

Citar como:

Sarmiento, L. 2006. Grazing impact on vegetation structure and plant species richness in an old-field succession of the Venezuelan Páramos. In: Spehn, E., Liberman, M., Körner, C. (Eds): Land use changes and Mountain Biodiversity. CRC Press LLC, Boca Raton FL, USA. pp. 119-135.

9 Grazing Impact on Vegetation Structure and Plant Species Richness in an Old-Field Succession of the Venezuelan Páramos

Lina Sarmiento

INTRODUCTION

Páramos occupy the alpine belt of northern South America, between 3000 and 4800 masl. Giant rosettes of the genera *Espeletia*, together with sclerophilous shrubs and bunch grasses, dominate the vegetation. In pre-Columbian times, the páramo was almost exclusively used for hunting and gathering (Wagner 1978), and only after the arrival of the Spanish, and mainly during the 18th century, did it begin to be extensively grazed by introduced domestic animals, mainly cattle, horses, and mules. Consequently, the páramo evolved until recent times without domestic herbivory. Many plant species, mostly the endemic ones, probably did not develop specific adaptations to this kind of disturbance and are potentially sensitive.

The carrying capacity of the Venezuelan páramos is low. The main offering of forage is concentrated in small marshes and fens situated in the valley bottoms or in areas with poor drainage and dominated by palatable grasses and sedges (Molinillo and Monasterio 1997). The more widespread páramo vegetation, in which dwarf shrubs, rosette plants, and tussock grasses predominate, presents a lower availability of forage (Molinillo and Monasterio 1997). In the wetter páramos of Colombia, where the cover of tussock grasses is higher and more continuous than in Venezuela, the palatability of the vegetation is commonly improved by

burning (Hofstede et al. 1995), but in the drier páramos of Venezuela, where grasses are less abundant, burning is not practiced, and the strategy of the farmers is to develop a closer relationship between agricultural activities and cattle management, complementing the natural sources of forage with crop residues, fodder, and grazing on fallow plots (Molinillo and Monasterio 2002).

To analyze the human impact on páramo vegetation, it is essential to differentiate the Andean and high-Andean ecological belts (Monasterio 1980). In the Andean belt (3000 to 4000 m), night frosts are concentrated during the dry season, allowing crops to develop during the rainy season. In Venezuela, a rapid process of agricultural expansion is taking place in this belt, with potatoes as the main cash crop and livestock husbandry as a complementary activity. The high-Andean belt (above 4000 m), where frosts occur throughout the year, is not suitable for cropping and is only used for extensive grazing. Nevertheless, these two belts are not managed independently, and continuous animal displacements occur between them. Animals used as draft power in agriculture and milking cows are maintained temporally in the Andean belt, where crop residues and fodder are used to complement their diet (Molinillo and Monasterio 1997; Pérez 2000).

Long-fallow agriculture is still practiced in some areas of the Andean belt. This agricultural

system generates a landscape mosaic of areas under cultivation, under natural vegetation and at different stages of the fallow period, which can last from 5 to more than 10 years. Fallow areas are important sources of forage for domestic animals maintained in the agricultural belt (Pérez 2000). Fallow agriculture provides a unique opportunity to analyze the rate and mechanisms of páramo regeneration after agricultural disturbance, an essential knowledge to evaluate the reversibility of human impacts and to design future strategies for páramo restoration and management.

Our general objective is to assess if páramo regeneration after agricultural disturbance is affected by grazing and to evaluate this activity as to whether or not it can be compatible with páramo restoration plans. From the literature, it is well known that herbivory causes a pronounced impact on cover, structure, and diversity of plant communities, affecting the functioning of the ecosystems and the environmental services that they provide (Milchunas et al. 1988; Huntly 1991; Pacala and Crawley 1992; Gough and Grace 1998). Herbivory also affects the rates of succession and can produce divergence in successional pathways (Davidson 1993; Van Oene et al. 1999). Nevertheless, the specific consequences of grazing depend on herbivore density and on the characteristics of each particular system, such as the level of soil fertility, the importance of competition for light as a driving successional force, and the sensitivity and adaptive mechanisms of the dominant and subordinate species. As the vegetation response to grazing depends on so many different factors, it is necessary to perform specific studies in each ecosystem to design particular management strategies to preserve ecosystem biodiversity and functioning.

In the páramos, some studies were carried out on the effect of grazing on vegetation, but most of them were based on comparing vegetation relevés between sites with different grazing intensities. Few data come from experimental exclusions, except the unrepliated 1-year experiment of Molinillo and Monasterio (1997). Moreover, in most of the studies, it is not possible to differentiate the impact of grazing from that of burning. We

did not find specific studies on the effect of grazing on páramo regeneration after agricultural disturbance.

The objective of this study is to assess the impact of grazing on páramo secondary succession, including the effect on (1) general ecosystem attributes such as plant biomass, height, and percentage of bare soil, (2) the life-form spectrum of vegetation, (3) plant species richness, (4) individual plant species, including identification of the more susceptible and tolerant ones in different stages of the succession, and (5) the probability of invasion by introduced species more adapted to this kind of disturbance. With these aims, an enclosure experiment was conducted over a period of 4 years in plots at two different stages of páramo succession.

METHODOLOGY

STUDY AREA

The study was carried out in the Páramo de Gavidia, located in the northern Andes in Venezuela, at 8°40 latitude N and 70°55 longitude W. The area lies within the Sierra Nevada de Mérida National Park, at 3400 masl and is a narrow glacial valley, with well-drained inceptisols (*Ustic Humitropept*) of a sandy-loam texture, low pH (4.25 to 5.5), and high content of organic matter (up to 20%) (Abadin et al. 2002). Agriculture is practiced on steep slopes and also on small colluvial and alluvial deposits in the valley bottom. The precipitation regime is unimodal, with the dry season between December and March. The mean temperature ranges between 9 and 5°C, depending on the altitude, and the mean annual precipitation is 1300 mm.

A present population of 400 inhabitants established the settlement at the end of the 19th century, giving the valley a relatively short land use history (Smith 1995). The land-use system is long-fallow agriculture. Potatoes are grown during an agricultural phase lasting from 1 to 3 years. The agricultural practices include the incorporation of the successional vegetation as a green manure and mineral fertilization with an average dose of 300 kg N ha⁻¹ a⁻¹. After cultivation, the fields are abandoned, and the fallow period begins. The current average fal-

low length is 4.6 years, but there is a large variability, with times ranging from 2 to more than 15 years (Sarmiento et al. 2002). During the fallow period, fields are used for extensive grazing, mainly by cattle and horses.

VEGETATION DYNAMICS DURING OLD-FIELD SUCCESSION: MAIN TRENDS

A previous study on plant succession, carried out by Sarmiento et al. (2003), indicated that, as in other extreme environments, succession in the páramo proceeds as an *autosuccession*; the characteristic species of the mature ecosystem colonize very early and succession takes place more by changes in the abundance of these species than by a true replacement. Only a few herbaceous, mostly introduced species (e.g. *Rumex acetosella*) act as strict pioneers and strongly dominate the early stages. Then they undergo a progressive decline, whereas native forbs (e.g. *Lupinus meridanus*) and grasses (e.g. *Trisetum irazuense*) have their peaks of abundance at intermediate stages (4 to 5 years). The characteristic páramo life-forms, sclerophilous shrubs (e.g. *Baccharis prunifolia*, *Hypericum laricifolium*) and giant rosettes (e.g. *Espeletia schultzii*), appear very early and gradually increase in abundance, becoming dominant after only 7 to 8 years. Vegetation regeneration takes place relatively fast, but despite a rapid reestablishment of the general physiognomy of the ecosystem, the high diversity of the natural páramo is not reached in the current successional times (Sarmiento et al. 2003).

EXPERIMENTAL DESIGN

Eight areas were selected in different parts of the valley: four had just been abandoned after potato cultivation (early plots), and four had already passed through 5 years of grazed succession (intermediate plots). In each area, an enclosure of 200 m² was established and divided into two parts, each of 100 m² (20 m × 5 m). One of these parts was excluded from grazing, and the other was grazed for 1 h every 3 weeks, equivalent to a stocking rate of 0.4 cows ha⁻¹, considering that a cow grazes 12 h per day. The experiment lasted 4 years, from February 1998 to November 2001, and, in total,

60 different events of grazing were carried out. Controlled grazing was preferred instead of free grazing, to have an identical stocking rate in all the repetitions.

