

# Seed Bank Dynamics and Germination Ecology in *Espeletia timotensis* (Compositae), an Andean Giant Rosette<sup>1</sup>

Manuel R. Guariguata<sup>2</sup>

Departamento de Estudios Ambientales, Universidad Simon Bolivar, Apartado 80659, Caracas, Venezuela 1080  
and

Aura Azocar

Facultad de Ciencias, Universidad de Los Andes, Merida, Venezuela 5101

## ABSTRACT

The dynamics of a seed cohort over a one-year period and its laboratory germination requirements at eight constant temperatures in light and darkness were studied in *Espeletia timotensis* Cuatr., a giant rosette species from the Venezuelan Andes (paramo) at 4200 m elevation. After one year (coinciding with the end of the rainy season) 55 percent of the seeds remained viable, 17 percent had germinated, and mortality accounted for 30 percent. Soil samples collected at the beginning and the end of the rainy season and sieved to separate the buried seeds revealed naturally occurring viable seeds on both occasions. In the laboratory, maximum germination percentages were 80 and 67 percent in light and darkness, respectively, much higher than the germination percentage observed in the field. The adaptive significance of the asynchronous germination pattern in the seed bank of *E. timotensis* and the differences between field and laboratory germination are discussed.

IN THE VENEZUELAN ANDES, páramo vegetation ranges from altitudes of 2800–4600 m where giant rosette plants of the genus *Espeletia* comprise a conspicuous physiognomic element. One of the dominant species in the highest páramo zone, *Espeletia timotensis* Cuatr., is a long-lived caulescent rosette growing to 3 m tall and restricted to well-drained slopes above 4000 m (Fig. 1). The frequent occurrence of night freezing temperatures throughout the year is a common feature in high tropical mountain environments (Hedberg 1964, Coe 1967, Troll 1968, Monasterio and Reyes 1980) and may limit germination and establishment (Smith 1980, 1981; Smith & Young 1982). For this reason and because it lacks vegetative propagation and reproduces polyannually (Monasterio 1983, Berry & Calvo 1987), we might expect adaptive characteristics in the timing and degree of germination synchrony of the *E. timotensis* seed bank. To date, very few studies have focused on the seed biology of páramo species. Pannier (1969) found in *E. schultzii*, a widely distributed giant rosette, that germination percentages were higher in light and increased by drying and wetting cycles. Smith's (1975) studies of germination optima from altitudinal populations in five species showed that only seeds from high-elevation populations could germinate at temperature regimes other than that of their natural habitat.

The objectives of this paper are to evaluate the dy-

namics of a seed cohort of *E. timotensis* over a one-year period and to characterize its germination requirements under laboratory conditions. Although the population dynamics and ecophysiological aspects in this species are fairly well known (Monasterio 1983; Goldstein *et al.* 1984, 1985; Rada *et al.* 1985), basic features of its seed biology have remained unstudied.

## STUDY SITE

The study was conducted in the Páramo Las Cruces, Estado Mérida, Venezuela (8°51'N, 70°49'W), at 4200 m elevation. The vegetation is described by Monasterio (1980) as "desert páramo" with total plant cover ranging from 5 to 30 percent. The slope of the site varies between 10° and 30°. Other characteristic plant life forms in the area include tussock grasses, cushion plants, and small acaltescent rosettes. The zone was subjected to glacial events during the late Pleistocene (Schubert 1980); soils were formed by the accumulation of colluvial deposits and are composed primarily of sand. The climate is strongly seasonal with a 4- to 5-mo dry period (December–March) followed by an 8-mo rainy season during which 76 percent of the mean annual rainfall of approximately 800 mm is received. Daily temperature fluctuations are far greater than seasonal ones. Mean annual temperature is 2.8°C, with a mean monthly difference of about 2.7°C between the warmest and coldest months. In contrast, daily cycles recorded during the dry and wet season at soil surface have given extreme (day/night) values of 40°/–10° and 26°/0°C, respectively (Monasterio 1983).

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<sup>2</sup> Present address: Department of Botany, University of Florida, Gainesville, Florida 32611, U.S.A.



FIGURE 1. Individual of *E. timotensis* from the Venezuelan paramos at 4200 m. Approximate height is 2 m.

## METHODS

Seeds were collected for seed bank dynamics and laboratory germination experiments prior to dispersal in December 1983 from 25 randomly selected fruiting individuals inside a 20 × 50 m plot. Mean seed weight is 0.92 mg (SD = 0.16,  $N = 100$  seeds). Since this species forms a seed coat regardless of whether the ovule has been fertilized, filled and empty seeds were distinguished by applying light pressure to each seed with a pair of tweezers. The seeds were stored in paper bags at room temperature for use in the two experiments.

