DOI: 10.1007/s11099-012-0050-6 PHOTOSYNTHETICA 50 (3): 429-436, 2012

Water relations and gas exchange in *Coespeletia moritziana* (Sch. Bip) Cuatrec., a giant rosette species of the high tropical Andes

F. RADA[*,+], A. AZÓCAR[*], and A. ROJAS-ALTUVE[**]

Instituto de Ciencias Ambientales y Ecológicas, Facultad de Ciencias, Universidad de Los Andes. Mérida, Venezuela[*]
Departamento de Cristalografía y Biología Estructural, Instituto de Química-Física "Rocasolano", CSIC, Serrano 119, 28006-Madrid, Spain[**]

Abstract

Giant rosettes are ones of the most striking features of the vegetation in the high tropical Andes, with *Coespeletia moritziana* reaching the highest altitudes up to 4,600 m a.s.l. Different from other giant rosettes, this species grows on rock outcrops with poorly developed soils and where water availability may be limited. Two questions are addressed in this study: How does this species respond in terms of water relations to maintain favorable gas-exchange conditions? Considering that adult plants rely on a water-reserving central pith, how do early stages respond to this environment´s extreme conditions? Water relations and gas-exchange studies were carried out on juveniles, intermediate and adult *C. moritziana* plants during wet and dry seasons in Páramo de Piedras Blancas at 4,200 m a.s.l. Adult plants maintained higher leaf water potentials (Ψ_L) during the wet season, however, no differences between stages were found for the dry season. Minimum dry season Ψ_L were never near the turgor loss point in any of the stages. Juveniles show a more strict stomatal control during the dry season to maintain a favorable water status. Net photosynthesis significantly decreased in intermediate and juvenile stages from wet to dry seasons. Our results suggest that *C. moritziana* resists more extreme conditions compared to other Andean giant rosettes.

Additional key words: net photosynthetic rate; osmotic adjustment; plant growth stages; stomatal conductance; tropical mountains.

Introduction

Tropical high mountains combine an assortment of unique features to produce a very particular environment. Temperature plays an essential role in the existence of different plant life forms. Below zero temperatures may occur any night of the year, while daytime high incoming radiation inputs, with a greater frequency during the dry season, may generate high temperature conditions at leaf surfaces and near the ground. These conditions led Hedberg (1964) to describe this environment as one where summer occurs every day and winter every night of the year. In addition, water availability and high evaporative demand conditions are also critical features which determine plant survival at these altitudes. A distinctive dry season lasts from 2 to 4 months. Also, extremely low relative humidities, together with high solar radiation inputs determine a significant difference between leaf and air temperatures, leading to large water vapor pressure differences, which in turn have an impact on plant gas-exchange responses. Both temperature and water effects act differentially along soil level to air gradients. Therefore, plant survival may also be dependent on differential responses throughout the growing stages.

The páramos, in a very broad sense, may be defined as a characteristic ecosystem of the tropical high Andes composed mainly of low strata vegetation dominated by shrubs, grasses and giant rosettes. Within this latter plant life form, different species of the genus *Coespeletia* reach the highest altitudes of the high tropical Andes up to 4,600 m. As adults, these plants consist of a single rosette of large pubescent leaves supported by an erect, unbranched stem which in some cases may reach a few meters. This stem holds a large central parenchymatic pith and is protected by a large layer of marcescent leaves. It is interesting to point out that this life form, presenting very similar structures, has evolved in other

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Received 28 April 2011, *accepted* 26 April 2012.

[+]Corresponding author; tel.: (58) 274 2441575, fax: (58) 274 2401255, e-mail: frada@ula.ve

Abbreviations: E – transpiration rate; g_s – stomatal conductance; L – leaf area; P_N – net photosynthetic rate; PPFD – photosynthetic photon flux density; RH – relative humidity; T_a – air temperature; T_L – leaf temperature; V – chamber volume; VPD – leaf to air vapor pressure difference; WUE – water-use efficiency; ΔCO_2 – difference in CO_2 concentration; Δtime – difference in time; Ψ_L – leaf water potential; Ψ_L^{min} – minimum leaf water potential; Ψ_π^0 – osmotic potential at turgor loss.

tropical high mountain regions of the world (Hedberg and Hedberg 1979, Halloy 1983, Smith and Young 1987, Bussmann 2006), suggesting that they have developed as a response to a tropical environment characterized by extreme daily temperature fluctuations, frequent night frosts, seasonal and daily water availability limitations and high incoming radiation inputs.

Night-time low temperature resistance has been studied for many of the giant rosettes of the Venezuelan high Andes (Goldstein *et al.* 1985b, Rada *et al.* 1985). In all cases, a high supercooling capacity of the leaves together with isolating marcescent leaf layers protecting stems, permit these rosettes to avoid freezing of their tissues. However, giant rosettes species of the African tropical mountains (*Dendrosenecio* and *Lobelia* spp.) are able to tolerate ice formation in leaf tissues (Beck *et al.* 1984). With respect to daytime temperature, water availability, and evaporative demand studies, Goldstein *et al.* (1984) described how adult giant rosettes depend on a high capacitance generated by the water-storage pith in order to resist water deficit periods. In addition, Rada *et al.* (1987, 1998) and Goldstein *et al.* (1989) showed how *Espeletia schultzii*, *Coespeletia timotensis* and *Coespeletia spicata* rely on strong stomatal control to avoid large water losses under high water vapor pressure differences between leaf and air, mainly during the dry season. Both of these responses result in the maintenance of high Ψ_L throughout the year with the accompanying cost in reductions of net photosynthetic rates. Low net photosynthetic rates were described for Andean giant rosette species (Baruch 1979, Baruch and Smith 1979, Goldstein *et al.* 1989, Rada *et al.* 1998). Schulze *et al.* (1985) described relatively high net photosynthetic rates for different giant rosette species of the Afroalpine vegetation. It is important to mention that most major studies on giant rosette plants worldwide have been carried out on adult plants. Responses of early establishing or nonreproductive stages of these rosette plants have been scarcely described for *C. spicata* and *C. timotensis* in the literature (Estrada *et al.* 1991, Goldstein *et al.* 1985a). These authors consider only water relations aspects and to our knowledge no gas-exchange results have been presented.