VEGETATION SAMPLING

Twice a year, during the dry and rainy seasons (in March and October), the vegetation was sampled in the grazed and excluded part of each plot, for a total of eight sequential samplings during the 4 years of the experiment (8 sampling dates × 8 plots × 2 treatments = 128 vegetation relevés). The first sampling was carried out just before the start of the experiment. The point intercept method was used (Greig-Smith 1983). Five parallel lines of 20 m length were located at 1-m intervals. Along these lines a pin (diameter, 2.5 mm) was placed vertically every meter, and the contacts of each species in height intervals of 10 cm were recorded.

Using the data obtained from the point intercept method, the biovolume per species, the percentage of bare soil, and the weighted height of the vegetation were calculated. The biovolume was computed as the sum of all the contacts of the species in the 100 points. The average weighted height of the vegetation was calculated by weighing the number of contacts in each 10 cm by the height of the stratum. The percentage of bare soil was calculated from the points that no species touched.

Slope, stoniness, soil texture, and soil total C and N were also measured to characterize the different plots.

ANALYSIS OF THE DATA

Biovolume data can be transformed into biomass using coefficients for each species. The relative abundance of the species is different when data are expressed in one or the other of these units, as the coefficients to transform biovolume to biomass are different for each species, depending on architecture, wood density, specific leaf area, vertical distribution, etc. These coefficients were established for each species from simultaneous measurements of biovolume and biomass in several plots of 2500 cm² (20 plots by species in average), selected to include a large variation in species

abundance. The relationship between biovolume and biomass was linear for all the species, and the regression coefficient was always significant. The best correlation was obtained for *Acaena elongata* ($r^2 = 0.90$, $p < 0.0001$) and the worst for *Poa annua* ($r^2 = 0.50$, $p = 0.049$). The coefficients were obtained forcing the linear regression to the origin. Values oscillate in the range from 39 to 1774 g m⁻², which means that a biovolume of 1 (100 touches in 100 points) corresponds to a biomass of 1774 g m⁻² for the species with the largest coefficient (*Espeletia schultzei*). As biovolume can be higher than 1, this coefficient does not represent a top limit to biomass. For some less-abundant species, coefficients were not available, and we used those of the more similar species in terms of architecture.

A repeated-measures statistical analysis (GLM) was carried out to test the overall significance of the differences and to identify the effect of the different factors. The age of the plot (young and intermediate) was considered as the between-subject factor; treatment (grazed and excluded) and time (eight sampling occasions) were the within-subject factors. Additionally, paired t-tests were used to compare the mean values between the grazed and excluded treatments over the 4 years. For these paired tests, each pair consisted of the mean values of the grazed and ungrazed treatments of the same plot for a given variable. Statistical analyses were carried out using SPSS (version 7.5). Biomass data were log +1 transformed for the statistical tests.

An index of damage by grazing (ID) was calculated for the different species from their relative abundance in the grazed (G) and ungrazed treatments (NG):

$$(NG-G)/G \leq -0.5$$

ID = -2, very positively affected

$$-0.5 < (NG-G)/G < -0.1$$

ID = -1, positively affected

$$-0.1 \leq (NG-G)/G \leq 0.1$$

ID = 0, not affected

$$0.1 < (NG-G)/G < 0.5$$

ID = +1, negatively affected

$$(NG-G)/G \geq 0.5$$

ID = +2, severely affected

RESULTS

PLANT BIOMASS, VEGETATION HEIGHT, AND PERCENTAGE OF BARE SOIL

The effect of grazing on aboveground biomass, vegetation height, and cover is presented in Figure 9.1, and the results of the repeated-measures analysis is shown in Table 9.1. It can be observed that: (1) The total aboveground biomass was significantly lower in the young, compared to the intermediate plots (age effect). (2) Grazing significantly reduced plant biomass (grazing effect). (3) The effect of grazing was similar in the two successional ages (grazing-age interaction). (4) Biomass changed significantly over time (time effect). (5) The effect of time was different in the two successional ages (time-age interaction). (6) In the grazing treatment, biomass increased at a faster rate than in the excluded one (grazing-time interaction). (7) The effect of grazing over time was similar in both successional ages (grazing-time-age interaction). On the average in the 4 years of the experiment, aboveground biomass was 338 g m⁻² and 585 g m⁻² in the grazed and ungrazed young plots, and 606 g m⁻² and 878 g m⁻² in the grazed and ungrazed intermediate plots, respectively (Table 9.2). The final biomass in the grazed young plots was higher than the initial biomass in the intermediate plots, indicating that the stocking rate in our experiment was probably lower than that existing before the enclosures were made.

Another clear consequence of grazing was the significant reduction in the weighed height of the vegetation. For this variable, no significant differences were detected between young and intermediate plots (Table 9.1). In the grazed young plots, the vegetation remained very low during the 4 years of the experiment (weighed average = 8.8 cm) compared to the ungrazed plots in which the weighed height increased from 7 to 20 cm. In the intermediate plots, the height increased in both treatments but more in the ungrazed one, passing from 8.5 to 15 cm under grazing and to 19 cm under ungrazed conditions.

The percentage of bare soil was also very sensitive to grazing. At the beginning of the experiment, 57% of the surface was uncovered

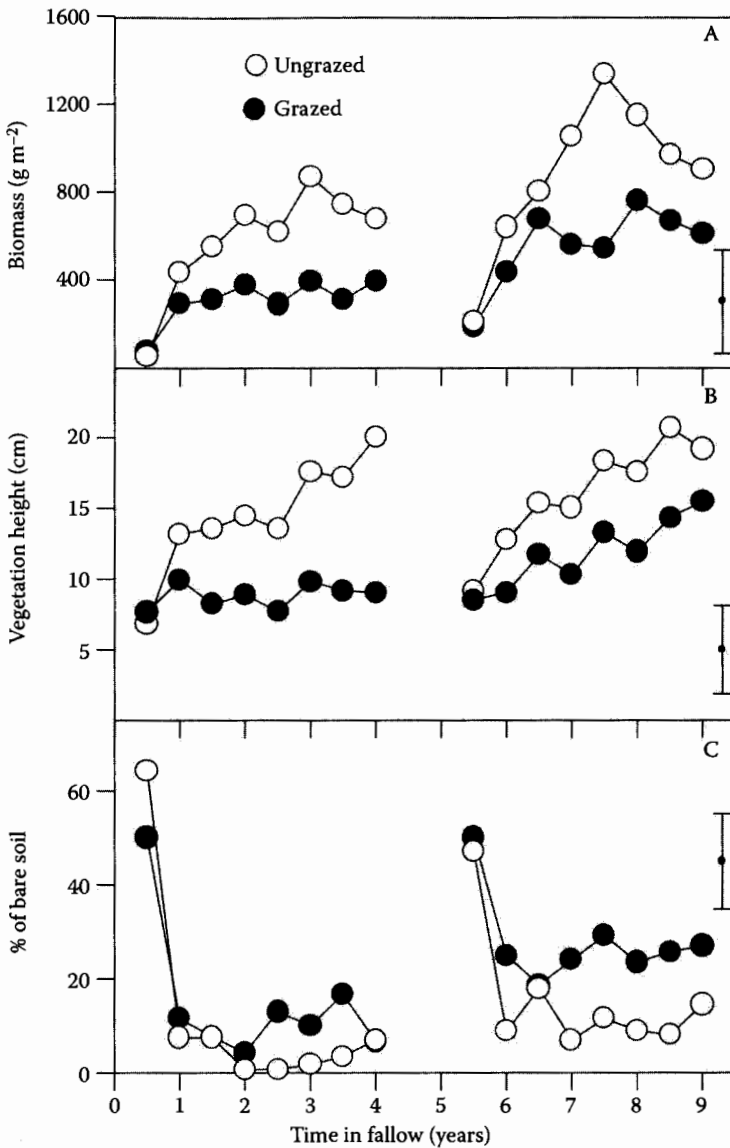


FIGURE 9.1 (A) Aboveground biomass, (B) weighted height of the vegetation, and (C) percentage of bare soil in the excluded and grazed treatments. The bars of error represent the average standard deviation.

in the young plots and 49% in the intermediate plots (Figure 9.1). After 6 months, the percentages of bare soil decreased in all cases but remained higher in the grazed treatment. On average, the percentages of bare soil were 4 and 10 in the ungrazed and grazed young plots, and 11 and 25 in the intermediate ungrazed and grazed plots, respectively. Differences between grazed and ungrazed treatments were significant but not between young and intermediate plots. However, a very significant interaction

was found between grazing and time, indicating that the reduction in the percentage of bare soil occurred faster in the ungrazed treatment for both ages. The high percentage of bare soil at the beginning of the experiment in the young plots is due to their recent abandonment after harvest. In the case of the intermediate plots, the high percentage of bare soil at the first sampling date indicates, again, a possible higher grazing pressure before the installation of the experiment.

