Adaptive Radiation of *Espeletia* in the Cold Andean Tropics

Maximina Monasterio and Lina Sarmiento

The genus Espeletia *(Asteraceae) underwent an accelerated adaptive radiation in the new habitats of the high tropical Andes after the retreat of the glaciers. From the ancestral rainforest species, with tree-like forms, the genus diversified at high altitude, developing morphological and physiological adaptations to the peculiar combination of low-temperature, energy and nutrient stresses of the tropical periglacial environments.* Espeletia *offers an exceptional example of a taxon undergoing a rapid evolutionary process through the colonization of a totally original environment: the cold tropics. Here we review recent research on the ecological, biogeographical, taxonomic, morphological and physiological traits that have led to the adaptive radiation of* Espeletia *in this extreme habitat.*

The high tropical montane environments have been, since their appearance in the Pleistocene, subjected to a series of climatic fluctuations resulting from glacial and interglacial oscillations. As a result, a new kind of environment appeared, combining the tropical climatic regime (yearly isothermy and daily 'seasonality') with low temperatures and frequent frost. When these equatorial high mountains, on either the continents or oceanic islands, have high rainfall, similar environments result. These are the cold humid tropics, which are regionally differentiated into *páramo* (northern Andes), afro-alpine (East Africa) and tropical-alpine (Hawaii and Malesia) habitats[1]. At an intercontinental level of comparison, the plants of these environments seem to show 'convergent' evolutionary responses in both morphology and physiology. Among the most interesting examples are *Espeletia* in the *páramo* and *Dendrosenecio* in the afroalpine region[2,3].

Espeletia is one of the best examples of diversification and adaptive radiation in a novel environment. Recent and current research is addressing the following questions[4]. What ecological role does *Espeletia* play in the high tropical Andes? How did *Espeletia* differentiate? What specific ecological niches are filled during the process

Maximina Monasterio and Lina Sarmiento are at the Centro de Investigaciones Ecológicas de Los Andes Tropicales (CIELAT), Facultad de Ciencias, Universidad de Los Andes, Mérida 5101, Venezuela.

of adaptive radiation? What kinds of morphological and ecophysiological diversification accompany the ecological diversification? Much research is needed to answer these questions, but on the basis of the still fragmentary evidence, we shall discuss some key problems and the major hypotheses they suggest.

Patterns of diversification and radiation

The genus *Espeletia* (Asteraceae, Heliantheae) contains about 130 species endemic to the northern tropical Andes, extending from the isolated Sierra Nevada de Santa Marta in northern Colombia (11°N) and the Coastal Caribbean Range in Venezuela, southward to northern Ecuador (2°S) (Ref. 2).

The distribution of the main architectural types and reproductive patterns within the genus is shown in Fig. 1. Branched forms, more primitive and closer to the ancestral type[5,2], are primarily distributed in the northern part of this area: the montane forests (1500–3000 m) of the Sierra Nevada de Santa Marta, the Coastal Caribbean Range, the Sierra de Perijá and the Cordillera de Mérida.

The greatest richness of taxa occurs in the Cordillera de Mérida, where there are 63 endemic species of *Espeletia*; these include a wide array of growth forms, from branched trees to dwarf or giant rosette trees. The Cordillera de Mérida contains a highly diversified set of mountain environments, where the most contrasting habitats of the northern Andes may be found[6]. In the montane forests, various species of tree-like *Espeletia* occur (Fig. 2), whereas above the treeline a variety of growth forms colonize the rich diversity of substrates resulting from glacial and periglacial events. From this center of diversification and radiation, only the polycarpic rosette forms migrated south and westwards. In the Coastal Range, only the more primitive, branched, tree-like forms occur.

