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Growth and Population
Dynamics
of *Espeletia* (Compositae)
in the Venezuelan Andes

ALAN P. SMITH

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ABSTRACT

Smith, Alan P. Growth and Population Dynamics of *Espeletia* (Compositae) in the Venezuelan Andes. *Smithsonian Contributions to Botany*, number 48, 45 pages, 19 figures, 20 tables, 1981.—*Espeletia* (Compositae, Heliantheae) is a major component of alpine and subalpine plant communities in the Venezuelan Andes. A detailed analysis of population dynamics was undertaken for *Espeletia* species representing the arborescent, caulescent rosette, and acaulescent rosette forms. Mortality, growth, and reproduction were recorded during a 15-month period for *E. schultzei*, and *E. lutescens* (caulescent rosette species), *E. floccosa* and *E. atropurpurea* (acaulescent rosette species), and *E. humbertii* (an arborescent species of treeline forests). *Espeletia floccosa* is obligately semelparous; all other study species are iteroparous. Microenvironmental variables were measured at all sites.

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Contents

	<i>Page</i>
Introduction	1
Acknowledgments	4
General Methods	4
Research Design	4
Plot Design	6
Environmental Measurements	7
The Páramo Environment	7
Studies of Juveniles	10
Recruitment	10
Size Class Distribution	11
Growth	12
Mortality	14
Studies of Adults	19
Size Class Distribution	19
Growth	20
Rosette Turnover Time	26
Mortality	26
Reproductive Phenology	29
Effects of Slope Aspect on Growth and Population Density	33
Experimental Study of Growth	35
Discussion	35
Relationship between Growth Form and Population Dynamics	35
Population Control and Stability	38
Summary: Tables	38
Appendix: Tables	40
Literature Cited	44

Growth and Population Dynamics of *Espeletia* (Compositae) in the Venezuelan Andes

Alan P. Smith

Introduction

The presence of perennial caulescent rosette plants differentiates many high elevation ecosystems in the tropics from alpine communities of the temperate latitudes (Cuatrecasas, 1968; see also Figure 1). Such plants are characterized by rosettes of large leaves supported by unbranched or little-branched stems. Immature leaves form a dense bud around the apical meristem. Dead leaves are often persistent, forming a thick cylinder around the stem. This form has evolved independently in the alpine regions of the East Africa (*Senecio*, *Carduus* and *Lobelia*), South America (*Puya* and *Espeletia*), Hawaii (*Argyroxiphium*), New Guinea (*Cyathea*), and the Canary Islands (*Echium*), but is absent in extra-tropical alpine regions. It is therefore assumed that the form is an adaptive response to tropical alpine environments (Hedberg, 1964; Mabberly, 1973). Ecological studies of these plants may help us understand plant forms characteristic of high tropical mountains.

The giant rosette form is particularly well suited for studies of plant population biology: plants are small enough to make thorough growth measurements feasible, yet large enough to permit precise measurements; the rosette form permits

accurate description of spatial relationships because each plant's location can be described as a point on an "X-Y" coordinate system, a technique far less appropriate for plants with asymmetrical canopies; plants can be easily manipulated for experimental studies; associated plants are also small in stature, facilitating characterization of competitive neighborhoods; many giant rosette species are abundant, permitting adequate replication of measurements.

This paper describes seasonal variation in growth, mortality, and reproduction in relation to environment for *Espeletia* species of contrasting growth forms. Long-term studies of year-to-year variation in population dynamics are continuing, and will be presented in later papers. This research is part of a larger study of convergent evolution among tropical alpine giant rosette species of the New and Old World tropics.

Espeletia (Compositae, Heliantheae) is endemic to the Andes of Venezuela, Colombia, and northern Ecuador. The genus probably evolved in place from the genus *Polymnia*, which occurs in tropical montane forests (J. Cuatrecasas, pers. comm., Mar 1973). At least 90 species are recognized, of which 45 occur in Venezuela (Cuatrecasas, 1954, 1977; Aristeguieta, 1965). The most "primitive" member of the genus is probably *E. neriifolia* Sch. Bip., a very widely distributed ar-

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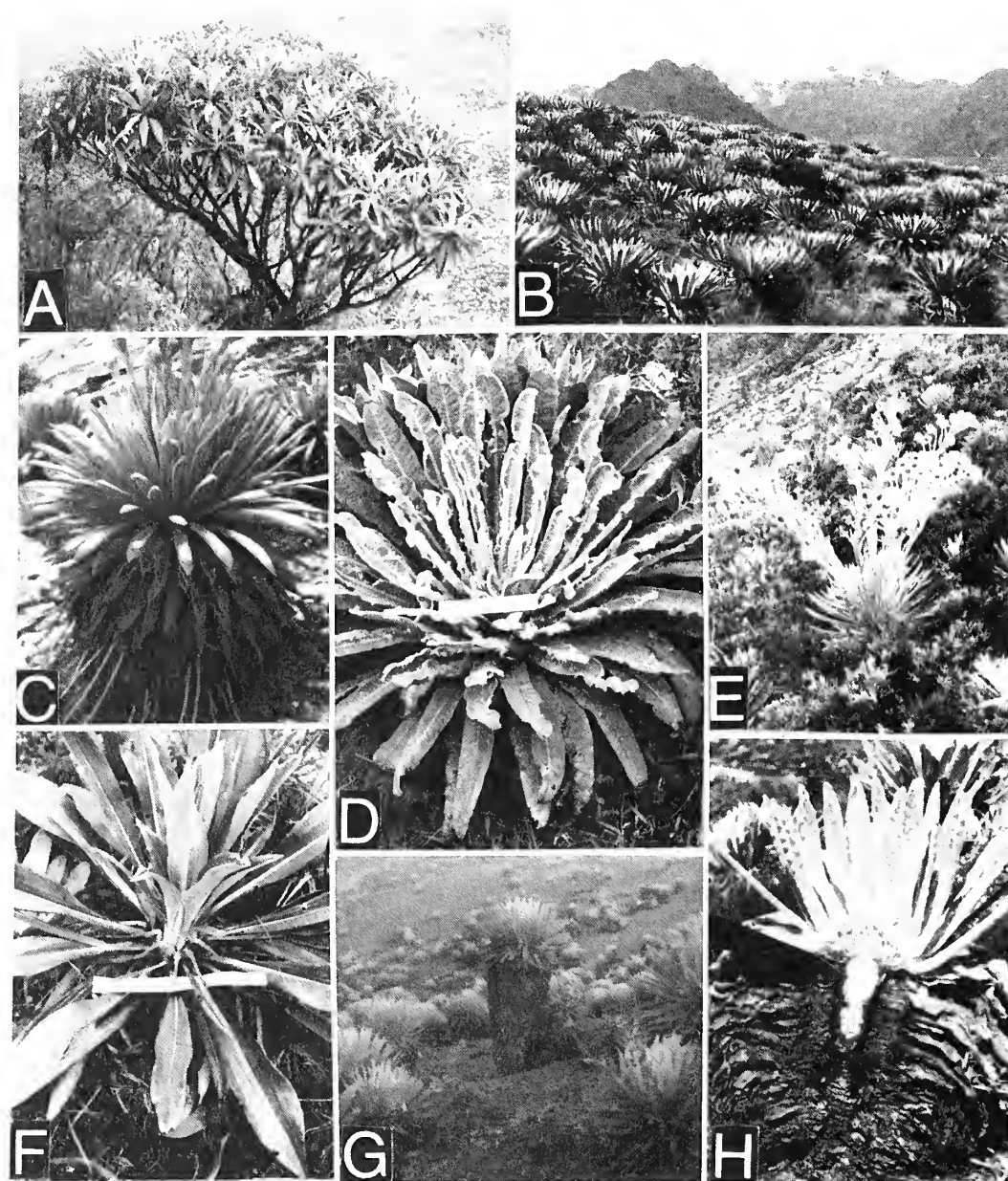


FIGURE 1.—Study species: A, *E. humbertii* on talus slope at 3500 m; plant is approximately 4 m tall; B, *E. schultzei* at 3600 m on leeward slope; C, *E. schultzei* at 4200 m; D, *E. schultzei* at 3000 m, showing insect damage to leaves; E, *E. floccosa* at 3600 m, an acaulescent, monocarpic species; F, *E. atropurpurea* at La Aguada at 3400 m, an acaulescent, glabrous-leaved species; G, *E. lutescens* at 4200 m; largest plant is approximately 1.5 m tall; H, longitudinal section of *E. schultzei* plant at 3600 m.

borescent species of subalpine forests (Cuatrecasas, 1954; Chardon, 1951; Smith and Koch, 1935). There are 15 other arborescent species, all occupying restricted geographical ranges. Arbo-

rescent species occur at elevations of about 2600 m to 3600 m in elevation.

The majority of *Espeletia* species occurs in the páramo (alpine and/or subalpine) zone. Most

páramo species have the caulescent rosette growth form, but there are also several acaulescent páramo species. Caulescent and acaulescent rosette species occur at elevations of about 2700 m to 4600 m. Nomenclature of *Espeletia* spp. is that of Aristeguieta (1965); for other plants, Vareschi (1970) is followed.

Montane forest tree line occurs between 2700 m and 3400 m in the Venezuelan Andes around Mérida, Estado Mérida (9°N), depending on exposure and degree of human disturbance. Pockets of woodland extend up to 4200 m in sheltered valleys and on talus slopes. Forests have been eliminated altogether in many areas, so that páramo vegetation merges gradually with manmade montane pastures. The upper limit of vascular plants occurs at approximately 4800 m, just below snowline.

The Andes began to rise during the Cretaceous, reaching their present height during the Pliocene and the Pleistocene (Vuillemier, 1971). Pleistocene glaciations caused fluctuations of climatic zones (Van der Hammen, 1968). Glaciers extended downward to approximately 2600 m in the Andes around Mérida (R. Giegengack, pers. comm., Feb 1974). Modern snowline occurs at approximately 4850 m and, in Venezuela, apparently is retreating. Anecdotal accounts suggest that in the early 20th century snowline occurred at approximately 4400 m to 4500 m (R. Giegengack, pers. comm., Feb 1974).

Sierran "islands" with alpine or subalpine environments were produced as the Andes rose. The invasion of these islands by *Espeletia*—presumably by genotypes of arborescent forest species similar to *E. neriifolia*—produced numerous isolated populations. This comparative isolation, combined with new selective forces imposed by the páramo environment, apparently contributed to extensive speciation (Chardon, 1951; J. Cuatrecasas, pers. comm., March 1973). The arborescent type was apparently ancestral to the more compact caulescent rosette form, which requires lower energy allocation for nonphotosynthetic support tissue and provides greater buffering against intense

diurnal temperature fluctuations (Smith, 1974a, 1974b, 1979). The arborescent form persists in *Espeletia* species of subalpine forests. A similar evolutionary pattern has been proposed for the genus *Senecio* in the East African high mountains (Mabberley, 1973).

Only one previous study has dealt with growth and population dynamics of *Espeletia*. Pannier (1969) grew *E. schultzi* under phytotron conditions. He found that germination percentage was increased by wetting and drying cycles, and that the degree of seed dormancy varied seasonally. Leaf color and amount of leaf pubescence varied with the temperature regime under which the plants were grown, suggesting a high degree of phenotypic plasticity. Pannier recorded mortality of *E. schultzi* seedlings in a 1 m² plot in the páramo at 3600 m. Highest mortality occurred in the dry season. Baruch (1972) studied water relations in *E. neriifolia* under both field and phytotron conditions. He found that increased leaf pubescence and density thickness (dry weight per cm² of leaf surface) is correlated with reduced transpiration.

The anatomy of *Espeletia* has been studied by Carlquist (1958), Roth (1973), Weber (1956), and Rock (pers. comm., May 1972). Powell and Cuatrecasas (1970) found that 30 *Espeletia* species all had a chromosome number of N=19.

Observations on the distribution, growth form, and anatomy of certain Afroalpine caulescent rosette species (*Lobelia* spp. and *Senecio* spp.) were made by Cotton (1943), Hauman (1934, 1935), and Mabberley (1973), but no quantitative ecological data were collected. Hedberg (1964) and Coe (1967) found that nyctinastic leaf movement and retention of dead leaves on the stem in these species result in maintenance of tissue temperatures above ambient at night. Hedberg (1969) found that annual height increase in *Senecio keniodendron* was approximately 2.5 cm. Studies of the population biology of the alpine *Senecio* species were initiated in 1977 and are continuing (Smith, unpublished data). Less extensive, but similarly

long-term studies of growth, mortality, and recruitment for alpine *Cyathea* species on Mount Wilhelm were initiated in 1975 (Smith, unpublished data).

Information on within- and between-species variation in population dynamics is essential for an interpretation of growth form patterns in *Espeletia*. Data on net growth rate and longevity are necessary in order to determine the immediate causes of trends in plant height. It is also necessary to determine which environmental factors reduce growth and reproduction and increase mortality; the capacity of the caulescent rosette growth form to moderate the effects of these specific factors can then be evaluated.

Knowledge of population dynamics in *Espeletia* is also essential for an understanding of the functioning of alpine and subalpine ecosystems of the north tropical Andes, where *Espeletia* is a dominant component of the community.

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General Methods

RESEARCH DESIGN.—The research provided (1) elevational comparisons within a wide-ranging caulescent rosette species (*E. schultzii*), (2) comparisons within *E. schultzii* at an intermediate elevation along a topographic gradient, and (3) comparisons among *Espeletia* species representing different growth forms. All sites were located in the Andes near Mérida, Estado Mérida, Venezuela (Figure 2).

Elevational Comparisons: Elevational comparisons for *E. schultzii* were made among sites at 3000 m (Zerpa site), 3600 m (Mucubají site), and 4200 m (Aguila site). *Espeletia schultzii* is abundant at 3000 m and 3600 m, growing in dense stands from ridge tops to bog edges. At 4200 m, at the upper limit of its range, *E. schultzii* occurs primarily in gently sloping, rocky drainage areas. These three sites were all on gentle slopes exposed to the prevailing NE winds. The 3000 m and 3600 m sites were located on morainal deposits. The 4200 m site was never glaciated.

Topographic Comparisons: Comparisons within *E. schultzii* were made along a small morainal ridge-bog gradient at 3600 m (Mucubají). The total relief from ridge to bog was about 10 m. Sites were located at the base of the slope; on a mid-slope exposed to the prevailing NE winds; at the top of the slope, also exposed to the wind; and on a leeward midslope. Some data were also collected on plants growing on the edge of the bog (Figure 3). This gradient was in a fenced research area referred to as the "upper enclosure."

Three other sites at 3600 m were used for studies of *E. schultzii*: (1) a steep xeric slope of a terminal moraine north of Laguna Mucubají (Figure 2); (2) a gently sloping talus slope at 3600 m; (3) a series of windward and leeward slopes in

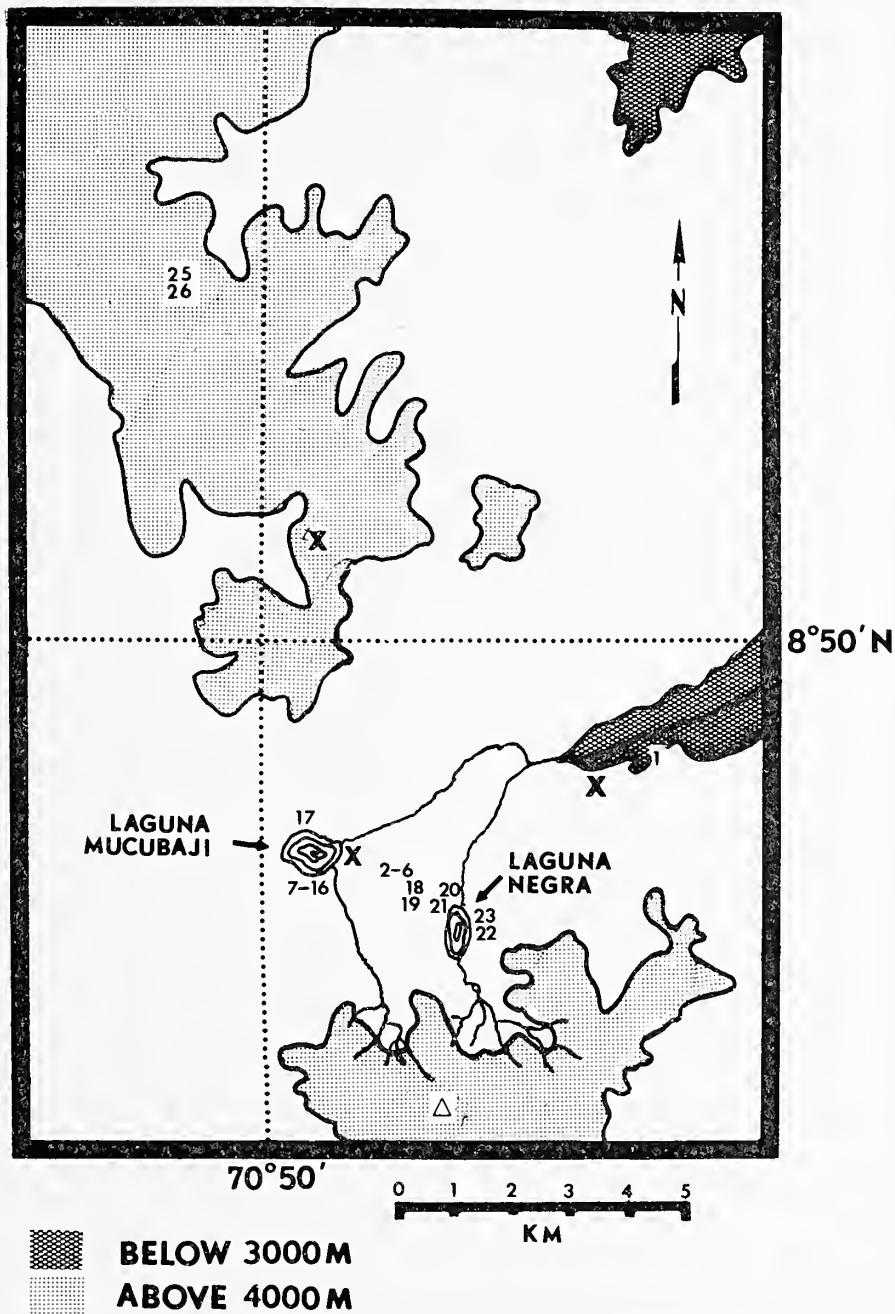


FIGURE 2.—Map of research sites (numbers = study site numbers given in Appendix (Table A); X = locations of government weather stations; triangle = Pico Mucuñuque, 4765 m).

the “lower enclosure,” a fenced research area adjacent to Laguna Mucubají (Figure 2).

Interspecific Comparisons: *Espeletia schultzei* was compared with several other species differing

from it in growth form. An arborescent species, *E. humbertii* Cuatrecasas, was studied at Laguna Negra, approximately 1 km southeast of the Mucubají topographic site, at 3500 m (Figure 2).

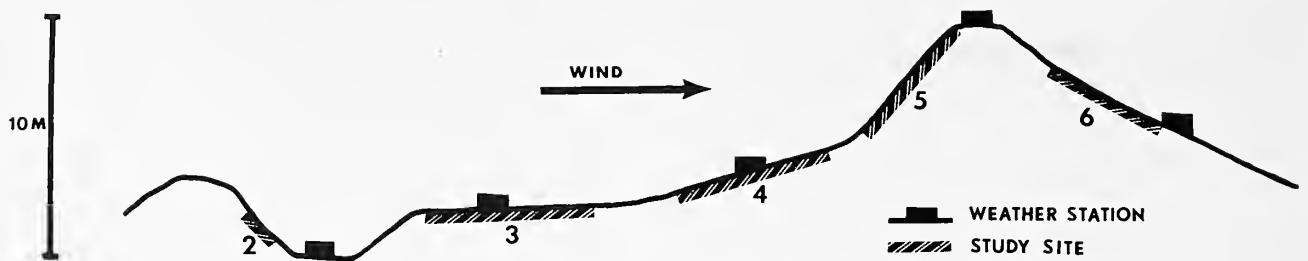


FIGURE 3.—Topographic gradient used for study of *E. schultzei* at 3600 m (numbers = site numbers in Appendix Table A).

Populations were located on a talus slope, in a closed forest, and in a treefall in an otherwise closed forest.

A semelparous acaulescent rosette species, *E. floccosa*, was studied at 3600 m (Mucubají). Populations were small and were located on rocky windward slopes, surrounding by *E. schultzei*. A study plot was established in such a population (Mucubají), approximately 300 m from the main topographic site used for *E. schultzei* and a few meters above the *E. schultzei* plot located on talus.

An acaulescent, glabrous-leaved species, *E. atropurpurea*, was studied at La Aguada, a station on the Mérida Teleférico (cable car) at 3400 m. Data on this species are presented elsewhere (Baruch and Smith, 1979).

