



Comparative demography of two giant caulescent rosettes (*Espeletia timotensis* and *E. spicata*) from the high tropical Andes

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ABSTRACT

Using field data from previous studies we built matrix models for two populations of giant rosettes, *Espeletia timotensis* Cuatrec. and *E. spicata* Sch. Bip. Wedd., from the Andes Cordillera in Mérida, Venezuela. We analysed the models and calculated population growth rate (λ), sensitivities, elasticities and the sensitivity of the elasticities to changes in the vital rates. The analysis showed that the two species behave alike in general demographic terms. In both models, population growth rate is positive and sensitivities of λ to changes in vital rates decrease markedly in this order: plant establishment, progression of juvenile–adult, germination and survival. The relative contributions of vital rates to λ (elasticities) are very similar to those of other woody plant species: a higher contribution of survival and a very low contribution of fecundity. Transition

from seedling to juvenile is most important and the younger established stages (juveniles and young adults) play a predominant demographic role in both populations. Seed banks and older adults are playing a relatively minor role in the dynamics of both populations. However, they may be important in relation to unpredictable, favourable or detrimental events. Perturbation analysis of elasticities showed that increasing the rate of plant establishment will decrease the relative importance of stasis. We conclude that both species are demographically very close, and similar to other long-lived woody plant species. However, the two species differ in the role of the seed bank, which seems more important in the demography of *E. spicata* than in *E. timotensis*.

Key words Demography, elasticity, *Espeletia*, giant rosettes, matrix models, paramos, population ecology, sensitivity, tropical alpine, tropical Andes

INTRODUCTION

At above 4000 m elevation in the Andean Cordillera in Venezuela, a very harsh periglacial habitat has been available for plant colonization since the retreat of the ice around 10–12 000 years ago (Salgado-Labouriau, 1986). This habitat has been described as a ‘cold desert paramo’, dominated by giant caulescent rosettes belonging to the genus *Espeletia* in the Compositae (Asteraceae) family (Monasterio, 1979). The giant rosettes grow up to 2–3 m high, forming a discontinuous cover. There is also a very discontinuous ground layer formed by ‘dwarf cushions and small rosettes of

various species. The discontinuity of the vegetation leaves large areas of bare ground, resulting in a very open community.

Paramos dominated by giant rosettes of *Espeletia* are also found in the Colombian high Andes, where they have been named ‘super paramo’ (van der Hammen & Cleff, 1986). Similar ecosystems are also found in other high tropical mountains in Africa and Hawaii (Smith, 1994). These are dominated by giant rosettes from other genera of Compositae (*Argyroxiphium* in Hawaii, *Dendrosenecio* in Tropical Africa). One interesting feature of all these tropical communities is that despite the morphological

and ecological similarities of the various giant rosette species they tend to exclude each other, forming almost pure patches in adjacent areas, usually accompanied by a specific set of ground-layer species (Young & Peacock, 1992).

Another common feature of all these ecosystems is the remarkable dominance of each giant rosette species, in terms of size, number and biomass. Accordingly, these populations should play a dominant role in the functioning of the whole ecosystem and in the dynamics of the communities. Furthermore, these rosettes represent extraordinary models of evolutionary radiation and life form and physiological adaptation. Advancing knowledge of the population biology of these long-lived species will provide the basis for understanding community responses to environmental changes (Rundel *et al.*, 1994). This is especially important, since tropical high mountains are key ecosystems in global environmental monitoring.

Several studies have addressed the adaptive features, especially the physiological mechanisms, which allow these species to colonize these habitats (Goldstein *et al.*, 1984; Monasterio & Sarmiento, 1991; Meinzer *et al.*, 1994). Some aspects of the population biology of giant rosette species have been studied in *Senecio keniodendron* R.E. & T.C.E. Fr. (Smith & Young, 1982, 1994), and in *Lobelia* species (Young, 1984, 1985, 1994), both from Mount Kenya, as well as in *Argyroxiphium sandwicense* DC. from Maui (Rundel & Witter, 1994). Several studies have also been made of populations of *Espeletia* in the high tropical Andes (Smith, 1981; Monasterio, 1986; Berry, 1987; Guariguata & Azócar, 1988; Berry & Calvo, 1989; Estrada & Monasterio, 1991). These studies address different components of population biology including pollination, seed set, germination and seedling survival.