TABLE 9.1

Effects of age (young vs. intermediate plots), grazing (treatments), and time (consecutive sampling dates during 4 years) on several vegetation parameters using a repeated-measures analysis

Source Parameter	df	Age	Grazing	Grazing × Age	Time	Time × Age	Grazing × Time	Grazing × Time × Age
		1	1	1	7	7	7	7
Biomass	F	5.95*	49.29**	0.47	14.46**	2.18*	4.93**	1.47
	P			ns				ns
Height	F	2.91	33.96**	1.61	9.03**	1.12	6.05**	1.94
	P	ns		ns		ns		ns
Percentage of bare soil	F	5.17	32.65**	0.17	13.42**	2.30*	6.20**	1.44
	P	ns		ns				ns
Percentage forbs	F	28.75*	0.05	3.45	6.35**	2.03	2.26*	1.69
	P		ns	ns		ns		ns
Percentage grasses	F	0.40	0.98	3.35	1.53	1.84	5.24**	1.34
	P	ns	ns	ns	ns	ns		ns
Percentage shrubs	F	11.91*	0.36	0.00	17.73**	14.09**	1.05	0.38
	P		ns	ns			ns	ns
Percentage rosettes	F	24.23*	0.05	0.03	2.61*	0.22	1.59	1.97
	P		ns	ns		ns	ns	ns
Species richness	F	5.12*	21.03**	3.43	14.97**	4.55**	2.88*	0.51
	P			ns				ns

*Significant at $p < .05$.

**Significant at $p < .001$.

TABLE 9.2

Total aboveground biomass and its distribution among the different life-forms in the ungrazed (NG) and grazed (G) treatments

	1–4 years		5–8 years	
	NG g m ⁻² (%)	G g m ⁻² (%)	NG g m ⁻² (%)	G g m ⁻² (%)
Total aboveground	585 ^a (100)	338 ^b (100)	878 ^c (100)	606 ^a (100)
Forbs	370 ^a (63 ^a)	206 ^b (61 ^a)	87 ^c (10 ^b)	62 ^d (10 ^b)
Grasses	123 ^a (21 ^a)	70 ^b (21 ^a)	119 ^a (14 ^a)	50 ^b (8 ^b)
Shrubs	82 ^a (14 ^a)	48 ^b (14 ^a)	358 ^c (41 ^b)	204 ^d (34 ^b)
Giant rosettes	9 ^a (2 ^a)	15 ^a (4 ^a)	314 ^b (36 ^b)	291 ^b (48 ^c)

Note: Values are the average over the 4 years of the experiment, excluding the first sampling.

^{a-d} Different letters indicate significant differences between treatments ($p < 0.05$; t-test for dependent samples).

LIFE-FORM SPECTRUM OF THE VEGETATION

The relative contribution of the main life-forms (forbs, grasses, giant rosettes, and shrubs) to the total aboveground biomass is shown in Figure 9.2. In Table 9.1, the results of the repeated-measures analysis are shown and in Table 9.2, the mean values over the study period. The relative contribution of forbs to the total aboveground biomass experienced a clear and significant decrease over time, whereas shrubs and rosettes increased. No significant temporal trends were detected using the repeated-measures analysis in the percentage of grasses (age and time effects not significant).

Despite the reduction in total biomass by grazing, the repeated-measures analysis shows that the effect of grazing on the life-form spectrum was not significant, indicating a proportional reduction in the biomass of the four life-forms. Nevertheless, for forbs and grasses, there is an interaction between grazing and time (Table 9.1). The comparison of the mean values over time (Table 9.2), using a t-test for depen-

dent samples, shows that grazing did not change the perceptual contribution of the different life-forms in the young plots. However, in the intermediate plots, grazing caused a significant reduction in the percentage of grasses (from 14 to 8% of total aboveground biomass) and an increase in giant rosettes (from 36 to 48%).

It is rather surprising that grasses and forbs, the main targets of herbivory, do not experience a more important proportional decrease in biomass. An explanation will arise from the analysis of the response of the individual species.

PLANT SPECIES RICHNESS

The method used to quantify plant species richness (100 points in 100 m⁻²) underestimates the total number of species in the plot, as curves of numbers of species do not saturate after 100 points (results not shown). Consequently, values have to be interpreted only comparatively. The maximum number of species recorded in a particular plot was 23, which is low compared to the almost 200 species reported for the whole valley.

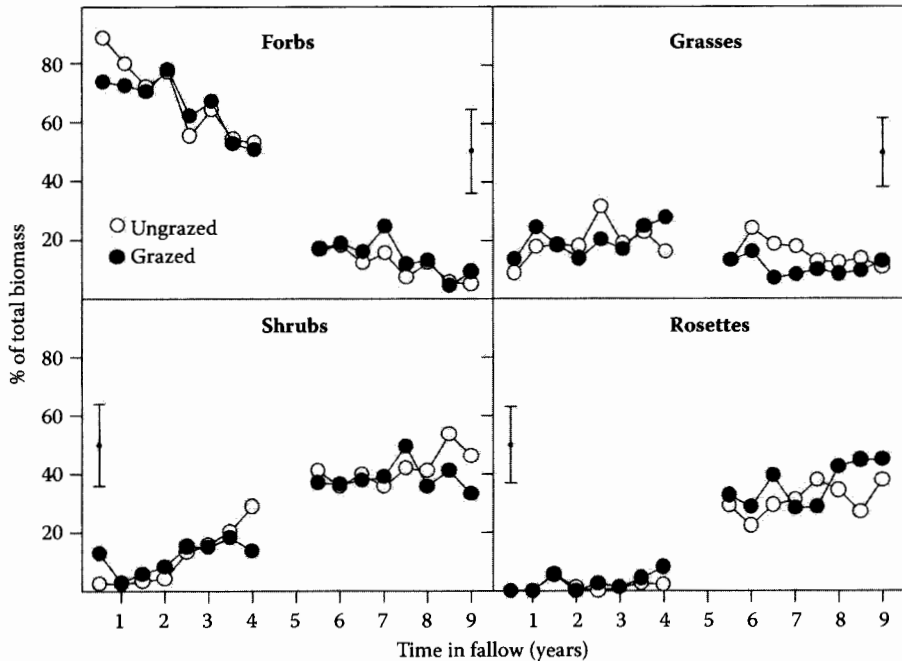


FIGURE 9.2 Percentage of the total aboveground biomass represented by the different life-forms in the excluded and grazed treatments. The bars of error represent the average standard deviation.

There is a significant effect of age and time on plant species richness (Figure 9.3 and Table 9.1), indicating that diversity increases during succession. The rate of increase was significantly higher in the young compared to the intermediate plots. In the intermediate plots, the most important change in the number of species was between the first and the second samplings, when the number of species increased from an average of 8 to an average of 16 as a consequence of fencing out the plots.

Grazing produced a statistically significant but slight reduction in plant species richness (Table 9.1), but it is remarkable that richness did not differ at the last sampling date, suggesting that the effect of grazing at this stocking rate could be only temporal (Figure 9.3). The initial richness of the intermediate plots, at the first sampling date, was lower than at the end point of the young plots, again suggesting a higher grazing pressure before the start of the experiment. Consequently, a bigger effect of grazing on plant richness could be expected at higher grazing pressures.

To analyze the factors that influence plant diversity in this old-field succession, a multiple regression (forward stepwise) was carried out using plant richness as dependent variable, and successional time, percentage of bare soil, total aboveground biomass, weighed height of the vegetation, stoniness, slope, soil texture, total soil nitrogen, and soil total carbon as indepen-

dent variables. The forward stepwise procedure selected four variables that explained 69% of the variability in plant richness. The included variables were: biomass (B, in g m⁻²), which explains 47% of the variability, slope of the plot (S, in degrees), which explains an additional 11% of the variability, bare soil (BS, in %), which explains 7%, and successional age (SA, in years), which explains 3.6% more. The inclusion of further variables did not significantly increase the total amount of variance explained. The equation for the multiple regression is:

$$\text{Richness} = 5.02 + 0.06 B + 0.11 S - 0.07 BS + 0.41 SA$$

A logarithmic function of plant biomass explains more variability (74%) than the multiple lineal regression (Figure 9.4).