We can take as a starting point the montane forest environment, which underwent altitudinal oscillations

and fragmentation during the succession of glacial–interglacial events, as clearly shown in the palynological record[7]. The 'proto-*Espeletia*'[2] (up to then a restricted forest taxon) underwent an accelerated process of adaptive radiation, colonizing the whole range of postglacial and periglacial habitats, from cold deserts to permanent swamps, giving rise to remarkable life forms and reproductive patterns. The most successful form within the *páramo* belt was undoubtedly the unbranched polycarpic rosette, which extends for more than 1000 km from Venezuela to Ecuador. Outside the Cordillera de Mérida, more than 60 species with this growth form are found, from 2500 m to the border of the present glaciers at 4600 m (Ref. 2). Several species of unbranched monocarpic (semelparous) rosettes occur in this
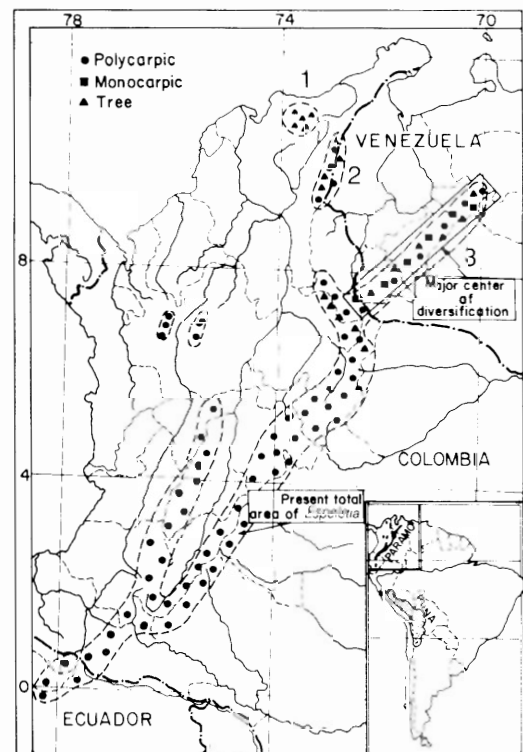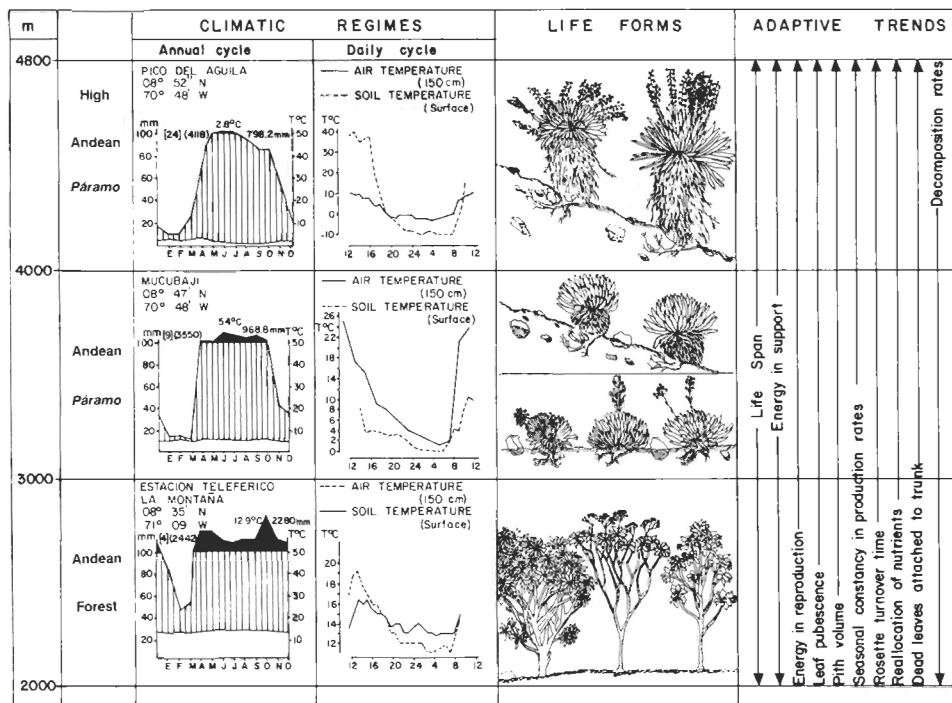

Fig. 1. Geographical area of *Espeletia* and distribution of some of its growth forms. 1: Sierra Nevada de Santa Marta. 2: Sierra de Perijá. 3: Cordillera de Mérida. The Coastal Caribbean Range lies to the east of the Cordillera de Mérida. Adapted from Ref. 2.