C. moritziana is distributed between 4,000 and 4,600 m a.s.l. and mainly associated to rock outcrops with poorly developed soils presenting a large quantity of fractured rocks. Due to these characteristics, water availability may be limited. As stated previously, all described Andean giant rosette species avoid drought and/or high evaporative demand conditions through very strict stomatal control and a high capacitance obtained through the large water reservoirs of the central pith. Due to the more extreme conditions in which this species is found, several questions are addressed in this study: Does it respond, as all other giant rosettes, through a severe stomatal control during the unfavorable periods, or does it resist lower plant water potentials in order to maintain favorable gas-exchange conditions? Considering that the environment near the ground is more extreme, and that smaller rosettes have not yet formed a large water reserving central pith, how do these stages respond to the extreme conditions previously described? Additionally, Azócar *et al.* (2000) describe how all Andean giant rosettes respond to water and temperature stresses in a similar manner, and therefore they suggest that any change in the environmental conditions, *i.e.* harsher water-stress conditions, would affect them as an important functional group of the páramo. As a consequence, this ecosystem would be functionally unstable under present climate change scenarios. Does this species fall outside of the general pattern described for all giant rosette species?

Materials and methods

Study site and plant characteristics: The study was carried out in the Páramo de Piedras Blancas (08º52'N, 70º48'S) at an altitude of 4,200 m. This area corresponds to an open vegetation páramo (mainly rosette-shrub associations) of the Desert Páramo (Monasterio 1980) with different species of the genus *Coespeletia* with their characteristic tall stems (1–3 m) and narrow oblong-lanceolate pubescent leaves. Bare soils may vary between 50 and 90%. Mean annual temperature is 2.8ºC with little seasonal variation and extreme daily variations with maximum above 30ºC and night minimum below –10ºC. Mean annual precipitation is 790 mm falling mainly between April and December and a marked dry season between December and March.

As previously mentioned, *C. moritziana* grows on rock outcroppings with well drained and poorly developed soils. Three well differentiated size classes were selected: juvenile, intermediate, and adult stages.

Stage	Rosette diameter; plant height [cm]	Leaf length [cm]	Leaf width [cm]
Juvenile	20–25; 20–25	15–18	0.8–1.5
Intermediate	30–35; 30–35	20–25	1.5–2.5
Adult	55–60; 90–100	25–30	2.0–2.5

Juveniles grew close to the ground and did not show an apparent stem and rosettes appeared sessile. Intermediate plants had an early developing stem. Adult individuals presented a well-developed stem of approximately 40 cm in length, covered with marcescent leaves. Adult individuals were the only ones that had any signs of earlier reproductive events.

Three daily courses of water relations and gas-exchange measurements were carried out during each the month of February for the dry and between July and November for the wet seasons. All measurements were done at 1–1.5 h intervals for all courses. It is important to point out that measurement times for all wet season courses, on one hand, and all the dry season courses, on the other, were done at exactly the same hour periods, therefore, results presented correspond to means for each hour of the three daily courses considered for each season.

Microclimatic variables: Daily courses of microclimatic variables (air temperature (T_a, n = 3), relative humidity (RH, n = 3) and photosynthetic photon flux density (PPFD, n = 3) and leaf temperatures (T_L, n = 3) were carried out. T_a and T_L were measured with copper-constantan thermocouples connected to a digital thermometer for all three developmental stages. RH was measured with a digital hygrometer at the different plant heights. T_a, T_L, and RH were used to calculate leaf-to-air vapor pressure difference (VPD). PPFD was obtained through the selenium photocell of the leaf chamber of the gas-exchange system described further ahead.

Water relations: Ψ_L was measured in each of the studied daily cycles. Two leaves from three individuals in each size category were selected. Measurements were carried out with a pressure bomb (*Model 600, PMS Instruments Inc., Corwallis*, Oregon, USA).

Seasonal pressure-volume curves were generated to observe differences in osmotic potential at turgor loss (Ψ_π^0) in order to determine if there were any osmotic adjustments between seasons. Leaves from the three stages were collected in the field, placed in containers and then recut under water. The containers were covered with plastic bags to avoid water losses through transpiration and transported to the laboratory where they remained in dark for 16 h to obtain complete saturation. Leaf water potential at saturation and leaf mass were initially determined and leaves were placed on the laboratory bench in order to let them transpire. Thereafter, Ψ_L and leaf mass were continuously determined until changes in Ψ_L between measurements towards the end of the experiment were consistently small from one hour to the next. Leaves were then oven dried at 60ºC to obtain dry mass. Ψ_L components were obtained through the methods proposed by Tyree and Hammel (1972).

