High Altitude Tropical Biogeography

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Adaptive Strategies of Espeletia in the Andean Desert Páramo

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THE DESERT PÁRAMO

The desert páramo, with its characteristic and spectacular giant rosettes of *Espeletia* (Fig. 3–1), is the most representative plant formation of the high Andean zone. It occurs intermingled with the periglacial desert that occupies the most fragile habitats, where scattered dwarf cushions, sessile rosettes, and lichens form a sparse cover that dots the prevailing bare ground.

The desert páramo is the most extreme environment colonized by *Espeletia* at the present time. The major area of this tropical, high Andean ecosystem is found in the Cordillera de Mérida, Venezuela, above 4000 m, where it reaches the very border of the glaciers at 4600 m.

According to Tricart (1970), in the Andes of Mérida it is possible to fix at about 4000 m the lower limit of definite periglacial features. This same level marks the boundary between two clear-cut ecological zones: the Andean belt, downward, and the high Andean belt, toward the summits (Monasterio, 1980a).

The high Andean belt shows an insular pattern of distribution (Fig. 3–2), each "island" corresponding to one main sierra (Sierra Nevada, Sierra de Santo Domingo, Sierra de la Culata, etc.). Below 4000 m, the desert páramo is replaced by various páramo formations characterized by a wider diversity of life forms and by

FIG. 3–1. *E. timotensis* at the páramo of Pico del Aguila, Sierra de la Culata, 4200 m. Photo by M. Fariñas.
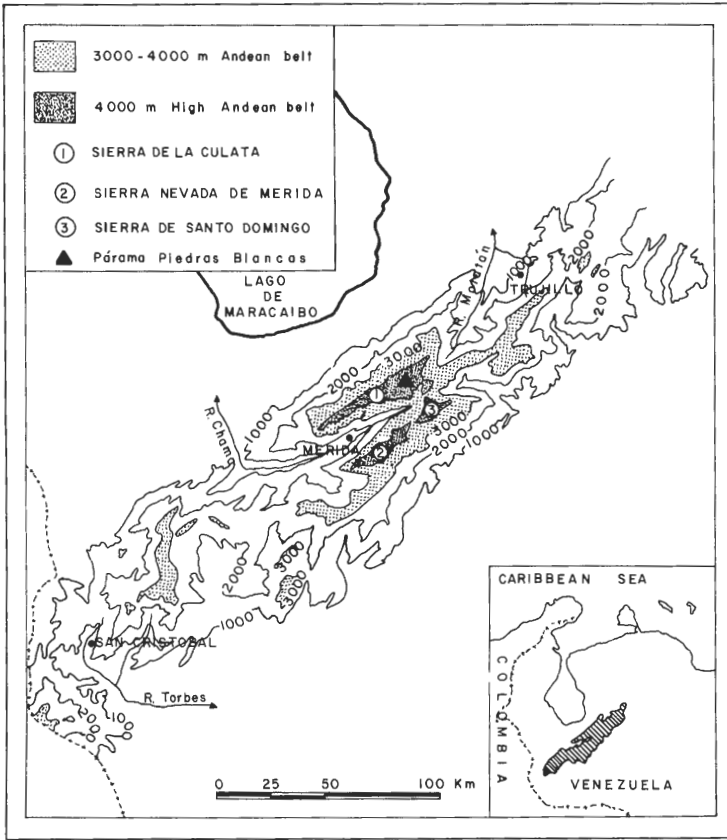
FIG. 3–2. Map of the surface corresponding to different altitudinal levels in the Cordillera de Mérida. At the 4000-m level, the highlands become discontinuous, giving rise to three separate areas or "islands."

the prevalence of small rosettes of *Espeletia* together with some branched forms (see Chap. 11).

The Periglacial Climate and Its Ecological Constraints

The desert páramo corresponds to the periglacial belt of low-latitude mountains where frost action and daily cycles of freeze–thaw promote specific geomorphogenetic processes and soil movements of profound ecological consequences. These climatic effects are reinforced by the open nature of the vegetation cover that leaves large areas of bare ground, favoring thus the alternation of rapid cooling and heating of the soil surface that lead to the daily cycles of freeze and thaw during most of the year. Soil particles gradually move down the slopes in the process of cryoturbation that induces such typical surface features as patterned ground in small-scale structures, due to their formation in daily cycles (Schubert, 1976).

The most common feature of patterned ground in the desert páramo is striped ground. Malagon (1982) analyzed this feature at Pico del Aguila, at

4118 m. He reported a mobile mantle of solifluction, about 7 cm thick, that migrates easily along the steep slopes prevailing in the highest areas. It is this moving mantle, porous and unstable, that receives the achenes of *Espeletia*, constituting its germinative niche. Seedlings thus have a low survival probability, since they can be swept away in the migrating solifluction mantle. Low temperature acts then indirectly on the survivorship of seedlings and juveniles, through the instability of the substrate rather than by its direct effect on plant tissues. We will return to this point, but it is worthwhile to emphasize now how the principal impact of the periglacial ecology occurs just at ground level (Fig. 3–3).

Besides the scarce cushions at ground level (Fig. 3–1), the desert páramo shows a conspicuous layer of giant rosettes that constitute an open stratum 1 to 3 m high. To understand this sharp contrast in the vertical distribution of the vegetation biomass, it is convenient to refer to microclimatic gradients along the soil and air in close contact with it. The main climatic features of the desert páramo within the framework of the high mountain climates have already been discussed by Sarmiento (Chap. 2), and therefore I will men-

tion only a few additional environmental pulsations that may aid in the interpretation of the adaptive mechanisms of the giant rosettes of *Espeletia*.

Pico del Aguila, a representative site for the desert páramo, shows the annual constancy in mean daily temperature and in incoming radiation that characterizes low latitudes (Fig. 3–4), with a difference of only 2.7° between the mean temperature of the coldest and the warmest months: 1° and 3.7°, respectively. As was already pointed out, in high tropical mountains, daily cycles become the major cyclic environmental pulsations. However, rainfall seasonality also induces seasonal contrasts and amplifies daily cycles. At Pico del Aguila, wet and dry seasons are quite contrasted, since during the four months of the dry season (December to March) rainfall amounts to only 76 mm, that is, 8% of the annual total (Fig. 3–4). This contrasts sharply with the wettest months (May to August), which may be considered as perhumid, whereas the remaining months are intermediate between these two extremes. As a direct consequence of this rainfall pattern, the equatorial constancy is partially broken, introducing an annual pulsation that affects daily cycles inducing slight but noticeable changes in the solar radiation reaching the surface, as well as in air and soil temperatures and humidity. Two daily cycles, one in the moist, the other in the dry season, illustrate these facts (Table 3–1 and Figs. 3–5 and 3–6). Air temperatures were recorded hourly at 150 cm and 10 cm, as well as at the soil surface, and soil temperatures were recorded at 5, 10, 20 and 50 cm below the surface.

During the daily cycle in the dry season, air temperatures at 150 cm ranged from −2.5° to 11°, remaining at or below zero for 13 consecutive hours (8 P.M.–9 A.M.). At 10 cm, the pattern was similar but the daily oscillation was more pronounced: from −5° to 12°. During the night hours, air temperatures were consistently 2°–3° lower at 10 cm than at 150 cm. That is, from a thermal standpoint, the air level at 150 cm where most of the leaf and reproductive biomass of *Espeletia* is located, has more moderate conditions than the levels nearer to the ground. As far as soil temperature is concerned, an amplitude of 50° was recorded at the soil surface (bare ground), between a minimum of −10° and a maximum of 40°. As may be seen in Fig. 3–5, the ground surface remained at below freezing temperatures for 14 consecutive hours. The amplitude of daily oscillations dampened gradually with depth: 21° at 5 cm, 5° at 20 cm, and only 1° at 50 cm. Moreover, the freezing point was never
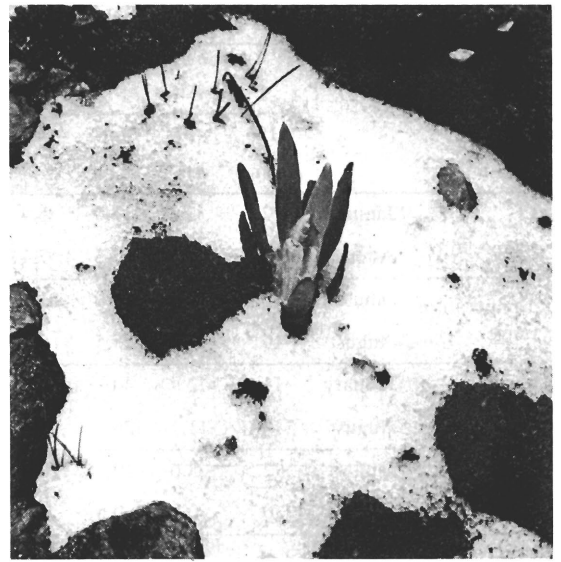

FIG. 3–3. A juvenile of *E. timotensis* surrounded by ice formed in the night and gradually melting in the morning. Páramo of Pico del Aguila, 4200 m. Photo by M. Fariñas.
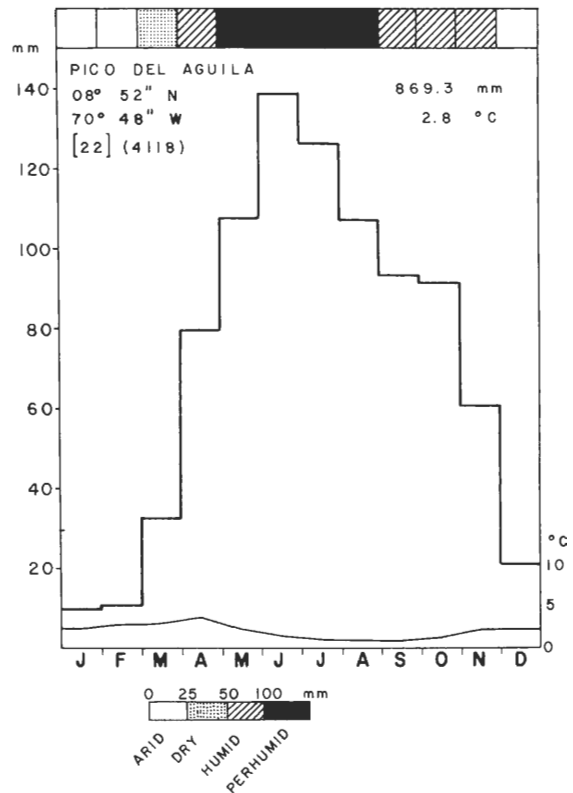

FIG. 3–4. Climate diagram for Pico del Aguila in the Sierra de la Culata, a typical desert páramo station. Periods of contrasting humidity conditions are shown from the arid to the perhumid.

TABLE 3–1. Microclimatic records in the Páramo de Piedras Blancas at 4200 m.

Micro-climatic factors (°C)		Air			Soil			E. moritziana (69 cm)			E. timotensis (165 cm)		
		150 cm	10 cm	Sur-face	−5	−20	−50	bud	ext. leaf	air	bud	ext. leaf	air
Mean temperature	January	2.7	2.3	7.0	5.4	6.5	6.0	5.5	2.4	2.4	5.4	4.3	2.5
	August	4.5	5	7.6	7.7	6.8	5.6	7.1	5.1	4.2	5.8	5.6	4.4
Temperature range	January	13.5	17.0	50.0	21.0	5.0	1.0	21.0	27.0	19.0	20.5	13.5	13.0
	August	10	11.1	25.5	9	3.9	1.4	16.3	14.5	10	11.6	15.2	12.1
Maximum temperature	January	11	12	40	19	9	6.5	19	21	16	19	11	11
	August	10	11.1	26	13	8.9	6.2	17.5	14	10	12.5	14.9	12
Minimum temperature	January	−2.5	−5.0	−10	−20	4	5.5	−2.0	−6.0	−3.0	−1.5	−2.5	−2.0
	August	0	0	0.5	4	5	4.8	1.2	−0.5	0	0.9	−0.3	−0.1

Note: Measurements were made hourly during two days, one in the dry season (January 12–13, 1978), the other in the rainy season (August 1–2, 1978). Extreme temperatures recorded at 10 cm above the ground were −14°C and 18°C in the dry season day, and −3°C and 15°C in the rainy season daily cycle.

reached at these two lowest levels. But we must keep in mind that most of the below–ground biomass of *Espeletia* occurs in the first 20 cm of soil.

Besides this daily pattern of air and soil temperature, in typical dry season days, the sky remains clear except for a few hours in the evening. Relative humidity varies from 20%–25% in the early morning to 70%–90% in the evening, whereas wind speed remains feeble all day.

During the wet season, the vertical gradient of temperature disappears; the minima are higher, whereas the maxima and the daily ranges are lower than in the dry period. Both cloudiness and relative humidity remain high for most of the day.

From the analysis of these two cycles, we may conclude that rather low air temperatures prevail all day and all year at the crown level of *Espeletia*. During the dry season, air and soil moisture are lower and daily ranges more pronounced, but the strong insulation may make the energy balance of the plant more favorable. By contrast, in the wet season moisture conditions improve and the minima are higher, but the lower incoming radiation and diurnal temperatures make the energy budget of plants less favorable. We see that neither season appears to be optimal, and thus that a given period cannot be considered the most favorable to all plant processes. In the wet season, for instance, pollination is negatively affected by the continuous rains and the frequent snowfalls, whereas growth is favored by the abundant water available in the soil.

Espeletia as a Colonizer of High Mountain Habitats

In previous works (Monasterio, 1979, 1980b) I analyzed several aspects of the desert páramo vegetation. This plant formation is structured by several species of giant rosettes of *Espeletia*. Since it occurs in a very open and discontinuous pattern (Figs. 3–1 and 3–7), the desert páramo leaves large areas of ground bare. Thus, it converges physiognomically toward other desert formations, particularly those of some mountain deserts in the Central Andes dominated by columnar cacti. In both cases we are dealing with cold deserts, though the desert páramo is much moister than the succulent deserts of the Central Andes.

