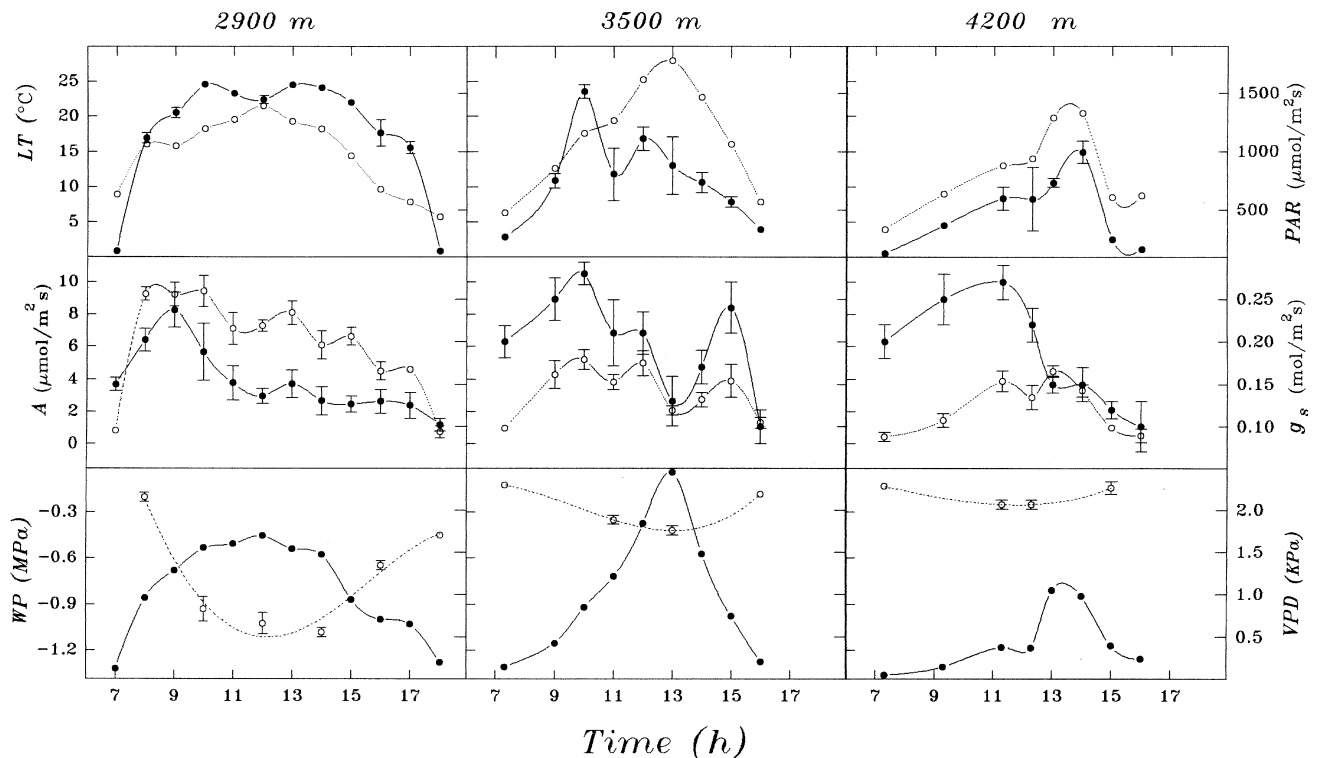


Fig. 1 Daily courses of leaf temperature (*LT*, ○), photosynthetically active radiation (*PAR*, ●), CO₂ assimilation rate (*A*, ○), leaf conductance (*g_s*, ●), leaf water potential (*WP*, ○) and leaf to air vapor pressure difference (*VPD*, ●) for *Acaena cylindrostachya* along the altitudinal gradient. Bars represent means \pm 1 SE ($n = 5$; for *LT* data are means for three thermocouples and variation was less than 0.5°C; for Ψ_L , $n = 4$)