In some studies, an attempt has been made to produce a more integrated view of the dynamics of the population. Estrada & Monasterio (1988) estimated seed production and height-specific mortality rates, and determined population structure and causes of mortality in *Espeletia spicata* Sch. Bip. Wedd. A graphic model of a population of *E. timotensis* Cuatrec. was developed by Monasterio & Lamotte (1989), based on field data of size structure and reproductive output. Vermeij (1995) developed a life table of *E.*

hartwegiana Cuatrec. based on size structure of adults. Although these studies focused on demographic aspects of the giant rosette populations, they are still far from providing an integrated picture of the dynamics of these populations, and consequently the demographic processes involved in the colonization of open ground and in the persistence of these species are still largely unknown. Collection of complete demographic field data under high mountain conditions and the methodological complexities involved in their analysis are each problematic.

The development of a methodology based on the construction and analysis of projection matrix models (Caswell, 1989) has facilitated the use of demographic data in an analytical approach allowing comparative studies. In this paper we present a demographic study of two closely related giant-rosette species from the desert paramo in Venezuela. They, and the paramos where they live, have been subjects of research in our group for more than two decades. Attempting to develop an integrated picture of giant-rosette demography, we use data from previous field studies to build and analyse projection matrix models of the two species and their peculiarities as colonizing species of high tropical mountains.

STUDY SITE AND SPECIES

The data used in this study were collected originally from permanent plots located in the Paramo de Piedras Blancas (8°52'N, 70°55'W) in the most northward section of the Sierra de La Culata, above 4100 m, in the Cordillera de Los Andes, State of Mérida, Venezuela.

We selected two giant-rosette species growing in the desert paramo (Fig. 1): *E. timotensis* Cuatrec. and *E. spicata* Sch. Bip. Wedd. (Aristeguieta, 1964). Taxonomically, they are closely related species and share many morphological traits. Both are polycarpic, monoaxial trees with indeterminate growth and lateral inflorescences (Monasterio, 1986). Both species reproduce only by seeds. In *E. timotensis*, each reproductive event takes as long as 21 months from the emergence of inflorescences in September of year 1 to the completion of seed dispersal in June of year 3. In *E. spicata*, each reproductive event takes little more than 1 year to completion.

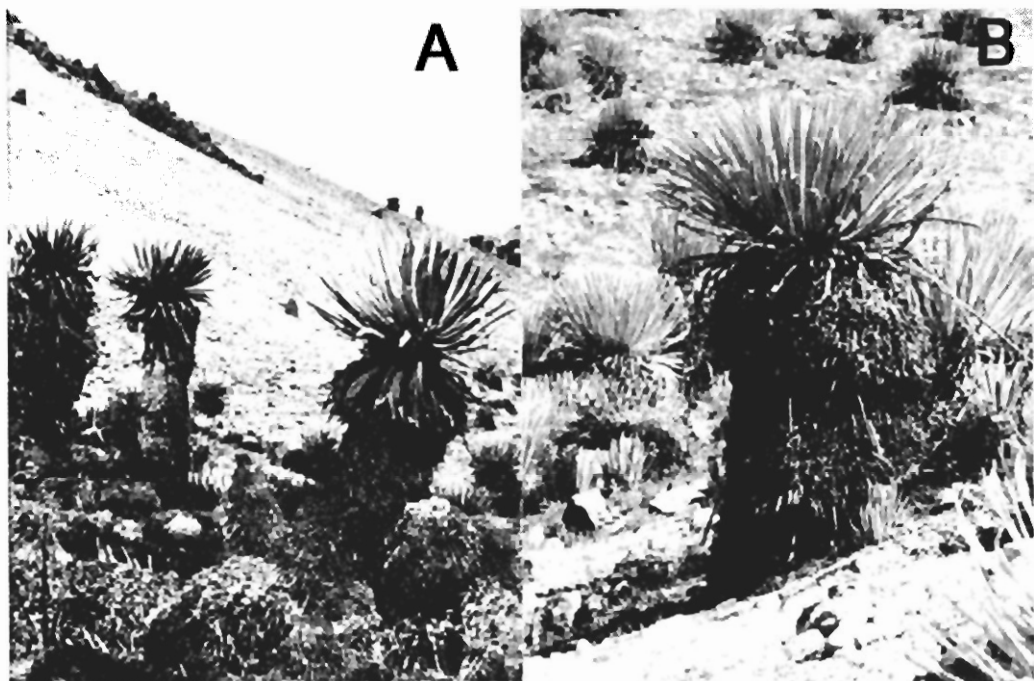


Fig. 1 *Espeletia timotensis* Cuatrec. (A) and *E. spicata* Sch. Bip. Wedd. (B) in their natural habitats above 4000 m in Sierra de La Culata, Merida, Venezuela.

