

The role of capacitance in the water balance of Andean giant rosette species

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Abstract. Pith water storage capacity and its role in plant-water relations were studied in seven giant rosette species of the genus *Espeletia* from the Venezuelan Andes. Readily available water from the pith was calculated to be capable of sustaining mean transpiration for up to 2.5 h. The relative importance of water stored in the pith, however, differed among species. The species that grow in the higher and colder environments tended to have a greater capacitance than the species that grow in the lower and less extreme environments. The pith volume per unit leaf area (PV/LA) was found to be a good indicator of the relative water storage capacity of the adult individuals of each species. Diurnal fluctuations in leaf water potential were not as pronounced in the species with higher PV/LA values. The species-specific PV/LA was highly correlated with the leaf turgor loss point and with the total resistance to water flow from soil to leaves. These results suggested that species-specific capacitance in the genus *Espeletia* is a response to temperature-limited soil water availability and that cold tropical environments with frequent subfreezing temperatures tend to select for high water storage capacity in giant rosette plants.

Key-words: *Espeletia*; Compositae; Frailejón; plant capacitance; water balance; hydraulic resistance; low temperature effects; tissue water potential components; páramo.

Introduction

Caulescent giant rosette species belonging to the genus *Espeletia* grow at elevations up to 4600 m in the high tropical Andes (páramo). This genus has experienced an intense radiative speciation process (Cuatrecasas, 1979) and is composed mainly of endemic species which are generally restricted to a limited number of habitats. All of the high elevation species have stems protected by a layer of marcescent leaves and a voluminous central pith made up of parenchymatous tissue.

In a previous study (Goldstein & Meinzer, 1983) we found that the pith of *Espeletia timotensis* Cuatr. is an important source of stored water that helps to maintain a favourable water balance. This study

demonstrated that the pith water reservoir has good hydraulic connections with the rest of the plant and continuously provides water to the external xylem thereby contributing significantly to the total transpiration stream. The pith is recharged during the night when water potential equilibrium tends to be established between the plant and soil.

The high tropical environments where these caulescent rosettes grow are characterized by daily rather than seasonal temperature fluctuations and by frequent freezing temperatures (Monasterio, 1980; Monasterio & Reyes, 1980). As a consequence of this harsh tropical temperature regime, water is not always readily available to meet transpirational demand despite relatively abundant precipitation. During most of the year moisture availability can be severely limited, particularly during the early morning hours when soil water is frozen or water uptake impeded by low root membrane permeability. The pith reservoir is therefore of adaptive value because it minimizes the distance and resistance between water source and atmospheric sink.

Most discussions of water transfer through the soil-plant-atmosphere continuum have considered the soil as the only source of water even for meeting short-term demands. Only recently has the importance of plant tissues as an important source of water in some species been emphasized (Jarvis, 1975; Powell & Thorpe, 1977; Waring & Running, 1978; Lassoie, 1979). Hinckley, Lassoie & Running (1978) have distinguished two categories of internal water reservoirs: (i) elastic tissues (such as fruits, buds and foliage) which undergo dimensional changes when water is exchanged with the transpirational stream, and (ii) inelastic tissues (such as mature lignified sapwood) that do not undergo dimensional changes. Inelastic storage seems to account for the most significant amount of water lost from internal water sources in trees (Jarvis, 1975; Hinckley *et al.*, 1978). The study of the role of stem-sapwood in the internal water economy of trees is complex because sapwood has diffuse boundaries with adjacent tissues, particularly in species with a vessel anatomy, and functions both in storage and conduction. Elastic tissues, on the other hand, have more defined boundaries, but the resistances to flow between the transpiring foliage and the internal storage tissue tend to be generally high, such as in the phloem and

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Table 1. Physical and climatic characteristics of the sites where *Espeletia* populations were sampled

Páramo site and elevation (m)	Species studied	Annual precipitation (mm)	Distinct wet-dry season	Average Monthly temperature (°C)
Piedras Blancas (4200)	<i>Espeletia lutescens</i> Cuatr. & Aristeg. <i>Espeletia moritziana</i> Sch. Bip ex Wedd. <i>Espeletia spicata</i> Sch. Bip. ex Wedd.	798	Yes	2.8
Mucubají (3600)	<i>Espeletia schultzi</i> Wedd. <i>Espeletia floccosa</i> Standl.	969	Yes	5.4
El Batallón (3100)	<i>Espeletia marcana</i> Cuatr. <i>Espeletia atropurpurea</i> A. C. Sm.	1213	No	9.3

associated living tissues (Molz & Klepper, 1972). An ideal system for studying the role of capacitance in a plant would be one where the storage tissue is discrete, serves a single function, and has good hydraulic connections with the transpiring surface. The pith of many *Espeletia* species appears to fulfill these requirements.

