

# Physiological and Mechanical Factors in Relation to Size-dependent Mortality in an Andean Giant Rosette Species

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## ABSTRACT

Physical and physiological factors affecting age dependent mortality in *Espeletia timotensis*, an Andean caulescent rosette species, were analysed in a combination of field and laboratory studies. Mortality was highest among smaller individuals, relatively low in intermediate size classes, and increased with increasing height at older ages. This suggested that different kinds of environmental stresses were responsible for mortality in juvenile versus taller adult plants. Small plants with low stem pith water storage capacity experienced lower leaf water potentials than taller plants with larger pith volume, particularly during the dry season. The leaf water potentials observed in small individuals during the dry season were below the turgor loss point and very close to the irreversible damage point, suggesting that the high risk of mortality in small plants was a consequence of their small capacitance and lack of ability to osmotically adjust to periods of low soil water availability. Solifluction processes in the high paramos where *E. timotensis* grows cause substrate instability resulting in tilting of taller individuals until they are prostrate over the soil surface. Symptoms of senescence were not observed before the tall plants were completely tilted. It appears that selection in tropical high altitude caulescent rosette plants has favored rapid growth to "escape" from frequent diurnal water stress by rapidly increasing the volume of tissues with high water storage capacity instead of favoring physiological characteristics of more slow growing species adapted to withstand long periods of seasonal water stress.

KEY-WORDS: *Espeletia timotensis* - *Paramo* - *Size-dependent mortality* -  
*Water relations* - *Supercooling*.

## RÉSUMÉ

Les facteurs physiques et physiologiques qui influent sur l'évolution en fonction de l'âge de la mortalité chez *Espeletia timotensis*, une Composée caulescente à rosette des Andes, ont été analysés en se basant sur une combinaison d'études de terrain et de laboratoire. La mortalité la plus élevée a été observée parmi les individus de petite taille; elle est relativement faible chez les individus de taille intermédiaire et augmente à nouveau en fonction de la taille chez les individus âgés. Ceci suggère que ce sont des contraintes écologiques différentes qui sont responsables de la mortalité des plantes juvéniles d'une part et de celle des plantes adultes de grande taille d'autre part. Les plantes de petite taille, à faible capacité de stockage de l'eau dans la moelle des tiges, atteignent des potentiels hydriques plus bas que les plantes de grande taille chez lesquelles la moelle occupe un espace plus important; ceci est particulièrement important au cours de la saison sèche. Les potentiels hydriques foliaires observés au cours de la saison sèche chez les individus de petite taille étaient inférieurs au

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point de turgescence nulle et très proches du point de dommages irréversibles. Ceci suggère que le risque élevé de mortalité chez les plantes de petite taille est une conséquence de leur faible capacité de stockage de l'eau et du manque de pouvoir d'ajustement osmotique lors des périodes de faible disponibilité de l'eau dans le sol. Les processus de solifluction dans les zones où pousse *E. timotensis* entraînent une instabilité du substrat qui occasionne une inclinaison des individus les plus grands, lesquels finissent par être couchés sur le sol. On n'a pas observé de symptômes de sénescence avant que les tiges des plantes ne soient entièrement couchées.

En conclusion, il apparaît que, dans les zones tropicales de haute altitude, la sélection a favorisé chez les espèces caulescentes à rosette une croissance rapide permettant d'échapper aux fréquentes contraintes hydriques journalières grâce à une augmentation des tissus à forte capacité de stockage pour l'eau plutôt que de favoriser les caractéristiques physiologiques d'espèces à croissance lente, lesquelles sont mieux adaptées pour résister à de longues périodes de sécheresse.

MOTS-CLÉS : *Espeletia* - Compositae - Paramo - Démographie - Régime hydrique.

## INTRODUCTION

Populations of caulescent giant rosette species belonging to the genus *Espeletia* grow at elevations up to 4 600 m in the high tropical Andes (Paramo). Even at this elevation germination and establishment of new members of the uneven age populations are very frequent. Adult plants can attain a height of 3 m. The unbranched stem contains a voluminous central pith made up of parenchymatous tissue and is surrounded by an insulating layer of marcescent leaves.

Similar morphological features have evolved independently in other equatorial high mountains (HEDBERG, 1964; SMITH, 1974). This great morphological convergence in disjunct regions suggests that the giant rosette form represents an adaptive solution to the unique selective pressures that prevail in high altitude tropical environments, in which daily temperature variations are more important than seasonal ones, freezing temperatures are very frequent and can occur any night of the year (COE, 1967; TROLL, 1968), and gelifluction processes, particularly in Andean desert paramos, induce strong soil particle displacement (SCHUBERT, 1976; MALAGON, 1982).

Mechanical instability, on slopes strongly affected by soil movement, may influence germination, seedling establishment and survivorship of tall rosette plants. The low prevailing nighttime temperatures not only may directly affect exposed tissues such as external leaves of the rosettes, but also water uptake by the roots and therefore water balance of the whole plant. Soil moisture availability can be severely limited when water is frozen or water uptake impeded by low root membrane permeability (ref. *i. e.* RUNNING & REID, 1980; KAUFMANN, 1977).