Fig. 2. Climatic regimes, life forms and adaptive trends in the species of *Espeletia* along an altitudinal gradient in the Cordillera de Mérida, Venezuela. Shown for the annual cycle are: the number of years with meteorological records, | |; the altitude in metres, ( ); the mean annual temperature in °C; and rainfall in mm. The areas shaded in black correspond to monthly rainfall above 100 mm.

genus *Dendrosenecio* in the afro-alpine environments of Mt Kenya[11], suggesting that similar underlying selective forces operated in both cases.

Adaptation of giant rosettes to the Andean periglacial habitats

We will now focus on the giant polycarpic rosettes, the only growth form adapted to the most extreme ecological conditions of the high tropical mountains. This ecological accomplishment can be understood as the result of the evolution and integration of a series of adaptive traits along the altitudinal gradients. In this way, *Espeletia* was able to move from the relatively constant montane rainforest environment to the almost permanently stress-generating cold-desert conditions (Fig. 3) of the high tropical mountains.

In the high-Andean belt, low mean temperatures prevail all year, and there are wide daily oscillations. There is a high frequency of frosts all year round. The 24-hour rhythm is the key external factor regulating plant functioning: plants have to overcome low night temperatures through responses that allow the continuity of the assimilative process during daytime hours. Poor soils constitute an additional important stress in the high-Andean belt; this is a consequence both of the periglacial climatic conditions and of the short evolution of these soils. The availability of some nutrients falls within the range typical for the most nutrient-poor ecosystems.

How is the morphological structure of the giant rosette adaptive with respect to the water, nutrient and carbon budgets? Enough information is available to permit a preliminary review. We follow previous models that have been applied to various plant forms and ecosystems, and that involve the separate analysis of the water, nutrient and carbon economy of plants[12–14].

Biomass and energy allocation

The allocation of plant biomass among different organs and structures, expressed as caloric values, is one of the most revealing aspects of the overall adaptive strategy. Each pattern of biomass allocation, in mature individuals, may be considered as a functional alternative op-
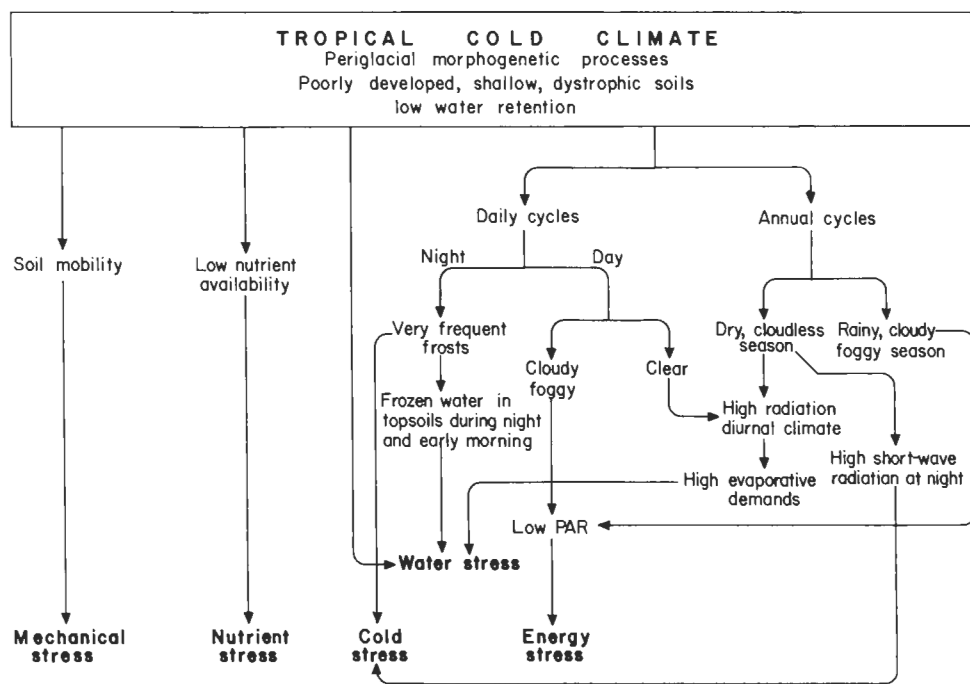
belt, showing a convergent strategy with *Lobelia* in the afroalpine zone, *Argyroxiphium* in the tropical-alpine zone of Hawaii and *Lupinus* and *Puya* in the Central Andean *puna*[8].

