

Effects of fire and grazing on *Espeletia hartwegiana* populations

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Abstract. In the bunchgrass páramo of Parque Nacional Natural Los Nevados, Colombia, aspects of population dynamics of the stem rosette *Espeletia hartwegiana* ssp. *centro-andina* were studied in relation to different grazing intensities and regeneration stages after burning. Life tables corresponding to different management situations are presented. A basal growth rate of 8.8 cm per year was determined for adults in undisturbed situations. In burned sites, an increased growth rate was observed, including a fire-induced stimulation factor which is dependent on initial plant height at the time of burning. In burned situations, adult mortality increases with height and is more than twice the natural mortality rate for the tallest individuals. After initial high juvenile mortality, increased seedling survival and higher juvenile growth rate at burnt sites quickly compensate for this loss. In intensively grazed situations, clustering of individuals was observed; this may provide protection against trampling and scraping impact by cattle. Mortality rates are likewise increased.

Resumen. En el páramo de pajonal del Parque Nacional Natural Los Nevados, Colombia, aspectos de la dinámica de poblaciones del frailejón *Espeletia hartwegiana* ssp. *centro-andina* fueron estudiados en relación a diferentes intensidades de pastoreo y etapas de regeneración después de quemadas. Se presentan las tablas demográficas correspondientes a las diferentes situaciones de manejo. Se determinó una tasa basal de crecimiento de 8.8 cm por año en adultos bajo condiciones inalteradas. En sitios quemados se determinaron tasas mayores, debidas a la estimulación causada por la quema. Se estableció una correlación entre este incremento y el tamaño inicial de la planta en el momento de la quema. Se observó también que la mortalidad de adultos aumenta con su altura en situaciones de quema, siendo, para los individuos más altos, más del doble de la tasa de mortalidad natural. Entre los juveniles, la alta mortalidad inicial en sitios de quema se ve rápidamente compensada por el mayor número de plántulas que sobreviven y por el mayor ritmo de crecimiento de los juveniles en estos sitios. Bajo pastoreo intensivo, se observó la ocurrencia de frailejones en grupos, posiblemente como forma de protección contra el impacto del ganado a través del

pisoteo y el raspado. Los índices de mortalidad se ven incrementados en esta situación al igual que lo observado después de una quema.

Introduction

In montane landscapes of Andean páramo, caulescent giant rosettes of *Espeletia* (Asteraceae) and related genera are a characteristic feature. Natural selection favors longevity; in comparison to recently established plants, taller and thus older individuals are more successful in maintaining a favorable water balance in the growing tissues, which increases their chance of survival (Smith, 1981; Monasterio, 1986). The leaf rosette of the adult is situated at a "safe height" above ground level, where fluctuations between day and night temperatures are greatest. On the other hand, the water-storing pith tissues in the center of the stem are protected by dead leaves. Damage from frost is thus reduced by retention of dead leaves on the stem of giant rosettes. Experimental removal of these leaves caused higher mortality during the dry season in *Espeletia schultzii* (Smith, 1979; Goldstein and Meinzer, 1983). Furthermore, the densely packed bases of dead leaves probably serve as a protection against fire.

Little has been reported on the effects of fire and grazing on *Espeletia* populations. In many páramos of the Colombian Andes, the bunchgrass vegetation is purposely burned by local farmers. This management practice serves to stimulate forage regrowth for cattle. In a Venezuelan páramo, Smith (1981) found that as much as 55% of adult *E. schultzii* plants could be killed in a dry season fire.

It was the objective of this study to investigate the impact of grazing and burning practices on the following aspects of the *Espeletia hartwegiana* population dynamics: 1) growth of individuals of different age classes; 2) demographic aspects, such as age-specific mortality rates and survival of juveniles; and 3) population density.

This study attempts to characterize *Espeletia* growth patterns as affected by burning and grazing, in terms of mathematical functions. It was hypothesized that burning and/or grazing causes increased mortality, particularly among adult individuals. Although cows rarely eat from the stem rosettes, their trampling may exert significant influence.

Reproductive patterns of *Espeletia* populations have only been taken into account indirectly. As was demonstrated by Monasterio (1986) for the Venezuelan páramo, a massive seed production occurs at irregular time intervals, but yet sufficiently to replenish the soil seed bank. An important portion of the seeds is also retained on the inflorescence stalks. As long as population density does not decrease dramatically, we assume that availability of viable seeds is not as limiting for regeneration from seedlings as is the availability of space, light, and nutrients. This study forms part of the ECOANDES research program.