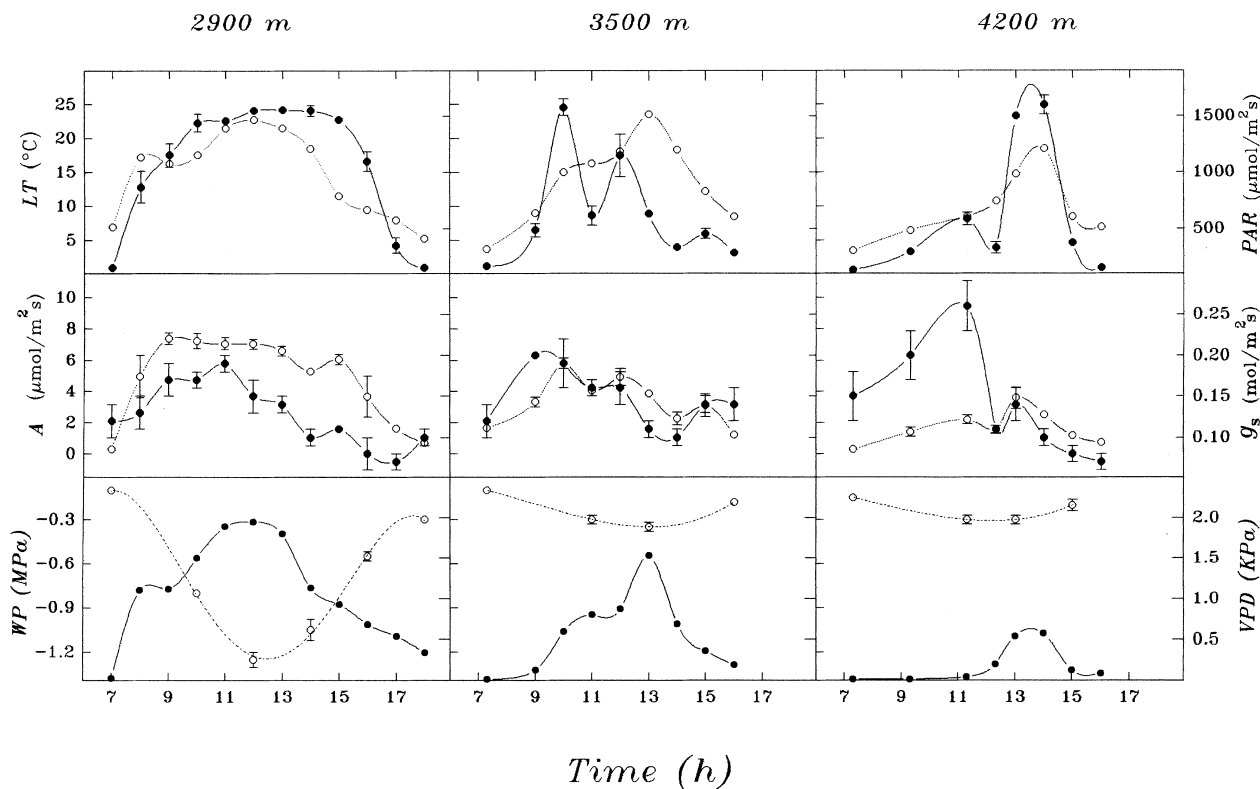


Fig. 2 Daily courses of leaf temperature (LT , \circ), photosynthetic active radiation (PAR , \bullet), CO_2 assimilation rate (A , \circ), leaf conductance (g_s , \bullet), leaf water potential (WP , \circ) and leaf to air vapor pressure difference (VPD , \bullet) for *Senecio formosus* along the altitudinal gradient. Bars represent means ± 1 SE ($n = 5$; for LT data are means for three thermocouples and variation were less than $0.5^\circ C$; for Ψ_L $n = 4$)

associated to high vapor pressure differences, c. 1.5–2.0 KPa, and as a consequence of these conditions, lower leaf conductances were observed.