A caulescent rosette species, *E. lutescens*, similar to *E. schultzei* but much taller, was studied at 4200 m (Aguila). It is one of the most widespread species at this altitude, occurring from ridge tops to the edges of drainage areas and bogs. A plot was established in a population of *E. lutescens* adjacent to the *E. schultzei* plot at 4200 m.

Descriptions of all sites are summarized in Appendix A. Locations are given in Figure 2.

PLOT DESIGN.—10 × 10 m plots were used for population studies. Height, stem diameter (for arborescent species), rosette or crown diameter, and distance to nearest adult neighbor of the same species were recorded for each *Espeletia* adult within a 10 × 10 m plot. In most cases, 1 m² random quadrats, located within the 10 × 10 m plots, were used to sample juvenile plants. A preliminary survey was carried out for each spe-

cies to find the reproductive adult with the smallest rosette diameter. A reproductive adult was defined as any plant with new or old flower stalks. This minimum rosette diameter was then used to distinguish between adults and juveniles. For *E. schultzei* this critical diameter is 25 cm, for *E. floccosa* it is 10 cm, and for *E. lutescens* it is 40 cm. For *E. humbertii* it was not necessary to distinguish between adult and juvenile stages: the large plots used for surveys of adults were also used for complete counts of juveniles, because juvenile densities were low at most sites.

Sampling was initiated on the north edge of a given 10 × 10 m plot. The first 120 adults encountered were marked with a metal stake and numbered aluminum tag. If there were fewer than 120 adults in the plot, the first adults encountered beyond the plot were tagged in order to give a uniform sample size from site to site. These 120 marked adults were used for measurement of growth and mortality. Dates for surveys are given in Appendix Tables C and D.

Ten 1 × 1 m quadrats were located at random within each 10 × 10 m plot, using coordinates from a random number table. Height to highest leaf tip, rosette diameter, and distance to nearest adult neighbor were recorded for every *Espeletia* juvenile in each quadrat. Each juvenile was marked with a numbered plastic pot marker. Each marker was located 2 cm upslope from its plant, with the marker edges oriented east-west to minimize shading. Great care was taken to locate all juveniles present, including seedlings

(cotyledon stages). Dates for surveys of juveniles are given in Appendix Table E.

The original research design called for a minimum of two replicate 10×10 m plots for each site. However, because insufficient time was available during the initial wet season survey, only one plot per site was established, each divided into two subplots.

ENVIRONMENTAL MEASUREMENTS.—Descriptions of elevational gradients in rainfall and temperature are based primarily on data from Venezuelan government weather stations. These stations are located at 3100 m (Los Plantios), 1 km from the 3000 m study site; at 3550 m (Mucubají), 0.5 km from the main Mucubají study site; at 4095 m (Pico del Aguila), 5 km from the 4200 m study site. These stations are visited daily by government personnel.

Soil moisture, measured gravimetrically, was determined periodically for most study sites. Cores of soil were extracted from depths of 0–5, 5–10, and 10–15 cm for several points around each study plot. Soil moisture content under 15 atmospheres pressure was determined in the laboratory for soil from each site, using the methods of Richard (1949).

Weather stations were established at the topographic gradient site in the upper enclosure at 3600 m (Figure 3). Each station had a white, double-roofed, louvered, instrument shelter (Chabot and Billings, 1972) placed at ground level. Each shelter contained a Taylor maximum-minimum thermometer. A Bendix-Friez 3-cup anemometer was located at 100 cm above the ground adjacent to each shelter. Weather stations were serviced weekly from early June 1972 through mid-January 1973.

Percentage cover by vascular plants, moss, lichens, rock, litter, and bare soil was estimated for each 1 m^2 random quadrat used for surveys of juveniles. In addition, vegetation cover was estimated for the area within a 1 cm radius of the canopy margin of each juvenile present in the 1 m^2 quadrats.

A brief microclimatic study was made on a 20° NE-facing slope (windward) and the adjacent 20°

SW-facing slope (leeward) at 3550 m in the lower enclosure (Figure 2). The leeward slope at this site was far more sheltered from the prevailing NE wind than was the leeward slope studied in the upper enclosure. The lower enclosure site thus provided a clearer demonstration of the effects of wind on microclimate. These data were used to interpret patterns of flowering phenology on windward and leeward slopes. The study was carried out in clear weather on 24–25 Mar 1973. Measurement sites were located 6–7 m below the crest. Distance from ridge crest to base of the NE-facing slope was 13.4 m; distance from crest to base of the SW-facing slope was 18.0 m. Air temperatures were measured with shaded thermocouples at 50 cm. Wind speed was recorded with a hand-held anemometer (Deuta-Werke) at 1.5 m above the ground.

For each of seven adult *E. schultzei* plants on each slope, one thermocouple was placed in the center of the apical bud, a second in the tissue of one of the outermost bud leaves on the north side of the bud, and a third in the tissue of a mature leaf at a 45° angle on the north side of the rosette.

The Páramo Environment

Elevational trends in climate are summarized in Table 1. Total annual precipitation decreased from the 3100 m site to the 4095 m site. Wet season soil moisture levels also decreased with increasing elevation (Table 1). Snowfall is rare at 3550 m, but occurs occasionally at 4200 m in the wet season. There are seldom more than few cm of accumulation, and this rarely persists for more than 24 hours.

Rainfall is strongly seasonal. The dry season generally lasts from December through March or April. The transition from wet season to dry season, and from dry season to wet season, can be very gradual. Rainfall data and other climatic variables for Mucubají (3550 m) are summarized in Figure 4. Seasonal precipitation patterns vary greatly from year to year. Figure 5 summarizes 30 years of precipitation data for the months of

TABLE 1.—Elevational differences in environment at research location (except where noted, data are from Venezuelan government weather stations near *Espeletia* study sites)

Factors	3100 m	3550 m	4095 m
Mean maximum temperature, 1972	12.6°C	10.5°C	5.2°C ²
Mean minimum temperature, 1972	4.2°C	1.9°C	1.1°C ²
Precipitation	1304 mm	1118 mm	980 mm
Evaporation, open pan, Nov 1970	108 mm	78 mm	74 mm
Soil moisture ¹			
1 Aug 1972	62%	47%	35%
26 Mar 1973	27%	30%	18%
Wilting percentage	18%	18%	11%
Vegetation cover ¹	94±2.6%	78±4.0%	38±8.1%
Cover by rock	0%	2±1.0%	37±9.1%

¹ Data from *E. schultzei* study plots at 3000 m and 3600 m and *E. lutescens* study plot at 4200 m; soil moisture expressed on oven-dry weight basis.

² Temperature data from June 1968–May 1969.

February (mid dry season) and May (early wet season) at Páramo de Mucuchies (4118 m), located between the 4200 m (Aguila) and 3550 m (Mucubají) research sites.

Mean monthly temperatures are relatively constant throughout the year. However, the diurnal temperature range is greater in the dry season than in the wet season (Figure 4). Heavy cloud cover and frequent fog, as well as rain and snow, are characteristic of the wet season. In the wet season, clear weather often occurs early in the morning but seldom persists beyond 0900 or 1000 hours. Completely clear days are common in the dry season. Relative humidity can drop to 15% to 20% at ground level during the dry season but often remains near 100% all day in the wet season. Wind is nearly continuous during the day in both wet and dry seasons. Wind speeds seldom exceeds 20 mph, except on high mountain peaks. Highest wind speeds occur in the wet season. Winds are almost entirely from the northeast during the wet season, but occasionally shift to the southwest during the dry season. Such shifts generally last for less than a day.

The effects of topography on microclimate for the primary study site at 3600 m are summarized in Table 2. The lowest dry season temperatures occurred in the bog, as a result of cold air drainage. Highest dry season temperatures occurred on the leeward slope, because this slope was sheltered from the wind. Differences between topographic sites were greatly reduced during the wet season.

Short-term data on wind speed and air temperature on a NE-facing (windward) slope and the adjacent SW-facing (leeward) slope are summarized in Figure 6. Data on tissue temperatures for *E. schultzei* plants on these slopes are summarized in Figure 7. The slopes were located in the lower enclosure at 3550 m (Figure 2).

Air and plant temperatures early in the morning rose faster on the NE-facing slope than they did on the SW-facing slope because the sun hit the NE-facing slope first. However, by 1130 hours wind speed had increased and the sun was almost directly overhead. By this time, plant temperatures for the more sheltered SW-facing had risen above those for the NE-facing slope and remained higher during the afternoon. Soil moisture measured at a depth of 0–15 cm on 25 March 1973 was 28.9% on the NE-facing slope and 16.2% on the SW-facing slope.

Needle ice formation occurred at elevations above 3000 m on bare soil wherever soil moisture was high enough. At 4200 m there were extensive areas of bare soil, probably maintained by intense frost activity; needle ice occurred on most nights. At 3600 m there was extensive cover by moss, lichens, and higher plants, and only small patches of bare soil a few cm² in size surrounded by vegetation. Needle ice formation was restricted to these small areas and occurred only on clear nights. Soil frost activity was most intense in the early dry season when clear nights were common and soil moisture was still high. By mid dry season, soil moisture was too low to permit needle ice formation except in wet swales and bogs.

Cattle and horses graze throughout and páramo zone. Cattle were seen at elevations up to 4600 m. However, grazing was eliminated at 3600

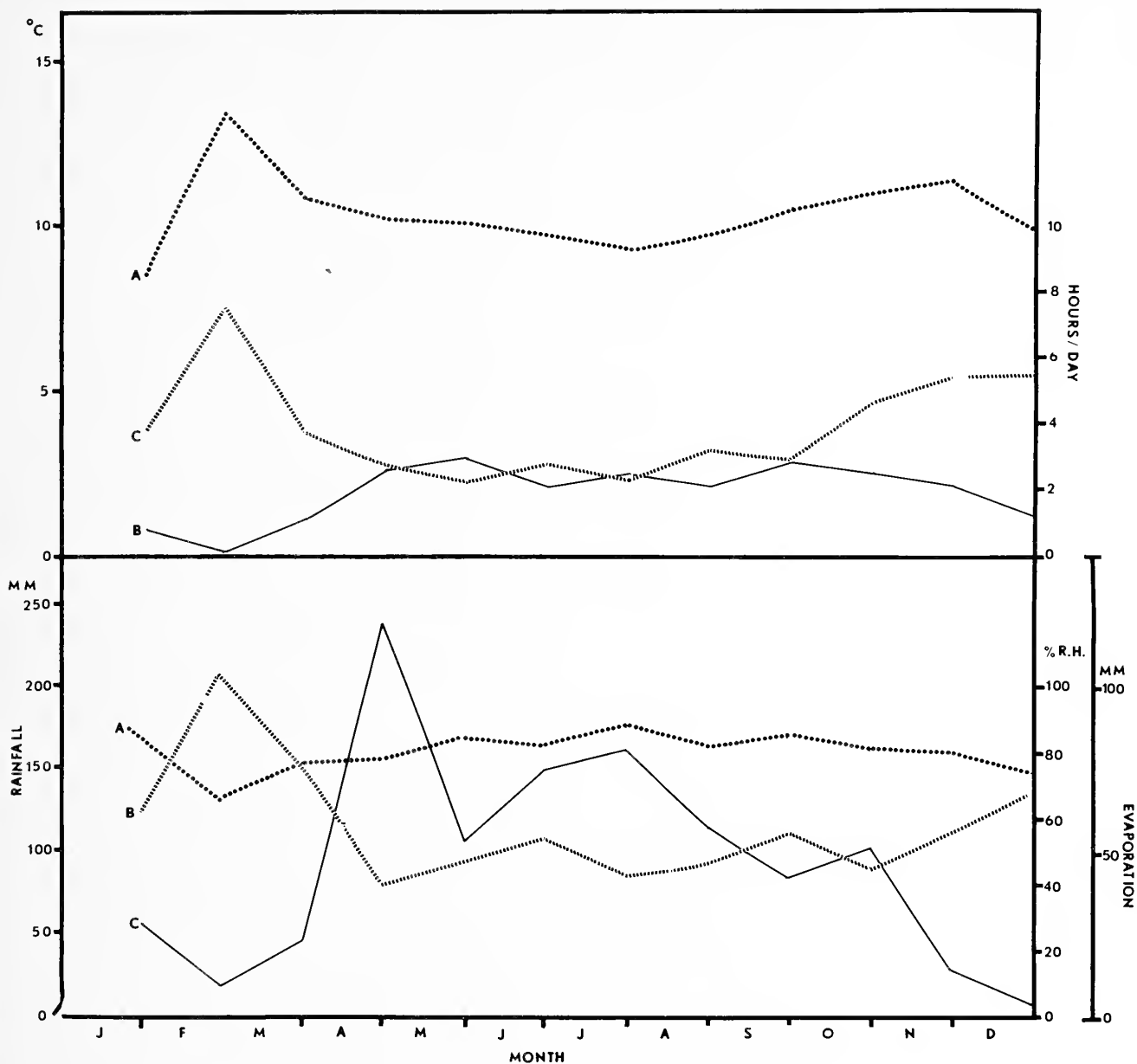


FIGURE 4.—Seasonal variation in climate at Mucubají (3550 m) (data from government weather station). *Top:* A, mean maximum temperature (monthly); B, mean minimum temperature (monthly); C, mean number of hours of sunshine per day for each month. *Bottom:* A, mean relative humidity (monthly); B, total mm evaporation per month; C, total precipitation per month (mean maximum and mean minimum temperatures were calculated from daily maximum and daily minimum temperatures, recorded with hygrothermographs; hours of sunshine recorded with Campbell Stokes sunshine recorder—"sunshine" defined as solar radiation at or above intensity of $0.33 \text{ cal}^{-1} \text{ cm}^{-2} \text{ min}^{-1}$ (Stringer, 1972).

m (Mucubají) approximately 15 years ago. There was light grazing at 3000 m (Zerpa) and at 4200 m (Aguila). An attempt was made to enclose the study plots at Zerpa and Aguila with barbed

wire, but the fences were stolen or vandalized. However, no cattle or horses were observed feeding on *Espeletia* and no evidence of such grazing was found for any of the species studied.

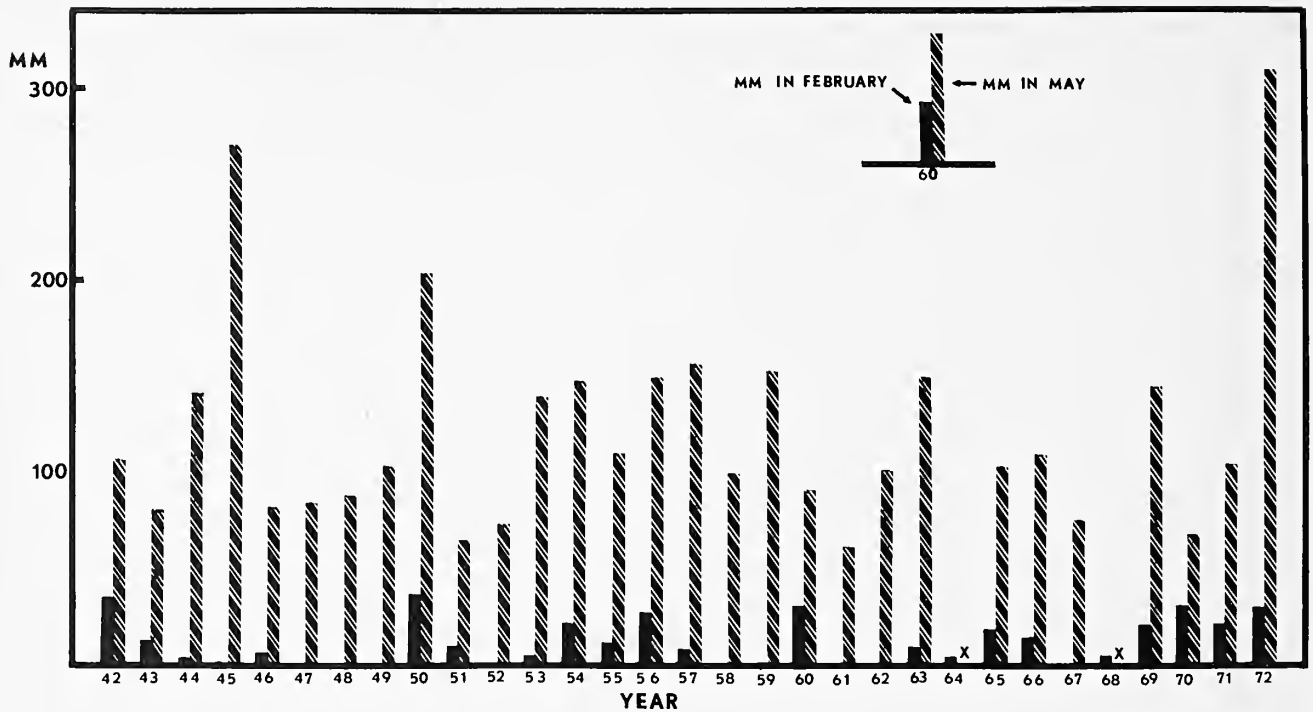


FIGURE 5.—Thirty years of precipitation data for February and May, Páramo de Mucuchies, 4118 m (data from government weather station; X = missing data).

Studies of Juveniles

RECRUITMENT.—The 1 m² random quadrats used for studies of juveniles were resurveyed periodically. New seedlings were marked and measured during each resurvey. Data were collected for *E. schultzi*, *E. lutescens*, and *E. floccosa*. *Espeletia humbertii* seedlings were too rare on the talus slope site to make studies of seedling dynamics practical. Extensive excavations of young plants indicated that, of all species studied, only *E. atropurpurea* reproduces vegetatively. Thus, the new plants recorded for *E. schultzi*, *E. lutescens*, and *E. floccosa* were all derived from seed.

Elevational Comparisons in *E. schultzi*: Results are summarized in Table 3 and Figure 8. Seedling production decreased with increasing elevation. New seedlings were relatively common at both 3000 m and 3600 m. Only two new seedlings were recorded during the year at 4200 m. Seedling production occurred entirely in the wet season at 3000 m and 4200 m. At 3600 m, all but four of

the 91 new seedlings produced during the year appeared during the wet season.

Topographic Comparisons in *E. schultzi* at 3600 m: Seedling production decreased from leeward to windward slope sites and from slope base to ridge (Table 3). Highest rates of seedling production thus occurred in the sites most sheltered from the prevailing wind (Table 2).

Interspecific Comparisons: Seedling recruitment rate was low in *E. lutescens* (only one new seedling was recorded during the year), but was similar to that for the adjacent *E. schultzi* population at 4200 m (two seedlings).

Twenty-five new seedlings were recorded for *E. floccosa* during the year. All of these seedlings appeared during the wet season. There were only five 1 m² quadrats for *E. floccosa* versus 10 for other species. On a per area basis, the recruitment rate for *E. floccosa* was therefore similar to that for *E. schultzi* on the ridge site at 3600 m (50 seedlings per 10 m² per year).

The low number of new seedlings recorded for

TABLE 2.—Variation in environment along a topographic gradient at 3600 m (site described in Figure 3 and Appendix Table A)

<i>Factors</i>	<i>Bog</i>	<i>Slope base</i>	<i>Midslope windward</i>	<i>Ridge</i>	<i>Midslope leeward</i>
Temperature (°C)*					
25 Jun -23 Jul 1972					
Mean maximum	12.8	13.3	13.9	14.4	15.6
Mean minimum	1.1	1.1	1.1	1.1	1.1
17 Dec 1972 -14 Jan 1973					
Mean maximum	17.8	16.7	20.0	19.4	23.6
Mean minimum	-9.8	-5.9	-3.6	-1.8	-5.0
Soil moisture (% oven-dry weight)					
24 Jul 1972	94.5	57.0	51.6	54.6	49.6
24 Aug 1972	109.2	54.6	49.5	47.1	48.9
2 Jan 1973	66.4	34.9	31.0	26.7	28.5
26 Feb 1973	53.4	20.0	20.6	20.6	21.8
Wilting percentage	24.3	17.9	18.0	17.5	17.6
Mean wind speed (mph)					
8 Jun 1972 -14 Jan 1973	1.5	3.1	3.6	6.4	2.7
Percent of cover					
Vegetation	-	81±5.5	78±4.0	72±5.8	79±2.6
Rock	-	<1	2±1.0	3±1.2	0

* Mean temperatures are based on weekly readings of maximum-minimum thermometers.

both *E. schultzi* and *E. lutescens* at 4200 m could have been the result, in part, of intense, nightly, soil frost activity. Most seedlings are destroyed by frost heaving as soon as they germinate and thus disappeared too quickly to be recorded during the quadrat resurveys. Most of the established juvenile plants at 4200 m grow among rocks, or are surrounded by vegetation, and are protected from soil frost activity.

