

## Leaf dynamics and water relations of *Espeletia spicata* and *E. timotensis*, two giant rosettes of the desert Paramo in the tropical Andes

C. Estrada \*, G. Goldstein \*\* and M. Monasterio \*

\* Centro de Investigaciones Ecológicas de los Andes Tropicales (CIELAT), Facultad de Ciencias, Universidad de Los Andes, Mérida 5101, Venezuela.

\*\* Laboratory of Biomedical and Environmental Sciences, UCLA, 900 Veteran Avenue, Los Angeles, CA 90024, USA.

### Abstract

The relationships between leaf production and ecophysiological parameters [water potential, water storage capacity (pith volume/leaf area), transpiration and hydraulic conductivity] in two giant rosettes, *Espeletia spicata* and *E. timotensis* (Compositae) were studied at different life cycle stages and in contrasting seasons, at 4,200 m in the Venezuelan Tropical Andes. *E. spicata* grows at intermediate topographic positions in slopes of glacial cirques. It shows significant seasonal changes in leaf production between life cycle stages and throughout the year. *E. timotensis*, which grows in more extreme environments, has almost constant leaf production rates within each stage of the life cycle. These different behaviors may be explained by differences in hydraulic conductivity between the pith water storage and the leaves of each species. *E. timotensis* showed an efficient hydraulic conductivity with low stomatal control, while *E. spicata* exhibited a low hydraulic conductivity with an important stomatal control, particularly in adult individuals.

**Keywords:** Leaf production, water relations, life cycle, *Espeletia*, Compositae, Tropical Andes, Paramo, Venezuela.

### Résumé

Les relations entre la production foliaire et les paramètres écophysologiques (potentiel hydrique, capacité de stockage d'eau - volume du cœur/surface foliaire -, transpiration et conductivité hydraulique) ont été analysées chez deux rosettes géantes, *Espeletia spicata* et *E. timotensis* (Compositae) à différents stades du cycle de vie et au cours de saisons contrastées à 4200 m dans les Andes tropicales au Venezuela. *E. spicata* croît à des étages topographiques moyens dans la pente des cirques glaciaires. Elle présente des modifications saisonnières significatives de la production foliaire entre les différents stades et au cours de l'année. *E. timotensis* qui colonise des milieux plus extrêmes présente des taux de production foliaire presque constants pour chaque classe d'âge. Ces différences de comportement peuvent être expliquées par des différences de la conductivité hydraulique entre l'eau accumulée dans le cœur et les feuilles de chaque espèce. *E. timotensis* présente une conductivité hydraulique efficace avec un faible contrôle stomatique, tandis que *E. spicata* a une faible conductivité hydraulique associée à un contrôle stomatique important, surtout chez les individus adultes.

## INTRODUCTION

In high mountain equatorial environments, the African and Andean "paramos", where giant rosettes of the genera *Dendrosenecio* and *Espeletia* have evolved convergently, studies on growth (BECK *et al.*, 1980, 1984; ESTRADA, 1983; MONASTERIO 1986*a*) and ecophysiology (GOLDSTEIN & MEINZER, 1983; GOLDSTEIN *et al.*, 1984; SCHULZE *et al.*, 1985) have been carried out. In the Andean páramos, GOLDSTEIN *et al.* (1985) studied the interphase between population ecology and ecophysiology. It is important to analyze leaf production and water status in the cold tropics in relation to annual water seasonality and to the changes in plant size because it would increase our knowledge on the ecophysiological plant behavior during its life cycle.

The Desert Páramo, one of the most extreme environments of the tropical high Andes, is characterized by a tropical periglacial climate with daily thermal fluctuations greater than seasonal ones and with frequent nighttime freezing temperatures (MONASTERIO, 1986*b*). A factor which has to be considered is the seasonal precipitation regime in the Desert Páramo, that may induce seasonal changes on daily cycles with significant effects in the functioning and dynamics of plant populations (MONASTERIO, 1986*a*).

Giant rosettes of the genus *Espeletia* are the dominant life form of the Desert Páramo and represent a very particular adaptation to cold tropical conditions (MONASTERIO, 1986*a*). This life form has an unbranched stem with a terminal rosette which shows little seasonal variation in total biomass. The marcescent leaves protect the stem and pith from low nighttime temperatures (SMITH, 1979; GOLDSTEIN & MEINZER, 1983; RADA *et al.*, 1985). The pith also plays an important role in the water balance of these plants (GOLDSTEIN & MEINZER, 1983; GOLDSTEIN *et al.*, 1984). According to these authors, the pith water storage supplies daily transpirational needs, functioning as a buffer both against daily fluctuations (since water is not available for a few hours when freezing temperatures occur) and against seasonal ones (water shortage during the dry season). This storage may be estimated through a "relative capacitance" index (pith volume per unit of leaf area).

The purpose of this study is to document, in two *Espeletia* species with long life cycles (MONASTERIO, 1986*b*; ESTRADA & MONASTERIO, 1988), leaf production dynamics and to establish the relationship between leaf dynamics and water status of plants with respect to size-age and water seasonality.