To assess the density of seeds buried in the soil within the plot, 60 samples (30 × 30 × 5 cm deep) were collected at random intervals along two 50-m transects on 12 March and 4 December 1984, at the beginning and end of the rainy season. Samples were placed in plastic bags and transported promptly to the laboratory where they were

stored at 4°C in the dark. Each sample was air-dried, sieved into >1.0-mm and >0.5-mm fractions and the filled seeds hand-sorted. Since a great number of samples contained either no seeds or only empty ones, all replicates were combined for each date, and seed density was estimated by dividing the number of filled seeds by the total area sampled (5.4 m<sup>2</sup>).

**SEED BANK DYNAMICS.**—Thirty nylon 1-mm mesh bags of 100 seeds each were buried in January 1984, at the onset of natural seed dispersal, at randomly chosen locations inside the plot. The bags were filled with sieved soil from the burial site and placed within 2–3 cm of the soil surface. Approximately every 2 mo over an entire year, 5 randomly selected bags were taken to the laboratory and kept at 4°C in the dark for ≤2 days. Recovered seeds were designated either germinated, viable, or dead. Because seed coats are not easily degraded under natural conditions and emerging seedlings might have died, the criterion for designating germinated seeds was the detection of a longitudinal incision in the coat and the presence of the tegument that surrounds the embryo. The remaining intact seeds were incubated in tetrazolium chloride, and stained embryos were designated viable. If the sum of the seeds in the three categories did not total 100 for each bag, the difference was designated unrecovered.

**LABORATORY GERMINATION.**—Germination tests were conducted on an aluminium thermogradient bar connected at both ends to constant temperature baths. Treatments used were 5°, 10°, 13°, 16°, 19°, 23°, 26°, and 28°C, in both constant light and constant darkness. Fifty seeds per treatment were placed on strips of filter paper inside glass tubes (1 cm diameter × 25 cm long) and arranged at the selected temperatures along the bar. Samples were moistened every 2 days with 1 ml distilled water. Light was provided by fluorescent tubes with quantum flux of 18 μmol/m<sup>2</sup> × sec. The glass tubes were covered with aluminium foil in the dark treatments. A seed was considered to have germinated when both the extrusion of the radicle and a longitudinal split in the seed coat were observed. Germinated seeds were counted every day and dark treatments inspected with a dim green safelight for no more than 2 min. For each treatment, the experiment was terminated following 5 consecutive days in which no germination was recorded. Experiments were repeated three times over a 3-mo period during which the viability of the stored seeds remained high (94.5%;  $N = 400$  seeds). For each treatment, mean germination time (MGT) was calculated in every replicate according to the formula:

$$\text{MGT} = \frac{\sum (N_i \times T_i)}{\sum N_i}$$

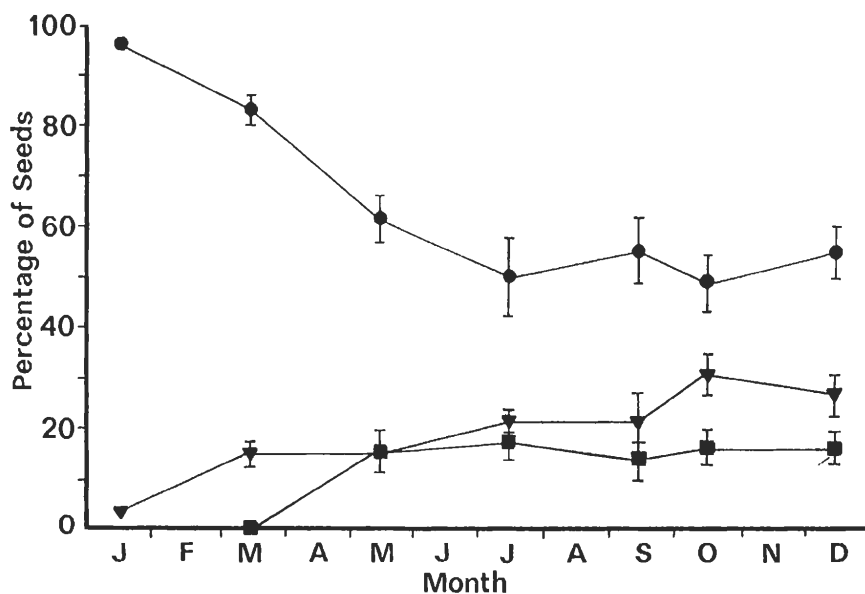


FIGURE 2. Percentage of germinated (squares), viable (circles), and dead (triangles) seeds of *E. timotensis* at each sampling date during 1984. Percentages of viable and dead seeds for the date of burial (January) were obtained with a tetrazolium test in a lot of 500 seeds. Each value represents the mean ( $\pm$ SD) of five replicates of 100 seeds each.