In previous works we have analysed this last aspect of low temperature effects, particularly the role of pith water storage in the water economy of giant rosette plants. Pith water storage in this extreme environment is of adaptive value not only because it helps to replace transpirational losses (particularly during the early morning hours when soil temperature is low and evaporative demand is high), but also because it minimizes the distance and resistance between water source and atmospheric sink (GOLDSTEIN & MEINZER, 1983; GOLDSTEIN *et al.*, 1984; MEINZER & GOLDSTEIN, 1985). Diurnal fluctuations in leaf water status are less pronounced in *Espeletia* species with higher relative pith water storage capacity (pith volume/total leaf area) (GOLDSTEIN *et al.*, 1984). In tall caulescent species this ratio of pith volume to total leaf area undergoes large variations during the life cycle of an individual because rosette area typically increases and stabilizes before appreciable stem elongation

and pith volume increase occur. These intraspecific age-dependent variations in relative water storage should influence diurnal water relations and therefore could affect the size or age-specific mortality of the individuals in high, cold habitats with severe short-term reduction in water availability.

In most plant populations with overlapping generations, mortality rates tend to vary with the age or size of the individuals. Three theoretical survivorship distributions were established long ago (PEARL & MINER, 1935). The negative skew rectangular (Type I) indicates low mortality among young cohorts and a rapidly increasing mortality rate at older ages. The Type III distributions have high mortality rate in the youngest age classes with the probability of death decreasing with age. Type II is intermediate and implies a constant mortality rate throughout the lifespan of the population. Other more complicated functions have been also used to describe age depletions in long-lived tree species (HETT & LOUCKS, 1976). Death rates in giant caulescent *Espeletia* species appears to be greatest during the first years and at old age (M. MONASTERIO, manuscript in preparation). These two distinctive periods in the life cycle of several *Espeletia* species probably implies that mortality in each period is caused by different factors. The objective of this study was to document the size-specific changes in mortality rate in *Espeletia timotensis* and to investigate physiological and ecological factors that may cause the mortality patterns observed.

## MATERIALS AND METHODS

All studies were carried out with individuals of *Espeletia timotensis* Cuatr. (nomenclature according to ARISTEGUIETA, 1964) from the Paramo de Piedras Blancas (08°52'N, 70°48'W) at 4,200 m elevation. This is one of highest and driest Venezuelan paramos and the vegetation has an open desert-like appearance. The study site was described in detail by MONASTERIO (1984). Plant cover is approximately 10 to 30 % of the total soil surface. Grasses, cushion plants and other typical growth forms of temperate alpine zones are represented here by a few sparse members. The mean annual temperature is 2.8° C and the difference in mean monthly temperature between the coldest and warmest months is only 2.7° C. The mean annual precipitation of approximately 800 mm falls mainly between April and December. *E. timotensis*, one of the dominant giant caulescent rosette species in the Paramo de Piedras Blancas, is a long-lived polycarpic species that reproduces approximately once every three years. The leaves are active for two years after full expansion (ESTRADA, 1984) and remain attached to the stem after senescence, thus forming an insulating cylinder of marcescent leaves. In addition to well-developed secondary xylem, this species has a large volume of parenchymatous pith in the center of the stem.

Previous work at the study area (MONASTERIO, 1984) consisted of establishing 4 permanent plots of 100 m<sup>2</sup> each at regular intervals along a topographic gradient dominated by *E. timotensis*. Every individual was marked and plant establishment and death were recorded from 1977 to 1983. On both sides of the permanent plots 5 contiguous sample plots 10 × 10 m were established in the present study parallel to the contour lines. In each sample plot total plant height, stem length, rosette diameter and number of inflorescences per individual were recorded.

Leaf water potential ( $\Psi_L$ ) was measured with a pressure chamber several times during the wet and dry seasons in individuals of different total height in a site dominated by *E. timotensis* plants similar to the permanent plots. Midday  $\Psi_L$  values observed under conditions of maximum evaporative demand were considered to be the minimum leaf water potential ( $\Psi_L^{\min}$ ) attained during the day. Individuals from the same site were excavated with roots and soil and transported to the laboratory to determine the ratio of pith volume to total leaf area. Area of all living expanded leaves was measured with a LI-3000 portable area meter connected to a LI-3050 a belt conveyer (LI-COR, Lincoln, Nebraska). The stems were stripped, cut in short sections and the pith diameter and length of each cylindrical section measured to the nearest millimeter in order to calculate pith volume.

Individuals were also excavated with soil and transported to the laboratory to study the leaf water potential response to short term water deficit. The plants were rewatered, the rosette covered with plastic bags and kept overnight at 6° C. Early in the next morning the root systems were completely excised and the bags removed. Leaf water potential was determined every 20-45 minutes. Only one leaf at a time in each individual was used to avoid a significant decrease in total leaf area as time progressed.