Field measurements of air, soil and leaf temperature

A strong relationship was found between leaf temperature and air or soil temperature over the diurnal course for each species. Linear regressions showed that, for the two higher sites, leaf temperatures for *Acaena* were similar and closely related to soil temperatures, whereas *Senecio* leaf temperatures were coupled to air temperatures (Fig. 3). Soil temperatures reached values near $30^\circ C$ at noon on several days for each of the altitudes selected over this gradient of decreasing temperature. Leaf temperatures for *Acaena* reached $10^\circ C$ and $12^\circ C$ above air temperature at noon at 4200 and 3550 m, respectively. However, at the lower altitude leaf temperatures for both species showed similar values, without a strong relationship with air or soil temperatures. These results for 2900 m could be related to the more humid climate and greater ground cover at this altitude compared to Mucubaji or Las Cruces.

Field net photosynthesis-leaf temperature relations

CO_2 exchange rates in the field were plotted against leaf temperature. Only those assimilation rates with irradiances above $500 \mu mol m^{-2} s^{-1}$ were used, to avoid limitations imposed by PAR . A similar optimum temperature for photosynthesis ($A_{o.t.}$) was found for *Acaena* at each site along the gradient, between $18^\circ C$ and $19^\circ C$ (Fig. 4a). On the other hand, *Senecio* showed a clear trend that followed the expected air temperature decrease with altitude (Fig. 4b). This species showed an $A_{o.t.}$ of c. $21^\circ C$ and $18^\circ C$, at 2900 and 3550 m, respectively. A lower value of c. $15^\circ C$ was obtained at 4200 m.

Laboratory net photosynthesis-leaf temperature relations

Net photosynthesis-leaf temperature relations obtained in the laboratory for *Acaena* plants from different altitudes are shown in Fig. 5. $A_{o.t.}$ was similar for the two lowest altitudes with $19.1^\circ C$ at 2900 m and $19.6^\circ C$ at 3550 m; while at 4200 m there was an increase in leaf temperature optimum ($21.7^\circ C$). Maximum photosynthetic rates (A_{max}) for plants at each altitude were between 5.5 and $6.0 \mu mol m^{-2} s^{-1}$.

$A_{o.t.}$ decreased with increasing altitude of origin from $21.7^\circ C$ at 2900 m, to $19.7^\circ C$ at 3550 m and to $15.5^\circ C$ at 4200 m for *Senecio* (Fig. 6). A_{max} was progressively lower with increasing altitude. Plants from 2900 m showed rates of $6.0 \mu mol m^{-2} s^{-1}$, nearly $2.5 \mu mol m^{-2} s^{-1}$ higher than the rates found at 4200 m ($3.5 \mu mol m^{-2} s^{-1}$).