It has been pointed out that growth processes in plants are affected by low water availability and a consequent internal water deficit (KRAMER, 1980). As a consequence of the cold climate in the Desert Páramo, water is not always available to cover transpirational demands in spite of relatively abundant precipitation (GOLDSTEIN *et al.*, 1984). On the other hand, for *Espeletia* caulescent rosettes, the ratio pith volume/leaf area changes during the life cycle due to an increase in plant's height, and therefore pith volume, while leaf surface area remains relatively constant (ESTRADA, 1983; GOLDSTEIN *et al.*, 1985). Our initial working hypotheses were:

(1) A stable leaf production rhythm, as observed for adult *E. timotensis* plants (MONASTERIO, 1986*a*), will be associated with a relatively constant internal water status in these plants.

(2) A greater water deficit should be observed in juveniles as compared to adults, associated with a greater seasonal variability in juvenile leaf production.

If these hypotheses are supported, we will try to explain them through three alternative mechanisms for the regulation of the water balance:

(1) The stem pith functions as a water source which satisfies the transpirational demands.

(2) A stomatal control may act as a regulating mechanism of the plant water status under transpirational demand conditions.

(3) Efficient hydraulic conductivity between pith storage and leaves may help to maintain a positive water balance under low water availability conditions, even if there is no stomatal control.

In this work the term "hydraulic conductivity" is used as a measure of the efficiency by which water moves from the pith to the peripheral xylem and into the leaves.

## MATERIALS AND METHODS

### Site and species characteristics

The study was done in the Páramo de Piedras Blancas (08°52'N, 70°48'W) at 4,200 m, Cordillera de Mérida, Venezuela, with *E. spicata* Sch. Bip. and *E. timotensis* Cuatr. (nomenclature by ARISTEGUIETA, 1964). The vegetation corresponds to the "Altiandino" Desert Páramo with a higher open stratum constituted by *Espeletia* giant rosettes leaving large areas of bare soil. The lower stratum is composed of different plant life forms such as cushions, small rosettes and *Espeletia* juveniles (MONASTERIO, 1986a). Climatic records for 24 continuous years show that the area has a mean annual temperature of 2.8°C and the difference between the coldest and warmest month is 2.7°C. The daily temperature fluctuations are approximately 10°C, and the mean annual precipitation (800 mm) falls between April and November. Some microclimate measurements are available for the desert Paramo vegetation (MONASTERIO, 1986a): For the dry season (January 12-13, 1978), daily temperature fluctuations at 150 and 10 cm above soil, as well as the soil surface were 13.5, 17.0 and 50°C, respectively; likewise, the minimum temperatures were -2.5, -5.0 and -10.0°C, respectively. During the wet season (August 1-2, 1978), daily ranges were 10°C at 150 cm, 11.1°C at 10 cm and 25.5°C at the soil surface; the minimum temperatures were 0, 0, and 0.5°C, respectively. In other words, for the wet season, the vertical temperature gradient disappears; minimum are higher, whereas the daily ranges are lower than for the dry season. *E. timotensis* has an altitudinal range from 4,000 to 4,600 m, occupying the highest and steeper slopes of the glacial cirques, on poorly differentiated substrates, while *E. spicata* grows on intermediate topographic positions, on deeper and organic substrates where periglacial conditions, although present, are not as intense as in *E. timotensis* substrates (figs. 1 and 2).

### Life cycle stages

We have chosen four different life cycle stages for *E. spicata* and *E. timotensis*. In unproductive juvenile plants, we distinguished three stages (I, II and III). Mature reproductive plants were grouped in stage IV. The following information may morphologically differentiate plants from different stages. Stage I: plants with stems between 2 and 6 cm above ground and leaf rosettes between 10 and 22 cm in diameter. Stage II: stems between 6 and 12 cm and leaf rosettes between 22 and 50 cm in diameter. Stage III: stems between 10 and 26 cm in height and leaf rosettes between 50 and 80 cm in diameter. Stage IV: stems between 24 and 110 cm in height and rosettes between 60 and 100 cm in diameter.

Individuals of stages I and II belong to the first age and size classes of the population and show relatively high mortality rates. Individuals of stage III show moderate mortality rates. Stage IV has the



FIG. 1. — *E. spicata* is normally found in intermediate habitats, covered by boulders and small angular debris. Páramo de Piedras Blancas, 4,200 m. Photo Estrada.

lowest mortality rates and its individuals belong to intermediate and advanced age and size classes (ESTRADA & MONASTERIO, 1988).

