



# Water relations and gas exchange in *Ruilopezia atropurpurea* (Asteraceae), a giant rosette growing under contrasting microclimates in the high tropical Andes

Relaciones hídricas e intercambio de gases en *Ruilopezia atropurpurea* (Asteraceae), una roseta gigante que crece en microclimas contrastantes en los altos Andes tropicales

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## ABSTRACT

Tropical high andean ecosystems, known as paramos, are unique because they are highly diverse, have a high number of endemic species, and play an essential role in different ecosystem services, but are especially susceptible to climate change. Most of the giant rosettes, a dominant growth-form in the paramos, depend on unique features like stems protected by marcescent leaves, voluminous stem pith, and leaf pubescence. However, *Ruilopezia atropurpurea* lacks these characteristics and must respond differently to endure the paramo extreme conditions. Additionally, unlike other rosettes, this species is found under contrasting exposed and understory microenvironments so that intraspecific plasticity is also expected. We evaluated the responses of *R. atropurpurea* in terms of leaf water relations, gas exchange, and morphological characteristics in temporal (seasonal and daily variations) and spatial (microsite differences) scales in a Venezuelan paramo. *R. atropurpurea* displayed lower leaf water potentials (minimum leaf water potentials of -1.5 MPa and -1.8 MPa at the turgor loss point), higher leaf conductance ( $620 \text{ mmol m}^{-2}\text{s}^{-1}$ ), transpiration ( $5 \text{ mol m}^{-2}\text{s}^{-1}$ ), and  $\text{CO}_2$  assimilation ( $13 \text{ } \mu\text{mol m}^{-2}\text{s}^{-1}$ ) rates compared to other paramo giant rosettes. A reduction in leaf area and specific leaf area occurred from understory to exposed sites. *R. atropurpurea* diverges from the typical responses of most paramo giant rosettes to the extreme environmental conditions. This species' morphological and physiological plasticity permits it inhabit under variable microclimatic conditions, but despite its confirmed plasticity, it is not able to reach higher elevations as other giant rosettes successfully have.

**Keywords:**  $\text{CO}_2$  assimilation rate, leaf water potential, paramo, phenotypic plasticity, plant functional traits.

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## RESUMEN

Los ecosistemas tropicales de las partes altas de los Andes, conocidos como páramos, son únicos debido a su alta diversidad, gran número de especies endémicas y rol esencial en distintos servicios ecosistémicos, pero son especialmente susceptibles al cambio climático. La mayoría de las rosetas gigantes, que es la forma dominante de crecimiento en los páramos, poseen características únicas como tallo cubierto por hojas marcescentes, médula de tallo voluminosa y pubescencia foliar. Sin embargo, *Rui-lopezia atropurpurea* no posee estas características y depende de respuestas particulares para sobrevivir en estos ambientes extremos. Adicionalmente, a diferencia de otras rosetas gigantes, esta especie habita microambientes contrastantes bajo copas de plantas y expuestas por lo que esperaríamos cierta plasticidad intraespecífica. Evaluamos las respuestas de *R. atropurpurea* en términos de relaciones hídricas, intercambio de gases y características morfológicas en tiempo (variaciones estacionales y diarias) y espacio (diferencias entre micrositos) en un páramo de los Andes venezolanos. *R. atropurpurea* mostró potenciales hídricos foliares menores (potenciales hídricos foliares mínimos de -1,5 MPa y -1,8 MPa de pérdida de turgor), mayor conductancia foliar ( $620 \text{ mmol m}^{-2}\text{s}^{-1}$ ), transpiración ( $5 \text{ mol m}^{-2}\text{s}^{-1}$ ) y asimilación de  $\text{CO}_2$  ( $13 \text{ } \mu\text{mol m}^{-2}\text{s}^{-1}$ ) en comparación con otras rosetas gigantes. Se encontró una reducción en el área foliar y área foliar específica entre plantas bajo copas y expuestas. Las respuestas de *R. atropurpurea* a las condiciones ambientales extremas contrastan con aquellas de la mayoría de las rosetas gigantes de páramo. Su plasticidad morfológica y fisiológica le permite establecerse en condiciones microclimáticas variables, pero a pesar de esta plasticidad, no tiene la capacidad para alcanzar mayores elevaciones como lo logran exitosamente otras rosetas gigantes.

**Palabras clave:** Páramo, plasticidad fenotípica, potencial hídrico foliar, rasgos funcionales de plantas, tasa de asimilación de  $\text{CO}_2$ .

## INTRODUCTION

High tropical mountains integrate a set of environmental conditions which make them very unique ecosystems and to which plants must, through different strategies, adapt to survive. Even though at first hand these areas are defined as cold environments; both low and high temperatures play a fundamental role in the survival of plants. High radiation inputs during the day may directly affect exposed plant tissues and indirectly have an effect through higher surface temperatures, while freezing temperatures may occur any night. Therefore, plants are exposed to ‘summer’ during the day and ‘winter’ at night (Hedberg 1964). With regard to water conditions, to a greater or lesser extent, high tropical mountains are subjected to a marked seasonality in precipitation. In addition, low relative humidity and high soil surface temperatures on clear days give rise to high evaporative demands. These high evaporative demands together with limited seasonal water availability determine extreme demanding conditions for plants (Rada *et al.* 2019).

The paramo ecosystems of the high tropical Andes, occur above the tree line and consist of predominantly low stature vegetation, mainly dominated by tussock grasses, shrubs and giant rosettes growth-forms. The paramo is the most floristically diverse and holds the highest number of endemic species of any other mountain ecosystem in the world (Luteyn *et al.* 1999, Beniston 2003, Sklenář *et al.* 2014, Pouchon *et al.* 2018). These highly endemic, biologically diverse ecosystems have been described as critical biodiversity hotspots (Myers *et al.* 2000) and are especially susceptible to climate change (Buytaert *et al.* 2010, Cuesta *et al.* 2019).