The upper, woody layer in the desert páramo is formed by the giant rosettes of several species of *Espeletia*, while the ground layer is made of dwarf cushions (including *Mona*, *Azorella*, *Arenaria*, and *Calandrinia*), small rosettes (such as *Draba* and *Senecio*), and juveniles of *Espeletia*. As we have seen, the ground layer is subjected to hard microclimatic conditions. The adult rosettes of *Espeletia* in the upper layer live under a more stable thermal microclimate, since the crowns of the rosette trees are located well above the ground. A conspicuous feature of this plant formation is the maintenance of dead leaves attached to the trunks of *Espeletia* (Fig. 3–1), forming a thick mantle of slowly decomposing tissues that insulate the vascular system of the plant.
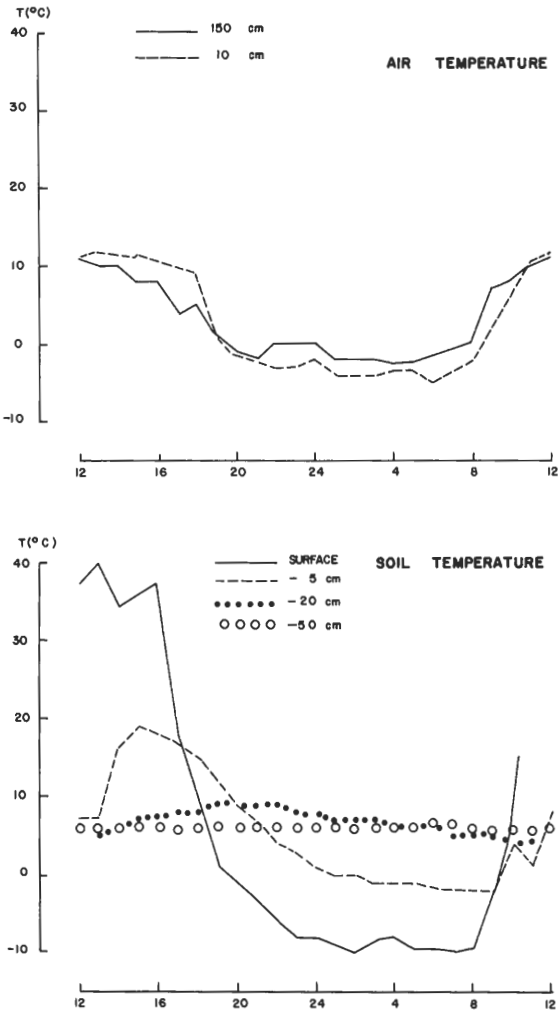
FIG. 3–5. *Top*: Daily course of air temperature 150 cm and 10 cm above ground for a 24-hour cycle in the dry season (January 12–13, 1978), at the Páramo de Piedras Blancas. *Bottom*: Daily course of soil temperature at various soil depths.
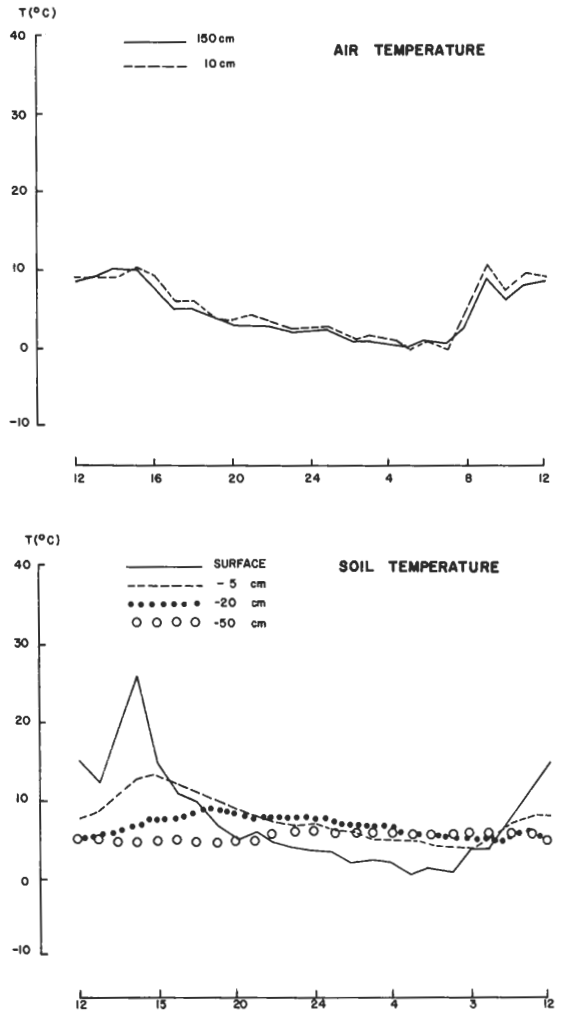
FIG. 3–6. *Top*: Daily course of air temperature 150 cm and 10 cm above ground for a 24-hour cycle in the wet season (August 1–2, 1978), at the Páramo de Piedras Blancas. *Bottom*: Daily course of soil temperature at various soil depths.

The total cover of *Espeletia* varies widely according to both altitude and habitat conditions, particularly the slope and the nature of parent materials. On gentle slopes, valley bottoms, and depressions, *Espeletia* may account for as much as 30% of ground cover. On steep slopes, instead, where most of the ground remains completely bare, the rosettes scarcely attain a cover of about 5%. The same factors affect the occurrence of the ground layer, which ranges in cover from 40% down to 2%.

Three species of *Espeletia* have colonized the periglacial habitats of the desert páramo in the Andes of Mérida: *E. timotensis* with its forma

lutescens (see Cuatrecasas, Chap. 11), *E. spicata*, and *E. moritziana* (Cuatrecasas considers that these three species belong to his genus *Coespeletia*; see Chap. 11). Each of these species is exclusive of a given habitat where it coexists with a different set of ground layer species. Therefore, three different associations were distinguished in the desert páramo (Monasterio, 1979, 1980a). Given that each species population colonizes a different habitat and that the various types of habitats form a mosaic of small patches, any type of interspecific competition is avoided, with the possible exception of competition for biotic resources, such as pollinators, that might be
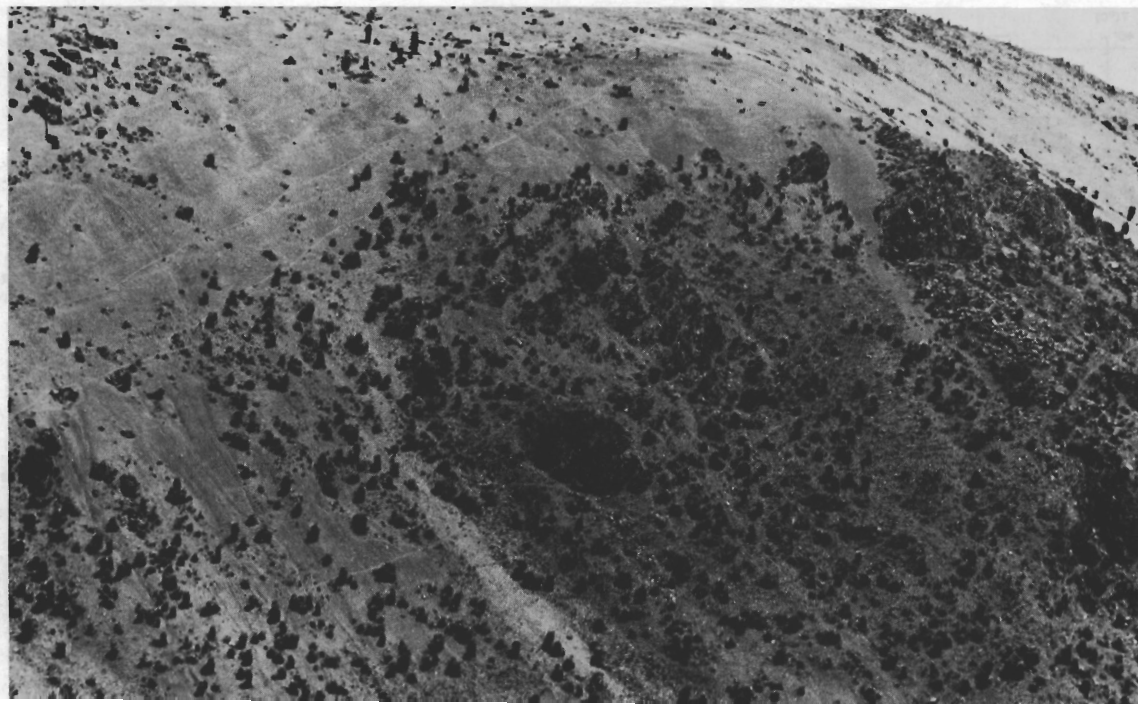
FIG. 3–7. A population of *E. timotensis* in the desert páramo. Páramo de Piedras Blancas, Sierra de la Culata, 4100–4300 m. Notice the distribution and cover of the rosettes. Our permanent plots are located at this site. Photo by Nuni Sarmiento.

shared by several of the adjacent species populations.

The desert páramo extends over a landscape modeled by late Pleistocene glacial events that left the characteristic features of glacial sculpture and depositions, such as glacial troughs, hanging valleys, roches moutonnées, cirques, horns, and till deposits. *E. timotensis* shows the widest ecological distribution and occurs between 4000 and 4500 m. Its habitats are the steep slopes covered by slope deposits, together with some erosion forms, like walls of cirques and valleys, covered with debris ranging in size from 2 to 20 cm, smaller sizes predominating. This is the species of *Espeletia* able to colonize the finest materials. Fine debris, together with the steep slopes, leads to great soil instability. However, when *E. timotensis* succeeds in colonizing this substrate, it acts as a stabilizing agent, slowing down the sliding of the solifluction mantle. The main soil pattern associated with these habitats is the striped ground.

E. timotensis shows true pioneer attributes, since it normally colonizes bare ground not previously occupied by other species. This means that a typical plant succession from lower plants to flowering species does not occur in this case. This pioneer behavior must be of great adaptive value in environments in which a sequence of glacial and interglacial events has continually changed ecological conditions. Besides, and in another temporal scale, that of present-day morphodynamics, the cryoturbation structures originating in the daily frost–defrost cycles hinder any possible stabilization of these high Andean habitats. The populations that colonize this environment play an important moderating role, fixing and wedging the mobile ground that thus forms small platforms or microterraces, as happens with *E. timotensis* on many of the steep slopes where it becomes established.

E. moritziana occurs on rocky sites, such as rocky summits, aretes, and horns, or over coarse periglacial debris formed by large boulders that carpet certain slopes in cirques and troughs (Fig. 3–8). Altitudinally, it ranges from 4100 to 4600 m, its upper limit surpassing that of *E. timotensis* because *E. moritziana* colonizes summits and mountain crests. The morphoclimatic effects of the periglacial climate are attenuated in the habitat of this species because rock interstices behave like thermal refuges by maintaining a more temperate microclimate that allows these populations to reach higher elevations.

E. spicata is found between 4000 and 4300 m, in habitats intermediate between those of the two
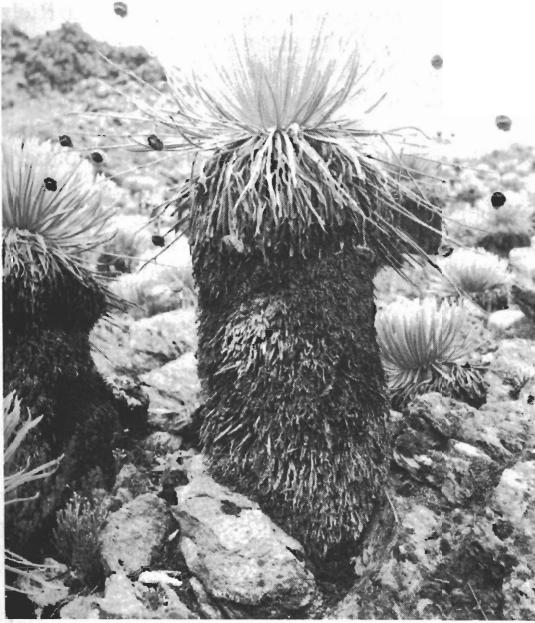
FIG. 3–8. *E. moritziana* growing on rocky crevices in the Páramo de Piedras Blancas, 4200 m. Photo by Carlos Estrada.

FIG. 3–9. *E. spicata* is normally found in intermediate habitats, covered by boulders and small angular debris. Páramo de Piedras Blancas, 4200 m. Photo by Carlos Estrada.

aforementioned species (Fig. 3–9), that is, on gentle slopes of cirques and valleys covered with medium-sized debris up to 50 cm in length.

Finally, I have to mention two additional species. In the desert páramo *E. semiglobulata* occurs in peat bogs between the steps of cirques and at the base of retreating glaciers, a perhumid environment where its decumbent trunks form giant cushions. *E. schultzii*, the most important species of *Espeletia* in the contiguous and lower Andean belt, reaches up to 4200 m in the desert páramo, where it occupies small areas having wetter conditions. This is not a giant rosette since it has only a small trunk. It is unable to colonize the extreme habitats of the high Andean belt, but its occurrence in small patches within the desert páramo is important, as we will see later, when the phenological niches of high Andean *Espeletia* are considered as a whole.

A Global Project Involving *Espeletia* of the Desert Páramo

As one approach to an understanding of the desert páramo ecosystem, my colleagues and I undertook a detailed analysis of the global strategies of the main species occurring in this belt: *E. timotensis*, *E. spicata*, and *E. moritziana*. Our study was carried out in the Páramo de Piedras Blancas (Fig. 3–2) between 4100 and 4300 m. The

fieldwork began in 1971; intensive sampling in permanent plots started in 1977 and continues up to now.

Three main lines of research were followed. The first deals with the global strategy of these species, including aspects of demography, phenology, and growth. The second concerns the temperature balance and the water and photosynthetic budgets, and the third line covers reproductive aspects with particular emphasis on pollination. In this chapter I refer mainly to the first approach, mentioning very briefly some ecophysiological results that may aid in the interpretation of plant strategies.

As elements of the global adaptive strategy allowing the ecological success of *Espeletia* populations in the harsh environment of the desert páramo, we selected several events and processes of their life cycle. These include the architectural pattern, the vegetative and reproductive phenodynamics, leaf production and its rhythmicity, growth of leaves and reproductive structures, attainment of sexual maturity, reproductive effort, and seed rain. Field data were obtained from several hundred marked individuals in permanent plots. Several thousand additional individuals were sampled at regular intervals near the permanent plots. As the Páramo de Piedras Blancas can be reached after a two-hour drive from our laboratory in Mérida, we were able to make the intensive sampling required for this type of

analysis. The results on populations dynamics will appear in another publication, and part of the ecophysiological aspects has already been published (Goldstein and Meinzer, 1983; Goldstein, Meinzer, and Monasterio, 1984).

THE DYNAMICS OF GROWTH AND REPRODUCTION IN *ESPELETIA*

In order to understand the adaptive strategies of *Espeletia* in the desert páramo, it seems essential to know the dynamics, capacity, and seasonal modalities of growth, as well as the part of the annual energy budget assigned to each organ and function. The phenological patterns and the reproductive behavior of their populations and individuals are also fundamental in the interpretation of their success as colonizers of the highest elevations of the cold tropics. To start with, we consider the architectural model of *Espeletia*, since it is the basis for an explanation of its dynamics of growth and reproduction.

Architectural Pattern

The three species of *Espeletia* that characterize the desert páramo belong to the Corner architectural model, defined by Hallé, Oldeman, and Tomlinson (1978) as monoaxial trees with indeterminate growth and lateral inflorescences. The Corner model corresponds to the life form *tall*, *polycarpic*, *pachycaulis*, *caulirosula* (Cuatrecasas, 1979), and to what Mabberley (1974) con-
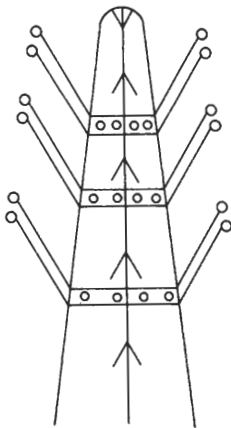
sidered as "unbranched pachycaulis." Du Rietz (1931) employed the attractive name of "rosette tree." The advantage of architectural models over traditional life-form systems is that they imply and synthesize the dynamics of growth that expresses itself in a precise architectural pattern through the patterns of meristematic activity throughout the life cycle of the plant. In this sense, the ecological constraints of the desert páramo are reflected in the sequential growth patterns of the various plant parts as well as in their spatial distribution.

Specific Elements of the Corner Model in Desert Páramo Espeletia

In accordance with Corner's model, *E. timotensis*, *E. spicata*, and *E. moritziana* have a monocaulous structure built by a single shoot apical meristem responsible for the aboveground vegetative biomass (trunk and leaves). In contrast, the root system is built by various independent buds. The inflorescences are lateral, produced by
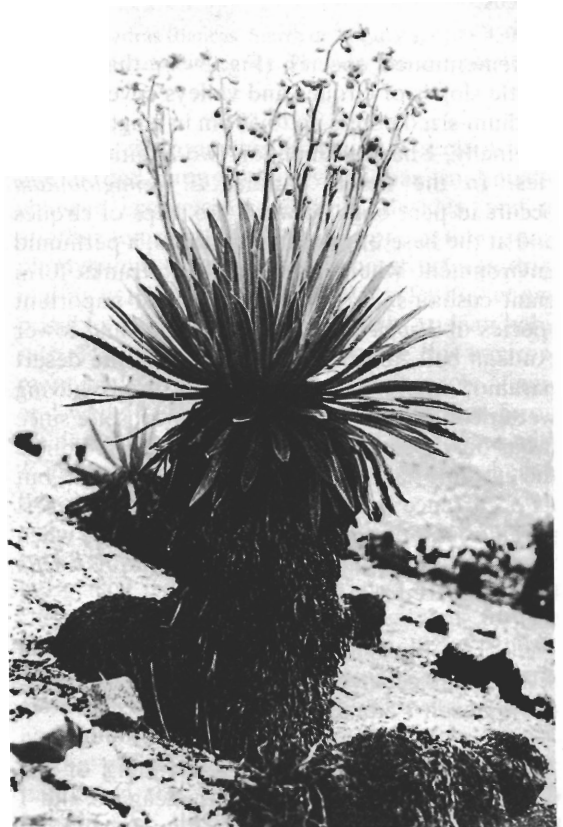

FIG. 3–11. The most conspicuous representative of the Corner Model is *E. timotensis*. Notice how the active leaves and the reproductive structures are located well above ground level. Photo by Nuni Sarmiento.