Higher rates of seedling recruitment in more sheltered sites could have resulted from increased seed production, as well as from the direct effects of microclimate on germination and establishment. The number of adult plants that flowered and the number of flower heads per plant were both highest in more sheltered places (Table 15-17).

SIZE CLASS DISTRIBUTION.—The number of juveniles present in the 1 m² random quadrats was recorded at each site. Height to highest leaf tip was then recorded for each plant. These data were used to construct size class distributions. Size class distributions were based on data from the initial survey.

Height class intervals were based on a geometric sequence with a common quotient of 2 (0-0.5, 0.6-1.0, 1.1-2.0, 2.1-4.0 cm, etc.). This sequence was used because for the smallest plants a difference in plant height of a few mm was associated with major differences in mortality rate, whereas for larger plants a difference of several cm had little effect. These same height classes were used to summarize data on juvenile mortality and growth.

Elevational Comparisons in E. schultzi: Size class distributions are shown in Figure 8. The greatest number of juvenile plants occurred in the smallest height classes. At 4200 m there were far fewer plants in the smallest size classes than was the case at either 3600 m or 3000 m. Total number of juveniles per 10 m² was highest at 3000 m and lowest at 4200 m (Appendix Table B).

Comparisons within E. schultzi at 3600 m along a Topographic Gradient: For the upper enclosure sites the number of juveniles decreased from smallest to largest height classes (Figure 9). Juvenile density was highest on the slope base site

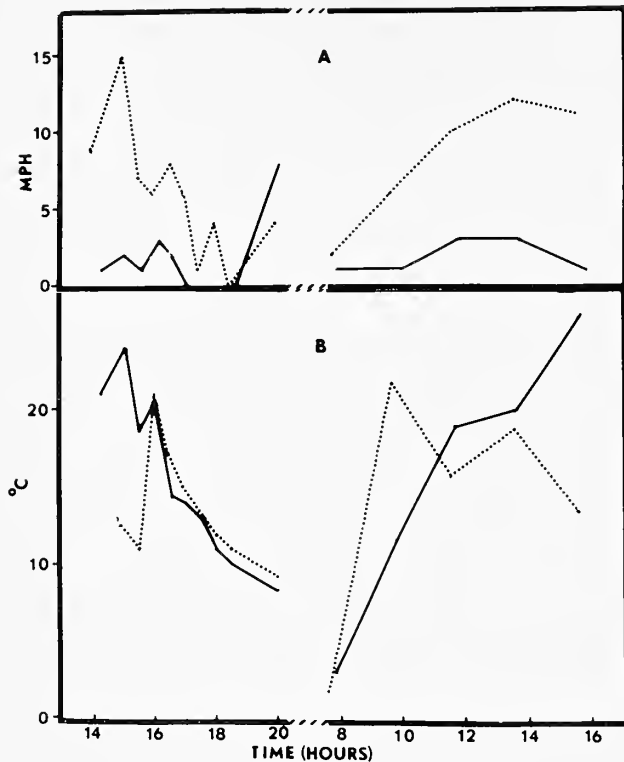


FIGURE 6.—Comparison of microclimate on NE-facing (windward) and SW-facing (leeward) slopes at 3550 m: A, wind speed; B, air temperature at 50 cm (dotted lines = windward slope data).

and lowest on the ridge. Density was higher on the leeward slope than on the windward slope (Appendix B). On the xeric slope site at 3550 m, the greatest number of juveniles occurred in the intermediate size classes, with lowest numbers in the smallest classes (Figure 10A). On the talus slope at 3600 m, only three juveniles, all cotyledon stage seedlings, were found (Figure 10B). These were located in small pockets of moist organic debris.

Interspecific Comparisons: Juvenile density in *E. lutescens* was too low to yield a clear pattern of size class distribution (Figure 11B).

In *E. floccosa* the greatest number of juveniles occurred in intermediate size classes (Figure 11A). The only other population showing a similar pattern was *E. schultzei* on the xeric slope at 3550 m.

For *E. humbertii*, young plants were too rare on

the talus slope site and the closed-canopy forest site to yield clear size distribution patterns (Figure 12A–B). High juvenile densities occurred only on the treefall site within otherwise closed forest (Figure 12C). At this site, the number of juveniles decreased from the smallest to the largest size classes.

For *E. floccosa* at 3600 m and *E. schultzei* on the xeric slope site at 3600 m, juveniles were concentrated in the intermediate rather than the lowest size classes. Both of these populations had shorter generation times and fewer large adults than was the case in other populations. The relative scarcity of large adults may have resulted in decreased competition between adults and juveniles. This could lead to an increased probability that newly recruited seedlings reach higher size classes.

GROWTH.—All juveniles of *E. schultzei*, *E. lutescens*, and *E. floccosa* present in the 1 m² quadrats at the initial survey were marked with plastic tags. Height, measured to the highest leaf tip, was recorded. The surviving plants were remeasured one year later. Change in plant height was used as a measure of growth. Distance to nearest adult of the same species was recorded for each plant.

Elevational, Topographic, and Interspecific Comparisons: Growth rates are summarized in Figures 8, 9, and 11. Growth was highly variable; there were no clear-cut patterns along either altitudinal or topographic gradients. Mean annual growth rate was negative for *E. schultzei* on the midslope windward site at 3600 m and for *E. lutescens* at 4200 m, indicating that, on the average, juveniles decreased in size during the year. This was the result of extensive leaf wilting during the dry season. For most plants, leaf regrowth during the next wet season was too slow to permit full recovery from this wilting. Some juveniles in both populations increased in size, however.

Growth occurred primarily in the wet season for all populations. Wilting of older leaves in the dry season caused a reduction in size, even for plants that showed a net increase in height over the entire year.

For *E. schultzei* at 3000 m, annual height growth increased with increasing initial plant height (r_{xy}

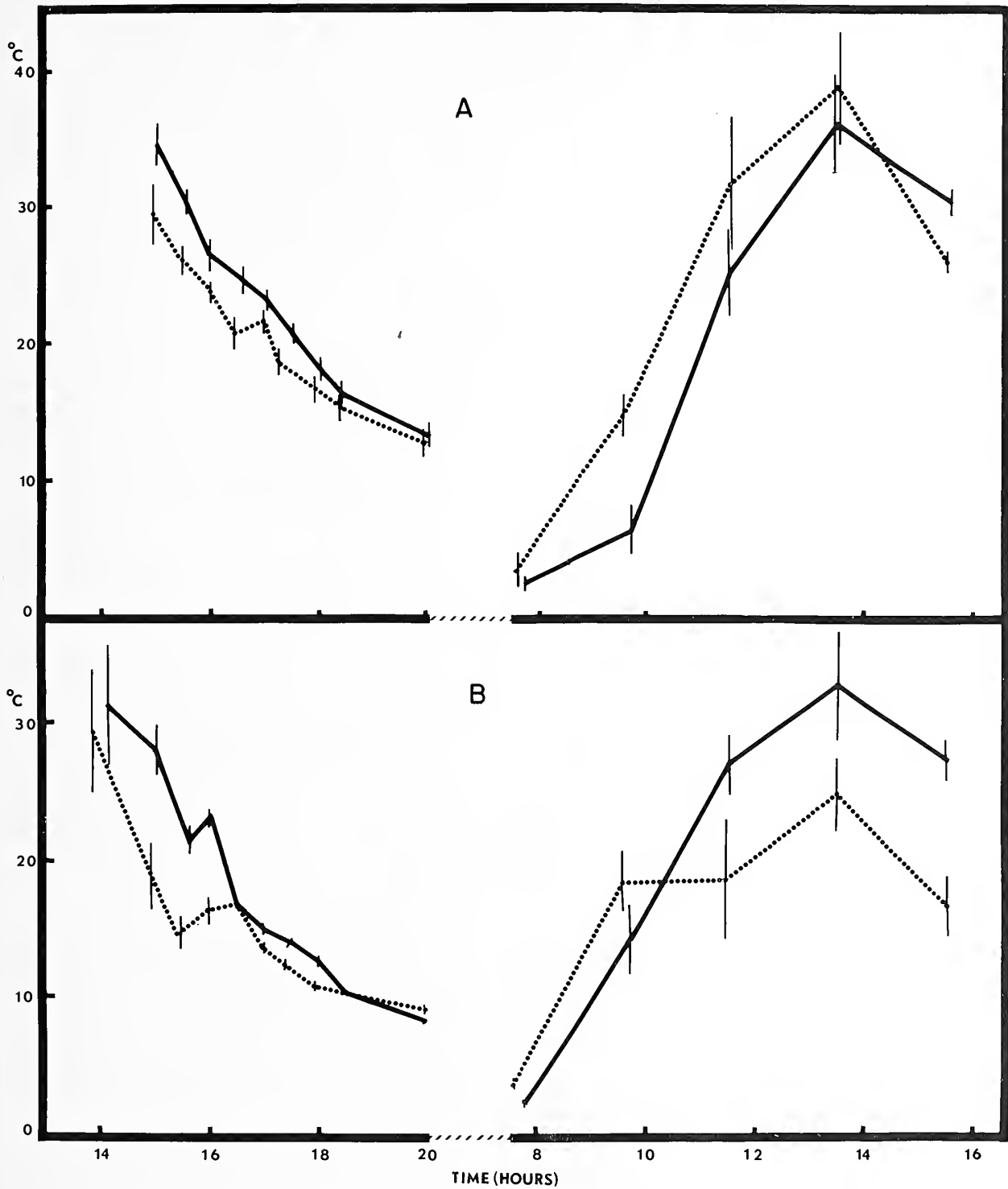


FIGURE 7.—Comparison of *E. schultzei* tissue temperatures on windward NE-facing (dotted line) slope and leeward SW-facing (solid line) slope at 3550 m: A, bud core temperature; B, mature leaf temperature (vertical lines represent 95% confidence intervals).

TABLE 3.—Seedling production at various times of year (each figure = number of new seedlings in ten 1-m² quadrats (five quadrats for *E. floccosa*) at the end of given time period; dates for all surveys given in Appendix Tables C-E)

Species and sites	Wet season 1972	Early dry season 1972-3	Late dry season 1973	Wet season 1973	Total new seedlings in one year
<i>E. schultzei</i>					
3000 m	54	0	0	71	125
3600 m					
Slope base	116	3	0	7	126
Windward slope	84	4	0	3	91
Ridge	45	1	0	4	50
Leeward slope	137	1	0	24	162
4200 m	2	0	0	0	2
<i>E. floccosa</i>					
3600 m	23	0	0	2	25
<i>E. lutescens</i>					
4200 m	0	0	0	1	1

= 0.340; $P < 0.01$). This same relationship was found for *E. schultzei* on the leeward slope site at 3600 m ($r_{xy} = 0.225$; $P < 0.05$). However, for *E. schultzei* on the windward slope site at 3600 m, annual height growth decreased with increasing initial plant height ($r_{xy} = -0.451$; $P < 0.005$). This was also the case for *E. lutescens* at 4200 m ($r_{xy} = -0.709$; $P < 0.005$). For other populations, there was no significant correlation between annual height growth and initial plant height.

Nearest Neighbor Effects: Annual height growth of juveniles increased with decreasing nearest neighbor distance for *E. schultzei* at 3000 m and for *E. floccosa* at 3600 m (Table 4). Adults could shelter juveniles from wind and intense insolation. They might also inhibit interspecific competitors. However, adults simply may occupy the most favorable microsite. In any case, the closer a juvenile was to an adult, the more nearly optimal its own microsite would be. Increased intraspecific competition close to the adult might be outweighed by these effects.

Effects of Vegetation: No significant correlations were found between juvenile growth and vegetation cover (Table 5). Experimental studies strongly suggest that vegetation reduces juvenile growth (manuscript in preparation).

MORTALITY.—The 1 m² quadrats were resurveyed periodically to determine the numbers of marked juveniles that had died since the last

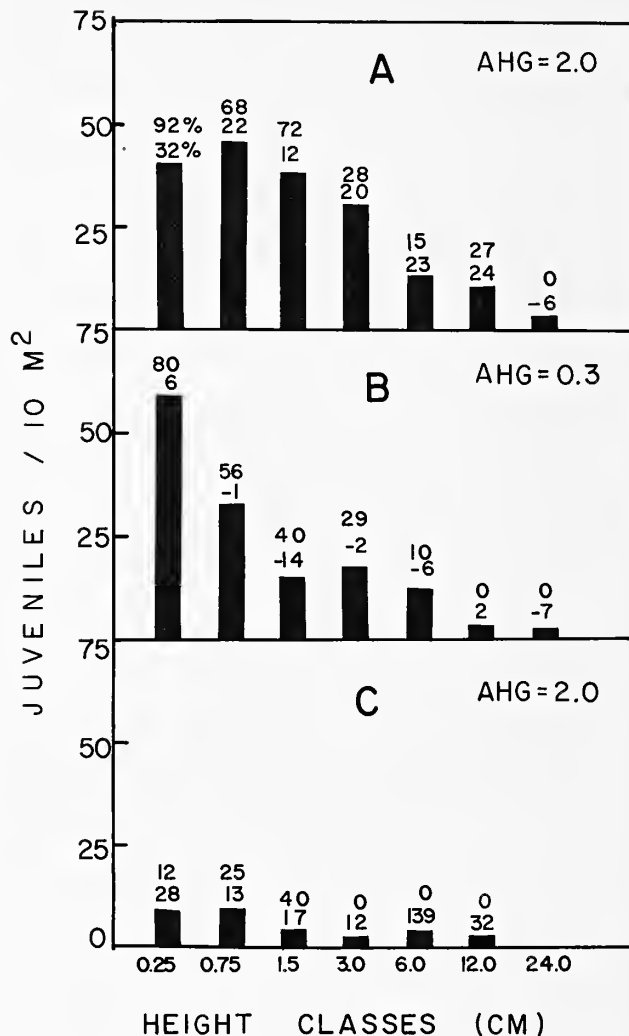


FIGURE 8.—Altitudinal variation in population structure and dynamics for *E. schultzei* juveniles: A, 3000 m; B, 3600 m; C, 4200 m (juvenile = plant with rosette diameter of less than 25 cm; AHG = annual height growth (cm); bar = number of juveniles found in each height class; top number = percent of mortality in one year; lower number = percent of height increase in one year).

survey. Newly recruited seedlings were marked during the resurvey. Subsequent mortality rates for these new seedlings were compared with mortality of previously established juveniles. Distance to nearest adult of the same species and percentage of cover by vegetation in the plant's immediate vicinity were recorded for each marked plant.

Elevational Comparisons in *E. schultzei*: For juve-

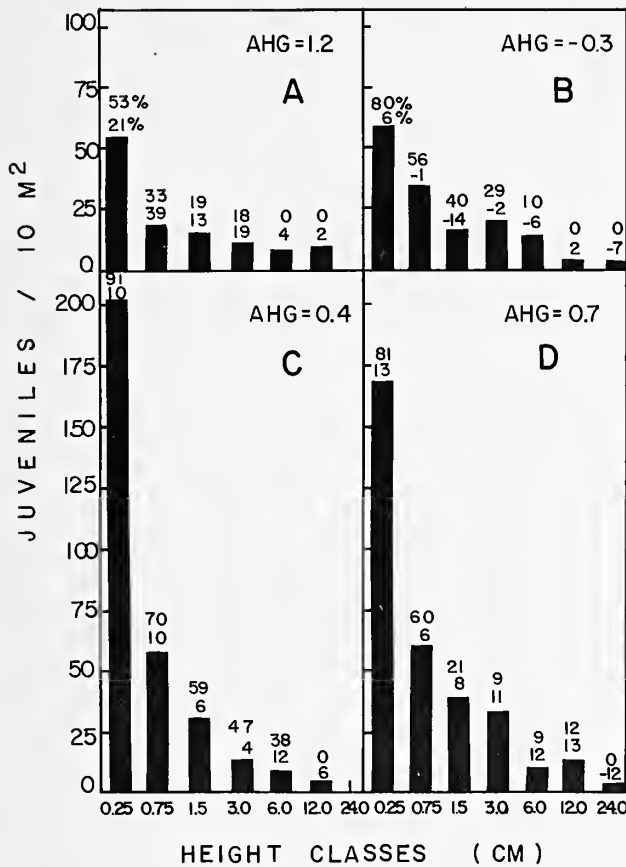


FIGURE 9.—Topographic variation in population structure and dynamics for *E. schultzei* juveniles at 3600 m: A, ridge; B, midslope windward; C, slope base; D, midslope leeward (juvenile = plant with rosette diameter of less than 25 cm; AHG = annual height growth (cm); bar = number of juveniles; top number = percent mortality in one year; lower number = height increase in one year).

niles present at the initial survey, there was a slight decrease in annual mortality rate from 3000 m to 3600 m, and a large decrease from 3600 m to 4200 m for midslope windward sites (Table 6). At 3000 m, 87% of all mortality occurred during the dry season, compared with 64% at 3600 m (Table 6). At 4200 m, only four deaths occurred during the year, too few to accurately estimate seasonal trends.

Mortality rates for each size class are shown in Figure 8. Mortality decreased with increasing plant size for the midslope windward sites at 3000 m and 3600 m (cf. Hett, 1971; Sarukhan and Harper, 1973). For both sites, there was a negative

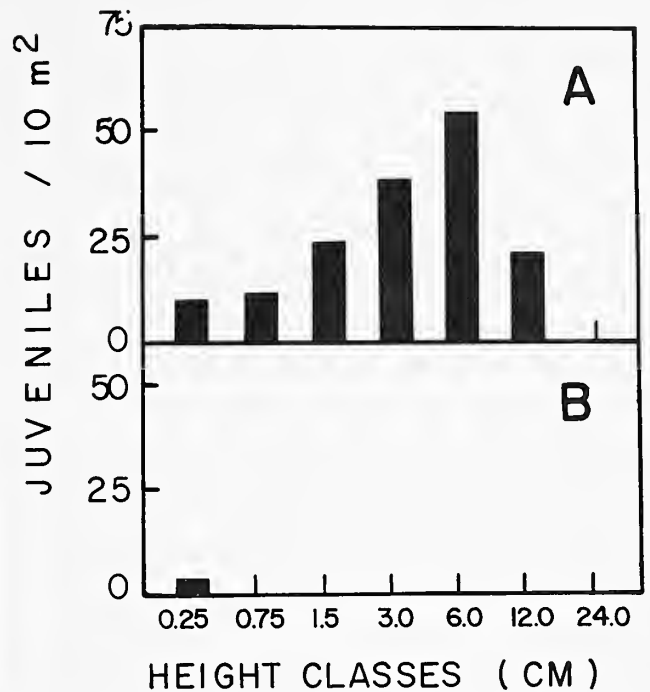


FIGURE 10.—Size class distributions of *E. schultzei* juveniles at 3600 m: A, xeric slope; B, talus slope (juvenile = plant with rosette diameter of less than 25 cm).

linear relationship between percent mortality in each size class and the natural log of the median value (in cm) for each height class (Figure 13). The regression of mortality rate against plant size was not statistically significant for *E. schultzei* at 4200 m. However, mean initial height for juveniles that died was significantly lower than mean initial height for juveniles that survived one year (0.7 cm versus 3.8 cm; $P < 0.02$).

Topographic Comparisons in E. schultzei at 3600 m: Annual mortality rate of juveniles decreased from slope base to ridge (Table 6). Annual mortality rate on the leeward slope (58%) was similar to that on the windward slope (54%).

The proportion of total mortality that occurred during the dry season was greater on the slope base site than on the ridge, and was greater on the leeward slope than on the windward slope (Table 6). With the exception of the ridge site, mortality was always greatest during the dry season.

For all four topographic sites, mortality de-

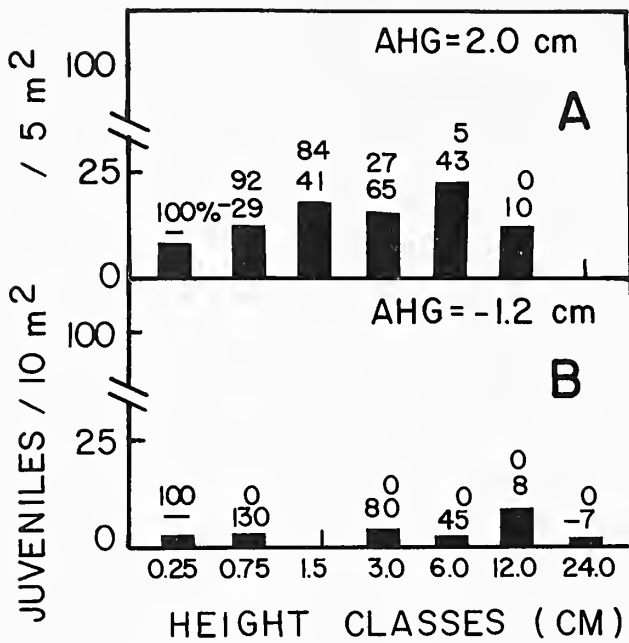


FIGURE 11.—Population structure and dynamics for juveniles: A, *E. floccosa* at 3600 m; B, *E. lutescens* at 4200 m (for *E. floccosa* juvenile = plant with rosette diameter of less than 15 cm; for *E. lutescens* juvenile = plant with rosette diameter of less than 40 cm; AHG = annual height growth (cm); bar = juveniles; top number = percent mortality in one year; lower number = height increase in one year).

creased with increasing plant size (Figure 9). There were negative linear relationships between percent mortality in each size class and the natural log of the median value for each size class (Figure 13). For the midslope leeward site, the apparent sigmoidal relationship between these two variables (Figure 13, middle) was not statistically significant; a polynomial regression was not significantly better than a linear regression.