Gas exchange: Net photosynthetic rate (P_N), transpiration rate (E), and stomatal conductance (g_s) were measured on two completely developed leaves of three different individuals for each of the categories. A portable system (*LCA-4, ADC Ltd.,* Hoddesdon, UK) consisting of a leaf chamber and an infrared gas analyzer unit, operating in an open mode was used. All measurements were made under ambient conditions with CO_2 and water vapor circulating through the leaf chamber being supplied *via* a 5-m air probe. Mean ambient CO_2 concentration did not show significant differences between seasons in any of the size classes, with means of 359.9 ± 2.6 for the wet- and 355.9 ± 3.3 for the dry season. Mean relative humidity within the leaf chamber was 82.7 ± 5.0% during the wet- and 54.6 ± 3.9% during the dry season for all size classes. Leaves were sealed within the chamber for approximately 30 s, time in which stable measurements were obtained. Gas-exchange rates were determined according to von Caemmerer and Farquhar (1981).

PPFD-P_N curves for both wet- and dry seasons were constructed using field data. In addition, a P_N-T_L curve was constructed for adult plants from data obtained in the laboratory. Several adult plants (n = 3) were excavated from the study site and transported to the laboratory. Curves were carried out using a gas-exchange system with an infrared gas analyzer (*LCA-2, ADC Ltd.,* Hoddesdon, UK) and a plant chamber (0.014 m^3). The chamber was equipped with copper-constantan thermocouples connected to a digital thermometer. A 1,000 $\mu mol\ m^{-2}\ s^{-1}$ light source was placed above the chamber. A refrigerated bath with hose connections to a radiator installed within the chamber was used to increase and decrease T_a and consequently T_L. Five leaves from a single rosette were placed within the chamber. Measurements were done at 1-min intervals for 5 min at each chosen temperature. Plants were left 10–15 min at each set temperature. P_N was determined through CO_2 depletion from the chamber and calculated through:

$$P_N = V\ \Delta CO_2/(L\ \Delta time),$$

where V is the chamber volume [m^3], L is the leaf area [m^2], ΔCO_2 corresponds to differences in CO_2 concentration [$\mu mol\ m^{-3}$] and Δtime to differences in time [s] (Field *et al.* 1989).

Results

Differences in Ψ_L between stages were more pronounced during the wet season (Table 1, Fig. 1). Adult plants showed less negative Ψ_L between midmorning and early afternoon compared to intermediate or juvenile plants. These higher Ψ_L may be explained by lower VPD (non-significant trend) and significant differences in g_s, giving rise to significantly lower E in adult plants compared to the other two stages (Table 2). With respect to the dry season, VPD conditions were significantly higher compared to the wet season, while no significant differences were observed between stages (Table 2, Fig. 1). Lower Ψ_L were obtained for the dry season, however, no significant differences between stages were observed throughout the daily courses, showing similar minimum leaf water potentials (Ψ_L^{min}) at midday. Juveniles showed a more severe stomatal control during the dry season, closing stomata after early morning maximum leaf conductances and reaching lowest g_s at midday (Fig. 1). Even though Ψ_L were much lower during the dry season in all stages, none of them fell close to the turgor loss

Table 1. Mean (Ψ_L^{mean}) and minimum (Ψ_L^{min}) leaf water potential, and osmotic potential at the turgor loss point (Ψ_π^0) for the different growth stages of *Coespeletia moritziana* during both wet and dry seasons. Values presented correspond to mean ± SE ($n = 6$ for the wet and $n = 7$ for the dry season). *Different superscript letters* correspond to significant seasonal differences for each parameter within each stage (*U-Mann-Whitney*, $p<0.05$). *Different superscript numbers* correspond to significant differences between growth stages for each season (*Kruskal-Wallis*, $p<0.05$).

Stage	Season	Ψ_L^{mean} [MPa]	Ψ_L^{min} [MPa]	Ψ_π^0 [MPa]
Adult	Wet	$-0.78 \pm 0.04^{a,1}$	$-1.12 \pm 0.08^{a,1}$	$-1.69 \pm 0.13^{a,1}$
	Dry	$-1.39 \pm 0.06^{b,1}$	$-1.84 \pm 0.06^{b,1}$	$-2.30 \pm 0.07^{b,1}$
Intermediate	Wet	$-0.90 \pm 0.04^{a,2}$	$-1.18 \pm 0.07^{a,1}$	$-2.10 \pm 0.04^{a,2}$
	Dry	$-1.46 \pm 0.04^{b,1}$	$-1.90 \pm 0.06^{b,1}$	$-2.35 \pm 0.04^{b,1}$
Juvenile	Wet	$-0.94 \pm 0.04^{a,2}$	$-1.12 \pm 0.08^{a,1}$	$-1.93 \pm 0.08^{a,1,2}$
	Dry	$-1.43 \pm 0.06^{b,1}$	$-1.84 \pm 0.06^{b,1}$	$-2.30 \pm 0.14^{b,1}$