FIG. 3–10. Corner Model "monocaulous polycarpic tree," corresponding to all the species of *Espeletia* of the desert páramo. The stem has continuous growth and leaf production, but reproductive events occur at various frequencies throughout the adult plant life.

TABLE 3–2. Morphological and life cycle characteristics of *Espeletia* spp. in the desert páramo.

Species	Size adults (m)	Annual growth/ trunk (mm)	Estimated length of life cycle (years)	Mean number of leaves per rosette	Leaf size (length, width) (cm)	Length of inflor- escences (cm)	Average no. of heads/ inflor- escence	Head diameter (cm)
E. timotensis	2–3	15	170	240	50 × 3.5	110	11	3.5–4
E. spicata	1.5–2.5	20	130	590	35 × 2	80	22	2–2.5
E. moritziana	0.5–1	15	70	264	45 × 2	55	1	4–6

active buds in the axil of the young leaves of the rosette. Consequently, growth is indeterminate since it is not interrupted by reproduction, and the species are polycarpic. Monocarpic *Espeletia* differ from polycarpic ones in that their growth stops at the moment of reproduction, and they occur only below 4000 m, not being able to pass the barrier of the periglacial climate above 4000 m.

The three species have continuous growth, both in length of the trunk and in leaf production. The inflorescences, emergent from the axil of leaves, vary in their times of expansion at the specific, population, and individual levels (we will discuss this later). Corner's model of desert páramo *Espeletia* is exemplified in Figs. 3–10 and 3–11. Other elements associated with this architecture are presented in Table 3–2.

The growth in length of the unique axis and the production of leaves are continuous and synchronized as evidenced by the uniform pattern of leaf scars that may be observed on the denuded trunks. Phyllotaxis is typically spiral; the rosettes have spirally arranged leaves and congested persistent leaf scars on the trunk. Leaf abscission does not occur in these species; the leaves remain attached to the trunk and decompose very slowly during the life cycle of each individual, thus forming a case of marcescent leaves down to its base. Cuatrecases (Chap. 11) says: "The leaves of these species have enlarged imbricated sheaths arranged in multispiral circles at the end of the stem. The older, marcescent leaves attached to the stem embraced it with their closely imbricated sheaths." The trunk appears to be several times thicker than the real stem and acquires a columnar aspect. The adaptive significance of this bulky covering of dead leaves on the stem will be discussed later.

Biomass and Energy Allocation

The architectural pattern of *Espeletia* in the desert páramo reflects the allocation of their available energy to each plant organ or function. Consequently the architecture has great ecological importance since it controls the spatial distribution, both vertical and horizontal, of the energy incorporated into the ecosystem. Thus, architectural model and energy pattern are closely coupled.

It is of great interest to know how individuals growing under periglacial constraints allocate their resources to different functions, and to consider whether these allocation patterns constitute successful "decisions" that maximise their fitness in this environment. The proportion of the biomass allocated to aboveground and underground organs, to vegetative and reproductive structures, to assimilative organs, and to cryoprotection is particularly indicative in this context.

All three species of *Espeletia* in the desert páramo have the same pattern of resource distribution, only small features distinguishing each other. Figure 3–12 represents the case of a medium-sized individual of *E. timotensis*. The caloric values of the various plant parts appear in Table 3–3. Some main points to note are:

1. The aerial parts accumulate an overwhelming proportion of the total calories (96.6%) against only 3.4% represented by the underground biomass.
2. Within the aerial parts, the allocation of energy favors leaves (79.27%) over reproductive structures (inflorescences, heads, achenes: 11%), while only 4.4% is devoted to the stem.
3. Most of the energy stored in leaves corresponds to dead leaves (71.6%); green leaves instead accumulate 17.97% of the total stored energy.
4. The investment for rooting and support in these rosette trees is small—about 7% of their total energy. Given the unstable nature of the substrate, the root system has to be highly efficient to anchor the plant, and the stem is indeed very efficient to support
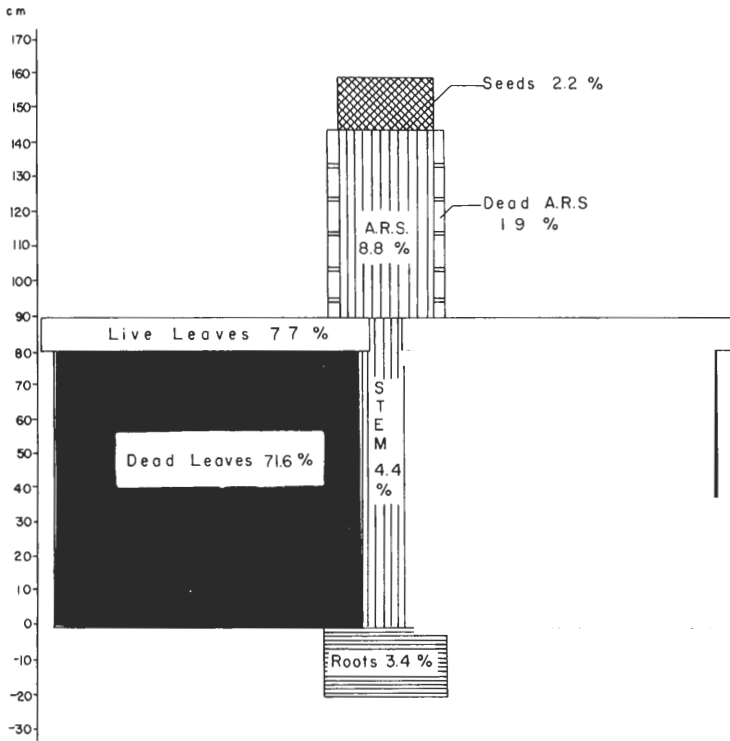
FIG. 3–12. Biomass allocation (%) in calories toward different plant organs in *E. timotensis*. Each figure is the mean of 10 replicates corresponding to 10 adult plants.

TABLE 3–3. Caloric values per gram of various plant structures in *E. timotensis*.

		Kcal/g
Live leaves		
Leaves of the bank		4.2
Juvenile leaves	(14– 28 cm²)	4.1
	(28– 56 cm²)	3.9
	(56– 84 cm²)	4.5
Adult leaves	(84– 98 cm²)	4.5
Mature leaves	(98–130 cm²)	4.5
Pre-senescent leaves	(130–140 cm²)	4.9
Senescent leaves		4.7
Dead leaves		4.4
Stem		
Cortex		4.7
Pith		4.3
Roots		4.9
Reproductive parts		
Inflorescences		4.4
Heads		4.7
Achenes		4.9
Maximum biomass per plant (g)	:	8,441.91
Maximum biomass per plant (Kcal)	:	38,339.5
Estimated annual leaf production (Kcal)	:	3,150.0

Note: Each figure is the mean of 10 samples corresponding to 10 adult individuals.

the large mass of green and dead leaves and the reproductive structures as well.

5. *E. timotensis* clearly assigns the greater part of its energy to its photosynthetic structures, and most of it remains on the plant forming the cover of dead leaves around the trunk. However, this dead material, attached to the stem for the life span of the individual plant, does not represent a reservoir of energy to be used again, but it plays an important role in the transfer of nutrients from decaying leaves to actively growing tissues (Monasterio, 1980b). Besides this function as a nutrient sink, the cover of dead leaves isolates the living tissues of the stem, protecting them against low temperatures and regulating their water balance (Goldstein and Meinzer, 1983). Furthermore, the necromass is colonized by rich and diversified meso- and microfaunas that contribute to the cycling of nutrients in this ecosystem (Garay, Sarmiento-Monasterio, and Monasterio, 1982).

A first general conclusion that follows from this pattern of energy allocation is that the energy produced throughout the life cycle of the desert páramo *Espeletia* accumulates not just in their growing organs, such as stem and roots, but

chiefly in the slowly decomposing cover of dead leaves that encloses the whole stem. The only energy dispersed by these plants is that forming part of the reproductive structures, mostly the achenes, since even the old inflorescences remain attached to the stem for a relatively long time.

The investment in reproduction appears to be rather high (11%), particularly if we consider that only one reproductive event was considered in our energy budget. A substantial part of the energy allocated to sexual reproduction goes to auxiliary structures (8.2%), but achenes represent only 2.2%. Thus most of the reproductive effort goes to structures that protect flowers or, like the axis of the inflorescences, dispose them at a favorable level either to facilitate pollination or to escape frost injury. The high investment in auxiliary reproductive structures gives a certain protection to all stages of the long reproductive process from buds to anthesis and seed dispersal. Figure 3–11 illustrates how the inflorescences of *E. timotensis* reach an air layer somewhat higher, and possibly with a more stable microclimate, than that of the rosette of green leaves.

Finally, it must be considered that the energy accumulated at any given moment in the life cycle of individuals of these species constitutes a fair approximation of the total energy allocated to vegetative plant parts throughout their life span. This is because the biomass allocation carries the whole history of the individual, since besides those parts with increasing biomass accumulation (e.g. the stem and roots), all leaves produced by an individual, as well as a part of the inflorescences, remain attached to the stem until its death. I will return to these aspects when dealing with reproduction.

Dynamics of Vegetative Growth

The rosette trees, ever-growing and with continuous activity, present the same aspect at any time of the year: the composition of the rosettes always looks uniform, and no ostensible changes in cover and biomass are noticeable at first sight. In this section, I analyze the rosette as a population of parts, considering the number of leaves existing at any given time, the rhythms of leaf initiation, expansion, and death in the dry and wet seasons, and the rates of leaf growth and turnover times of the rosette.

The principal problem is whether, in spite of their continuous growth, *E. timotensis*, *E. spicata*, and *E. moritziana* show a difference in rhythmicity along the seasons coupled with environmental changes, or whether an almost absolute constancy predominates, or else whether the dynamics of growth shows some endogenous rhythmicity.

The Demographic Structure of the Rosette

If the rosette is considered a whole composed of modular units, i.e., the leaves, a demographic approach can be applied to this ensemble. The knowledge of the demographic structure of leaves provides data useful to interpret the dynamics of leaf growth and the turnover time of the rosette.

The demographic approach applied to modular plant units is of recent use (Harper, 1977; Harper and Bell, 1979), but the concepts on which it is based are somewhat older (White, 1979). White (1979) considers the plant to be a metapopulation of parts.

In the cases of *E. timotensis*, *E. spicata*, and *E. moritziana*, which reproduce only by seeds, the modular units, the leaves, of a given individual all belong to one particular genet and in this sense they constitute a homogeneous ensemble.

The rosette with its spiral and compact arrangement of leaves presents at any given time the same sequence of developmental stages in its population of leaves. In its center (Figs. 3–13 and 3–14), a compact core of immature, not yet expanded, leaves, here named the *leaf bank* (foliar primordium and immature leaves), surrounds the apical meristem. Near or very near this center stand the recently expanded young leaves, and in sequence from the center to the periphery are all the other developmental stages, corresponding with increasing age to young, adult, mature, to senescent and finally dry leaves, thus gradually adding to the collar of dead leaves around the trunk.

Figure 3–15 represents the demographic structure of the rosette of *E. timotensis* on the basis of foliar area, which our data indicate has a 100% correlation with leaf length in this species. Two maxima appear in the frequency distribution, the first and higher one corresponding to the unexpanded units in the leaf bank (0–14 cm^2). This maximum is followed by a conspicuous inflection that corresponds to young leaves of intermediate sizes: 28–42, 42–56, 56–70, and 70–84 cm^2. Each successive age class has a smaller number of leaf units. The second maximum, which gives rise to a quite abrupt discontinuity in the graph, corresponds to adult leaves in the range of 84–126 cm^2, already in the final stages of their growth and development. The last class corresponds to leaves that are old but still alive. This increase in foliar

FIG. 3–13. Rosette of *E. timotensis*. In its center appears the leaf bank surrounding the single apical bud. Photo by Carlos Estrada.
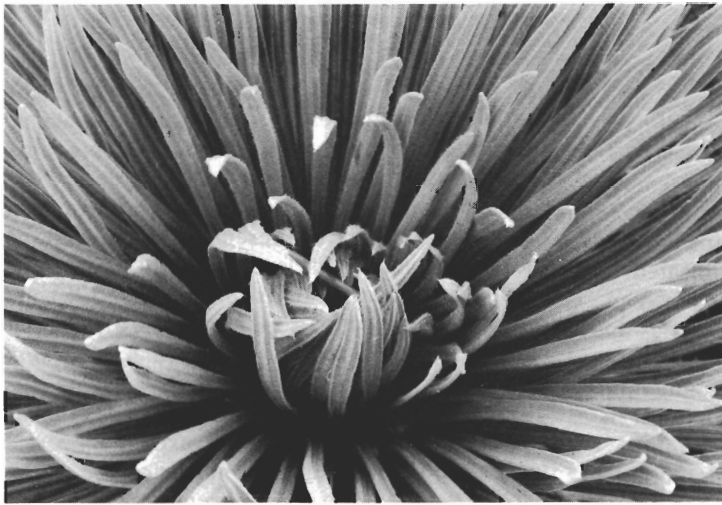

FIG. 3–14. Rosette of *E. spicata*; various developmental leaf stages may be seen. Photo by Carlos Estrada.

area agrees with the disposition of leaves from the center to the top of the rosette. The distribution from center to periphery corresponds to sequential stages of development, and this arrangement agrees with the phyllotaxis in spiral.

The static vision of the rosette as represented in Fig. 3–15 needs for its interpretation the analysis of each leaf-area class in terms of its dynamics of growth and of the role of each leaf class in the productive process. Figure 3–16 indicates the dry weight of leaves per size class. In this example, the total dry weight of live leaves in the rosette attains 1665 g, while the leaf bank, with 174 units, attains 8.5 g, that is, 0.33% of the total weight. The leaf bank is not in contact with the external environment, their units do not photosynthesize, are yellow-white in color, and show only minimal growth, remaining in a state of dormancy or rest. For this reason we consider them to be a bank or reservoir of foliar resources. These very imma-

ture leaves behave as consumers and importers of resources from the rest of the plant.

In the external part of the rosette, the class of 14–28 cm^2 corresponds to freshly expanded leaves that still behave as consumers, their color being pale yellow. In the next several classes and up to 84 cm^2 of foliar area, a transitional and gradual process occurs that changes them from consumers to producers. But together with assimilation, leaf growth and elongation become the most conspicuous processes at this stage. The "residence time" in each of these classes is quite short.