The giant rosettes, considered a classical example of convergent evolution, are the result of particular adaptations to cold tropical environments, and have evolved independently in different mountain ranges as exemplified by the genera: *Coespeletia* Cuatrec. and *Espeletia* Mutis ex Bonpl. in the Andes; *Senecio* L., *Dendrosenecio* (Hauman ex Hedberg) B. Nord. and *Lobelia* L. for Equatorial Africa; and *Argyroxiphium* DC. in Hawaii (Monasterio and Vuillemier 1986). In the particular case of the Andes, the

*Espeletia* complex (Rauscher 2002), represented by genera including *Carramboia* Cuatrec., *Coespeletia*, *Espeletia*, *Espeletiopsis* Cuatrec., *Libanothamnus* Ernst, *Tamania* Cuatrec., and *Ruilopezia* Cuatrec. (Cuatrecasas 1976, see Mavárez *et al.* (2019) for a differing stand on this division criteria), is an example of rapid diversification and adaptive radiation in island ecosystems like the paramos (Monasterio and Sarmiento 1991).

Most of the giant rosettes in the paramo present very conspicuous morphological characteristics which differentiate them from other growth forms: A thick layer of marcescent leaves surrounding the stem, a voluminous central stem pith and densely pubescent leaves (Monasterio and Sarmiento 1991, Rada 2016). Marcescent leaves protect stem and pith from freezing temperatures (Smith 1979, Goldstein and Meinzer 1983, Rada *et al.* 1985, Cárdenas *et al.* 2018) and the stem pith functions as a water storage compartment permitting the rosettes to maintain positive leaf water potentials under limiting water availability (Goldstein *et al.* 1984, Estrada *et al.* 1991). Different studies suggest that pubescence plays an essential role in the leaf thermal balance through a coupling between incident radiation, air, and leaf temperatures (Meinzer *et al.* 1994) and through a high reflection of incident radiation which helps prevent heat overloads. Between 13 % and 21 % of the radiation that reaches the leaf surface in different species of *Coespeletia* and *Espeletia* is reflected (Baruch and Smith 1979, Goldstein *et al.* 1989, Rosquete 2004). A reduction in leaf area in response to colder and drier environments has also been reported for giant rosettes (Meinzer *et al.* 1985). Different authors describe relatively high leaf water potentials ( $\Psi_L$ ) for several pubescent *Coespeletia* and *Espeletia* species (Baruch and Smith 1979, Goldstein *et al.* 1984, Rada *et al.* 1998) and severe stomatal closure under limiting water conditions occur resulting in lower CO<sub>2</sub> assimilation rates. An exception to these  $\Psi_L$  patterns is displayed by *Coespeletia moritziana* (Sch. Bip. ex Wedd.) Cuatrec. which at extreme elevations (> 4000 m altitude) in a particularly dry paramo reaches lower  $\Psi_L$  and rely on osmotic adjustments under drought periods (Rada *et al.* 2012).

Nonetheless, other giant rosettes that inhabit these regions do not depend on these adaptations such as large central stem pith and pubescent leaves, to respond to the particular conditions of the paramos and therefore must exhibit other mechanisms that guarantee their survival.

The genus *Ruilopezia* is composed of approximately 26 species (Briceño and Morillo 2002), their main feature being monocarpic caulescent rosettes. *Ruilopezia atropurpurea* (A.C. SM.) Cuatrec., unlike previously described giant rosettes, shows important morphological differences such as coriaceous leaves which vary greatly in size and are glabrous on the abaxial surface and scarcely pubescent on the adaxial surface, and presents a small or nonexistent stem pith. Baruch and Smith (1979) and Goldstein *et al.* (1985) have described the ability of *Ruilopezia atropurpurea* and *R. floccosa* (Standl.) Cuatrec. to withstand lower  $\Psi_L$ . Additionally, Baruch and Smith (1979) have indicated that *Ruilopezia atropurpurea*, similarly to the great majority of other giant rosettes, establishes in open paramo conditions, but contrarily to most of them, it is also found beneath the canopy of other plants.

In view of the morphological differences in *Ruilopezia atropurpurea*, in relation to the other dominant paramo rosettes, we would expect different ecophysiological responses in order to cope with variable seasonal and daily temperature and water availability conditions occurring in these high tropical mountain environments. Additionally, since *R. atropurpurea* is found under contrasting microenvironmental conditions, we would expect to find intraspecific adjustments in different morphological and/or water relations characteristics depending on the corresponding microenvironment, fully exposed or under the canopy of other plant growth-forms, mainly shrubs and other grasses. Our main objective was to study the responses of *R. atropurpurea* in terms of water relations and gas exchange characteristics in temporal (seasonal and daily variations) and spatial (microsite differences) scales in the Venezuelan Andes. We also aim to compare the responses of *R. atropurpurea* with those of other dominant giant rosette species of the paramo which present contrasting morphological characteristics.

## MATERIALS AND METHODS

This study was carried out in the Paramo de San Jose, Venezuelan Andes (8°19' North, 71°18' West) at an elevation of 3150 m. The study site corresponds to a border limit between two slopes, a more humid one with an annual rainfall of 1300 mm and a drier one with 900 mm, with two dry periods, one between January and the beginning of March and a briefer one between June and July (Monasterio and Reyes 1980). Dulhoste (2010) reported an 8

°C mean annual temperature for this site. The vegetation of the Paramo de San Jose represents a typical formation of the Paramo Andino (Monasterio 1980), dominated by tussock grasses, caulescent rosettes (mainly *Espeletia schultzei*, *Ruilopezia atropurpurea* and *R. lindenbergii* (Sch. Bip. ex Wedd.) Cuatrec.) and clustered shrubs (mostly *Hypericum* L.) (Fig. 1a).

