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ABSTRACT

The production of leaves, inflorescences, and growth rates were measured during 1985 for 547 plants of *Espeletia barclayana*, a giant rosette species in the high Andes of Colombia. There were differences in leaf production between individuals of different sizes, with a maximum for plants 61–90 cm in height (27.9 leaves yr⁻¹) and a minimum for plants less than 30 cm (5.1 leaves yr⁻¹). For plants more than 61 cm in height there was a minimum in leaf production during February, coinciding with the minimum in rainfall, and also during June coinciding with a decrease in rainfall, low temperature, and a peak in fog and condensation. There was a great variation in the number of reproductive plants from one year to the next. There was also a positive relationship between total production of inflorescences at the population level and annual rainfall. Trunk growth rates ranged from 1.1 cm yr⁻¹ for plants less than 30 cm in height to 3.8 cm yr⁻¹ for plants 61–90 cm in height. The tallest plant in the population (150 cm) was about 93 yr old. The results of this study suggest that *E. barclayana* is subject to seasonal drought and that the variation in water supply and temperature have an effect on leaf production and probably on growth rates. Because of the very slow growth rates of *E. barclayana*, it will take a considerable time to recover the actual population and vegetation structure of those areas which have been turned into agricultural fields.

RESUMEN

La producción de hojas e inflorescencias y las tasas de crecimiento de 547 individuos de *Espeletia barclayana*, una roseta gigante de los Andes de Colombia, fueron medidas durante 1985. Hubo diferencias en la producción de hojas entre individuos de diferentes clases de tamaño, con un máximo para plantas entre 61–90 cm de altura (27.9 hojas año⁻¹) y un mínimo para plantas de menos de 30 cm (5.1 hojas año⁻¹). Para plantas de más de 61 cm de altura hubo un mínimo en la producción de hojas durante febrero, coincidiendo con un mínimo en las lluvias y también durante junio, coincidiendo con una disminución de las lluvias y la temperatura, y un máximo de neblina y condensación. Hubo una gran variación en el número de individuos reproductivos de un año para otro, y una correlación positiva entre la producción total de inflorescencias a nivel de la población y la lluvia anual. Las tasas de crecimiento de troncos variaron entre 1.1 cm año⁻¹ para plantas de menos de 30 cm de altura y 3.8 cm año⁻¹ para plantas 61–90 cm de altura. El individuo más alto de la población (150 cm) tenía aproximadamente 93 años. Los resultados de este estudio sugieren que *E. barclayana* esta sujeta a sequía estacional y que las variaciones en los aportes de agua y temperatura tienen efecto sobre las tasas de producción de hojas y probablemente sobre las tasas de crecimiento. Debido al lento crecimeinto de *E. barclayana*, tomará muchisimo tiempo en recuperar la estructura poblacional y de la vegetación de estas areas que estan siendo convertidas a la agricultura.

THE ENDEMIC ROSETTES of the Espeletiinae (Helian-theae, Compositae) occur in the Andes of Colombia, Venezuela, and northern Ecuador, and are the most characteristic element of the paramos (Cuatrecasas 1968, 1979). The majority of the species occur at elevations between 2700 and 4600 m and have caulescent rosettes. The trunks are covered with a dense layer of old leaves (marcescent leaves), apparently reducing freezing damage to the stem (Smith 1979, Goldstein & Meinzer 1983). Leaves are densely pubescent and this seems to increase bound-ary layer thickness and resistance to convective and latent heat transfer, thus increasing leaf temperature without increasing transpiration (Meinzer & Gold-stein 1985). Leaves are arranged spirally around the meristem forming a huge rosette with a parabolic geometry probably improving capture and retention of solar radiation, thus increasing leaf temperature (Smith 1974, Meinzer *et al.* 1985).

In high altitude, neotropical environments there is strong daily variation in air temperature, and there is little seasonal variation in the mean monthly tem-perature (Troll 1968, Monasterio 1979, Azocar & Monasterio 1979, Monasterio & Reyes 1979, Sar-miento 1986). Above the upper limit of forest growth, annual rainfall varies between 700 and

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3000 mm, resulting in dry paramos on leeward slopes (dry bunchgrass paramo) and wet paramos on windward slopes (humid bamboo paramos) according to Cleef (1981). Paramos experience a rainfall seasonality having one or two rainy seasons (Guhl 1974, Monasterio 1979, Smith 1981). Although fog is common during the wet season (Smith 1972, 1974) and may also be common during the dry season (Smith & Young 1987), there are no systematic records of this important environmental factor in paramo vegetation.

In contrast to the knowledge of the adaptive significance of morphology and physiology of rosette plants in relation to climatic conditions, there is little information on the effect of climate on plant growth (Smith 1981, Orozco 1986), reproduction and population dynamics (Monasterio 1979, Smith 1981, Estrada & Monasterio 1988). In this study we would like to answer the following questions: What are the effects of seasonal variations in rainfall on leaf production for *E. barclayana*? Are the effects of seasonality of rainfall on leaf production the same for all individuals in the population? What are the growth rates of individuals of different size classes, and what are the ages of these plants? What other climatic factors may control the production of leaves and inflorescences in this species?

MATERIALS AND METHODS

THE SPECIES AND THE STUDY SITE.—*Espeletia barclayana* is a caulescent rosette endemic of the Zipaquira-Neusa region, northwest of Bogota (Cuatrecasas 1986). The study was carried out near Lagua Verde, Paramo de Guerrero (3540 m), in a site described as a "lower *Calamagrostis effusa* bunchgrass paramo with Espeletia" (Cleef 1981). The site was on a gentle slope (10°) with no permanent or seasonal flooding. A detailed vegetation map of this paramo (1:25,000) was published by Bekker and Cleef (1990). At this site, in addition to *E. barclayana*, *E. argenta*, *E. chocontana*, and *Espeletiopsis corymbosa* were also present. We chose to study *E. barclayana* because it was one of the most abundant species in this paramo.

In a meteorological station near the study site (Neusa watershed at 3100 m), mean annual rainfall (1956–1987) was 985 mm. Rainfall was distributed bimodally, with peaks in April (131 mm) and October (125 mm). There was a dry season between December and March when pan evaporation was higher than rainfall (Fig. 1). Mean annual sunshine was 1383 hr, with a maximum during January (176 hr month⁻¹) and a minimum during May and June (88 hr month⁻¹). At higher altitudes there were only short term climatic records. At 3465 m (Hato 4 rainfall station) mean annual rainfall (1973–1977) was 1314 mm with the same bimodal distribution that occurs for the Neusa watershed. Although there were no records of evaporation at the Hato 4 rainfall station, the dry season was likely to be shorter than that of Neusa because of the lower temperatures and thus lower evaporative demands. If the vertical temperature gradient is $0.55°C/100$ m (Guhl 1968) and mean annual temperature at 3000 m (Pantano Redondo) is 8.9°C (Molano 1983), mean annual temperature at Laguna Verde would be around 6.0°C. Temperatures below 0°C occur between December and March (Beekman & Verweij 1987).