The second maximum, 84–126 cm^2, corresponds to leaves at the peak of their assimilation process, the most efficient producers in the rosette, with gray-green color. Their growth slows while the residence time increases, and these assimilating leaves attain their optimum and become stable. As Fig. 3–16 shows, the dry
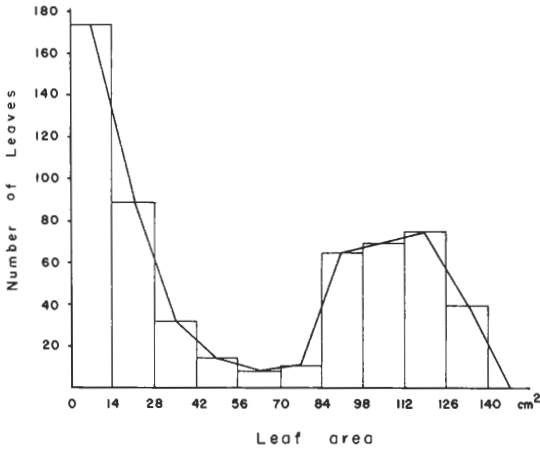
FIG. 3–15. Demographic structure of the rosette in *E. timotensis* showing the distribution of the population of leaves in leaf area classes.
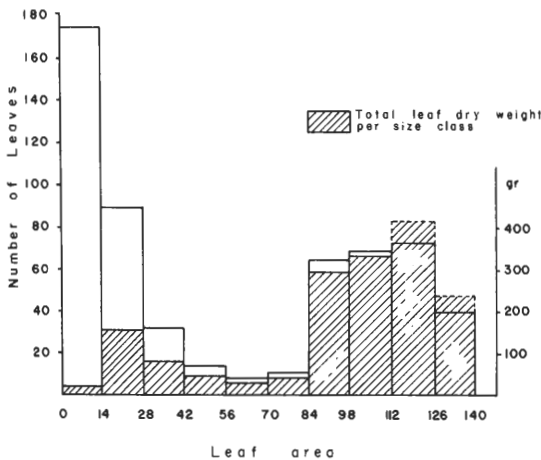

FIG. 3–16. Relationship between leaf area and leaf dry weight in *E. timotensis*.

weight of leaves in the classes from 84 to 126 cm^2 reaches 1050 g, which represents 63% of the total weight of the rosette. The last class reaches the top size and growth is then finished; the first signs of decay are already apparent. It is a fragile class, but assimilation remains active.

Leaf Life Cycle

As pointed out by Harper (1977), "a leaf has a life history, a changing pattern of behavior from birth, as a primordium on a meristem, to death from senescence or some environmental hazard." Figures 3–17 and 3–18 depict the leaf life cycles of *E. timotensis* and *E. spicata*, respectively. In the case of *E. timotensis* the measurement of leaf length of a cohort of leaves starts at the point of

leaf expansion from the leaf bank. In the initial stages, the growth in length is only 1 mm/day, with a gradual increase up to a maximum rate of 2.5 mm/day. During the first six months, the growth rate curve shows a steep slope. During this period, the leaves expand up to 40 cm in length until they retain the maximum size of 50 cm. The maximal growth rates correspond to foliar areas between 45 and 100 cm^2, the minimal rates with areas up to their top size. Correspondence between length, area, and dry weight was obtained for about 500 leaves. In Fig. 3–17, at the start of the measurements, the recently expanded leaves have a dry weight of 0.68 g. After seven months of growth and assimilation, they reach the top weight of 6.29 g per leaf—an increase on the order of 6 g.

The top size and weight are reached seven months after the start of growth. After that, leaves remain in the apogee of their function for 14 or 15 consecutive months, and the first signs of senescence begin only 22 months after their start. The cohort studied since November 1978 showed two years later clear signs of withering but their basal parts were still active. Therefore, the leaf life cycle in *E. timotensis*, from the start of growth from the leaf bank and its incorporation into the external rosette, covers at least 20 months of optimal activity. But we must also consider the length of time they remain in the leaf bank, which we estimated to be 1.4 years. The total life cycle of the leaves in this species would then be over three years.

As each leaf develops, its position in the rosette changes. Thus, a spiral from the apical bud to the border of the rosette is traced during the leaf life cycle. Hence, the microenvironment of the leaf varies along this pathway, from the refuge conditions in the leaf bank, when leaves are totally dependent, to leaf expansion. This implies not only growth and assimilative autonomy, but also gradual changes in leaf angles that become greater as they approach senescence and then become incorporated into the collar of dead leaves. This angle has great significance, since it controls the incident light on the leaf surface, therefore influencing phtosynthesis and the temperature balance of the leaf. Following their spiral trajectory for two years, each leaf traverses a gradient of microenvironmental conditions within the rosette.

Leaf mortality is closely linked with leaf senescence, and each leaf dies when its life cycle is completed. The only mortality observed during field measurements was due to predation, mainly by insects, and it was quite low since insects produce some leaf damage but rarely leaf death. It
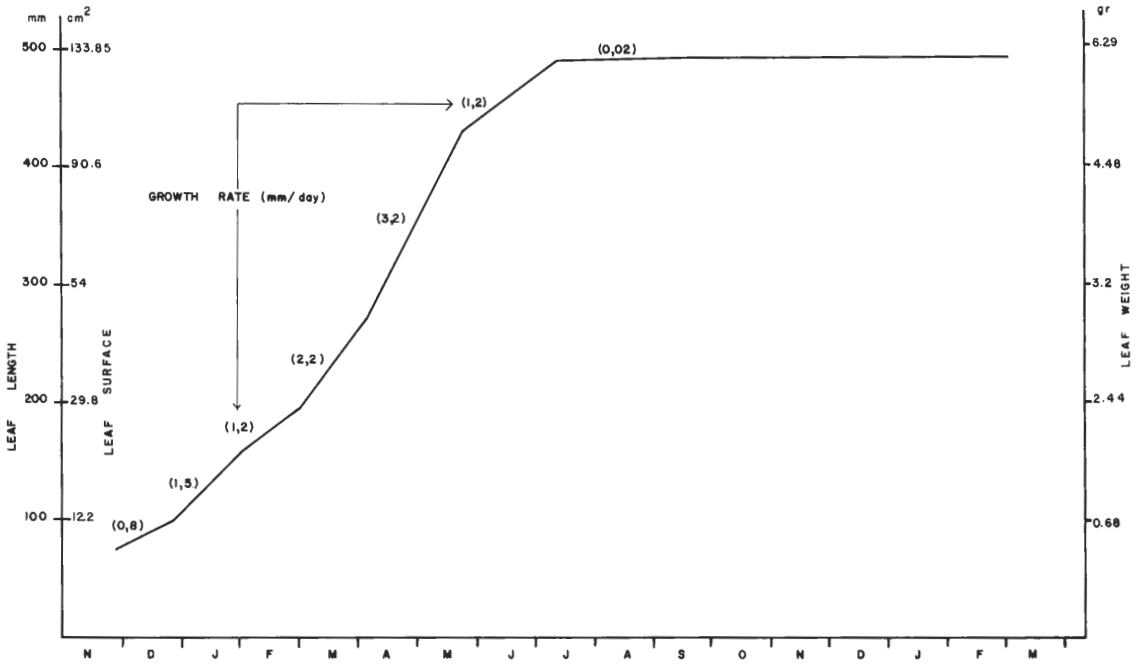
FIG. 3–17. Life cycle of leaves in *E. timotensis* corresponding to a leaf cohort that started in November 1978. Growth rates in each developmental stage are indicated as well as the correlation between leaf length, area, and dry weight.
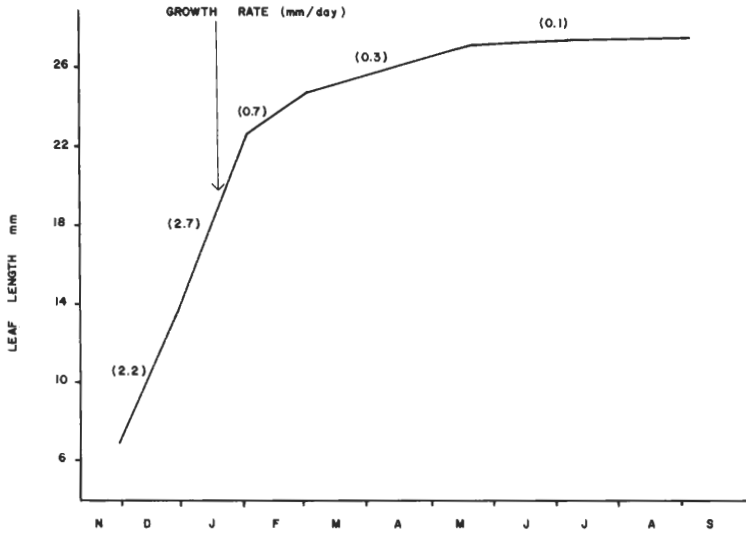

FIG. 3–18. Life cycle of leaves in *E. spicata* corresponding to a leaf cohort that started in November 1978. Growth rates in each developmental stage are indicated.

was not apparent whether any mortality was due to environmental hazards, caused either by the weight of the snow over the leaves during periods of heavy snowfall, or by frost for many consecutive days. However, during some exceptionally dry years, whole plants as well as certain leaves may die.

I refer now to the leaf cycle in *E. spicata* (Fig. 3–18). Its behavior is similar to that of *E. timotensis*, although development is more rapid during the first four months to reach the top size

six months after their start. Nevertheless, the leaf span in the external rosette is shorter, being totally accomplished in 12 or 14 months. In *E. moritziana* it is less than one year.

Leaf Life Cycle and the Demographic Structure of the Rosette

The analysis of differential growth rates along the development of the leaves of *E. timotensis* allows one to interpret the demographic structure of the

leaf population in the rosette. Why do leaf units accumulate in the leaf bank and also in adult size classes? Why are there so few leaves in other intermediate developmental stages?

Comparing Figs. 3–15 and 3–17, we see that low growth rates correspond with the accumulation of leaves in a given size-class, whereas a high growth rate, such as the one characterizing young leaves, brings about a rapid change toward the larger size classes.

Growth Rates in the Wet and Dry Seasons

Leaf growth seems to depend on different factors. Some are ontogenetic and relate to the developmental stage reached by each leaf, whereas others correspond to moisture seasons (Figs. 3–17 and 3–18). Maximal growth rates are found in young leaves: 14–30 cm in length in *E. timotensis*, 10–20 cm in *E. spicata*. In the latter species, maximum rates of 3.45 mm/day were recorded in leaves of 10–15 cm during the wet season, but this size class only attained 3.0 mm/day during the dry season. Similar results may be seen in Tables 3–4 and 3–5.

In the foliage of the ever-growing *Espeletia* of the desert páramo, growth takes place continuously, but not at constant rates. This implies that leaves incorporated from the leaf bank into the external rosette will receive different impulses for their initial development or for their maturation according to the season of the year. Nevertheless, given the extended leaf life cycle in these species, particularly in *E. timotensis*, each leaf, independent of its time of inception, will later be subjected to the influence of several dry and wet periods. Besides, its spiral trajectory will be conditioned by other leaves preceding or following it in the rosette. Observations by Estrada and Monasterio (unpublished) suggest that the duration of the leaf life cycle in these species is constant and unrelated to the starting period of each leaf as well as to the age of the individual to which they belong.

Rosette Turnover Time

Long-term measurements of leaf expansion (three years) were made to determine the total number of leaves expanded per unit time during several different seasons of the year. Several individuals of each species were marked, and the total number of expanded leaves was counted at monthly intervals. We define rosette turnover time as the time taken to renew all leaves in the rosette.

As Fig. 3–19 indicates, the total number of leaves incorporated into the rosette in two consecutive years in *E. timotensis* is 240. The mean rate of leaf expansion in this species is 0.3 leaves per day; that is, a new leaf departs from the leaf bank toward the external rosette approximately every three days.

If the expansion rates during the wet and dry seasons are compared, it can be seen that their differences are not significant. Thus, of the two greatest expansion rates recorded, one was in the wet (0.41 leaves per day), the other in the dry season (0.49 leaves per day). Of two lowest values attained, one was in the dry (0.23 leaves per day), and the other in the wet season (0.21 leaves per day).

Certain anomalies in these expansion rates, however, deserve further comment. At the beginning of 1980 (Fig. 3–19), in the middle of the dry season, no leaf departure was recorded during a period of 35 days. But during this time, the leaf bank increased noticeably in all three observed species. A possible explanation for this is that normally the lowest temperatures occur in January, when there are frosts during many consecutive nights. But are there any mechanisms that might hinder the departure of leaves from the leaf bank? If the answer is yes, it could be the same

TABLE 3–4. Leaf growth rates of *E. timotensis* in the dry and rainy seasons for different size classes. Mean and standard error for 26 leaves in three plants.

Size class (cm)	Growth rate (mm/day)	
	Dry season	Wet season
6–13	1.51 ± 0.15	–
13–21	1.72 ± 0.16	–
21–29	1.93 ± 0.14	3.11 ± 0.15
29–36	1.83 ± 0.2	2.12 ± 0.29
36–43	0.56 ± 0.09	0.52 ± 0.12
43–50	0.11 ± 0.02	0.20 ± 0.04

TABLE 3–5. Leaf growth rates of *E. spicata* in the dry and rainy seasons for the different size classes. Mean and standard error for five plants.

Size class (cm)	Growth rate (mm/day)	
	Dry season	Wet season
5–10	2.55 ± 0.18	2.94 ± 0.12
11–15	3.00 ± 0.13	3.45 ± 0.09
16–20	2.78 ± 0.15	3.11 ± 0.12
21–25	1.83 ± 0.16	2.20 ± 0.11
26–30	0.40 ± 0.09	0.48 ± 0.06
31–35	0.05 ± 0.02	0.17 ± 0.03
36–40	−0.02 ± 0.03	–

type of mechanism as that of nyctaginasis (daily rhythm of opening and closing of the rosette), but in this case blocking leaf expansion. Anyway, the leaf bank appreciably increased during that cold and dry period, but remember that this is precisely the most stable and protected microenvironment within the rosette, and indeed the whole plant.

The mean number of expanded leaves per year was 120; individual variation is rather small. The rosette turnover time for *E. timotensis*, about 24 months, was the greatest determined in any of the three species. The dynamics of leaf production in *E. spicata* is shown in Fig. 3–20. In this species too, leaf expansion seems to be continuous, with an average rate of about one leaf per day. In total, 370 leaves are incorporated into the rosette yearly. These values are roughly double those obtained in *E. timotensis*; however, both leaf size and leaf weight are much higher in the latter species. Rosette turnover time is also shorter in *E. spicata*, about 13 or 14 months.
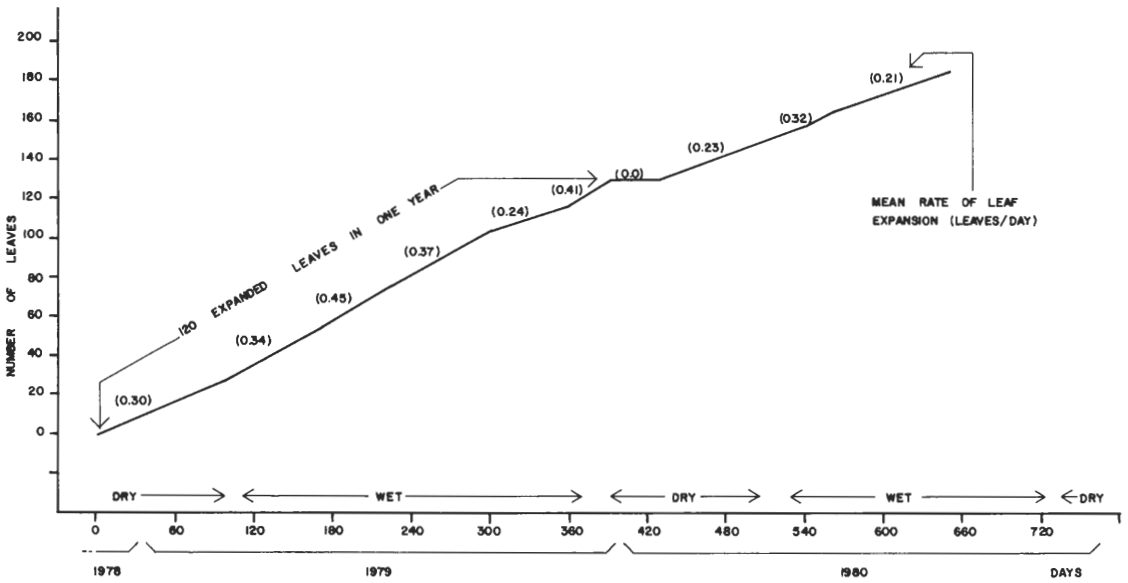

FIG. 3–19. Dynamics of leaf production in *E. timotensis* in contrasting seasons. The estimated rosette turnover time was 24 months.
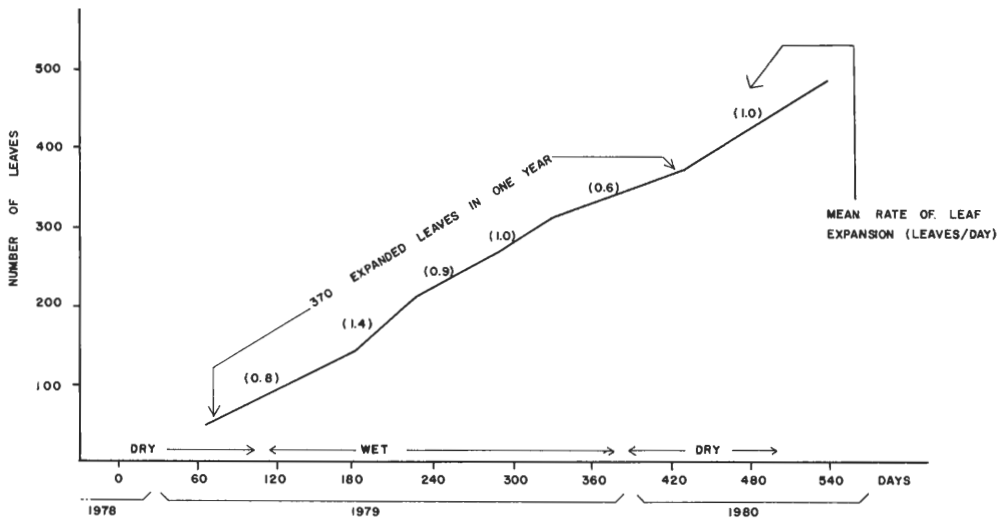

FIG. 3–20. Dynamics of leaf production in *E. spicata* in contrasting seasons. The estimated rosette turnover time was 14 months.