Figure 2 shows the altitudinal distribution of *Espeletia* in the Cordillera de Mérida. The branched forms occur in the Andean forests, where there are no drastic water or temperature limitations. Immedi-

ately above this belt, in the Andean *páramo*, which has a widespread variety of local climates and habitats, *Espeletia* radiated in various forms with quite divergent life cycles, physiology and reproductive patterns[9–11]. Finally, in the most extreme environment, the high-Andean cold desert, only the giant polycarpic rosettes are found. These same trends in morphology with altitude are shown by the

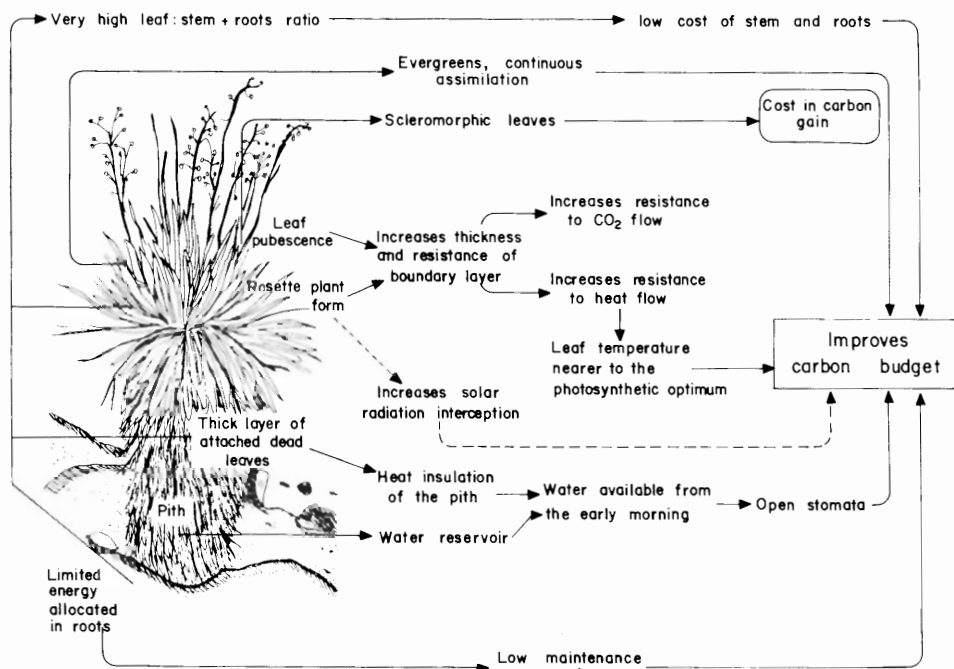**Fig. 3.** Major ecological consequences arising from environmental characteristics in the cold Andean tropics.

Fig. 4. Morphological traits and functional mechanisms involved in the carbon economy of giant rosettes of *Espeletia*.

timized through natural selection. Some remarkable aspects of the pattern of energy allocation in the giant Espeletias[10] (see Table I) are as follows:

(1) A major proportion (73.5%) of the total plant material occurs as standing necromass (dead leaves and dead auxiliary reproductive structures), whereas only 26.5% is live biomass, including roots, stem, leaves, inflorescences and seeds. This surprisingly high proportion of dead material attached to the plant transforms each individual into a microecosystem with a functional integration of the productive and degradative subsystems, the latter being represented by the decomposing plant parts and their accompanying decomposers. The energy stored in live plant parts is divided in the following proportions: roots, 13%; stem, 17%; leaves, 29%; ARS, 33%; and seeds, 8%.

(2) The low investment in roots indicates that the plant does not exploit a large volume of soil, as has been reported for some high-Andean cushion plants (L. Sarmiento, unpublished data). Instead, the plant optimizes the cycling of its nutrients and the capture of nutrients from rainfall.

(3) The low investment in nonassimilative structures reduces the maintenance cost and improves the carbon budget (Fig. 4).

(4) A very high ratio of assimilative to nonassimilative parts (Fig. 4), close to 1.0 in *E. timotensis*, contrasts with a ratio of 0.1 to 0.01 in more 'typical' trees[15,16].

(5) A high proportion of the total energy invested in reproduction, as well as a high reproductive effort, are essential aspects of the overall plant strategy, given that mortality rates are very high during the first stages of the life cycle.