Methods

Study area. The study area is part of Parque Nacional Natural Los Nevados on the western flank of the central cordillera of Colombia ($4^{\circ}35\text{--}60'\text{N}$, $75^{\circ}10\text{--}30'\text{W}$). Of the three main páramo belts (Cuatrecasas, 1958, 1968), the study sites fall within the middle belt of the grass páramo. Its dominant vegetation components are bunchgrasses of *Calamagrostis* and *Festuca* and stem rosettes of *Espeletia hartwegiana* ssp. *centro-andina*. Characteristics of the study area are described elsewhere (Verweij and Budde, 1992). Before establishment of Parque Nacional Natural Los Nevados in 1973, harvesting of *Espeletia* plants occurred occasionally on the surrounding farms. Stems were used as a fuel resource for cooking, heating, and as insulation material in the walls of farmers' huts. Extensive collecting might have led to the present scarcity or absence of *E. hartwegiana* in the vicinity of formerly inhabited places.

The selection of sites was based on an initial grazing and burning gradient determined by Verweij and Budde (1992). Ten experimental sites were chosen at elevations of 4000–4150 m. An attempt was made to locate them in places with similar topographic conditions, *i.e.*, moderate slopes. However, in reality, heavily grazed situations where *Espeletia* populations still occur, only existed on flat valley bottoms and the slightly undulating ridge tops of lateral moraines. Furthermore, grazing influence is common at burned sites, especially after recent fires when the vegetation is most attractive to the cattle. Fire age was determined by evaluation of aerial photographs from different dates (10 series from 1955–1989) and through interviews with farmers and park guards. The study sites are characterized in Table 1.

Population structure. Plots of approximately 300 square meters were established so that at least 150 adult stem rosettes per site were covered. An adult was defined as an individual taller than 30 cm. The following parameters were recorded for each adult *Espeletia* encountered: total height from ground level to the highest leaf tip, height of dead leaf column from lower to upper point of attachment of the dead leaves, height of bare stem due to burning, traces of scraping by cattle, and phenological stage, *i.e.*, vegetative or flowering. In juveniles, only height was measured. Furthermore, it was noted whether the stem rosettes occurred in groups, and if so, group size. If distance to nearest neighbor of juveniles was smaller than 5 cm, they were considered to be part of a group, whereas the critical distance for adults was defined as 25 cm.

Growth measurements. Growth of *Espeletia hartwegiana* was determined in three different ways: by measuring annual height increments, by establishing the leaf expansion in one year, and by evaluating height increment

Table 1. Site characteristics for the *Espeletia hartwegiana* populations. Grazing intensity: 1= very low, 2= low, 3= medium, 4= high. Terrain form: GLF= glacial lava fields, LM= lateral moraine, BLF= block lava flow. Total = total number of individuals per site; ad. = number of individuals > 30 cm. Undist.= undisturbed sites

Site	Fire age (years)	Grazing intensity	Aspect	Slope (°)	Terrain form	Tussock cover (%)	Bare soil (%)	Total ad.	juv.
Undist. 1	-	-	SW	30	GLF	55	10	173	379
Undist. 2	-	-	SW	10	GLF	40	15	151	403
Undist. 3	-	1	SW	25	LM	20	5	374	316
Fire 1a	1	-	NW	20	LM	25	45	100	168
Fire 1b	1	-	N	35	LM	20	40	187	192
Fire 2	2	3	S	30	LM	25	40	295	151
Fire 6	6	2	S	30	LM	60	10	269	150
Block lava	15	-	-	0-10	BLF	35	10	271	197
Grazed 1	-	3	SE	35	LM	<5	<5	278	122
Grazed 2	-	4	SE	2	LM	5	5	403	206

of regenerating stem rosette populations after fire events of a known age.

Annual height increment was measured in four different plots corresponding to different management conditions (Undist. 3, Fire 2, Fire 6, and Grazed 1). In each, 30–50 individuals were measured, starting from a place chosen at random. The same parameters were recorded as for the description of population structure. Additionally, dead leaf columns of the plants were marked during the initial survey with a horizontal line of red paint close to the rosette. Height up to this red line was recorded as a fixed reference in order to avoid variation of height due to soil erosion or irregular ground surfaces. These measurements were taken in April 1989 and repeated twice, about 1 and 1.5 years later.