For this study (1985) rainfall was measured with a locally constructed rain gauge (9.5 cm in diameter). "Occult precipitation" (fog + condensation) was measured with a "fog catcher." Fog catchers were constructed with plastic mesh (26.0 × 5.5 cm, of which 36% was interception surface = 51.5 cm²) placed on top of funnels 9.5 cm in diameter. In a different study fog inputs in elfin cloud forests were calculated in mm after applying a conversion factor of 318 cm³ (fog catcher) to 1 mm (throughfall) as described in Cavelier and Goldstein (1989). In the present study, occult precipitation was calculated as the difference between the water volume in the rain gauge and in the fog catcher (cm³), divided by the area of interception. Thus, the absolute values of fog may not be related to the absolute inputs of water to the vegetation.

According to Molano (1983), soils are acid (pH = 4.9–5.5), low in "available" phosphorus (Bray II = <5.0 Kg P/ha), total nitrogen (0.33–1.48%), exchangeable bases (total bases = 1.8–3.7 meq/100 g), and high in organic carbon (12.5–22.9%) and cation exchange capacity (18.8–25.4 meq/100 g). Soils were derived from sandstones of the Guadalupe Formation (sedimentary rocks of the Lower Tertiary) and periodic ash supply from the volcanoes of the Cordillera Central (Cleef 1981).

ENUMERATION OF PLOTS AND INDIVIDUALS.—Fifteen plots, 5 m by 5 m, were permanently marked along three transects. The distance between plots varied between 1 and 9 m (a stratified random design). For each plant, total height, trunk height, and rosette diameter were measured at the beginning of the study (October 1984). To measure leaf production, a nylon ring was placed around the younger leaves in the inner rosette, and the number of leaves inside the ring were counted every month. Leaf production was calculated for five size classes be-

NEUSA   STATION   3100 m
LOC: 05° 09'N , 73° 58'W
MEAN   ANNUAL   RAINFALL = 985 mm
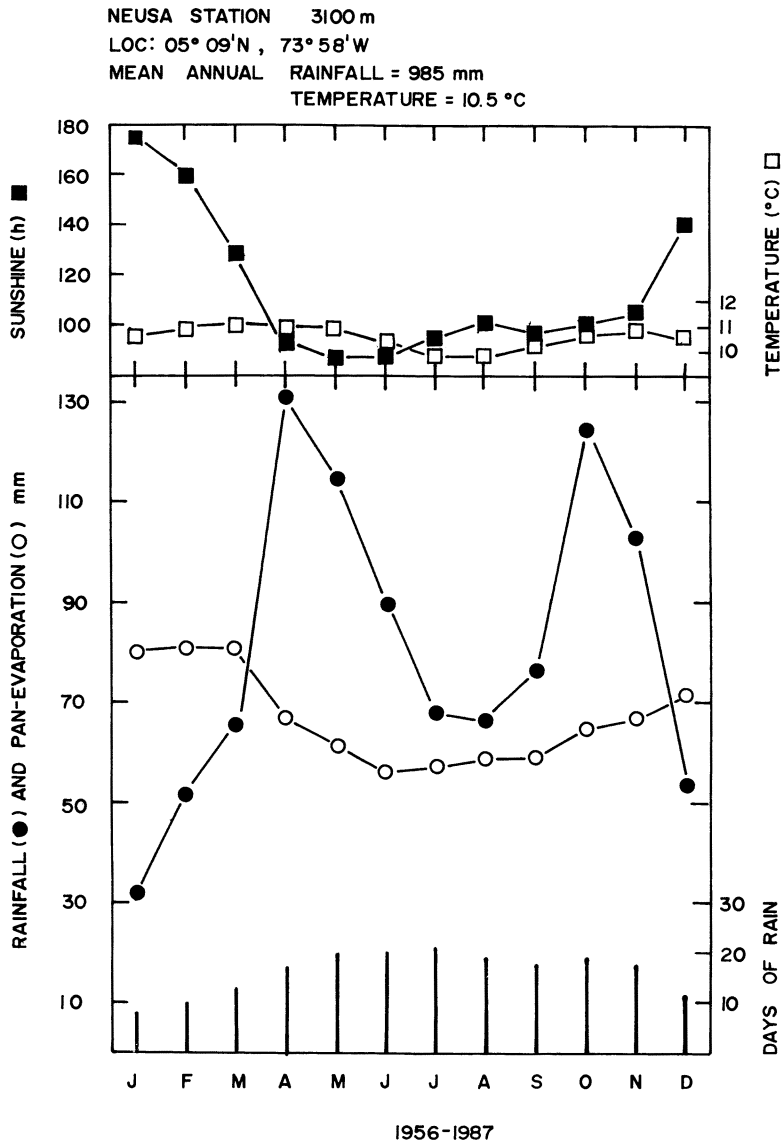   TEMPERATURE = 10.5 °C

FIGURE 1.   Mean sunshine duration, monthly temperature, rainfall, pan evaporation, and rainy days at Neusa weather station (1956–1987).

tween February and December 1985. The size classes were <30, 31–60, 61–90, 91–120, and 121–150 cm. For individuals <30 cm in height, leaf production rates were calculated for subclasses of 5 cm, because there were important morphological differences among individuals of this size class (*i.e.,* individuals with and without trunks). The annual growth rate for each size class was calculated as the difference in total height measured at the tip of the tallest leaf, between 7 October 1984 and 17 No-

vember 1985. Age was estimated from the relationship between size and growth rates. In juveniles (<30 cm), age was also estimated for six subclasses of 5 cm.