Leaf rosette

These evergreen rosettes produce leaves all year round. The leaves are thick, densely pubescent and scleromorphic, with small cells and protected stomata.

The spatial arrangement of leaves in a terminal rosette has many consequences for plant function.

(1) The leaves become more vertical along the elevation gradient[17]. This parabolic geometry of the rosette improves photosynthetic assimilation, since high rates occur at mid-morning and early afternoon, when the oblique sun rays are more efficiently intercepted by the upright leaves[18].

(2) Within the rosette, every possible leaf orientation is found, which may increase the interception of solar radiation (Fig. 4). At each hour of the day, the amount of radiation intercepted by a particular leaf will be different, and this relationship changes with the position of the sun. This feature allows a better use of solar radiation throughout the day and the seasons, as well as a more favourable thermal balance[18].

(3) The arrangement of leaves in the rosette insulates the apical bud and the youngest leaves, which remain protected by the older ones[19,20]. Nyctaginistic movements increase this thermal protection[21].

(4) The geometry of the rosette influences the surrounding atmosphere, forming a permanent boundary layer. This aerodynamic effect reinforces the one induced by each individual leaf. The consequences of the boundary layer on the thermal and photosynthetic balances are discussed below[22].

(5) The rosette intercepts and channels rainfall, a process whose magnitude and importance are often neglected (Fig. 5). The rosette acts as a collecting funnel that directs a significant part of the total rainfall towards the layer of dead leaves, through which it flows towards the site at the foot of the trunk where active roots concentrate. Thus, rain water is directed towards the most favourable place to be taken up by roots, improving water and solute availability. A similar channelling of rain water occurs in the epiphytic bromeliads of tropical rain forests.

Dying and dead leaves

All high-Andean species have a thick layer of dying and dead leaves surrounding the stem. As the process of dying is gradual, it favours the reallocation of nutrients to developing leaves[10]. Removal of the dead leaves significantly increases the probability of death of the

Table I. (a) Biomass allocation (% of total biomass in calories) in different plant organs in E. *timotensis*. (b) Ratios between the energy allocated to various plant parts

(a)

	Live	Dead
Seeds	2.2	–
ARS[a]	8.8	1.9
Leaves	7.7	71.6
Stem	4.4	–
Roots	3.4	–

(b)

$\dfrac{\text{live}}{\text{dead}}$	0.36
$\dfrac{\text{live reproductive}}{\text{live vegetative}}$	0.70
$\dfrac{\text{assimilative}}{\text{nonassimilative}} = \dfrac{\text{leaves}}{\text{stem + roots}}$	0.99

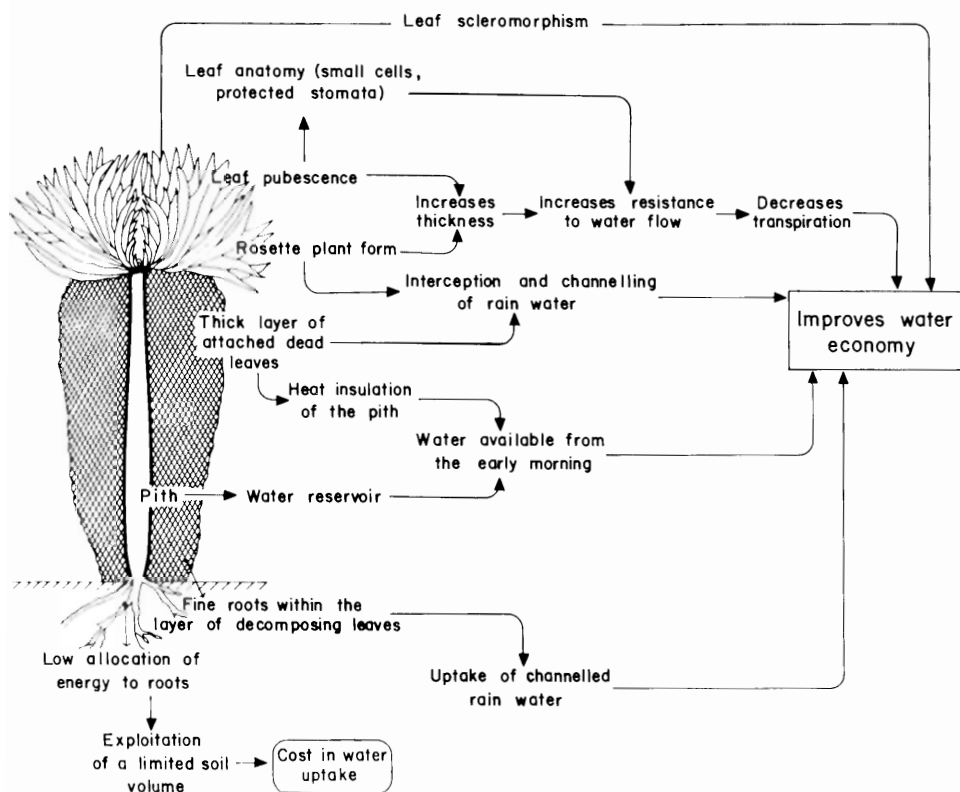[a]ARS = Auxiliary reproductive structures: inflorescences, heads, etc.