A comparison of the three species shows that *E. timotensis* has the longest turnover time (24 months), whereas in *E. spicata* and *E. moritziana* the respective values were 13–14 months and 12 months. Considering the life cycle of the three species, we see that *E. timotensis* has the longest life span followed by *E. spicata*, and *E. moritziana* (see Table 3–2). Thus, the longest-lived species seems to have the longest renewal rhythms, longevity being expressed not only by the length of the individual life cycle, but also by the longer turnover time of all organs, as I shall confirm later when considering reproductive aspects.

In comparative terms and as a point of reference, I want to consider the rosette turnover time in *E. schultzii*. Smith (1974) presented short-term measurements in populations of this species at various altitudes. At its upper altitudinal limit, about 4200 mm, *E. schultzii* shows a longer turnover time (12 months) than at 3600 m (7 months). Moreover, the various ecotypes along the altitudinal range of the species have different life spans, the most long-lived being at the highest altitude in the desert páramo.

Phenological Patterns

Reproduction is the most conspicuous process in the giant rosettes of the desert páramo. It implies a transitory rupture with the monocaulous form due to the appearance of numerous inflorescences emerging from the axils of the youngest leaves. Although reproduction is a long-term process in these polycarpic *Espeletia*, which reproduce only sexually, it does not interrupt leaf production or growth.

In the first part of this chapter I emphasized the spatial partition of the niche during the vegetative phases, each species of *Espeletia* having its own closely delimited habitat. This separation implies a sharp division of physical resources such as water, light, and nutrients. Apparently, there is no actual competition among these populations, since the niche is spatially partitioned. But what happens with the phenological niche? Are the reproductive processes synchronous in the various species or are the homologous phenological phases asynchronous? An analysis of the phenological pattern of each species may also provide a key to the degree of reproductive isolation among these closely related taxa.

I shall discuss in some detail the phenological pattern and the reproductive behavior of *E. timotensis*; the other *Espeletia* of the high Andean belt will be considered for comparative purposes only. Our phenological studies in the desert páramo started in 1971, and from 1977 on we gathered quantitative data on several hundred individuals in permanent plots.

The Phenological Pattern of E. timotensis

Our preliminary observations since 1971 suggested that this species has aperiodic reproductive behavior, because during several consecutive years its populations remained entirely vegetative. This was not the case with the other *Espeletia* in the desert páramo, which entered reproductive phases each year, as also pointed out by Smith (1974). In order to study this behavior more closely, we established permanent plots to follow reproduction at both the population and at the individual levels.

Apart from its aperiodic reproductive activity, when a given reproductive event erupted, the various phenophases followed a precise chronology. I give as an example the 1978–79 phenological cycle, for which I have data from 344 inflorescences that gave rise to 3677 heads.

The reproductive phenorhythm of *E. timotensis* may be summarized as follows (Fig. 3–21). The reproductive process starts in the middle of September with the emergence of the inflorescences, which are no more than 5 mm long and are scarcely perceptible hidden inside the rosette. From this starting point, a slow process of axis elongation and head maturation continues for almost one year. A maximal elongation rate of 4.98 mm/day was recorded in April–May when the axes were 21–30 mm long. When full grown, the inflorescences surpass 1 m (Fig. 3–21). A huge energetic investment is therefore directed toward the auxiliary reproductive structures whose building up takes about one year. In May, the first female flowers begin to open, followed by the normal sequence of phenophases in the processes of flowering and fruiting. A peak in the blooming of female flowers occurs in August, and a peak in pollination in September, but both processes go on for several consecutive months, from May to December. The maturing and dispersal of the achenes also continue for several months. Toward the end of June of the next year, most achenes have already dispersed, but a few remain on the heads.

In summary we have a period of 21 months from the starting point of reproduction in September 1978 to seed dispersal in June 1980. Thus, the reproductive schedule of this species does not follow an annual cycle but rather extends over a
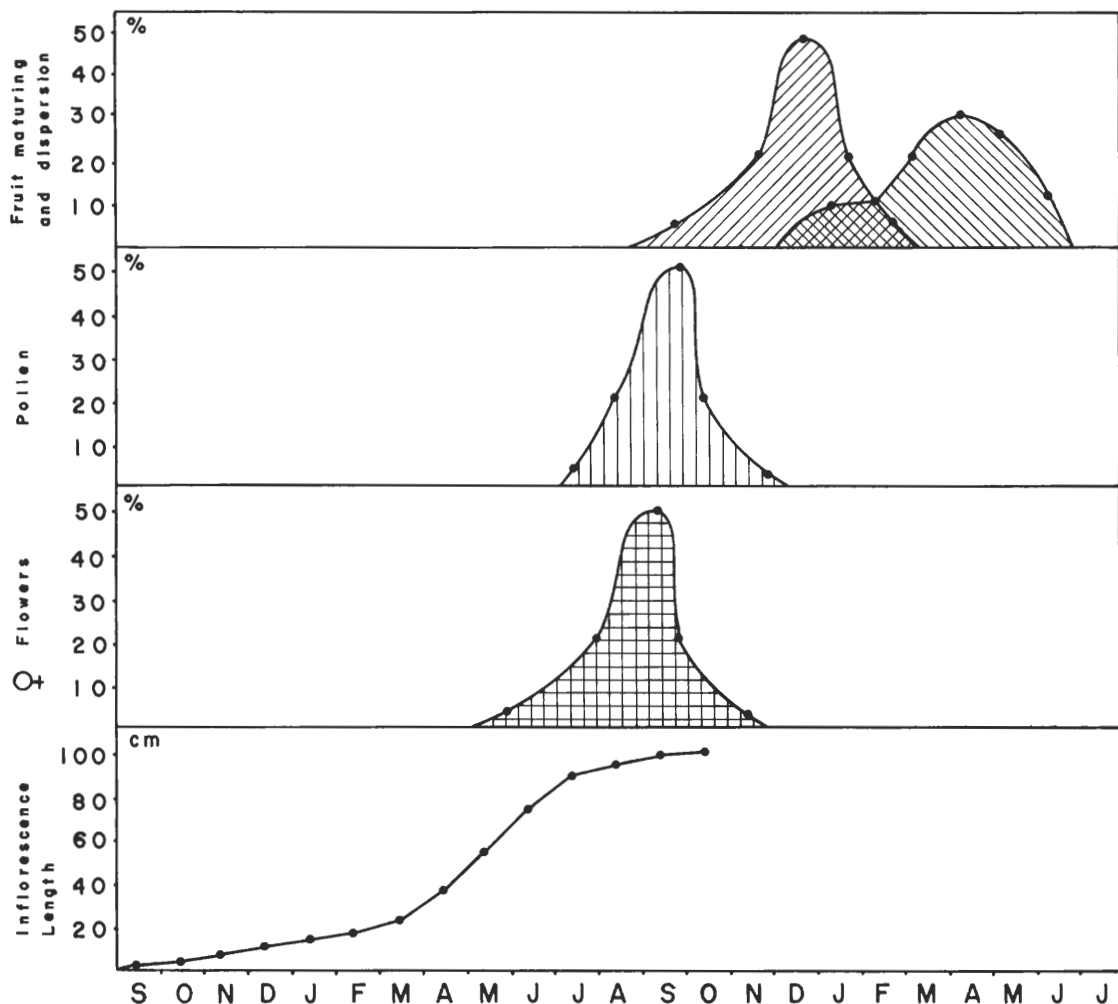
FIG. 3–21. Reproductive phenorhythm of *E. timotensis* in the Páramo de Piedras Blancas at 4200 m showing inflorescence elongation rate, production of female flowers, pollen, and fruit maturation and dispersal. This reproductive process started in September 1978 and the dispersal of achenes still continued in June 1980. Data based on 344 inflorescences that produced 3677 heads.

longer period, of the same order as the rosette turnover time.

I would like to remark on two aspects. The first is the duration of each phenophase for a relatively long period of time. This avoids the risks of losses due to environmental hazards and affords a greater probability of success for some key phases such as pollination and fertilization. The second aspect is the co-occurrence in a given population and in each individual of various phenological phases that may also contribute to avoid the risks of a total synchrony.

The reproductive process in *E. timotensis* extends over several moist seasons. The greatest energetic investment, that of building up the inflorescences, takes place mostly in the dry sea-son, whereas pollination and fertilization occur in the wet season.

Reproductive Behavior of Individuals of E. timotensis

Long-term phenological observations were made on individuals of *E. timotensis* in permanent plots, in order to analyze reproductive behavior at the individual level as well as intrapopulation variability. Table 3–6 synthesizes seven years of observations (1976–82) on all adults in the perme-nent plots (58 individuals). Five different patterns were observed in this period. The first, shown by 25.8% of the population, is one in which no indi-vidual entered into reproduction during the seven

TABLE 3–6. Reproductive frequency in a population of 58 adults of *E. timotensis* in the period 1976–82.

Year							Number of reproductive events in 7 years	Number of individuals
1976	1977	1978	1979	1980	1981	1982		
1ᵃ	0	1ᵃ	0		1ᵃ	1ᵃ	4	2
1ᵇ		1ᵇ		1ᵇ		1ᵇ		
1ᵃ		1ᵃ 2ᵈ			1ᵃ 2ᵈ	2ᵈ		
1ᵇ	0		0	1ᵇ	1ᵇ		3	10
1ᶜ		1ᶜ 4ᵉ		4ᵉ	4ᶜ	1ᶜ		
		1ᶠ		1ᶠ		1ᶠ		
1ᵃ		1ᵃ 2ᶜ		2ᶜ				
	0		0			0	2	15
		8ᵇ		4ᵈ	8ᵇ 4ᵈ			
1	0	9	0	2	3	1	1	16
0	0	0	0	0	0	0	0	15
Total number of reproductive individuals per year								
7	0	31	0	15	24	⁀7		

Note: Columns 1–7 show the individuals that started their reproductive cycle in each year; a letter (a to f) indicates those whose reproductive cycle is linked together in the same years. Five patterns are distinguished according to reproductive frequency. The number of plants showing each pattern is given in the last column.

consecutive years. A second pattern corresponds to those plants reproducing just once in that period (27.5% of the population); a third, to plants reproducing twice (25.8% of the population); a fourth, shown by individuals with three reproductive events (17%); and a fifth, shown by individuals with four reproductive events (3.4%).

The data in Table 3–6 also suggest relative synchrony in the reproductive behavior of individuals of this population. Thus, in 1977 and 1979 not a single plant bloomed. Although the sample is relatively small, this conclusion was supported by the additional sampling of 1500 plants each year outside the permanent plots. It appers then that the whole population of *E. timotensis* in the Páramo de Piedras Blancas fails to bloom in some years, as in 1977 and 1979. In contrast, in 1978 and 1981 a relatively large proportion of the population entered into reproduction (53% and 41% respectively).

On the other hand, individuals that flower more than twice in seven years seem to repeat their reproductive cycles together. This linkage implies highly variable pollen production and seed crops, with years when these resources are almost nil alternating with periods of abundant production.

Table 3–6 groups the different reproductive schedules into three main patterns that take into account rhythms and frequency of sexual reproduction (Fig. 3–22). The first one, (top of Fig. 3–22), corresponds to those plants in which variable periods set apart two successive repro-

ductive events that never overlap. The minimum period to avoid overlapping would be two years, and the longest observed period is seven years. The second reproductive pattern (middle of Fig. 3–22), corresponds to those individuals that reproduced twice in seven years. Their behavior shows two successive reproductive events in two years. This led to an overlapping of phenological phases, since the last reproductive process started when the previous event was still far from being completed. This overlap, with the implied additional cost, was followed by several years without further reproduction. The third repro-
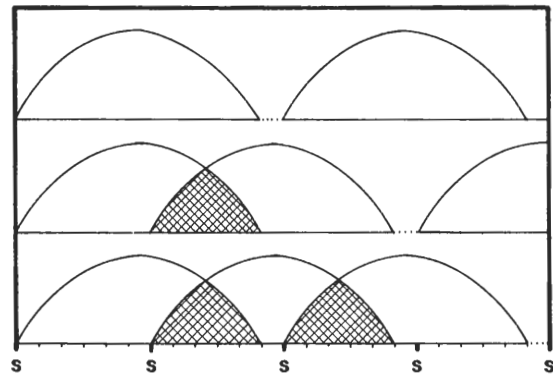

FIG. 3–22. Main reproductive patterns in *E. timotensis* during seven consecutive years. *Top:* Individuals without overlapping of reproductive events. *Middle:* Plants that reproduced twice in seven years (one overlap). *Bottom:* Plants that reproduced four times in seven years. S (September) indicates the start of reproduction.
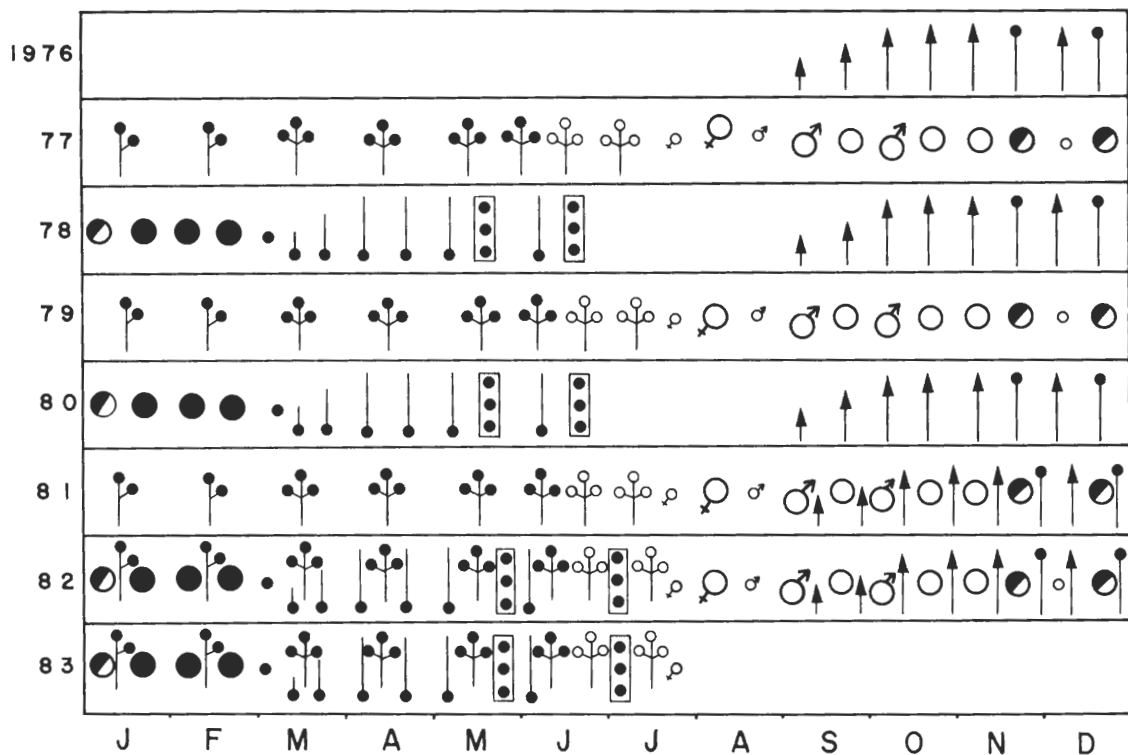
FIG. 3–23. Diversity of the phenological space in populations of *E. timotensis* (1976–82). A change is shown from an empty phenological space (first months of 1976) to one of maximal diversity in 1982 when several phenological phases coexisted.