RESPONSE OF INDIVIDUAL SPECIES

Over the whole experiment, 61 species were recorded: 17 grasses, 33 forbs, 10 shrubs, and 1 giant rosette. Among these, 28 had a very low abundance and will not be considered further. The successional behavior of the 33 other species and their response to grazing is presented in Table 9.3, including the consumption preference by cattle of the different plant species, according to Molinillo and Monasterio (1997), complemented with personal observations.

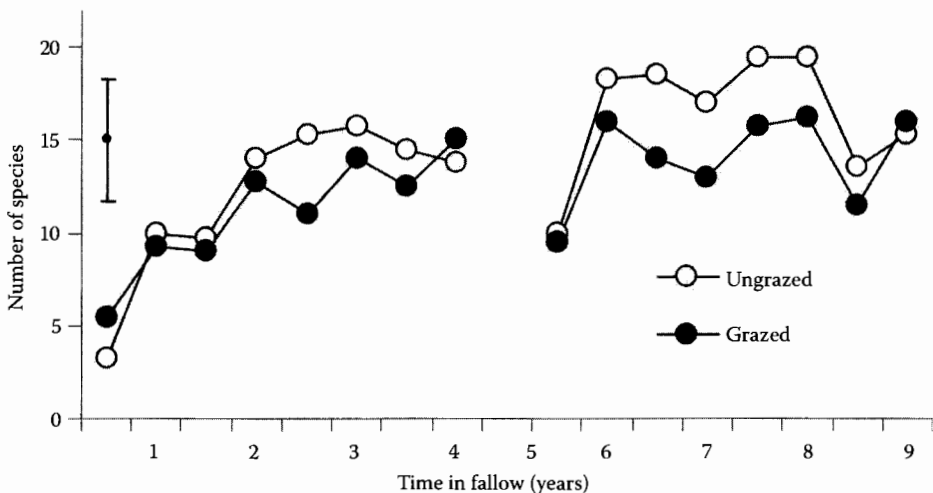


FIGURE 9.3 Species richness in the excluded and grazed treatments. The bar of error represents the average standard deviation.

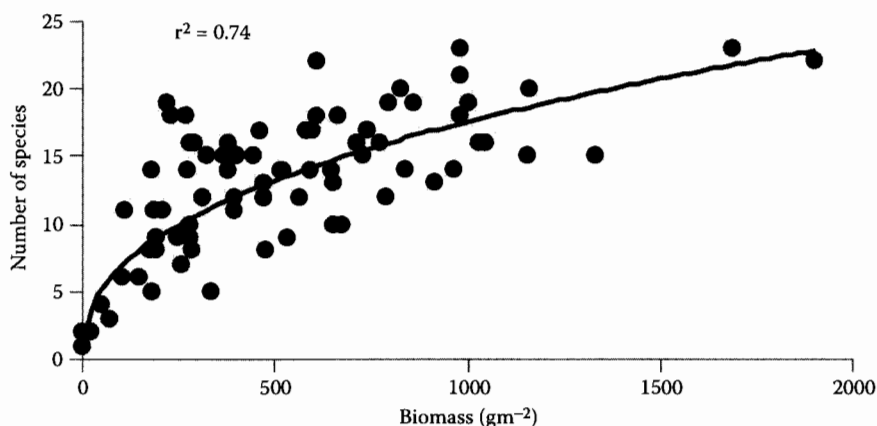


FIGURE 9.4 Relationships between plant biomass and richness using the data of all vegetation samplings. A logarithmic function was adjusted to the points ($p < 0.001$).

There are contrasting successional patterns (Table 9.3 and Figure 9.5). A group of species was more abundant in early succession compared to intermediate succession: *Rumex acetosella*, *Erodium cicutarium*, *Gnaphalium elegans*, *Penisetum clandestinum*, *Bromus carinatus*, *Poa annua*, *Lachemilla moritziana*, and *Lupinus meridanus*; all of them, except the last two, introduced species. Another group of species was more abundant during the intermediate succession: *Espeletia schultzii*, *Acaena elongata*, *Aciachne pulvinata*, *Hypericum laricifolium*, *Oenothera epilobifolia*, *Orthosanthus chimboracensis*, *Brachypodium mexicanum*, and *Nassella linerifolia*, all of them native species. The rest of the species did not present significant differences between young and intermediate plots.

In Figure 9.5, the successional behavior of some representative species can be observed. For example, *Rumex acetosella* decreased regularly with time, with a very significant effect of age and time (Table 9.4). *Lachemilla moritziana* and *Trisetum irazuense* have their peaks of abundance after 2 and 4 years of succession, respectively, with very regular curves of increase and posterior decrease in abundance. Other species, such as *Espeletia schultzii* and *Hypericum laricoides*, showed a progressive and significant increase in abundance with time.

Analyzing the effect of grazing on above-ground biomass (absolute values in Table 9.3), it can be observed that only four species sig-

nificantly increased their biomass and can be considered as promoted by grazing: *Aciachne pulvinata*, *Erodium cicutarium*, *Penisetum clandestinum*, and *Poa annua*. Three of these species are introduced. Twelve species decreased their biomass and can be considered as damaged by grazing: *Acaena elongata*, *Baccharis prunifolia*, *Brachypodium mexicanum*, *Gamochaeta americana*, *Geranium chamaense*, *Hypericum laricifolium*, *Lachemilla moritziana*, *Nassella linerifolia*, *Noticastrum marginatum*, *Rumex acetosella*, *Sisyrinchium tinctorum*, and *Trisetum irazuense*. The remaining 17 species listed in Table 9.3 did not show a significant change in biomass and can be considered as not affected by grazing. In this unaffected group, there are several grasses, such as *Agrostis jahnii*, *Agrostis trichodes*, and *Vulpia myurus*, that are consumed by animals but with an intermediate preference; the only giant rosette recorded, *Espeletia schultzii*, which is not consumed by cattle; a legume, *Lupinus meridanus*, rejected due to its toxic composition; and several forbs that are not consumed by animals, such as *Gnaphalium elegans* and *Gnaphalium meridanum*.

Apart from the absolute changes in biomass, grazing also affected the relative proportion between species (values in parentheses in Table 9.3). These relative changes give additional information concerning the structural transformation of the vegetation. Several

TABLE 9.3

Aboveground biomass and perceptual contribution (in parentheses) of the main species in the ungrazed (NG) and grazed (G) treatments