Fig. 5. Morphological structures and processes influencing the water economy of giant rosettes of *Espeletia*.

standing leaf litter[25,26]. This undoubtedly suggests a continuous liberation of the soluble fraction of leaf nutrients. A working hypothesis is that liberated nutrients are leached by the flow of water through the litter, accumulating at the stem's base and progressively reaching the zone of fine-root development. Furthermore, fine roots also develop within the layer of dying leaves. In this way, nutrients could be reutilized in a time that depends upon the decomposition rates and the rates of downward leaching towards the zone of absorption. As a sharp nutrient limitation seems to be a widespread feature of the periglacial habitats colonized by these giant rosettes, studies on nutrient utilization and recycling should be made in order to attain a better understanding of the whole adaptive strategy of these *Espeletia*.

(3) The standing dead litter increases the individual basal area and lowers its centre of gravity, providing the plant with increased stability. All factors concerning mechanical equilibrium appear as highly favourable for survival, given that falling as a consequence of their height and weight is one of the major mortality causes among adult individuals.

plant[23]. Their functional role has been the object of several alternative, nonexclusive interpretations.

(1) The layer of dead leaves insulates the pith[24], maintaining its temperature above 0°C even when the air temperature is several degrees lower. Because of this, the pith water reservoir does not freeze (Fig. 5).

(2) The dead leaves are a reservoir of nutrients, although their contribution to the nutrient economy remains unknown (Fig. 6). There is ample evidence of the existence of an abundant and diversified community of decomposers inside the

Voluminous central pith

One of the most peculiar aspects in the adaptive strategy of *Espeletia* is the gradual increase in pith size and water-storage capacity in those species occurring in habitats with greater frequency of frost[9]. A voluminous central pith made up of parenchymatous tissue stores water during the night to sustain up to two and a half hours of morning transpiration. That seems to be important, since, during the early morning, temperatures may remain below the freezing point, impeding water uptake by freezing the soil water and by reducing root permeability[9] (Fig. 5).