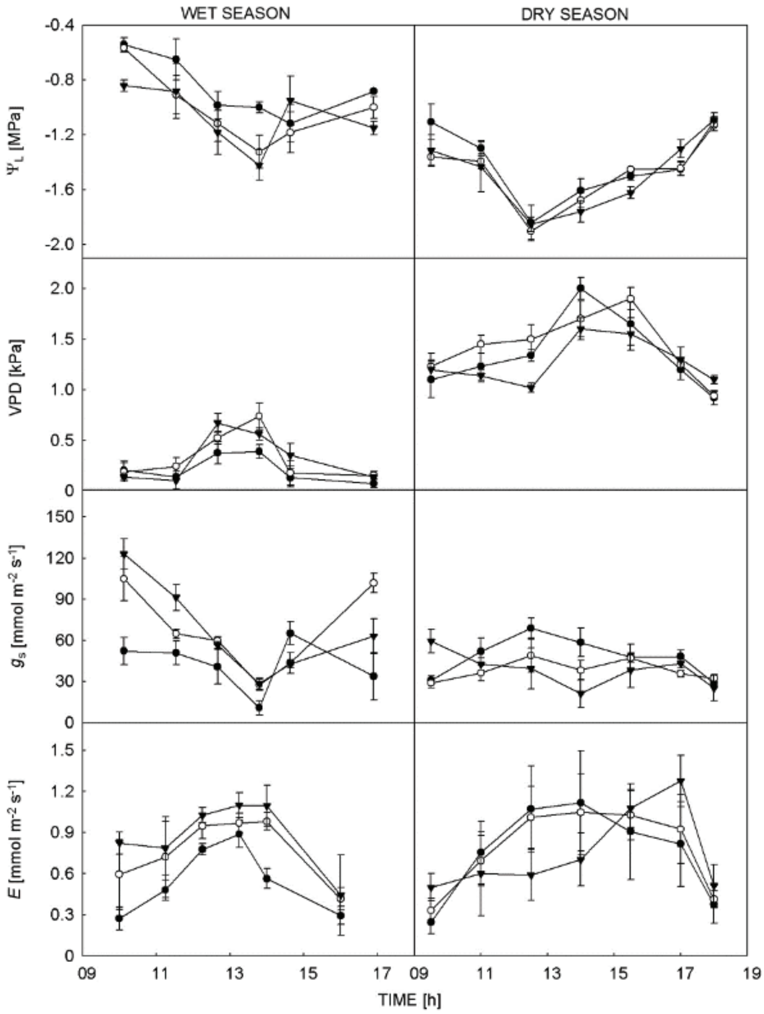

Fig. 1. Wet- and dry season courses for the different water relations parameters measured in the study: Leaf water potential (Ψ_L), vapor pressure difference between leaf and air (VPD), leaf stomatal conductance (g_s) and transpiration rate (E). Results correspond to the mean of three different daily courses taken for each of the seasons. Adults (●), intermediate (○), juveniles (▼). Values presented correspond to mean ± SE ($n = 9$ for both wet- and dry seasons).

point which was approximately –2.3 MPa for all stages (Table 1). Adult plants showed an important degree of seasonal osmotic adjustment with an approximate difference of 0.6 MPa between wet and dry season. Whereas, intermediate and juvenile stages showed a slight adjustment between 0.2 and 0.4 MPa from wet- to dry seasons due to the significantly lower Ψ_L at turgor loss during the wet season.

Incoming PPFD is much higher during the dry season resulting in higher T_L (Table 2, Fig. 2), lower RH (data not presented) and, therefore, higher VPD (Table 2). Even though adult plants decreased P_N from wet to dry season, differences were not significant, while intermediate and juvenile stages significantly decreased their photosynthetic rates. In relation to water use efficiency (WUE), the juvenile stage was the only one showing

Table 2. Mean photosynthetic photon flux density (PPFD), leaf temperature (T_L), vapor pressure difference between leaf and air (VPD), leaf stomatal conductance (g_s), transpiration rate (E), net photosynthetic rate (P_N,) and water-use efficiency (WUE) for the different growth stages of *Coespeletia moritziana* during both wet- and dry seasons. Values presented correspond to mean ± SE ($n = 6$ for the wet- and $n = 7$ for the dry season). *Different superscript letters* correspond to significant seasonal differences for each parameter within each stage (*U-Mann-Whitney*, $p<0.05$). *Different superscript numbers* correspond to significant differences between growth stages for each season (*Kruskal-Wallis*, $p<0.05$).

Stage	Season	PPFD [μmol m^{-2} s^{-1}]	T_L [°C]	VPD [kPa]	g_s [mmol m^{-2} s^{-1}]	E [mmol m^{-2} s^{-1}]	P_N [μmol m^{-2} s^{-1}]	WUE [mmol mol^{-1}]
Adult	Wet	$919 \pm 175^{a.1}$	$7.9 \pm 0.4^{a,1}$	$0.28 \pm 0.06^{a,1}$	$52.3 \pm 3.9^{a,1}$	$0.68 \pm 0.04^{a,1}$	$3.7 \pm 0.3^{a,1}$	$5.4 \pm 0.6^{a,1}$
	Dry	$1355 \pm 199^{b,1}$	$11.0 \pm 0.5^{b,1}$	$1.34 \pm 0.16^{b,1}$	$61.9 \pm 7.2^{a,1}$	$0.97 \pm 0.07^{b,1}$	$3.2 \pm 0.4^{a,1}$	$4.1 \pm 0.3^{b,1}$
Intermediate	Wet	$911 \pm 178^{a,1}$	$8.8 \pm 0.5^{a,1}$	$0.33 \pm 0.07^{a,1}$	$69.3 \pm 5.1^{a,2}$	$1.11 \pm 0.06^{a,2}$	$4.8 \pm 0.3^{a,2}$	$4.8 \pm 0.8^{a,1}$
	Dry	$1269 \pm 197^{b,1}$	$12.8 \pm 0.6^{b,2}$	$1.39 \pm 0.13^{b,1}$	$53.2 \pm 5.5^{b,1,2}$	$0.77 \pm 0.08^{b,2}$	$2.9 \pm 0.4^{b,1}$	$4.0 \pm 0.4^{a,1}$
Juvenile	Wet	$973 \pm 181^{a,1}$	$9.6 \pm 0.6^{a,1,2}$	$0.39 \pm 0.07^{a,1}$	$79.7 \pm 8.2^{a,2}$	$1.70 \pm 0.06^{a,3}$	$5.3 \pm 0.4^{a,2}$	$2.9 \pm 0.6^{a,2}$
	Dry	$1402 \pm 194^{b,1}$	$12.2 \pm 0.7^{b,2}$	$1.24 \pm 0.08^{b,1}$	$43.9 \pm 7.8^{b,2}$	$0.67 \pm 0.09^{b,2}$	$3.5 \pm 0.5^{b,1}$	$4.8 \pm 0.4^{b,1}$