E. spicata is found in an altitudinal range from 3900 to 4300 m, on intermediate slopes with a rocky substrate formed by small blocks and gravel. *E. timotensis* occurs between 4000 and 4500 m, on steeper slopes with substrates predominantly formed by small debris (Monasterio, 1986).

METHODS

The models

Based on more than 20 years of previous observations on the two species' reproductive behaviour, growth and survival, we constructed a six-stage classified model to represent different life stages in these populations. Figure 2 shows the graph of the life cycle in which the time for each transition equals 1 year. The first three stages are common to both species: stage 1, the seed bank in the soil; stage 2, the seedlings, which are small plants still bearing cotyledons; stage 3, established plants below 20 cm height; these are considered juveniles since plants do not flower in this stage

except for very few precocious individuals. Height in this and in the adult stages described below is the height of the stem from the soil surface to the base of the rosette. The three adult stages in *E. timotensis* are: stage 4, plants from 21 to 100 cm, stage 5, plants from 101 to 160 cm and stage 6, plants above 160 cm. The three adult stages for *E. spicata* are: stage 4, plants from 21 to 80 cm, stage 5, plants from 81 to 100 cm and stage 6, plants above 100 cm.

For each population, a non-negative matrix can be formulated from the graph in Fig. 2. The matrix, which we denote by A , is the population projection matrix and its element a_{ij} represents the contribution of individuals in stage j at time t to stage i at time $t + 1$. The population dynamics are determined by a linear time-invariant model:

$$n(t + 1) = A n(t) \quad (1)$$

where $n(t)$ is a column vector containing the abundance of individuals in each stage at time t (Caswell, 1989).

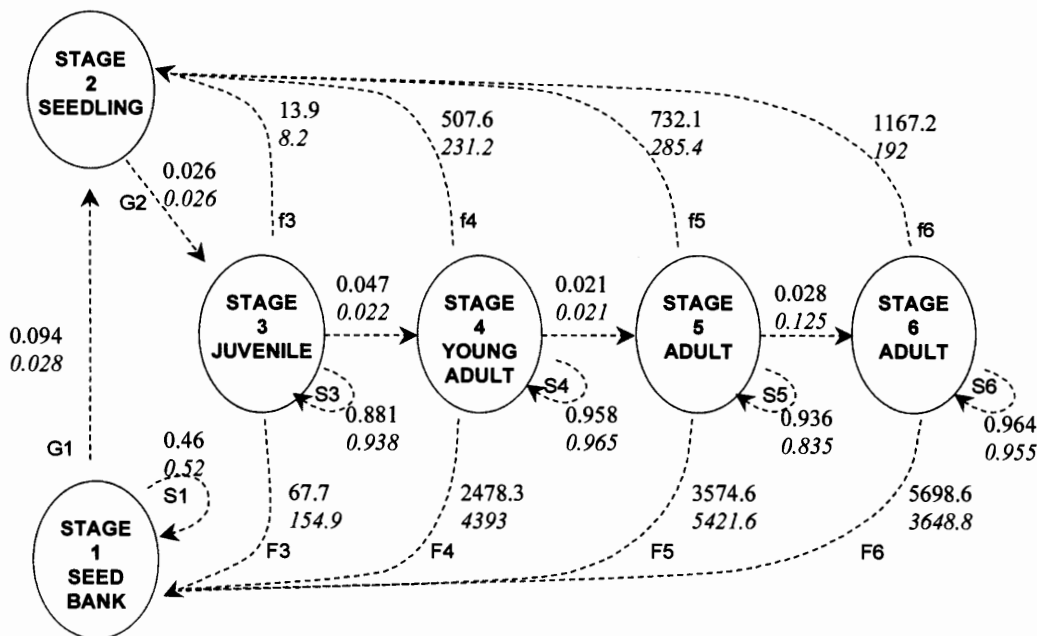


Fig. 2 Graph model and vital rates for the life cycle of the two species, *Espeletia timotensis* and *E. spicata*. Transitions between stages are of three types: growth from one stage to the next (G), survival within a stage (S) and fecundity (F, f). We distinguish two components of fecundity, seed recruitment into the soil seed-bank (F) and seedling recruitment from currently produced seeds (f). Vital rates for the projection matrices are included close to each transition, upper figure for *E. timotensis*, lower figure (*italics*) for *E. spicata*.

Vital rates

The vital rates for the models were estimated from field data taken by several authors in the study site described above. The sampling procedures and the treatment of field data for each projection matrix are explained briefly below. They are varied and come from different sources and years.