To evaluate the effect of mechanical stability on plant survivorship, four pure *E. timotensis* stands were chosen. Each one of them had similar plant densities but different slope angles. The deviation angle (deviation from vertical) of at least 30 plants in each stand was measured with an inclinometer.

Components of leaf water potential for plants of different ages were estimated in the laboratory by means of the pressure-volume technique (TYREE & HAMMEL, 1972). Leaves of the same developmental stage were cut in the late afternoon and the cut end was 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  $1/\Psi_L = \beta_0 + \beta_1 \cdot RWC$  was fitted to the linear portion (TYREE & RICHTER, 1981, 1982).

For thermal analysis (*TA*) studies leaf pieces 3 cm long and 1 cm wide were cut and immediately enclosed in small tubes tightly sealed to avoid changes in tissue water content. Copper-constantan thermocouples (36 gauge) were inserted in the leaf sample and changes in temperature were continuously monitored with a strip chart recorder fitted with an electronic 0° C reference. Prior to immersion in a refrigerated alcohol bath the tubes were placed in an aluminium cylinder which acted as a heat sink and provided temperature stabilization during cooling (QUAMME *et al.*, 1972). The temperature of the bath was lowered to -30° C at a rate of 10-12° C h<sup>-1</sup>.

To evaluate the sensitivity of the leaf tissue to changes in water content, several detached leaves were saturated overnight and then left to dehydrate to various water saturation deficits. The leaves were then weighed, allowed to resaturate during 24 h, reweighed, and oven dried for determination of dry weight (SLAVIK, 1974). The results were graphed by plotting % resaturation against the corresponding water saturation deficit value. The critical or sublethal water saturation deficit was considered to occur when the weight of resaturated leaf tissue was 10 % smaller than the initial saturated weight (OPPENHEIMER, 1963; RYCHNOVSKA, 1963).

## RESULTS

### *Height and Age Structure*

Height in caulescent giant rosette species seems to be linearly related to age, except for the first few cm (ESTRADA, 1984). Height and relative age, therefore, will be used interchangeably here. Under the assumption of stable age (height) distribution and constant recruitment, the slope of the frequency-age class distribution in figure 1 may be considered as an estimate of the age specific mortality rate (HARPER, 1977). The more pronounced the slope of the relationship the higher the number of dead plants per unit time or unit height. Three regions can be distinguished in figure 1: 1) an initial steep slope indicating high mortality rate, 2) a very small decrease in population size with increasing height between 40 and 100 cm, and 3) above this plant height a rapidly increasing mortality rate at older ages. Death rates seemed to be greatest during the first years and at old age. A third degree polynomial function was used to describe the changes in population size as a function of plant height. The inflection point of the function around 40 to 100 cm in height again indicated a changing risk of death with time.

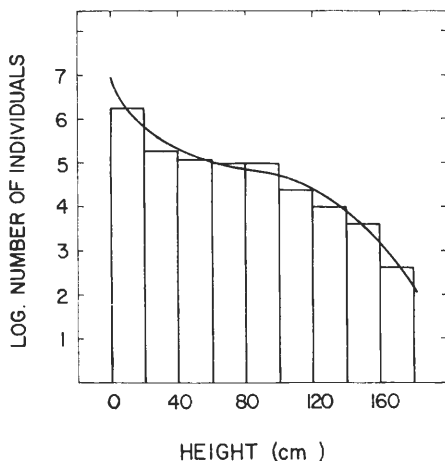


FIG. 1. — Distribution of height of *E. timotensis* using 20 cm height intervals. A few individuals taller than 180 cm were not included in the histogram. The curve describes a 3-degree polynomial function fitted to the data ( $R^2 = 0.98$ ).

Records of annual mortality rates in permanent plots seemed to confirm this pattern. The mean annual mortality is 7.2 % for small individuals (0-40 cm) (small seedlings were not monitored), decreased to 2.1 % mortality in 1 year for individuals 40 to 100 cm tall and increased again for individuals above 100 cm tall (e. g. 3.6 % for the 120-140 height class). The initial population size ( $n = 124$ ) of the permanent plots was small and therefore the cross section of the population was used to describe the changes in mortality rate with age.

#### *Pith Water Storage and Water Balance*

In the caulescent giant rosette species that grow at high elevations pith relative water storage capacity was expected to show large variations during the life of an individual. Figure 2a confirms this expected change. In *E. timotensis* relative water storage capacity initially increases slowly as both rosette area and stem length, and therefore pith volume, are increasing. As the rosette area begins to stabilize a rapid linear increase in relative pith water storage capacity occurs. The importance of these changes is reflected in patterns of water stress in individuals of different ages (fig. 2b). The curves in figure 2b represent size-dependent minimum leaf water potentials during wet and dry season days. During the humid wet season day practically no differences were observed in  $\Psi_L^{\min}$  between tall and short individuals. During the dry season, however,  $\Psi_L^{\min}$  of adult individuals remained well above the turgor loss point while minimum water potentials were lower and wilting occurred in younger plants. Individuals with smaller pith water storage capacity exhibit lower  $\Psi_L^{\min}$  particularly during the dry season when the evaporative demand is relatively high and soil water availability is not only affected by more frequent freezing temperatures (SARMIENTO, 1984), but also by lower soil water potentials. This size-specific water balance behavior may reflect not only differences in water storage capacity of internal tissues but also differences in root system size. Roots systems of tall

plants tend to be more extensive and explore a larger volume of soil than smaller plants.