To monitor leaf expansion, the same individuals were followed by marking the leaf tips of both the youngest visible and the oldest living leaves during the initial survey. After one year, the number of newly developed leaves was counted. In addition, total number of leaves present in the rosette was counted.

As a third method, an average growth rate was derived from the regrowth of the dead leaf column of burned stem rosettes where the age of the fire was known.

Growth of juveniles was estimated in a different way in view of the absence of a fixed reference point. In the sites Undist. 1, Fire 1b, and Fire 2, all juveniles were marked in 1989. In 1990, the number of newly unmarked juveniles was recorded. The mean height of the new individuals within one year's time served as an indication of juvenile growth rate.

Mortality rates. Mortality rates of adults were determined in two different ways. First, all dead individuals within the experimental plots were marked during the initial survey. After one year, the number of individuals that had died, and their corresponding height, was recorded. In this way mortality per height class was obtained. In grazed situations, however, fragmentation of dead specimens by trampling of cows made it impossible to measure original height. Besides it was not always clear when an individual had died, and low numbers of dead plants per height class interfered even more with the collection of reliable data using this first method. Therefore, estimates of mortality were based mainly on population structures by combining the decrease in the number of individuals per height class with the measured growth rates.

The survival of juveniles was monitored at the site Fire 1a which had been burnt exactly one year before. From the analysis of the results, it appeared that, for *Espeletia* individuals, 30 cm is the critical height, below which they mostly do not survive a fire. Furthermore, individuals below this height showed more fluctuations in density, due to variations in the rates of recruitment, growth, and mortality. Therefore, the upper limit of 30 cm in the definition of juveniles seems to be justified and they were analyzed separately.

Regression analysis. Due to the fact that populations were not normally distributed, simple analysis of variance was not possible (Sokal and Rohlf, 1981). Thus, an alternative method had to be used in order to compare the size and age distributions of *Espeletia hartwegiana* populations between the different management situations. Different regressions between density and stem rosette height were compared in order to obtain the best fit. The ln-transformation of density per size class showed the best correlation with height. In the same way, for recently burned populations, a correlation between regrowth after fire and the initial height at the time of fire was established. It was tested whether the obtained regression coefficients differed significantly from zero (Sokal and Rohlf, 1981), and at what significance level, in order to determine whether these relationships were different from the undisturbed situation. Subsequently, the mean of annual height increments was taken from the different recently burned plots and in this way a general fire-influenced growth equation was derived.

Demography. For each study site, life tables of numbers of *Espeletia* individuals per height class were filled out, complete with values of height-specific mortality indices (M_x) calculated from the population structures. Tables produced by this method are known as static or vertical life tables. Dynamic or horizontal life tables, in which a cohort of seedlings is followed taking censuses at intervals, are less subject to error (Silvertown, 1987). Obviously it would be rather impractical in the case of long-lived plants like *Espeletia* to make a census throughout their lifetime. The assumption of a

constant yearly input of seedlings to the zero-age class, however, enables the treatment of a static life table as though it was a dynamic one. For this purpose an average delay time per height class was calculated for all populations using the obtained growth equations. Subsequently, height-specific mortality was divided by delay time to obtain mortality rates (per time unit). A dynamic life table representative for each management situation was calculated. Based on these theoretical mortality figures and starting from the same number of individuals in the initial adult height class, a theoretical population structure was calculated. These values were compared with data from the field in order to validate the described model.

Results and discussion

Growth. According to annual height increment measurements in undisturbed situations, a growth rate of 8.8 ± 3.5 cm per year (mean \pm s.e., $n = 80$) was recorded for all individuals over 30 cm regardless of their age. Annual height increments of giant rosette species that have been reported are within a range of 1–5 cm (Hedberg, 1969; Smith, 1981; Monasterio, 1986; Smith and Young, 1987; Monasterio and Lamotte, 1989). The high figures obtained in this study, compared to similar ecosystems, are not yet fully understood. A possible explanation could be the input of extra nutrients originating from volcanic ash products of the frequent eruptions of the Ruiz-Tolima mountain chain.

Growth rates of burned individuals varied considerably. In contrast to the undisturbed situation, the growth rate, as based on regrowth measurements, related linearly to the initial stem height at the time of fire. Regressions are plotted in Figure 1. A weighted annual average of regrowth of burned *Espeletia* individuals in the five study sites was derived. The mean (r_{xy}) is 0.050 ± 0.0095 and the mean (c) is 7.3 ± 1.2 ($n = 5$), which leads to the following growth equation for burned individuals:

$$Y_{an} = 0.05 X_f + 7.3 \quad (1)$$

where Y_{an} = annual regrowth (cm) and X_f = stem height at time of fire (cm).