Symbol	Description
↓ ↑ ↑	Starting and growth of the inflorescences
↑ ↑• ↑•	Various stages in head formation and inflorescence elongation
⚘	Open heads, flower buds
♀	Female flowers
♂	Pollen
○	Maturing fruits
◐	Maturing and mature fruits
↓	Mature fruits
▦	Fruit dispersal
•	Seed bank

ductive pattern (bottom of Fig. 3–22), corresponds to plants that flowered four ties in seven years. It is characterized by more than one overlap between successive reproductive events. This case might almost be considered as a pattern for continuous production of flowers, pollen, and fruit. As can be seen, these patterns range between two extremes: extended unfertility and multiple reproduction.

Diversity of Phenological Resources

The reproductive patterns exhibited by *E. timotensis* contribute to increase the phenological diversity of the plant community throughout the years. In seven years of records, the phenological space showed variable degrees of diversity (Fig. 3–23). Thus, up to September 1976 there was no reproductive activity in this population. At that time, a few plants started their reproductive cycles, which were completed in 1978. As I have shown, reproductive events were not started in 1977 or in 1979. From 1981 on, a certain overlap of reproductive events at the individual level began, with the consequent overlap at the population level, thus enriching the phenological diversity at any given time. A switch occurred then from an empty phenological space to one showing the greatest diversity. The consequences of these oscillations for pollinators

(mostly arthropods) and granivores (mostly birds; see Vuilleumier and Ewert [1978, p. 78], especially *Phrygilus unicolor* in desert páramo), as well as for the renewal of the seed bank, can be easily visualized.

Phenological Niches: Interspecific Comparisons

In the desert páramo, reproductive processes do not acquire their real significance at the level of the whole ecosystem unless all the species of *Espeletia* can be considered together as populations producing phenological resources according to various interdigitated patterns. Figure 3–24 shows the temporal division of the phenological niche between the four main species of *Espeletia*: *E. timotensis*, *E. spicata*, *E. moritziana* and *E. schultzii*. The asynchrony between homologous phases in the first three species is readily apparent, whereas *E. schultzii* shows more continuous production. Apparently, the three typical species

of the high Andean belt have an almost complete separation of their reproductive phenophases. This might permit the sharing of the same population of pollinators during the year. Even if more than one species attains the flowering phases at more or less the same time, the accomplishment of the successive flowering stages is not synchronous.

This way, the flowering behavior of each species suggests both a precise synchronization at the intrapopulation level and a conspicuous desynchronization of homologous phenophases among the different species. This behavior may have an adaptive value, since it allows the sequential utilization of one of the most limiting resources in this ecosystem: the populations of pollinators. Furthermore, this desynchronization contributes to the genetic isolation of the species of *Espeletia* in the desert páramo, promoting both their biological diversification and their ecological restriction to different habitats in the high Andean belt.
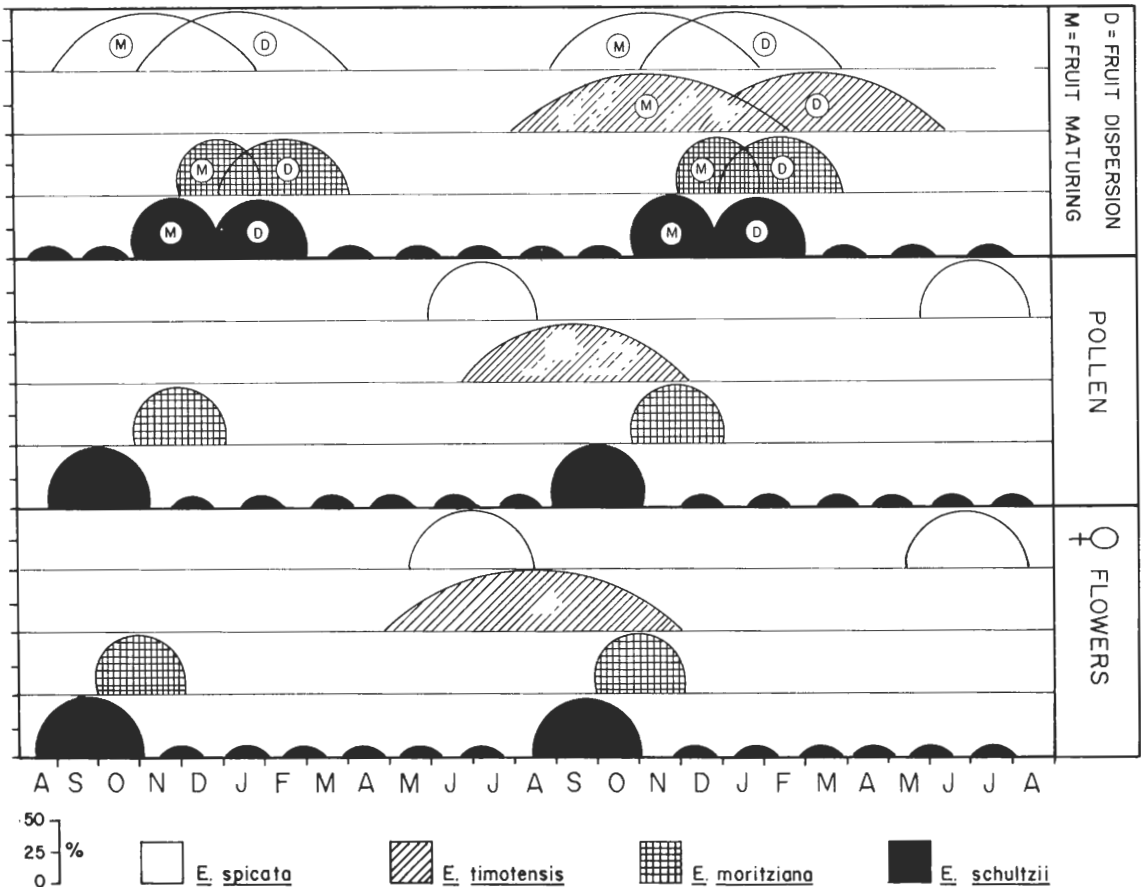

FIG. 3–24. Temporal partition of the phenological niche between the main species of the uppermost vegetation layer in the desert páramo: *E. timotensis*, *E. spicata*, and *E. moritziana*. Production of female flowers, pollen, and seeds is shown. Notice the desynchronization between these crucial phenophases in homologous species. *E. schultzii*, in contrast, has a continuous succession of reproductive phases throughout the year, although there is a major peak.
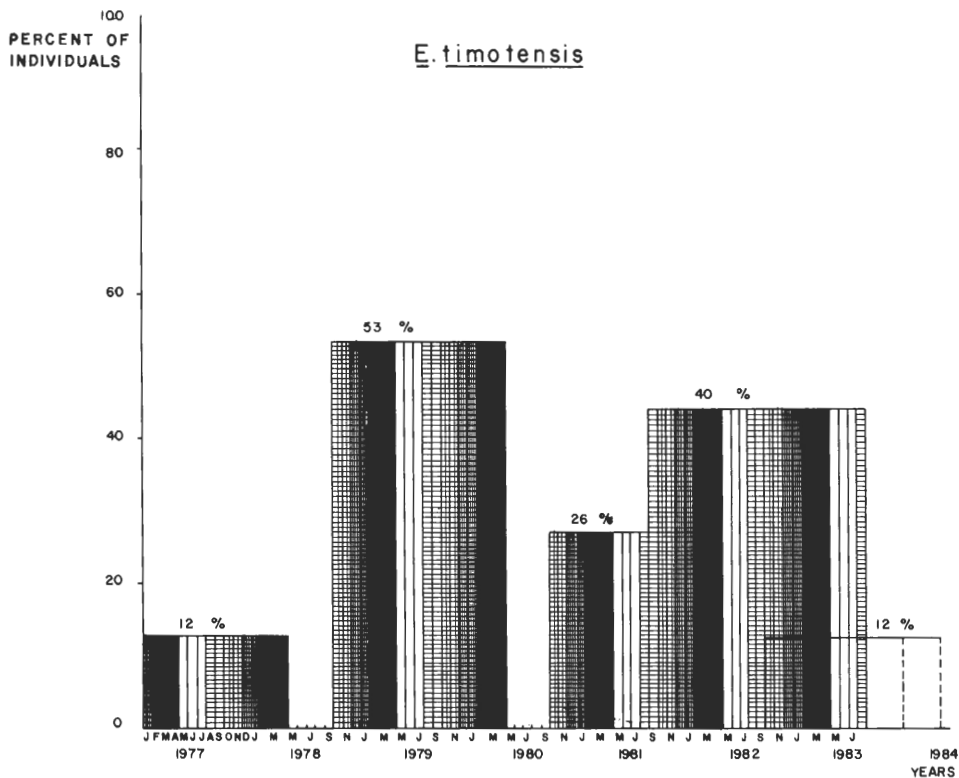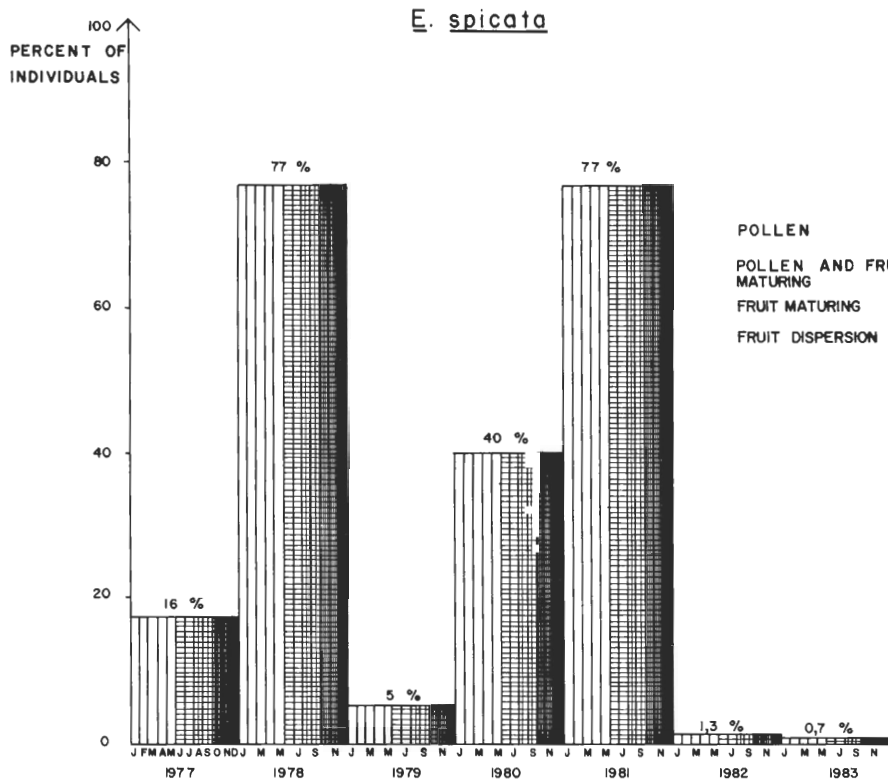
FIG. 3–25. Comparison of reproductive behavior in *E. spicata* and *E. timotensis* in seven years of observations. A clear desynchronization is readily apparent, since years with a higher proportion of reproductive plants in one species correspond with years of higher sterility in the other.

As indicated in Fig. 3–24, the period of pollen production extends from June–July in *E. spicata*, to August–October in *E. timotensis*, and to November–December in *E. moritziana*. *E. schultzii* produces small quantities all year, though flowering attains a peak in September––October.

If the reproductive behavior of *E. timotensis* and *E. spicata* is compared for the seven years with field records (Fig. 3–25), we see how the complementarity of resources also operates. In fact, those years with a greater proportion of reproducing individuals in *E. spicata* are those with a lower proportion of flowering in *E. timotensis*. This desynchronization at the specific level might also have an adaptive value since it allows a more regular distribution of resources through time. We must remember that in these desert páramo *Espeletia*, reproduction is a long-term, high-energy-demanding process and that most frequently reproductive cycles at the individual level appear well distributed along the years.
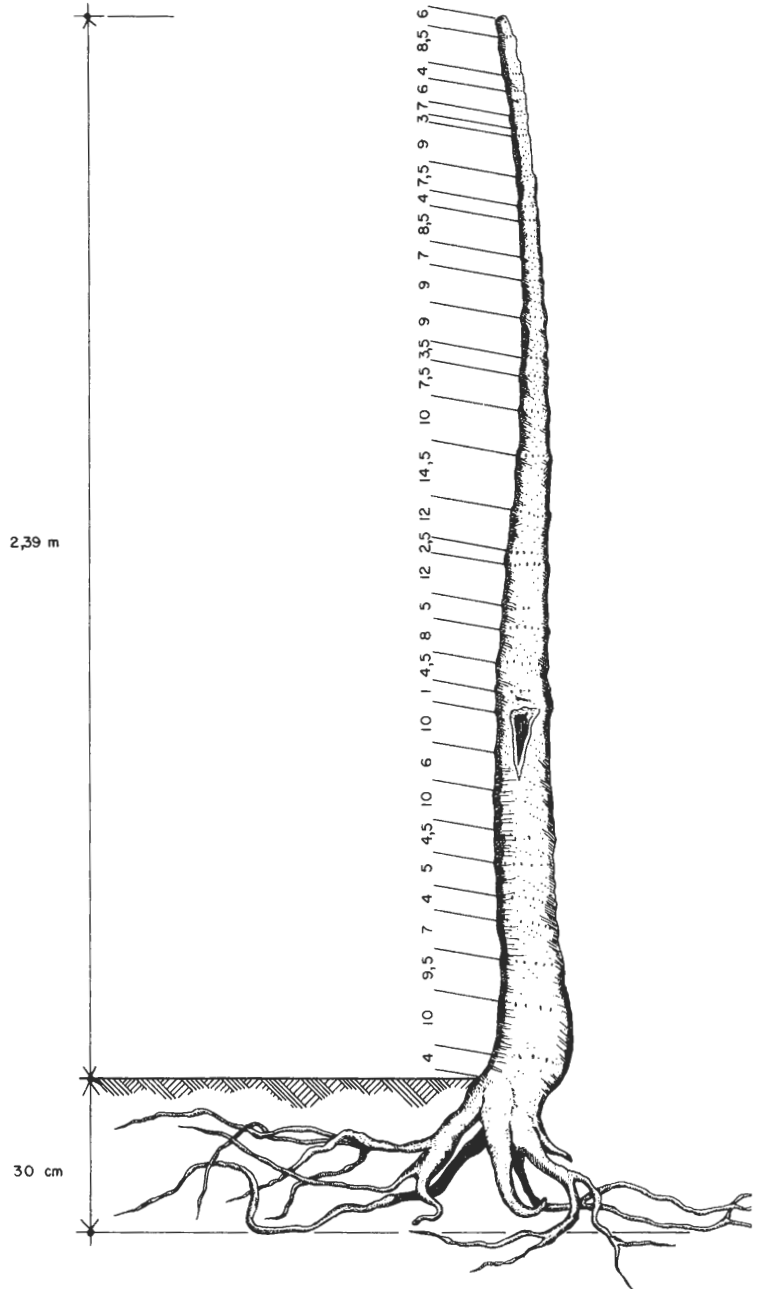
2,39 m