Interspecific Comparisons: Annual mortality rate for *E. floccosa* juveniles at 3600 m was 49%. The proportion of total annual mortality that occurred during the dry season was higher for *E. floccosa* (98%) than for any other population studied (Table 6). Mortality rates for each class are given in Figure 11A. The relationship between percent mortality in each size class and the natural log of the median value for each size class was linear (Figure 13). The apparent sigmoidal

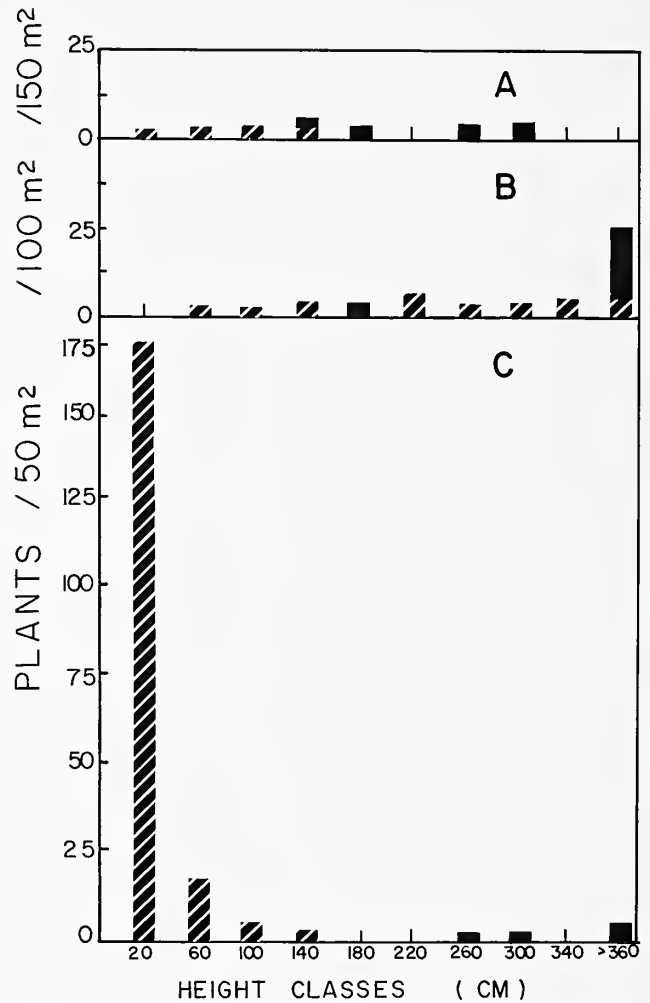


FIGURE 12.—Population structures for *E. humbertii* at 3500 m: A, talus slope (plants/150 m²); B, closed forest (plants/100 m²); C, treefall (plants/50 m²) (growth rate for talus slope population = 4.2 cm/year based on 50 marked plants, all over 75 cm in height; growth data not recorded for other populations; solid bar = reproductives; striped bar = pre-reproductives).

relationship between these two variables was not statistically significant.

In *E. lutescens* at 4200 m, only two of the marked juveniles died (Table 6), making a detailed analysis of mortality impossible.

Comparisons between Newly Recruited and Previously Established Juveniles: The figures for juvenile mortality discussed so far have been based on those sets of juveniles present in the quadrats during the initial survey in mid wet season, 1972. These quadrats were resurveyed in early December 1972

TABLE 4.—Distance to nearest adult neighbor in relation to juvenile growth, mortality, and initial height (juvenile and adult always of same species)

Species and sites	Height growth vs. nearest neighbor r_{xy}	Height growth vs. initial height r_{xy}	Initial height vs. nearest neighbor		Mean nearest neighbor distance	
			All juveniles r_{xy}	Survivors only r_{xy}	Survivors	Mortalities
<i>E. schultzi</i>						
3000 m	-0.276**	0.340**	-0.114	-0.077	29.3	42.1***
3600 m						
Slope base	0.023	0.136	-0.024	-0.323**	42.3	44.1***
Midslope windward	-0.118	-0.451***	-0.085	-0.133	49.7	49.9
Ridge	0.100	0.024	0.509***	0.415***	67.6	34.9***
Midslope leeward	0.034	0.225*	0.012	-0.026	32.7	28.5*
4200 m	-0.046	0.291	0.042	-0.268	43.4	17.8***
<i>E. floccosa</i>						
3600 m	-0.394*	0.000	0.152	0.392*	29.5	33.8
<i>E. lutescens</i>						
4200 m	-0.182	-0.709***	0.359	0.427†	-	-

* P<0.05 ** P<0.01 *** P<0.005 † P<0.1

TABLE 5.—Effects of vegetation on juveniles (vegetation cover measured in immediate vicinity of each juvenile)

Species and sites	Height growth vs. vegetation cover r_{xy}	Vegetation cover (%)		Initial height vs. vegetation cover (%)	
		Survivors	Mortalities	All juveniles r_{xy}	Survivors only r_{xy}
<i>E. schultzi</i>					
3000 m	-0.011	83.9	69.3**	0.299***	-0.077
3600 m					
Slope base	-0.069	59.9	47.2*	0.237**	0.357**
Midslope windward	-0.248†	73.0	48.0***	0.336***	0.329*
Ridge	-0.070	62.6	42.3**	0.303**	0.320**
Midslope leeward	0.086	53.8	26.1***	0.367***	0.326***
4200 m	0.211	42.2	38.5**	0.346†	0.504*
<i>E. floccosa</i>					
3600 m	0.222	84.5	61.0***	0.102	0.220
<i>E. lutescens</i>					
4200 m	0.100	-	-	0.045	-0.065

* P<0.05 ** P<0.01 *** P<0.005 † P<0.1

(wet season-dry season transition), and seedlings that had appeared since the initial survey were marked and measured. Mortality during the following dry season was, in general, much greater than mortality for juveniles already present at the time of the initial survey (Table 7). The only exception to this trend occurred in *E. schultzi* at

4200 m. In this case, however, only two newly recruited seedlings were present, making a meaningful analysis impossible.

Nearest Neighbor Effects: For *E. schultzi* at 3000 m, mean distance to nearest conspecific adult neighbor was significantly lower for juveniles that survived one year than for those that died. This

TABLE 6.—Seedling mortality for seedlings present in initial survey (wet season, 1972) (survey dates summarized in Appendix Table E)

Species and sites	Initial number seedlings	Percent mortality in 1 year	Percent of all mortality occurring			New seedlings present at final survey	Total seedlings present at final survey
			Wet season 1972	Dry season 1972-3	Wet season 1973		
<i>E. schultzei</i>							
3000 m	178	60.7	8.3	87.0	4.7	73	143
3600 m							
Slope base	314	79.3	20.5	79.1	0.4	19	84
Midslope windward	134	53.7	29.2	63.9	6.9	17	79
Ridge	118	33.0	43.6	48.7	7.7	13	92
Midslope leeward	197	57.7	17.9	78.8	3.3	29	164
4200 m	29	13.8	25.0	75.0	0	2	27
<i>E. floccosa</i>							
3600 m*	82	48.8	0	97.5	2.5	2	44
<i>E. lutescens</i>							
4200 m	21	9.5	50.0	50.0	0	1	20

* Number of seedlings per 5 m², rather than 10 m².

same relationship was found for *E. schultzei* at 3600 m on the slope base plot and for *E. floccosa* at 3600 m.

On the ridge and leeward slope plots at 3600 m, surviving juveniles of *E. schultzei* had a greater mean nearest neighbor distance than did mortalities. Dry season soil moisture levels for those two plots were the lowest recorded at this site. Competition between adults and juveniles for water could have outweighed any moderating effects of the adults on microenvironment on these plots.

Effects of Vegetation: At all sites, vegetation cover around juveniles that survived one year was greater than cover around those that died. With the exception of the *E. floccosa* and *E. lutescens* populations, initial plant height was positively correlated with vegetation cover (Table 5). Mortality rate decreases as juvenile height increases (Table 5). Mortality rates were therefore lower in sites with higher vegetation cover, in part because the size of juveniles was greater.

Herbivory: Herbivory on juveniles was rare. Insect damage to leaves was noted in two of the marked *E. schultzei* juveniles at 3000 m (1% of all juveniles at this site) and in three marked *E. lutescens* juveniles at 4200 m (14% of all juveniles). The damage was caused by beetle larvae burrow-

ing in the apical buds. However, these plants survived. No herbivory on juveniles was recorded at other sites. Elimination of juveniles by grazers apparently is not a major factor. At all sites, marked juveniles that died could always be located and showed no signs of insect damage.

Discussion: Data on juvenile mortality in *Espeletia* suggest two general patterns: (1) the probability of mortality decreases as plant size increases, and (2) the probability of mortality is greatest in the dry season. Potentially, these two patterns could result in several kinds of selection on *Espeletia* populations: (1) selection on adult stages for production of larger numbers of seedlings, increasing the probability that some will survive despite high mortality rates; (2) selection on juvenile stages for rapid growth rates, reducing the duration of the most vulnerable stage in the life cycle; and (3) selection on juvenile stages for physiological and/or morphological adaptations that confer protection against environmental extremes of the dry season. Further studies will be required to determine the relative importance of such selective pressures in various *Espeletia* populations.

The positive correlation of juvenile size with vegetation cover within 1 cm of the rosette margin

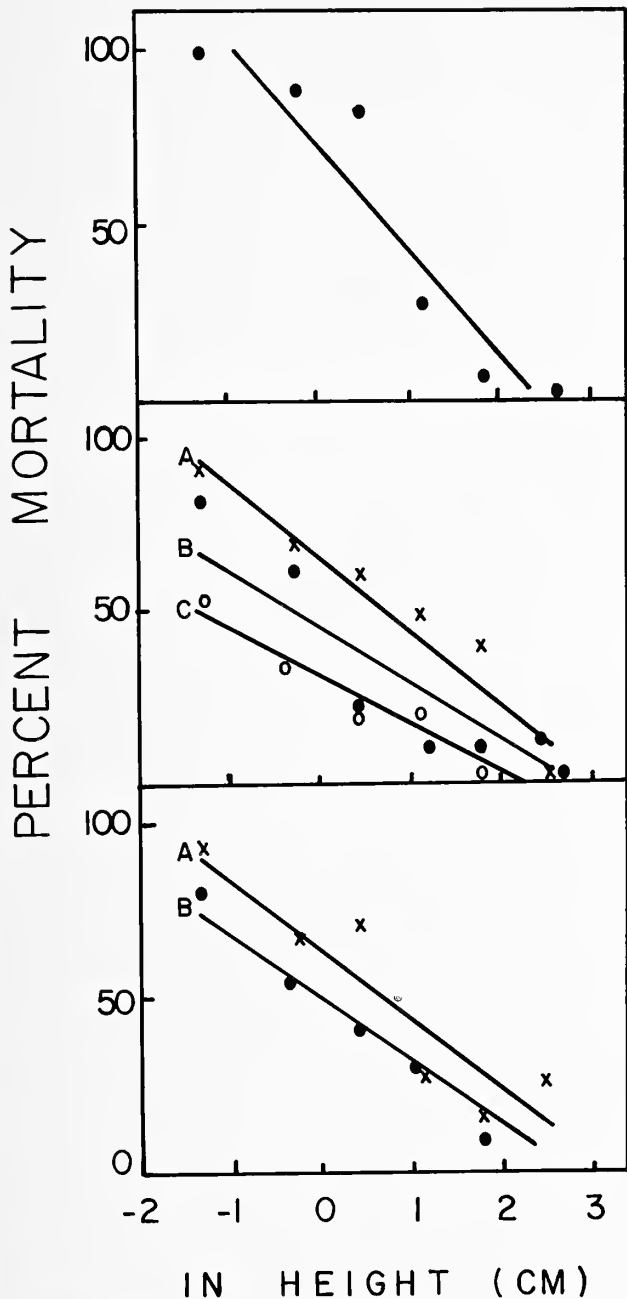


FIGURE 13.—Relationships between seedling height class and percent mortality in each height class during one year. *Top*: *E. floccosa* at 3600 m ($y = 72.2 - 30.5 \ln X$, $r = -0.939$). *Middle*: A, slope base *E. schultzei* plot at 3600 m ($y = 65.3 - 20.9 \ln X$, $r = -0.977$); B, midslope leeward *E. schultzei* plot at 3600 m ($y = 45.5 - 37.4 \ln X$, $r = -0.903$); C, ridge plot for *E. schultzei* at 3600 m ($y = 30.1 - 34.0 \ln X$, $r = -0.976$) *Bottom*: A, *E. schultzei* at 3000 m ($y = 64.1 - 20.1 \ln X$, $r = -0.941$); B, *E. schultzei* at 3600 m, midslope windward plot ($y = 50.1 - 18.6 \ln X$, $r = -0.985$).

TABLE 7.—Dry season mortality (December 1972 to April 1973) for seedlings present at initial survey (wet season, 1972), and for seedlings produced after initial survey, but before December 1972 (survey dates summarized in Appendix Table E)

Species and sites	Number of initial seedlings present Dec 1972	Mortality (%)	Number of new seedlings present Dec 1972	Mortality (%)
<i>E. schultzei</i>				
3000 m	163	57.7	54	96.3
3600 m				
Slope base	250	78.8	116	94.0
Windward slope	95	68.7	84	89.3
ridge	67	28.4	45	82.2
Leeward slope	262	55.3	137	97.1
4200 m	28	10.7	2	0
<i>E. floccosa</i>				
3600 m	82	47.6	23	87.0
<i>E. lutescens</i>				
4200 m	20	5.0	0	0

is probably an inevitable consequence of increase in rosette diameter. Nonvegetated patches at most sites typically cover only a few square centimeters. A very small juvenile within such a patch could be free of vegetation in its immediate vicinity. As the rosette expands, it will outgrow the bare site. As a result, large juveniles will seldom be free vegetation.

Studies of Adults

SIZE CLASS DISTRIBUTION.—Size class distributions are based on height data for adults within each study plot. Plant height was measured to the base of the apical bud in all species except *E. floccosa*. In *E. floccosa*, height was measured to the highest leaf tip because the apical bud was poorly defined. Annual height growth was recorded for 120 adults in most study plots. Size class distributions can be transposed into very approximate adult age class distributions by using these annual height growth data as conversion factors. However, such approximations must be interpreted with care because rate of height growth for adults is probably correlated with initial plant height: rate of leaf expansion is positively correlated with plant height in many populations, and plant height growth and leaf expansion rates are closely related in caulescent rosette plants. A more de-

tailed analysis of height-age relationships will be presented in a later paper.

Elevational Comparisons within E. schultzei: The 4200 m population had fewer plants in small size classes than did populations at 3000 m and 3600 m. However, considering similar topographic sites, the tallest and hence oldest plants occurred at highest elevations. Mean adult height, calculated for 120 plants at each elevation, was 23.8 cm at 3000 m, 26.0 cm at 3600 m, and 29.6 cm at 4200 m. These means are significantly different from each other ($P < 0.01$) according to the *F* test and least significant range test (Sokal and Rohlf, 1969). This relationship is discussed in detail in Smith (1980).

Topographic Comparisons in E. schultzei at 3600 m: Maximum height and hence maximum age were greatest on the slope base site and lowest on the ridge (Figure 15). Mean plant height decreased from slope base to ridge and from windward slope to leeward slope.

On the xeric slope site at 3550 m, high adult mortality apparently resulted in a very young population, with no plants in the larger size classes (Figure 16A). On the talus slope site at 3600 m, there were comparatively few small plants, but maximum plant height was nearly one meter (Figure 16B). Mortality data were not collected for the talus slope population. However, wet season leaf expansion rates were similar for the two populations, suggesting that differential mortality, rather than differential growth, may be largely responsible for these two contrasting size class distribution patterns.

Interspecific Comparisons: Small size in *E. floccosa* (Figure 17A) combined with rapid height growth suggest that it may have the shortest generation time of the species studied. The largest plants measured in 1972 flowered and died in late 1975 (see "Reproductive Phenology", page 31).

The largest *E. lutescens* adults at 4200 m were 160 to 170 cm tall (Figure 17B). It is possible that these plants were at least 100 years old, because annual height increase was 1.5 cm at this site. Mean rate of branch elongation in *E. humbertii* on the talus slope at 3500 m was 4.2 cm per year.

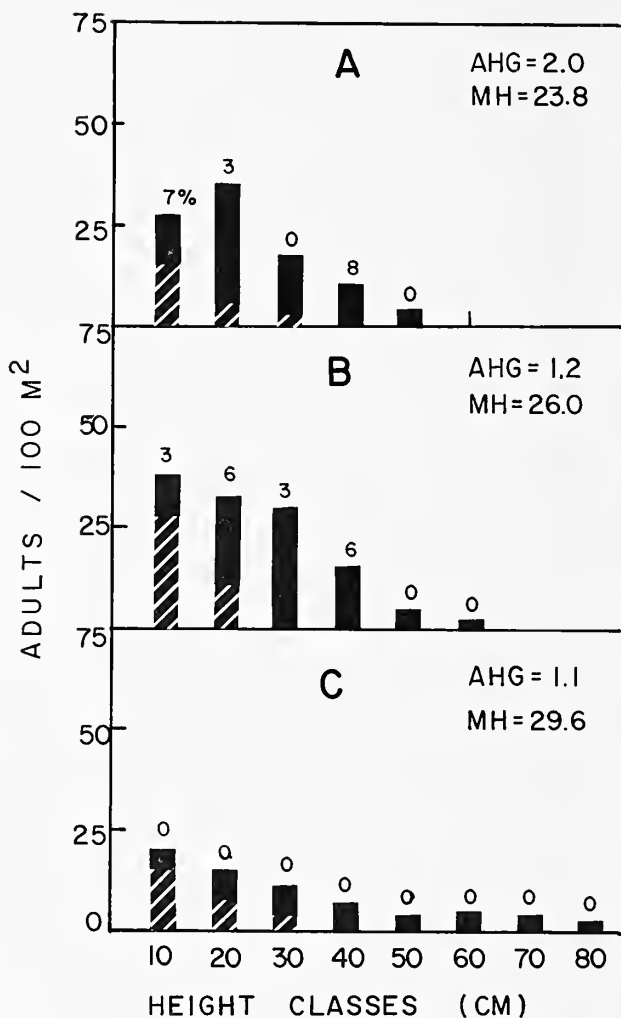


FIGURE 14.—Altitudinal variation in population structure and dynamics for *E. schultzei* adults on midslope windward sites: A, 3000 m; B, 3600 m; C, 4200 m (adult = plant with rosette diameter of 25 cm or greater; AHG = annual height growth (cm); MH = mean height; solid bar = reproductives; striped bar = prereproductives; number on bar = percent mortality in one year).

Using this rate to convert height to approximate age, it appears that the tallest individuals may have been at least 70 to 80 years old (Figure 18).