### Field and laboratory measurements

Forty (40) individuals of both species (five in each stage) were labelled and their stem height and rosette diameter measured. At approximately 30 day intervals leaf production was analyzed by counting



FIG. 2. — *E. timotensis* at the Páramo de Piedras Blancas, 4,200 m. Photo Sarmiento.

number of leaves which expanded from the central leaf bud. These measurements were done between August 1982 and January 1984. Some environmental variables (air temperature, relative humidity) and plant responses (leaf water potential, leaf conductance, leaf temperature) were measured, for each stage, during midday (between 11:00 and 14:00 h). These measurements were done on March and April during the dry season of 1984 and on November during the wet season of 1987. Leaf water potential of expanded adult leaves was measured with a pressure chamber: 2-3 leaves/plant in 1-2 plants/stage (wet season) and 2 leaves/plant in two plants/stage (dry season). Leaf conductance was determined with a steady-state porometer: 4 leaves/plant in 1 plant/stage during the wet season, and 3 leaves/plant in 2 plants/stage for the dry season. Leaf temperature was measured with 36-gauge copper-constantan thermocouples: 1 leaf/plant and one plant/stage. Relative humidity was measured with an Assman psychrometer following a vertical gradient from 10 cm to 150 cm above ground at 20 cm intervals. Leaf temperatures and relative humidity were determined every half-hour between 11:00 and 14:00 h. For each species, four to five individuals from each stage were used to determine leaf area and pith volume. To determine hydraulic conductivity between pith and leaves, an adult individual of each species with roots and soil was taken to the laboratory and placed in a growth chamber (Percival, Iowa) simulating field conditions (12-hour photoperiod and 10-12°C temperatures); these plants were irrigated several times before the roots were removed; at this point water potentials of leaves ( $\Psi_{leaf}$ ) and pith ( $\Psi_{pith}$ ) were simultaneously measured. These measurements were made at 1-2 hour intervals at the beginning of the experiment, and at 2-3 hour intervals towards the end.  $\Psi_{pith}$  determinations were done with psychrometric chambers (C-52, Wescor, Utah) attached to a dew point microvoltmeter (HR 33, Wescor, Utah).

## RESULTS

### Leaf production dynamics

Figure 3 shows an annual cycle of leaf production in *E. spicata* and *E. timotensis*. Four important aspects may be observed: (1) In both species, a

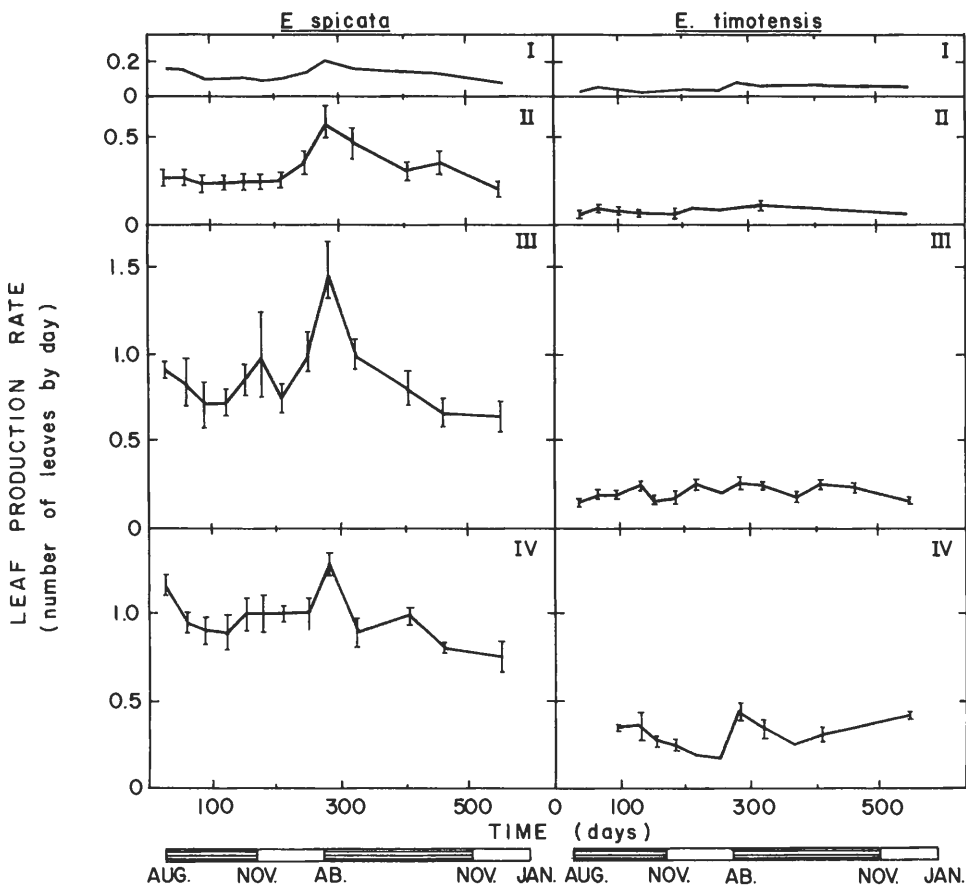


FIG. 3. — Leaf production seasonal courses from August 1982 to January 1984 in *E. spicata* and *E. timotensis*. Roman numerals indicate different life cycle stages (I, II, III=juveniles in different developmental categories, IV=adults). Each curve represents the mean of 4-5 individuals per stage. Vertical bars show standard error from mean. Horizontal bars in X-axis indicate wet season (with lines) and dry season (without lines).