Species	P	LF	Biomass 1–4 years g m ⁻² (%)		Biomass 5–8 years g m ⁻² (%)		ID
			NG	G	NG	G	
<i>Acaena elongata</i>	3	S	7.8 ^a (1.2 ^a)	3.9 ^b (1.2 ^a)	68.8 ^c (7.1 ^b)	40.2 ^d (6.6 ^b)	0
<i>Aciachne pulvinata</i>	5	G	0.1 ^a (0.0 ^a)	0.0 ^a (0.0 ^a)	7.8 ^b (0.8 ^b)	12.9 ^c (2.1 ^c)	-2
<i>Agrostis jahni</i>	2	G	22.4 ^a (3.4 ^a)	13.9 ^a (4.1 ^a)	5.3 ^{ab} (0.6 ^{ab})	3.3 ^b (0.5 ^b)	0
<i>Agrostis trichodes</i>	2	G	11.9 ^a (1.8 ^{ac})	3.2 ^b (0.9 ^b)	35.1 ^a (3.6 ^{ab})	13.5 ^a (2.2 ^c)	+1
<i>Baccharis prunifolia</i>	5	S	67.7 ^{ab} (10.4 ^a)	44.0 ^a (13.0 ^b)	91.8 ^b (9.4 ^{ab})	43.6 ^a (7.2 ^{ab})	0
<i>Brachypodium mexicanum</i>	1	G	0.0 ^a (0.0 ^a)	0.0 ^a (0.0 ^a)	2.9 ^b (0.3 ^b)	0.0 ^a (0.0 ^a)	+2
<i>Bromus carinatus</i>	1	G	22.1 ^a (3.4 ^a)	18.2 ^a (5.4 ^a)	4.5 ^b (0.5 ^b)	1.1 ^c (0.2 ^c)	0
<i>Erodium cicutarium</i>	—	F	0.3 ^a (0.0 ^a)	2.6 ^b (0.8 ^b)	0.0 ^a (0.0 ^a)	0.0 ^a (0.0 ^a)	-2
<i>Espelletia schultzii</i>	5	R	10.8 ^a (1.6 ^a)	15.2 ^a (4.5 ^b)	349.1 ^b (35.7 ^b)	291.4 ^b (48.0 ^c)	-2
<i>Gamochaeta americana</i>	4	F	8.1 ^a (1.2 ^a)	2.6 ^b (0.8 ^{ab})	6.0 ^a (0.6 ^b)	2.6 ^a (0.4 ^b)	+1
<i>Geranium chamaense</i>	3	F	16.0 ^a (2.5 ^a)	7.1 ^{bc} (2.1 ^{ab})	8.4 ^b (0.9 ^{bc})	3.5 ^c (0.6 ^c)	+1
<i>Gnaphalium elegans</i>	4	F	3.5 ^{ab} (0.5 ^{ab})	0.3 ^a (0.1 ^a)	0.0 ^b (0.0 ^b)	0.0 ^b (0.0 ^b)	+2
<i>Gnaphalium meridanum</i>	4	F	1.4 ^a (0.2 ^{ab})	0.5 ^a (0.2 ^{ab})	0.9 ^a (0.1 ^b)	1.1 ^a (0.2 ^a)	-1
<i>Hypericum laricifolium</i>	5	S	16.0 ^a (2.5 ^a)	2.7 ^b (0.8 ^b)	210.2 ^c (21.5 ^c)	108.0 ^d (17.8 ^c)	+1
<i>Lachemilla moritziana</i>	3	F	42.5 ^a (6.5 ^a)	33.0 ^b (9.8 ^b)	13.3 ^c (1.4 ^c)	8.7 ^d (1.4 ^c)	-1
<i>Laennecia mima</i>	5	F	2.5 ^a (0.4 ^a)	1.1 ^a (0.3 ^a)	0.2 ^a (0.0 ^{ab})	0.1 ^a (0.0 ^a)	+1
<i>Lupinus meridanus</i>	5	F	14.1 ^a (2.1 ^a)	7.4 ^{ab} (2.2 ^a)	2.2 ^b (0.2 ^b)	1.5 ^b (0.3 ^b)	0
<i>Nassella linerifolia</i>	1	G	1.2 ^a (0.2 ^a)	0.0 ^b (0.0 ^b)	30.4 ^c (3.1 ^c)	1.0 ^a (0.2 ^a)	+2
<i>Nassella mexicana</i>	2	G	4.6 ^a (0.7 ^a)	0.0 ^a (0.0 ^a)	1.4 ^a (0.1 ^a)	0.2 ^a (0.0 ^a)	+2
<i>Nassella mucronata</i>	1	G	1.1 ^a (0.2 ^a)	0.1 ^a (0.0 ^{ab})	0.0 ^a (0.0 ^a)	0.0 ^a (0.0 ^a)	+1
<i>Noticastrum marginatum</i>	—	F	0.9 ^a (0.1 ^{ab})	0.3 ^a (0.1 ^a)	2.8 ^b (0.3 ^b)	1.7 ^a (0.3 ^{ab})	+1
<i>Oenothera epilobifolia</i>	—	F	0.0 ^a (0.0 ^a)	0.8 ^a (0.2 ^{ab})	3.3 ^b (0.3 ^b)	3.5 ^b (0.6 ^c)	-2
<i>Orthosanthus chimboracensis</i>	5	F	0.5 ^a (0.1 ^a)	0.4 ^a (0.1 ^a)	5.7 ^b (0.6 ^b)	4.5 ^b (0.7 ^b)	-1
<i>Oxylobus glanduliferus</i>	5	F	0.4 ^{ab} (0.1 ^{ab})	0.1 ^a (0.1 ^b)	2.1 ^{ab} (0.1 ^a)	1.8 ^b (0.3 ^a)	0
<i>Paspalum pygmaeum</i>	1	G	0.2 ^a (0.0 ^a)	0.3 ^a (0.1 ^a)	0.5 ^a (0.1 ^a)	1.0 ^a (0.2 ^a)	-2
<i>Penisetum clandestinum</i>	1	G	0.1 ^a (0.0 ^a)	10.1 ^b (3.0 ^b)	0.0 ^a (0.0 ^a)	0.0 ^a (0.0 ^a)	-2
<i>Poa annua</i>	2	G	2.8 ^a (0.4 ^a)	5.2 ^b (1.6 ^b)	0.0 ^c (0.0 ^c)	0.0 ^c (0.0 ^c)	-2
<i>Rumex acetosella</i>	3	F	320.4 ^a (49.7 ^a)	148.2 ^b (43.5 ^a)	44.9 ^c (4.6 ^b)	31.4 ^d (5.1 ^b)	0
<i>Sisyrinchium tinctorum</i>	5	F	5.7 ^a (0.9 ^a)	1.8 ^{bc} (0.5 ^a)	8.6 ^a (0.9 ^a)	3.7 ^c (0.6 ^a)	+1
<i>Stevia elatior</i>	5	F	1.1 ^a (0.2 ^a)	0.6 ^a (0.2 ^a)	1.2 ^a (0.1 ^a)	0.5 ^a (0.1 ^a)	0
<i>Stevia lucida</i>	5	S	0.0 ^a (0.0 ^a)	0.0 ^a (0.0 ^a)	15.4 ^b (1.6 ^b)	9.5 ^b (1.6 ^b)	0
<i>Trisetum irazuense</i>	1	G	42.8 ^a (6.6 ^a)	3.5 ^b (1.0 ^b)	28.2 ^a (2.9 ^a)	2.5 ^b (0.4 ^b)	+2
<i>Vulpia myurus</i>	3	G	17.0 ^a (2.6 ^a)	8.2 ^a (2.4 ^a)	12.2 ^a (1.2 ^a)	9.4 ^a (1.5 ^a)	0

Note: The values are averages for the 4 years of the experiment. The values of the palatability index were taken from Molinillo and Monasterio (1997), and completed or modified using personal observations.

P is an index of palatability in a relative scale 1 = preferred, 2 = good, 3 = regular, 4 = insufficient, 5 = rejected. Life-form (LF) abbreviations are F = forb, G = grass, S = shrub, R = giant rosette. The index of damage (ID) is: -2 = very positively affected, -1 = positively affected, 0 = not affected, +1 = negatively affected, and +2 = very negatively affected.

^{a-d}Different letters indicate significant differences between treatments ($p < .05$, t-test for dependent samples).

trends are possible: (1) a reduction in biomass not accompanied by a reduction in the relative contribution of the species, (2) a reduction in

biomass and in the relative contribution of the species, (3) a reduction in biomass but an increase in the relative contribution of the spe-