GROWTH.—Growth in adults was measured in two ways. First, annual increase in height was recorded for the 120 marked adults in each plot. Techniques are given in the preceding section. The second measure of growth was rate of leaf expansion. Fifty of the 120 marked adults were randomly selected for these measurements. The

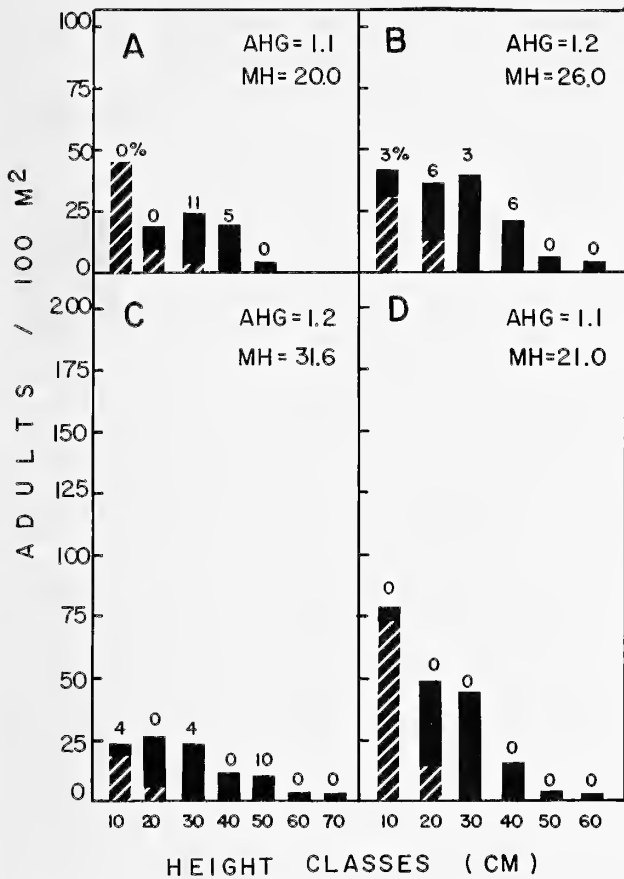


FIGURE 15.—Topographic variation in population structure and dynamics for *E. schultzii* adults at 3600 m: A, ridge; B, midslope windward; C, slope base; D, midslope leeward (adult = plant with rosette diameter of 25 cm or greater; solid bar = reproductives; striped bar = prereproductives; number on bar = percent mortality in one year).

oldest leaves in the apical bud were marked on the tip with indelible ink (Nursery Marker, Horta Craft Corporation), and the number of leaves expanding from the bud during the next 4 to 6 weeks was recorded. This procedure was carried out in the wet and dry seasons and in a wet season-dry season transition period, providing a measure of the seasonality of growth. In *E. floccosa* there was no clear differentiation between bud leaves and rosette leaves. Thus, leaf expansion rates could not be determined accurately for this species.

Two plants could produce the same number of leaves per unit time yet produce very different

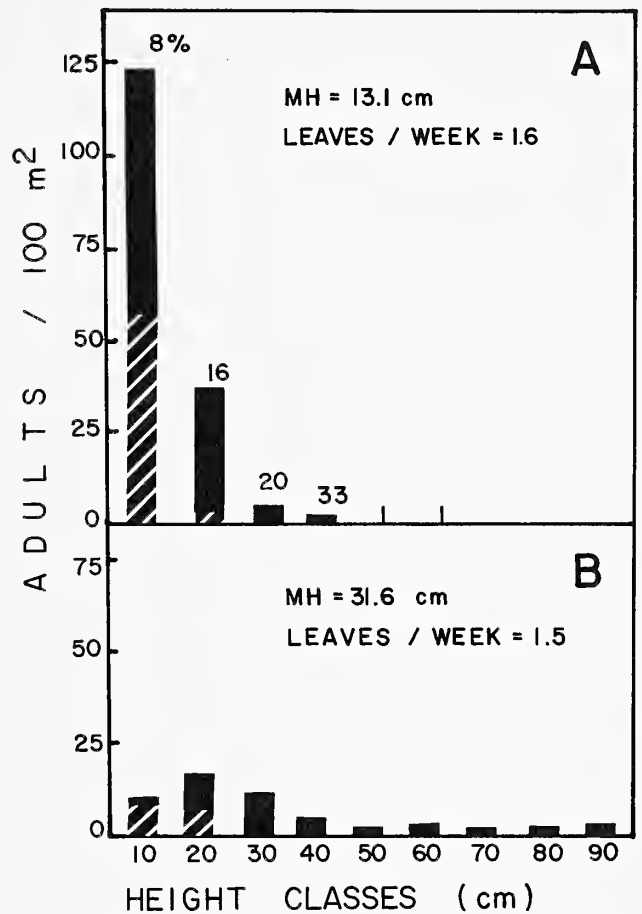


FIGURE 16.—Population structure and dynamics for *E. schultzii* adults at 3600 m: on A, xeric slope; B, talus slope (adult = plant with rosette diameter of 25 cm or greater; rate of leaf production measured during the wet season; solid bar = reproductives; striped bar = prereproductives; number on bar = percent mortality in one year; MH = mean height).

amounts of leaf tissue, since leaf size varied greatly from plant to plant. Therefore, for each of the 50 plants at each site, the outline of the outermost mature leaf was traced in situ, and the area of the outlines determined with a planimeter. In converting from number of leaves expanded per unit time to leaf area produced per unit time, the number of leaves was multiplied by this area.

Leaf area produced per unit time was converted to dry weight of leaf tissue produced per unit time. To do this, mature leaves from 50 additional plants were collected at each site. Each leaf was traced and the area determined with a

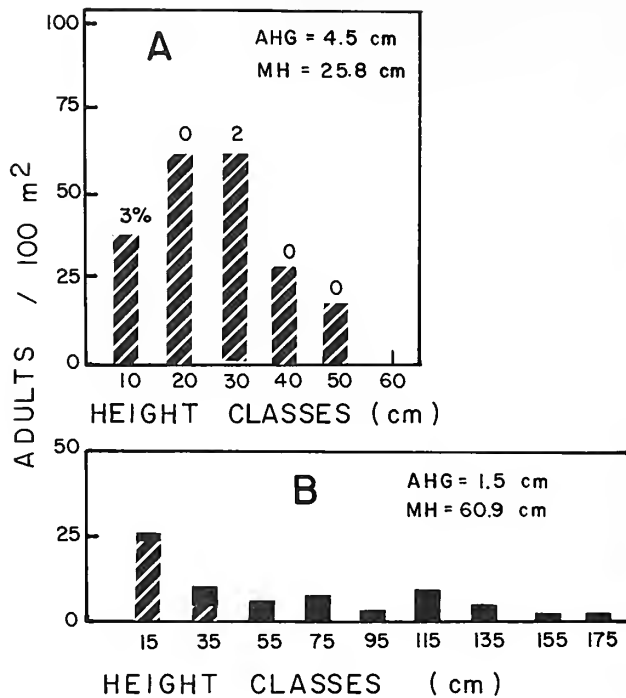


FIGURE 17.—Population structure and dynamics for adults: A, *E. floccosa* at 3600 m; B, *E. lutescens* at 4200 m (*E. floccosa* adult = plant with rosette diameter of 15 cm or greater; *E. lutescens* adult = plant with rosette diameter of 40 cm or greater; AHG = annual height growth (cm); MH = mean height; solid bar = reproductives; striped bar = prereproductives; number on bar = percent mortality in one year).

planimeter. Oven-dry weight was determined for each leaf and dry weight per unit surface was calculated. Dry weight per unit surface area was regressed against total area per leaf. If there was a significant correlation at a given site, the resulting regression line was used to determine dry weight per surface area for each intensively studied plant. If there was no correlation, the mean figure for dry weight per unit leaf area was used. The figure for grams dry weight per cm² of leaf surface was multiplied by the figure for leaf area produced per week by each plant.

Growth was highly seasonal at most sites. A quantitative index was developed to express this seasonality. For each plant, the rate of leaf expansion during the dry season was divided by the rate of expansion during the wet season. The results for all plants at a given site were then

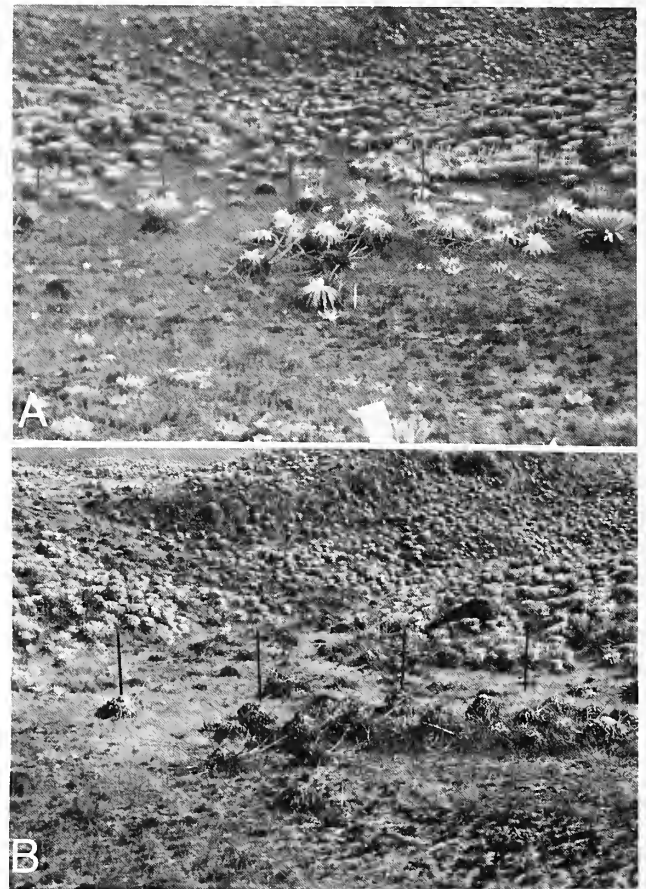


FIGURE 18.—Effect of flooding on *E. schultzei* in a swale at 3600 m; A, June 1972; B, March 1973.

summed and averaged, and the resulting mean multiplied by 100. Seasonality (S) is calculated by

$$S = \frac{\sum_{i=1}^n \frac{D_i}{W_i} \times 100}{n}$$

where S is seasonality, D_i is rate of leaf production for the i th individual in the dry season, W_i is rate of leaf expansion for the i th individual in the wet season, and n is the number of individuals.

Altitudinal Trends within E. schultzei: Seasonality decreased with increasing elevation for midslope windward sites (Table 8) because dry season growth rates increased with increasing elevation, and for the same sites in the wet season, growth rates decreased with increasing elevation.

TABLE 8.—Growth rates and seasonality (dry season growth rate as percentage of wet season growth rate) (dates for sampling periods given in Appendix Tables C-E; see page 22 for definition of "seasonality")

Species and sites	Wet to dry season transition		Dry season		Wet season		Leaves/ year	Grams/ year	Seasonality
	Lvs/week	Gm/week	Lvs/week	Gm/week	Lvs/week	Gm/week			
<i>E. schultzi</i>									
3000 m	3.5±0.18	5.4±0.48	1.0±0.09	1.6±0.21	3.2±0.18	5.4±0.43	125	210	28.2±2.6
3600 m									
Bog edge	-	-	1.1±0.09	1.9±0.24	2.6±0.17	4.6±0.54	-	-	44.8±3.6
Slope base	2.6±0.21	5.2±0.83	1.4±0.12	2.6±0.43	3.0±0.29	6.1±1.05	119	236	50.8±5.5
Windward slope	2.2±0.12	4.0±0.37	1.1±0.09	2.1±0.26	2.4±0.18	4.4±0.49	96	177	55.0±6.1
Ridge	1.9±0.12	3.5±0.42	1.4±0.11	2.5±0.32	2.0±0.15	3.6±0.48	88	163	74.2±5.3
Leeward slope	2.0±0.12	3.6±0.46	0.8±0.09	1.4±0.20	2.0±0.16	3.6±0.54	81	146	43.9±4.4
4200 m	1.6±0.11	3.9±0.40	1.3±0.12	3.0±0.36	1.3±0.12	3.2±0.38	72	172	92.4±11.1
<i>E. lutescens</i>	1.2±0.11	4.4±0.67	1.0±0.14	3.4±0.81	1.6±0.19	5.7±0.84	64	231	68.4±15.0
<i>E. humbertii</i> *	0.1±0.01	0.3±0.05	0.1±0.02	0.3±0.05	0.4±0.04	0.9±0.12	10	25	34.3±7.1

* Leaf expansion recorded for single leaf rosettes, rather than for whole trees.

Decreasing vegetation cover with increasing altitude might result in decreasing interspecific competition for water in the dry season, causing reduced seasonality. Decreased intraspecific competition could also be a factor. At 3000 m, there was a significant positive correlation between nearest neighbor distance and growth rate in the dry season ($r_{xy} = 0.491$), but a weaker correlation during the wet season ($r_{xy} = 0.272$) (Table 10), suggesting that the plants at this site were competing for water. No such correlations were found at higher elevations. Frequency of juvenile plants of *E. schultzi* decreases with increasing elevation. Competitive effects of juveniles on adults would therefore decrease, further improving dry season growth at 4200 m. Leaf pubescence increases with increasing elevation in *E. schultzi* (Z. Baruch, pers. comm., Nov 1973). This might result in greater buffering against drought stress, reducing seasonality of growth.

Topographic Trends in E. schultzi at 3600 m. Seasonality decreased from bog edge to ridge and from leeward slope to windward. This trend occurred despite the fact that the ridge and windward slope sites both had lower soil moisture levels than did the bog edge and both were more exposed to the prevailing wind than was the leeward slope.

Greater seasonality of growth for the bog edge plants could be related to rapid leaf senescence and resulting decrease in total leaf surface area during the dry season. Reduction in dry season leaf number on the bog edge site was far greater than on the midslope site (Table 9). This reduction was due to wilting of the outermost rosette leaves. Rates of dry season leaf expansion were the same for the bog edge and midslope plants. Windward and leeward halves of each rosette were distinguished when leaves were counted in the early dry season. For the bog edge there was no significant difference between number of leaves in the two rosette halves. For midslope plants, however, the mean number of leaves in the leeward rosette halves was 30.6 versus 24.9 for the windward halves. These means were significantly different ($P < 0.005$). The midslope site was subject to far stronger winds than was the bog edge site. In the wet season, there was no significant difference between mean leaf number in the leeward and windward rosette halves for the midslope plants. Rosette halves were not sampled separately when the bog edge plants were resurveyed.

Greatest total wilting occurred on the bog edge despite greater wind-related wilting on the midslope site. It is unlikely that the wilting was

TABLE 9.—Number of leaves per rosette and leaf expansion rates for *E. schultzii* at 3600 m (50 adult plants measured at each site)

Sites and seasons	Leaves/ rosette	$\frac{\text{Leaves/rosette, dry season}}{\text{Leaves/rosette, wet season}} \times 100$		Leaves/ week	$\frac{\text{Leaves/rosette, dry season}}{\text{Leaves/rosette, wet season}} \times 100$	
Midslope windward						
Wet season	68±16.1			2.4±0.18		
Dry season	55± 4.3	81.6%		1.1±0.09	55.0%	
Bog edge						
Wet season	60± 4.4			2.6±0.17		
Dry season	34± 2.5	57.0%		1.1±0.09	44.8%	

related to soil moisture. On 2 January 1973, soil moisture on the bog edge was 46%, versus 31% on the midslope windward site. Mean minimum temperatures in the dry season were much lower in the bog (and hence on the bog edge) than on the midslope site. Greater leaf wilting on the bog edge might have been related to an interaction of (1) freezing stress and (2) drought stress due to rapid heating of leaves early in the morning when, because of cold stem and roots, water transport to leaves is inefficient. Presumably, this second factor would be more important on the bog edge than on the midslope site because of lower stem and root temperatures imposed by dry season cold air drainage.

The difference in seasonality between the leeward and the windward slopes might have been the result of (1) greater adult density on the leeward slope, leading to greater dry season competition for water (199 adults per 100 m² on the leeward slope versus 122 on the midslope windward site); (2) higher dry season mean maximum temperature on the leeward slope, possibly resulting in greater dry season evapotranspiration; (3) slightly lower dry season soil moisture levels on the leeward slope.

There was a significant positive correlation between seasonality and distance to nearest adult neighbor on the midslope leeward site (Table 10). With increasing distance between an adult plant and its nearest adult neighbor, growth became progressively less seasonal. This suggests that some form of intraspecific interference may be controlling seasonality at this site.

There was a significant negative correlation between seasonality and distance to nearest neighbor on the midslope windward side. Thus, growth becomes progressively more seasonal with increasing distance between an adult plant and its nearest adult neighbor. There is probably a sheltering effect on one plant by another on the gently sloping windward site, reducing wind-induced drought stress. This would be most important for short plants located on the leeward sides of taller plants. On steeper windward sites, such as the ridge plot, an adult located on the windward (downslope) side of a second plant might provide little or no shelter, even if taller than the second plant.

Further studies will be required to determine the causes of these patterns in seasonality. However, the data do suggest that there is strong intraspecific control over seasonality within local populations and that the nature of this control changes qualitatively with change of topography.

Interspecific Comparisons: Growth in *E. lutescens* was more seasonal than growth in the adjacent *E. schultzii* population (Table 8). *Espeletia schultzii* at 4200 m was restricted to shallow swales that received runoff from the surrounding páramo during the wet season. The *E. schultzii* population studied was on ground 1 to 3 dm lower than the adjacent *E. lutescens* population. Soil moisture, measured on 26 Mar 1973, at 0–10 cm was 20% for the *E. schultzii* plot versus 16% for the *E. lutescens* plot. Percentage moisture content under 15 atmospheres pressure (laboratory determina-

TABLE 10.—Correlations of nearest neighbor distance with adult leaf production (g/week) and with seasonality of leaf production

Species and sites	G/week versus nearest neighbor		Seasonality versus nearest neighbor r_{xy}
	Dry season r_{xy}	Wet season r_{xy}	
<i>E. schultzii</i>			
3000 m	0.491 P<0.001	0.272 P<0.1	0.214 P<0.05
3600 m			
Slope base	0.268 P<0.1	0.145	-0.036
Windward slope	-0.222	-0.100	-0.278 P<0.05
Ridge	-0.219	-0.259	-0.108
Leeward slope	-0.117	-0.168	0.384 P<0.01
4200 m	-0.041	0.163	-0.174
<i>E. lutescens</i>			
4200 m	-0.209	-0.126	0.311
<i>E. humbertii</i>			
3500 m	0.171	0.182	0.057

tion) was 14% for the *E. schultzii* plot and 11% for the *E. lutescens* plot. Vegetation cover was slightly lower on the *E. schultzii* plot ($29 \pm 8.6\%$ versus $38 \pm 8.1\%$), and percentage cover by bare rock was higher ($55 \pm 8.7\%$ versus $38 \pm 9.1\%$).

Height growth in *E. floccosa* at 3600 m was faster than in any other species studied. This species generally grows on rocky, windward slopes—sites where both vegetation cover and density of *E. schultzii* are generally lowest. Fast growth, occupation of apparently unfavorable sites, short generation time, and semelparous reproduction are characters often attributed to “r-selected” species (Gadgil and Solbrig, 1972).

The growth rates for *E. humbertii* (Table 8) were much lower than for other species because rate of leaf expansion was recorded for a single leaf rosette, rather than for the entire crown. With the exception of unbranched saplings, crowns were made up of many leaf rosettes located on branch apices. Number of rosettes per tree ranged from 1 to 46, with a mean of 10 ± 2.4 . There was no significant correlation between the total number of rosettes making up a given tree crown and the growth rate measured for one of these rosettes. Overall growth rate for a given tree will therefore be proportional to the number of rosettes making up the crown.

Growth was highly seasonal in *E. humbertii* (Table 8). The leaves on several trees growing on a

rock outcrop at Laguna Negra showed signs of wilting toward the end of the dry season. Cross-sections of *E. humbertii* trunks showed distinct growth rings, providing further evidence of seasonal growth.

For *E. humbertii* no significant correlations were found between growth rate and distance to nearest neighbor or between seasonality and distance to nearest neighbor (Table 10). However, there were significant positive correlations between nearest neighbor distance and plant size (Table 11), suggesting that interference of some sort has occurred in the past. There was a weak positive correlation between basal stem diameter and nearest neighbor distance for the 50 trees used for growth studies. These plants were scattered throughout the talus population, from the bottom to the top of the slope (a distance of about 30 m). For the plants occurring in plot 1, near the base of the slope, there was no correlation. For the plants occurring in plot 2, near the top of the slope, there was a strong positive correlation.

In both the closed forest plot and the treefall site, there were positive correlations between plant size and nearest neighbor distance. The seedlings in the treefall produced dense cover several dm above ground level. Both sites therefore had essentially closed canopies. Competition for light as well as for water and nutrients could have enforced the observed spacing patterns at these sites.

TABLE 11.—Correlation of distance to nearest conspecific adult with adult plant height

Species and sites	Mean distance to nearest neighbor (cm)	Height vs. nearest neighbor distance (r_{xy})	
<i>E. schultzei</i>			
3000 m	7.2± 2.5	0.104	
3600 m			
Slope base	18.3± 3.5	0.055	
Windward slope	25.9± 1.8	0.146	
Ridge	15.4± 3.1	0.280	P<0.01
Leeward slope	9.4± 1.5	0.078	
4200 m	24.5± 5.1	-0.103	
<i>E. floccosa</i>			
3600 m	12.0± 3.1	-0.103	
<i>E. lutescens</i>			
4200 m	22.1± 4.0	0.041	
<i>E. humbertii</i> *			
Talus plot 1	108.1±18.8	0.262	
Talus plot 2	98.6±22.1	0.515	P<0.01
50 growth-study plants	91.5±16.4	0.248	P<0.1
Closed forest	62.1±10.9	0.416	P<0.01
Forest treefall	18.9± 1.8	0.190	P<0.01

* With exception of treefall plot, all *E. humbertii* analyses carried out for basal stem diameters, rather than height. Plant heights used for treefall plot.