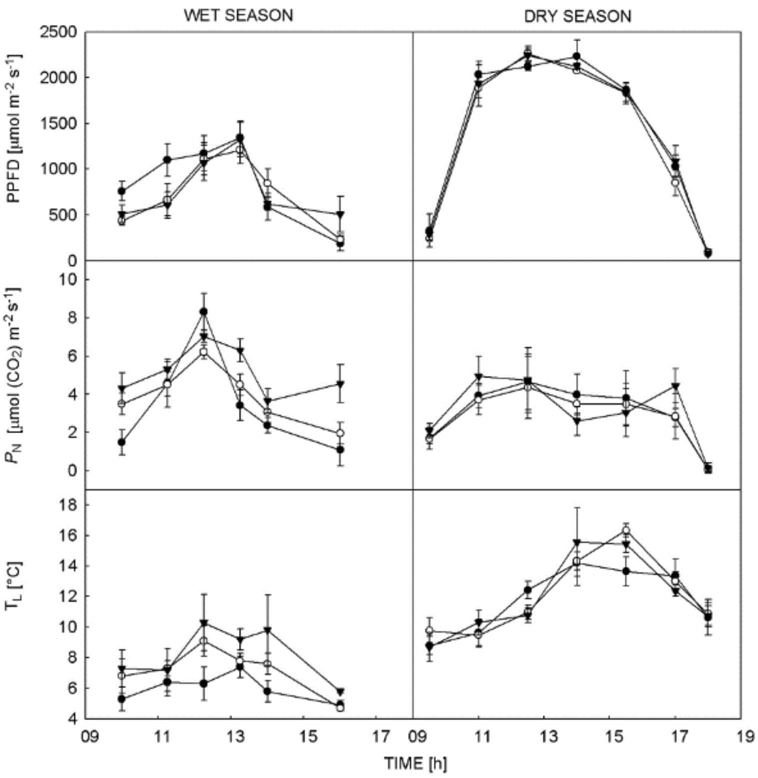

Fig. 2. Wet- and dry season courses for photosynthetic photon flux density (PPFD), net photosynthetic rate (P_N), and leaf temperature (T_L). Results correspond to the mean of three different daily courses taken for each of the seasons. Adults (●), intermediate (○), juveniles (▼). Values presented correspond to mean ± SE ($n = 9$ for both wet and dry seasons).

a significant increase from wet to dry season (Table 2). The significant seasonal decrease in P_N from one season to the other in intermediate and juvenile stages may be explained by the extremely high incoming radiation inputs from midmorning to midafternoon during the dry season. One can observe from the PPFD-P_N curves (Fig. 3) how P_N values decreased in these two stages at radiation inputs of 2,000 μmol m^{-2} s^{-1} or above. This decrease in P_N may also be explained by the significant decreases in g_s observed in these two stages (Table 2). Light compensation points were 20.7 and 24.5 μmol m^{-2} s^{-1} for adults, 20.3 and 37.6 μmol m^{-2} s^{-1} for intermediate and 45.7 and 27.2 μmol m^{-2} s^{-1} for juveniles during wet and dry seasons, respectively.

T_L may also be an important factor determining P_N differences from one season to the other. From T_L-P_N curves carried out on adult individuals one can determine that optimum T_L for photosynthesis for *C. moritziana* was 10.2ºC (Fig. 4) at maximum P_N of 4.1 μmol m^{-2} s^{-1}. Considering mean T_L obtained for wet and dry seasons, P_N rates were 3.7 μmol m^{-2} s^{-1} (T_L = 7.9ºC) and 4.0 μmol m^{-2} s^{-1} (T_L = 11.0ºC) for wet- and dry seasons, respectively. These values correspond to a 10% and 3% reduction in P_N from the optimum T_L for wet- and dry seasons, respectively.

Discussion

Water relations studies in Andean tropical mountains have suggested that giant rosette plants are not able to resist low Ψ_L. Rada *et al.* (1998) report very high Ψ_L^{min} for both wet (–0.6 MPa) and dry (–1.0 MPa) seasons in *Espeletia schultzii* at 4,200 m a.s.l. in the Venezuelan Andes. Baruch (1979) reports Ψ_L^{min} of –1.5 MPa for *E. schultzii* adult plants at 4,200 m. These authors also describe that a severe stomatal control was necessary to maintain these high Ψ_L. Estrada *et al.* (1991) describe Ψ_L^{min} for *Coespeletia spicata* of –1.6 MPa and –1.4 MPa for adult and juvenile plants, respectively, and values above –1.0 MPa for both adult and juveniles of *Coespeletia timotensis* in the same region of the Andes in which our study was carried out. These authors also suggest a strong stomatal control in *C. spicata*, while *C. timotensis* would rely on its efficient hydraulic connections between pith and leaves to maintain positive Ψ_L during the dry season. In a different study, *C. timotensis* small plants experienced lower Ψ_L compared to taller plants during the dry season, while no differences were observed during the wet season (Goldstein *et al.* 1985a). These authors report Ψ_L^{min} of –1.4 to –1.5 MPa for juveniles (20–30 cm in height) compared to values of –1.2 MPa for adults (90 cm in height). Goldstein *et al.* (1985a) describe a turgor loss point of –1.4 MPa for all height classes indicating this species does not have the ability to osmotically adjust. These authors conclude that this inability together with a smaller water-storage capacity during periods of low water availability result in a high risk of mortality in establishing stages for this species. Ψ_L^{min} (–1.8 to –1.9 MPa for all stages) described in our study are lower compared to those of other giant rosettes of the Andes. Additionally, turgor loss for *C. moritziana* is reached at a Ψ_L of –2.3 MPa, suggesting that it resists more extreme water-deficit conditions. Schulze *et al.* (1985) report very low diurnal Ψ_L (–2.2 MPa) for *Lobelia telekii*, an Afroalpine giant rosette during the dry season. Additionally, these authors report that these low water potentials did not have any effects on leaf conductance. It is important to note that Beck *et al.* (1984) have described extremely low Ψ_L (–6.7 MPa) in afroalpine giant rosettes when leaves are frozen at night. Since the freezing process involves water movement from intracellular to intercellular spaces in leaves, it is necessary that plants be extremely resistant to water deficits in order to survive. Therefore, it is not surprising that leaf conductance is not affected by low Ψ_L as has been reported by Schulze *et al.* (1985). In contrast, the *Coespeletias* do not have the ability to tolerate ice formation; consequently one would not expect these plants to be very resistant to water deficits.