The *Espeletia* species that grow in the Andean páramos differ not only in pith volume but also in the ratio between leaf surface area and the volume of the water reservoir. If the conspicuous pith plays a role in the water economy of other high elevation species of *Espeletia* as it does in *Espeletia timotensis* (Goldstein & Meinzer, 1983), its relative importance should be a function of its relationship to the total evaporating surface of the plant. The objective of this study is to document the differences in potential water storage capacity in the pith and to investigate the role that this plays in the regulation of water balance in several *Espeletia* species that grow along a climatic and altitudinal gradient.

Materials and methods

Site characteristics and plant material

Seven *Espeletia* species were chosen from three different páramos characterized by different climate and altitude (Table 1). The páramo sites were selected to provide a range of conditions. All species studied are the dominant rosette species in each páramo and are characterized by a stem with a central pith and a single terminal rosette. *E. floccosa* and *E. atropurpurea* are acaulescent while the other species exhibit varying degrees of caulescence with *E. lutescens* being the tallest. Although *E. schultzi* also occurs as restricted patches of individuals in the Piedras Blancas páramo, it was studied only in the Mucubají páramo where it is the dominant caulescent rosette species.

In Piedras Blancas, the driest and highest páramo (08°52'N, 70°48'W), where temperatures can drop below freezing during any night of the year, the vegetation has an open desert-like appearance and the *Espeletia* species can attain 3–4 m in height (Monasterio, 1980). The Batallón páramo (08°07'N, 71°55'W) is one of the lower and wetter páramos in

the Venezuelan Andes and represents the other extreme of the altitudinal and climatic gradient. Here bunch grasses dominate the plant cover and the caulescent rosettes attain no more than 0.75 m in height. The Mucubají páramo (08°50'N, 70°50'W) is intermediate in precipitation and altitude and the vegetation is dominated by caulescent rosettes 0.5–1.25 m in height (Azócar & Monasterio, 1980).

Field and laboratory measurements

Five adult individuals of each species were used to determine leaf surface area and pith volume. They were excavated with roots and soil and transported to the laboratory. Area of all living expanded leaves was measured with a LI-3000 portable area meter connected to a LI-3050a belt conveyer (LI-COR, Lincoln, Nebraska). The rosettes have many small leaves densely packed around the terminal bud which were not measured because they do not contribute significantly to the total evaporative surface of the plant. The stems were stripped, cut in short sections and the pith diameter and length of each cylindrical section measure to the nearest millimetre.

Daily courses of environmental variables and plant responses were measured in each páramo on three occasions during the 1982 and 1983 dry season. The days selected were representative of the dry period. A pressure chamber was used to measure water potential (ψ_L) of mature expanded leaves which had been placed in plastic bags immediately after excision. At least three leaves were used for each species and the difference between replicates never exceeded 0.2 MPa. Leaf conductance was determined with a locally-constructed steady-state porometer. Humidity and temperature in the porometer chamber were measured with a Vaisala HMP 14 (Vaisala Oy, Helsinki, Finland) relative humidity and temperature probe. Leaf temperatures for transpiration calculations were measured with 36-gauge copper-constantan thermocouples attached to the lower leaf surface. Wet and dry bulb temperatures were measured with two Assman psychrometers, one installed at 1.5 m and the other at the level of the average height of adult individuals of the smallest species. The absolute humidity

Table 2. Summary of pith volume per unit leaf area (PV/LA), pith volume (PV), leaf turgor loss point ($\psi_{0(TLP)}$) estimated from pressure-volume curves, leaf surface area (LA), the range of relative water content corresponding to the water readily available in the pith (ΔRWC), the mass of available water in the pith (ΔM), transpiration (T) of the rosette ($82.2 \text{ g m}^{-2} \text{ h}^{-1} \cdot \text{LA}$), and the period of time during which the water removed from the pith could replace the water transpired (h of T)