Height of burned *Espeletia* individuals is then given by:

$$X_t = (1 + 0.05 \times t) \times X_f + 7.3 \times t \quad (2)$$

where t = time after burning in y.

From equations (1) and (2), the general equation of height growth after fire can be derived:

$$dx/dt = [0.05 \times X_t / (1 + 0.05 \times t)] + [7.3 / (1 + 0.05 \times t)] \quad (3)$$

The constant term of 7.3 cm annual regrowth of equation (1) does not vary significantly from the determined natural growth rate of 8.8 cm per year. This implies that *Espeletia* growth is stimulated by fire with a certain increment on top of the natural growth rate, represented by the first term of equation (1).

Survival and growth of juveniles. In the recently burned situations in Fire 1a and Fire 1b, a growth rate of 26 and 25 cm per year, respectively, was determined for juveniles established after the fire. In Fire 2, the growth rate of newly recruited juveniles was 20 cm per year and in Undist. 1 a rate of 9 cm per year was found. Standard errors in these estimates are high, but do not indicate the real variation of the growth rates, as many juveniles have been recruited within less than one year's time. Juvenile growth or germination appears to be stimulated immediately after burning. This effect decreases with time since fire, until the growth of juveniles stabilizes at a similar rate to that of adults in undisturbed situations. Smith (1981) found a juvenile growth of 0.3–2.0 cm per year in a natural situation which also corresponds to adult growth rates.

Not only do juvenile growth rates vary considerably in the different management situations, but the same holds for the number of juveniles surviving. Juvenile density immediately after fire is low; one year after

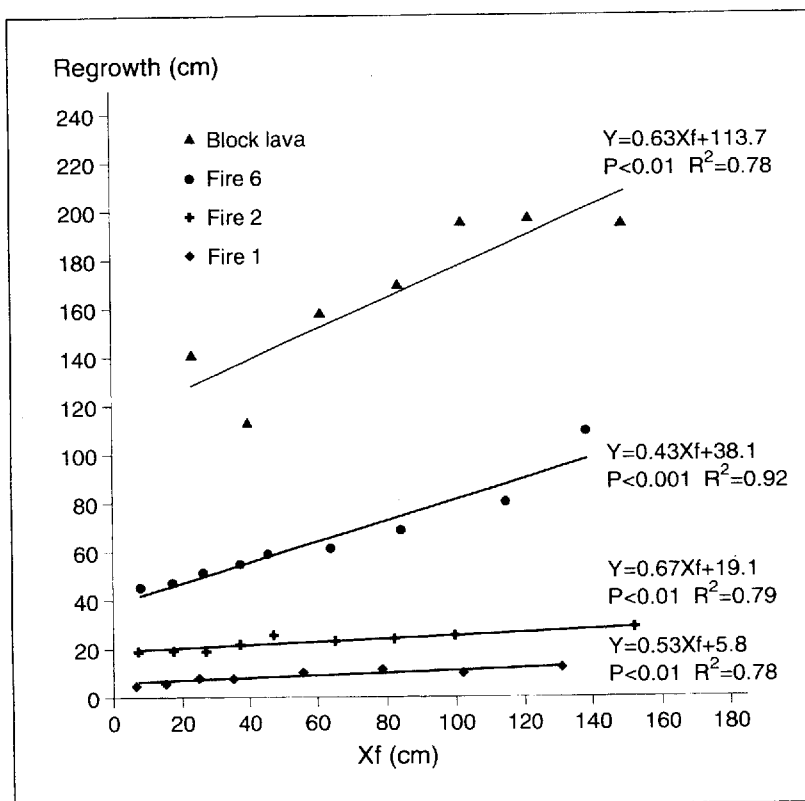


Figure 1. Regression lines of regeneration height (y , in cm) of *Espeletia hartwegiana* as a function of their stem height at the time of burning (X_f). $Y = r_{xy} \times X_f + c$. The significance level at which r_{xy} is different from zero is indicated by probability P .

fire, 27 and 75 individuals per 100 square meters were recorded in comparison to 151 newly recruited juveniles in the undisturbed situation. In the Fire 2 site, a number of 4.5 individuals per 100 square meters was found reflecting a possible trampling impact. However, juvenile densities are rather variable here related to local micro-climate and -relief.