ROSETTE TURNOVER TIME.—Short-term measurements of leaf expansion were used to estimate total number of leaves expanded in one year (Table 8). Wet season, dry season, and transitional periods were each assumed to make up one-third of the year. For each plant, the number of rosette leaves present during the wet season of 1973 was then divided by the estimated number of leaves expanded during the year, to provide an estimate of the time required to renew an entire complement of rosette leaves.

For *E. schultzei*, turnover time increased with increasing elevation because leaf production rates decreased (Table 12). Slow rate of leaf replacement might in part explain the upper elevational limit of *E. schultzei*: above 4200 m leaf damage and senescence might occur more rapidly than leaf growth. At 4200 m, turnover time was greater for *E. lutescens* than for *E. schultzei*. This was due

TABLE 12.—Time required for complete replacement of rosette leaves (turnover time) (leaf expansion rates not measured in *E. floccosa*)

Species and sites	Number leaves/year	Mean number of leaves/rosette ²	Leaves/rosette/Leaves/year
<i>E. schultzei</i>			
3000 m	125	70.5± 4.80	0.56
3600 m			
Slope base	119	74.6± 6.60	0.63
Windward slope	96	68.0±16.10	0.71
Ridge	88	66.3± 5.40	0.75
Leeward slope	81	58.9± 4.90	0.74
4200 m	72	77.9± 6.10	1.08
<i>E. lutescens</i>			
4200 m	64	95.5± 7.90	1.49
<i>E. humbertii</i> ¹			
3500 m	10	13.4± 0.93	1.34

¹ Per leaf rosette, not per tree.

² Mid-wet season, 1973.

in part to a slower rate of leaf expansion in *E. lutescens*, but also resulted from a larger number of leaves per rosette. Long turnover time for the *E. humbertii* population on talus was due to the low rate of leaf expansion. This slow expansion rate might have resulted in part from the large energy input required for maintenance and growth of an arborescent support system.

MORTALITY.—Data on adult mortality during one year were based on death of marked plants at each study site (Figures 14–16; also see “Experimental Study of Growth”). Mortality rates were very low. Many qualitative observations on adult mortality were made and these provide information on seasonal, altitudinal, and topographic patterns.

Flooding: For *E. schultzei*, high wet season mortality was observed in several swales at 3000 m and 3600 m. These swales were apparently subject to flooding only during periods of extremely intense rainfall. Rainfall during the month of May 1972 was the highest recorded for this month during 30 years of measurements (Figure 5). The preceding dry season also had unusually heavy rainfall. In May 1972, at both 3000 m and 3600 m, a number of swales had standing water for

several days. Flooding recurred periodically during June. These swales had populations of *E. schultzi* with adults up to 40 or 50 cm tall. In late May and early June, these plants began to wilt. In one typical swale at 3600 m (Figure 18), all seedlings and adults had died by the end of the wet season. These plants had evidently become established in the swales during a long period of more moderate rainfall. High dry season rainfall then resulted in extensive soil flooding, killing the plants.

Local distribution patterns of *E. schultzi* along certain moisture gradients apparently undergo long-term fluctuations—gradual expansion into swales during drier periods and rapid contraction during extreme wet periods. This pattern would be well developed in those few swales that, because of topography, receive heavy flooding only during extreme wet years. For most swale-upland ecotones, annual flooding presumably eliminates any seedlings that germinate in the swale.

No wet season mortality was observed in *E. schultzi* at 4200 m. At this elevation, *E. schultzi* populations were largely restricted to drainage areas that often had running water during heavy wet season rains. However, the soil in these areas was extremely rocky so that drainage might be sufficient to prevent flooding of roots. At this site, populations of *E. schultzi* did not occur in swales that retained standing water.

Drought and Temperature Stress: At 3600 m, dry season mortality was common in three habitats: (1) xeric slopes; (2) valley floors and other frost pocket sites; and (3) edges of bogs and wet meadows, with or without cold-air drainage.

Extensive dry-season mortality in *E. schultzi* occurred on a steep, S-facing slope located on a terminal moraine above Laguna Mucubají (Figure 16A). Soil moisture measured on 26 February 1973 at 0–15 cm was 5.8%. Wilting percentage (percent moisture content under –15 atmospheres pressure) was 10.6%. This was the only site studied for which soil moisture dropped below the wilting range. On the same date, soil moisture for the midslope windward plot at 3600 m was 20.6%. Wilting percentage for this site was 18.0%.

There was a positive linear correlation between height class and mortality rate ($r = 0.977$, $P < 0.05$). No other population showed a significant correlation between adult size and mortality rate. Mean nearest neighbor distance for survivors was not significantly different from that for mortalities. It appears that adult mortality at this site is comparatively low during moderate dry seasons, permitting survival of older, taller individuals. During occasional severe droughts, however, these taller plants may be more susceptible to drought stress than shorter adults both because of greater wind exposure and because of greater stem resistance to water transport (cf. Zimmerman and Brown, 1971). *Espeletia* stems may store water (Smith, 1979) but very severe droughts may deplete this, eliminating this beneficial aspect of greater stem height.

Mortality was common among *E. schultzi* adults on the floor of a large morainal valley at 3600 m. This area received extensive cold-air drainage.

Extensive *E. schultzi* mortality was commonly observed on the edges of sloping wet meadows. These sites are not frost pockets. The meadow edges were flooded during the intense rainfall of May 1972. It is hypothesized that this flooding, though less extensive than in swales and not sufficient to cause immediate death, was sufficient to cause some initially nonlethal root die-back. Reduced efficiency of water uptake might then have caused mortality.

Fire: Páramo fires can cause adult mortality in the dry season. One such fire was observed at 3200 m (Laguna Victoria). The burned site was on a gentle NE-facing slope. Of 137 adult *E. schultzi* plants in a 10 × 10 m sample plot, 55% had been killed by the fire. Damage appeared to have taken two forms. For plants 1–2 dm tall, the apical meristem seemed to have been burned. In taller plants, mortality occurred if the dead leaves retained around the stem had been burned off and the stem itself had been burned.

Herbivory: Insect damage to leaves was extensive in *E. schultzi* at 3000 m and below, but was much less common at 3600 m and 4200 m during 1972–

1973 (Table 13). Longer-term data suggest that elevational trends are extremely variable from year to year (Smith, ms. in prep.). Insect larvae (unidentified) burrowed in the apical bud. Mature click beetles (Elateridae) were observed feeding on bud leaves, on some plants. They consumed all leaf tissue except the midvein. No insects were observed feeding on mature leaves. Insect damage could not be linked directly to mortality, but it is possible that the larvae may occasionally burrow through the apical meristem, causing death. Reduced photosynthetic area due to predation could reduce competitive ability and fruit production.

Leaf herbivory was more common in the *E. lutescens* population than in the adjacent *E. schultzii* population at 4200 m. No mortality was recorded for the research plants of *E. lutescens* that had been subject to predation. However, there was an area that appeared to have been the site of extensive insect-related mortality approximately 200 m upslope from the *E. lutescens* study plot. The area was approximately one hectare in size. Near the center of the area there were many fallen dead stems of *E. lutescens* and no live adults. Further out from the center there were *E. lutescens* plants that appeared to have died more recently; they were still standing. Toward the edge of the area were many *E. lutescens* plants in which a large portion of the rosette leaves had been elim-

inated, apparently through larval herbivory. The apical buds of many of these plants were inspected and all had insect larvae burrowing in them. Beyond these heavily attacked plants, *E. lutescens* plants with moderate levels of herbivory were found. This pattern suggests that a long-term buildup of insects may be resulting in a very local elimination of *E. lutescens* over an area of several hundred meters. Reduced seed production, combined with naturally low probability of seedling establishment at this elevation, will make reestablishment of the population a slow process.

Leafhoppers (Homoptera) attacked the mature and immature leaves of *E. atropurpurea*, *E. humbertii*, and *E. neriifolia*. Every plant inspected had at least a few damaged leaves. These three species lack pubescence on their upper leaf surfaces. Levin (1973) has suggested that, in many plants, leaf pubescence may provide protection against leaf herbivory. However, other factors such as toxin production and nutrient levels could also be involved.

Semelparity: The only clear-cut mortality pattern noted for *E. floccosa* adults was that associated with flowering. If plants live to reproduce, death occurs immediately after fruiting. Flowering occurs in the early to mid wet season, so adult mortality is also concentrated in this period. Several hundred dead plants with flower stalks were observed at Mucubají. None of these showed

TABLE 13.—Number of adult plants in study plots that had insect-damaged leaves

Species and sites	Wet season 1972		Wet season 1973		Number of plants damaged in 1973 that were also damaged in 1972		Total	
	Plants	Percent	Plants	Percent	Plants	Percent	Plants	Percent
	<i>E. schultzii</i>							
3000 m	103	86	105	90	96	83	112	93
3600 m								
Slope base	2	2	12	10	1	1	13	11
Windward	11	9	16	14	2	2	25	21
Ridge	1	1	8	7	0	0	9	8
Leeward	16	13	30	25	6	5	40	33
4200 m	7	6	0	0	0	0	7	6
<i>E. lutescens</i>	30	25	29	27	17	16	42	35
<i>E. floccosa</i>	9	8	13	11	5	4	17	12

evidence of resprouting. No live adults with flower stalks were observed.

Effects of Man: Harvesting of *Espeletia* plants for medicinal and other uses may have a significant impact on some species. *Espeletia weddellii*, an acaulescent herbaceous species, is collected for use as a cure for respiratory diseases (Faustino Diaz, pers. comm., June 1973). This species is never abundant, so that such collecting could cause local extinction. Its present scarcity might be the result, in part, from past collecting. Roots of *E. schultzii* are reportedly used in the manufacture of local butter and *E. schultzii* leaves are used to package the butter.

The branches of *E. humbertii* and *E. neriifolia* are collected and the resin extracted for use as incense in churches. Cutting of subalpine forests is rapidly reducing population size in these arborescent species.

Intense agriculture in the main valley of the Río Chama, between Mucuchies and Mucubají, has resulted in almost complete elimination of *Espeletia* (both arborescent and rosette species) below 3400 m, although *Espeletia* does occur in less heavily used side valleys.

REPRODUCTIVE PHENOLOGY.—For each species, the number of individuals in each plot that flowered during the field research period was recorded. A more detailed study of reproductive biology was carried out for *E. schultzii* at 3600 m. Flower and fruit production were recorded monthly for 100 *E. schultzii* plants on the floor of a sheltered morainal valley and for 100 plants on a windy ridge 140 m above the valley floor. The plants studied were the first reproductive adults (adults in flower or which had flowered in the past) encountered along a line transect at each site. In addition, flowering of *E. schultzii* was recorded on a series of seven low ridges at 3600 m. The ridges had NE-facing (windward) and SW-facing (leeward) slopes, with relief of 3 to 5 m. For each ridge, one line transect was run across the SW-facing slope and a second along the adjacent NE-facing slope. The transects were located 2 m below the ridge crests. Presence or absence of flower buds, flowers, and fruit

(achenes) was recorded for the first 100 reproductive adults along each transect. The 14 transects were run in October 1972 and were resurveyed in November 1972.

A comparison of flowering on the windward and leeward sides of *E. schultzii* plants was made at Mucubají (3600 m). The research site was on the crest of a terminal moraine immediately west of Laguna Mucubají. This site received the full force of the prevailing NE winds. The number of flower stalks, and flower stalk length, was recorded for the NE-facing (windward) and SW-facing (leeward) halves of each rosette. Fifty plants were studied. All plants had completed flowering and had set fruit.

Flower and fruiting heads were collected from 50 *E. schultzii* plants at 3000, 3600, and 4200 m. The fruiting heads were collected just before fruit dispersal began and were taken from the same plants from which flower heads were obtained. Fruiting heads generally remained tightly closed until just before the fruit were dispersed. Number of ray (male) and disc (female) flowers were recorded for the flower heads. Number of achenes and number of insect larvae were recorded for each fruiting head.

Mature fruit were collected from 50 plants at the same three sites. Fruit size and weight per whole fruit were recorded. Fruit were cut open to determine the proportion of apparently normal fruit that were hollow.

A detailed study of pollen flow and seed dispersal was made, and will be reported elsewhere (Teeri and Smith, unpublished data).

Elevational Comparisons of Flowering Phenology in E. schultzii: At 3000 m and 3600 m, flowering was concentrated in the wet season and the wet season-dry season transition period (Table 14). Fruit production and dispersal at these sites began during the wet season and continued throughout the dry season and into the next wet season. However, most fruit had already been dispersed by the beginning of the next wet season. Germination at all sites generally began with the onset of the wet season rains.

At 4200 m, *E. schultzii* produced flowers and

TABLE 14.—Number of plants that flowered within each 100 m² study plot (figures in parentheses = number of flowering plants as percentage of all adults in plots)

<i>Species and sites</i>	<i>Plants in 1972 with 1971 seedheads</i>	<i>Plants flowering in 1972 wet season</i>	<i>Plants flowering in 1972-73 dry season</i>	<i>Plants with flowers or buds by mid-wet season 1973^b</i>
<i>E. schultzi</i>				
3000 m	10 (9.7)	29 (28.2)	0	9 (9.1)
3600 m				
Slope base	5 (5.2)	4 (4.2)	0	11 (11.7)
Midslope windward	12 (9.8)	0	0	5 (4.1)
Ridge	13 (11.2) ^c	0	0	5 (4.4)
Midslope leeward	26 (21.7)	0	0	7 (3.5) ^d
4200 m	3 (3.8)	19 (23.8)	10 (12.5)	29 (36.3)
<i>E. lutescens</i>				
4200 m	0	7 (8.1)	0	0
<i>E. floccosa</i>				
3600 m	0	0	0	0
<i>E. humbertii</i>				
3500 m ^a	Not recorded	21 (42.0)	0	10 (20.0)

^a Based on 50 marked adults used for growth studies.

^b Final observations were made in August 1973, before the end of the wet season.

^c Based on 120 marked adults in the plot.

^d Based on all 199 adults in the plot.

fruit throughout the year. Here *E. schultzi* populations were generally restricted to rocky drainage areas that received runoff from the surrounding areas. This aseasonality in flowering was associated with aseasonality of growth as well (Table 8). Possible explanations for this lack of seasonality were discussed in an earlier section.

At 4200 m, flower heads produced during the dry season frequently were killed by frost during clear cold nights. Generally, only expanded flower heads were killed; flower buds were seldom damaged. At 3600 m (Mucubají) frost damage to flower heads was observed occasionally in the few plants producing flowers in late December 1972, at the end of the flowering season. Such damage was observed again for the few plants coming into flower in April and May 1973, at the beginning of the 1973 flowering season. The damage occurred during several periods of unusually low rainfall, when clear cold nights were more common. It was most pronounced on the floor of a large morainal valley (see Smith, 1980).

No population of *E. schultzi* was found in

which all reproductive adults were in flower during a given wet season. Some plants flowered during both wet seasons (1972 and 1973), but many other plants flowered in only one. Many plants that had flowered during past years did not flower during the period of this study.

Topographic Comparison of Flowering Phenology in E. schultzi at 3600 m: Flowering occurred first on leeward slopes and valley floors and last on exposed ridges and windward slopes. The proportion of all reproductive adults that flowered at any given time also decreased from leeward to windward slopes and from valley floors to ridge tops (Figure 19). Plants that did flower on ridge tops produced fewer flower heads than plants on the valley floor (Table 15).

Table 16 summarizes data on flowering on a series of NE-facing (windward) and SW-facing (leeward) slopes. On 1 October 1972, 31 plants on the SW-facing slopes were in fruit (24.2% of all plants that flowered during the year), whereas only one plant (4.9% of all plants which flowered during the year) had come into fruit on the NE-

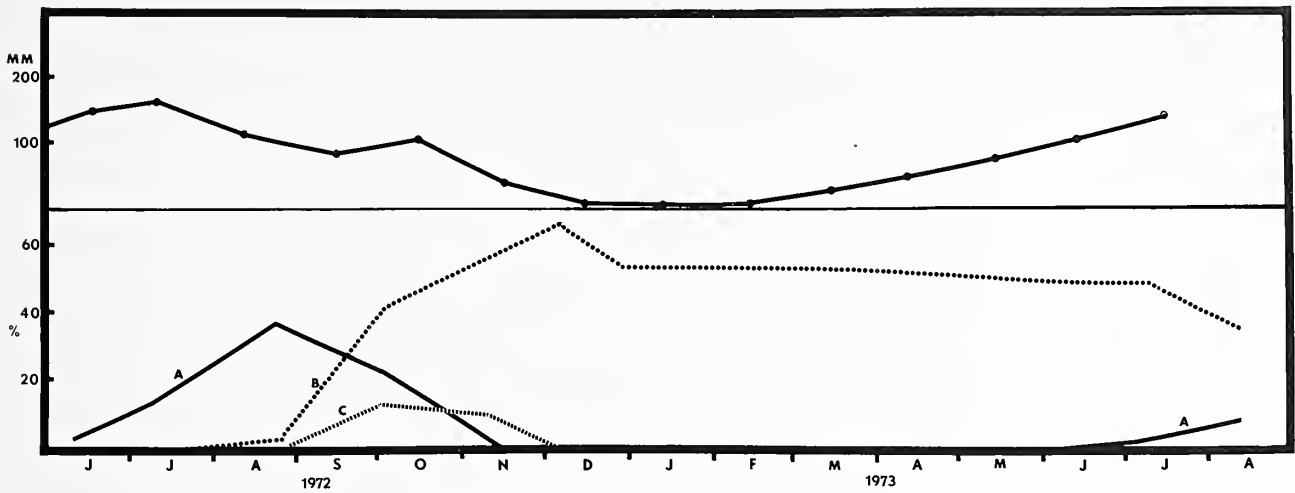


FIGURE 19.—*Top*: Monthly precipitation at Mucubají (3550 m). *Bottom*: Flower and fruit production in *E. schultzei* at 3600 m (A = percent of plants in flower on valley floor; B = percent of plants in fruit on valley floor; C = percent of plants in flower, windy ridge, 140 m above valley floor).

TABLE 15.—Mean number of flower heads per flowering plant for *E. schultzei*, recorded at five sites within a morainal valley at 3600 m (relief was 140 m)

Site	Number of flower heads
East moraine	
Ridge top	43.6±10.48
Midslope leeward	88.2±19.74
Valley floor	169.9±33.03
West moraine	
Midslope windward	45.9± 8.95
Ridge top	39.8±14.60

TABLE 16.—Flowering on NE-facing (windward) and SW-facing (leeward) slopes at 3600 m (figures = number of flowering or fruiting plants per 100 adults sampled at each of seven sites; each figure = mean of seven sites)

Sites and stages	1 Oct 1972	18 Nov 1972
NE-facing slopes		
Flower buds only	1.0±0.69	0
In flower	1.6±0.48	0.4±0.79
Seed heads only	0.1±0.14	3.6±1.43
SW-facing slopes		
Flower buds only	3.3±0.81	0
In flower	10.7±1.91	1.7±0.68
Seed heads only	4.4±1.19	17.3±2.12

facing slope. Of 700 plants monitored on the NE-facing slope, only 17 flowered in 1972 versus 128 on the SW-facing slopes. Environmental differences between windward (NE-facing) and leeward (NW-facing) slopes are discussed elsewhere (Figure 6, 7).

Within-Plant Effects of Wind in E. schultzei at 3600 m: The mean number of windward flower stalks was 1.6 ± 0.4 ; the mean number of leeward flower stalks was 3.3 ± 0.5 . These means are significantly different ($P < 0.005$). The windward stalks were shorter than the leeward stalks (70.9 ± 1.3 cm versus 82.3 ± 1.4 cm). Shorter stalks on the windward sides of plants might have resulted from greater mechanical stimulation by wind, resulting in inhibition of elongation (Jaffe, 1980). Flower bud initiation, however, takes place inside the apical bud. The windward side of each plant was presumably cooler than the leeward, or suffered more drought stress, perhaps resulting in differential rates of flower bud formation.

Interspecific Comparisons of Flowering Phenology: The *E. lutescens* population at 4200 m flowered in the late wet season and wet season-dry season transition period of 1972, but did not flower in 1973. No recent *E. lutescens* flower stalks were found in the early wet season of 1972, suggesting

that flowering probably did not occur during 1971. Flowering occurred again during 1975; no flowering occurred in 1976 or 1977. These observations suggest that *E. lutescens* flowering occurs less than once a year, but that it may occur synchronously within the population.