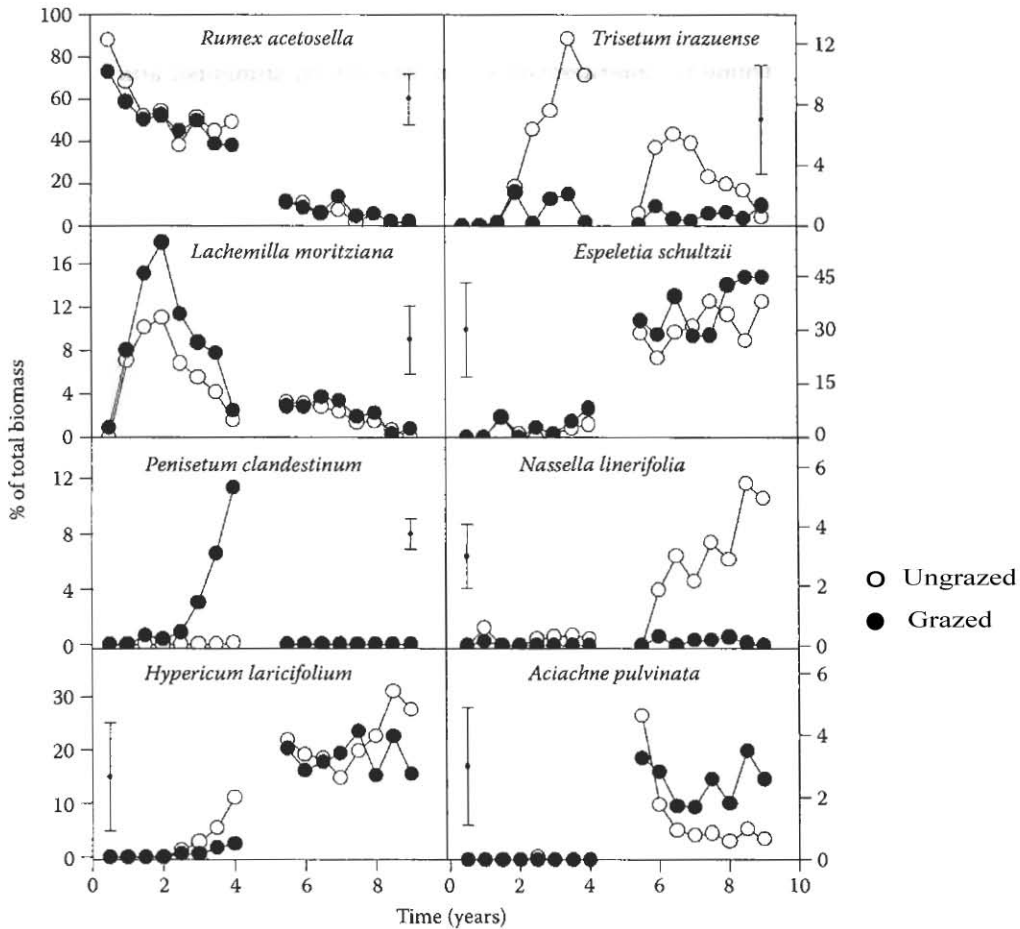


FIGURE 9.5 Percentage of the total biomass of some representative species along the 4 years of the study in the excluded and grazed treatments. The bars of error represent the average standard deviation.

cies, (4) an increase in the absolute and proportional biomass, and (5) no change in biomass but an increase in proportion. Situation 1 indicates that the species is consumed or damaged as a function of its biomass, without a preferential positive or negative selection. This is the case of *Rumex acetosella* (see also Figure 9.5), *Acaena elongata*, *Baccharis prunifolia*, and *Hypericum laricoides* (Figure 9.5), among others. Situation 2 indicates a preferential consumption or damage, as is the case with only three species: *Trisetum irazuense* (Figure 9.5), *Brachypodium mexicanum*, and *Nassella linerifolia* (Figure 9.5), all tall grasses with a very high palatability and accessibility to animals. Situation 3 indicates a little negative selection and is only found in the case of *Noticastrum marginatum*.

Situation 4 indicates that the effect of grazing is positive, as in the case of *Poa annua*, *Aciachne pulvinata* (Figure 9.5), *Erodium cicutarium*, and *Penisetum clandestinum* (Figure 9.5). Situation 5 indicates that the species is not consumed or damaged by animals but indirectly favored as its proportion in the total biomass increased. This is the case of *Espeletia schultzei* (Figure 9.5), whose biomass remained constant but increased its relative contribution from 36 to 48% in the intermediate plots. Another species with the same behavior is *Oenothera epilobifolia*, a prostrate forb.

The last column of Table 9.3 presents the index of damage by grazing. The more fragile species are grasses with a high palatability, such as *Trisetum irazuense*, *Brachypodium mexi-*

TABLE 9.4

Effects of age (young vs. intermediate plots), grazing (treatments), and time (consecutive sampling dates during 4 years) on several vegetation parameters using a repeated-measures analysis

Parameter	df	Age	Grazing	Grazing ^a	Time	Time ^a	Grazing ^a	Grazing ^a
		1	1	Age 1	7	Age 7	Time 7	Time ^a Age 7
<i>Rumex acetosella</i>	F	85.5**	0.17	4.31	6.49**	2.32*	2.41*	1.67
<i>Lachemilla moritziana</i>	P		ns	ns				ns
<i>Trisetum irazuense</i>	F	10.48*	7.47*	2.13	11.28**	1.57	1.14	0.34
<i>Penisetum clandestinum</i>	P			ns		ns	ns	ns
<i>Espeletia schultzii</i>	F	0.04	11.84*	0.28	1.51	3.87*	1.12	3.84*
<i>Hypericum laricifolium</i>	P			ns		ns	ns	
<i>Nassella linerifolia</i>	F	3.38	3.61	3.61	4.35*	4.35*	4.27*	4.27*
<i>Aciachne pulvinata</i>	P			ns				ns
<i>Poa annua</i>	F	45.58**	0.03	0.07	2.49*	0.31	1.60	2.25*
	P			ns		ns	ns	
	F	11.41*	3.50	0.35	4.21*	1.72	2.26*	0.51
	P			ns		ns		ns
	F	2.86	5.10*	2.91	0.29	0.54	1.26	1.36
	P			ns		ns	ns	ns
	F	1.16	1.33	1.51	1.29	1.15	0.84	1.27
	P			ns		ns	ns	ns
	F	15.19*	3.67	3.44	9.90**	9.89**	3.17*	2.9*
	P			ns				

*Significant at $p < .05$.

**Significant at $p < .001$.

canum, and *Nassella linerifolia*, which are preferentially consumed by cattle but apparently do not have efficient mechanisms to resist this kind of disturbance. The shrub *Hypericum laricoides* also appears as a fragile species, probably due to trampling.

Data in Table 9.3 also suggest that the introduced species *Bromus carinatus* and *Penisetum clandestinum*, and in a lesser measure, the native species *Agrostis jahnii*, are good sources of forage. These species have a high palatability but do not suffer significant damage when grazed.

Some species that are not negatively affected by grazing are *Espeletia schultzii*, *Rumex acetosella*, *Paspalum pygmaeum*, *Stevia lucida*, and *Vulpia myurus*. *Espeletia schultzii* is rejected by cattle and is not sensitive to trampling. *Paspalum pygmaeum* evades grazing by its creeping habit. *Rumex acetosella*, a European weed, is not preferentially selected but, as

it is the most abundant species at the beginning of the succession, it represents an important percentage of animal diets. Nevertheless the growth form of this species (a rhizomatous herb) allows it to tolerate grazing.

Table 9.3 shows that the lack of response to grazing of the grasses, as a life-form, is due to a very contrasting response of the individual species. Caespitose grasses (such as *Penisetum clandestinum* and *Aciachne pulvinata*) and creeping grasses (such as *Poa annua* and *Paspalum pygmaeum*) are favored by grazing, probably because they are tolerant, as does *Penisetum clandestinum*, or because they have mechanisms of evasion, as does *Aciachne pulvinata*, a thorny prostrate species, or *Paspalum pygmaeum*, a very small species that concentrates its biomass in 1 or 2 cm above the soil surface. On the other hand, tall grasses (such as *Trisetum irazuense* and *Bromus carinatus*) are preferentially consumed.

DISCUSSION

The aboveground biomass after 8 to 9 years of succession (606 and 878 g m⁻² on average for the grazed and ungrazed treatment, respectively) lies in the low part of the range reported by Hofstede (1995) for several Colombian páramos (735 to 3486 g m⁻²). This difference can be explained considering that our plots are still in a relatively early successional phase and that Venezuelan páramos are drier and probably less productive than the Colombian ones. Our estimations are closer to the values reported by Ramsay and Oxley (2001) for a grassland páramo in Ecuador (800 g m⁻²), but this kind of páramo does not have giant rosettes and shrubs, which account for an important part of the total aboveground biomass in late succession in Venezuela. In the same area of our study, Montilla et al. (2002) measured, using harvest techniques, a total aboveground biomass of 952 g m⁻² in a 12-year successional plot, in the same order of magnitude as the figures obtained using the biovolume–biomass coefficients in the 9-year plots, a result that partially validates our method.

One of the most noticeable effects of grazing in this secondary succession was the reduction of plant aboveground biomass under extensive grazing. Other studies in the páramo confirm this trend; for example, Hofstede (1995) reported a total aboveground biomass of 3486 g m⁻² in an undisturbed Colombian páramo, compared to 2567 g m⁻² in a similar but extensively grazed area. This 26% reduction in biomass can be compared to the 30 to 40% reduction found in this study. Furthermore, Molinillo and Monasterio (1997) also reported an increase in biovolume of 52% after 1 year of grazing exclusion for a Venezuelan rosette–shrub páramo community.

A decrease in biomass is not an obvious or generalized response of vegetation to grazing. For example, in natural alpine grasslands in the Alps, Körner (1999) found that very extensive grazing had a positive effect on biomass due to the stimulation of nutrient cycling. An increase in biomass, production, richness, or other ecosystem properties under moderate disturbance is reported in many ecosystems and is explained by the intermediate disturbance hypothesis.