For *E. timotensis*, the basic data come from a field study directed by M. Monasterio (Monasterio, 1986). In that study, 1423 plants present in a 5000-m² plot were monitored for a 7-year period from 1976 to 1982. Also, 116 plants present in four 100-m² subplots were tagged and monitored for more detailed measurements and the flowering of 58 adults during 1978 and 1981 was closely followed. This field dataset allowed us to calculate size-specific annual mortality rates and annual stem growth. Furthermore, annual viable seed production was estimated by multiplying the average number of

inflorescences by the average number of viable seeds per inflorescence for each stage.

For *E. spicata*, we used information from a 5.5-year study conducted by C. Estrada between 1978 and 1984 in four 500-m² transects with 1561 individual plants. Mortality was monitored in a subsample of 238 plants in four 100-m² plots and growth was monitored in a subsample of 30 plants of various sizes during that period. During 1981–82, reproductive activity was followed closely, allowing us to estimate the viable seed production for each year (more details in Estrada & Monasterio, 1988, 1991).

In our models, fecundity has two components (Fig. 2): (1) the fraction of viable seeds that germinate within the year they are produced, called here 'seedling recruitment' (following Silvertown *et al.*, 1993) and designated by f_i ($i = 3, \dots, 6$), where i represents stages; and (2) the fraction of viable seeds that do not germinate and that enters the seed bank in the soil,

called here 'seed recruitment' (also following Silvertown *et al.*, 1993) and designated by F_i ($i = 3, \dots, 6$). To calculate these vital rates we used: $f_i = \text{viable seed crop} \times p_g$ and $F_i = \text{viable seed crop} \times (1 - p_g)$, where p_g is the probability of germinating within the year the seed is produced. For *E. timotensis*, $p_g = 0.17$ was taken from Guariguata & Azócar (1988). For *E. spicata* we used an estimate from an unpublished study conducted by A. Azócar during 1977–80. In 1977 and 1979 few plants flowered in the area, but in 1978 there was a flowering boom. Seed dispersal of this episode took place during the first half of 1979, allowing Azócar to estimate the average seed rain per square metre and the fraction of viable seeds. Between May 1979 and October 1980, she monitored seven plots (100×50 cm) weekly, counting and labelling emerging seedlings. On the basis of this dataset, she estimated the probability of germination during the first year as $p_g = 0.05$.

To calculate annual rates of germination from the seed bank (G1, Fig. 2) and seed stasis in the seed bank (S1, Fig. 2), we use the following: $G1 = p_g \times p_s$ and $S1 = (1 - p_g) \times p_s$, where p_g is as above and p_s is the probability of survival of a seed in the seed bank. From Guariguata & Azócar (1988) we have estimates for the probability of survival of *E. timotensis* seeds in the soil after 1 year (0.55) and, as already mentioned, for the probability of germination (p_g) during the first year (0.17). These authors expect seeds of *E. timotensis* to remain viable in the soil for 5 years. We do not have information on the probability of survival in the soil of *E. spicata* seeds. For this study, we have assumed that: (a) based on the strong morphological similarities between their seeds, the probabilities of survival in the soil are similar for both species, and (b) the probabilities of survival and germination do not change throughout the estimated 5 years of seed life span in the soil. According to this, we lumped together seeds of different age in the seed bank and used 0.55 as the probability of seed survival in the soil in both species. Then, we calculated G1 and S1 for each species as described above.

Survivorship and growth from seedlings to juveniles (G2, Fig. 2) was estimated by A. Azócar for *E. spicata* in her unpublished study. A total of 2175 emerging seedlings were labelled and

monitored in a 2-year period. She estimated transition from seedlings to juveniles to be 0.0026, and concluded that seedlings either die or become established as juveniles within the first year of life. This vital rate is unknown for *E. timotensis*. Since seedlings in both species are morphologically very similar we assume that the pattern of seedling growth to established juvenile in *E. timotensis* is similar to that in *E. spicata* and used the data provided by A. Azócar for this species.

Demographic analyses

The dominant eigenvalue of matrix **A** in (1) is the population growth rate (λ) when the population reaches its stable stage distribution. The positive right (**w**) and left (**v**) eigenvectors associated with this eigenvalue represent the stable stage distribution and the stable reproductive value distribution, respectively.

In order to evaluate the sensitivity of the growth rate λ to small changes in the vital rates, the following formula is used (Caswell, 1989):

$$s_{ij} = \delta\lambda / \delta a_{ij} = v_i w_j / \langle v, w \rangle$$

where the subscripts in **v** and **w** denote vector components, and $\langle \dots \rangle$ is the inner product.