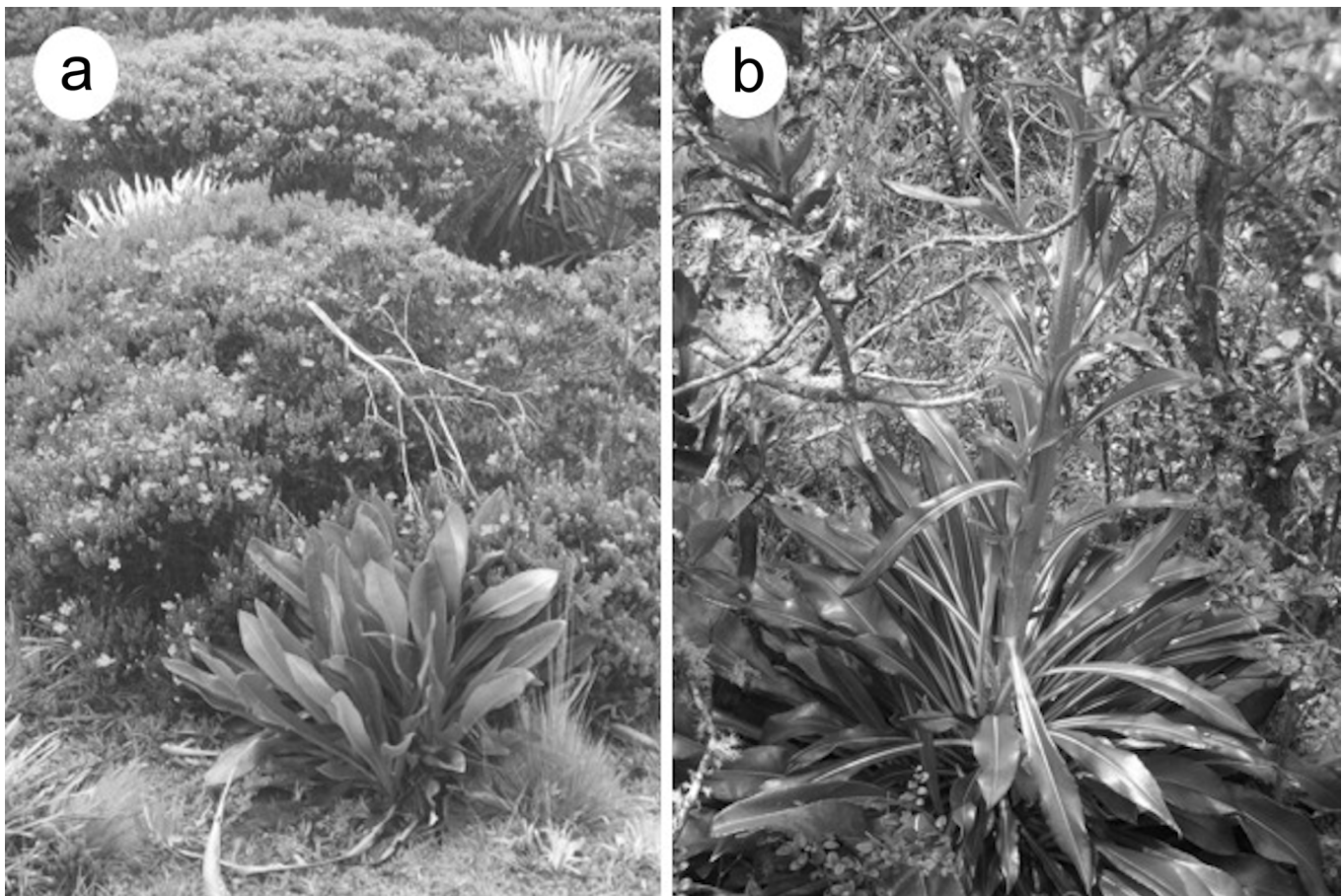
*Ruilopezia atropurpurea* (Asteraceae) is a monocarpic caulescent rosette with a relatively small stem pith and large leaves, glabrous on the adaxial and scarcely pubescent on the undersurface (Fig. 1b). Leaves are variable in size, ranging between 80 and 220 cm<sup>2</sup>. Our studied individuals were chosen from the drier slope sites, however, it is important to note that cloudiness begins in the early afternoon on both slopes practically every day of the year. Since this species is monocarpic, we had to consider a differentiating criterion to ensure that completely grown plants were chosen for the study. To differentiate these ‘adult’ plants from juveniles, individuals which presented more than one ring of marcescent leaves at their base were chosen.

Seven three-day field trips were carried out, four during the wet and three during the dry season, in which different microclimatic and plant morphological and physiological variables were measured for exposed and understory *R. atropurpurea* individuals.

#### Microclimatic variables

External sensors connected to dataloggers (HOBO Onset Corp.) were placed totally exposed and under the canopy of shrubs to measure continuously at 10 min intervals air temperature and incoming radiation (20 cm above the soil surface) throughout the study period (November 2010 to February 2012). Additionally, a soil moisture sensor connected to the datalogger was horizontally placed at a depth of 5 cm in the exposed site to measure soil water content.

During the field trips, other microclimatic variables were assessed at 2 h intervals from 06:00 to 16:00 h in exposed and understory sites. These parameters were: Photosynthetic photon flux density (PPFD), relative humidity (RH), air temperature ( $T_A$ ) and leaf temperature ( $T_L$ ). PPFD was



**Figure 1.** Representative vegetation of Paramo de San Jose. **a** An individual of *R. atropurpurea* (foreground) and pubescent giant rosettes of *Espeletia schultzei* and the shrub *Hypericum* sp. in the background. **b** Close up of an *R. atropurpurea* individual.

obtained from a quantum sensor located on the leaf chamber of the portable gas exchange system described further down.  $T_A$  and  $T_L$  were measured with constantan-copper thermocouples connected to a digital thermometer and RH with a digital hygrometer. Temperatures and relative humidity measurements were used to calculate leaf to air vapor pressure differences (VPD).

#### Leaf water potentials and its components

Leaf water potential ( $\Psi_L$ ,  $N=3$  per condition) were measured in fully developed leaves. Measurements were carried out every two hours between 06:00 and 16:00 h using a pressure chamber.

In order to determine the different components of the leaf water potential (leaf osmotic potential at turgor loss ( $\Psi_L^{tp}$ ), elasticity modulus ( $\epsilon$ ), relative water content at turgor loss ( $RW^{ctp}$ )), pressure-volume curves from five individuals for each microclimatic condition were carried out in the laboratory for leaves collected during three different times: the end of the wet season (December 2010), the beginning of the wet season (March 2011) and in the middle of the dry season (January 2012). Leaves were cut in the field, submerged in containers with water, then cut again under water to restore continuity in xylem and ensure rehydration of the samples. This material was taken to the laboratory and placed in darkness in a growth chamber at 8 °C for 12 h before beginning the curves.