The number of inflorescence stalks were measured for each individual during 1985 and 1986. Since inflorescence stalks remained attached to the trunk at different heights and are in different stages of decomposition, it was also possible to count the
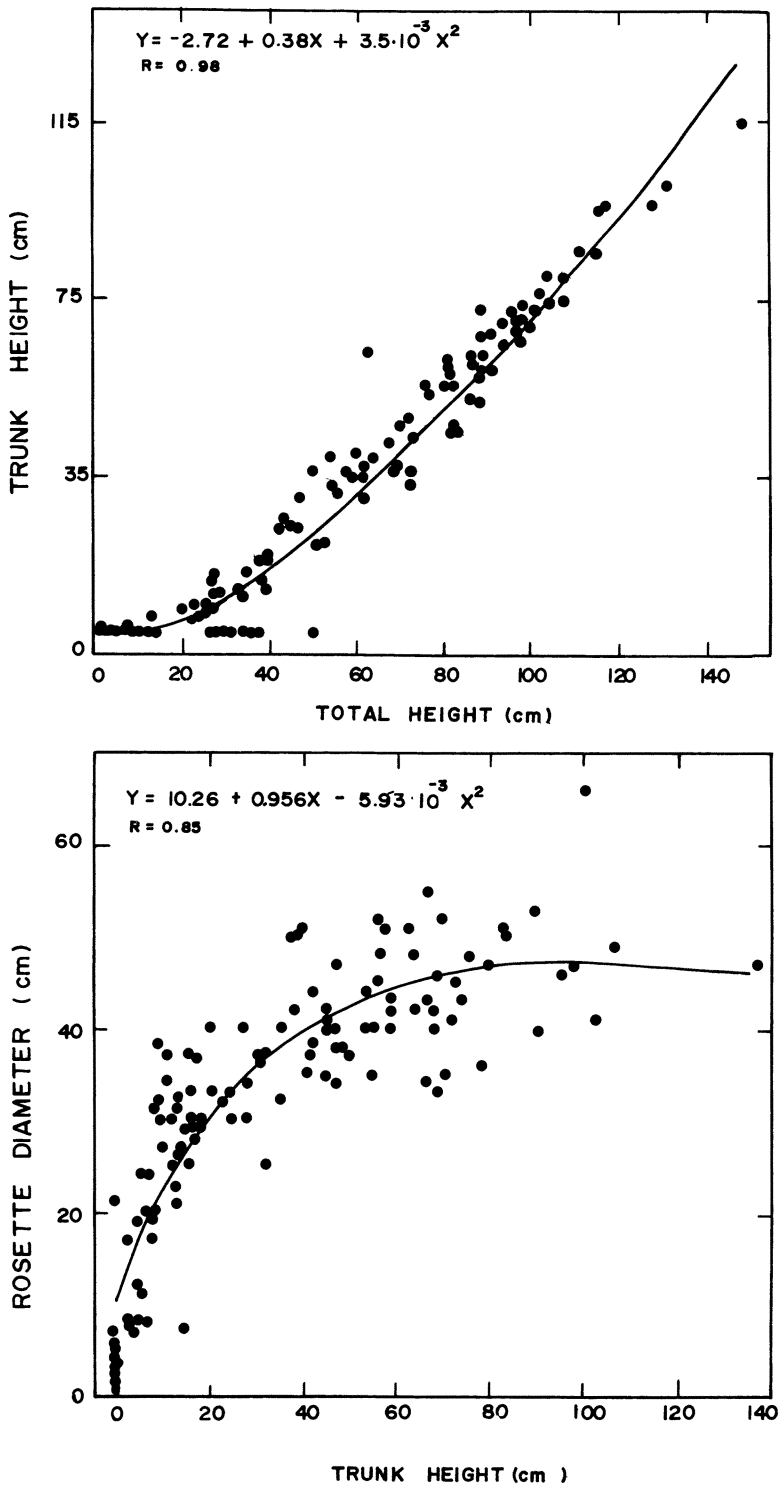
FIGURE 2. In the upper panel, relationship between total plant height and trunk height. In the lower panel, relationship between trunk height and rosette diameter. Each point represents one plant in the population of *E. barclayana* studied in the Zipaquira-Neusa region (Colombia).
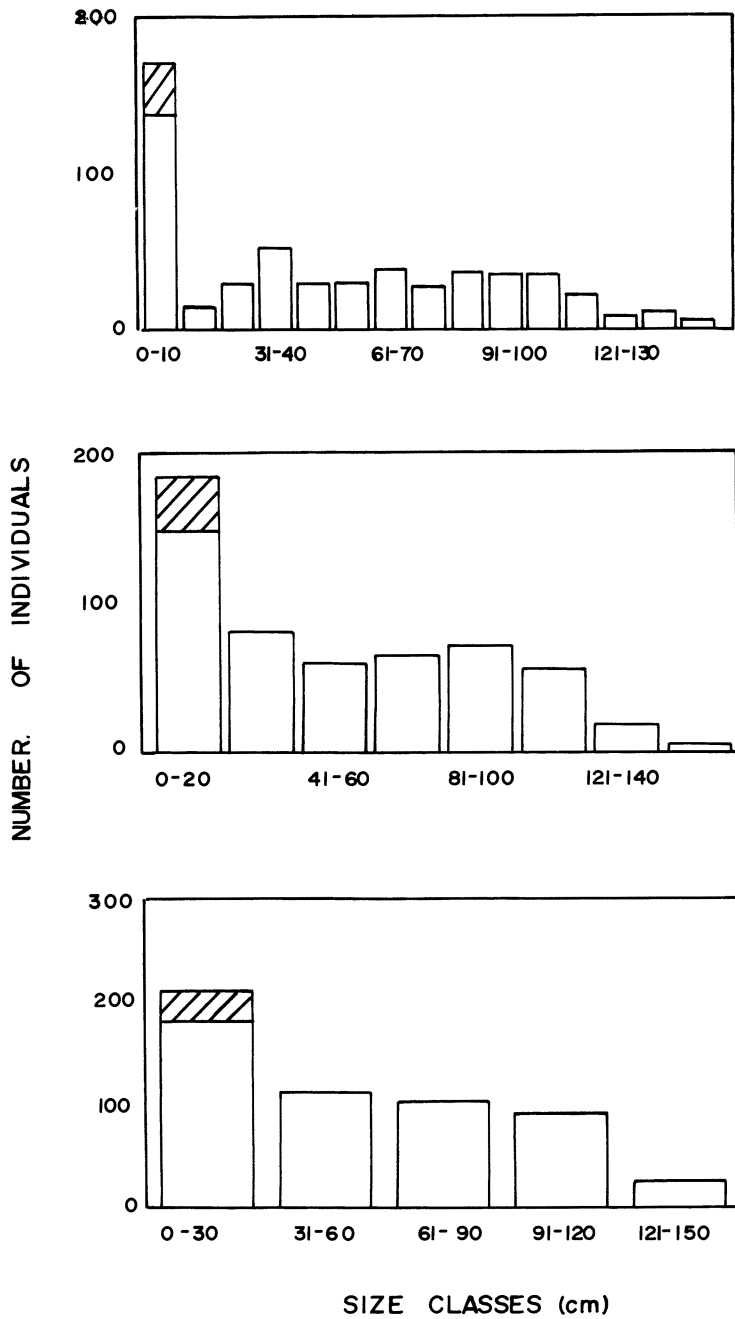
FIGURE 3. Size (total height) class distribution of rosettes of *Espeletia barclayana* using classes of 10, 20, and 30 cm. The dashed areas represent the individuals that died between February and December 1985.
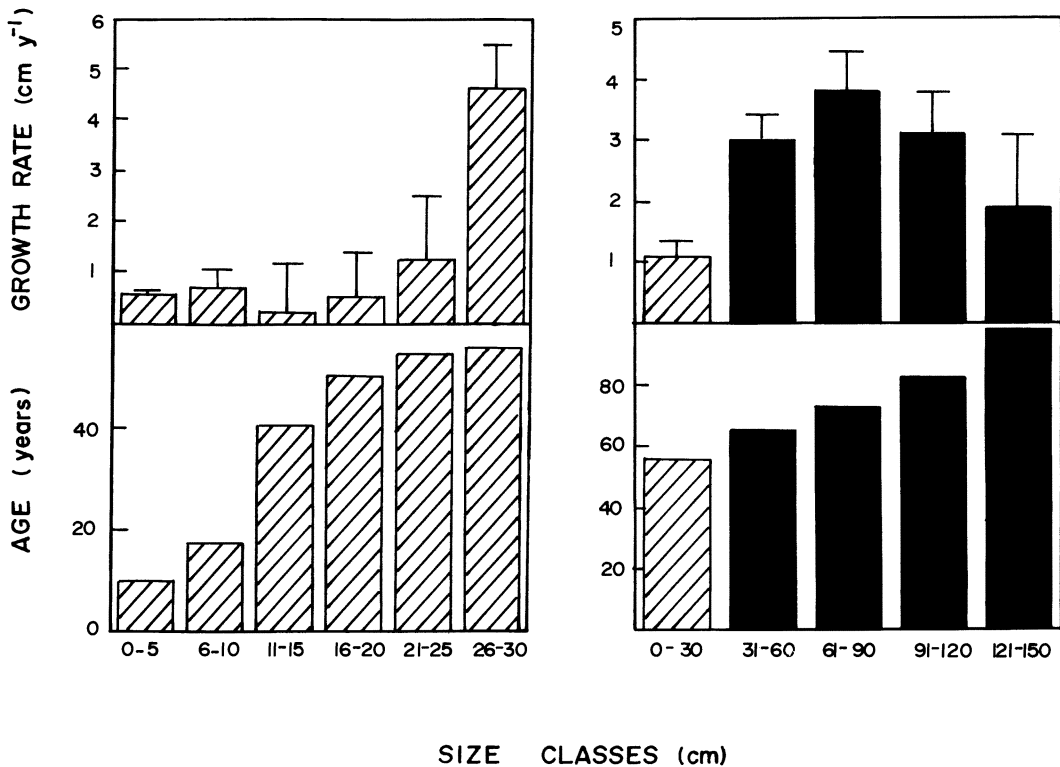
FIGURE 4.   Mean annual growth rates (±1 SEM) and age for juveniles (dash bars) and adults (black bars) of *Espeletia barclayana* in Paramo de Guerrero. Size classes of 5 cm for juveniles, and of 30 cm for adults.