In which  $T_i$  = time (in days) since the start of the experiment, and  $N_i$  = number of seeds germinated at time  $T_i$ . Germination percentages were arcsine-transformed and compared using 1-way ANOVA. *A posteriori* comparisons were performed with a Tukey's test (Sokal & Rohlf 1981). Final germination percentages for each treatment in light and darkness were compared with a  $G$ -independence test.

## RESULTS

The percentage of viable seeds decreased exponentially with time in the seed bank, as described by the equation  $\ln(\text{percentage dormant seeds}) = 4.499 - 0.055T$ , where  $T$  = months ( $r^2 = 0.72$ ; slope  $t$  value =  $-3.66$ ,  $df = 5$ ,  $P < 0.01$ ; 95% C.I. for slope =  $-0.093$ ,  $-0.017$ ). After one year, about 55 percent of the buried seeds remained viable (Fig. 2). Germination started after the first rains in May and did not exceed 17 percent/mo during the whole year. Seed mortality was more common than germination, reaching about 30 percent by the end of the experiment. No signs of external damage (e.g., by seed predators) were observed. The percentage of unrecovered seeds varied from 1.6 in January to 10.8 in July and declined to 3.4 and 2.2 in October and December, respectively. If coat degradation contributed to the lack of seed recovery, an increase of seed loss with time would be expected; but no significant relationship was found. Mean density and percent viability in the seeds sampled in the study plot (Table 1) decreased between the beginning and the end

of the rainy season (probably caused by germination). Viability percentages, however, were lower on both dates than those for the bagged seeds: 67 vs 83 percent in March and 39 vs 55 percent in December.

At all temperatures, germination percentages were consistently higher in the light, but the highest percentages in darkness tended to occur at warmer temperatures (Table 2). Germination percentages were influenced differently by light and darkness as temperature increased, as a significant interaction component was found (2-way ANOVA,  $F = 20.9$ ,  $df = 7, 32$ ,  $P < 0.001$ ). In the light, the highest percentages were obtained between 5° and 19°C, whereas in darkness no germination occurred after 40 days at 23°, 26°, and 28°C. A tetrazolium test applied to these treatments showed a decline in viability of approximately 40 percent, suggesting that the seeds may have been damaged by the higher experimental temperatures. The mean germination time increased as the tem-

TABLE 1. Mean density and percent viability of *E. timotensis* seeds in the study plot at the beginning (March) and the end (December) of the rainy season during 1984. All replicates were pooled and divided by the total area sampled, 5.4 m<sup>2</sup>.

Date	No. seeds/m <sup>2</sup>	% viability	Total no. of seeds sampled
March	68.5	67.8	370
December	23.5	39.8	127

TABLE 2. Mean ( $\pm$ SD) of final germination percentages and mean germination times (MGT, in days) at constant temperatures in *E. timotensis* seeds. Within the light and dark conditions, mean final germination percentages followed by different letters differ significantly at  $P < 0.05$ . At all temperatures, germination was higher in the light (G-independence test,  $P < 0.05$  in all cases).

Temp. (°C)	Light		Dark	
	% germination	MGT	% germination	MGT
5	76.00 (5.29)a	10.81 (2.71)	50.00 (2.00)a	19.23 (1.98)
10	81.33 (2.30)a	6.75 (1.75)	65.33 (7.02)b	14.08 (1.27)
13	78.00 (5.29)a	5.92 (0.97)	67.33 (2.30)b	8.77 (0.57)
16	80.00 (3.46)a	6.28 (1.32)	45.33 (2.30)a	8.19 (1.04)
19	77.33 (4.16)a	4.76 (1.56)	30.00 (2.00)c	6.25 (2.89)
23	28.66 (4.16)b	5.00 (2.45)	0.00 (0.00)	—
26	8.66 (5.03)c	3.20 (2.98)	0.00 (0.00)	—
28	0.66 (1.15)d	—*	0.00 (0.00)	—

\* At 28°C in the light, mean germination time was not recorded due to small sample size.

perature decreased and was always greater in the dark treatments (Table 2).