30 cm

FIG. 3–26. Stem of an adult *Espeletia timotensis* where the scars of all reproductive events along its entire life cycle are new. The distance between consecutive flowering events is also shown.
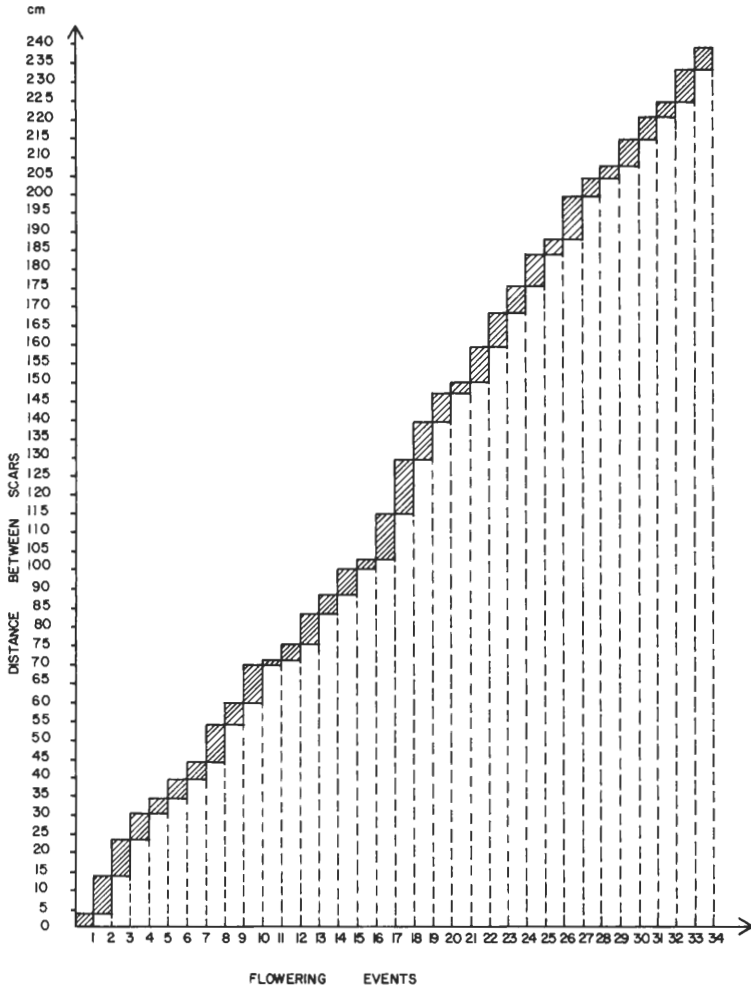
FIG. 3–27. Reproductive frequency by size or age, in the same plant shown in Fig. 3–26.

Reproductive Events and Production During the Life Cycle

In species with long cycles, such as these *Espeletia*, very long term observations, beyond the reach of a normal research program, would be necessary to disclose the reproductive behavior at the individual level. However, it is possible to obtain a picture of all reproductive cycles during the life span of individual plants by analyzing the scars left on the stem. Thus, Figure 3–26 depicts a dead adult plant whose trunk attained a length of 239 cm. On this trunk all the scars indicating reproductive events during its entire life cycle were marked, a total of 34, and the distance between each was measured. The reproductive rhythmicity appears clearly in Fig. 3–27. On the basis of these data, one may suggest, first, that sexual reproduction began at an early age, a conclusion also supported by other field observations; and second, that the intervals between reproductive cycles seem to be highly variable during the life span of the plant. If one considers that the stem of *E. timotensis* grows about 15 mm per year, by measuring distances between the scars we may conclude that in this particular plant, the first two reproductive cycles show a distance equivalent to two years of growth, then one reproductive event followed a period of about six or seven years without reproductive traces, followed again by a similar gap without flowering. Figure 3–27 suggests, third, that this individual has had periods of high fecundity, with quite rapid reproductive cycles, and other vegetative phases lasting up to 10 years.

In the context of the whole plant, it is interesting to know the total energy allocated by an individual to each plant part during its life cycle. I have already pointed out how the energy allocated in a given period of time represents in these *Espeletia* an estimate of the whole investment during the life cycle. However, it is possible to

TABLE 3–7. Reproductive events during the life cycle of an individual of *E. timotensis*.

Number of repro-ductive events	Distance between consecutive scars	Number of inflorescences	Estimated head number	Estimated achene number	Weight of achene yield (g)	Weight of inflorescence (g)	Total weight of reproductive structures (g)
1	–	3	33	9,647	5.4	76.3	81.7
2	4.0	2	22	6,358	4.7	50.90	55.6
3	13.0	20	220	63,580	47.68	509.0	556.68
4	7.0	25	275	79,475	59.6	636.25	695.85
5	3.0	10	110	31,790	23.8	254.5	278.3
6	8.5	29	319	92,191	69.1	738.05	807.15
7	8.0	8	88	25,432	19.0	203.60	226.60
8	7.5	19	209	60,401	45.3	485.55	530.85
9	9.0	10	110	31,790	23.8	254.5	278.3
10	6.0	18	198	57,222	42.9	458.10	501.0
11	8.0	24	264	76,296	57.2	600.80	658.0
12	11.5	26	286	82,654	61.9	661.70	723.60
13	11.5	29	319	92,191	69.1	738.05	807.15
14	11.0	35	385	101,265	75.94	890.75	966.69
15	6.0	26	286	82,654	61.9	661.70	723.60
16	4.5	12	132	37,148	41.86	305.40	347.26
17*	3.0	–	–	–	–	–	–
18*	1.5	–	–	–	–	–	–
Totals 18	124	290	3566	929,794	709.18	7525.15	8234.33

Note: Reproductive frequency is based on the distance between inflorescence scars on the stem. Each reproductive yield is estimated by counting the inflorescence scars. Data on head number per axis, seed number per head, and their respective weights, from Azócar and Monasterio (unpublished). *17 and 18 are events in the process of development.

obtain a more adequate picture, closer to the real allocation to different plant organs and functions. To do this, a living individual of E. *timotensis* with a trunk length of 121 cm was harvested. All the attached leaves, either living or dead, were counted (8500 leaves). Since we know that the blade or photosynthetic portion of an adult leaf has an average dry weight of 6.9 g, a figure of 61,200 g is obtained for the total leaf mass produced in its lifetime. The actual living leaf biomass, considering the leaf bank and the external rosette, amounted to 1700 g, corresponding to 420 leaves. This biomass constitutes the leaf production of more than two years. Given that the number of expanded leaves per year is about 120, this particular plant produced its standing mass of dead leaves in a period of 70 or 80 years. In this calculation the number of leaves produced by unit time and the size of the rosette were considered to become stable during the first two years of the plant's life (Estrada, personal communication).

Each reproductive event thus leaves clear traces on the stem. Furthermore, each inflorescence axis leaves its mark on the stem, thus allowing one to count the number of axes produced. We also know the mean number of heads per inflorescence and the mean number of flowers and achenes per head. On the basis of these data (Table 3–7) I arrived at a fair estimate of each reproductive crop during the life cycle of the individual, and hence of the total energy allocated to sexual reproduction. The harvested plant showed 16 different reproductive events. The initiation of two further reproductive cycles inside the rosette could also be observed. Table 3–7 indicates the distance between two successive events, the total number of floral axes, the estimated number of heads and achenes, and their corresponding total dry weight. The biomass allocated to each plant part or function throughout the life span of this particular individual is given in Table 3–7.

A first comparison to be made is between the vegetative and the reproductive investments. The ratio

$$\frac{\text{Reproductive biomass}}{\text{Vegetative biomass}} = \frac{8200 \text{ g}}{66,100 \text{ g}} = 0.12$$

and the reproductive effort:

$$\frac{\text{Reproductive biomass}}{\text{Total biomass}} = \frac{8200 \text{ g}}{74,300 \text{ g}} = 0.11$$

are both rather low. The ratio between below- and aboveground biomass is also low:

$$\frac{\text{Belowground biomass}}{\text{Aboveground biomass}} = \frac{784 \text{ g}}{74,300 \text{ g}} = 0.011$$

The biomass allocated to the various vegetative parts is:

Live leaves	1720	g =	2.2% of the total biomass			
Dead leaves	61,200	g =	82.5%	,, ,,	,,	,,
Stem	2417	g =	3.2%	,, ,,	,,	,,
bark	837.6 g					
pith	1567	g				
Roots	784	g =	1.06%	,, ,,	,,	,,

Within the reproductive allocation we have:

Auxiliary reproductive structures 7525 g = 10% of the total biomass

Achenes 709 g = 0.9% of the total biomass

These data validate those previously considered on the energy allocated to plant parts at a given time. They confirm the minimal allocation to belowground organs, even if we keep in mind the errors in the measurement of root biomass due to harvest techniques. The low allocation to the stem is also striking, and it is interesting to notice how most of it corresponds to the pith, which as we will see later functions in these species as a water reservoir. The greatest allocation is to leaves; the total biomass allocated to reproduction appears relatively modest, and most of it is directed to the building of auxiliary structures. However, given the small size of the achenes in these *Espeletia*, the small biomass allocated to them throughout the life span of the plant corresponds to about one million achenes.

The strategy of energy allocation in E. *timotensis* might be described as continuous addition to the foliage in contrast with occasional or intermittent allocation to reproduction. Roots and stem do accumulate biomass, but apparently the belowground parts have shorter turnover times, being decomposed faster than the aerial organs. As a final observation, I want to emphasize that E. *timotensis* seems to be highly efficient in the capture and accumulation of energy, particularly if the very adverse environmental conditions under which it maintains itself in the desert páramo are considered.

SOME FUNCTIONAL ASPECTS

The giant caulescent rosettes of high altitude tropical regions have long been noted for their remarkable adaptations. The tall *Espeletia* of the desert páramo in the Venezuelan Andes have their equivalent in the genera *Senecio* (*Dendrose-*

necio) and *Lobelia* from equatorial Africa, which also contain several giant caulescent rosette species (Hedberg, 1964; Coe, 1967; Chap. 4). This striking morphological convergence in plants from disjunct tropical regions suggests that the giant rosette form represents an adaptive solution to high altitude tropical environments characterized by year-round low temperatures. These low temperatures make the soil water physiologically unavailable during the early morning hours, either because the soil water may be frozen, or because water uptake is impeded by freezing or near-freezing soil temperatures.

The Role of the Pith and Dead Leaves
in the Water Balance

In the Andes as well as in Africa, the stems of giant rosette plants contain a voluminous parenchymatous pith that acts as a water source during periods of low water availability (Hedberg, 1964; Goldstein, Meinzer and Monasterio, 1984). The *Espeletia* that grow in the Andean páramos differ from each other not only in pith volume, but also in the ratio between the volume of the water reservoir and the transpiring surface (PV/LA) (Table 3–8). Species from higher and colder páramos have a higher PV/LA and can provide water to the transpirational stream for a longer period of time than species from lower páramos with smaller water storage capacities. The pith of the high Andean belt species can provide more than one and a half hours of water to satisfy the transpirational needs during the critical morning hours when soil temperture is low and evaporative demand relatively high.

Daily patterns of transpiration and leaf water potential show the buffering effect of the water stored in the pith (Fig. 3–28). The species from the desert páramo (4200 m) that show the highest storage capacity also exhibit small changes in leaf water potential, whereas the species from the wettest and lowest páramos (e.g., Páramo Batallón, 3100 m), with small pith reservoirs, exhibit pronounced changes in water potential under conditions of similar evaporative demand.

Variations in water storage capacity of the pith would also be expected during the life cycle of an individual. In *E. timotensis*, relative water storage capacity measured as PV/LA seems to increase rather linearly with plant height above 60 cm (Fig. 3–29). The importance of these changes in relative water storage is reflected in patterns of water balance in individuals of different sizes (Fig. 3–29). During the dry season, minimum leaf water potentials of adult individuals remain high, while minimum water potentials are significantly lower and wilting may occur in smaller plants (Goldstein and Meinzer, 1983; Goldstein et al., 1984). One could speculate that for this reason the risk of death is greater in small plants. Initial observations that tend to confirm these ideas show a high correlation between size, specific mortality, and water storage capacity of the pith for individuals up to 1 m tall.

The potential importance of the pith of the *Espeletia* of the desert páramo can be seen in the relationship between the plants and the bird *Cinclodes fuscus* (family Furnariidae). A nest of this species was found in September 1981 in the decaying pith of the fallen trunk of an individual of *Espeletia* (?*timotensis*) at 4100 m at Páramo de Piedras Blancas near the permanent plots (Vuilleumier, pers. comm.).

Another conspicuous feature shared by both Andean and African caulescent giant rosette species is the 10–30 cm thick layer of marcescent leaves surrounding the stem. This layer provides considerable temperature insulation and prevents stem temperatures from falling below 0°C during the night (Smith, 1979; Goldstein, Meinzer and Monasterio, 1984). Stem core temperatures for *E. timotensis* growing at 4200 m in the desert pár-

TABLE 3–8. Factors related to water budget in species of *Espeletia* in two contrasting páramos, one (Piedras Blancas) in the high Andean, the other (Batallón) in the Andean belt.

Páramo site	Mean temp. (°C)	Species	PV/LA (cm³/cm²)	ΔM (g)	T (gh⁻¹)	TH
Piedras Blancas (4200 m)	2.8	*E. timotensis*	0.105	176	70.7	2.5
		E. spicata	0.056	160	81.9	2.0
		E. moritziana	0.057	57	39.7	1.4
Batallón (3100 m)	9.3	*E. marcana*	0.038	68	55.3	1.6
		E. atropurpurea	0.018	9	16.3	0.6

Note: PV/LA, Pith volume/leaf area is a measure of relative capacitance; ΔM, mass of water stored in the pith; T, transpiration rate; TH, transpiration hours needed to spend all the water stored in the pith; obtained by dividing ΔM by T.

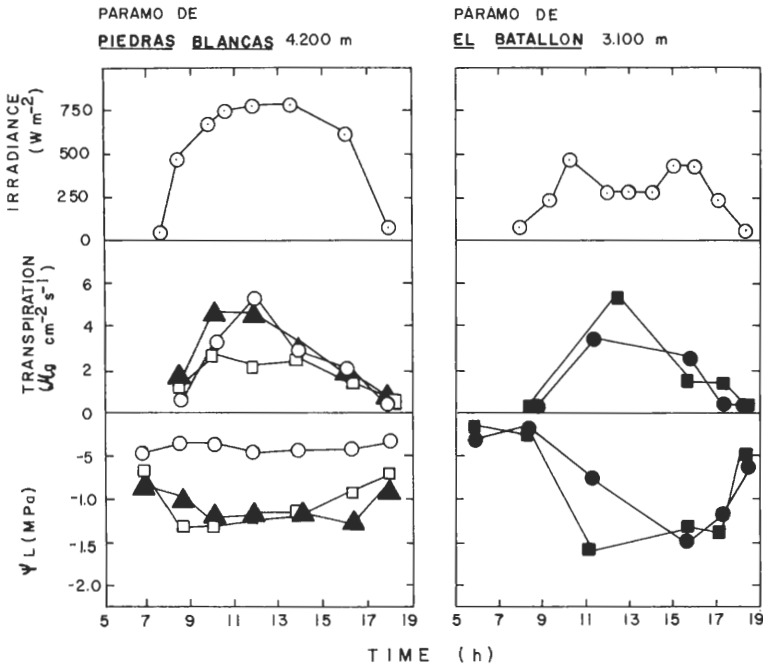*Source*: Adapted from Goldstein et al., 1984.