number of reproductive individuals that reproduced in 1982, 1983, and 1984.

STATISTICAL ANALYSES.—Patterns of plant growth were determined by using regression analysis on size characteristics (heights and diameter) of the 547 individuals. The differences in leaf production between size classes and months were analyzed with a two-way ANOVA (SAS 1984).

RESULTS

MORPHOMETRICS.—Total plant and trunk height were positively correlated ($r = 0.98$; $P < 0.01$) as shown in Figure 2. On average, individuals 15 cm or less in total height had no trunk, although there were plants up to 50 cm in which the total plant height was the rosette height. There was a correlation between height and diameter of the rosette (not shown) and between trunk height and rosette diameter ($r = 0.85$; $P < 0.01$; Fig. 2). The shape (curve) of this relationship suggests that for plants less than 30 cm, increments in rosette diameter were greater than increments in trunk height, in contrast to plants 31-60 cm.

POPULATION STRUCTURE AND GROWTH RATES.—There were 547 individual *E. barclayana* plants in the 15 plots (14,586 plants ha^{-1}). The distribution of size classes showed a larger number of the small sizes and a decline in numbers with increasing size. When the individuals were regrouped in classes of 10 cm, there were very few individuals in the 11–20 and 21–30 cm classes, suggesting that recruitment can be very low during long periods (Fig. 3).

Growth rates during 1985 were higher for plants 61–90 cm tall (3.8 ± 0.63 cm yr^{-1}, mean ± SE, $N = 107$) than for plants less than 30 cm tall (1.1 ± 0.27 cm yr^{-1}, $N = 139$). There were no statistically significant differences in the growth rates of plants 31–60 cm (3.0 ± 0.40 cm yr^{-1}, $N = 117$), 61–90 cm (3.8 ± 0.63 cm yr^{-1}, $N = 107$), and 91–120 cm (3.1 ± 0.67 cm yr^{-1}, $N = 78$). For small individuals (<30 cm), growth rates were significantly higher for plants 26–30 cm (4.6 ± 0.84 cm yr^{-1}, $N = 15$), than for plants less than 25 cm
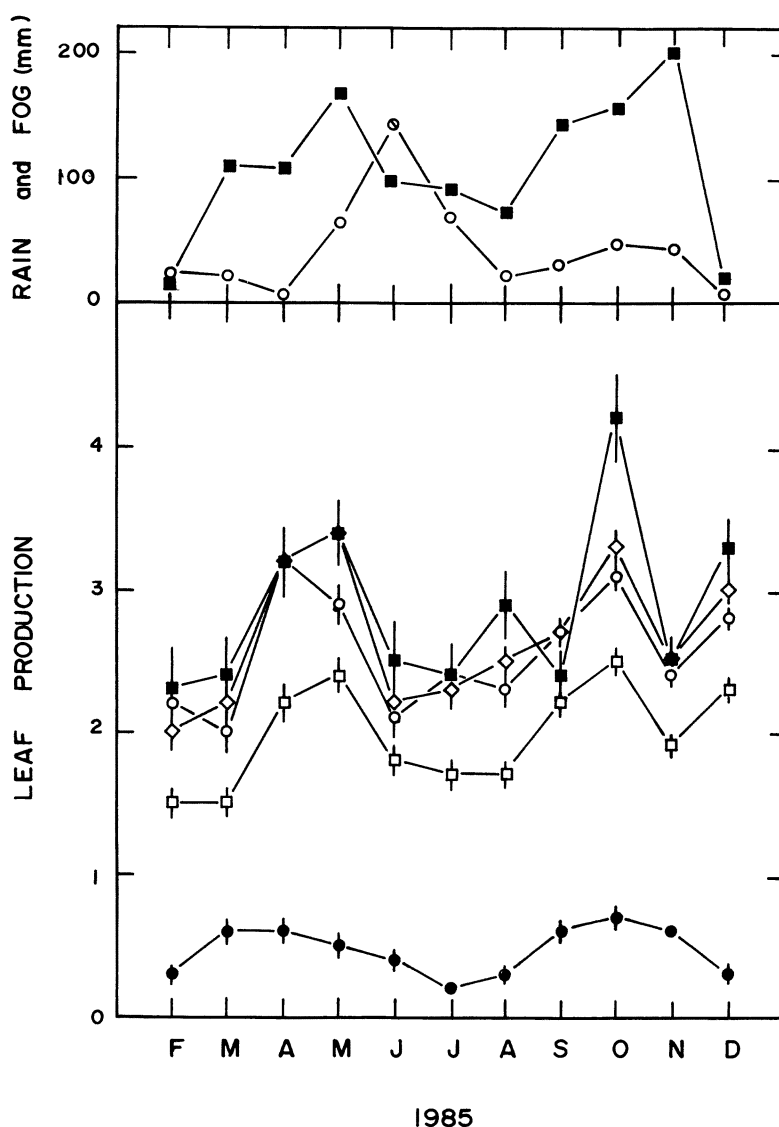
FIGURE 5. In the upper panel, rainfall (■) and fog + condensation (O) during 1985 in Paramo de Guerrero. In the lower panel, mean monthly leaf production (± 1 SE) for plant heights of <30 cm (●), 31–60 cm (□), 61–90 (O) 91–120 cm (◇), and 121–150 cm (■). For all size classes there were significant seasonal variations in leaf production ($P < 0.05$). Leaf production was significantly different between plants <30 cm and 31–60 cm tall, and between plants 31–60 and 61–90 cm ($P < 0.05$) tall. There were no significant differences between leaf production in plants 61–90, 91–120, and 121–150 cm tall.