The development of a voluminous pith also appears crucial for water and carbon balance, since it allows the maintenance of open stomata early in the morning (Fig. 4). The gradual increase in pith volume could explain the greater height attained by individuals in the high-Andean species, as well as the greater probability of death in seed-
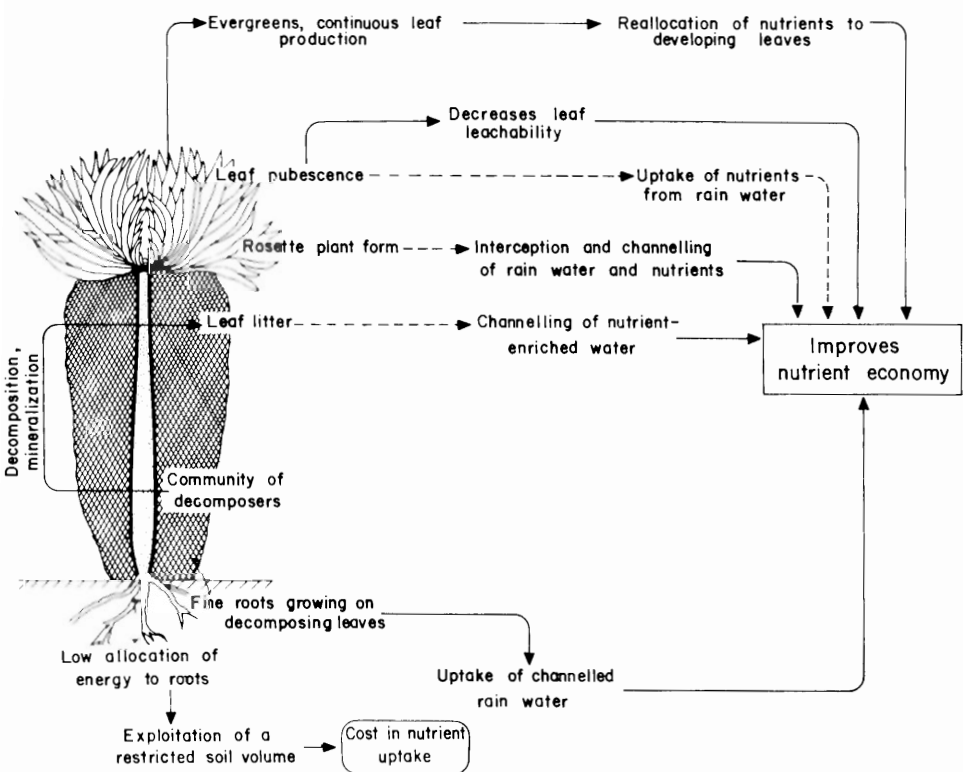

Fig. 6. Some morphological features and functional mechanisms that affect the nutrient economy of giant rosettes of *Espeletia*.

lings and juveniles without a well-developed pith[27].

Leaf pubescence

In *E. timotensis*, the effect of leaf pubescence on leaf temperatures has been clearly demonstrated[24]. Pubescence acts through the formation of a boundary layer that restricts convection and latent heat losses without greatly affecting the absorption of the incoming solar radiation (Fig. 4). In this species the photosynthetically active radiation (PAR) reaching the leaf blade decreases by about 15% and there is also a stronger resistance to CO_2 diffusion[18]. This effect of leaf pubescence is the opposite of its known effect on warm desert plants[28]. But the increase in leaf temperatures has a positive effect on carbon gain since they become closer to the photosynthetic optimum[17]. As the boundary layer lowers transpiration rates, its action on the water budget is positive, but as it hinders CO_2 exchange, it represents a cost in carbon assimilation (Fig. 4). The dense leaf pubescence also hinders wetting of the leaf surface, decreasing the freezing risk[22] and the leaching of nutrients.

Other adaptive mechanisms

Seed latency

Seed latency has been found in some of these species[29]. Given the strong interannual variability in climate that characterizes the high-Andean environments, seed latency would certainly increase the probability of germination under more favourable weather conditions. Furthermore, in each seed crop, some seeds germinate in the year of production, while the germination of the others is spread through several years, giving rise to a persistent seed bank.

Supercooling

Only the assimilating leaves are exposed to freezing temperatures, the remaining plant structures either develop in sites with higher temperatures or are protected by insulating structures or tissues[20]. The live leaves avoid the formation of ice by supercooling to temperatures of −13°C to −16°C, a fact apparently made possible by the small cell sizes and the small intercellular spaces for ice nucleation[30,31].

Conclusion

Figures 4 to 6 summarize the whole set of morphological traits and functional interactions that have led to the colonization of extreme environments by *Espeletia*. As we have shown, each particular trait is involved in a diversity of functions related to the overcoming of various environmental stresses, such as cold, drought and nutrient shortage. Thus, for instance, the thick layer of attached dead leaves insulates the pith and channels rainfall, while its mineralization provides nutrients.

One of the most remarkable features of high-Andean *Espeletia* is their ability to survive through optimization of the use of critical resources. This results from the development of an integrated ecological system composed of both the living plant and the standing dead litter and its decomposers[10]. The gradual mineralization of the sequestered nutrients, together with the humification of part of the organic materials, leads to the formation of an aerial, plant-linked soil environment. This coherent system established within the living individuals of *Espeletia* greatly contrasts with the surrounding desert ground.