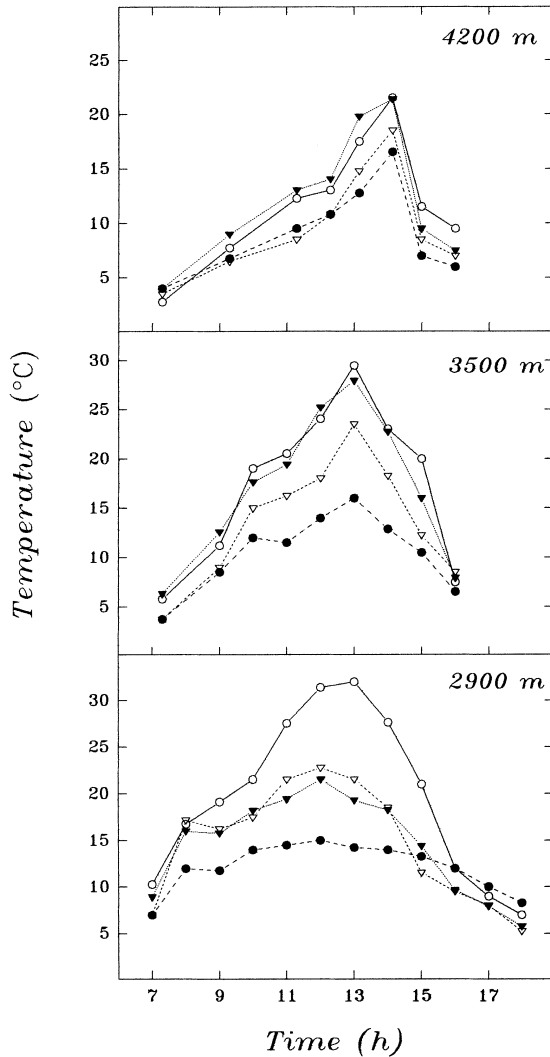


Fig. 3 Diurnal courses of soil (○), air (●), and leaf temperatures of *A. cylindrostachya* (▼) and *S. formosus* (▽) along the altitudinal gradient. Data for each temperature are means for three thermocouples and variation about the mean was generally less than 0.5°C. Linear regression analysis: 4200 m [*A. cylindrostachya* (*A.c.*) leaf (l) and soil (s) $r = 0.98$, $r^2 = 96$, $P < 0.05$ and *A.c.* l-air (a), $r = 0.95$, $r^2 = 89.5$, $P < 0.05$; *S. formosus* (*S.f.*) l-s, $r = 0.92$, $r^2 = 85$, $P > 0.1$ and *S.f.* l-a, $r = 0.95$, $r^2 = 89.5$, $P > 0.1$]. 3550 m [*A.c.* l-s, $r = 0.96$, $r^2 = 92.5$, $P > 0.1$ and *A.c.* l-a, $r = 0.92$, $r^2 = 84.5$, $P > 0.1$; *S.f.* l-s, $r = 0.93$, $r^2 = 87.5$, $P > 0.1$ and *S.f.* l-a, $r = 0.97$, $r^2 = 94.5$, $P > 0.1$]. 2900 m [*A.c.* l-s, $r = 0.87$, $r^2 = 75.5$, $P > 0.1$ and *A.c.* l-a, $r = 0.79$, $r^2 = 63$, $P > 0.1$; *S.f.* l-s, $r = 0.91$, $r^2 = 82$, $P < 0.05$ and *S.f.* l-a, $r = 0.79$, $r^2 = 63$, $P > 0.1$]

s⁻¹). Plants from 3550 m showed intermediate rates. For this species, there were no differences in terms of net photosynthesis between field and laboratory measurements when different altitudes were compared.

Discussion

Plant-ambient temperature relations and photosynthetic characteristics, influenced by soil or air temperatures,