that grew between 0.2 and 1.2 cm yr^{-1} as shown in Figure 4.

Age was estimated from the relationship between size and growth rates (Fig. 4). On average, plants 30 cm in height were about 55 yr old, while the tallest individual in the population (150 cm) was approximately 93 yr old.

LEAF PRODUCTION.—Leaf production was significantly different between size classes (Fig. 5). Small individuals (<30 cm) produced fewer leaves (5.1 $\pm$ 0.25 leaves yr^{-1}) than individuals 31–60 cm tall (21.7 $\pm$ 0.61 leaves yr^{-1}), and these, less than individuals 61–90 cm tall (27.9 $\pm$ 2.9 leaves yr^{-1}). Leaf production was not significantly different be-

TABLE 1.   *Leaf production in leaves per year, and dry weight per year, leaf duration (Ld), leaves per rosette, turnover (leaf production/leaves per rosette = T), and growth rates for species of* Espeletia *and* Senecio. *Data for* E. schultzii, E. lutescens, *and* E. humbertii *(Smith 1981), for* Senecio keniodendron *in Hedberg (1969), Beck* et al. *(1980, 1984) and Smith and Young (1982), and for* E. lutescens[b], *Espeletia* spicata, *and* E. moritziana *in Monasterio (1986). Rain value for* E. barclayana *includes occult precipitation (fog + condensation).*

Species	Alt. (m)	Rain (mm)	Temp. (°C)	Leaves (n) dry wt (g) Year		Ld (da)	Leaves Rosette (m)	T	Growth (cm/yr)
E. barclayana	3500	1785	5.6	—	—	—	—	—	—
Size 000–030 cm				5	8	—	—	—	1.1
031–060 cm				22	61	323	17	0.81	3.0
061–090 cm				28	81	432	33	1.19	3.8
091–120 cm				29	87	543	36	1.25	3.1
121–150 cm				31	99	467	39	1.26	1.8
E. schultzii	3000	1304	9.6[a]	204	—	—	—	—	2.0
Slope base				119	236	—	74	0.65	—
Windward side				96	177	—	68	0.70	—
Ridge				88	163	—	66	0.75	—
Leeward side				81	143	—	58	0.71	—
	3600	1118	5.0[a]	125	210	229	70	0.56	1.2
	4200	980	2.0[a]	72	172	394	77	1.00	1.1
E. lutescens	4200	980	2.0[a]	64	231	543	95	1.49	1.5
	4200[b]			120	832[c]	720	240	2.00	1.5
E. spicata	4200			370	—	390	590	1.59	2.0
E. moritziana	4200			264[d]	—	360	264	1.00	1.5
E. humbertii	3500			10	25	489	13	1.31	—
S. keniodendron	4180			1154	—	—	—	2.5–4.5[e]	

[a] Soil temperatures at −30 cm (Schubert 1979).
[b] *E. timotensis* in Monasterio (1986).
[c] Calculated as half of the standing leaf biomass.
[d] Estimated from turnover rates.
[e] 2.5–3.0 cm yr⁻¹ for unbranched plants, 5.3 for plants having flowered once, 4.5 for plants having flowered twice and 4.0 for plants having flowered 3 or more times.

tween individuals 61–90, 91–120 (29.1 ± 0.53) and 121–150 (31.1 ± 1.11) cm tall. Production of leaf biomass per plant increased from 8.0 g yr⁻¹ in individuals <30 cm in height to 99 g yr⁻¹ in individuals 121–150 cm tall (Table 1). Total leaf biomass production at the population level, calculated with the number of plants per size class (5586 individuals ha⁻¹ for <30 cm size class, 2926 for 31–60 cm, 2660 for 61–90, 2394 for 91–120 and 665 for 212–150 cm), the number of leaves produced, and the leaf mass, was around 710 kg ha⁻¹ yr⁻¹, with 60 percent of this value produced by individuals 61 to 120 cm tall.

There was substantial seasonal variation in leaf production (Fig. 5). While for the smallest size class (<30 cm) leaf production varied from 0.24 to 0.74 leaves month⁻¹, a 3 fold change, leaf production in plants 31–150 cm tall varied on average from 2.0 to 3.3 leaves month⁻¹, a 1.7 fold change. Production of leaves in plants 60 cm and over was low during

February coinciding with a minimum in rainfall (42 mm month⁻¹), and also during June coinciding with the second dry season and with the maximum of occult precipitation.