References

1 Monasterio, M. and Vuilleumier, F. (1986) in *High Altitude Tropical Biogeography* (Vuilleumier, F. and Monasterio, M., eds), pp. 3–7, Oxford University Press
2 Cuatrecasas, J. (1986) in *High Altitude Tropical Biogeography* (Vuilleumier, F. and Monasterio, M., eds), pp. 275–280, Oxford University Press
3 Hedberg, O. (1964) *Acta Phytogeogr. Suec.* 49, 1–114
4 Vuilleumier, F. and Monasterio, M. (1986) in *High Altitude Tropical Biogeography* (Vuilleumier, F. and Monasterio, M., eds), pp. 265–266, Oxford University Press
5 Smith, A.C. and Koch, M.F. (1935) *Brittonia* 1, 479–530
6 Monasterio, M. (1980) in *Estudios Ecológicos en los Páramos Andinos* (Monasterio, M., ed.), pp. 171–176, Ediciones de la Universidad de Los Andes
7 Van der Hammen, T. and Cleef, A.M. (1986) in *High Altitude Tropical Biogeography* (Vuilleumier, F. and Monasterio, M., eds), pp. 153–201, Oxford University Press
8 Young, T.P. and Augspurger, C.K. (1991) *Trends Ecol. Evol.* 6, 285–289
9 Goldstein, G., Meinzer, F. and Monasterio, M. (1984) *Plant Cell Environ.* 7, 179–186
10 Monasterio, M. (1986) in *High Altitude Tropical Biogeography* (Vuilleumier, F. and Monasterio, M., eds), pp. 49–80, Oxford University Press
11 Smith, A.P. and Young, P. (1987) *Annu. Rev. Ecol. Syst.* 18, 137–158
12 Mooney, H.A. and Dunn, E.L. (1970) *Evolution* 24, 292–303
13 Chapin, F.S., III (1980) *Annu. Rev. Ecol. Syst.* 2, 233–260
14 Sarmiento, G., Goldstein, G. and Meinzer, F. (1985) *Biol. Rev.* 60, 315–355
15 Kira, T. (1978) in *Tropical Trees as Living Systems* (Tomlinson, P.B. and Zimmermann, M.H., eds), pp. 561–590, Cambridge University Press
16 Lemée, G. (1976) in *Ecosystèmes Terrestres* (Lamotte, M. and Bourliere, F., eds), pp. 75–121, Masson
17 Menzier, F., Goldstein, G. and Rundel, P. (1985) *Oecologia* 65, 278–283
18 Goldstein, G., Rada, F., Canales, M.O. and Zabala, O. (1989) *Acta Oecol.* 10, 359–370
19 Beck, E., Senser, M., Scheibe, R., Steiger, H-M. and Pongratz, P. (1982) *Plant Cell Environ.* 5, 215–222
20 Rada, F., Goldstein, G., Azócar, A. and Meinzer, F. (1985) *Plant Cell Environ.* 8, 501–507
21 Smith, A.P. (1974) *Biotropica* 6, 263–266
22 Meinzer, F. and Goldstein, G. (1984) *Ecology* 66, 512–520
23 Smith, A.P. (1979) *Biotropica* 11, 43–47
24 Goldstein, G. and Meinzer, F. (1983) *Plant Cell Environ.* 7, 179–185
25 Garay, I. (1981) *Rev. Ecol. Biol. Sol.* 18, 209–219
26 Garay, I., Sarmiento-Monasterio, L. and Monasterio, M. (1982) in *New Trends in Soil Biology (Proceedings of the VIII International Colloquium of Soil Zoology)* (Lebrun, Ph., Andre, H.M., De Medts, A., Gregoire-Wibo, C. and Wauthy, G., eds), pp. 127–133, Louvain-La Neuve
27 Goldstein, G., Meinzer, F. and Monasterio, M. (1985) *Oecol. Plant.* 6, 263–275
28 Ehleeringer, J. and Björkman (1978) *Oecologia* 36, 151–162
29 Guariguata, M.R. and Azócar, A. (1988) *Biotropica* 20, 54–59
30 Goldstein, G., Rada, F. and Azócar, A. (1985) *Oecologia* 68, 147–152
31 Rada, R., Goldstein, G., Azócar, A. and Torres, F. (1987) *J. Exp. Bot.* 38, 491–497