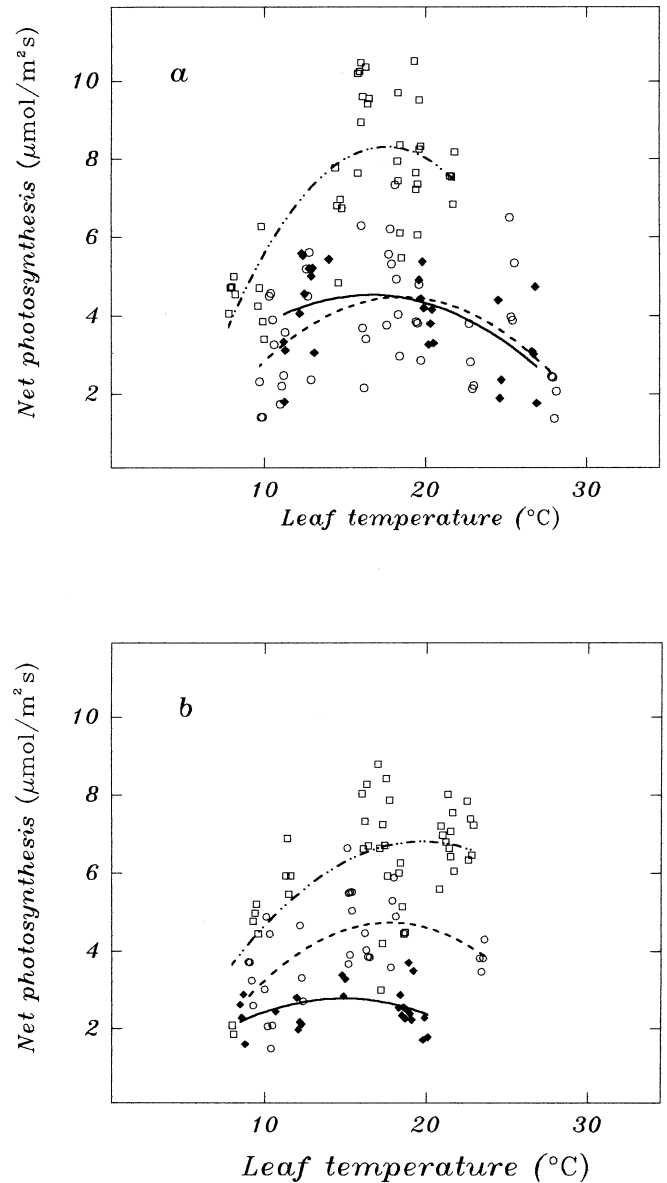


Fig. 4 Net photosynthesis-leaf temperature relations in the field for **a** *A. cylindrostachya* and **b** *S. formosus* along the altitudinal gradient. Net photosynthetic rates measured at PAR greater than 500 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Symbols correspond to: 2900 m (—□—), 3550 m (—○—) and 4200 m (—◆—)

differ along the altitudinal gradient and between the two morphologically contrasting species. Leaf-air temperature differences above 10°C were found for the acaulescent rosette *Acaena*, while they were below 6°C for the herb *Senecio*. In addition to these differences, a correlation between leaf and soil or air temperatures along the altitudinal gradient was found. On clear midsummer days in Australia's Snowy Mountains, leaf-air temperature differences were 13°C for shrubs, 21°C for dwarf shrubs, 24°C for rosette plants and 30°C for a moss cushion (Körner and Cochrane 1983).

The acaulescent rosette *Acaena*, strongly influenced by soil temperature, showed similar optimum tempera-