The elasticity e_{ij} gives the results of proportional changes in λ due to proportional changes in a_{ij} , and quantifies the contribution of this coefficient to population growth rate (de Kroon *et al.*, 1986; Caswell, 1989):

$$e_{ij} = (a_{ij} / \lambda) (\delta\lambda / \delta a_{ij})$$

Elasticities sum to one and may be summed across selected paths of the life cycle to measure the importance of these paths to population growth.

We also used the perturbation analysis of elasticities to study their response to changes in the vital rates (Caswell, 1996). This can be done by differentiating e_{ij} with respect to a_{ki} :

$$(\delta e_{ij} / \delta a_{ki}) = (a_{ij} / \lambda) (\delta^2 \lambda / \delta a_{ij} \delta a_{ki}) - (a_{ij} / \lambda^2) (\delta \lambda / \delta a_{ij}) (\delta \lambda / \delta a_{ki}) + (\delta_j \delta_{ki} / \lambda) (\delta \lambda / \delta a_{ij})$$

where the second derivative is given in terms of the sensitivities of the eigenvalues (Caswell, 1996), and $\delta_j = 1$, if $i = k$; 0 otherwise. The perturbation

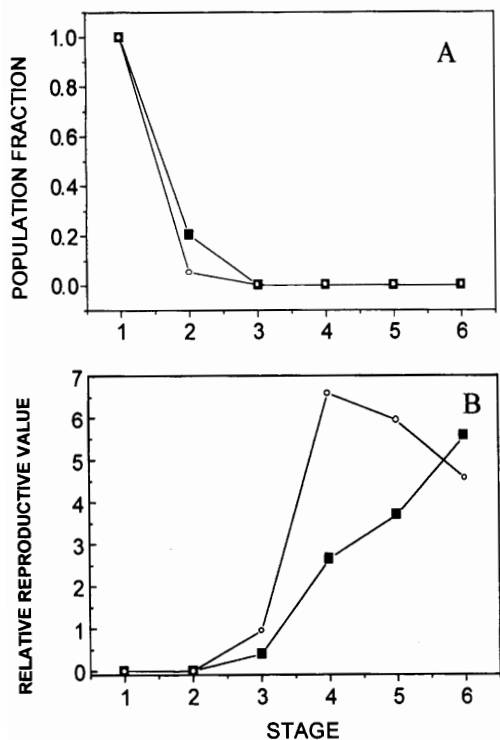


Fig. 3 Stable stage distribution (A) and reproductive value distribution (B). Both calculated from the matrix models and normalized to stage one. Filled squares = *Espeletia timotensis*, open circles = *E. spicata*.

analysis is interesting not only because it can help to explain the differences in elasticity values, but also because it may allow us to detect general patterns relating to how life history structure determines elasticity patterns (Caswell, 1996).

RESULTS

The projection matrices

The elements of the two projection matrices represent the vital rates or transitions of the graph model, as presented in Fig. 2 for each of the two species. The lowest vital rate is plant establishment after the seedling stage. After plants are established they have a high probability of survival within a stage (stasis) and very slow growth, resulting in slow progression

from one stage to the next. Germination from the seed bank (G1), here called emergence, is more than three times higher in *E. timotensis* than in *E. spicata*. In adults of *E. timotensis*, fecundity increases with size, and stage 6 has the highest average value. In contrast, adults of *E. spicata* reach maximum fecundity in stage 5.

Population growth rate

The population model of *E. timotensis* grows at $\lambda = 1.24$, which means a positive growth rate ($r = 0.22$). The *E. spicata* population model grows at $\lambda = 1.13$, also a positive growth rate ($r = 0.12$).

Reproductive value and stable distribution

Reproductive value increases with size throughout the life span of *E. timotensis* (Fig. 3), whereas in *E. spicata* there is a maximum value at stage 4 (young adults). Reproductive values for plant stages 4 and 5 are as much as two times higher in *E. spicata* than in *E. timotensis*.

Stable distributions are very similar for the two species (Fig. 3) and follow the well-known inverted-J shape.

Sensitivity analysis

Sensitivities are comparable in both species (Fig. 4). Population growth rate is extremely sensitive to changes in plant establishment (G2) in both species, with values in *E. timotensis* even higher than in *E. spicata*. Sensitivity to progression from juvenile to young adult (G3) ranks second, one order of magnitude below sensitivity to plant establishment. Sensitivity to emergence (G1, germination from the seed bank) is third, almost three times higher in *E. spicata* than in *E. timotensis*. Sensitivity to stasis (S) is fourth, two orders of magnitude below seedling establishment. Sensitivity values for both components of fecundity (f, F) are extremely low in both species.