In terms of gas exchange, stomatal control has been described as one of the main mechanisms by which giant rosettes resist low water availability and/or high evaporative demand periods in the high Andean environments. In fact, all *Coespeletia* studies establish important leaf conductance reductions from wet to dry seasons to avoid reaching low Ψ_L. Rada *et al.* (1998) describe reductions from 120 to 40 mmol m^{-2} s^{-1} from wet to dry seasons in *E. schultzii* in order to maintain Ψ_L above –1.0 MPa. In contrast, our results for *C. moritziana* show no seasonal differences in g_s for adult rosettes while intermediate and juvenile stages do have a stronger stomatal control during the dry season. Schulze *et al.* (1985) report g_s between 100 and 150 mmol m^{-2} s^{-1} for *Lobelia spp.* during the dry season. They also show how g_s is more strongly related to VPD and as previously stated Ψ_L did not have an immediate effect on g_s.

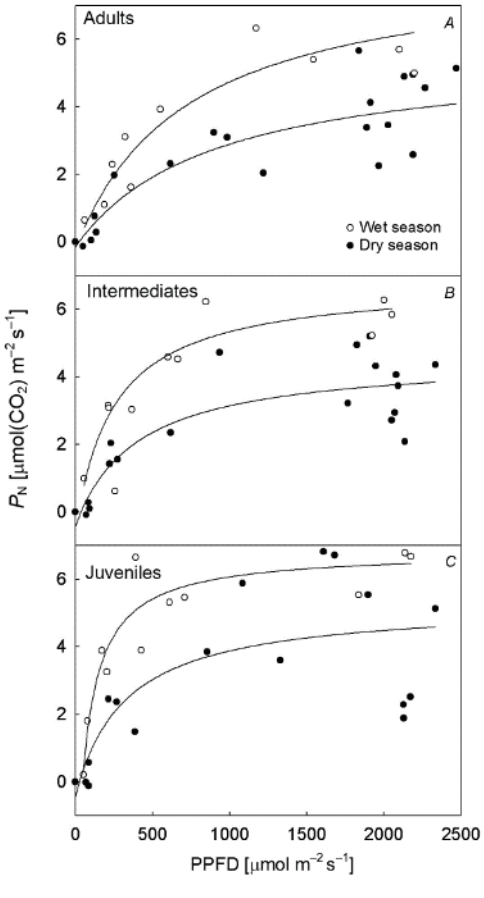

Fig. 3. Photosynthetic photon flux density (PPFD)-net photosynthetic rate (P_N) curves for *C. moritziana*'s three growth stages. *Open circles* correspond to the wet- and *solid circles* to the dry season. (*A*) wet season: P_N = 8.3 (–20.7 + PPFD)/(–20.7 + 733.7 + PPFD), r^2=0.78; dry season: P_N = 5.6 (–24.5 + PPFD)/(–24.5 + 916.7 + PPFD), r^2=0.71. (*B*) wet season: P_N = 6.8 (–20.3 + PPFD)/(–20.3 + 270.5 + PPFD), r^2=0.64; dry season: P_N = 4.6 (–37.6 + PPFD)/(–37.6 + 435.5 + PPFD), r^2=0.72. (*C*): wet season: P_N = 6.8 (–45.7 + PPFD)/(–45.7 + 117.8 + PPFD), r^2=0.84; dry season: P_N = 5.3 (–27.2 + PPFD)/(–27.2 + 350.7 + PPFD), r^2=0.62.

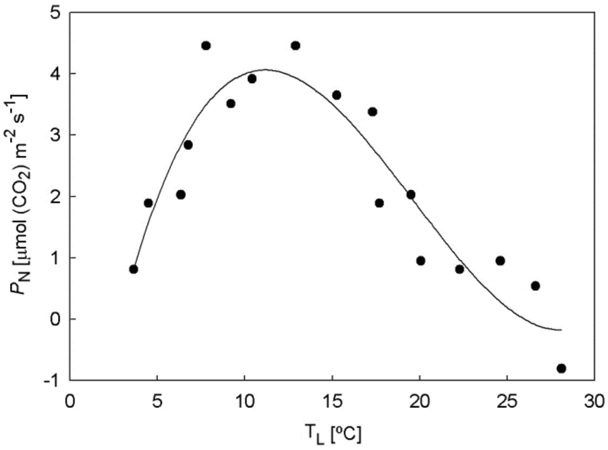

Fig. 4. Leaf temperature (T_L)-net photosynthetic rate (P_N) curve for adult plants of *Coespeletia moritziana*. Optimum temperature for photosynthesis corresponded to 10.2ºC. A fourth order polynomic function was fitted to the data ($P_N = -0.00007\ T_L^4 + 0.0065T_L^3 - 0.208T_L^2 + 2.508T_L - 6.064$, r^2=0.88).