Species name	PV/LA ($\times 10^{-2} \text{ cm}^3 \text{ cm}^{-2}$)	PV (cm^3)	$\psi_{0(TLP)}$ (MPa)	ΔRWC	ΔM (g)	LA ($\times 10^3 \text{ cm}^2$)	T (g h^{-1})	Hours of T
<i>E. lutescens</i>	10.5	967.7	-1.37	0.212	176.0	8.60	70.7	2.50
<i>E. moritziana</i>	5.7	268.2	-1.60	0.247	57.0	4.85	39.7	1.44
<i>E. spicata</i>	5.6	565.7	-1.66	0.330	160.4	9.96	81.9	1.96
<i>E. schultzii</i>	4.7	465.6	-1.60	0.247	98.8	11.58	95.2	1.04
<i>E. marcana</i>	3.8	269.9	-1.80	0.373	86.5	6.73	55.3	1.56
<i>E. atropurpurea</i>	1.8	28.6	-1.82	0.378	9.3	1.98	16.3	0.57
<i>E. floccosa</i>	1.3	72.0	-2.04	0.433	26.8	5.45	44.8	0.59

difference between the leaf and the air was determined from leaf temperature and wet and dry bulb temperatures obtained with the psychrometer. The multiplication of these values of humidity difference ($\mu\text{g cm}^{-3}$) by conductance (cm s^{-1}) resulted in an estimate of transpiration ($\mu\text{g cm}^{-2} \text{ s}^{-1}$). Global solar radiation was recorded with a pyranometer (LI-COR model LI-200S) connected to an integrator (LI-COR model LI-500).

Components of leaf water potential were estimated in the laboratory by means of the pressure-volume technique (Tyree & Hammel, 1972). Leaves of the same developmental stage in each species were cut in the late afternoon and the cut end immediately recut under water. The leaves were allowed to fully saturate overnight under a polyethylene cover. The following day the submerged ends were cut, the leaves quickly weighed and the initial balancing pressure determined with a pressure chamber. The leaves were allowed to transpire freely and fresh weight and balancing pressure determinations were continued until several points on the linear portion of the pressure-volume curve had been obtained. Curves were analysed using plots of $1/\psi_L$ versus relative water content (RWC). A regression of the form $1/\psi_L = \beta_0 + \beta_1 \text{ RWC}$ was fitted to the linear portion (Tyree & Richter, 1981, 1982).

The water potential components of the pith were determined with small discs of tissue. Several tissue samples were left in Petri dishes with a source of moisture for 2 d at 4°C until they became fully saturated. The discs were never allowed to come in direct contact with the moisture source. After saturation the samples were weighed, allowed to desiccate for different times (from 0 to 1 h), reweighed and immediately placed inside a thermocouple psychrometer sample chamber (Wescor C-51, Logan Utah). After 1 h equilibration the tissue water potential was measured with a Wescor HR-33T dew point microvoltmeter (dew-point mode). This system was frequently calibrated with filter paper discs soaked in known solutions of sodium chloride. After oven drying at 70°C for 24 h the RWC of each disc was calculated and plotted against the inverse of tissue water potential as with the leaf material.

Results

The pith volume per unit leaf area (PV/LA), a measure of relative capacitance, was calculated for several adult individuals of each species in the study sites indicated in Table 1. Although there was some variability between individuals, the PV/LA differences between species were generally significant (Table 2). Pith volume per unit leaf area, rather than its inverse, was thought to be a better measure of relative capacitance for *Espeletia* since total leaf area of the rosettes remains essentially constant once the plants reach a certain age. Thus between and within species differences in relative water storage capacity of adult plants are due primarily to differences in stem length and therefore pith volume. Species from high and dry páramos tended to have higher PV/LA than species from low and wet sites. This was particularly true for the three species that are mostly restricted to the highest and harsher environments: *E. lutescens*, *E. moritziana* and *E. spicata*. Some of the other species, such as *E. schultzii*, have a broader altitudinal range and the PV/LA ratio of different populations along an altitudinal gradient shows a trend similar to the one reported here for all seven species (Meinzer, Goldstein & Rundel, unpublished observations).