Leaf production. The mean number of leaves produced per year is 118 ± 28 (mean \pm s.e., $n = 80$), showing a high variation. An increase of both number of leaves present and leaf production with stem height was observed. The average number of leaves per rosette is 70 and the mean rosette turnover time 0.59 ± 0.07 years ($n = 80$). Monasterio (1986) found higher turnover periods of 1–2 years for different *Espeletia* species. The only species known from the literature with a similar rapid rosette turnover of 0.56 years is *E. schultzei* at 3600 m (Smith, 1981). Effects of fire and grazing on leaf production were not investigated.

Population parameters. Concerning reproduction, none of the individuals defined as juveniles was observed in flower. Nor did adult individuals to a height of 90 cm flower in undisturbed or grazed situations. In the case of recently burned plots, however, this height class had entered the reproductive phase. The percentage of flowering individuals in the other height classes was $4.3 \pm 2.0\%$ ($n = 8$, height classes of 40 cm) in undisturbed and grazed situations. Until two years after fire, an increase (35–64%) of the flowering percentage was noted. Even two flowering cycles instead of one per year, were recognized. Nevertheless, among different sites and within one population, the reproductive pattern could vary considerably, which agrees with reports by Smith (1981), Monasterio and Lamotte (1989), and Sobrevila (1989) for the Venezuelan páramo.

In Figure 2, plant size distributions from undisturbed and burned sites are compared. In Table 2, some population parameters are presented for all study sites. The observed decrease of individuals as a function of height (Fig. 2) was analyzed by means of regressions. This height-dependent mortality proved to be constant over all height classes with high coefficients of regression ($R^2 > 0.9$). In order to be able to compare the mortality rate for the different management situations, the varying growth rates have to be taken into account.

Mean adult height is smaller (96–104 cm) in recently burned situations, compared to undisturbed conditions (153 cm). The presence of big rocks in the irregular terrain of the block lava, which was burned 15 years before, explains the lower adult density in comparison to other sites. On the other hand, they provide a shelter and thus a better chance of survival for the adults. This is expressed in a lower mortality per height class resulting in a higher average height (190 cm).

The burned plots are characterized by a lower adult and juvenile density (Table 2). In the most intensively grazed plot, adult density is

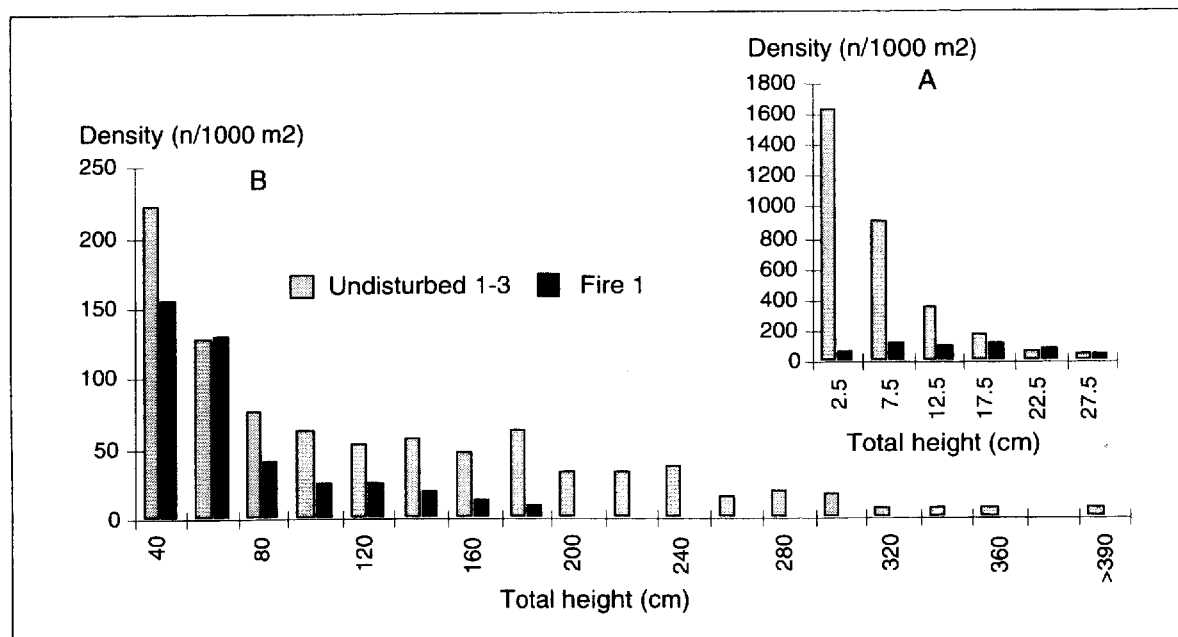


Figure 2. Plant size distribution of *Espeletia hartwegiana* populations in burned and undisturbed situations. A. Juveniles (0–30 cm). B. Adults (over 30 cm).