Maximum P_N of 8 μmol m^{-2} s^{-1} found in this study for *C. moritziana* adult plants are comparable to those of *C. spicata* (Goldstein *et al.* 1989), and higher than those of *C. timotensis* (Goldstein *et al.* 1989) and *E. schultzii* (Rada *et al.* 1998), all giant rosettes growing at 4,200 m in the Venezuelan Andes. Both Goldstein *et al.* (1989) and Rada *et al.* (1998) describe how, during the dry season, P_N for different adult giant rosettes may fall down to the CO_2 compensation point during the day. In the case of *C. moritziana*, P_N remained constant between seasons in adult plants. In the case of the other two stages, even though P_N decreased from the wet to the dry season, it did not reach values close to the CO_2 compensation point, therefore suggesting that this species may maintain a more positive leaf carbon balance throughout the year compared to the other giant rosettes studied. Likewise, the wide range of maximum P_N described for giant rosettes in the Andes persists in African and/or Asian giant rosettes. Fetene *et al.* (1997) observed maximum P_N of 6–7 μmol m^{-2} s^{-1} in *Lobelia rhynchopetalum*, a giant rosette plant growing at 4,000 m in the tropical alpine regions of Ethiopia. Schulze *et al.* (1985) describe rates between 8–11 μmol m^{-2} s^{-1} for afroalpine rosettes of the genus *Dendrosenecio spp.* and *Lobelia spp.* during the dry season. While Terashima *et al.* (1993) measured P_N of 10–16 μmol m^{-2} s^{-1} and no stomatal restrictions for *Rheum nobile*, a monocarpic giant rosette, at 4,300 m in the Eastern Himalaya during the wet season, however no data is presented for the dry season. With respect to optimum temperature for photosynthesis, our result (10.2ºC) contrasts that of 7.9ºC for *E. schultzii* (Rada *et al.* 1992). However, temperature does not seem to be a major limitation since daily mean T_L for photosynthesis are always above the 90% for P_N in relation to the optimum T_L measured for adult plants. Schulze *et al.* (1985) mention that maximum P_N for different *Lobelia* and *Dendrosenecio* species occur between 8ºC and 13ºC. In addition, high radiation inputs may be limiting *C. moritziana*'s photosynthetic capacity. As observed in our work, at high radiation inputs P_N decreases. Fetene *et al.* (1997) report CO_2 uptake inhibition in *L. rhynchopetalum* at high PPFD. Cui *et al.* (2004) describe how high radiation induces photoinhibition, limiting photosynthetic carbon gain in *Saussurea superba*, a dwarf rosette plant of the Qinghai-Tibet Plateau.

With respect to the comparison between life cycle stages, the importance of the pith water storage of the giant rosettes stands out. However, *C. moritziana*'s intermediate and juvenile stages appear to overcome its lack by having higher g_s, mainly during early morning and late afternoon hours of the wet season. The ability to maintain low osmotic potentials at turgor loss, even in the wet season, allows these two stages to have higher g_s and higher P_N during both seasons. Even though P_N decreased during the dry season in intermediates and juveniles, mean rates are still very positive (2.9 and 3.5 μmol m^{-2} s^{-1}, respectively). For instance, *E. schultzii* growing at 4,200 m in the Venezuelan Andes had maximum and mean P_N of 2.2 and 0.9 μmol m^{-2} s^{-1}, respectively; almost four times below *C. moritziana*'s dry season rates for any of the stages. According to Fetene *et al.* (1998), for *L. rhynchopetalum* adult plants, water relations are not important due to roots that reach the deep soil. However, juveniles, with superficial roots are subjected to severe drought during the dry season. They suggest this would be one of the main reasons why very few individuals survive. Other authors also report a high mortality rate in establishing phases of *C. timotensis* and *C. spicata* in the high Venezuelan Andes (Estrada and Monasterio 1988, Guariguata and Azócar 1998). All these results point to the importance of the establishing phase as a main filter in the success of plants. However, it is still necessary to study *C. moritziana*'s survival rates in these phases due to its apparent more resistant characteristics under these extreme environments. We suggest that the success of these rosettes depends on how they are able to get away from the most extreme conditions of the ground surface to reach the more favorable conditions well above ground level.

Giant rosettes had been described as having very similar responses to water and temperature stress (Azócar *et al.* 2000). These authors suggested that under a change in ambient conditions, *i.e.* more extreme water deficits and/or higher temperature effects, all giant rosettes would be negatively affected, thus jeopardizing this ecosystem's functional stability. Although our intention is not to conclude on this stability, as we are clear that there are many other factors involved, our results do suggest that *C. moritziana* is capable of resisting, throughout all stages, more extreme conditions than other studied giant rosettes of the tropical high Andes.

References

Azócar, A., Rada, F., García-Núñez, C.: [Ecophysiological aspects for the conservation of contrasting tropical ecosystems.] – B. Soc. Bot. Mex. **65**: 89-94, 2000. [In Span.]

Baruch, Z.: Elevation differentiation in *Espeletia schultzii* (Compositae), a giant rosette plant of the Venezuelan paramos. – Ecology **60**: 85-98, 1979.

Baruch, Z., Smith, A.P.: Morphological and physiological correlates of niche breadth in two species of Espeletia (Compositae) in the Venezuelan Andes. – Oecologia **38**: 71-82, 1979.