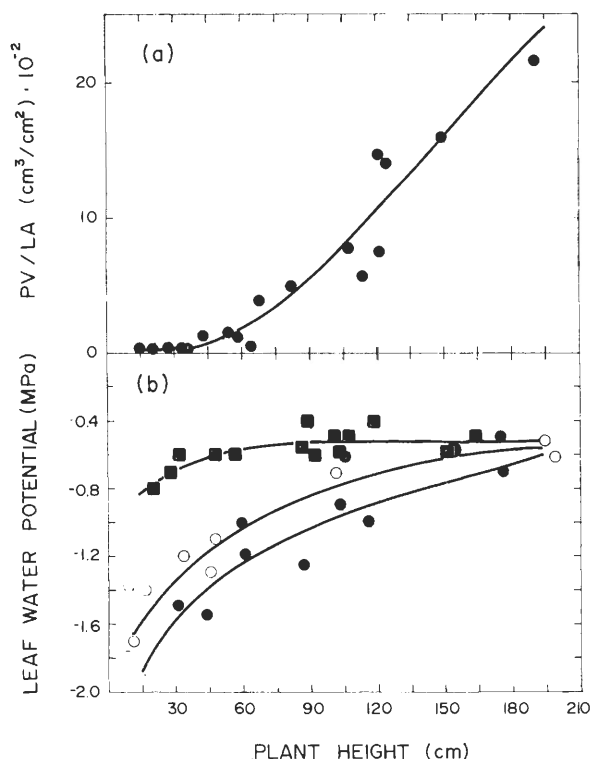


FIG. 2. — Changes in (a) pith volume/leaf area ( $PV/LA$ ), and (b) minimum leaf water potential as a function of plant height. Each one of the curves in the lower panel are relationships between leaf water potential and plant height measured during a wet season day (■) and two dry season days (●, ○).

Figure 3 shows the time course of  $\Psi_L$  of individuals with different pith water storage capacity under laboratory conditions. Individuals with smaller capacitance tended to exhibit more negative  $\Psi_L$  after 1 to 2 h of root excision. Individuals with high capacitance showed only a small  $\Psi_L$  decrease. These results coincide with  $\Psi_L$  patterns observed in the field. Tall caulescent rosette plants do not exhibit pronounced changes in  $\Psi_L$ , even at mid-day when transpiration rates are maximum (GOLDSTEIN *et al.*, 1984).

Pressure volume curve analyses (fig. 4) show that turgor loss points in leaves of individuals of different ages were nearly identical. The curves exhibited the characteristic two phases; an initial nonlinear portion at high values of  $RWC$  and a linear relationship at lower values of  $RWC$ . The inverse  $Y$ -intercept of the linear portion (about  $-1.1$  MPa) is an estimate of the osmotic potential at full saturation ( $\Psi_0(SAT)$ ). There were no significant differences in  $\Psi_0(SAT)$  obtained with leaf material from plants of different heights. The turgor loss point ( $\Psi_0(TLP)$ ) was also

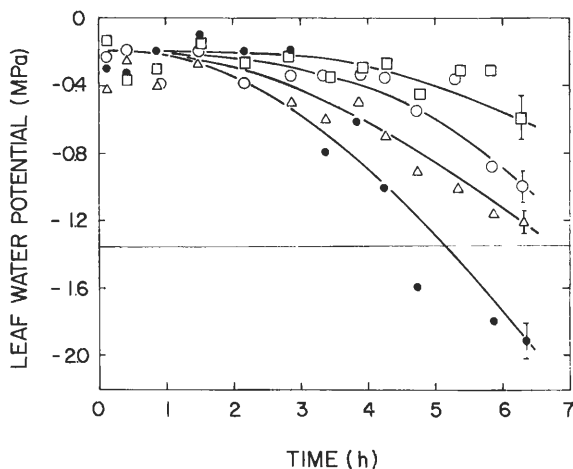


FIG. 3. — Time course of leaf water potential after root excision for individuals 26 (●), 40 (△), 66 (○) and 100 (□) cm tall under laboratory conditions. Pith volume/leaf area ratios are  $0.07 \times 10^{-2}$ ,  $0.4 \times 10^{-2}$ ,  $3.92 \times 10^{-2}$  and  $9.00 \times 10^{-2}$   $\text{cm}^3/\text{cm}^2$  respectively. Bars are  $\pm 1$  SE of the means ( $n = 3$ ). Line indicates the turgor loss point of expanded leaves.

similar among height classes and was approximately  $-1.4$  MPa. Another water relations characteristic, the relative water content at zero turgor ( $RWC^0$ ) tended to be lower in younger plants. The difference in  $RWC^0$  between the leaves of the tallest and shortest individuals, however, was only 6 %.