Elasticity analysis

In *E. timotensis*, the most important relative contribution to population growth (Fig. 5) comes from stasis (survival within a stage), with a

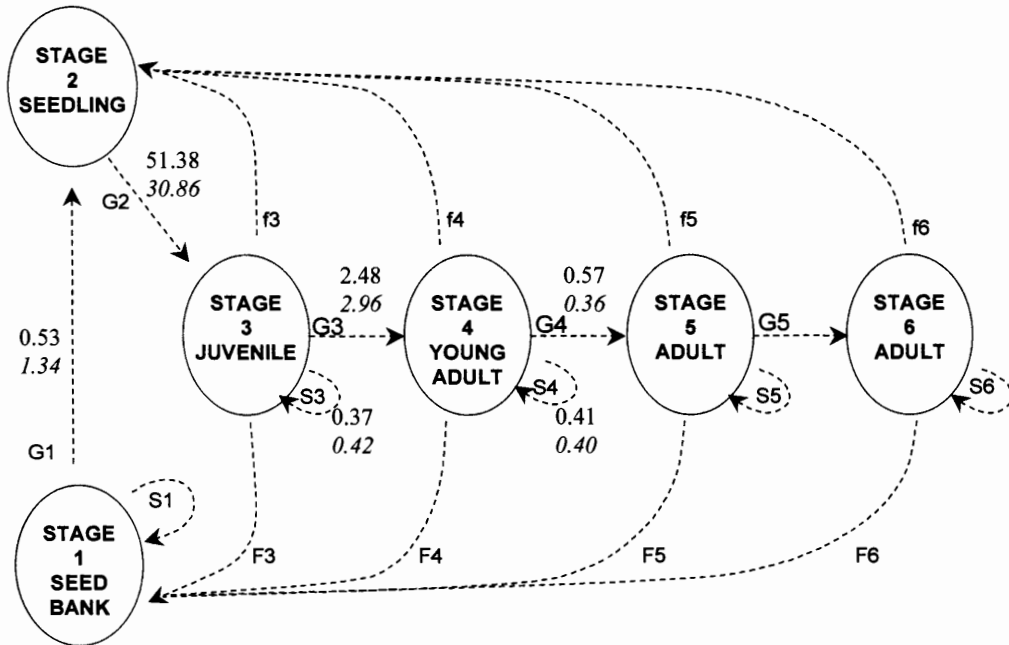


Fig. 4 Sensitivity of population growth rate (λ) to changes in each vital rate. Upper figure for *Espeletia timotensis*, lower figure (italics) for *E. spicata*. For simplicity, only values higher than 0.1 are shown.

sum of elasticity values of 64%, followed by progression (transition from one stage to the next) with a sum of elasticity values of 25% and lastly by fecundity with a sum of elasticity values of 11%. Fecundity components differ in their total elasticity values, since seedling recruitment sums 6.79% and seed recruitment sums only 3.98%.

Elasticities in *E. spicata* are similar to those in *E. timotensis*, except that the relative contribution from stasis is even higher (75.8%). Progression and fecundity contribute less (17.1 and 7%, respectively). Another difference is that in *E. spicata*, the importance of seedling recruitment (3.2%) is comparable to seed recruitment (3.8%).

Transitions from and to stages 3 (juveniles) and 4 (young adults) contribute equally highly, and together add 90% of the population growth rate in both models. In contrast, seed survival and seed germination together contribute 6% and transitions from and to older adults (stages 5 and 6) contribute very little.

Perturbation analysis

Estimation of the sensitivities of elasticities to changes in the vital rates in each species renders 36 matrices, one for each elasticity value, each matrix with 36 sensitivity values. We examined all matrices to rank sensitivity values in both species and selected all values above unity. Both species behave similarly, since sensitive elasticities all respond to changes in G2, plant establishment. Also, in both species, elasticity of S4 showed the highest absolute sensitivity, a negative value, followed by the elasticities of G2 and G3, which were positive (Table 1). In response to changes in G2, all stasis elasticities are negative and all others are positive.