No flowering occurred in the *E. floccosa* plot during 1972–1973, although widely scattered individuals did flower in several populations at 3600 m during the wet season. Extensive flowering occurred in all populations observed in 1975. Only very scattered flowering occurred in 1976 and 1977. All plants that flowered died after fruit maturation.

Flowering in *E. humbertii* populations at 3600 m was concentrated in the wet season. Flowering occurred in 1972 and 1973. In the early wet season of 1972, stalks with fruit were still present, suggesting that flowering also occurred in 1971. During any given flowering period only a portion of all reproductive-age plants actually produced flowers.

Fruit Size: Data on flower and fruit production in *E. schultzi*, *E. floccosa*, and *E. humbertii* are summarized in Table 17. The most consistent trend was an increase in *E. schultzi* fruit weight with increased elevation. Larger fruit contain either more endosperm or larger embryos. The thickness of the achene wall did not appear to

vary with elevation. Larger fruit could produce more vigorous, rapidly growing, seedlings. At 4200 m this would increase the probability of seedling establishment during periods of low soil frost activity. It would also facilitate seedling growth in a rocky substrate or in dense mats of vegetation—habitats conferring protection from frost heaving.

Size-specific Reproduction: Number of flower stalks was recorded for 121 reproductive *E. schultzi* plants of known size on a valley floor site at 3600 m (Mucubají). Number of stalks (y) was linearly correlated with plant height (x) ($y = 3.94 + 0.13x$, $r = 0.34$, $P < 0.01$).

Number of flower heads was recorded for 73 reproductive *E. floccosa* plants on a windward slope at 3600 m (Mucubají). Rosette height was measured shortly before flowering began. Number of flower heads (y) was linearly correlated with plant height (x) ($y = 7.54X - 105.8$, $r = 0.59$, $P < 0.05$).

Hybridization: Putative hybrids between *E. schultzi* and *E. weddellii* (an acaulescent herbaceous species) were common wherever the two species occurred together in large numbers. Both species are insect-pollinated and have conspicuous yellow inflorescences.

A putative hybrid between *E. schultzi* and *E. humbertii* was found at 3500 m, on the edge of a

TABLE 17.—Flower and seed production

Species and sites	Number disc (male) flowers per head	Number ray (female) flowers per head	Number fruits per head ¹	Percent		Number flower heads per plant ³	Dry weight per fruit (mg)	Dry weight (g) per flower stalk
				hollow fruit ²	fruiting heads with insect larvae			
<i>E. schultzi</i>								
3000 m	101±7.7	82±2.8	75±4.6	32	36	104±31.7	0.3±0.02	23.2±1.19
3600	102±6.7	83±4.6	71±4.3	32	58	(see Table 15)	0.4±0.03 ⁴	16.9±0.67
4200 m	92±6.3	87±4.4	86±4.2	67	12	74±4.3	0.8±0.05	19.4±0.93
<i>E. floccosa</i>	—	—	32±3.5	—	100	656±105.3	1.2±0.08	28.4±5.00
<i>E. humbertii</i>	—	—	16±1.4	—	48	—	1.5±0.10	35.6±4.91

¹ Number of fruit that appeared undamaged.

² Percent based on number of seeds that appeared undamaged.

³ Number of heads per plant produced during the entire year.

⁴ The difference between mean seed weights for *E. schultzi* at 3000 m and 3600 m is weakly significant ($P < 0.1$); difference between 3600 m and 4200 m means is highly significant ($P < 0.001$).

talus slope near Laguna Negra. The hybrid was completely intermediate in leaf shape, leaf pubescence, apical bud structure, stem form, and flower stalk form. The flower stalks were old and badly weathered, with no flower or seed heads remaining. The putative hybrid plant was located on the edge of an *E. humbertii* population where *E. humbertii* plants were intermixed with *E. schultzii* plants. Inflorescences in *E. humbertii* are yellowish-white and smaller than those of *E. schultzii*, but both are insect-pollinated.

The occurrence of apparent hybrids between arborescent and caulescent rosette species and between caulescent and acaulescent species suggests that, despite great differences in growth form, the species are closely related. Barrett Rock (pers. comm., May 1972) found that there are no fundamental differences between arborescent, caulescent rosette, and acaulescent rosette *Espeletia* species with respect to the anatomy of the stem. He found that the anatomy of acaulescent rosette species such as *E. weddellii* closely resembles that of seedlings in the caulescent rosette and arborescent species.

EFFECTS OF SLOPE ASPECT ON GROWTH AND POPULATION DENSITY.—A special study was done to determine the effects of slope aspect on population density and adult growth rates in *E. schultzii* at 3550 m. The study was carried out in the lower enclosure, adjacent to Laguna Mucubají. Leeward slopes at this site were far more sheltered from the prevailing NE winds than was the leeward slope studied at the upper enclosure. The lower enclosure thus provided a clearer demonstration of the effects of wind.

The slopes were located on a series of small terminal moraines (Figure 2). Slope angles varied from 15° to 20°. Relief varied from 10 to 20 m. Four NE-facing (windward) slopes were compared with the adjacent WNW-facing slope. A 24-m transect was run along each slope, 2 m below the ridge crest. On the largest NE-SW slope system, with approximately 20 m of relief, two parallel transects located 2 m and 4 m below the crest were used. At 3 m intervals along each transect, the point-centered quarter method (Cot-

tam, et al., 1953) was used to determine adult density. Transect data were converted to number of adults per hectare.

Growth rates were measured for plants on a 20° NE-facing slope and the adjacent 20° SW-facing slope at 3550 m. Fifty adults on each slope were marked with metal stakes and numbered aluminum tags. The plants were located from 4 to 7 m below the ridge crest. In the dry season and again in the wet season the tips of the outermost bud leaves were marked with indelible ink. After several weeks the leaves that had expanded were counted. Dates for measurements are summarized in Appendix Tables C–E.

Wind speeds were measured at each of the transect sites with a Deuta-Werke hand-held anemometer at 1.5 m above the ground. Readings were taken between 1500 and 1515 hours on 28 July 1973. Each slope was visited twice and the readings averaged. These wind speed data are in agreement with those taken at the same sites on other days.

More intensive studies were not carried out at this site because it was susceptible to vandalism by visitors.

Adult Density: Data on *E. schultzii* adult density, along with data on wind speed for various slope types at 3550 m, are shown in Table 18. Mean adult density for the four NE-facing slopes was 49.5% of that on the four adjacent SW-facing slopes. This suggests that the prevailing NE wind may create a less favorable environment for *E. schultzii* on windward slopes.

Adult density on the ESE-facing slope was 26.3% of that on the WNW-facing slope—a greater difference than between the NE- and SW-

TABLE 18.—Number of *E. schultzii* adults (per hectare) and wind speed (mph) in relation to slope aspect

<i>Slope aspect</i>	<i>Adults</i>	<i>Wind speed</i>
NE-facing	14,690	16.3
SW-facing	29,680	4.1
NE/SW × 100	(49.5%)	(397.6%)
ESE-facing	5,730	12.0
WNW-facing	21,830	8.5
ESE/WNW × 100	(26.3%)	(141.2%)

facing slopes. However, wind speed on the ESE-facing slope was only about 1.4 times that on the WNW-facing slope—a smaller difference than between the NE- and SW-facing slopes. One possible explanation for this apparent discrepancy is that the ESE-facing slope faces more directly into the rising sun than does the NE-facing slope. As suggested earlier, rapid heating of leaves when soil, roots, and stem are still near freezing could result in early morning drought stress (cf. Mayland, 1972). All the slopes studied had similar slope angles and all were located on the same system of terminal moraines. Thus, differences in slope angle and substrate probably were not involved.

It was shown earlier that the proportion of adult plants flowering on NE-facing slopes was lower than on SW-facing slopes. It is thus possible that low population density on NE-facing slopes could result, at least in part, from lower seed input. No comparison of NE-facing and ESE-facing slopes were made with respect to flowering.

Growth: Data on growth of *E. schultzi* plants on a NE-facing slope and the adjacent SW-facing slope are present in Table 19. Microclimatic data for these same slopes are given in Figures 6 and 7.

Growth was faster in the SW-facing slope plants and was also less seasonal. Because soil moisture was highest on the NE-facing slope (28.9% versus 16.2%, measured on 25 March 1973), soil moisture was apparently not the cause of this effect. It is possible that more rapid heating

of leaves might have caused some early morning drought stress in the NE-facing slope plants. However, this effect would probably not be a major factor in the wet season. Dew formation on *E. schultzi* leaves is greater in the wet season; in the mornings, it seldom evaporates completely before the sun is obscured by fog or clouds, making drought stress unlikely. Because growth differences between the slopes persisted in the wet season, it is probable that other factors, such as wind-induced leaf water stress and wind-cooling, may be acting. Tissue temperatures were lower on the NE-facing slope (Figure 7) perhaps resulting in lower metabolic rates. On the midslope windward plot at the topographic gradient, it was found that there was greater wilting of leaves on the windward halves of rosettes than on leeward sides. The effect was observed only in the dry season, however.

Leaf width was measured for a single mature leaf from each of the 50 marked plants on each slope. Leaf width for the NE-facing slope plants was 3.2 cm versus 3.9 cm for the SW-facing slope plants. These means were significantly different ($P < 0.001$). Narrow leaves could be interpreted as a response to wind-related drought areas (Parkhurst and Loucks, 1972). No attempt was made to determine if this leaf width difference was genetically based.

Comparisons of the upper and lower exclosures with respect to *E. schultzi* growth and population density suggest that small differences in aspect and topography can have major effects on these parameters. Population density in the upper exclosure was estimated using the 100 m² plots as samples. Population density was 19,900 adults per hectare on the leeward slope and 12,200 on the windward slope. The windward-leeward ratio was 61% versus 50% on the lower exclosure. The upper exclosure is located on the crest of a large morainal system that may partially shelter the lower exclosure from the prevailing wind.

Leaf expansion rates on the windward slopes in the upper exclosure were significantly greater than on the leeward slope (Table 8; $P < 0.01$, according to the F test). This is the reverse of the

TABLE 19.—Growth rates (leaves per week) and seasonality (dry season growth as percentage of wet season growth) for *E. schultzi* adults on a windward (NE-facing) slope and adjacent leeward (SW-facing) slope at 3550 m

Parameter	Windward slope	Leeward slope
Leaves per week		
Wet season	2.7±0.15	3.8±0.23*
Dry season	1.8±0.15	2.9±0.25*
Seasonality	68±5%	77±6%

* Mean for leeward slope significantly greater than mean for windward slope, $P < 0.05$.

trend in the lower enclosure. The leeward slope in the upper enclosure was less sheltered from the prevailing wind than was the leeward slope in the lower enclosure. Greater exposure may have interacted with greater intraspecific competition caused by high adult density, resulting in reduced growth rates on the leeward slope.

Although adult growth rates in the upper enclosure are higher on the windward slope, seedling recruitment rates and juvenile growth rates are higher on the leeward slope (Tables 3, 6; Figure 9). As pointed out earlier (Table 16), rates of seed production are lower on windward slopes. Annual juvenile mortality rates were similar on the two slopes (Table 6). Adult mortality rates after one year were too low to permit meaningful comparisons. These data suggest that control of population density at this site might occur largely in the seedling stage.

Experimental Study of Growth

Experimental and descriptive studies of *Espeletia* adults suggest that inter- and intraspecific competition for water may be a major factor controlling growth. However, these results do not eliminate the possibility that plants may also compete for nutrients. An experiment was designed to determine if lack of nutrients can limit growth in *E. schultzii* adults. Further studies will be required to determine if competition for nutrients is actually occurring.

Thirty-two pairs of *E. schultzii* adults were selected at 3600 m. Fertilizer was applied to one of the members of each pair (500 g per m², 10% N, 10% P₂O₅ and 15% K₂). Leaf expansion rate was recorded before and after application. Before application of fertilizer, no significant difference in leaf expansion was found. After application, leaf expansion in the experimental plants was slightly higher than in the control plants ($P < 0.1$), suggesting the possibility that lack of mineral nutrients could limit growth.

Comparisons of elevational populations of *E. schultzii* in the field indicated that growth rate varies with elevation (Table 8). However, these

data do not permit discrimination between genetically controlled growth rate differences and differences imposed directly by elevational variation in environment. Plants were therefore grown in a controlled phytotron environment (17°C day, 11°C night; 16hr photoperiod) from seed collected at 2800 m, 3550 m, and 4100 m. After three years, growth rate (grams dry weight of leaves per plant per week) was measured over a 3-month period (Table 20). These rates are similar to those recorded for the windward slope populations at 3000 m, 3600 m, and 4200 m during the wet season (Table 8). This suggests that there are genetically based differences between the three populations with respect to plant growth rates. However, field rates for the dry season increased with increasing elevation. As suggested earlier (see "Studies of Adults: Growth"), dry season growth patterns may be controlled primarily by inter- and intraspecific competition, both of which decrease with increasing elevation (Smith, 1980). Experimental studies of population control will be presented elsewhere (Smith, 1980; ms. in prep.).

Discussion

RELATIONSHIP BETWEEN GROWTH FORM AND POPULATION DYNAMICS.—Two aspects of growth form in *Espeletia* must be considered in the context of population dynamics: (1) the presence of both caulescent and acaulescent forms, and (2) the increase in plant height, both within and between

TABLE 20.—Growth rates for phytotron-grown *E. schultzii* adults

Parameter	Seed source			
	2800 m	3550 m	4100 m	
Plants	12	10	8	
Grams/leaf ¹	1.67	1.25	1.03	$P < 0.01^2$
Leaves/week	3.15	3.32	2.79	Not tested
Grams/week ¹	5.28	4.12	2.68	$P < 0.05^2$

¹ Oven-dry weight.

² Mean for 3550 m significantly different from both mean for 2800 m and for 4100 m, according to F test and least significant range test (Sokal and Rohlf, 1969).

species, with increasing elevation. Data on population dynamics provide information on the types of life histories that produce plants of characteristic size and shape, and also suggest possible explanations for the evolution of the life histories themselves.

Major patterns in plant height are correlated primarily with generation time. Comparing *E. schultzi* populations on midslope windward sites at 3000 m, 3600 m, and 4200 m shows both maximum and mean adult height increased with increasing elevation. However, annual rate of height growth decreased from 3000 m to 3600 m, and did not change significantly from 3600 m to 4200 m. Thus, increase in height with increasing altitude is apparently the result of greater life span.

Mean height in the *E. lutescens* population at 4200 m was twice that of the adjacent *E. schultzi* population. Annual rates of height growth were not significantly different in the two populations, suggesting much longer generation time in *E. lutescens*.

Very long-term data on mortality and growth will be required to determine if these populations have reached stable age distributions. However, the presence of dead adults of all sizes in these populations suggests that they could be in equilibrium, such that the differences between them with respect to plant height will be maintained.

The acaulescent habit in *E. floccosa* at 3600 m is associated with very short generation time. This species appears to reach age of first reproduction more quickly than any other species measured, and dies after flowering. In a second acaulescent species investigated, *E. atropurpurea*, a similar pattern was observed. In this species, however, new rosettes sprout from the old rosette base (see Baruch and Smith, 1979).

The tallest *Espeletia* plants occur in arborescent species such as *E. humbertii* and *E. nertiifolia*. In *E. humbertii*, apparent generation time is probably comparable to that in *E. lutescens* at 4200 m. However, rate of shoot elongation is greater than for any other population studied. Size increase in *E. floccosa* rosettes, although similarly rapid, is due

almost entirely to production of progressively longer leaves rather than to shoot elongation. Thus, in *E. humbertii*, rapid height growth interacts with long generation time to result in tall plants. Such a growth pattern might be expected in a forest environment where there is strong selection for the ability to compete for light.

Selection for Iteroparity and Semelparity: If rates of seedling recruitment are low and/or unpredictable, a population must be composed of individuals that survive and reproduce over a long time period to guarantee production of successful offspring (Stearns, 1976; Schaffer, 1974). In the absence of such iteroparity, or delayed germination in a portion of the seed, the population would go extinct.

Selection for increased iteroparity could have occurred in *E. schultzi* and *E. lutescens* at 4200 m. Seedling recruitment is lower for these two populations than for any other population studied, perhaps because of intense soil frost activity. Apparent generation times are greater than for any other páramo population studied.

Three major growth patterns could be associated with iteroparity in rosette species of *Espeletia*: (1) production of lateral shoots followed by death of the parent rosette, as in *E. atropurpurea*; (2) continued growth of the original rosette, with or without production of lateral shoots, resulting in continued height growth; and (3) continued growth of the original rosette, but in a horizontal direction, resulting in a prostrate caulescent form. The rarity of the first and third patterns, and the dominance of the second among páramo species of *Espeletia* suggest that selection for iteroparity, if present, may have interacted with selection for height growth (cf. Smith, 1980).

The two populations with shortest apparent generation times (*E. schultzi* at 3000 m and *E. floccosa* at 3600 m) both had high seedling recruitment rates. In both populations, juveniles growth rates increased and juvenile mortality rates decreased with increasing proximity to adults. This "nurse tree" effect could increase the probability that an *E. schultzi* adult that dies is replaced by its own progeny, and ought therefore to reduce

intensity of selection for great iteroparity (see Smith 1980).

There might be little selection for continued resource allocation to vegetative growth in adults if, despite such input, adults generally die early. Under these conditions, there should be selection for greater allocation of resources to early reproduction. In an expanding population, reproductive value would be increased by such early reproduction (Gadgil and Solbrig, 1972; Schaffer, 1974). *Espeletia floccosa* generally occurs on steep, rocky, windward slopes. The *E. schultzii* xeric slope population at 3600 m occupies a similar site. This is the only *E. schultzii* population studied in which adult mortality was positively correlated with size (and, thus, age) (Figure 16A). It also had a higher frequency of reproductive plants in the smallest size class than did other populations. Both trends are consistent with the hypothesis that on such sites selection can, at least periodically, favor semelparity and early reproduction.

Selection for Vegetative Spread: Vegetative spread (vegetative "reproduction") represents a form of iteroparity in that it maintains the parent genotype in the population, permitting repeated sexual reproduction. It permits population maintenance in the face of high and unpredictable juvenile mortality. Vegetatively spreading plants are most frequent in extreme environments where the probability of successful sexual reproduction is low (Billings and Mooney, 1968; cf. Janzen, 1977; Cook, 1979; Harper, 1977).

The occurrence of vegetative spread in *E. atropurpurea* at 3400 m may be related to this species' great susceptibility to dry season stress. For glabrous-leaved *E. atropurpurea* plants, dry season growth rate (Kcal of leaf tissue per week) was only 3% of that in the wet season. Reduced growth was combined with severe stunting of dry season leaves. For pubescent-leaved *E. schultzii* plants growing in association with *E. atropurpurea*, mean dry season growth rate was 91% of the wet season rate and no leaf stunting occurred. Adult mortality rate was 5% for *E. atropurpurea* in the dry season. No adults died in the *E. schultzii* population. Data on seedling mortality were not

collected. The relation between growth and leaf pubescence in these two species are discussed in more detail elsewhere (Baruch and Smith, 1979). These data suggest that the páramo dry season is, in effect, more extreme for *E. atropurpurea* than for adjacent plants of *E. schultzii*. It is possible that vegetative spread might represent an evolutionary response to such stress.

Death of the parent rosette after first flowering—the immediate cause of the acaulescent habit in *E. atropurpurea*—might be selected for if it improved survival, growth, and reproduction by daughter rosettes. Such mortality might release daughter rosettes from apical dominance effects of the parent, or might reduce within-clone competition. In either case, death of the parent rosette would probably increase the reproductive value of the clone by (1) increasing the rate of vegetative reproduction, and (2) increasing the rate of sexual reproduction by reducing time to first reproduction in daughter rosettes.

In this discussion, it has been suggested that variation in plant height in *Espeletia* is due primarily to variation in generation time, the one partial exception being *E. humbertii*, where generation time interacts with rapid height growth to produce tall plants. It has also been hypothesized that variation in generation time could be explained, in part, by selection for particular life history strategies: semelparity, iteroparity, and vegetative spread. However, it is possible that there has been direct selection for particular height growth patterns. That is, at high elevation, selection may favor plants capable of growing tall; elevation differences in longevity would then be an incidental consequence of this selection. Finally, it may be that height patterns, particularly intraspecific patterns in *E. schultzii*, do not result directly from elevational differences in selection pressure. Rather, greater adult survivorship at high elevations may result directly from less competition or less herbivory. These possibilities are considered in Smith (1980).

Selection for Growth Form: The climatic extremes of the dry season have a major influence on demographic patterns in *Espeletia*. Juvenile and

adult growth is reduced and mortality is increased in the dry season. Flowering is generally restricted to the wet season; plants that do flower in the dry season (primarily *E. schultzii* at 4200 m) frequently suffer extensive frost damage to flowers.