higher, although the height of most of the individuals is below 100 cm. The highest mortality per height interval was found here, reflecting a high grazing pressure upon the population. It appeared that *Espeletia* exhibits a special survival strategy. High percentages of both adults and juveniles (75 and 96%, respectively) occur in groups. This phenomenon of clustering of individuals may be a product of trampling impact at the same time as it provides a certain protection against it. Those individuals standing in the middle of a group are expected to be less subject to scraping and trampling, which is especially important for juveniles. A similar tendency, although less pronounced, can be observed under low intensity grazing. Smith (1981) demonstrated a positive correlation between climatic stress in the form of seasonality and decreasing nearest neighbor distance. This confirms our observations of a clustered distribution of stem rosettes under unfavorable conditions.

Table 2 shows a remarkable clustering effect of juveniles in recently burned situations, mainly around adults. This might be explained by two different mechanisms. First, the higher amount of bare soil available, due to the absence of bunchgrass cover, is important for rapid colonization close to the parent individual. Second, the possible presence of higher

Table 2. Main characteristics of *Espeletia hartwegiana* populations in different management situations. X = total height; M_x = average height dependent mortality per size classes of adult and juvenile individuals, mean \pm s.e.; Age of maximum = age of the tallest individual measured; ad. = adult, i.e., individual > 30 cm high; juv. = juvenile, i.e. individual < 30 cm high.

Site	Density (n/100 m ²)		Mean X (cm)		Occurring in group (%)		Mx (%) (per 20cm) (per 5cm)		Age of maximum (cm) (years)	
	ad.	juv.	ad.	juv.	ad.	juv.	ad.	juv.	max X	age
Undist.	91	323	153.7	11.1	25.3 \pm 2.9	39.0 \pm 9.9	440	51.5		
Fire 1	44	59	100.8	8.9	28.1 \pm 8.6	30.7 \pm 5.6	220	19.4		
Fire 2	39	44	95.8	11.4	31.2 \pm 8.8	48.3 \pm 9.2	260	20.9		
Fire 6	49	43	103.9	6.6	28.1 \pm 8.8	33.3 \pm 5.6	310	24.6		
Bl. 1.	30	56	190.1	16.4	9.4 \pm 0.8	36.3 \pm 9.1	465	43.2		
Grazed 1	81	44	156.3	25.6	13.1 \pm 2.0	31.2 \pm 4.1	325	40.2		
Grazed 2	158	172	78.4	74.8	41.9 \pm 9.8	0	225	23.9		

nutrient concentrations immediately around the stem of *Espeletia* individuals, which was demonstrated by Garay *et al.* (1983), may favor the observed clustering. Trampling is supposed not to play a role in determining the clustered distribution, as the recently burnt plots are not grazed.

The number of dead individuals per height class encountered in the plots divided by the number of living individuals could be used as a validation for the mortality rates derived from population structures. A constant mortality rate of $13.0 \pm 2.8\%$ ($n = 10$) of adult individuals within each 20 cm height class was determined for the unburned plots, and for the burned plots a range of 7.6–25% was found. The higher rates corresponded to taller individuals.

Table 2 finally demonstrates that the maximum age that can be reached varies considerably between the different populations. In stable populations, this maximum age can be considered a maximum turnover time. The tallest individuals in the undisturbed plots reach an estimated age of more than 50 years, whereas the maximum turnover in recently burned plots is diminished by more than half.