The pressure volume curves obtained for the pith tissue of three species, two extreme and one intermediate in terms of PV/LA values, exhibited the characteristic two phases; an initial non-linear portion at high values of RWC and a linear relationship at lower values (Fig. 1). The turgor loss point $\psi_{0(TLP)}$ on each of the three curves was similar and was approximately -1.22 MPa . There was no significant difference between the linear portions of the three curves because the standard errors of the estimates of the slopes (approximately ± 0.2) and of the y -intercepts (± 0.06) overlapped. The inverse y -intercept of the linear portion (about -0.96 MPa) is an estimate of the osmotic potential at saturation [$\psi_{0(SAT)}$]. Because there were no significant differences in pith water potential components for the two extreme and one intermediate species, a combined pressure-volume curve was used for all

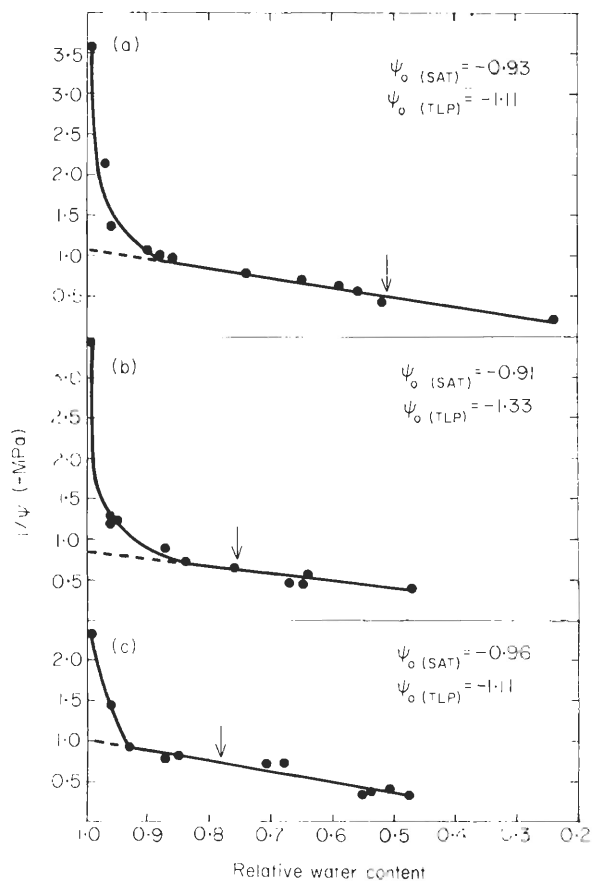


Figure 1. Pressure volume curves for pith tissue of *E. floccosa* (a), *E. schultzei* (b), and *E. lutescens* (c) showing the turgor loss point [$\psi_{0(TLP)}$] and the osmotic potential at full saturation [$\psi_{0(SAT)}$]. Arrows represent the leaf turgor loss point of each species.

seven species to calculate pith water storage capacity. The linear portion of this curve is described by $1/\psi = -0.128 + 1.089 \text{ RWC}$. In a previous study we found that the pith water potential of *E. timotensis* can drop down to leaf $\psi_{0(TLP)}$ and recover rapidly upon rewatering (Goldstein & Meinzer, 1983). We decided therefore to use a conservative criterion and define the range of RWC corresponding to the use of available water as:

$$\Delta \text{RWC} = 1 - \text{RWC}_{(TLP)}$$

where $\text{RWC}_{(TLP)}$ is the relative water content of the pith tissue at the turgor loss point. The combined curve was entered with the leaf $\psi_{0(TLP)}$ of each species and the change in RWC that the pith tissue experiences between this value and saturation was calculated as described above.

Information used to calculate the water storage capacity for each species is presented in Table 2. The mass of available water in the pith reservoir was calculated as:

$$\Delta M = V \cdot \alpha \cdot \rho \cdot \Delta \text{RWC},$$

where V is the volume of the pith tissue, α is the fraction of the pith which is water filled (0.859), and ρ (1 g cm^{-3}) is the density of water (Jarvis, 1975). Total transpiration was calculated as transpirational flux density (TFD) multiplied by leaf area of the rosette. Since the aim was to calculate storage capacity under similar conditions, the same average TFD was used for all the species. There was complete overlap between all seven species in the range of typical TFD values measured in the field. The mass of available water stored (ΔM) was compared with diurnal average transpiration rates to give the period of time during which the water removed from the pith could replace the water transpired (final column in Table 2).