However, at a high intensity of disturbance, the normal response is a reduction in biomass due to the diminution of the LAI and of the photosynthetic capacity of the vegetation. In the case of the páramo, we have no evidences of a possible augmentation of biomass under very extensive grazing, but our data suggest that the deleterious effect occurs at relatively low grazing pressure.

The stocking rate of this experiment, estimated at 0.4 cows ha⁻¹, can be considered as high compared to the carrying capacity of 0.1 cows ha⁻¹ reported by Molinillo and Monasterio (1997) for a drier rosette–shrub páramo and to the mean animal stocking rate of the valley estimated in 0.13 cows ha⁻¹ (Pérez 2000). Nevertheless, we consider that the effective stocking rate was not as high as it seems. According to Schmidt and Verweij (1992), the daily dry matter intake by adult cows grazing in páramo ecosystems is around 11.8 kg. Assuming 12 h of grazing per day, the consumption in 1 h can be estimated in 980 g, or 9.8 g m⁻² for a 100-m² plot. This figure corresponds to a consumption of 2 to 4% of the total aboveground biomass per month, which is not a very high proportion of the total biomass. In addition, the rotative grazing method (only 1 h each, 3 weeks) probably allows vegetation to recover between two consecutive events of grazing. Furthermore, our results suggest that the stocking rate before the installation of the fences was higher than under the grazing treatment (lower biomass and richness and higher percentage of bare soil in the initial intermediate plots compared with the final point of the grazed young plots). Further research is needed to arrive at more conclusive results concerning the response of biomass and other attributes to different intensities of grazing in this ecosystem.

The decrease in plant biomass observed under this stocking rate can have different consequences for the functioning and stability of the ecosystem, but an accurate prediction is difficult to make because of the existence of compensatory mechanisms and nonlinear processes in ecosystems. As a first approximation, we can predict that a reduction in biomass, mainly in the photosynthetic one, may produce a reduction in net primary production due to less light interception. Consequently, a

reduced amount of necromass would be incorporated into the soil, leading to a progressive depletion in soil organic matter (SOM), which in turn can reduce the soil's capacity to retain water and nutrients. However, trends in SOM are only detectable in mean and long-term studies, due to the large amount initially present in these mountain soils. A decrease in SOM, together with the increase in the proportion of bare soil under grazing, could favor erosive processes and could negatively affect the sustainability of the system. This is the case documented by Podwojewski et al. (2002) in an intensive sheep-grazed páramo in Ecuador, where a dramatic decrease of SOM took place as a consequence of the decrease in plant biomass, the exportation of sheep manure, and by soil surface erosion favored by the increased percentage of bare soil and the mechanical effect of animals. Nevertheless, in our case, contrabalancing processes can also be taking place; for example, if the species with higher nitrogen content were consumed preferentially, litter quality and also decomposition rates would decrease, compensating for the reduction in the amount of litter. No definitive conclusions concerning the effect of grazing on ecosystem properties can be derived from this experiment, and further experimental work is necessary to test the consequences of changes in quality and quantity of plant biomass. Also, a simulation approach could give further insights.

Only small changes were detected in the life-form spectrum of the vegetation. Possible trends toward a reduction in the proportion of grasses and an increase in the proportion of giant rosettes were observed at the end of the experiment in the intermediate plots. In a Colombian páramo, Hofstede (1995) observed an increase in the density and biomass of giant rosettes (*Espeletia hartwegiana*) as a consequence of grazing and in absence of burning. However, Verweij and Kok (1992) reported different results for the same species. Vargas et al. (2002) reported a deleterious effect of grazing on *Espeletia killipii*. These inconsistencies can be related to different grazing intensities or to the interaction between grazing and burning.

The classification of the species in four life-forms is too general to analyze the structural

changes produced by grazing, as species belonging to the same life-form can present different responses. A more detailed classification is necessary to assess the effect of grazing on functional types of plants, which should take into consideration more specific traits influencing the way plants are affected by grazing (palatability, mechanical fragility, grazing defenses, etc.). This approach could be interesting when comparing different sites in terms of ecological equivalents. Using a more detailed classification of grasses, the diminution of tall and short grasses, and the increase in creeping and rhizomatous grasses can be identified as grazing effects. Other authors also reported the replacement of tall and tussock grasses by a short carpet grass vegetation in páramo ecosystems (Verweij and Budde 1992; Hofstede 1995; Podwojewski et al. 2002).

Independently of grazing, the abundance of giant rosettes and shrubs increases in the succession and, consequently, the offer of forage decreases. Early plots seem to be more suitable for grazing than intermediate and late ones, and decisions by farmers concerning the duration of the fallow period probably take this aspect into consideration.

In this experiment, grazing produced a slight but consistent reduction in plant diversity. In literature, different responses of plant richness have been reported, depending on the intensity of grazing and on the characteristics of the species that conform the community. Körner (1999) reported, for an alpine grassland in the Alps, a positive effect of extensive grazing, whereas Podwojewski et al. (2002) reported a diminution of the number of species under intensive grazing in the páramo. In our experiment, the abundance of some of the species was dramatically reduced, but they did not disappear completely, explaining the small changes observed in plant richness. A stronger effect would be expected with higher grazing pressures.

The observed reduction in biodiversity is in accordance with the hypothesis that in poor environments such as the páramo, grazing reduces plant richness, whereas in rich environments, plant richness can be increased (Milchunas and Lauenroth 1993). Grazing can promote plant biodiversity by balancing competitive

interactions between species, reducing competition for light, promoting dispersion, and creating more recruitment opportunities for subordinate species (Berendse 1985; Milchunas and Lauenroth 1993; Bakker 2003). For example, Bakker (2003) found, in a grassland in the Netherlands, a negative correlation between the height of the vegetation and plant richness and a positive correlation between richness and the percentage of bare soil, indicating that in this environment, competition for light and the existence of opportunities for establishment are the main factors controlling plant richness. However, in the páramo, the situation seems to be the opposite. Plant richness is positively correlated to plant biomass and negatively correlated to the amount of bare soil, indicating that other factors are controlling plant biodiversity. Light competition does not appear to be an important factor controlling diversity, probably because even without grazing, there is a significant proportion of bare soil. In general, the effect of herbivory on plant species diversity is mainly determined by the response of the subordinate species. In the páramo, grazing seems to enhance the abundance of the dominant species that are less palatable and to promote the extinction of some of the subordinate species that are more palatable. On the other hand, regeneration niches do not seem to be limiting, and herbivores are not expected to increase the opportunities of colonization. In this páramo, succession grazing seems to promote extinction without favoring colonization.

At the level of individual species, the effect of grazing in this old-field succession is clear; it promotes some species, damages others, and does not affect a third group. This differential effect can be related to the palatability of the species, their adaptations to tolerate or avoid herbivory, and their mechanical fragility. According to Körner (1999), the impact of grazing on alpine vegetation is much more severe by trampling than by direct consumption due to the extreme sensitivity of shrub communities. The sensitivity of *Hypericum laricifolium* observed in this study and by Molinillo and Monasterio (1997), and explained by the fragility of its branches, supports this affirmation.

The positive effect of grazing on some páramo species, mainly creeping and prostrate

life-forms such as *Aciachne pulvinata* and *Lachemilla orbiculata*, is widely recognized in the literature (Verweij and Budde 1992; Hoftede 1995). Also, the positive impact on some introduced species, such as *Poa annua*, *Taraxacum officinaris*, and *Rumex acetosella*, is reported in other studies (Velázquez 1992; Verweij and Budde 1992; Pels and Verweij 1992; Podwojewski et al. 2002).

The positive response to grazing of the introduced species and their strong dominance in early succession, documented in a previous study by Sarmiento et al. (2003), indicate that current management favors the invasion of the páramo by ruderal species. These probably have more adaptations to herbivory, because they evolved in other environments in which this kind of disturbance is common.

As a conclusion, it can be said that at the moderate stocking rate used in this experiment, some negative effects of grazing were detected, but they are less important than expected, considering the short history of grazing of this ecosystem. A certain level of grazing is probably compatible with the restoration of the páramo ecosystem without severely threatening plant biodiversity. Nevertheless, additional studies are necessary to evaluate more accurately the impact of grazing on SOM and on the long-term stability of the system, and to determine the appropriate stocking rate.