If an individual plant possesses adaptations to these dry season stresses, such that it matures faster, has a lower probability of mortality, and/or has a higher rate of reproduction than other members of the population, then, all other factors being equal, this individual will contribute more progeny to subsequent generations than will others lacking the adaptations. Population growth rate will increase and probability of extinction will decrease as the proportion of individuals possessing such adaptations increases.

It was hypothesized that the caulescent rosette form represents such an adaptation to climatic stress. Field studies (Smith, 1974a, 1974b, 1979; Baruch and Smith, 1979) demonstrate that apical bud structure, leaf pubescence, rosette geometry, nyctinastic movement of rosette leaves, stem height, and retention of dead leaves on the stem all confer protection from the climatic extremes of the páramo dry season.

POPULATION CONTROL AND STABILITY.—Descriptive data given here, and experimental data (Smith, 1980; ms. in prep.), suggest that a wide range of environmental stresses acting on *E. schultzii* populations at worst cause only temporary reductions in density. This is due primarily to density-dependent control of growth, reproduction, and mortality. In this respect, *E. schultzii* populations are highly stable. For example, extreme reduction in juvenile density without concomitant reduction in adult density might result from extensive frost and pest damage to flowers and seed, or from high seedling mortality caused by drought or temperature stress. Reduction in juvenile density will increase adult growth rate, and may increase adult survivorship. Number of seeds produced per plant is positively correlated with plant size. Seed production will therefore increase, increasing the potential for seedling recruitment. However, because average adult size and adult biomass per unit area are

now greater than they were before the reduction in juvenile density, actual recruitment may remain low until adult mortality occurs. A form of feedback inhibition may operate: high juvenile density will cause a reduction in seed production by adults, followed by reduced recruitment of new seedlings, and a gradual decrease in juvenile density.

Similar feedback responses result if adult mortality is increased by predation, interspecific competition, or physical stress without concomitant increase in juvenile mortality. Reduction in adult density increases juvenile growth, speeding rate of replacement of dead adults, and also increases growth and seed production in remaining adults, speeding recruitment into smallest juvenile size classes.

A decrease in density is likely to persist only if all adults and all or most juveniles are killed over a large area, perhaps by intense fire or prolonged intense insect damage. Seed dispersal over more than 3 m to 4 m is rare, because the seeds lack adaptations for wind and animal dispersal. Re-invasion would therefore be slow. In the absence of abundant cover by *Espeletia* plants, cover by tussock grasses, shrubs, and other associated plants will increase. Greater interspecific competition will then further retard re-invasion of the site by *Espeletia*. However, death of all adults and all or most juveniles is probably a rare event. Morphological buffering against physical stresses, and strongly density-dependent population control apparently permit maintenance of dense populations of *E. schultzii* over a wide range of habitats.

Summary

The páramo climate is highly seasonal, with lower soil moisture, more intense insolation, colder night temperatures, and warmer daytime temperatures during the dry season than in the wet season. True mean monthly temperatures remain nearly constant all year.

Flowering generally occurs in the wet season and wet season-dry season transition period.

Fruit dispersal begins in the wet season and continues throughout the dry season. Germination begins in the early wet season. Below 4200 m, seedling production is abundant; juveniles were common for *E. schultzi*, *E. floccosa* and, in treefall sites, for *E. humbertii*. Juveniles were uncommon at 4200 m, where diurnal needle ice formation may eliminate them.

Juvenile mortality is highest in the dry season. For all species, the probability of juvenile mortality decreases as plant size increases. Adult *Espeletia* plants in some populations appear to shelter juveniles, thus reducing mortality. In other populations, mortality is greatest for juveniles in close proximity to adults. Insect predation was rare in juveniles.

In some populations, mean yearly juvenile height growth was negative due to extensive dry season die-back. For *E. schultzi* at 3000 m and *E. floccosa* at 3600 m, growth was greatest for juveniles closest to adults of their own species.

Growth of adult plants is highly seasonal at most sites. Seasonality of growth decreases from 3000 m to 4200 m for *E. schultzi*. Intraspecific competition was documented on some sites and is most pronounced in the dry season. However, sheltering of one adult by another may also occur. Competition between *E. schultzi* adults and surrounding vegetation can greatly reduce growth in

the dry season. Conspecific juveniles can also reduce adult growth. Annual growth rate in *E. schultzi* decreases from low to high elevations, and from slope bases to ridge tops. Mortality of *E. schultzi* adults can result from drought, fire and, in rare cases, flooding. Variation in plant height in páramo species is correlated primarily with longevity. In *E. schultzi*, plant height and longevity both increased with increasing elevation. The *E. lutescens* population at 4200 m had a greater mean plant height than any other páramo population studied, and had the greatest apparent longevity. The acaulescent rosette form in *E. floccosa* at 3600 m was correlated with very short generation time: plants reproduced early and died after first reproduction. The other acaulescent rosette species, *E. atropurpurea*, had a similar pattern, but new rosettes sprouted from old rosette bases.

The species showing greatest iteroparity, *E. lutescens*, occurs on sites where seedling establishment is rare. The semelparous species, *E. floccosa*, occurs on sites where adult mortality is greatest among the largest size classes, and where seedling establishment is comparatively common.

Population control is strongly density dependent. Reduction in density in one size class results in increased growth and/or reproduction among remaining plants. Thus, populations rapidly recover from most perturbations.

Appendix

Tables

TABLE A.—Site characteristics (site locations shown in Figure 2)

<i>Site number, name, and location</i>	<i>Elevation</i>	<i>Slope</i>	<i>Aspect</i>	<i>Species</i>
1. Zerpa Mucubají Upper exclosure	3000 m	12°	40°E	<i>E. schultzi</i>
2. Bog edge	3600 m	20°	260°W	<i>E. schultzi</i>
3. Slope base	3600 m	0°	—	<i>E. schultzi</i>
4. Windward slope	3600 m	13°	55°E	<i>E. schultzi</i>
5. Ridge	3600 m	32°	55°E	<i>E. schultzi</i>
6. Leeward slope	3600 m	15°	265°W	<i>E. schultzi</i>
Lower exclosure				
7. Windward slope	3550 m	19°	NNE	<i>E. schultzi</i>
8. Leeward slope	3550 m	21°	SSW	<i>E. schultzi</i>
9. Leeward slope	3550 m	21°	SW	<i>E. schultzi</i>
10. Windward slope	3550 m	15°	NE	<i>E. schultzi</i>
11. Leeward slope	3550 m	26°	SW	<i>E. schultzi</i>
12. Windward slope	3550 m	26°	NE	<i>E. schultzi</i>
13. Windward slope	3550 m	20°	NNE	<i>E. schultzi</i>
14. Leeward slope	3550 m	17°	SSW	<i>E. schultzi</i>
15. Leeward slope	3550 m	20°	ESE	<i>E. schultzi</i>
16. Leeward slope	3550 m	17°	WNW	<i>E. schultzi</i>
17. Xeric slope	3550 m	32°	S	<i>E. schultzi</i>
18. Talus slope	3600 m	10°	SSE	<i>E. schultzi</i>
19. <i>E. floccosa</i> plot.	3600 m	15°	SSE	<i>E. floccosa</i>
Laguna Negra Talus slope				
20. Plot 1	3500 m	31°	SSE	<i>E. humbertii</i>
21. Plot 2	3500 m	29°	NNW	<i>E. humbertii</i>
22. Closed forest	3500 m	38°	SW	<i>E. humbertii</i>
23. Treefall	3500 m	38°	SW	<i>E. humbertii</i>
24. La Aguada	3400 m	26°	W	<i>E. schultzi</i> , <i>E. atropurpurea</i>
25. Aguila	4200 m	16°	115°E	<i>E. schultzi</i>
26. Aguila	4200 m	16°	115°E	<i>E. lutescens</i>

TABLE B.—Plot description

<i>Species and sites</i>	<i>Plot size</i>	<i>Number of adults in plot</i>	<i>Number of marked seedlings</i>	<i>Number of marked adults</i>
<i>E. schultzei</i>				
Mucubají (3600 m)				
Windward slope	10×10 m	122	257	120
Leeward slope	10×10 m	199	456	120
Ridge	10×10 m	116	172	120
Base of windward slope	10×10 m	96	440	120
Xeric slope	10×10 m	146	167	120
Talus slope	20×5 m	57	3	—
Zerpa (3000 m)				
Windward slope	10×10 m	103	298	120
Aguila (4200 m)				
Windward slope	10×10 m	80	34	120
La Aguada (3400 m)	Plotless	—	—	50
<i>E. lutescens</i>				
Aguila (4200 m)				
Windward slope	10×10 m	86	23	120
<i>E. floccosa</i>				
Mucubají (3600 m)				
Rocky slope	20×5 m	103	105	120
<i>E. humbertii</i>				
Laguna Negra (3500 m)				
Open talus slope				
Plot 1	10×15 m	29 plants total		50
Plot 2	10×15 m	45 plants total		45
Closed Polylepis forest	10×10 m	52 plants total		52
Treefall in Polylepis forest	5×10 m	213 plants total		—
<i>E. atropurpurea</i>				
La Aguada (3400 m)	Plotless	—	—	50

TABLE C.—Dates on which bud leaves were marked and counted for measurement of adult leaf expansion rates

<i>Species and site</i>	<i>Dates</i>
<i>E. schultzi</i>	
3000 m Zerpa	
Descriptive plot	9 Oct-9 Dec 72, 15 Feb-16 Mar 72, 24 Jun-5 Aug 73
3550 m Mucubají	
NE-facing slope	27 Mar-25 Apr 73, 24 Jun-28 Jul 73
SW-facing slope	27 Mar-25 Apr 73, 24 Jun-28 Jul 73
3600 m Mucubají	
Bog edge	26 Jan-14 Mar 73, 25 Jun-31 Jul 73
Slope base	9 Oct-9 Dec 72, 25 Jan-14 Mar 73, 25 Jun-30 Jul 73
Windward slope	9 Oct-9 Dec 72, 25 Jan-14 Mar 73, 25 Jun-30 Jul 73
Ridge	9 Oct-9 Dec 72, 25 Jan-15 Mar 73, 25 Jun-30 Jul 73
Leeward slope	9 Oct-10 Dec 72, 26 Jan-15 Mar 73, 25 Jun-30 Jul 73
4200 m Aguila	10 Oct-10 Dec 72, 14 Feb-17 Mar 73, 24 Jun-11 Aug 73
3400 m La Aguada	3 Oct 72-14 Jun 73, 14 Jun-20 Jul 73
<i>E. lutescens</i>	
4200 m	10 Oct-10 Dec 72, 14 Feb-17 Mar 73, 24 Jun-11 Aug 73
<i>E. humbertii</i>	
3500 m	9 Oct-16 Dec 72, 29 Jan-28 Mar 73, 2 Jul-1 Aug 73
<i>E. atropurpurea</i>	
3400 m	3 Oct 72-14 Jun 73, 14 Jun-20 Jul 73

TABLE D.—Dates for juvenile mortality and recruitment observations (height measured on first and last dates)

<i>Species and site</i>	<i>Dates</i>
<i>E. schultzi</i>	
3000 m	
Descriptive plot	19 Aug 72, 9 Dec 72, 16 Mar 73, 28 Apr 73, 16 Aug 73
Transplant garden	9 Oct 72, 17 Dec 72, 23 Mar 73, 28 Apr 73, 4 Aug 73
3600 m	
Slope base	25 Jun 72, 5 Dec 72, 14 Mar 73, 26 Apr 73, 27 Jun 73
Windward slope	9 Jun 72, 5 Dec 72, 14 Mar 73, 26 Apr 73, 9 Jun 73
Ridge	20 Jun 72, 5 Dec 72, 14 Mar 73, 26 Apr 73, 26 Jun 73
Leeward slope	17 Jul 72, 8 Dec 72, 14 Mar 73, 27 Apr 73, 22 Jul 73
Transplant garden	8 Oct 72, 16 Dec 72, 22 Mar 73, 28 Apr 73, 5 Aug 73
Adult elimination experiment	21 Oct 72, 22 Mar 73, 29 Apr 73, 7 Aug 73
4200 m	7 Aug 72, 10 Dec 72, 17 Mar 73, 29 Apr 73, 18 Aug 73
<i>E. lutescens</i>	
4200 m	7 Aug 72, 10 Dec 72, 17 Mar 73, 29 Apr 73, 18 Aug 73
<i>E. floccosa</i>	
3600 m	6 Aug 72, 13 Dec 72, 28 Mar 73, 29 Apr 73, 3 Aug 73

TABLE E.—Dates for adult height measurements

<i>Species and site</i>	<i>Dates</i>
<i>E. schultzi</i>	
3000 m	18 Aug 72, 16 Aug 73
3600 m	
Slope base	16 Jul 72, 17 Jul 73
Windward slope	5 Jun 72, 6 Jun 73
Ridge	29 Jun 72, 25 Jun 73
Leeward slope	23 Jul 72, 22 Jul 73
4200 m	9 Aug 72, 18 Aug 73
<i>E. lutescens</i>	8 Aug 72, 18 Aug 73
<i>E. floccosa</i>	30 Jul 72, 3 Aug 73

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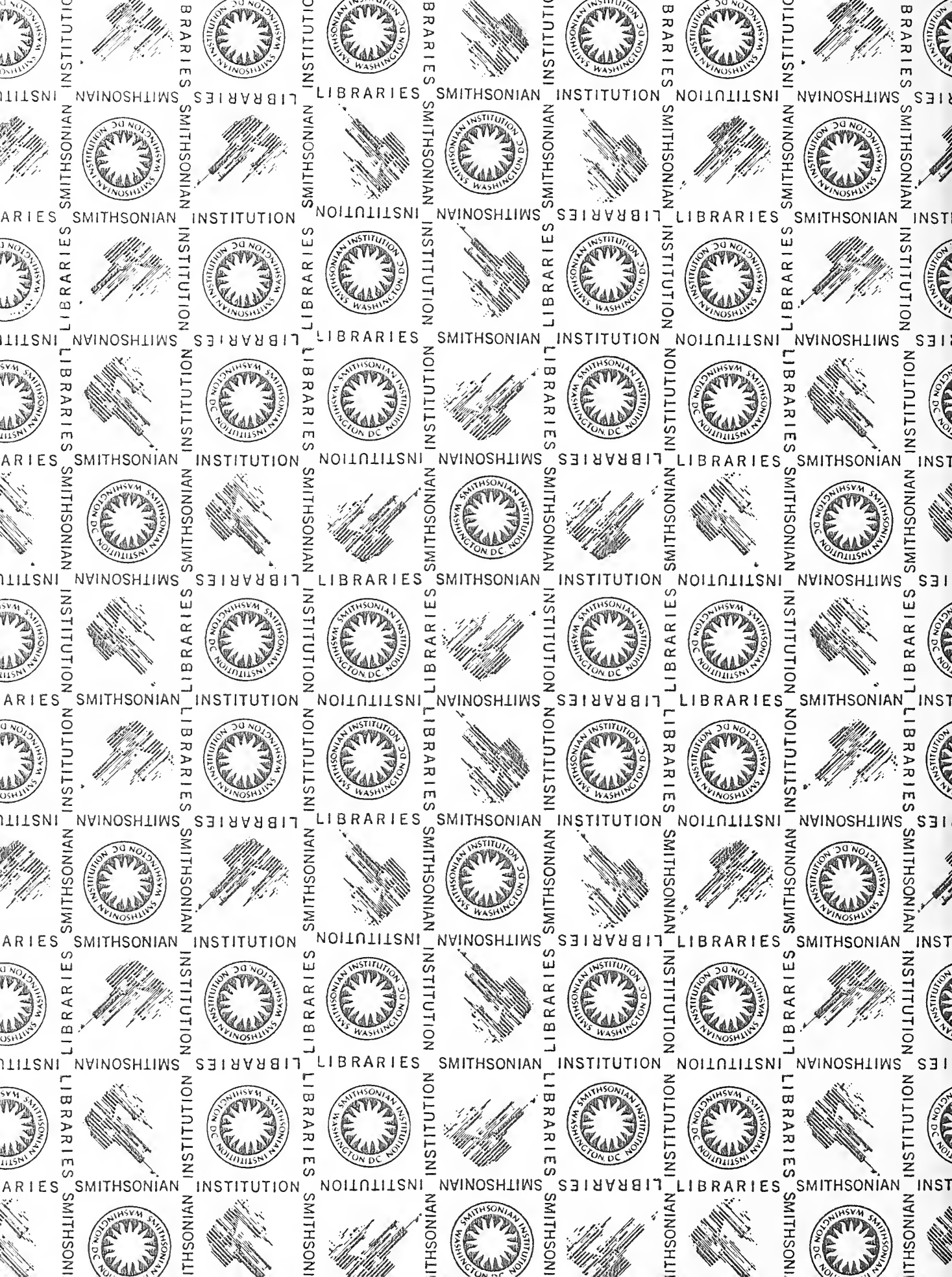
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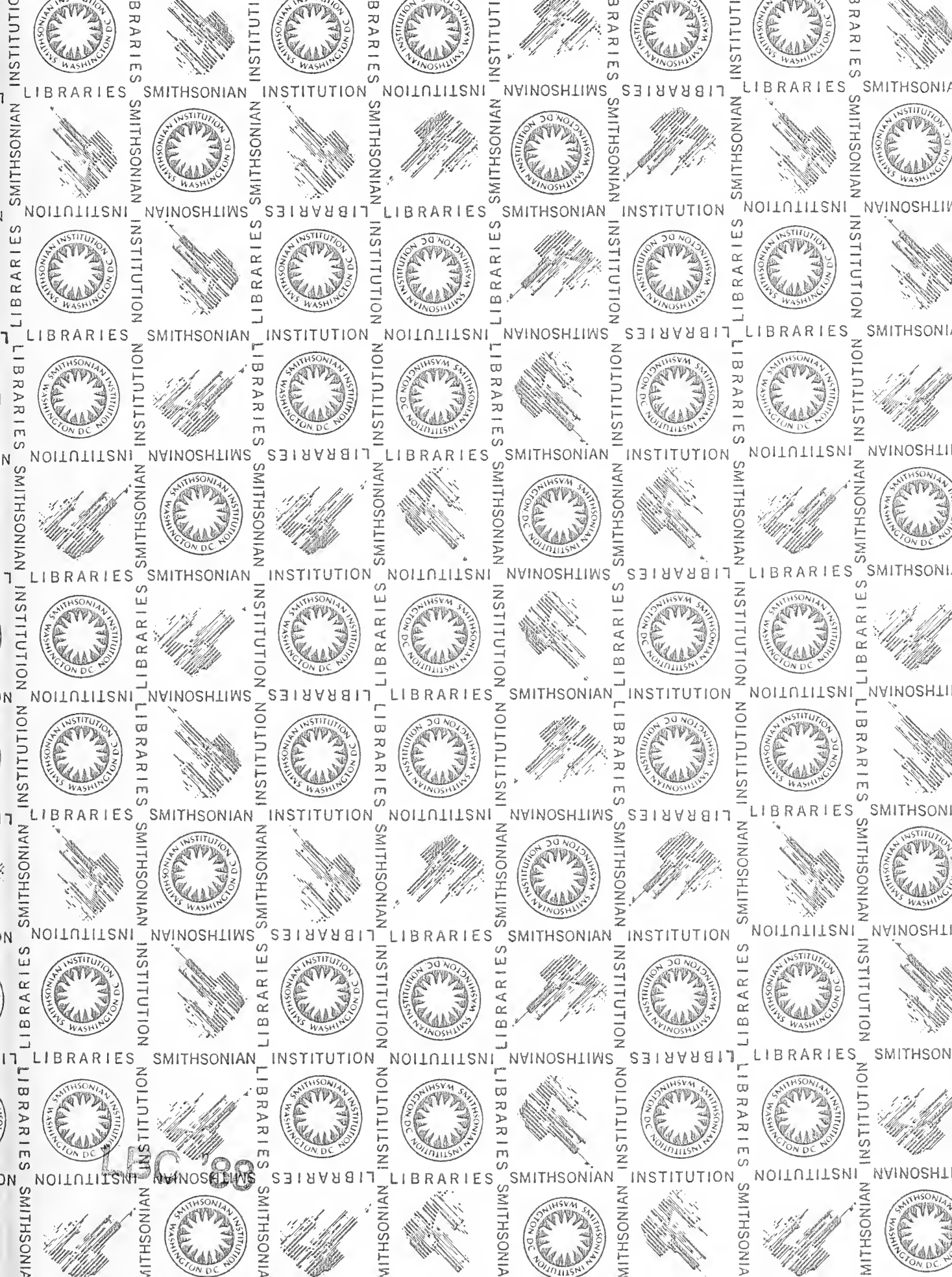
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