progressive increase in the leaf production rate from juvenile individuals of stage I to the more developed stage IV individuals. The same trend appears in terms of leaf dry weight, from 13 g/year in juveniles (I) to 600 g/year in adults (IV) for *E. spicata*, and from 7 g/year in juveniles to 450 g/year in adults of *E. timotensis* (ESTRADA & MONASTERIO, unpublished data); (2) During the measurement period, *E. spicata* produced a greater number of leaves for all stages as compared to *E. timotensis*; (3) Leaf production rates for individuals of *E. spicata* show greater seasonal variation than *E. timotensis*, which individuals show relatively constant leaf production rates (fig. 3, tab. I); (4) In *E. spicata*, the smallest juvenile individuals (I) show greater seasonal differences than adult individuals (IV) with respect to mean

TABLE I. - Analysis of variance (ANOVA) and Tukey-Kramer test (SOKAL & ROHLF, 1981) for leaf production measurements for the August 1982-January 1984 period. Roman numerals indicate different life cycle stages (I, II, III=juveniles in different developmental categories, IV=adults).  $F_s$ =F value of ANOVA,  $d_f$ =degrees of freedom ( $v_1$ =numerator,  $v_2$ =denominator), P=probability level, D=number of significantly different mean pairs (Tukey-Kramer test).

Species	Life cycle stages	$F_s$	$d_f$ ( $v_1, v_2$ )	P	D
<i>E. spicata</i> .	I	7.44	12,51	$P < 0.001$	16
	II	2.84	12,52	$0.005 < P < 0.010$	6
	III	3.17	12,52	$0.001 < P < 0.005$	8
	IV	3.27	12,49	$0.001 < P < 0.005$	4
<i>E. timotensis</i> .	I	3.16	12,48	$0.001 < P < 0.005$	1
	II	1.71	13,56	$0.050 < P < 0.100$	0
	III	2.87	13,43	$0.005 < P < 0.010$	1
	IV	0.83	10,22	$0.500 < P < 0.750$	0

leaf production rates throughout the year, with an intermediate behavior for stages II and III (See parameter "D" in tab. I). In *E. timotensis* instead, plants of each stage show little or no significant change in leaf production throughout the year.

### Water relations

**Leaf water potential ( $\Psi_{\text{leaf}}$ ):** Minimum  $\Psi_{\text{leaf}}$  showed different patterns for both species (fig. 4). In relation to life cycle, small juvenile individuals (I) of both species showed the lowest  $\Psi_{\text{leaf}}$  compared to individuals of stages III and IV. Comparing species,  $\Psi_{\text{leaf}}$  in *E. spicata* was always lower than in *E. timotensis* in any stage or season of the year. Comparing seasons, *E. timotensis* showed relatively constant  $\Psi_{\text{leaf}}$  for stages III and IV, while juveniles showed lower  $\Psi_{\text{leaf}}$  during the wet season (stage I) and dry season (stage II); on the contrary,  $\Psi_{\text{leaf}}$  in *E. spicata* during the dry season were always lower than in the wet season, for all life cycle stages.

**Pith water storage in stems:** Figure 5 shows the relationship between "relative capacitance" and stem height. In both species capacitance linearly increases from the smallest juvenile plants to the largest adult individuals. However, for individuals in different developmental stages, *E. spicata* showed a greater "relative capacitance" than individuals of *E. timotensis*, which means that the capacity to store water, relative to leaf area, is greater in *E. spicata* as compared to *E. timotensis*, independent of individual size.

**Transpiration:** Seasonal changes in rates of water loss at midday for plants at different stages are shown in figure 6. In *E. spicata*, individuals in stages III and IV tended to decrease their transpiration rates during the dry season, while the smallest juvenile plants (stage I) showed an inverse pattern; individuals in stage II did not show any significant difference in their transpiration rates. On the other hand, almost all the individuals of *E. timotensis* maintained relatively constant transpiration rates in both seasons, with the exception of adults in stage IV which significantly increased their transpiration rates during the dry season.

**Leaf and pith water potential:** Changes in leaf ( $\Psi_{\text{leaf}}$ ) and pith ( $\Psi_{\text{pith}}$ ) water potential were monitored in the laboratory under constant environmental conditions

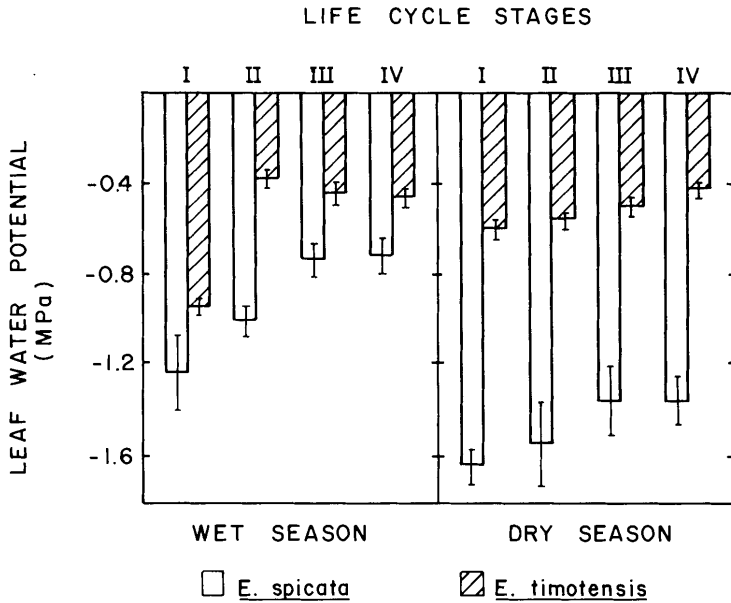


FIG. 4. — Minimum leaf water potential as a function of life cycle stage for *E. spicata* and *E. timotensis* for wet and dry seasons. Each bar represents the mean of 4-5 measurements (wet season) and 8 measurements (dry season). Standard error of mean is shown for each case.