REPRODUCTION.—Individuals less than 30 cm tall showed no inflorescence stalks. Most of the reproductive individuals were in the 61–90 cm size class, and there was a great variation in the number of reproductive individuals from year to year (Fig. 6). When the number of reproductive plants was high (*e.g.*, 1986) the average number of inflorescence stalks per plant was higher for tall (121–150 cm = 5.6 inflorescences plant⁻¹) than for small individuals (30–60 cm = 3.8 inflorescences plant⁻¹). In contrast, during years when few individuals flowered (*e.g.*, 1985) individuals 61–90 cm tall produced more inflorescence stalks than taller or smaller individuals (Fig. 6).

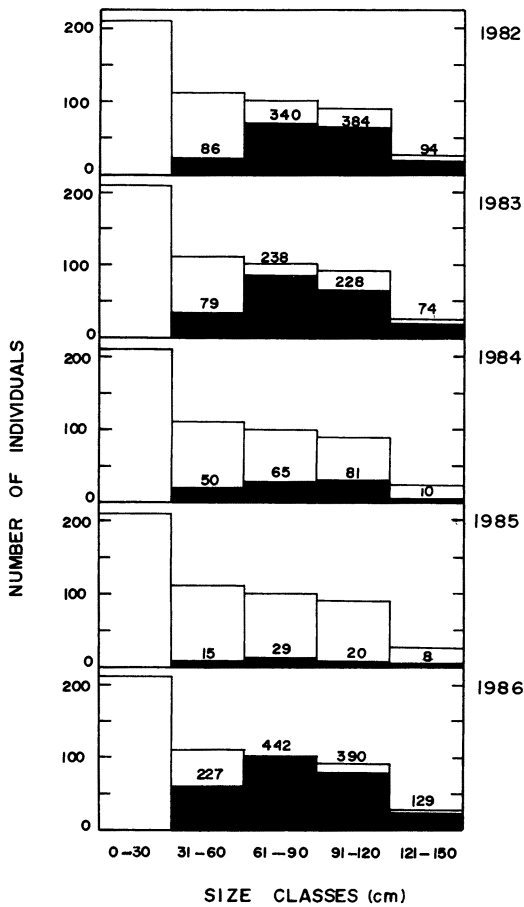The number of flower heads per inflorescence

FIGURE 6. Demographic structure of *Espeletia barclayana* in Paramo de Guerrero with the number of reproductive individuals (dark bars), and the total number of inflorescence stalks (numbers above the bars) between 1982 and 1986. The number of reproductive individuals between 1982 and 1984 were counted in 1985, using the inflorescence stalks that remained attached to the trunks, and for 1985 and 1986, by counting the new inflorescences.

TABLE 2. *Mean number of flower heads per inflorescence (±1 SEM) and mean number of seeds per flower head (±1 SEM) in a subsample of the population of E. barclayana (N = 5–12 for inflorescence and N = 4–5 for flower heads) collected between July 85 and January 86.*

Size class (cm)	Flower heads/ inflorescence (No.)	Seeds/head (No.)
000–030	—	—
031–060	6.0 (0.6)	73 (11.6)
061–090	6.5 (0.5)	65 (9.3)
091–120	6.3 (0.5)	52 (28.4)
121–160	9.4 (1.2)	63 (26.6)

0.90; $P < 0.01$) as shown in Figure 7. The number of reproductive individuals per year was also higher during wetter years, but the correlation was not statistically significant.

DISCUSSION

MORPHOMETRICS.—When information on morphology and leaf demography of *E. barclayana* are combined, it is possible to interpret the changes in shape and dynamics of growth of this species. Most of the variation in plant shape and leaf demography occurs in plants less than 30 cm in height. On the one hand, individuals less than 15 cm have no trunk, have low rates of leaf production, and show the highest relative seasonal variations in leaf production. On the other hand, plants 16–30 cm tall have a well defined trunk, although there are some individuals up to 50 cm with no visible trunk. The steep slope of the relationship between trunk height and rosette diameter (Fig. 2) for plants less than 30 cm suggests that rosette diameter is changing faster than total height. Although production of leaves for plants 31–60 cm tall is greater than for plants <30 cm tall, relative seasonality is significantly lower. In the 31–60 cm size class there are reproductive individuals, and this may be related to the decrease in rosette diameter increments. It is possible that some of the resources no longer used in vegetative growth are used in the construction of reproductive structures. Individuals 61–90 cm tall show the highest rates of growth and leaf production. This is the most active growth phase. Reproductive activity is also very high since the percentage of reproductive individuals in this class is the largest. Although plants more than 91 cm tall have annual leaf production and seasonal variations similar to those of plants 61–90 cm tall, rates of height and

stalk, and the number of seeds per flower head (Table 2), were more similar for the different size classes than the number of inflorescence stalks per plant. Thus, the contribution of each plant to the annual reproduction of the species can be estimated by the production of inflorescence stalks. No information for seed viability or germination was recorded for this species, but it is probably low as for other *Espeletia* species (Gauriguata & Azocar 1988).

Annual rainfall (El Salitre pluviometric station at 3140 m) and the number of inflorescence stalks in the population were significantly correlated ($r =$

rosette diameter changes are lower. Plants more than 91 cm show no changes in rosette dimensions and there are only small increments in plant height. There is also a reduction in reproduction activities, both in the number of reproductive individuals and in the number of inflorescence stalks. These variations in the form and productivity of *E. barclayana*, suggest that a plant's life cycle is subject to both environmental and endogenous growth controlling factors.

MICROCLIMATE AND LEAF PRODUCTION.—Seasonal variations in leaf production for *E. barclayana* seem to be related to changes in water supply and/or temperature. Low leaf production occurs during the driest part of the year (February) and also during the second dry season (June–August). Among monocaulous trees, lower leaf production with decreasing rainfall has been observed for several species of *Espeletia* in the Andes of Venezuela (Smith 1981) and for three species of *Espeletia* there is experimental evidence that plants can respond to an artificial wet season by producing new leaves (Orozco 1986, Orozco, unpublished data). Although lower nighttime temperatures are known to occur in paramo environments during the dry season rather than during the wet season (Troll 1968, Monasterio 1979), mean monthly temperature in the Neusa region seems to be lower in June than in February. Thus, the decrease in leaf production during midyear could be the result of a combination of low water supply, low temperatures, reduced sunlight, and a direct effect of occult precipitation (mist and fog).

BIOMASS PRODUCTION.—In Paramo de Guerrero, *E. barclayana* produces 710 kg dry weight ha^{-1} yr^{-1}, and grasses produce around 1120 kg ha^{-1} yr^{-1} (calculated from Lutz & Vader 1987). Thus, total production for this vegetation type would be around 1.8 ton ha^{-1} yr^{-1}, which is an underestimation because other less abundant species of *Espeletia* were not taken into account. This production value is lower than litter production in an elfin cloud forest (3.1 ton ha^{-1} yr^{-1}, Weaver *et al.* 1986) and other montane rain forests (2.7 to 27.0 ton ha^{-1} yr^{-1}, Proctor 1984), and agrees with the general reduction in biomass production with increasing altitude in wet, tropical mountains (Grubb 1977).