The critical relative water content of the leaf tissue (90 % resaturation) is shown in figure 5 and approximately coincides with the change in slope of the  $RWC$ -resaturation relationship. Irreversible damage began to occur at a relatively high  $RWC$  and close to the  $RWC$  and  $\Psi_L$  at zero turgor obtained with the pressure volume method.

#### Direct Temperature Effects

Attention was also focused on direct temperature effects, since frequent sub-freezing temperatures may produce leaf damage and therefore alter plant competitive or resistance ability. Leaves from individuals of different ages supercool (cool below the equilibrium freezing point) in the range of  $-6$  to  $-11^\circ\text{C}$  (table I). No visible symptoms of tissue damage were observed when leaf temperature was lowered to the corresponding supercooling temperature.

TABLE I. — Supercooling points for leaf tissue of different size individuals. Standard errors (SE) are included.

Plant height (cm)	15	25	60	90	120
Exotherm appearance ( $^\circ\text{C}$ )	-11.0	-8.73	-8.65	-8.07	-6.08
SE of the mean ( $n = 5$ )	0.47	0.78	0.50	0.40	0.84

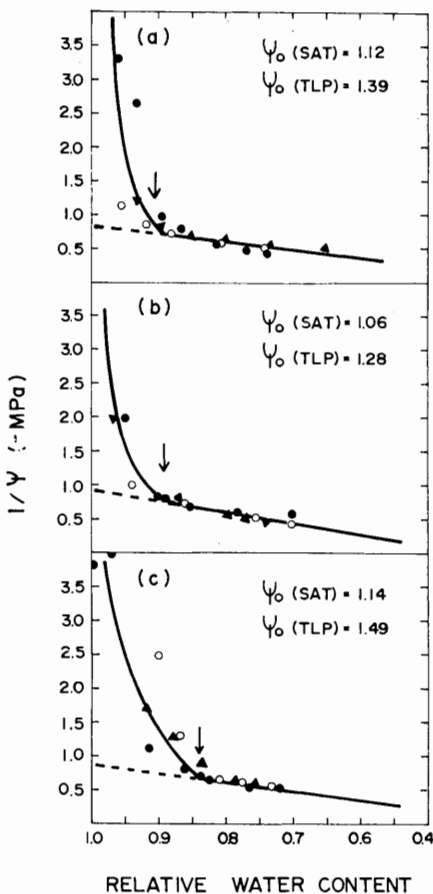


FIG. 4. — Pressure volume curves for leaves of *E. timotensis* individuals 150 cm tall (a), 85 cm tall (b) and 25-30 cm tall (c) showing the turgor loss point ( $\Psi_0$  (TLP)), and the osmotic potential at full saturation ( $\Psi_0$  (SAT)) in MPa. Arrows indicate the leaf turgor loss points for each group of individuals. The linear phase of the curves was obtained by regression analyses.

### Soil Instability and Risk of Death

To evaluate the effect of soil instability on the risk of death at older ages, exponential functions were fitted to the deviation angle/plant height relationship for different sites (fig. 6). An exponential function was preferable over a linear relationship not only because the  $R^2$  of the exponential regressions fitted to the data were generally higher, but also because it was more realistic from a mechanistic point of view.

The deviation angle of the individuals increased initially very slowly with increasing plant height and then more rapidly in individuals above 1 m tall. Figure 6 also shows that the deviation angle tended to be higher for a given size class in steeper sites. These results indicate that the risk of death in taller caulescent rosette plants may be affected by physical processes that produce strong soil movement in Andean desert paramos. No signs of senescence were found in tall erect individuals.



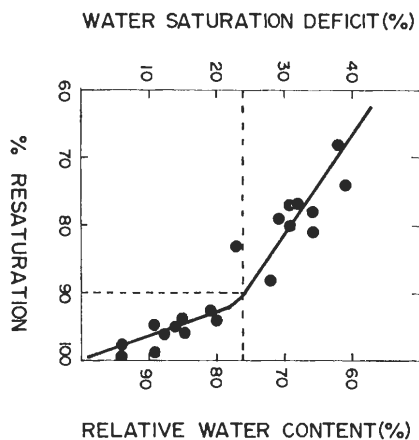


FIG. 5. — Relationship between water saturation deficit of leaf tissue and % resaturation. The critical or sublethal damage point (90 % resaturation) is indicated.