#### Gas exchange measurements

Stomatal conductance ( $G_s$ ,  $\text{mol m}^{-2}\text{s}^{-1}$ ),  $\text{CO}_2$  assimilation ( $A$ ,  $\mu\text{mol m}^{-2}\text{s}^{-1}$ ) and leaf transpiration ( $E$ ,  $\text{mmol m}^{-2}\text{s}^{-1}$ ) rates were determined during both wet and dry seasons for three exposed and understory adult individuals. Continuous measurements were attained between 09:00 and 12:00 h with a portable infrared gas analyzer (ADC Bio-Scientific Ltd, LCi). In order to compare  $A$  rates between sites, and knowing that leaf nitrogen content (LNC) may influence maximum assimilation rates, LNC were determined for understory and exposed plants using a micro-Kjeldahl method (Muller 1961). A composite sample from two leaves from three different plants were obtained at each microsite.

#### Leaf area and specific leaf area

Leaf area (LA) and specific leaf area (SLA) measurements were performed on fully expanded leaves of exposed and understory plants during wet and dry seasons. Seven leaves from three individuals were sampled. Plant mate-

rial was brought to the laboratory in plastic bags with wet absorbent towels to avoid drying out of the samples. LA was obtained by scanning leaves with the program Irfan-View (Skiljan 2012) and areas were calculated via Image J (Rasband 1997). To calibrate and verify the results, the same procedure was performed with known areas ( $N=10$ ) obtaining an error  $\leq 0.01$ . Leaves were then placed in a drying oven for 72 h at 60 °C; SLA (LA/dry weight,  $\text{cm}^2/\text{g}$ ) was then calculated.

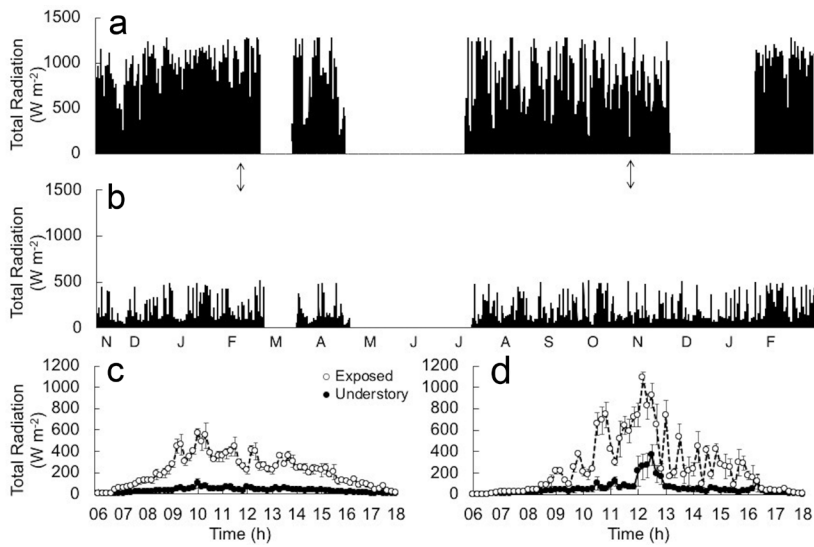
SPSS 10.0.7 (SPSS 2000) was used to carry out U Mann-Whitney non-parametric tests to determine whether or not there were differences between microclimatic conditions and for physiological and morphological variables within each season and for each microclimatic condition between seasons.

## RESULTS

#### Exposed and understory microclimate

Total radiation inputs for understories were 80 % lower compared to exposed sites (Figs. 2a-b). Exposed areas frequently received loads of  $1200 \text{ Wm}^{-2}$ , mainly during the drier months while understory sites seldom reached peaks (sunflecks) above  $600 \text{ Wm}^{-2}$  and mostly remained below  $400 \text{ Wm}^{-2}$ . Although cloudiness is a factor that plays an important role throughout the year, important seasonal differences were found in incoming radiation, with the months of January and February showing larger values compared to the rest of the year (March-November). Daily total radiation courses show typical patterns for wet and dry seasons (Figs. 2c-d). Lower radiation inputs ( $<600 \text{ Wm}^{-2}$ ) through the day for exposed sites during the wet season compared to higher inputs, reaching a maximum close to  $1200 \text{ Wm}^{-2}$  during the dry season. Understory plants received constantly low incoming radiation all day during the wet, while some small peaks were observed during the dry season.

The absolute maximum and minimum temperatures for exposed microsites were 35.7 °C and -3.6 °C respectively, both occurring on the same day (January 20, 2011) and resulting in an amplitude of approximately 40 °C (Fig. 3). Absolute maximum and minimum temperatures for the understory were 24.0 °C and -1.2 °C, respectively. Understory microsites presented an average temperature of 8.9 °C compared to 9.9 °C for exposed areas, a difference of just 1 °K, meaning that maximum and minimum tem-



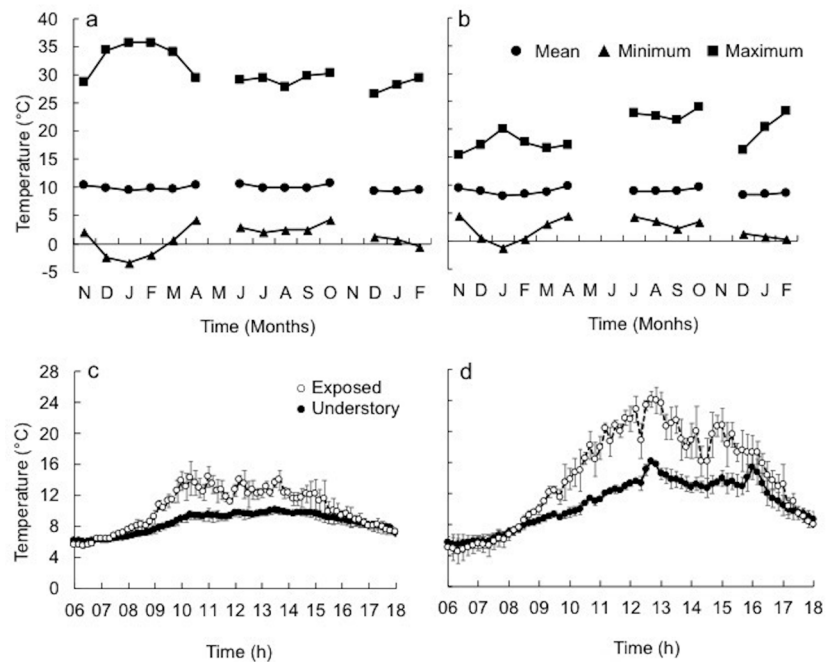
**Figure 2.** Seasonal and daily total radiation courses for the study period. **a** Seasonal pattern for exposed and **b** understory sites. **c** Daily radiation courses for exposed and understory sites during wet and **d** dry seasons. Bars represent one standard error from the mean. Arrows on panels **a** and **b** correspond to the chosen periods for daily courses shown in **c** and **d**. Open spaces in panels **a** and **b** refer to periods in which loggers were not available or sensor was disabled.