(fig. 7). These two parameters decreased in time for both species, but the difference in the rate of decrease in  $\Psi_{\text{leaf}}$  and  $\Psi_{\text{pith}}$  was significantly higher in *E. spicata* as compared with *E. timotensis*. For this latter species, a small decrease in  $\Psi_{\text{leaf}}$  synchronously produced a similar decrease in  $\Psi_{\text{pith}}$  while in *E. spicata*, large decreases in  $\Psi_{\text{leaf}}$  were accompanied by gradual changes in  $\Psi_{\text{pith}}$ . This indicates that the apparent hydraulic connection between the pith and the leaves is higher in *E. timotensis* compared with *E. spicata*. Since, previously, it was found that the transpiration rates are very similar between these two species. Besides, the hydraulic resistance  $[(\Delta\Psi_{\text{leaf}})/TF]$ , or the relative drop in water potential per unit of transpiration flux] for *E. spicata* was higher ( $\sim 120 \text{ MPa/mg.cm}^{-2}.\text{s}^{-1}$ ) than in *E. timotensis* ( $\sim 40 \text{ MPa/mg.cm}^{-2}.\text{s}^{-1}$ ) (GOLDSTEIN *et al.*, 1984, 1989).

## DISCUSSION

One of the most outstanding features of the giant rosettes in the Desert Paramo is their continuous vegetative activity, having a leaf biomass without significant changes throughout the year.

Some of our results show significant differences in the vegetative behavior of two *Espeletia* species. *E. spicata* shows a high seasonal variability in its leaf production rate with higher values for the wet season, while *E. timotensis* tends to constantly produce leaves. MONASTERIO (1986a) found similar trends for the period



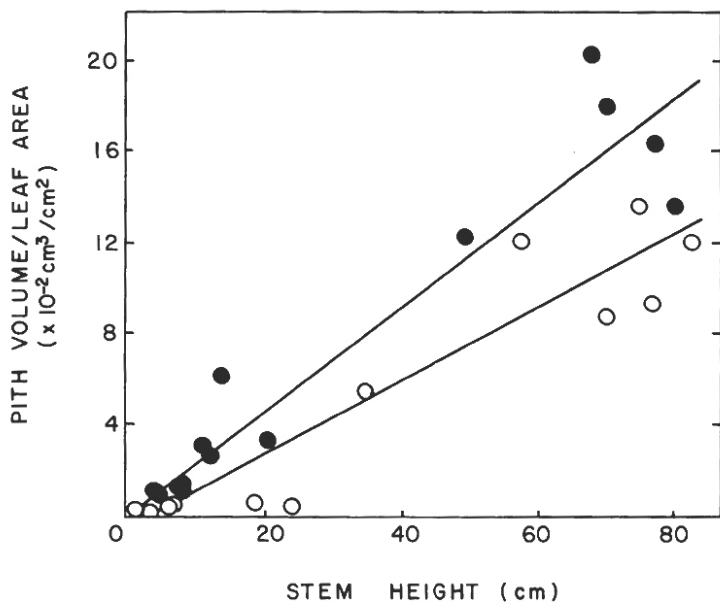


FIG. 5. — Relative capacitance (RC) as a function of stem height (H). (●) *E. spicata*, (○) *E. timotensis*. Each point represents a plant. Regressions: *E. spicata*:  $RC = 0.2311H - 0.06$  ( $n = 18$ ,  $r^2 = 0.93$ ). *E. timotensis*:  $RC = 0.16H - 0.48$  ( $n = 18$ ,  $r^2 = 0.91$ ).

1979-1980. Leaf growth rate also shows a similar pattern with more marked seasonal fluctuations in *E. spicata* leaves than in *E. timotensis* (ESTRADA, 1983; MONASTERIO, 1986a).

Neither of the seasons seems to be favorable for all plant processes in the Desert Páramo. In the wet season, air and soil temperature fluctuations are smaller, there is a high soil humidity content, but the energy balance is less favorable due to greater cloudiness during the day; the opposite occurs during the dry season (MONASTERIO, 1986a). A greater soil humidity during the wet months does not mean that it is available to the plants, due to nighttime low soil temperatures which may have adverse effects on the root hydraulic conductivity (KAUFMANN, 1977; RUNNING & REID, 1980; GOLDSTEIN, 1981). Soil water availability during the dry season may depend on both the effect of low nighttime temperatures and on low daily soil water potentials (GOLDSTEIN *et al.*, 1985; OROZCO, 1986).