Leaf production per rosette (g dry weight) for *E. barclayana* is significantly lower than for other species of Espeletiinae and Dendrosenecio (Africa), with the exception of *E. humbertii*, and arborescent species in the Andes of Venezuela (Table 3). This
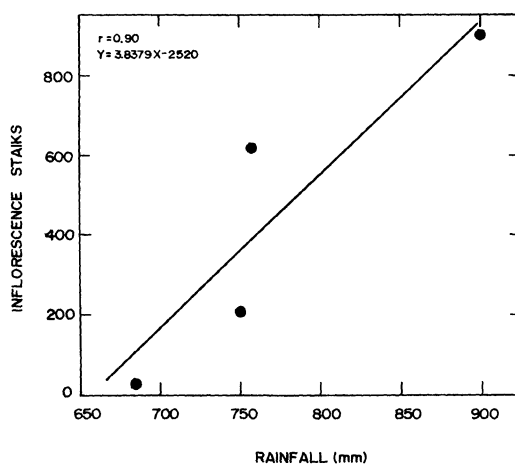

FIGURE 7. Relationship between annual rainfall (1982–1985) at El Salitre pluviometric station (3140 m) and the total number of inflorescence stalks in the population of *Espeletia barclayana* ($N = 547$) in Paramo de Guerrero.

low production for *E. barclayana* is partly the result of leaf duration (323–467 days) which is almost twice as high as for *E. schultzii* (229 days, Smith 1981) growing at similar altitudes in Venezuela. Even species like *E. lutescens*, with longer leaf life span (543–720 days, Monasterio 1986), produce more biomass per rosette than *E. barclayana*. In order to make more realistic comparisons among species with different leaf life spans, total number of leaves, and rosette dimensions, the time required for complete replacement of rosette leaves (turnover) was calculated. Turnover for *E. barclayana* in Colombia at 3500 m (0.81–1.26 years) was intermediate between species in Venezuela at 3000 m like *E. schultzii* (0.65–0.75 years), and species at 4200 m like *E. lutescens* (1.49–2.00 years) and *E. spicata* (1.59 years). In general, turnover tends to decrease with increasing altitude, although there are some exceptions (Table 1).

GROWTH RATE AND ESTIMATION OF AGE.—Growth rates for *E. barclayana* (1.1–3.8 cm yr^{-1}) are higher than for other *Espeletia* species in the Andes of Venezuela (1.1–1.5 cm yr^{-1}) with the exception of acaulescent *E. flocossa* for which growth was measured as the difference in height in the longest leaf (4.5 cm yr^{-1}, Smith 1981), and are lower than for *Senecio keniodendron* (2.5–4.5 cm yr^{-1}), in spite of the fact that the latter species grows at very high altitudes in Africa (4180 m). For this species, as for *E. barclayana*, there is an increase in growth rates to a given height and then a later decrease

with increasing age. This decrease in growth rate of E. barclayana is not the result of decreasing leaf production, since the tallest individuals in the population (121–150 cm) have leaf production rates similar to those of smaller individuals (91–120 cm).

In this study, we obtained growth rates for plants of different sizes, including juveniles. This makes our estimations of ages of adults more realistic than in some studies where only growth rates of adult individuals were measured (Hedberg 1969; Beck et al. 1980, 1984). For instance, if we had used a growth rate of 3.0 cm yr^{-1} to calculate the age of a plant 30 cm tall, we would have concluded that this plant was 10 yr old. In fact, our estimations using growth rates for juveniles suggest that this plant is 55 yr old, and that the tallest individual in the population (150 cm) is approximately 93 yr old. This means that a plant of E. barclayana spends more than half of its lifetime as a juvenile covered by grasses and without contributing to the reproduction of the species. Estimations of age could be further improved with more than one year of measurements, with the knowledge of the time of establishment, and a better estimation of the growth rate for the 121–150 size class. The growth rate for this class represents a significant source of error because the sample size was small and SE was large.

Currently, large areas of paramo vegetation are being burned during the dry season and these areas are then converted to agricultural fields. After the grasses are burned, the paramo is ploughed, the trunks of the caulescent Espeletia species piled up, and the field prepared for the cultivation of potatoes. If this trend continues, many Espeletia populations are in danger of disappearing. During a secondary succession, growth rates of E. barclayana could be potentially higher than the natural vegetation because most of the inter- and intraspecific competitors would be missing or infrequent. Nevertheless, the presence of introduced grasses and weeds would slow down or even stop the recovery of the natural vegetation. It is crucial to protect some areas of this paramo in its natural stage until enough information is obtained for the appropriate management of this vegetation type.

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LITERATURE CITED

AZOCAR, A., Y M. MONASTERIO. 1979. Variabilidad ambiental en el paramo de Mucubaji. In M. L. Salgado-Labouriau (Ed.). El Medio Ambiente Paramo. pp. 149–159. Actas del Seminario de Merida, Venezuela, 5 a 12 de noviembre de 1979. Ediciones Centro de Estudios Avanzados, Caracas.

BECK, E., R. SCHEIBE, M. SENSER, AND W. MULLER. 1980. Estimation of leaf and stem growth of unbranched Senecio keniodendron trees. Flora, (Jena) 170: 68–76.

———, I. SCHLUTTER, R. SCHEIBE, AND E.-D. SCHULZE. 1984. Growth rates and population rejuvenation of East African giant groundsels (Dendrosenecio keniodendron). Flora, (Jena) 175: 243–248.

BEEKMAN, A. M., AND P. VERWEIJ. 1987. Structure and nutrient status of a paramo bunchgrass vegetation in relation to soil and climate. Internal Report 233. Department of Palynology and Pelaeo/Actuo-Ecology. Hugo de Vries Laboratory, University of Amsterdam. The Netherlands.

BEKKER, R. P., AND A. M. CLEEF. 1990. La vegetacion del Paramo de la Laguna Verde (Mnpio. de Tausa, Cundinamarca). Analisis Geograficos No. 14. Instituto Geografico Agustin Codazii, Bogota.

CAVELIER, J., AND G. GOLDSTEIN. 1989. Mist and fog interception in elfin cloud forests in Colombia and Venezuela. J. Trop. Ecol. 5: 309–322.

CLEEF, A. M. 1981. The vegetation of the paramos of the Colombian Cordillera Oriental. Dissertationes Botaniceae 61. Cramer, Vaduz.