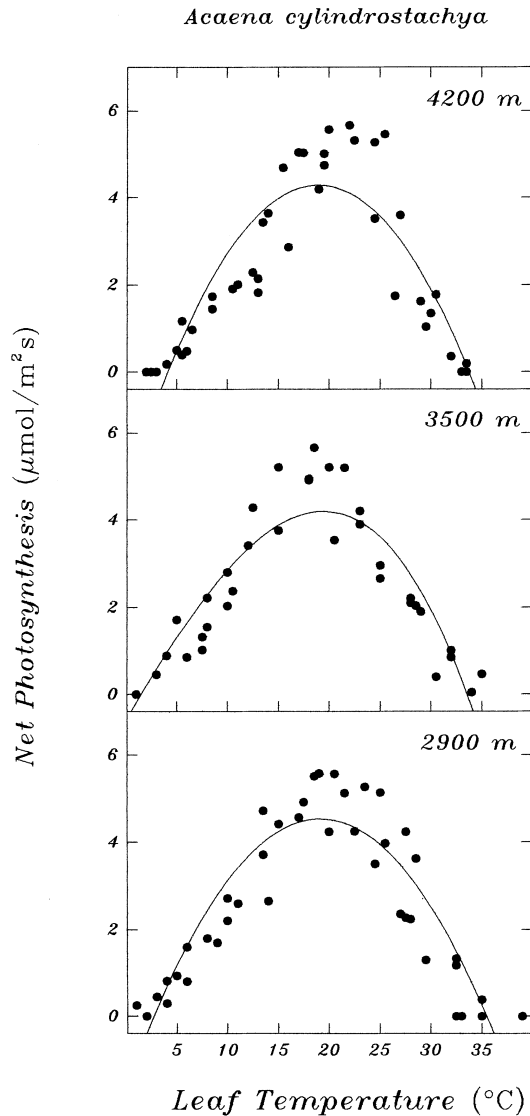


Fig. 5 Net photosynthesis-leaf temperature curves for *A. cylindrostachya* along the gradient. Curves are third-degree polynomial regression lines (95% confidence intervals) fitted to the data with coefficients of regression: 4200 m, $y = -(8.55 \times 10^{-4})x^3 - (2.63 \times 10^{-2})x^2 + (6.70 \times 10^{-2})x - 0.461$, $r^2 = 0.84$; 3550 m, $y = -(2.68 \times 10^{-4})x^3 - (2.08 \times 10^{-3})x^2 + 0.3899x - 0.642$, $r^2 = 0.78$; 2900 m, $y = -(8.35 \times 10^{-6})x^3 - (1.63 \times 10^{-2})x^2 + 0.6118x - 1.485$, $r^2 = 0.78$

tures for photosynthesis at 2900 and 3550 m, but this was more than 2°C higher at 4200 m. This increase at high altitude may be explained by a larger amount of bare soil, capable of warming up to a greater degree than at lower altitudes where ground cover is much greater. Leaf pubescence in *Acaena* may permit more efficient use of absorbed radiation at low environmental temperatures of the tropical high Andes, resulting in higher plant temperatures relative to air temperature, as described for two tropical Andean giant rosette plants (Meinzer and Goldstein 1985; Meinzer et al. 1985; Rada et al. 1985). Two acaulescent rosettes, *Hypochoeris setosus* and *Calandrinia acaulis*, showed similar or an increase, respectively, in optimum temperature for photosynthesis with