The species are ranked in Table 2 from high to low PV/LA values. It should be noted that species with higher PV/LA can provide water for transpiration needs during a longer period of time than species with smaller PV/LA. The ratio PV/LA is strictly morphological in character; however, it does bear relation to function, that is, the potential quantity of water available, as just shown. The ratio PV/LA can therefore be considered to be a good indicator of the water storage capacity of the plant.

Daily courses of global solar radiation, transpiration and water potential for the seven species are given in Fig. 2. These patterns are typical of the dry season and they reflect differences in regulation of water balance among the species studied. For example, *E. lutescens* in the Piedras Blancas páramo (Fig. 2a) did not exhibit pronounced changes in leaf water potential, even at mid-day when transpiration rates were maximum. Water potential in *E. moritziana* and *E. spicata* on the other hand dropped from a predawn value of -0.6 or -0.7 MPa to -1.3 MPa in only 4 h. These two species have a lower PV/LA than *E. lutescens* (Table 2). The differences in minimum ψ_L values cannot be explained by differences in transpiration rates because *E. lutescens* with the highest maximum transpiration rate maintained highest ψ_L .

E. floccosa and *E. schultzei*, the two species from the Mucubaji páramo (Fig. 2b) showed similar transpiration patterns. The development of water stress, however, progressed slower in *E. schultzei* than in *E. floccosa*. *E. floccosa* attained the lowest ψ_L and ψ_L of *E. floccosa* responded rapidly to changes in evaporative demand. This rapid response may reflect the low water storage capacity of the pith (Table 2).

Figure 2c shows ψ_L and TFD responses of *E. marcana* and *E. atropurpurea*. Again, in the species with the lowest storage capacity, ψ_L tended to be more responsive to changes in rate of water loss. In *E. atropurpurea* ψ_L decreased from -0.2 to -1.55 MPa while in *E. marcana* ψ_L dropped only 0.5 MPa during the same time interval.

In order to evaluate the effect of pith water storage capacity on the water economy of the species studied, the relationship between PV/LA and the