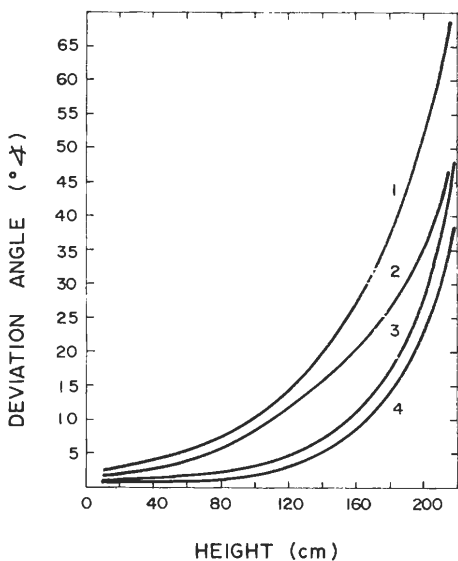


FIG. 6. — Deviation angle (deviation from vertical) as a function of plant height in sites with 25.4 % (1), 19.0 % (2), 10.0 % (3) and 14.5 % (4) slopes. Curves are exponential functions fitted to the data ( $0.35 \leq R^2 \leq 0.56$ ). All the regressions are significant at the 0.01 level.

DISCUSSION

Although several studies have shown that life history traits, and in particular mortality rate, vary predictably with size or age, there are few studies describing size or age dependent mortality patterns and their causal factors in long-lived plant

species. As a rule mortality in natural populations is concentrated in the smaller individuals or is constant throughout the life cycle (HARPER, 1977; ANTONOVICS & LEVIN, 1980). *E. timotensis* seems to be a case in which the probability of mortality is higher at the beginning and towards the end of the plant's lifespan. SARUKAN (1980) found in three tropical palm species mortality patterns similar to those observed in *E. timotensis*, however, he attributed the drop of survivorship at older ages to an artifact of the small sample size.

Most studies of sources of mortality have concentrated the analyses on the early prereproductive stage, not only because it is generally the most critical stage in the dynamics of a population, but also because it is perhaps the only stage where manipulative experiments, such as transplants, can be easily performed (TURNER *et al.*, 1966). Soil water deficit is one of the major sources of mortality in seedlings (COOK, 1980; JORDAN & NOBEL, 1981). The greatest susceptibility occurs shortly after germination when seedlings switch from internal to external sources of moisture. Grazing and pathogens are considered to be the other most important sources of mortality (AUGSPURGER & KELLY, 1984). In the majority of these studies some sort of correlation analysis in which an increase in mortality rate was quantitatively or qualitatively associated with a decrease in soil moisture or an increase in the intensity of the grazing effect was used. This approach, however, does not establish strong causal relationships between a possible source of mortality and the actual death of the plant, unless the mechanism that associates both terms of the relationship is well known. The two periods of high mortality risk observed in *E. timotensis* that occur when plants are experiencing different environmental stresses offer an opportunity to investigate the connections between physiological functioning and life history traits (mortality). Such a task has been theoretically proposed by MCGRAW & WULFF (1983).

### *Plant Water Balance*

The ability of caulescent giant rosette plants to dampen diurnal fluctuations in plant water potential seems to be associated with the decreasing risk of mortality during the early part of the lifespan. For example, 20-30 cm tall plants with very low pith volume/leaf area were very responsive to changes in evaporative demand and soil water availability (fig. 2). There was a wet to dry season difference in  $\Psi_L^{\min}$  of about 1 MPa for this size class. Tall caulescent individuals, however, with much higher pith water storage capacity and a more extensive root system exhibited a much smaller change in  $\Psi_L^{\min}$ . The leaf water potentials observed in some small individuals during the dry season were below the  $-1.4$  to  $-1.5$  MPa turgor loss point. Irreversible wilting in younger individuals of *E. timotensis* is fairly common in dry years. The  $\Psi_L$  observed in small plants during the peak of the dry season would produce irreversible damage in leaf tissues (77 % RWC =  $-1.6$  MPa) (figs. 4 and 5).

In a previous work (GOLDSTEIN *et al.*, 1984) we suggested that the high pith water storage capacity in tall *Espeletia* plants is a response to cold tropical environments where frequent subfreezing temperatures may reduce water uptake during the early morning hours. Results of figures 2 and 3 suggest that high pith storage capacity may also fulfill some role in the water relations of giant rosette plants on a seasonal basis. Under conditions of low soil water potential, high internal water storage capacity not only delays the  $\Psi_L$  decrease at mid-day by supplying water to the transpiring rosette, but also may aid the afternoon recovery before low nighttime soil temperatures affect water uptake and retard the establishment of water potential

equilibrium between soil and plant. The recovery is facilitated because water storage keeps diurnal  $\Psi_L$  fluctuations small.

Pressure-volume curve analyses showed that turgor loss points in leaves of individuals of different ages were nearly identical indicating that *E. timotensis* has little capacity to osmotically adjust. The leaves begin to experience irreversible damage at about incipient plasmolysis suggesting a trade-off between a stable water balance provided by high relative water storage capacity and resulting low dehydration tolerance. This represents an important constraint when water availability is limited by low soil moisture. We were surprised by this lack of ability of smaller plants to adopt a more negative turgor loss point and osmotic potential at full saturation, that is, properties of the leaf tissue that would increase tolerance of daily and seasonal water deficits without irreversible damage or wilting. It seems that selection in tropical caulescent rosette plants may have favored rapid growth to "escape" from frequent water stress conditions by rapidly increasing the volume of tissues with high water storage capacity, such as the pith, instead of favoring physiological characteristics of more slow growing species adapted to withstand longer periods of low soil water availability. This last physiological syndrome is represented in desert paramos by more tolerant plant species such as the shrub *Hypericum laricifolium*. Our results suggest that the high risk of mortality observed in small *E. timotensis* plants is a consequence of their small water storage capacity and their inability to osmotically adjust to periods of low soil water availability.