peratures are far more important to consider in terms of plant responses to contrasting microsites. With respect to daily cycles (Fig. 3d), the understory microsite maintained more stable mean maximum temperatures throughout the day during the wet season, compared to small variations during the dry season. On the other hand, the exposed site showed important maximum temperature fluctuations throughout the day, mainly during the dry season.

The two drier seasons were evident from the SWC measurements (data not shown). These periods occurred between the months of January and February. Although both

dry seasons were distinct, it is important to note that the second one was more extreme than the first. Soil water increased during the month of March and remained more or less stable from June to December when the next dry season set in.

Seasonal significant differences in maximum vapor pressure differences between leaf and air were found for each of the studied microsites (Table 1). Again, important differences in  $VPD_{max}$  between understory and exposed sites were obtained for the dry season, while there were no significant differences between sites for the wet season.



**Figure 3.** Absolute maximum and minimum, and mean air temperatures for **a** exposed and **b** understory sites throughout the study period. Representative daily temperature courses for the **c** wet and **d** dry season. Bars represent one standard error from the mean.

**Table 1.** Ecophysiological variables determined for understory and exposed *Ruilopezia atropurpurea* individuals during wet and dry seasons.

Ecophysiological variables	Wet season		Dry season	
	Understory	Exposed	Understory	Exposed
VPD <sub>max</sub> (KPa)	0.73±.15 <sup>a1</sup>	0.81±.24 <sup>a1</sup>	1.01±.12 <sup>b1</sup>	1.91±.18 <sup>b2</sup>
T <sub>L</sub> (°C)	11.0±.6 <sup>a1</sup>	13.6±.9 <sup>a2</sup>	13.4±.8 <sup>a1</sup>	17.4±1.1 <sup>b2</sup>
Ψ <sub>Lmin</sub> (MPa)	-0.58±.08 <sup>a1</sup>	-0.79±.09 <sup>a1</sup>	-1.19±.11 <sup>b1</sup>	-1.46±.15 <sup>b1</sup>
ε	15.3±3.7 <sup>a1</sup>	16.5±7.6 <sup>a1</sup>	10.7±.5 <sup>a1</sup>	16.2±2.0 <sup>a2</sup>
RWC <sup>tlp</sup>	0.85±.05 <sup>a1</sup>	0.89±.06 <sup>a1</sup>	0.79±.01 <sup>a1</sup>	0.74±.03 <sup>b1</sup>
G <sub>Smean</sub> (mmol m <sup>-2</sup> s <sup>-1</sup> )	351±23 <sup>a1</sup>	443±56 <sup>a1</sup>	136±8 <sup>b1</sup>	127±12 <sup>b1</sup>
G <sub>Smax</sub> (mmol m <sup>-2</sup> s <sup>-1</sup> )	478±9 <sup>a1</sup>	620±48 <sup>a2</sup>	246±5 <sup>b1</sup>	143±11 <sup>b2</sup>
A <sub>mean</sub> (μmol m <sup>-2</sup> s <sup>-1</sup> )	8.7±.3 <sup>a1</sup>	10.2±.6 <sup>a2</sup>	6.4±.1 <sup>b1</sup>	6.0±.1 <sup>b2</sup>
A <sub>max</sub> (μmol m <sup>-2</sup> s <sup>-1</sup> )	10.8±.2 <sup>a1</sup>	13.3±.2 <sup>a2</sup>	6.6±.1 <sup>b1</sup>	6.9±.1 <sup>b1</sup>
LA* (cm <sup>2</sup> )	127.4±4.6 <sup>1</sup>	85.6±8.0 <sup>2</sup>		
SLA* (cm <sup>2</sup> g <sup>-1</sup> )	50.6±2.5 <sup>1</sup>	36.1±2.4 <sup>2</sup>		
LNC* (%)	1.25±.06 <sup>1</sup>	1.07±.04 <sup>2</sup>		

VPD<sub>max</sub>= Maximum vapor pressure difference, T<sub>L</sub>= mean daily leaf temperature, Ψ<sub>Lmin</sub>= minimum leaf water potential, ε= mean modulus of elasticity, RWC<sup>tlp</sup>= relative water content at the turgor loss point, G<sub>Smean</sub>= mean leaf conductance, G<sub>Smax</sub>= maximum leaf conductance, A<sub>mean</sub>= mean CO<sub>2</sub> assimilation rate, A<sub>max</sub>= maximum CO<sub>2</sub> assimilation rate, LA= leaf area, SLA= specific leaf area, LNC= leaf nitrogen content. \*No significant seasonal differences were obtained for these variables, so data were grouped. Superscript letters and numbers show differences between seasons and between microclimate conditions, respectively according to U Mann-Whitney tests.

### Leaf water relations

No differences were found between leaf water potentials at the turgor loss point (Ψ<sub>L<sup>tlp</sup></sub>) between microsite conditions (Fig. 4a). On the contrary, significant differences between seasons (December and January) were a sign of important osmotic adjustments in this species. The month of March corresponded to a transition period between seasons. Moreover, due to this adjustment, Ψ<sub>L<sup>min</sup></sub> were always considerably above the turgor loss point during both seasons (Figs. 4b-c).

### Gas exchange characteristics

Mean PPFD was significantly lower in the understory compared to the exposed sites during the gas exchange measurements. Additionally, significant differences were also present between seasons for the understory (Fig. 5), and even though dry season PPFD conditions were slightly higher for the exposed microsite compared to the wet, these differences were not statistically significant.