The analysis of successive phases in *Espeletia*'s life cycles in the Desert Páramo acquires significant ecological importance. In this environment, plants of different developmental stages occupy microclimates characterized by great heterogeneity in a vertical gradient and by large daily variability. This must imply differences with respect to the manner and intensity of growth processes and ecophysiological responses of plants to the conditions of the microenvironments occupied by each life cycle stage. For example, the smallest size-age plants are the

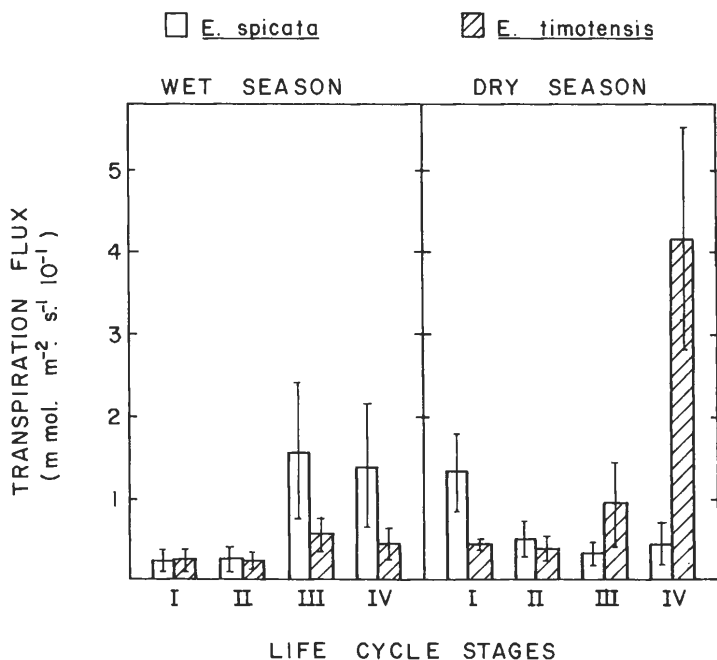


FIG. 6. - Midday transpiration rate as a function of life cycle stage for *E. spicata* and *E. timotensis* during wet and dry seasons. Each bar represents the mean of 4-6 measurements (dry season) and 4 measurements (wet season). Standard error of the mean is shown for each case.

closest to the ground, where the largest daily temperature fluctuations occur, and where nighttime freezing temperatures last longer and are more frequent. On the other hand, the oldest and tallest individuals are exposed to relative less fluctuating conditions in relation to the environmental factors found at the substrate level.

The lower  $\Psi_{\text{leaf}}$  exhibited for juveniles and higher  $\Psi_{\text{leaf}}$  in adult individuals of both species agree with the results of GOLDSTEIN *et al.* (1985) working with *E. timotensis*. This behavior is closely related to leaf production in *E. spicata* plants; in this case, in the early life cycle phases there is a greater seasonal variability in leaf production with respect to the more advanced stages. This may be explained by a smaller water capacitance in juveniles compared to adult plants. In this manner, an unfavorable water balance in juvenile individuals would increase their functional vulnerability to external fluctuations in water availability, causing therefore a highly variable leaf production throughout the year. This series of morphological controls which depend on the life cycle, and have important consequences at a functional level, is observed in a partial manner in *E. timotensis*. In this species, although changes in water capacitance and  $\Psi_{\text{leaf}}$  through its life cycle are similar to those observed in *E. spicata*, their functional consequences on the leaf production pattern are not evident. Within a given stage, *E. timotensis* plants produce leaves