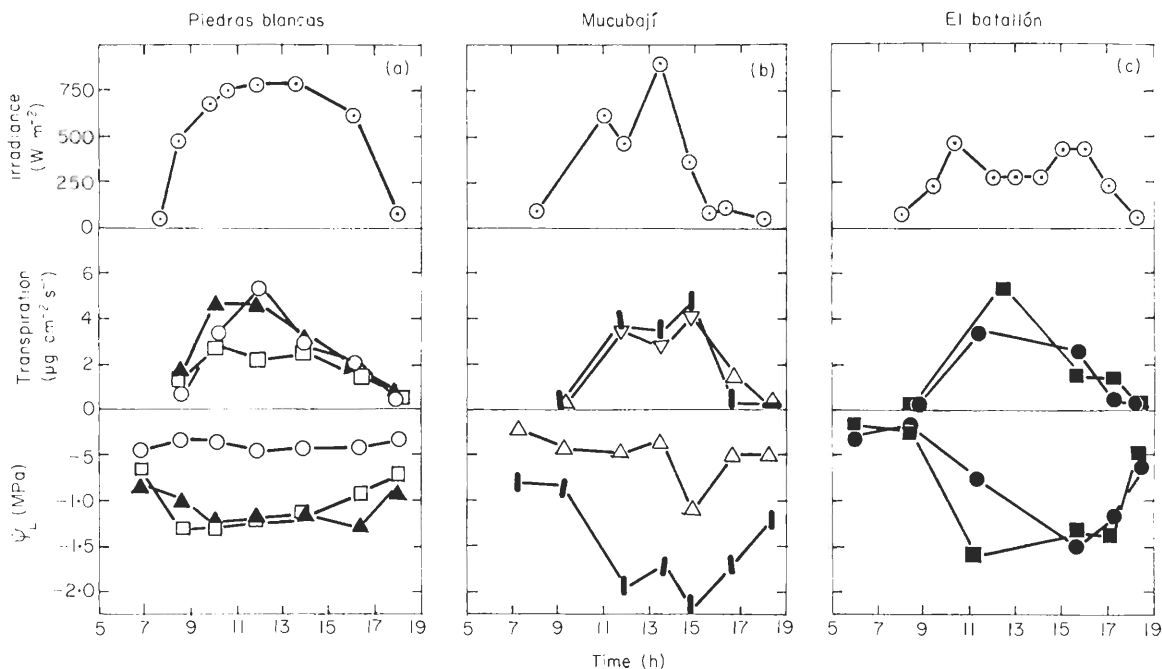


Figure 2. Daily courses of global solar radiation, transpiration flux density, and leaf water potential (ψ_L) during the dry season of 1982 for (a) *E. lutescens* (○), *E. spicata* (□), and *E. moritziana* (▲), (b) *E. schultzi* (△) and *E. floccosa* (■), and (c) *E. marcana* (●) and *E. atropurpurea* (■).

relative drop in water potential ($\Delta\psi_L$) per unit TFD was examined (Fig. 3). The ratio $\Delta\psi_L$ /TFD is a measure of total water flux resistance from the soil to the leaves (Elfving, Kaufmann & Hall, 1972; Boyer, 1974; Camacho-B, Hall & Kaufmann, 1974) and was obtained by averaging TFD and ψ_L data for 3 d from each site. To minimize hysteresis effects and to maximize the influence on hydraulic resistance of water transfer from the pith reservoir to the leaves, only measurements taken during the early morning,

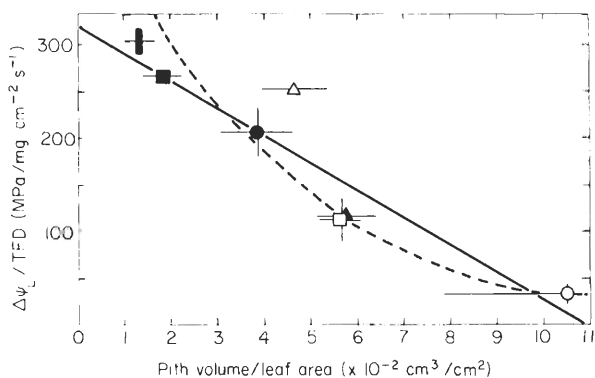


Figure 3. Hydraulic resistance ($\Delta\psi_L$ /TFD) versus pith volume per unit leaf area (PV/LA) in adult individuals of *E. lutescens*, *E. moritziana*, *E. spicata*, *E. marcana*, *E. schultzi*, *E. atropurpurea*, and *E. floccosa*. Symbols as in Fig. 2. The solid line represents a linear regression while the dashed line represents a negative exponential regression fitted to the data. Bars are ± 1 SE of the mean. Absence of bars indicates that the SE was smaller than the symbol.

under conditions of decreasing ψ_L and low soil and root temperatures, were used. A strong relationship was found between PV/LA and $\Delta\psi_L$ /TFD using either a linear function ($r^2 = 0.87$), or a negative exponential curve ($r^2 = 0.91$) suggesting that higher PV/LA's greatly reduce effective hydraulic resistance.

Figure 4 shows that there is also clearly a relationship between relative water storage capacity (i.e. effective hydraulic resistance) and leaf $\psi_{0(TLP)}$. The slope of the solid line in Fig. 5, determined by

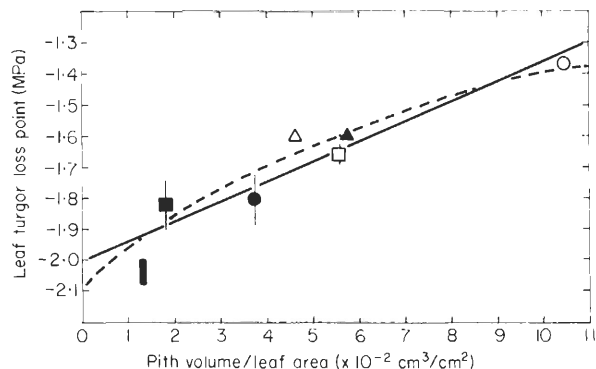


Figure 4. Species specific turgor loss point [$\psi_{0(TLP)}$] in relation to pith volume per unit leaf area (PV/LA) in adult individuals of *E. lutescens*, *E. moritziana*, *E. spicata*, *E. marcana*, *E. schultzi*, *E. atropurpurea*, and *E. floccosa*. Symbols as in Fig. 2. The solid line represents a linear regression while the dashed line represents a second degree polynomial regression fitted to the data. Vertical bars are ± 1 SE of $\psi_{0(TLP)}$. The SE of PV/LA values are represented in Fig. 3. Absence of vertical bars indicates that the SE was smaller than the symbol.