SMITH (1981) found that mortality decreased with increasing plant size in juvenile individuals of *E. schultzii*, another conspicuous caulescent rosette species from the high tropical Andes. He also observed that the probability of mortality in juveniles of *E. schultzii* and *E. lutescens* at 4,200 m was greatest during the dry season and that extensive leaf wilting even caused a transient reduction in plant height. Although mortality in young plants was not attributed to drought effects it was observed that herbivory and insect damage were rare on juveniles.

### *Frost Resistance*

Individuals of *E. timotensis* seem to be well protected against the effects of sub-freezing temperatures. Leaves of smaller individuals normally exposed to lower minimum temperatures near the soil surface tended to supercool more than those of taller individuals (table I). The degree of supercooling observed in leaves of small plants was considerable and coincided with values reported for *E. semiglobulata* (LARCHER & WAGNER, 1976) and other pronounced supercooling freezing avoiders (LEVITT, 1980). Leaf temperatures below the temperature at which the exotherms occurred were never measured in the high paramos (AZOCAR & MONASTERIO, 1980; RADA, 1983) and frost periods will never last more than a few hours. It thus seems unlikely that any of the mortality pattern observed can be attributed to frost damage.

### *Mortality in the Largest Size Classes*

Symptoms of senescence involving a breakdown in the efficiency of functioning were not apparent in the oldest erect individuals. Fecundity, for example, which may be considered a measure of plant vigor tends to increase with plant height (MONASTERIO, 1984). Pith water storage also increases with plant height (fig. 2). This implies that more water is available for replacing transpirational losses and dampening daily fluctuations in leaf water potential of tall plants. Tall individuals are severely affected

by soil movement, however, particularly on steep slopes (fig. 6). The relatively small root system (less than 5 % of total plant biomass is allocated into roots) evidently represents a very weak anchorage to counterbalance the strong soil particle displacement produced by solifluction processes. Once an individual has completely fallen over, a portion of the root system will be left exposed and possibly broken thus interfering with water and nutrient uptake. The stem lying on the soil surface is exposed to lower minimum temperatures and as a consequence the pith may be less effective as a water reservoir than the pith of protected erect stems. All of these factors may alter the water and energy relations of the largest individuals eventually causing its death.

### ACKNOWLEDGMENTS

We thank Dr. O. SOLBRIG, Dr. P. RUNDEL and BILL PFITSCH for their comments on the manuscript and Dr M. LAMOTTE for suggesting procedures to evaluate soil movement/risk of plant death relationships. Carlos ESTRADA and Oscar ZABALA provided invaluable assistance during the field and laboratory work. This research was supported by the Universidad de los Andes (CDCH) Grant no. C-180-81.

### REFERENCES

- ANTONOVICS J. & LEVIN D. A., 1980. — The ecological and genetic consequences of density-dependent regulation in plants. *Ann. Rev. Ecol. Syst.*, **11**, 411-452.
- ARISTEGUIETA L., 1964. — *Flora de Venezuela, Compositae*. Instituto Botanico, Caracas, 483 p.
- AUGSPURGER C. K. & KELLY C. K., 1984. — Pathogen mortality of tropical tree seedlings: experimental studies of the effects of dispersal distance, seedling density and light conditions. *Ecologia*, **61**, 211-217.
- AZOCAR A. & MONASTERIO M., 1980. — Características ecológicas del clima en el paramo de Mucubaji. In: M. MONASTERIO, ed., *Estudios ecológicos en los paramos andinos*. Ediciones de la Universidad de los Andes, Merida, p. 207-223.
- COE J. M., 1967. — *The ecology of the alpine zone of Mount Kenya*. Junk, The Hague, 136 p.
- COOK R. E., 1980. — Germination and size-dependent mortality in *Viola blanda*. *Ecologia*, **47**, 115-117.
- ESTRADA C., 1984. — Dinámica del crecimiento y reproducción de *Espeletia* en el paramo desértico. M. S. Thesis, Universidad de los Andes, Merida, 181 p.
- GOLDSTEIN G. & MEINZER F., 1983. — Influence of insulating dead leaves and low temperatures on water balance in an andean giant rosette plant. *Plant, Cell and 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 and Environ*, **7**, 179-186.
- HARPER J. L., 1977. — *Population biology of plants*. Academic Press, London, 892 p.
- HEDBERG O., 1964. — Features of afroalpine plant ecology. *Acta Phytogeographica Suecica*, **49**, 1-144.
- HETT J. M. & LOUCKS O. L., 1976. — Age structure models of balsam fir and eastern hemlock. *J. Ecol.*, **64**, 1029-1044.
- JORDAN P. W. & NOBEL P. S., 1981. — Seedling establishment of *Ferocactus acanthodes* in relation to drought. *Ecology*, **62**, 901-906.
- KAUFMANN M. R., 1977. — Soil temperature and drying cycle effects on water relations of *Pinus radiata*. *Canadian J. of Botany*, **55**, 2413-2418.
- LARCHER W. & WAGNER J., 1976. — Temperaturgrenzen der CO<sub>2</sub>-Aufnahme und Temperaturresistenz der Blätter von Gebirgspflanzen im vegetationsaktiven Zustand. *Ecolog. Plant.*, **11**, 361-374.
- LEVITT J., 1980. — *Responses of plants to environmental stresses. Vol. 1, Chilling, freezing and high temperatures stresses*. Academic Press, New York, 422 p.
- MCGRAW J. B. & WULFF R. D., 1983. — The study of plant growth: a link between the physiological ecology and population biology of plants. *J. Theor. Biol.*, **103**, 21-28.
- MALAGON D., 1982. — *Evolucion de los suelos en el Paramo Andino*. CIDIAT, Merida, 222 p.