DISCUSSION

E. timotensis and *E. spicata* are closely related, evolving from a common lineage as they invaded the paramo environment (Monasterio & Sarmiento,

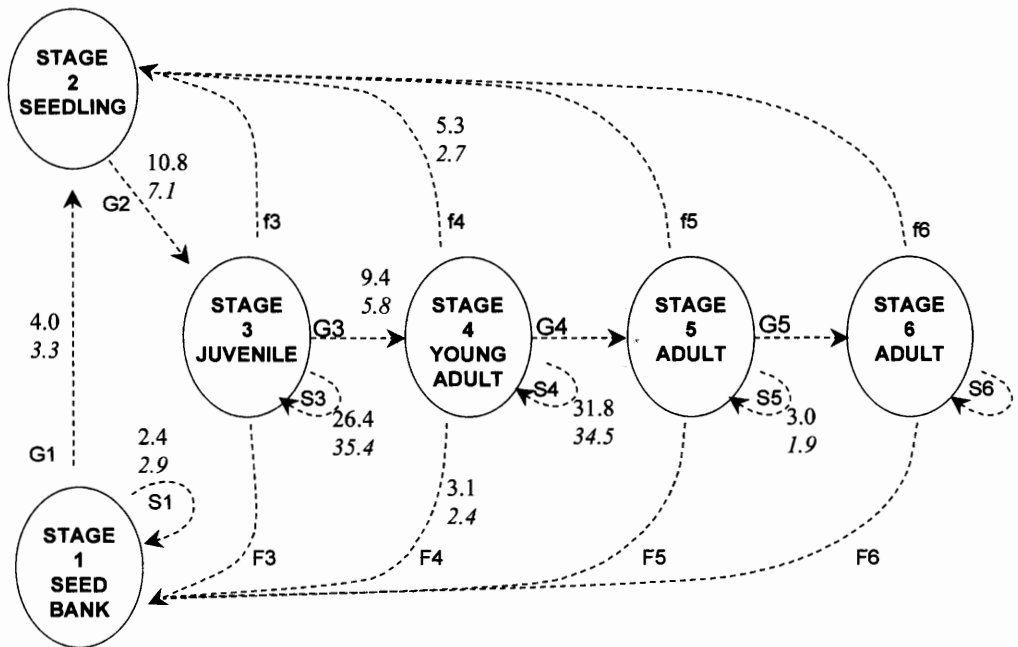


Fig. 5 Elasticity values or the relative contribution of each vital rate to the population growth rate (λ) as percentage of the total. Upper figure for *Espeletia timotensis*, lower figure (italics) for *E. spicata*. For simplicity, only values higher than 1% are shown.

Table 1 Summary of the results of the perturbation analysis of the two models. Only values higher than unity are shown. Vital rates are labelled as in Fig. 2, and elasticity values are included for comparison

<i>E. timotensis</i>			<i>E. spicata</i>		
Vital rate	Elasticity value	Sensitivity of elasticity	Vital rate	Elasticity value	Sensitivity of elasticity
S4	0.32	-23.42	S4	0.35	-24.79
G2	0.11	14.41	G2	0.07	11.26
G3	0.09	10.01	G3	0.06	6.82
f4	0.05	7.93	G1	0.03	4.39
S5	0.03	-7.12	f4	0.00	4.35
G1	0.04	3.75	S6	0.01	-3.94
f3	0.01	2.97	F4	0.02	2.64
F4	0.03	2.71	S5	0.02	-2.59
S3	0.26	-2.12	f3	0.01	2.53
S6	0.01	-0.196	S1	0.03	2.35
F3	0.01	1.42	F3	0.01	1.91
—	—	—	S3	0.35	-1.29

1991). They share some basic features in morphology and ecology. The population models built in this study suggest that both populations also behave similarly in demographic terms,

although vital rates estimates from field data showed some differences in the reproductive ecology of these species. *E. spicata* stores a larger fraction of seeds in the soil than

E. timotensis. Every year, three times more seeds from the current seed crop become a seedling in *E. timotensis* than in *E. spicata*, and for each seedling recruited, five seeds go to the seed bank in *E. timotensis* and 19 in *E. spicata*. The smaller importance of a seed bank in the former than in the latter species is emphasized by the sensitivity analysis. Sensitivity to seedling recruitment (f) is eight times higher than sensitivity to seed recruitment (F) in *E. timotensis*, whereas it is only two times higher in *E. spicata*. Furthermore, the latter species is almost three times more sensitive to seedling emergence ($G1$) than is *E. timotensis* (Fig. 4). Also, the response of λ to changes in seedling emergence from the seed bank ($G1$) will be greater in *E. spicata* than in *E. timotensis* (Fig. 4). These differences may be reflecting the fact that the substrate in communities dominated by *E. spicata* is more stable (less mobile) than in the communities dominated by *E. timotensis*, which is usually found on steeper slopes.