CUATRECASAS, J. 1968. Paramo vegetation and its life forms. In C. Troll (Ed.). Geo-ecology of the mountainous regions off the tropical Americas. Colloquium Geogr. 9: 163–186.

———. 1979. Comparacion fitogeografica de paramos entre varias cordilleras. En M. L. Salgado-Labouriau (Ed.). El Medio Ambiente Paramo, pp. 88–99. Actas del Seminario de Merida, Venezuela, 5 a 12 de noviembre de 1979. Ediciones Centro de Estudios Avanzados, Caracas.

———. 1986. Speciation and radiation of the Espeletiinae in the Andes. In F. Vuilleumier and M. Monasterio (Eds.). High altitude tropical biogeography, pp. 267–303. Oxford Univ. Press, Oxford–New York.

ESTRADA, C., Y M. MONASTERIO. 1988. Ecologia poblacional de una roseta gigante, Espeletia spicata SCH. BIP. (Compositae) del Paramo Desertico. Ecotropicos 1: 25–39.

GOLDSTEIN, G., AND F. C. MEINZER. 1983. Influence of insulating dead leaves and low temperatures on water balance in an Andean giant rosette plant. Plant, Cell & Environ. 6: 649–656.

GRUBB, P. J. 1977. Control of forest growth and distribution on wet tropical mountains: with special reference to mineral nutrition. Ann. Rev. Ecol. & Syst. 8: 83–107.

GUARIGUATA, M. R., AND A. AZOCAR. 1988. Seed bank dynamics and gemination ecology in *Espeletia timotensis* (Compositae), an Andean giant rosette. Biotropica 20: 54–59.

GUHL, E. 1968. Los paramos circundantes de la Sabana de Bogota, su ecologia y su importancia para el regimen hidrologico de la misma. *In* C. Troll (Ed.). Geo-ecology of the mountainous regions of the tropical Americas. Colloquium Geogr. 9: 195–212.

———. 1974. Las lluvias en el clima de los Andes ecuatoriales humedos de Colombia. Cuadernos Geograficos 1: 1–79 + Anexo Nos. 1–5. Universidad Nacional. Bogota, D.E.

HEDBERG, O. 1969. Growth rate of the East African Giant Senecios. Nature 222: 163–164.

LUTZ, R., AND P. VADER. 1987. Biomass, productivity and nutrient status in a Colombian bunchgrass paramo. Internal Report 229. Department of Palynology and Paleo/Actuo-Ecology, Hugo de Vries Laboratory, University of Amsterdam. The Netherlands.

MEINZER, F. C., G. GOLDSTEIN, AND P. W. RUNDEL. 1985. Morphological changes along an altitudinal gradient and their consequences for an Andean giant rosette plant. Oecologia 65: 278–283.

———, AND ———. 1985. Some consequences of leaf pubescence in the Andean giant rosette plant *Espeletia timotensis*. Ecology 66: 512–520.

MOLANO, J. 1983. Estudio biogeografico del Paramo de Guerrero (sin publicar). Facultad de Ciencias Humanas, Departamento de Geografia, Universidad Nacional, Bogota, Colombia. 315 pp.

MONASTERIO, M. 1979. El paramo desertico en el altiandino de Venezuela. *En* M. L. Salgado-Labouriau (Ed.). El Medio Ambiente Paramo. pp. 117–146. Actas del Seminario de Merida, Venezuela, 5 a 12 de noviembre de 1979. Ediciones Centro de Estudios Avanzados, Caracas.

———, Y S. REYES. 1979. Diversidad climatica y variacion de la vegetacion en los paramos de los Andes venezolanos. *En* M. Monasterio (Ed.). Estudios Ecologicos en los Paramos Andinos. pp. 47–91. Ediciones de la Universidad de los Andes, Merida, Venezuela.

———. 1986. Adaptive strategies of Espeletia in the Andean Desert Paramo. *In* F. Vuilleumier and M. Monasterio (Eds.). High altitude tropical biogeography. pp. 49–80. Oxford Univ. Press, Oxford–New York.

OROZCO, A. 1986. Economia hidrica en rosetas juveniles de Espeletia en el Paramo Desertico. Tesis de Maestria, Universidad de los Andes, Merida, Venezuela.

PROCTOR, J. 1984. Tropical rain forest litter. II. The data set. *In* S. L. Sutton and A. C. Chadwick (Eds.). Tropical rain forests: The Leeds Symposium. pp. 83–113. Leeds Philosophical and Literacy Society.

SAS. 1984. SAS/EST user's guide, 5th, edition. SAS Institute, Cary, North Carolina.

SARMIENTO, G. 1986. Ecological features of climate in high tropical mountains. *In* F. Vuilleumier and M. Monasterio (Eds.). High altitude tropical biogeography. pp. 11–45. Oxford Univ. Press, Oxford–New York.

SCHUBERT, C. 1979. La zona del paramo, morfologia glaciar y periglaciar de los Andes de Venezuela. *En* M. L. Salgado-Labouriau (Ed.). El Medio Ambiente Paramo. pp. 11–27. Actas del Seminario de Merida, Venezuela, 5 a 12 de noviembre de 1979. Ediciones Centro de Estudios Avanzados, Caracas.

SMITH, A. P. 1972. Notes on wind related growth patterns of paramo plants in Venezuela. Biotropica 4: 10–16.

———. 1974. Bud temperature in relation to nyctinastic leaf movement in an Andean giant rosette plant. Biotropica 6: 263–266.

———. 1979. Function of dead leaves in *Espeletia schultzii* (Compositae), an Andean rosette caulescent rosette species. Biotropica 11: 43–47.

———. 1981. Growth and population dynamics of Espeletia (Compositae) in the Venezuelan Andes. Smithson. Contr. Bot. No. 48.

———, AND T. P. YOUNG. 1982. The cost of reproduction in *Senecio keniodendron*, a giant rosette species of Mt. Kenya. Oecologia 55: 243–247.

———, AND ———. 1987. Tropical alpine plant ecology. Ann. Rev. Ecol. Syst. 18: 137–158.

TROLL, C. 1968. The cordilleras of the tropical Americas. Aspects of climate, phytogeography and agrarian ecology. *In* C. Troll (Ed.). Geo-ecology of the mountainous regions off the tropical Americas. Colloquium Geogr. 9: 15–56.

WEAVER, P. L., E. MEDINA, D. POOL, K. DUGGER, J. GONZALES-LIBOY, AND E. CUEVAS. 1986. Ecological observations in the dwarf cloud forest of Luquillo Mountains in Puerto Rico. Biotropica 18: 79–85.