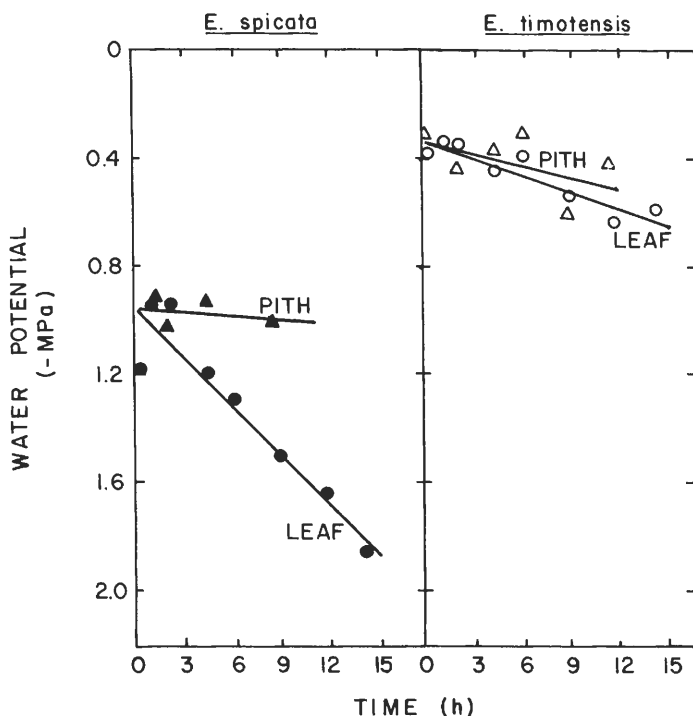


FIG. 7. — Leaf water potential ( $\Psi_{leaf}$ , circles) and pith water potential ( $\Psi_{pith}$ , triangles) as a function of time (T) for adult individuals of *E. spicata* and *E. timotensis*, with roots removed after saturation. The  $\Psi_{pith}$  regression values are actually 0.06 and 0.77 MPa lower (than what is shown in the figure) for *E. spicata* and *E. timotensis*, respectively. The origin of the  $\Psi_{pith}$  and  $\Psi_{leaf}$  regressions were put together to visualize differences in slope. *E. spicata*:  $\Psi_{leaf} = 0.96 + 0.06T$  ( $n = 8$ ,  $r^2 = 0.89$ ,  $s_y = 0.11$ );  $\Psi_{pith} = 1.02 + 0.004T$  ( $n = 4$ ,  $r^2 = 0.06$ ,  $s_y = 0.06$ ) and *E. timotensis*:  $\Psi_{leaf} = 0.34 + 0.02T$  ( $n = 8$ ,  $r^2 = 0.83$ ,  $s_y = 0.05$ );  $\Psi_{pith} = 1.12 + 0.014T$  ( $n = 6$ ,  $r^2 = 0.26$ ,  $s_y = 0.11$ ).

at an almost constant rate throughout the year. As will be discussed later, other water balance's regulating mechanisms may explain this behavior.

Up to this point we have analyzed the problem of the relation "water status-leaf production" from the point of view of the changes through the life cycle associated to morphological conditions (changes in water capacitance). However, when we compare species, we come to some kind of a paradox. We had established, at least for *E. spicata* that a lower water capacitance agrees with a more unstable behavior in terms of leaf production. But our results also indicate that, for any size range, *E. timotensis* plants exhibit a lower capacitance than *E. spicata* (fig. 5); in spite of this, the former species shows higher  $\Psi_{leaf}$  values than the latter one

(fig. 4), and also exhibits a relatively constant leaf production rhythm throughout the year (fig. 3). This may be explained in terms of a constant root water uptake in *E. timotensis* which could as well contribute to a favourable water balance, resulting in a constant leaf growth. Similar observations (lower  $\Psi_{\text{leaf}}$  in *E. spicata* and higher in *E. timotensis*) were described by GOLDSTEIN *et al.* (1984) in adult individuals and by OROZCO (1986) in juveniles.

These results show that "water capacitance", as a possible water balance's regulating mechanism for these giant rosettes, is not able to explain satisfactorily all the differences found between both species in terms of leaf production patterns and water status; furthermore, we found that a greater relative capacitance is not always associated neither with higher water potentials nor with greater water conductivity, as was previously suggested by GOLDSTEIN *et al.* (1984) in a broad comparison between *Espeletia* species.

If we now consider the role of stomatal control, we find that during the dry season, *E. timotensis* plants in stages III and IV showed relatively high transpirational rates (fig. 6) and maintained high  $\Psi_{\text{leaf}}$  values (fig. 4). In *E. spicata*, these same stages show a completely opposite behavior, low transpiration rates (fig. 6) and relatively low water potentials (fig. 4).

The latter seems to indicate that, comparing both species, transpiratory losses are not associated with seasonal variability in neither leaf production nor leaf water potentials, respectively. These results suggest that, in conditions of high air evaporative demand during the dry season, some kind of mechanism such as an efficient hydraulic conductivity between stem pith and leaves must exist. This permits high transpiration rates and at the same time a favorable water "status" (higher  $\Psi_{\text{leaf}}$ ), as in the case of adult *E. timotensis* plants (figs. 4 and 6), although a better water absorption capacity by the roots could also favor this. *E. spicata* behaves in a different manner during the dry season, maintaining a considerable stomatal control with reduced transpiration rates (fig. 6) in stages III and IV. However, this stomatal control does not seem to be sufficient to maintain a favorable water balance since its leaf water potentials were lower (fig. 4).

From these results we may infer that the stable water potentials and leaf production shown by *E. timotensis* may not be explained by a stomatal control mechanism since, as was previously shown, its maximum transpiration rates were relatively high, especially in adult individuals. *E. spicata* was characterized by a variable pattern (seasonal and through its life cycle) in its transpirational water losses, independent of the leaf water potential pattern observed which showed consistently lower values. Probably, during the dry season, *E. spicata* plants are vulnerable to any water lost by transpiration, suggesting a possible unbalance in the water flow from the stem pith to the leaves, in other words, an inefficient hydraulic conductivity between these compartments.

It has been stated that the leaf water potential is strongly dependent on the transpiration rate, and the degree of water potential change with transpiration is affected by the water flow resistance from soil to leaves and by the water availability to the roots (SCHULZE & HALL, 1982). In our case, the influence of the relatively high transpiration rates on the leaf water potentials of *E. timotensis* adult individuals during the dry season is counteracted by its high hydraulic conductivity between stem pith and leaves. This requires very efficient hydraulic connections

between roots and pith, and water absorption by roots. We conclude that *E. timotensis*, living in more extreme environments, maintains an almost constant vegetative behavior and a considerable water homeostasis, through its efficient hydraulic connections between the pith and the leaves, without an important stomatal control. On the other hand, *E. spicata* in less rigorous environments, shows significant changes in its vegetative behavior, a low water homeostasis and an appreciable stomatal control, particularly in adult individuals.