FIG. 3–28. Daily patterns of transpiration and leaf water potential in the giant rosettes of the Páramo de Piedras Blancas. *E. timotensis* (○), *E. moritziana* (▲), and *E. spicata* (□). In the Páramo El Batallón the acaulous rosettes of *E. marcana* (●) and *E. atropurpurea* (■) were studied. (After Goldstein et al., 1984.)
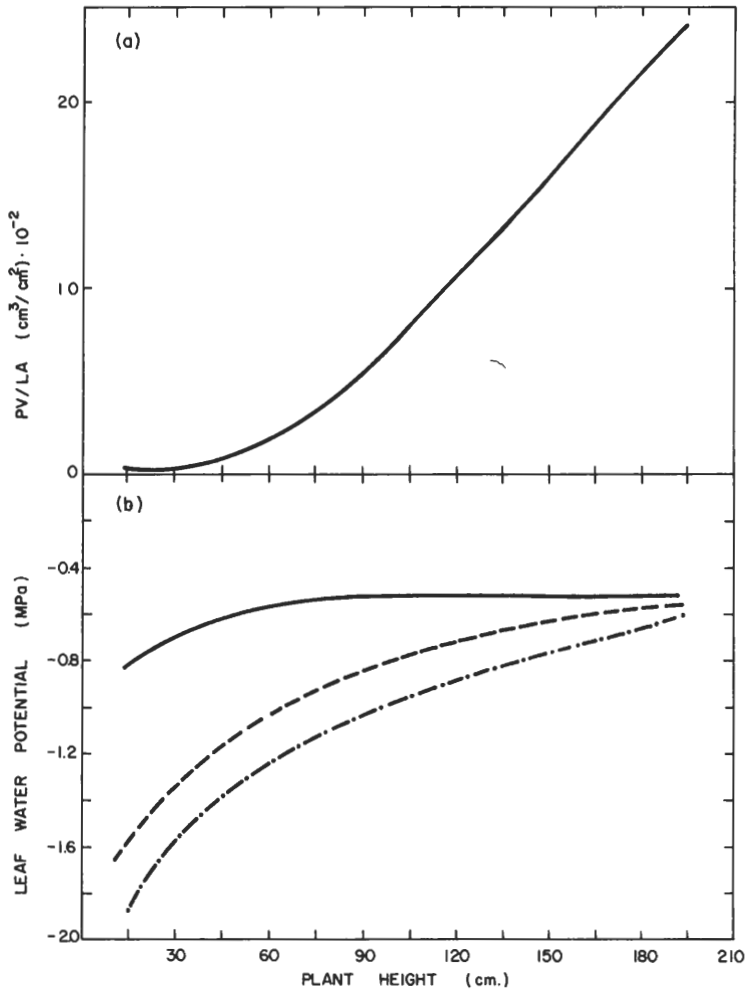

FIG. 3–29. (a) Variation in the capacity of water storage in the pith (PV/LA) in relation to size and age in *E. timotensis*. (b) Minimum leaf water potential reached in plants of *E. timotensis* of various sizes, in the wet (——) and in the dry (—————) season. (After Goldstein et al., 1984.)

FIG. 3–30. Stem temperature and leaf water potential in *E. timotensis* . (○) Intact plants, (●) denuded plants (removal of attached dead leaves). (a) One day after the experimental removal of dead leaves. (b) Fifteen days afterward. (After Goldstein and Meinzer, 1983.)
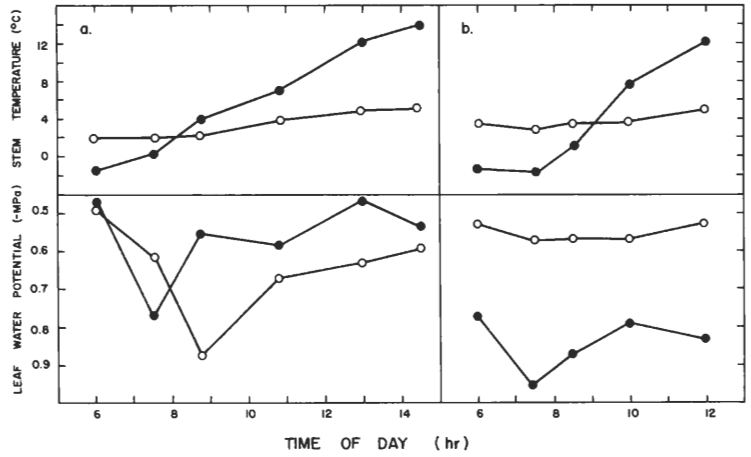
amo remain above 2°C for much of the day, but exposed stems show pronounced temperature changes (Fig. 3–30). Thus, at least during the day, marcescent leaves enhanced chances of survival due to avoidance of direct stem freezing. In manipulative experiments carried out at 4200 m, leaf removal improved water balance during the following day as a consequence of higher stem temperatures and therefore improved water flow between the soil and/or the pith reservoir and the transpiring leaves. Two weeks later, however, leaf water potential of stripped plants was lower than that of intact plants, and symptoms of damage were evident. Hydraulic resistance on this day was four times greater in the stripped plants. All stripped individuals died within two months. The lethal effects of dead leaf removal could be attributed to one or more of the following causes: (1) inhibition of pith recharge by subfreezing stem temperatures, (2) embolism in stem xylem, and (3) frost injury to pith tissue. These results suggested that an insulating layer of marcescent leaves and the presence of an internal water reservoir closer to the rosette than the soil water are important adaptations for maintenance of a favorable water balance in high altitude tropical habitats where freezing temperatures occur regularly but last only a few hours.

Leaf Pubescence and Thermal Balance

Another conspicuous characteristic of many giant rosette plants, shared by the desert páramo *Espeletia*, is the presence of a thick pubescence layer in the active leaves. Field and laboratory measurements were used to develop an energy balance model for leaves of *E. timotensis* (Meinzer and Goldstein, 1985). Results of model simulation predict that the most important effect of the leaf hairs was on the boundary layer and on

resistance to convective heat transfer, rather than on leaf absorbtion of solar radiation. Under clear-day conditions at 4200 m, the temperature of a pubescent leaf would be higher than that of a nonpubescent one in spite of the larger amount of solar radiation absorbed by the latter (Fig. 3–31). Thus, in contrast to many desert species in which leaf hairs reduce the radiant energy load and leaf temperatures by increasing reflectance, leaf hairs of *E. timotensis*, and probably of all the caulescent rosette species, result in greater daytime leaf temperatures by increasing the thickness of the boundary layer of unstirred air.
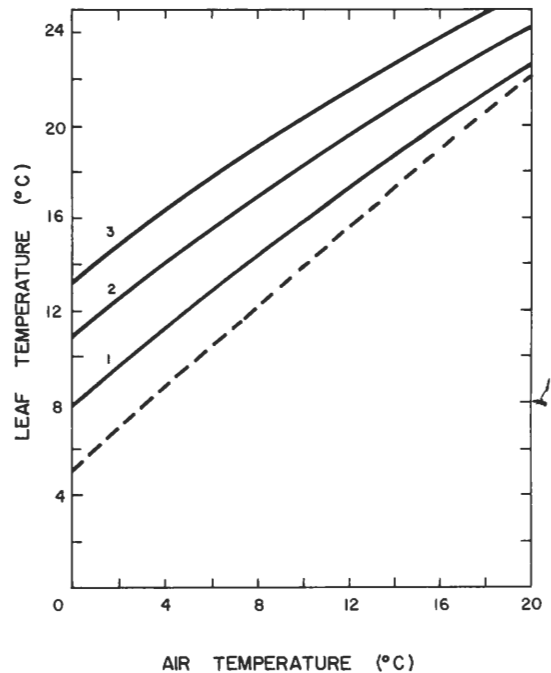

FIG. 3–31. Relation between simulated leaf temperature and air temperature in leaves of *E. timotensis* having 1, 2 and 3 cm of pubescence, and in glabrous leaves. (After Meinzer and Goldstein, 1985.)

Daytime leaf temperatures well above the low prevailing air temperatures would favor processes such as leaf growth and assimilate translocation. Leaf temperature can be increased without an accompanying increase in transpiration. This is important from an adaptive point of view because low temperatures severely limit water availability in the desert páramo.

Decomposition, Microfauna, and Nutrient Cycling

Variation in chemical composition with leaf age in the rosette leaves and in the standing leaf litter of *E. timotensis* and *E. schultzii* suggests a direct recycling of nutrients within the plant from dead leaves to growing tissues (Monasterio, 1980b). In this extreme environment where the periglacial climate hinders soil evolution (Malagon, 1982), this strategy would certainly favor greater efficiency in the use of nutrients, thus having clear adaptive advantages. Garay (1981) and Garay et al. (1982) analyzed the standing leaf litter of these two species, centering their attention on the relationships between nutrient stocks and the community of microarthropods, with the aim of understanding the role of microfauna in the processes of leaf decomposition and nutrient cycling.

Decomposition of the standing litter in *E. timotensis* follows two gradients, one toward the base of the stem, the other from outer to inner parts of the cover of dead leaves. Along both gradients, the proportion of amorphous organic matter increases. This organic matter appears to be formed almost exclusively of fecal pellets of arthropods (Garay, 1981). A high C:N ratio, induced by a low nitrogen content, in the dead leaves of the basal part of the stem also suggests a very low decomposition, and conversely, the weak decomposition of leaf sheaths may also be related to low nitrogen concentrations. Calcium and magnesium do not vary in the different parts of the standing litter, and potassium increases basipetally, probably due to the leaching of the upper leaves.

In *E. schultzii* (Diaz Rosales, 1983), the concentration of calcium and nitrogen is significantly higher than in *E. timotensis*, particularly in leaf sheaths, corresponding with higher decomposition rates. The protective function of the standing dead leaves thus would be less efficient in this predominantly Andean *Espeletia* than in *E. timotensis*, an exclusively high Andean species.

Garay (1981) reported a density of 130,000 microarthropods in the standing dead mass of a plant of *E. timotensis* with a trunk 110 cm high. Most of them occur toward the outer part of the standing litter and their abundance is highly correlated with nitrogen content.

From all these data we may conclude that leaf decomposition and its agents are of crucial importance to plants growing in soils with almost no chemical evolution and therefore with a very low content in available nutrients. In the long-lived species of *Espeletia*, like *E. timotensis*, nutrients once absorbed from the soil could be utilized repeatedly along numerous successive cycles of leafing and reproduction. Selection favoring longevity might therefore operate, since longevity appears correlated with better efficiency in nutrient use. On the other hand, a trade-off would be necessary between humification of the standing litter and its conservation as a protective cover against freezing temperatures. Thus, *E. schultzii*, with a more rapid decompositon and a shorter life span, is mostly restricted to the lower páramos and only occurs in protected sites in the high Andean belt.

Garay et al. (1982) also considered the decomposition-recycling system of the desert páramo *Espeletia* as giving rise to a strategy promoting the long-term maintenance of the colonized sites through the accumulation of organic matter, nutrients, and a rich fauna of decomposers in a single system that forms an integral part of the living plant.

Similar systems for more efficient cycling of minerals, but involving vertebrates instead of arthropods, may be found in ecologically similar areas elsewhere in the high tropical Andes. In the dry puna of Peru, where giant rosettes of *Puya raimondii* (Bromeliaceae) make up stands locally in the open grasslands (Vuilleumier, pers. comm.), a relationship between birds and plants has been postulated by Rees and Roe (1980). The sharply hooked leaves of *Puya raimondii* "catch" numerous birds which then die and remain as corpses for a long time in the rosette. Rees and Roe (1980) suggested that the dead birds, which decompose slowly in the dry climate of the puna, are a source of nutrients that would supplement the nutrient uptake by the root system.

CONCLUSIONS ON ADAPTIVE STRATEGIES

Several aspects of the adaptive behavior of the *Espeletia* in the desert páramo have been treated in this chapter, such as their dynamics of growth and reproduction, the patterns of biomass and energy allocation, the physioecological significance of the pith, dead leaves, and leaf pubescence, the fauna of the standing litter and its

relation to decomposition and mineral cycling. All of these aspects constitute key elements in the interpretation of the global strategy of *E. timotensis*, *E. spicata*, and *E. moritziana*.

More than 50 species of *Espeletia*, having different life forms and architectural models, exist in the Venezuelan Andes, yet only five of them cross the barrier of the periglacial climate at 4000 m. All five follow the Corner architectural model. Some species of the lower páramos also belong to this model, but they are low rosettes, less than 1 m high. Thus, giant rosettes that follow the Corner model are restricted to the desert páramo.

Two of the high Andean species, *E. schultzii* and *E. semiglobulata*, occur in protected habitats, and their rosettes are lower. What characteristics of the three most widespread and typical desert páramo *Espeletia* differentiate them from other species and allow them to survive under the periglacial climate of the high summits, where, at 4600 m they reach the uppermost limit of flowering plants in the tropical Andes?

Two types of adaptation are fundamental to the ecological success of these desert páramo *Espeletia*: adaptations related to the maintenance of favorable temperature and water balance, and features that increase the ability of individuals to remain in the colonized sites after having passed the critical seedling phase. Among the most important features in this context we may consider the following:

1. Selection favors longevity. In effect, the three species of the desert páramo belonging to the Corner model have a long life span compared with that of the species with the same architectural model growing in the Andean belt below. The latter species have an average life span of about 50 years, but the high Andean belt species may live as long as 150 years. In an environment where low rate of seedling survival represents the major obstacle to the maintenance of plant populations, longevity acquires an undisputed adaptive value.

2. Long lifespan appears to be correlated with greater plant size and with the development of a conspicuous pith, which is as important in the water economy of these *Espeletia*, as it is for the covergent African species *Dendrosencio keniodendron* (Hedberg and Hedberg, 1979; see Chap. 4).

3. The internal recycling of nutrients from slowly decomposing standing dead litter, and the role of the protective cover of dead leaves in the insulation of the stem are particularly significant.

4. Only polycarpic species of *Espeletia* reach the desert páramo. These species not only reproduce many times during their life cycle, but they also attain sexual maturity quite early and increase in fecundity with age. Thus, an individual, after having surmounted the critical seedling phase, will produce about one million seeds during its lifetime. That is, for about 100 years it is continuously feeding the seed bank and so contributing to the success of its regeneration and to population stability.

5. The reproductive patterns show very little, if any, overlap among homologous phenophases in different species. Pollen is more or less continuously available to pollinators, thus ensuring that only sexually reproducing species are successfully pollinated.

6. Both growth and reproduction proceed gradually and continuously through small increments synchronized with the daily cycles of the equatorial or tropical mountain climate. However small these increments, the year-long persistence of the process leads to a considerable annual production. An adult rosette of *E. timotensis* produces an estimated 700 g dry weight per year.

7. A remarkable feature of desert páramo *Espeletia* is their strategy of consolidation and maintenance of their sites by increasing the efficient use of critical resources. This is obtained by the coherent ecological system around each living plant, formed by its live biomass, the standing dead litter, and the microfauna that humifies and slowly decomposes the organic matter, gradually liberating the sequestered nutrients. A pattern arises in which each plant constitutes a stable and organized micro-ecosystem surrounded by a desert of bare ground.

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