## DISCUSSION

The seed bank experiment with *E. timotensis* showed that a high fraction of the seeds remained viable more than a year following production (a "persistent" seed bank; *sensu* Grime 1979). In addition, naturally occurring viable seeds were present in the soil along the study plot at the end of the rainy season, although their viability was relatively lower than those used in the seed bank experiment. This reduced viability might result from differences in sample sizes or from the presence of seeds in the soil from past fruiting episodes. Exponential decay of the seed bank has been reported in other species in studies of one year and longer (Roberts & Feast 1973, Sarukhan 1974, Yadav & Tripathi 1982, Anderson 1983). Assuming that the decay rate does not change with time, the expected longevity of seeds in the soil would be four to five years. The use of the bags, however, might have reduced the effects of seed predators or modified microenvironmental factors influencing seed survival, possibly leading to an overestimation of the expected longevity.

Asynchronous germination of the seed bank can be of adaptive value where selective pressures restrict establishment and early growth in plant populations (Angevine & Chabot 1979, Rathcke & Lacey 1985). In high-elevation tropical habitats, seedling establishment seems to be limited by such environmental factors as frequent nocturnal frosts and periods of low water availability. Smith (1981) reported low seedling survivorship at 4200 m in two common caulescent rosettes from the páramos, *E. schultzii* and *Espeletia lutescens*, especially during the dry season. Similarly, seedling survivorship was very low during a one-year survey at 4100 m of *Senecio keniodendron*, a giant rosette from African tropical mountains (Smith &

Young 1982). Our field observations over large areas in the study zone also suggest that seedling establishment is rare in *E. timotensis*, probably as a result of substrate instability that causes upper-soil movement (gelifluction) during repeated freezing and thawing cycles (Malagón 1982). Goldstein *et al.* (1985) found that *E. timotensis* juveniles (up to 40 cm tall) showed the highest risk of mortality in the population and attributed a low physiological capacity for drought tolerance as the main cause. A seven-year phenology study by Monasterio (1983) showed that reproductive cycles in *E. timotensis* tend to occur synchronously at the population level about every three years. This factor might also select for the persistence of seeds in the soil for more than one growing season.

Field germination percentages were usually lower than those obtained in the laboratory. Although laboratory results are difficult to extrapolate to field conditions, we suggest that enforced dormancy due to prevailing low ambient temperatures in the páramo restrict germination of *E. timotensis* seeds. Similar results have been obtained in arctic (Bell & Bliss 1980), alpine (Marchand & Roach 1980), and cool-climate populations from widely distributed temperate species (McNaughton 1966) and could be interpreted as a mechanism to "avoid" low temperatures that might lead to seedling mortality (see Angevine & Chabot 1979).

Our results of higher germination in the light, along with dark germination favored at warmer temperatures, were also reported in *E. schultzii* by Pannier (1969), who suggested the action of a photosensitive mechanism for this pattern. This author also showed that repeated drying and wetting cycles enhanced germination values. Although this treatment was not applied in *E. timotensis* seeds, germination values comparable to those obtained by Pannier (1969) have been found in *E. schultzii* without any treatment other than watering (M. R. Guariguata, pers. obs.). The lower germination times and the higher per-

centages within a broader temperature range found for *E. timotensis* seeds in the light suggests that germination is likely to be favored near the soil surface.

In summary, *E. timotensis* seed bank dynamics follows a "persistent" strategy, possibly as an adaptive response to a recruitment rate limited by extreme environmental conditions in the páramo habitat. How this pattern is maintained by the partial contribution of germination requirements of different genotypes, maternal effects during seed maturation, or dormancy enforced by low temperatures is unknown. Further studies on the seed biology in

high tropical mountain species are needed to better understand their regenerative processes in this environment.