Mean G<sub>s</sub> were not significantly different between understory and exposed microsites in either of the seasons (Fig. 5, Table 1), while seasonal significant differences were found for both microclimatic conditions. Reductions of 62 % and 67 % in mean G<sub>s</sub> between seasons were obtained for the understory and exposed sites, respectively; while a 77 % reduction in maximum G<sub>s</sub> was observed between wet and dry seasons for exposed *R. atropurpurea* plants (Table 1).

Mean A for plants under both microclimatic conditions were higher during the wet season, with maximum values of 10.8 and 13.3 μmol m<sup>-2</sup>s<sup>-1</sup> for understory and exposed plants, respectively (Fig. 5, Table 1). Mean A values fell approximately 25 % from wet to dry seasons in understory plants, while maximum A was reduced in 39 %. The decrease was larger for exposed plants, 41 % and 48 % for mean and maximum A, respectively (Table 1). Leaf nitrogen contents varied when compared understory to exposed plants. These contents were significantly higher for those individuals found under the shrubs' canopies (Table 1).

Given the severe stomatal closure, important reductions in  $E$  were found for both understory and exposed plants from the wet to the dry season (Fig. 5). Highest  $E$  corresponded to exposed plants during the wet season ( $5 \text{ mmol m}^{-2}\text{s}^{-1}$ ).

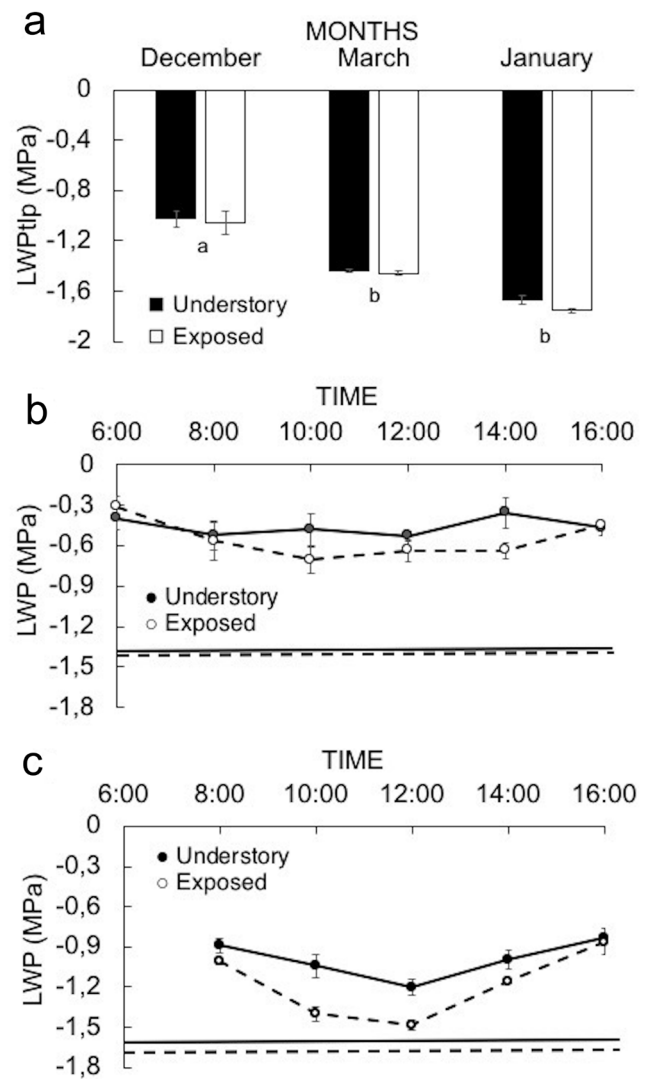
Finally, understory plants had significantly greater LA and SLA compared to exposed ones (Table 1).

## DISCUSSION

An important characteristic of our study site, and of paramos in general, is the highly variable cloud regime with persistent cloud events alternating with episodes of high solar radiation. This regime determines important seasonal and daily variations in microclimatic variables such as solar radiation, air temperature, air evaporative demand and water availability. *R. atropurpurea* responds to these variations by modifying several morphological and physiological traits.

Different leaf morphological characteristics, such as leaf size and pubescence, determine a plant's thermal balance. Despite large leaf sizes in an environment with periods of high solar incoming radiation, decoupling of air and leaf temperature in different *Espeletia* species from Venezuelan and Colombian paramos is achieved through leaf spectral and boundary layer characteristics defined mainly by leaf pubescence and orientation (Meinzer *et al.* 1994, Sánchez *et al.* 2014, León-García and Lasso 2019). One would expect that giant rosettes like *R. atropurpurea* would have higher leaf temperatures when present in open paramo habitats due to its upper glabrous surfaces compared to other pubescent rosettes. Yet, measured mean ( $17.4 \text{ }^{\circ}\text{C}$ ) and maximum ( $23.3 \text{ }^{\circ}\text{C}$ ) leaf temperatures for exposed *R. atropurpurea* were similar to those reported for *Coespeletias* and *Espeletias*, pubescent caulescent rosettes of Venezuelan and Colombian paramos (Goldstein *et al.* 1989, Rada *et al.* 1998, Sánchez *et al.* 2014, Sánchez *et al.* 2018). While pubescent leaves of giant rosettes reflect a significant proportion of incident solar radiation in order to maintain a favorable thermal balance (Goldstein *et al.* 1989), considerably higher transpiration rates in *R. atropurpurea* may play, to some extent, a role in controlling leaf temperature. This species displays  $E$  close to  $3 \text{ mmol m}^{-2}\text{s}^{-1}$  for the dry and occasionally above  $5 \text{ mmol m}^{-2}\text{s}^{-1}$  during the wet season, compared to values between 1 and  $2 \text{ mmol m}^{-2}\text{s}^{-1}$  for pubescent rosette species for both wet and dry seasons (Goldstein *et al.* 1989, Rada *et al.* 1998). Leaf

pubescence also plays an important role against increasing UV radiation at higher elevations in alpine environments (Barnes *et al.* 2017). In the particular case of *R. atropurpurea*, it is probable that this species relies on anthocyanins and other polyphenols as a protection mechanism against UV radiation as described for other alpine plants (Barnes *et al.* 2000, Apelt *et al.* 2019). In fact, this species was named 'atropurpurea' for its slight purple coloration of its leaves which may suggest the presence of these chemical compounds.