Demography. A dynamic life table, representative for each management situation, is given in Table 3. The values of these theoretical population structures are compared with data from the field. As demonstrated, a reasonable fit of predicted values with the real values is obtained. The conclusion can be drawn that the recently burned sites (Fire 1–6) are characterized by higher mortality rates as compared to the undisturbed plots. Mortality

ESPELETIA POPULATION	NATURAL CONDITIONS			
	constant growth rate constant mortality			
	FIRE		AND/OR GRAZING	
	adults	juveniles	adults	juveniles
Growth rate	stimulated (height dependent)	stimulated	unaffected (?)	?
mortality rate	stimulated (height dependent)	initially high	increased (constant)	increased by trampling
density	decrease	strong decrease	Increase <100 cm decrease \geq 100 cm	slight decrease
average height	unaffected (?)	—	decrease	—
clustered distribution	absent	around adult stems	present	almost exclusively

Figure 3. Schematic representation of the general effects of fire and grazing on *Espeletia hartwegiana* populations.

Table 3. Dynamic life table of *Espeletia hartwegiana* in different management situations. M_x = average height dependent mortality per size classes of adult individuals; delay = time required for an individual to pass from one height class to the next; n/area = number of individuals per area of ground surface; M(p) = predicted annual mortality in % per year per height class, based on M_x and delay time per height class; N(p) = predicted n per 100 square meters per height class; N(r) = observed n per 100 square meters per height class.

Site	Undisturbed	Grazed 1	Grazed 2	Block lava	Fire 6	Fire 2	Fire 1
M_x (%)	15.3	13.1	41.9	9.4	28.1	31.2	28.1
delay (y)	2.3	2.3	2.0				
n/area	91/100 m ²	81/100 m ²	158/100 m ²	300/1000 m ²	49/100 m ²	39/100 m ²	44/100 m ²

Class	M(p)	N(p)	N(r)	M(p)	N(p)	N(r)	M(p)	N(p)	N(r)	M(p)	N(p)	N(r)	M(p)	N(p)	N(r)
31-50	11.1	21	21	5.8	9	9	4.1	40	40	12.4	9	9	13.2	10	10
51-70	11.1	16	12	5.8	8	9	4.1	36	32	12.4	8	7	14.6	7	9
71-90	11.1	12	7	5.8	7	8	4.1	33	18	12.2	7	6	16.0	5	4
91-110	11.1	9	6	5.8	6	5	4.1	30	19	13.3	6	5	17.4	3	4
111-130	11.1	7	5	5.8	5	5	4.1	27	19	14.4	5	4	18.9	2	3
131-150	11.1	5	5	5.8	4	6	3.9	24	19	15.5	5	5	20.3	2	3
151-170	11.1	4	5	5.8	4	6	4.1	22	17	16.5	4	3	21.7	1	2
171-190	11.1	3	6	5.8	3	5	4.4	20	17	17.6	3	2	23.1	1	1
191-210	11.1	2	3	5.8	3	5	4.7	18	19	18.7	3	4	24.5	1	1
211-230	11.1	2	3	5.8	3	5	4.9	16	12	19.8	2	2	26.0	1	1
231-250	11.1	1	3	5.8	2	5	5.2	15	13	20.9	2	1			
251-270	11.1	1	2	5.8	2	4	5.5	13	14	21.9	1	1			
271-290	11.1	1	2	5.8	2	3	5.7	12	15						
291-310	11.1	1	2	5.8	1	3	6.0	11	10						
311-330	11.1	0	1	5.8	1	2	6.3	10	8						
331-350	11.1	0	1	5.8	1	1	6.5	9	8						
351-370	11.1	0	1				6.8	8	7						
371-390	11.1	0	1				7.1	7	6						
>390	11.1	0	1				7.4	7	5						

increases with stem rosette height. This effect is compensated for by increased growth rates of the taller individuals in such a way that the height-dependent mortality (M_x) remains constant throughout the life span of the *Espeletia* plants.

Mortality patterns in the block lava site, with a fire age of 15 years, and the site of low intensity grazing are in the same order of magnitude as the undisturbed situation. In Grazed 2, a constant mortality rate of 21% per height class of 20 cm was determined; this is comparable to that of the tallest recently burned individuals and almost twice the natural mortality rate. In Figure 3, a schematic representation of the main effects of grazing and burning is given.