In our models, population growth rate is slightly higher in *E. timotensis* ($\lambda = 1.24$) than in *E. spicata* ($\lambda = 1.13$), and both values are well within the range of values calculated for woody plants using projection matrix models (Silvertown *et al.*, 1993). It is important to emphasize that our estimates for the vital rates of the two models, from which these λ -values are derived, are based on several assumptions, as described in the Methods section. It is also important to recall that the deterministic models used here assume constant vital rates and exponential population growth. This is why we do not intend to forecast the growth of these two field populations, but rather gain an insight into their demographic structure and the relative importance of their components. Given the mixed nature of the field data used to estimate the vital rates, it was not possible to calculate confidence limits for the estimates of population growth rates (λ).

E. spicata has the peak of reproductive value as young adults, at the optimum of vegetative conditions (Fig. 3). In contrast, *E. timotensis* reaches the maximum reproductive value at the latest stage of the life cycle. These different patterns are reflecting a different energy allocation strategy throughout the plant's life. *E. spicata* is allocating more resources to reproduction

than to vegetative growth early in adult life, whereas *E. timotensis* allocates in reproduction more evenly throughout life.

The analysis of the models shows that the two species are very sensitive to changes in plant establishment, supporting the conclusions by Monasterio & Lamotte (1989). In this respect, *E. timotensis* is almost two times more sensitive than *E. spicata*. Sensitivities to changes in fecundity are extremely low in both species, even discounting for the fact that values for fecundity are generally much lower than values for survival and growth. This indicates that changes in this parameter have to be very large to affect population growth, and that observed fluctuations in flowering output (Monasterio, 1986) may not have major consequences upon population dynamics.

In both species, the relative contributions of vital rates to λ (elasticities) show a pattern very similar to that from woody plant species: a higher contribution of stasis and a very low contribution of fecundity (Silvertown *et al.*, 1993). However, the fact that the stasis of stages 3 (juvenile) and 4 (young adult) are the two most important vital rates contributing to λ , points out the prominent role of the smaller established rosettes in the growth of the population. Furthermore, sensitivities as well as elasticities show a similar pattern, being highest for transitions involving the first three plant stages, namely seedlings, juveniles and young adults. Eighty-seven per cent of the population growth rate is accounted by the subpopulation formed by plants smaller than 100 cm in *E. timotensis* and smaller than 80 cm in *E. spicata*. In terms of elasticity, the seed bank appears to be playing a relatively minor role in both models. The same can be said of the two taller stages of adults. If this is so, why does the population have a seed bank and why do the plants grow for so long to reach that height? Both the seed bank and the older adults may be important in relation to unpredictable events. These events may be detrimental to population growth but may also offer the important opportunity for seedling recruitment and establishment, as seem to be the case in arctic and alpine environments (McGraw & Vavrek, 1989). Drought spells may be an important type of event. Resistance to drought increases with size and age in these

giant caulescent rosettes (Goldstein *et al.*, 1985), and therefore mortality from this source should be lower in the older stages. The effects of consecutive failures to flower could be ameliorated by germination from the seed bank. This reserve of seeds may also increase recruitment during wet spells. Unfortunately, the available information at this time is not enough to test these hypotheses. Furthermore, since our matrices do not encompass temporal variations in the vital rates, the role of yearly fluctuations cannot be uncovered in our analysis.

However, we gain some insight into the way elasticities respond to changes in vital rates from the results of the perturbation analysis. In this respect, only changes in plant establishment will have effects on the structure of the elasticity matrix in both species. Changes leading to improved plant establishment, i.e. increasing the transition from seedling to juvenile, will decrease the relative importance of survival of young adults (S4) and will increase the relative contribution of plant establishment itself. We interpret this as an indication that the great importance of stasis of young adults is a direct consequence of the very low values of plant establishment.

Our analysis has shown that these two related giant rosette species are alike in general demographic behaviour, but differ in several important aspects. These differences may be related to the adaptation of these two species to different habitats in the desert paramo. However, the scanty field data available and the fact that we had to make several assumptions in the process of estimating vital rates limit the conclusions of this study. Further research is needed that would allow us to document the variations in vital rates through long-term field experiments and to explore further differences between the two species. The availability of demographic data from other giant rosette species in comparable habitats of other high tropical mountains would allow comparisons for a better understanding of the processes involved in the colonization of these habitats.

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