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## LITERATURE CITED

- ANDERSON, P. D. 1983. The dynamics and seed longevity of *Viola fimbriatula* seeds in the soil. Ph.D. Dissertation, Harvard University, Cambridge, Massachusetts.
- ANGEVINE, M., AND B. F. CHABOT. 1979. Seed germination syndromes in higher plants. In O. T. Solbrig, S. Jain, G. B. Johnson, and P. H. Raven (Eds.). Topics in plant population biology, pp. 188-206. Columbia University Press, New York.
- BELL, K. L., AND L. C. BLISS. 1980. Plant reproduction in a high arctic environment. *Arct. Alp. Res.* 12: 1-10.
- BERRY, P. E., AND R. CALVO. 1986. An overview of the reproductive biology of the Espeletiinae (Asteraceae) in the Venezuelan Andes. In P. W. Rundel and R. Meinzer (Eds.). Tropical Alpine environments: plant form and function, Springer-Verlag, Berlin. In press.
- COE, M. J. 1967. The ecology of the Alpine zone of Mount Kenya. Dr. W. Junk Publishers, The Hague.
- GOLDSTEIN, G., F. MEINZER, AND M. MONASTERIO. 1984. The role of capacitance in the water balance of Andean giant rosette species. *Plant Cell Environ.* 7: 179-186.
- , ———, AND ———. 1985. Physiological and mechanical factors in relation to size-dependent mortality in an Andean giant rosette species. *Oecol. Plant.* 6: 263-275.
- GRIME, J. P. 1979. Plant strategies and vegetation processes. John Wiley, London.
- HEDBERG, O. 1964. Features of Afro-Alpine plant ecology. *Acta Phytogeogr. Suec.* 49: 1-144.
- MALAGÓN, D. 1982. Evolucion de los suelos en el paramo andino. CIDIAT, Merida, Venezuela.
- MARCHAND, P. J., AND D. A. ROACH. 1980. Reproductive strategies of pioneering Alpine species: seed production, dispersal and germination. *Arct. Alp. Res.* 12: 137-146.
- MCNAUGHTON, S. J. 1966. Ecotype function in the *Typha* community type. *Ecol. Monogr.* 36: 297-325.
- MONASTERIO, M. 1980. Las formaciones vegetales de los paramos de Venezuela. In M. Monasterio (Ed.). Estudios ecologicos en los paramos andinos, pp. 93-158. Universidad de Los Andes, Merida, Venezuela.
- . 1983. Adaptacion de especies al tropico frio: el caso *Espeletia* en el paramo desertico. Tesis de Ascenso, Universidad de Los Andes, Merida, Venezuela.
- , AND S. REYES. 1980. Diversidad ambiental y variación de la vegetacion en los paramos de los Andes venezolanos. In M. Monasterio (Ed.). Estudios ecologicos en los paramos andinos, pp. 47-91. Universidad de Los Andes, Merida, Venezuela.
- PANNIER, F. 1969. Untersuchungen zur Keimung und Kultur von *Espeletia*, eines endemischen Megaphyten der alpinen zone (Paramos) der Venezolanischen-Kolumbianischen Anden. *Ber. Dtsch. Bot. Ges.* 82: 559-571.
- RADA, F., G. GOLDSTEIN, A. AZOCAR, AND F. MEINZER. 1985. Freezing avoidance in Andean giant rosette plants. *Plant Cell Environ.* 8: 501-507.
- RATHCKE, B., AND E. P. LACEY. 1985. Phenological patterns of terrestrial plants. *Annu. Rev. Ecol. Syst.* 16: 179-214.
- ROBERTS, H. A., AND P. M. FEAST. 1973. Emergence and longevity of seeds of annual weeds in cultivated and undisturbed soils. *J. Appl. Ecol.* 10: 133-143.
- SARUKHAN, J. 1974. Studies on plant demography: *Ranunculus repens*, *R. bulbosus* and *R. acris*. II. Reproductive strategies and seed population dynamics. *J. Ecol.* 62: 151-177.
- SCHUBERT, C. 1980. Aspectos geologicos de los Andes venezolanos: historia, breve sintesis, el Cuaternario y bibliografía. In M. Monasterio (Ed.). Estudios ecologicos en los paramos andinos, pp. 29-46. Universidad de Los Andes, Merida, Venezuela.
- SMITH, A. P. 1975. Altitudinal seed ecotypes in the Venezuelan Andes. *Am. Midl. Nat.* 94: 247-250.
- . 1980. The paradox of plant height in an Andean giant rosette species. *J. Ecol.* 68: 63-73.
- . 1981. Growth and population dynamics of *Espeletia* (Compositae) in the Venezuelan Andes. *Smithsonian Contributions to Botany*, No. 48. Smithsonian Institution Press, Washington, D.C.
- , AND T. P. YOUNG. 1982. The cost of reproduction in *Senecio keniodendron*, a giant rosette species of Mt. Kenya. *Oecologia (Berl.)* 55: 243-247.
- SOKAL, R., AND F. J. ROHLF. 1981. *Biometry*. W. H. Freeman, San Francisco.

- TROLL, C. 1968. The cordilleras of the tropical Americas: aspects of climate, phytogeographical and agrarian ecology. In C. Troll (Ed.). Geo-ecology of the mountain regions of the tropical Americas, pp. 13-56. Proceedings UNESCO Symposium, Mexico.
- YADAV, A. S., AND R. S. TRIPATHI. 1982. A study on seed population dynamics of three weedy species of *Eupatorium*. Weed Res. 22: 69-76.