linear regression analysis, indicates that species with a more negative $\psi_{0(TLP)}$ tend to have a smaller water storage capacity. Although a linear function was significant at $P \leq 0.01$ ($r^2 = 0.87$), an asymptotic relationship obtained by using a 2-degree polynomial regression ($r^2 = 0.90$) would better describe the data. This non-linear relationship suggests that a theoretical maximum $\psi_{0(TLP)}$ should exist at a very high relative water storage capacity. Both the linear and non-linear lines shown in Figs. 3 and 4 are significant. The non-linear relationships in both cases were preferable because they had (i) the higher r^2 and (ii), more importantly, a higher mechanistic reality.

Discussion

One of the most notable features of páramo environments is their high degree of seasonal temperature constancy combined with low prevailing temperatures. This poses a series of constraints for plant survival and growth because environmental and plant temperature frequently may be sub-optimal for processes such as water uptake, translocation of assimilates and leaf growth.

It is interesting that while the typical trend in temperate high mountains is a reduction in plant height with increasing elevation, the species of the genus *Espeletia* above timberline tend to be taller at higher altitudes. Several explanations have been offered for this apparent paradox. Larcher (1975) suggested that taller *Espeletia* plants would experience more favourable temperatures for photosynthesis and growth. However, because of the open desert-like appearance of the vegetation in the higher páramos (c. 4200 m), the temperature profiles above the soil surface change significantly only in the first 20 cm (Goldstein & Meinzer, unpublished observations). Thus growth above this height would not seem to be of additional adaptive value from the standpoint of carbon balance. Smith (1980), on the other hand, hypothesized that drought stress would select for taller *E. schultzii* plants in the higher and harsher environments because the portion of the 'water-filled pith' nearest the leaves, which would serve as a short-term water source when the soil is frozen, would have a lower probability of freezing in taller plants. His suggestion, however, was based on few measurements of microclimatic variables and no physiological measurements of plant responses to water deficits.

In this paper we suggest that the caulescent habit in the genus *Espeletia* plays an important role in water economy. The height of the *Espeletia* plants could be at least partially related to the maximization of the effectiveness of water storage. From the hydraulic point of view, long narrow cylindrical reservoirs that maximize the area of contact between xylem and pith are more efficient than short wide ones. In a previous study (Goldstein

& Meinzer, 1983), we demonstrated that the marcescent leaves thermally insulate the stem thus preventing frost injury of the pith tissue and ensuring its ability to store water. Soil temperatures frequently fall below freezing, particularly above 3600 m (Monasterio, 1980), and therefore water uptake during the early morning may be impeded by low root membrane permeability. The adverse effects of low soil temperatures on the hydraulic conductivity of roots is now well documented for several species (Running & Reid, 1980; Kaufmann, 1977; Goldstein, 1981). Large, insulated pith water reservoirs could therefore be an adaptive solution in high tropical mountains where freezing temperatures last only a few hours. The selective pressure for greater water storage capacity should increase with the intensity and duration of the frost.