- MEINZER F. & GOLDSTEIN G., 1985. — Adaptations for water and thermal balance in Andean rosette plants. In: T. GIVNISH, ed., *On the economy of plant form and function*. Cambridge University Press (*in press*).
- MONASTERIO M., 1984. — Adaptacion de especies al tropico frio: el caso *Espeletia* en el paramo desertico. Tesis de ascenso, Universidad de los Andes, Merida, 109 p.
- OPPENHEIMER H. R., 1963. — Zur Kenntnis kritischer Wassersättigungsdefizite in Blättern und ihrer Bestimmung. *Planta*, **60**, 51-69.
- PEARL R. & MINER J. R., 1935. — Experimental studies on the duration of life. XIV. The comparative mortality of certain lower organisms. *Q. Rev. Biol.*, **10**, 67-79.
- QUAMME H., STUSHNOFF C. & WEISER C., 1972. — The relationship of exotherms to cold injury in apple stem tissues. *J. Amer. Soc. Hort. Sci.*, **97**, 608-613.
- RADA F., 1983. — Resistencia a temperaturas congelantes en *Polylepis sericea* y *Espeletia spicata*. M. S. Thesis, Universidad de los Andes, Merida, 181 p.
- RUNNING S. W. & REID F. C., 1980. — Soil temperature influences of *Pinus contorta* seedlings. *Plant Physiol.*, **65**, 635-640.
- RYCHNOVSKA M., 1963. — Study of the reversibility of the water saturation deficit as one of the methods of causal phytogeography. *Biol. Plant.*, **5**, 173-178.
- SARMIENTO G., 1984. — Ecologically crucial features of climate in high tropical mountains. In: M. MONASTERIO & F. VUILLEUMIER, eds., *Adaptations and Evolution in Biota of High Tropical Montane Ecosystems*. Springer, Berlin (*in press*).
- SARUKHAN J., 1980. — Demographic problems in tropical system. In: O. T. SOLBRIG, ed., *Demography and Evolution in Plant Populations*. University of California Press, Berkeley & Los Angeles, 161-188.
- SCHUBERT C., 1976. — Glaciación y morfología periglacial en los Andes venezolanos noroccidentales. *Bol. Soc. Venez. Ciencias Nat.*, **32**, 149-178.
- SLAVIK B., 1974. — *Methods of Studying Plant Water Relations*. Ecological studies 9, Springer, Berlin, 449 p.
- SMITH A. P., 1974. — *Population dynamics and life form of Espeletia in the Venezuelan Andes*. Ph. D. dissertation, Duke University, Durham, North Carolina, 240 p.
- SMITH A. P., 1981. — Growth and population dynamics of *Espeletia (Compositae)* in the Venezuelan Andes. *Smithsonian contributions to botany* # 48, Smithsonian Institution Press, Washington DC., 45 p.
- TROLL C., 1968. — The cordilleras of the tropical Americas. Aspects of climate, Phytogeographical and agrarian ecology. In: C. TROLL, ed., *Geo-Ecology of the Mountain Regions of the Tropical Americas*. Proc. UNESCO Symposium-Mexico, 13-56.
- TURNER R. M., ALCORN S. M., OLIN G. & BOOTH J. A., 1966. — The influence of shade, soil and water on Saguaro seedling establishment. *Bot. Gaz.*, **127**, 95-102.
- TYREE M. T. & HAMMEL T. H., 1972. — The measurement of the turgor pressure and the water relations of plants by the pressure-bomb technique. *J. Exp. Botany*, **23**, 267-282.
- TYREE M. T. & RICHTER H., 1981. — Alternate methods of analysing water potential isotherms: some cautions and clarifications. I. The impact of nonideality and of some experimental errors. *J. Exp. Botany*, **32**, 643-653.
- TYREE M. T. & RICHTER H., 1982. — Alternate methods of analysing water potential isotherms: some cautions and clarifications. II. Curvilinearity in water potential isotherms. *Can. J. Botany*, **60**, 911-916.