**Figure 4.** Leaf water potential characteristics for understory and exposed *R. atropurpurea* during wet and dry seasons. **a** Leaf water potential at the turgor loss points ( $\Psi_{L}^{tip}$ ) for December 2010, March 2011 and January 2012. Different letters represent significant differences ( $P < 0.05$ ) between months, while there were no significant differences between microsite conditions. **b** and **c** Representative daily courses for wet and dry seasons, respectively. Solid and dotted lines correspond to the  $\Psi_{L}^{tip}$  for understory and exposed plants, respectively. Bars correspond to one standard error from the mean.

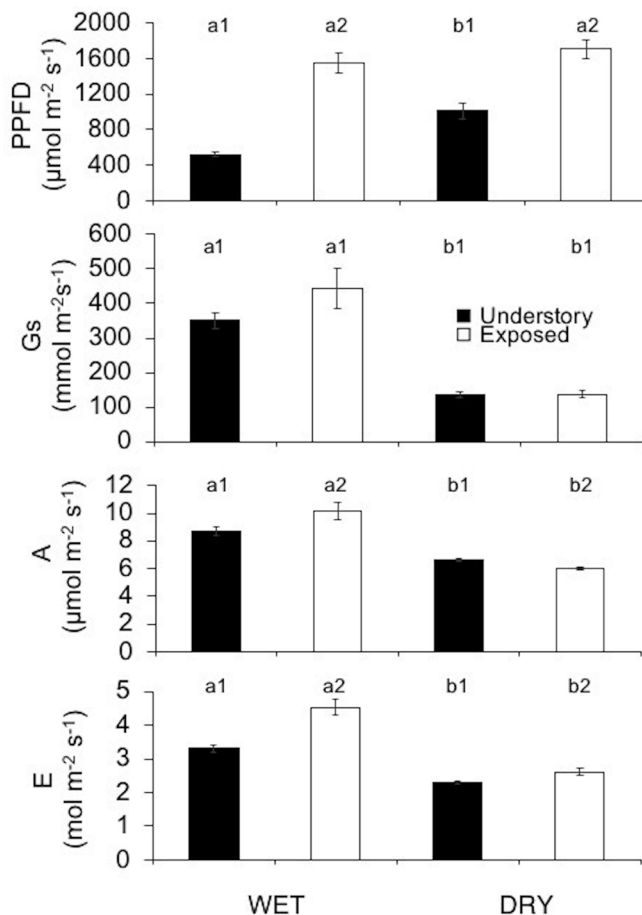


Different reports have highlighted the particularly positive leaf water potentials that Andean giant rosettes maintain, even under drought conditions (Goldstein *et al.* 1984, Rada *et al.* 1998, Rada 2016). *Coespeletia moritziana* diverges from this pattern with significantly more negative  $\Psi_L^{\min}$  (-1.8 MPa) and  $\Psi_L^{\text{tp}}$  (-2.3) compared to other giant rosettes (Rada *et al.* 2012). These authors also report important osmotic adjustments for *C. moritziana*, surviving under drought conditions and on poorly developed soils in rocky sites in one of the driest Venezuelan paramos at higher elevations (4300 m). *R. atropurpurea* also has the capacity to osmotically adjust from the wet season to the more unfavorable conditions of the dry season. This allows this species to maintain more negative  $\Psi_L^{\min}$  (-1.5 MPa) without losing turgor ( $\Psi_L^{\text{tp}} = -1.8$  MPa) in exposed conditions. As expected, plants growing under the canopy of other plants maintain more positive  $\Psi_L$  under the more

favorable conditions of the understory. Yet under these conditions, this species also osmotically adjusts from one season to the other, suggesting that *R. atropurpurea*'s ability to tolerate more negative  $\Psi_L$  allows this species to have the smallest pith volume and relative capacitance of all studied giant rosettes (Goldstein *et al.* 1985, Meinzer and Goldstein 1986).

The plant's water status, determined mainly by soil water availability and air evaporative demands, regulates leaf stomatal responses under fluctuating environments such as in the paramos. Low leaf conductances characterize most caulescent rosettes of the Venezuelan (Rada 2016) and Colombian (Mora-Osejo 2001) paramos in agreement with the fact that these rosettes maintain very positive leaf water potentials. *R. atropurpurea* may be considered an exception to this rule, more than doubling  $G_s$  of those other rosettes. Even though this species significantly reduces approximately 70 % stomatal opening from the wet to the dry season,  $G_s$  maintains high values compared to other rosette counterparts. This species' leaf conductance is comparable only to those of *Dendrosenecio* and *Lobelia*, Afroalpine giant rosettes reported to be tolerant to water deficit conditions (Schulze *et al.* 1985). This high  $G_s$  in *R. atropurpurea* explains the high transpiration rates described previously. Despite marked seasonal differences in  $G_s$ , they were not significant when microclimate conditions were considered. Significant differences found in  $E$  between understory and exposed plants during the dry season may be explained by higher VPD in this latter microsite. These adaptive characteristics (large stem piths, leaf pubescence and low leaf conductance) benefit most giant rosette plants of the paramo by maintaining a positive water balance under unfavorable conditions. *R. atropurpurea*, lacking these characteristics, is able to tolerate environmental water deficits.

Maximum  $\text{CO}_2$  assimilation rates (10-13  $\mu\text{mol m}^{-2}\text{s}^{-1}$ ) measured for *R. atropurpurea* in this study are remarkably higher than any other of the giant rosettes investigated in the Venezuelan paramos (Goldstein *et al.* 1989, Rada *et al.* 1998, Rada *et al.* 2012, Rada 2016) or *Lobelia rhynchopetalum* (Hochst. Ex A. Rich.) Hemsl., a giant rosette of the high tropical mountains of Ethiopia (Fetene *et al.* 1997) and are comparable to rates reported by León-García (2015) for *Espeletia grandiflora* Bonpl. in a Colombian paramo and for *Dendrosenecio* spp. and *Lobelia* spp., giant rosette species of Mt. Kenya (Schulze *et al.* 1985).