Beck, E., Schulze, E.D., Senser, M., Scheibe, R.: Equilibrium freezing of leaf water and extracellular ice formation in Afroalpine 'giant rosette' plants. – Planta **162**: 276-282, 1984.

Bussmann, R.W.: Vegetation zonation and nomenclature of African mountains – An overview. – Lyonia **11**: 41-66, 2006.

Cui, X., Tang, Y., Gu, S., Shi, S., Nishimura, S., Zhao, X.: Leaf orientation, incident sunlight and photosynthesis in the alpine species *Suassurea superba* and *Gentiana straminea* on the Qinghai-Tibet Plateau. – Arct. Antarct. Alp. Res. **36**: 219-228, 2004.

Estrada, C., Monasterio, M.: [Population Ecology of a giant rosette, *Espeletia spicata* Sch. Bip. (Compositae), from the Desert Páramo.] – Ecotrópicos **1**: 25-39, 1988. [In Span.]

Estrada, C., Goldstein, G., Monasterio, M.: Leaf dynamics and water relations of *Espeletia spicata* and *E. timotensis*, two giant rosettes of the desert Paramo in the tropical Andes. – Acta Oecol. **12**: 603-616, 1991.

Fetene, M., Nauke, P., Lüttge, U., Beck, E.: Photosynthesis and photoinhibition in a tropical alpine giant rosette plant, *Lobelia rhynchopetalum*. – New Phytol. **137**: 453-461, 1997.

Fetene, M., Gashaw, M., Hauke, P., Beck, E.: Microclimate and ecophysiological significance of the tree-like life-form of *Lobelia rhynchopetalum* in a tropical alpine environment. – Oecologia **113**: 332-340, 1998.

Field, C., Ball, J.T., Berry, J.A.: Photosynthesis: principles and field techniques. – In: Piercy, R.W., Ehleringer, J., Mooney, H.A., Rundel, P.W. (ed.): Plant Physiological Ecology. Field Methods and Instrumentation. Pp. 209-253. Chapman & Hall, London 1989.

Goldstein, G., Meinzer, F., Monasterio, M.: The role of capacitance in the water balance of Andean giant rosette species. – Plant Cell Environ. **7**: 179-186, 1984.

Goldstein, G., Meinzer, F., Monasterio, M.: Physiological and mechanical factors in relation to size-dependent mortality in an Andean giant rosette species. – Acta Oecol.-Oec. Plant. **6**: 263-275, 1985a.

Goldstein, G., Rada, F., Azócar, A.: Cold hardiness and supercooling along an actitudinal gradient in Andean giant rosette species. – Oecologia **68**: 147-152, 1985b.

Goldstein, G., Rada, F., Canales, M.O., Zabala, O.: Leaf gas exchange of two giant caulescent rosette species. – Acta Oecol. **10**: 358-370, 1989.

Guariguata, M.T., Azócar, A.: Seed bank dynamics and germination ecology in *Espeletia timotensis* (Compositae), an Andean giant rosette. – Biotropica **20**: 54-59, 1998.

Halloy, S.: The use of convergence and divergente in the interpretation of adaptation in high mountain biota. – Evol. Theor. **6**: 232-255, 1983.

Hedberg, O.: Features of afro-alpine plant ecology. – Acta Phytogeogr. Suecica **49**: 1-144, 1964.

Hedberg, I., Hedberg, O.: Tropical alpine life forms of vascular plants. – Oikos **33**: 297-307, 1979.

Monasterio, M.: [Vegetation formations of the Venezuelan Páramos.] – In: Monasterio, M. (ed.): [Ecological Studies of the Andean Páramos.] Pp. 93-158. Ediciones Univ Los Andes, Mérida, Venezuela, Mérida 1989. [In Span.]

Rada, F., Goldstein, G., Azócar, A., Meinzer, F.: Freezing avoidance in Andean giant rosette plants. – Plant Cell Environ. **8**: 501-507, 1985.

Rada, F., Goldstein, G., Azócar, A., Torres, F.: Supercooling along an altitudinal gradient in *Espeletia schultzii*, a caulescent giant rosette species. – J. Exp. Bot. **188**: 491-497, 1987.

Rada, F., González, J., Azócar, A., Briceño, B., Jaimez, R.: Net photosynthesis-leaf temperature relations in plant species with different height along an altitudinal gradient. – Acta Oecol. **13**: 535-542, 1992.

Rada, F., Azócar, A., González, J., Briceño, B.: Leaf gas exchange in *Espeletia schultzii* Wedd, a giant caulescent rosette species, along an actitudinal gradient in the Venezuelan Andes. – Acta Oecol. **19**: 73-79, 1998.

Schulze, E.D., Beck, E., Scheibe, R., Ziegler, P.: Carbon dioxide assimilation and stomatal response of afroalpine giant rosette plants. – Oecologia **65**: 207-213, 1985.

Smith, A.P., Young, T.P.: Tropical alpine plant ecology. – Annu. Rev. Ecol. Syst. **18**: 137-158, 1987.

Terashima, I., Masuzawa, T., Ohba, H.: Photosynthetic characteristics of a giant alpine plant, *Rheum nobile* Hood. f. et Thoms. and of some other alpine species measured at 4300 m, in the Eastern Himalaya, Nepal. – Oecologia **95**:194-201, 1993.

Tyree, M.T., Hammel, H.T.: The measurement of the turgor pressure and the water relations of plants by the pressure-bomb technique. – J. Exp. Bot. **23**: 267-282, 1972.

von Caemmerer, S., Farquhar, G.D.: Some relationships between the biochemistry of photosynthesis and the gas exchange of leaves. – Planta **153**: 376-387, 1981.