Conclusion

The fact that stem rosettes are not consumed, except occasionally the inflorescences, is apparently not a guarantee for their survival. Grazing by cattle has a major impact upon adult mortality of *Espeletia hartwegiana*. Clustering of individuals is a result of trampling impact and provides at the same time protection against trampling and scraping by cows. The main impacts of fire on *Espeletia* population dynamics can be summarized as follows: most juveniles (*i.e.*, over 80%) are killed immediately after a fire, though this height class is quickly replaced by individuals benefitting from the extra amount of space, light, and nutrients available, whereas adults have a higher risk of being killed because of fire damage. Silvertown (1983) mentioned the possible occurrence of peaks in age structures by the truncation of certain age classes. In this case, truncation of older age classes due to fire indeed does occur, whereas truncation of the younger age classes is partly compensated for by a more rapid replacement. On the lateral moraines, where a fire frequency of once every 5–10 years is common, stem rosette populations are able to survive in spite of a significant decrease of their average height and the higher adult mortality mentioned above. The increased growth rates and lower maximum turnover period are an effective response to the fire regime. These mechanisms are clearly different from the ones Silvertown (1983) listed; populations may be cushioned from local disturbances by immigration of plants from unaffected areas or by changes in fecundity or mortality in the population itself. Apparently, *E. hartwegiana* possesses certain unique fire adaptive traits which enlarge the capacity of populations to survive. But the limits to the stress that can be endured, especially in the case of combined burning and high intensity grazing, need further investigation.

Acknowledgments

We are grateful to A. M. Cleef, W. van Wijngaarden, and M. Oneka for useful comments to the manuscript and to M. de Zuviría for corrections of

the Spanish abstract. Further, we thank the Colombian institutes INDERENA and IGAC for their cooperation. The help from P. Budde during the measurements in the initial survey is gratefully acknowledged.

Literature cited

- Cuatrecasas, J. (1958). "Aspectos de la vegetación natural de Colombia." *Revista Acad. Colomb. C. Exact.* 10(40), 221-264.
- Cuatrecasas, J. (1968). "Páramo vegetation and its life forms." Pp. 163-186 in Troll, C. (ed.), "Geo-ecology of the mountainous regions of the tropical Americas." *Coll. Geogr.* 9.
- Garay, I., Sarmiento-M., L., and Monasterio, M. (1983). "Le páramo désertique: éléments biogènes, peuplements des microarthropodes et stratégies de survie de la végétation." Pp. 127-134 in Ph. Lebrun, H. André, M., De Medts, A., Grégoire-W., C. and Wauthy, G. (eds.), "Proc. VIII Int. Coll. Soil Zool. Louvain-la-Neuve, August 30-September 2, 1982." *Dieu-Brichart, Ottignies-Louvain-la-Neuve.*
- Goldstein, G. and Meinzer, F. C. (1983). "Influence of insulating dead leaves and lower temperatures on water balance in an Andean giant rosette plant." *Plant Cell Environ.* 6, 649-656.
- Hedberg, O. (1969). "Growth rates of the East African giant *Senecios*." *Nature* 22, 163-164.
- Monasterio, M. (1986). "Adaptive strategies of *Espeletia* in the Andean desert páramo." Pp. 49-80 in Vuilleumier, F. and Monasterio, M. (eds.), "High altitude tropical biogeography." *Oxford University Press, Oxford.*
- Monasterio, M. and Lamotte, M. (1989). "Les populations d'*Espeletia timonensis* dans le páramo désertique des Andes du Venezuela." *Rev. Ecol. (Terre Vie)* 44, 201-227.
- Silvertown, J. W. (1987). "Introduction to plant population ecology." 2nd ed. *Longman Scientific and Technical and Harlow and John Wiley & Sons, New York.*
- Smith, A. P. (1979). "The function of dead leaves in *Espeletia schultzii* (Compositae), an Andean giant rosette plant." *Biotropica* 11, 43-47.
- Smith, A. P. (1981). "Growth and population dynamics of *Espeletia* (Compositae) in the Venezuelan Andes." *Smithsonian Contrib. Bot.* 48, 1-45.
- Smith, A. P. and Young, T. P. (1987). "Tropical alpine plant ecology." *Ann. Rev. Ecol. Syst.* 18, 137-158.
- Sobrevila, C. (1989). "Effects of pollen donors on seed formation in *Espeletia schultzii* (Compositae) populations at different altitudes." *Pl. Syst. Evol.* 166, 45-67.
- Sokal, R. R. and Rohlf, F. J. (1981). "Biometry." 2nd ed. *W. H. Freeman and Company, New York.*

Verweij, P. A. and Budde, P. (1992). "Burning and grazing gradients in páramo vegetation: Initial ordination analyses." Pp. 177–195 in Balslev, H. and Luteyn, J. L. (eds.), "Páramo: An Andean ecosystem under human influence." *Academic Press, London*.