**Figure 5.** Photosynthetically photon flux density (PPFD), stomatal conductance ( $G_s$ ),  $\text{CO}_2$  assimilation rate ( $A$ ) and transpiration rate ( $E$ ) for understory and exposed plants during both wet and dry seasons. Bars represent one standard error from the mean. Different small letters correspond to significant differences ( $P < 0.05$ ) between seasons for each site condition. Different numbers correspond to significant differences ( $P < 0.05$ ) between site conditions for each season.

With respect to the contrasting microclimatic conditions, greater A for exposed compared to understory plants during the wet season may be mainly associated to PPFD differences, while strict stomatal closure affects plants equally from both microsites during the dry season. However, the extreme reduction in Gs from the wet to the dry season affected A to a lesser degree under either of the conditions, representing a 27 % and 39 % reduction in assimilation rates from one season to the other for understory and exposed plants, respectively.

A 17.1 °C optimum temperature for CO<sub>2</sub> assimilation was reported for *R. atropurpurea* (Rosquete 2004), with a 10.2 °C - 23.8 °C range in which this species is able to maintain above 80 % of maximum photosynthesis. All our measured leaf temperatures under any of the microclimatic conditions fall within this range, while the mean for exposed plants corresponded to 17.4 °C, suggesting that our measured photosynthetic rates were not temperature limited. This wide range in which *R. atropurpurea* maintains a high photosynthetic capacity has been reported for other giant rosettes (Rada *et al.* 1992) and these broad thermal safety margins suggest that paramo giant rosettes may manage warmer leaf temperatures (León-García and Lasso 2019) under changing temperature conditions. However, the effects of higher temperatures on other functions, e.g.

effects on higher evaporative demands, and consequent results on water relations and gas exchange characteristics have yet to be considered.

Leaf area and specific leaf area are factors of importance when analyzing plant performance under fluctuating environmental conditions. The latter one, which describes the trade-off between capture and conservation of resources (Poorter 2009), is tightly coupled to plant functions such as net photosynthetic capacity, relative growth rate and competitive ability (Reich *et al.* 1997) and has been described as a key trait under drought conditions (Wright *et al.* 2001). *R. atropurpurea* modifies both LA and SLA under contrasting microclimatic conditions, with exposed individuals showing lower values with a reduction from the understory to the exposed sites of 33 % and 29 % in LA and SLA, respectively. This reduction coincides with >25 % reductions in SLA reported by Siefert *et al.* (2015) in a world-wide study of 36 plant functional traits. Lower SLA is associated to slower growth rates under lower water availability (Reich *et al.* 1999, Villar *et al.* 2005, Poorter *et al.* 2009), to osmotic adjustments facilitating turgor maintenance (Marron *et al.* 2003) and has also been related to variations in light (Boardman 1977, Bazzaz and Bazzaz 1996, Castrillo 2006, Markesteijn *et al.* 2007) among oth-

**Table 2.** Comparison in morphophysiological responses between *R. atropurpurea* and *Espeletia schultzei*, two giant rosettes with different morphological characteristics and growing at similar elevations in the paramo.

Ecophysiological variables	Wet season		Dry season	
	<i>R. atropurpurea</i>	<i>E. schultzei</i>	<i>R. atropurpurea</i>	<i>E. schultzei</i>
LWP (MPa)	-0.6 (-0.8)	-0.3 (-0.6)	-1.2 (-1.5)	-0.6 (-0.9)
LWP <sub>tip</sub> (MPa)	-1.1	n.a.	-1.8	-1.6
G <sub>smean</sub> (mmol m <sup>-2</sup> s <sup>-1</sup> )	443 (620)	170 (320)	127 (143)	35 (53)
A <sub>mean</sub> (μmol m <sup>-2</sup> s <sup>-1</sup> )	10.2 (13.3)	2.5 (5.3)	6.0 (6.9)	0.8 (4.0)
LA (cm <sup>2</sup> )	85.6	161.9		
SLA (cm <sup>2</sup> g <sup>-1</sup> )	36.1	67		
Leaf pubescence	absent	present		
PV/LA (cm <sup>3</sup> cm <sup>-2</sup> )	1.7	3.8		

LWP= Leaf water potential, LWP<sub>tip</sub>= Leaf water potential at turgor loss point, G<sub>s</sub>= leaf conductance, A= CO<sub>2</sub> assimilation rate, LA= Leaf area, SLA= Specific leaf area, PV/LA= Relative water capacitance defined as the relationship between pith volume and leaf area (Goldstein *et al.* 1984). Values in parenthesis correspond to minimum LWP and maximum G<sub>smean</sub> and A<sub>mean</sub>. n.a.= data not available. Data for *E. schultzei* from Rada *et al.* (1998), Sierra (2016), and Rada (2016).

er environmental factors (Poorter 2009, Siefert *et al.* 2015, Wellstein *et al.* 2017).

The morphological and physiological responses of *R. atropurpurea* presented in this study contrast those of other typical giant rosettes which possess distinctive features such as pubescent leaves and large stem piths. To summarize these contrasting responses, some of the morphological and physiological characteristics of *R. atropurpurea* and *E. schultzei* growing at similar elevations in the Venezuelan paramos are presented (Table 2). These species, through different morphophysiological strategies, exhibit water relations and gas exchange characteristics which permit them to endure the harsh environments of the high tropical Andes.

In conclusion, phenotypic adjustments are important drivers of plant responses to contrasting environmental conditions. Studies on intra and interspecific plasticity of contrasting species are urgently needed to forecast species distribution and vegetation dynamics under future climate change scenarios (Valladares *et al.* 2014). *R. atropurpurea*'s morphological and physiological plasticity permits this species to compete under variable microclimatic conditions compared to other giant rosettes which have not been described to survive conditions under the canopy of other plants. However, we have to emphasize that despite *R. atropurpurea*'s confirmed plasticity, it is not able to reach higher elevations where many other giant rosettes have occupied exposed habitats successfully. *R. atropurpurea*'s upper limit stands at 3600 m compared to other pubescent giant rosettes which have reached above 4500 m. The question on which factors limit this species' ascent to higher habitats remains open.

## AUTHOR PARTICIPATION

FR and AN co-designed the research project and conducted field experiments. AN conducted laboratory experiments. AN performed statistical analyses. FR wrote the manuscript and carried out the final corrections. AN edited the final version of the manuscript.

## CONFLICT OF INTEREST

The authors declare that they have not conflict of interests.

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