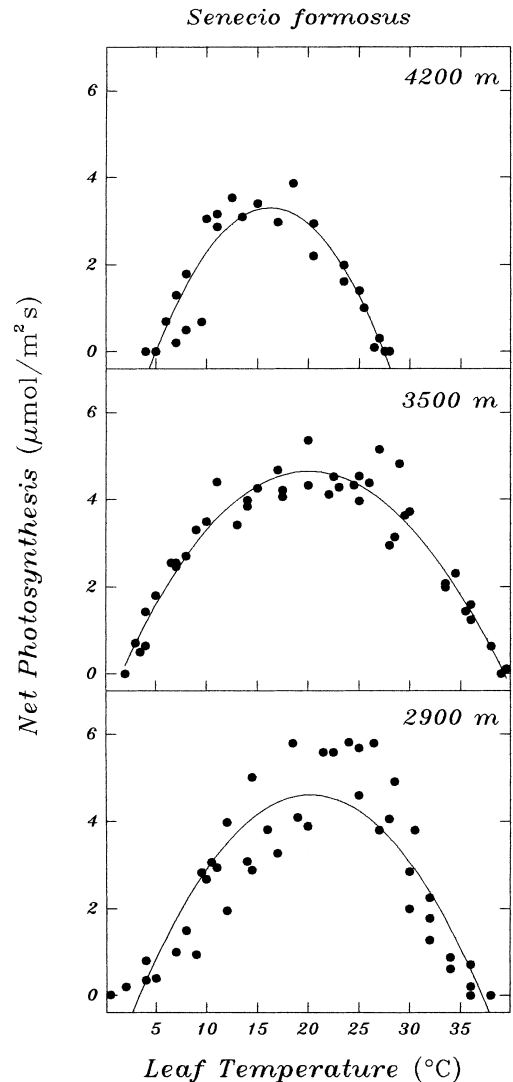


Fig. 6 Net photosynthesis-leaf temperature curves for *S. formosus* along the gradient. Curves are third-degree polynomial regression lines (95% confidence intervals) fitted to the data with coefficients of regression: 4200 m, $y = -(2.99 \times 10^{-4})x^3 - (4.08 \times 10^{-2})x^2 + 1.0517x - 4.258$, $r^2 = 0.87$; 3550 m, $y = -(5.94 \times 10^{-5})x^3 - (1.66 \times 10^{-2})x^2 + 0.5856x - 0.925$, $r^2 = 0.91$; 2900 m, $y = -(2.29 \times 10^{-4})x^3 - (4.87 \times 10^{-3})x^2 + 0.5367x - 2.119$, $r^2 = 0.82$

altitude (Rada et al. 1992). Körner and Diemer (1987) found similar optimum temperature for photosynthesis in different herbaceous plants along an altitudinal gradient in the Alps. In contrast, *Senecio* showed a decrease in the optimum leaf temperature for photosynthesis coupled to decreasing air temperatures with increasing elevation. This trend has also been described for species of different heights along this altitudinal gradient in the tropical high Andes (Rada et al. 1992). Phenotypic plasticity of this kind in woody species is common in cold environments (Tranquillini 1979) and results in lower optimum temperatures of plants at the colder higher altitudes than in plants growing at warmer low altitudes.

Vertical leaves often intercept nearly as much short-wave irradiation as do horizontal leaves over the course of a day, but they intercept less at midday, when air temperatures tend to be high (Nobel 1991). This characteristic would help explain the smaller differences found between air and leaf temperatures in *Senecio*. On the other hand, higher leaf temperatures at midday lead to greater transpiration for a given stomatal opening (Nobel 1991), and, therefore, this species would be faced with leaf temperatures well above photosynthetic optimum and/or greater stomatal control to avoid water losses. The temperature compensation points for net photosynthesis were similar for *Acaena* at all altitudes, with a range of approximately 35°C. *Senecio* plants show a wider temperature range (c. 40°C) at mid and low altitudes, compared to only c. 23°C for the highest site. These results confirm that *Senecio* shows a closer relation with the temperature regime at its specific habit, while *Acaena* is influenced by a warmer soil surface throughout the day and, therefore, effectively uncouples itself from low ambient temperatures along the altitudinal gradient. Larcher and Wagner (1976) reported a wider temperature range (40–55°C) for a positive carbon balance in alpine rosette and cushion plants, while the range for several species at different heights along a gradient for the tropical high Andes (Rada et al. 1992) is similar to those reported in this work.

Diurnal courses of CO₂ exchange for *Acaena* and *Senecio* along the altitudinal gradient show similar trends reported for other tropical Andean species: *Espeletia schultzii*, with lower CO₂ assimilation rates with increasing altitude (Baruch 1979; Rada et al. 1998). Changes in assimilation characteristics along the altitudinal gradient could be due to lower CO₂ partial pressures which can reduce photosynthetic rates (Friend and Woodward 1990), or to soil nitrogen deficiency at the higher altitudes (Malagon 1982) which would result in lower leaf nitrogen content, and therefore, reduced photosynthetic capacity (Vitousek et al. 1990; Rada 1993; Rada et al. 1998). Studies are being carried out on the CO₂ assimilation behavior of different plant species along the altitudinal gradient. For instance, why do *Acaena* plants show a differentiation in maximum assimilation rates along the gradient, but behave similarly when studied in the laboratory? Population differentiation for photosynthetic characteristics across altitudinal gradients is commonly observed in plants (Billings and Mooney 1968; Friend and Woodward 1990). The altitudinal distribution of *Acaena* and *Senecio* species depends on their capacity to adapt to the thermal conditions along the altitudinal gradient in the Andes. This photosynthetic plasticity in response to temperature is a major determinant for the success of plant species in different high mountain habitats and microenvironments.

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