SUMMARY

An enclosure experiment was carried out to analyze the effect of grazing on plant biomass and vegetation composition during secondary succession in a Venezuelan páramo. Four young plots (never in fallow) and four intermediate plots (5 years in fallow) of 200 m² each were fenced and divided into two parts; one was excluded and the other was grazed during 4 years using a stocking rate equivalent to 0.4 cows ha⁻¹. The vegetation was sampled twice a year using the point intercept method. At this stocking rate, grazing produced a reduction of 30 to 40% of total aboveground plant biomass. Vegetation height was reduced in the same order, and the percentage of bare soil increased significantly. Despite the reduction in aboveground biomass, the life-form spectrum of the

vegetation was only slightly affected, indicating that grazing impact was almost homogeneous for the different life-forms. A possible augmentation in the percentage of giant rosettes in the intermediate plots was detected at the end of the experiment in the grazed treatment. This is probably due to the total rejection of rosettes by cattle and to the low impact of trampling on this life-form. Grazing also reduced plant species richness slightly, but significantly, and a more severe effect could be expected from a higher grazing pressure. The response of individual species was very clear. An index of damage allowed classifying them into the following: damaged by grazing (e.g. *Trisetum irazuense*, *Nassella linerifolia*, *Brachypodium mexicanum*, etc.), unaffected (e.g. *Acaena elongata*, *Baccharis prunifolia*, *Lupinus meridanus*, etc.), and positively affected (e.g. *Aciachne pulvinata*, *Espeletia schultzei*, *Penisetum clandestinum*, etc.). Some explanations of the individual responses are advanced based on the preferences by cattle, plant architecture, and sensitivity to trampling.

ACKNOWLEDGMENTS

This research was supported by the International Foundation for Science (Grant C/2668) and by the EU project TROPANDES (IC18-CT98-0263). The author received a fellowship from the Wageningen Institute for Environment and Climate Research for the redaction of the paper. Thanks to A. Escalona, N. Marquez, A. Olivo, C. Molina, A. Berg, and B. Briceño for their participation in the fieldwork and in botanical identifications. J.K. Smith and L.D. Llambí also helped in the selection and installation of the plots. Special thanks to Cristobal, Alfonso, Gregorio, Sra. Rosa and Sra. Hilbina of the páramo de Gavidia for handling the animals that grazed the plots.

References

- Abadín, J., González-Prieto, S.J., Sarmiento, L., Villar, M.C., and Carballas, T. (2002), Successional dynamics of soil characteristics in a long fallow agricultural system of the high tropical Andes, *Soil Biology and Biochemistry*, 34(11): 1739–1748.
- Bakker, E. (2003), *Herbivores as Mediators of Their Environment: the Impact of Large and Small Species on Vegetation Dynamics*, Ph.D. thesis, Wageningen University, Wageningen.
- Berendse, F. (1985), The effect of grazing on the outcome of competition between plant species with different nutrients requirement, *Oikos*, 44: 35–39.
- Davidson, D.W. (1993), The effects of herbivory and granivory on terrestrial plant succession, *Oikos*, 68: 23–35.
- Gough, L. and Grace, J.B. (1998), Herbivore effects on plant species diversity at varying productivity levels, *Ecology*, 79: 1586–1594.
- Greig-Smith, P. (1983), *Quantitative Plant Ecology*, University of California Press, Berkeley.
- Hofstede, R.G.M. (1995), *Effects of Burning and Grazing on a Colombian páramo Ecosystem*. Ph.D. thesis, University of Amsterdam, Amsterdam.
- Hofstede, R.G.M., Modragon, M.X., and Rocha, C.M. (1995), Biomass of grazed, burned and undisturbed páramo grasslands, Colombia, Aboveground vegetation, *Arctic and Alpine Research*, 27: 1–12.
- Huntly, N.J. (1991), Herbivores and the dynamics of communities and ecosystems, *Annual Review of Ecology and Systematics*, 22: 477–503.
- Körner, C. (1999), *Alpine Plant Life: Functional Plant Ecology of High Mountain Ecosystems*, Springer-Verlag, Berlin.
- Milchunas, D.G. and Lauenroth, W.K. (1993), Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecological Monograph*, 63: 327–366.
- Milchunas, D.G., Sala, O.E., and Lauenroth, W.K. (1988), A generalized model of the effects of grazing by large herbivores on grassland community structure. *American Naturalist*, 132: 87–106.
- Molinillo, M. and Monasterio, M. (1997), Pastoralism in páramo environments: practices, forage, and impact on vegetation in the Cordillera de Mérida, Venezuela. *Mountain Research and Development*, 17(3): 197–211.

- Molinillo, M. and Monasterio, M. (2002), Patrones de vegetación y pastoreo en ambientes de páramo, *Ecotropicos*, 15(1): 19–34.
- Monasterio, M. (1980). Las formaciones vegetales de los Páramos venezolanos, in Monasterio, M. (Ed.), *Estudios Ecológicos en los Páramos Andinos*, Ediciones de la Universidad de los Andes, Mérida, pp. 93–159.
- Montilla, M., Monasterio, M., and Sarmiento, L. (2002), Dinámica sucesional de la fitomasa y los nutrientes en parcelas en sucesión-regeneración en un agroecosistema de páramo, *Ecotropicos*, 15(1): 75–84.
- Pacala, S.W. and Crawley, M.J. (1992), Herbivores and plant diversity, *American Naturalist*, 140: 243–260.
- Pérez, R. (2000), Interpretación ecológica de la ganadería extensiva y sus interrelaciones con la agricultura en el piso agrícola del Páramo de Gavidia, Andes venezolanos, M.Sc. thesis, Postgrado de Ecología Tropical, Facultad de Ciencias, Universidad de los Andes, Mérida, Venezuela.
- Podwojewski, P., Poulenard, J., Zambrano, T., Hofstede, R. (2002), Overgrazing effects on vegetation cover and properties of volcanic ash soil in the páramo of Llanguhua and La Esperanza (Tungurahua, Ecuador), *Soil Use and Management*, 18: 45–55.
- Ramsay, P. and Oxley, R.B. (2001), An assessment of aboveground net primary productivity in Andean grasslands of central Ecuador, *Mountain Research and Development*, 21: 161–167.
- Sarmiento, L., Smith, J., and Monasterio, M. (2002), Balancing conservation of biodiversity and economical profit in the agriculture of the high Venezuelan Andes: are fallow systems an alternative? In Körner, C. and Spehn, E. (Eds.), *Mountain Biodiversity — A Global Assessment*, Parthenon, pp. 285–295.
- Sarmiento, L., Llambí, L.D., Escalona, A., and Marquez, J. (2003), Vegetation patterns, regeneration rates and divergence in an old-field succession of the high tropical Andes, *Plant Ecology*, 166: 63–74.
- Schmidt, A.M. and Verweij, P.A. (1992), Forage intake and secondary production in extensive livestock systems in páramo, in Balslev, H. and Luteyn, J.L. (Eds.), *páramo: An Andean Ecosystem under Human Influence*. Academic Press, London, pp. 197–210.
- Smith, J.K. (1995), Die Auswirkungen der Intensivierung des Ackerbaus im Páramo de Gavidia — Landnutzungswandel an der oberen Anbaugrenze in den venezolanischen Anden, Diplomarbeit, University of Bonn, Germany.
- Van Oene, H., van Deursen, M., and Berendse, F. (1999), Plant-herbivore interaction and its consequences for succession in wetland ecosystems: a modeling approach, *Ecosystems*, 2: 122–138.
- Vargas, O., Premauer, J., and Cardenas, C. (2002), Efecto del pastoreo sobre la estructura de la vegetación en un páramo humedo de Colombia, *Ecotropicos*, 15: 35–50.
- Velázquez, A. (1992), Grazing and burning in grassland communities of high volcanoes in Mexico, in Balslev, H. and Luteyn, J.L. (Eds.), *páramo: An Andean Ecosystem under Human Influence*, Academic Press, London, pp. 231–241.
- Verweij, P.A. and Budde, P.E. (1992), Burning and grazing gradients in páramo vegetation: initial ordination analyses, in Balslev, H. and Luteyn, J.L. (Eds.), *páramo: An Andean Ecosystem under Human Influence*, Academic Press, London, pp. 177–195.
- Verweij, P.A. and Kok, K. (1992), Effects of fire and grazing on *Espeletia hartwegiana* populations, in Balslev, H. and Luteyn, J.L. (Eds.), *páramo: An Andean Ecosystem under Human Influence*, Academic Press, London, pp. 215–229.
- Wagner, E. (1978), Los Andes Venezolanos, arqueología y ecología cultural, *Ibero-Amerikanisches Archiv*, Neue Folge, Berlin. 4(1): 81–91.