## ACKNOWLEDGEMENTS

We are grateful to David Dugarte and Hely Saul Rangel for their field assistance. We also thank Fermin Rada for providing laboratory assistance, reviewing and translating the manuscript. We are also indebted to Prof. Guillermo Sarmiento for valuable comments on the manuscript.

This research was supported by the CDCHT-ULA (C-136-79 and C-289-86) and MAB-Unesco (ROSTLAC N° 241.768.7), we are grateful for their support.

This work is a contribution to the Program "Tropical Mountain Ecosystems" of the "Decade of the Tropics" IUBS, MAB-Unesco.

## REFERENCES

- ARISTEGUIETA L., 1964. — *Flora de Venezuela* (Compositae), vol. X. Parte Primera, Instituto Botánico. Dirección de RNR del MAC, Caracas.
- BECK E., SCHEIBE R., SENSER M. & MULLER W., 1980. — Estimation of leaf and stem growth of unbranched *Senecio keniodendron* trees. *Flora*, **170**, 68-76.
- BECK E., SCHLÜTTER I., SCHEIBE R. & SCHULZE E.-D., 1984. — Growth rates and population rejuvenation of East African giant groundsel (*Dendrosenecio keniodendron*). *Flora*, **175**, 243-248
- ESTRADA C., 1983. — Dinámica del crecimiento y reproducción de *Espeletia* en el Páramo Desértico. Tesis de Maestría. Universidad de Los Andes, Mérida, 143 p.
- ESTRADA C. & MONASTERIO M., 1988. — Ecología poblacional de una roseta gigante, *Espeletia spicata* Sch. Bip. (Compositae), del Páramo Desértico. *Ecorrópicos*, **1** (1), 25-39.
- GOLDSTEIN G., 1981. — Ecophysiological and demographic studies of white spruce (*Picea plauca* (Moench) Voss) at treeline in the Central Brooks range of Alaska. Ph. D. dissertation, University of Washington.
- GOLDSTEIN G. & MEINZER F., 1983. — Influence of insulating dead leaves and low temperatures on water balance in an Andean giant rosette plant. *Plant, Cell Environ.*, **6**, 649-656.
- GOLDSTEIN G., MEINZER F. & MONASTERIO M., 1984. — The role of capacitance in the water balance of Andean giant rosette species. *Plant, Cell Environ.*, **7**, 179-186.
- GOLDSTEIN G., MEINZER F. & MONASTERIO M., 1985. — Physiological and mechanical factors in relation to size-dependent mortality in an Andean giant rosette species. *Acta Oecologica, Oecol. Plant.*, **6** (3), 263-275.
- GOLDSTEIN G., RADA F., CANALES M. J. & ZABALA O., 1989. — Leaf gas exchange of two giant caulescent rosette species. *Acta Oecologica, Oecol. Plant.*, **10** (4), 359-370.
- KAUFMANN M. R., 1977. — Soil temperature and drying effects on water relations of *Pinus radiata*. *Can. J. Bot.*, **55**, 2413-2418.
- KRAMER P. J., 1980. — Drought, stress, and the origin of adaptations. In: TURNER N. C. & KRAMER P. J., Eds., *Adaptation of plants to water and high temperature stress*. John Wiley & Sons, New York, 7-20.
- MONASTERIO M., 1986a. — Adaptive strategies of *Espeletia* in the Andean Desert Páramo. In: VUILLEUMIER F. & MONASTERIO M., Eds., *High Altitude Tropical Biogeography*. Oxford University Press, 49-80.

- MONASTERIO M., 1986 b. — Recherches écologiques sur les *Espeletia* du Páramo Désertique des hautes Andes tropicales du Venezuela. Doctorat d'État en Sciences naturelles. Université Pierre-et-Marie-Curie, Paris-VI, 123 p.
- OROZCO A., 1986. — Economía hídrica en rosetas juveniles de *Espeletia* en el Páramo Desértico. Tesis de Maestría. Universidad de Los Andes, Mérida, 87 p.
- RADA F., GOLDSTEIN G., AZOCAR A. & MEINZER F., 1985. — Freezing avoidance in Andean giant rosette plants. *Plant, Cell Environ.*, **8**, 501-507.
- RUNNING S. W. & REID P. C., 1980. — Soil temperature influences of *Pinus contorta* seedlings. *Plant Physiol.*, **65**, 635-640.
- SCHULZE E.-D. & HALL A. E., 1982. — Stomatal responses, water loss and CO<sub>2</sub> assimilation rates of plants in contrasting environments. In: LANGE O. L., NOBEL P. S., OSMOND C. B. & ZIEGLER H., Eds., *Encyclopedia of Plant Physiology*, new ser., v. 12 B, Springer-Verlag, Berlin, 181-230.
- SCHULZE E.-D., BECK E., SCHEIBE R. & ZIEGLER P., 1985. — Carbon dioxide assimilation and stomatal response of afroalpine giant rosette plants. *Oecologia (Berl.)*, **65**, 207-213.
- SMITH A. P., 1979. — Function of dead leaves in *Espeletia schultzii* (Compositae), an Andean caulescent rosette species. *Biotropica*, **11** (1), 43-47.
- SOKAL R. R. & ROHLF F. L., 1981. — *Biometry*. W. H. Freeman and Company, San Francisco.