Our results suggest that a species-specific contribution of water stored in the pith to the transpirational stream, as well as plant height and pith volume per unit surface area tend to increase with increasing altitude (Table 2). The water storage capacity of the pith of the high elevation species (1.44–2.50 h) is higher than most of the capacitance values reported for elastic reservoirs (Hinckley *et al.*, 1981; Jarvis, 1975) and is similar to the range of values of sapwood capacitance calculated by Running (1980), Waring & Running (1978) and Richards (1973) for conifers. A similar trend in terms of PV/LA ratios and pith volume was found in several populations of *E. schultzii* along an altitudinal gradient from 2700 m to 4200 m (Meinzer, Goldstein & Rundel, unpublished observations). This intraspecific trend similar to the interspecific one described above, and the fact that the most primitive *Espeletia* species (Cuatrecasas, 1979) which do not have pith reservoirs, grow in the Venezuelan Andes at lower elevations below the continuous forest line, reinforce the idea that high tropical environments tend to select for great water storage capacity in giant rosette plants. *E. marcana* was the only species studied that did not follow the general capacitance pattern well since it has a relatively high water storage capacity and is found in some low elevation páramos. Cuatrecasas (1976) in a new classification scheme for the genus *Espeletia* has subdivided the genus into several new taxa and grouped *E. marcana* with the high elevation species in a new proposed genus, *Coespeletia*. Although we are suggesting that cold tropical environments select for high pith capacitance, a lower elevation species may possess this character if the cost of having a relatively voluminous pith does not affect competitive ability.

Daily patterns of transpiration and ψ_L show the buffering effect of the water stored in the pith (Fig. 2). The species that have the highest storage capacity in each páramo either do not exhibit pronounced changes in leaf water potential, or the drop in ψ_L exhibits a lag with respect to the other species. The

ψ_L of *E. lutescens*, which maintains the most stable water balance, changes no more than 0.15 MPa even during a relatively high evaporative demand day. This species, as well as *E. schultzei* exhibits a phase of increasing ψ_L during the morning. This apparent anomaly in behaviour may reflect the increase in soil temperature and therefore a decrease in hydraulic resistance of the roots. Initially water would move out of the pith storage protected from subfreezing temperatures by the insulating layer of dead leaves. Because this source is quite large in high elevation species and very close to the atmospheric sink, the potential does not drop considerably. Later in the morning and at higher root temperatures, the resistance to water uptake will tend to decrease and the soil water could supply the transpiration stream with enough water to cause an increase in the leaf water potential.

One could speculate that seedlings and small plants of the high elevation species such as *E. lutescens* would experience pronounced changes in ψ_L because the pith reservoir at this initial stage of plant development is not large enough to sustain prolonged high transpiration rates. One could also speculate that for this reason the risk of death is also greater in small plants. Initial observations that tend to confirm these ideas show a high correlation between size-specific mortality and water storage capacity of the pith for individuals up to 1 m tall (Goldstein, Meinzer & Monasterio, unpublished observations).

The asymptotic relationship between PV/LA (relative water storage capacity) and both hydraulic resistance (Fig. 3) and $\psi_{0(TLP)}$ (Fig. 4) indicates that the rate of change of these two variables decreases at high PV/LA values until a theoretical minimum resistance and maximum $\psi_{0(TLP)}$ is reached. At that point the hydraulic resistance and $\psi_{0(TLP)}$ should be independent of the capacitance of the pith. At this point the rate of water movement from the pith to xylem, rather than the absolute quantity of water stored in the pith, becomes the limiting factor. Figure 4 also implies that shoots of páramo plants without pith capacitance (y -intercept of the dashed line) should have a turgor loss point of -2.1 MPa. This prediction approximately coincides with the $\psi_{0(TLP)}$ values of another páramo growth form: *Hypericum laricifolium*, an evergreen shrub with a $\psi_{0(TLP)}$ of -2.0 to -2.2 MPa during the dry season. We were particularly surprised by the very high correlation between PV/LA and resistance, because each species may have other internal sources of water such as the conspicuous midribs of the leaves and different hydraulic conductivities between the pith reservoir and the peripheral xylem. Undoubtedly this functional relationship indicates that pith water storage significantly influences the apparent resistance to water flow between the roots and the leaves and therefore the capacity of the plant to dampen fluctuations in ψ_L during high potential

transpiration or low soil moisture availability periods. This would reduce the need for transpiration and therefore CO_2 uptake to be restricted by stomata.

Overall this work shows that the high elevation species of the genus *Espeletia* differ in their water storage capacity and that the species-specific capacitance is a function of the temperature-limited availability of water in the soil. This work also demonstrates that the genus *Espeletia* can be treated as a model system for studying the role of living water storage tissue in the regulation of plant water balance because the pith is easily differentiated anatomically from the other plant tissues, appears to function mainly as a water reservoir, has good hydraulic connections with the rest of the plant, and is involved in the maintenance of a favourable water balance by meeting peak demands when water uptake is impeded by low temperatures.

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