Spatial and temporal modelling of vegetation patterns–burning and grazing in the paramo of Los Nevados National Park, Colombia

1 author:

P.A. Verweij
Utrecht University

Burning and grazing gradients in páramo vegetation: Initial ordination analyses

P. A. Verweij and P. E. Budde

International Institute for Aerospace Survey and Earth Sciences (ITC), Enschede, The Netherlands

Abstract. In the bunchgrass páramo at 3900–4200 m elevation in Parque Nacional Natural Los Nevados, in the central cordillera of Colombia, vegetation patterns in relation to burning and grazing were characterized. Clustering and ordination techniques were applied to analyse variation of vegetation structure and floristic composition in relation to management variables. Zonal vegetation is dominated by species of *Calamagrostis* and the stem rosette *Espeletia hartwegiana* ssp. *centro-andina*. On moderate slopes the vegetation opens up under an intermediate grazing intensity. In these situations, coverage, height, and diameter of the bunchgrasses decrease, whereas percentage of bare soil and trampling impact increase. On more gentle slopes and flat terrains a short, matted grassland develops characterized by *Calamagrostis coarctata* and *Lachemilla orbiculata*. A list of species showing a positive or negative reaction to burning and grazing variables is presented.

Resumen. En el páramo de pajonal a 3900–4200 m de altitud del Parque Nacional Natural Los Nevados, se caracterizaron los patrones de vegetación relacionados con quemas y pastoreo. Se aplicaron técnicas de agrupación y de ordenamiento para analizar la variación de la estructura de vegetación y la composición florística en relación a variables de manejo. La vegetación zonal es dominada por *Calamagrostis* spp. y el frailejón *Espeletia hartwegiana* ssp. *centro-andina*. En laderas de inclinación moderada la vegetación se abre bajo una intensidad de pastoreo intermedia. En estas situaciones disminuyen cobertura, altura y diámetro de las macollas, mientras aumentan el porcentaje de suelo desnudo y el impacto de pisoteo. En laderas menos inclinadas y terrenos planos se desarrolla una estera de pastos cortos caracterizada por *Calamagrostis coarctata* y *Lachemilla orbiculata*. Se presenta un listado de especies que muestran una reacción positiva o negativa respecto a variables de quema y pastoreo.

PARAMO
ISBN 0-12-460442-0

Introduction

High-mountain vegetation in the Neotropics is often characterized by variation caused by human influence (Ellenberg, 1979). Under impact of extensive grazing, the tussock grasslands of the páramo ecosystem of the northern Andes frequently develop into a mosaic pattern of spatially and temporally alternating vegetation succession stages. In the Colombian páramo, it is a common management practice to combine extensive grazing with regular burning of the vegetation in order to stimulate the development of palatable young grass shoots. So far, few quantitative data exist that document the specific impact of this form of management on vegetation structure, floristic composition, soil characteristics, and micro-relief. This study aims at the characterization of vegetation patterns in páramo bunchgrasslands as a reflection of different grazing and burning situations. It forms part of the ECOANDES research program.

A list of the plant names mentioned in this contribution, complete with author names and life forms, is given in Table 1, following the nomenclature of Cleef (1981) and Rangel *et al.* (1983). Zonal páramo vegetation of the central cordillera of Colombia was described by Cuatrecasas (1958, 1968), Cleef (1981), Cleef *et al.* (1983), and Salomons (1989). The grass páramo, or "páramo propiamente dicho" *sensu* Cuatrecasas (1958), is dominated by tussocks of *Calamagrostis recta, C. effusa,* and species of *Festuca* accompanied by stem rosettes of *Espeletia hartwegiana* ssp. *centro-andina.* Two replacement communities under intensive grazing have been recognized: the *Aciachnetum pulvinatae* (Vareschi, 1953), a xerophytic association on dry plains, widely distributed throughout the tropical high-Andean ecosystems, and the *Agrostio breviculmis – Lachemilletum orbiculatae* (Cleef, 1981), on slightly humid grounds. The combined effects of grazing and burning have received less scientific attention so far.

Vegetation response to fire was described for a Costa Rican páramo by Janzen (1973), Chaverri *et al.* (1976), Williamson *et al.* (1986), and Horn (1989). A basis for comparison is furthermore provided by the post-fire succession on Mt. Wilhelm, Papua New Guinea, as studied by Corlett (1987), and by a description of recovery from fire of alpine vegetation at Mt. Kilimanjaro (Beck *et al.*, 1986). The general tendency in these tropical alpine grasslands is a quick regeneration of the grass tussocks within a few years after fire, whereas the shrubs are characterized by a slow recovery of several decades. Certain ericaceous shrubs exhibit a larger regeneration capacity.

Methods

Study area. The present study was carried out in Parque Nacional Natural Los Nevados in the central cordillera of the Colombian Andes (4°35–60'N, 75°10–30'W, Fig. 1). Mean annual precipitation is approximately 1300 mm; stable soil temperature is 7.3–7.5 °C (Salomons, 1989), which is generally accepted as being equal to the mean annual temperature. On top of a metamorphic basement of Palaeozoic and Mesozoic age, a number of high volcanoes was formed during the Plio-Pleistocene. Extrusive volcanic processes resulted in the formation of lava fields, block lava, and pyroclastic flows. During the Holocene and late Quaternary, glacial processes left their traces in the form of U-shaped valleys and moraine deposits. Layers of ash, lapilli, and other pyroclastic material produced by frequent explosive eruptions have covered the area. Volcán El Ruiz (5400 m) is still active. The volcanic ash products led to the development of Andosols (Andepts, USDA), characterized by a strong accumulation of humus and a quick

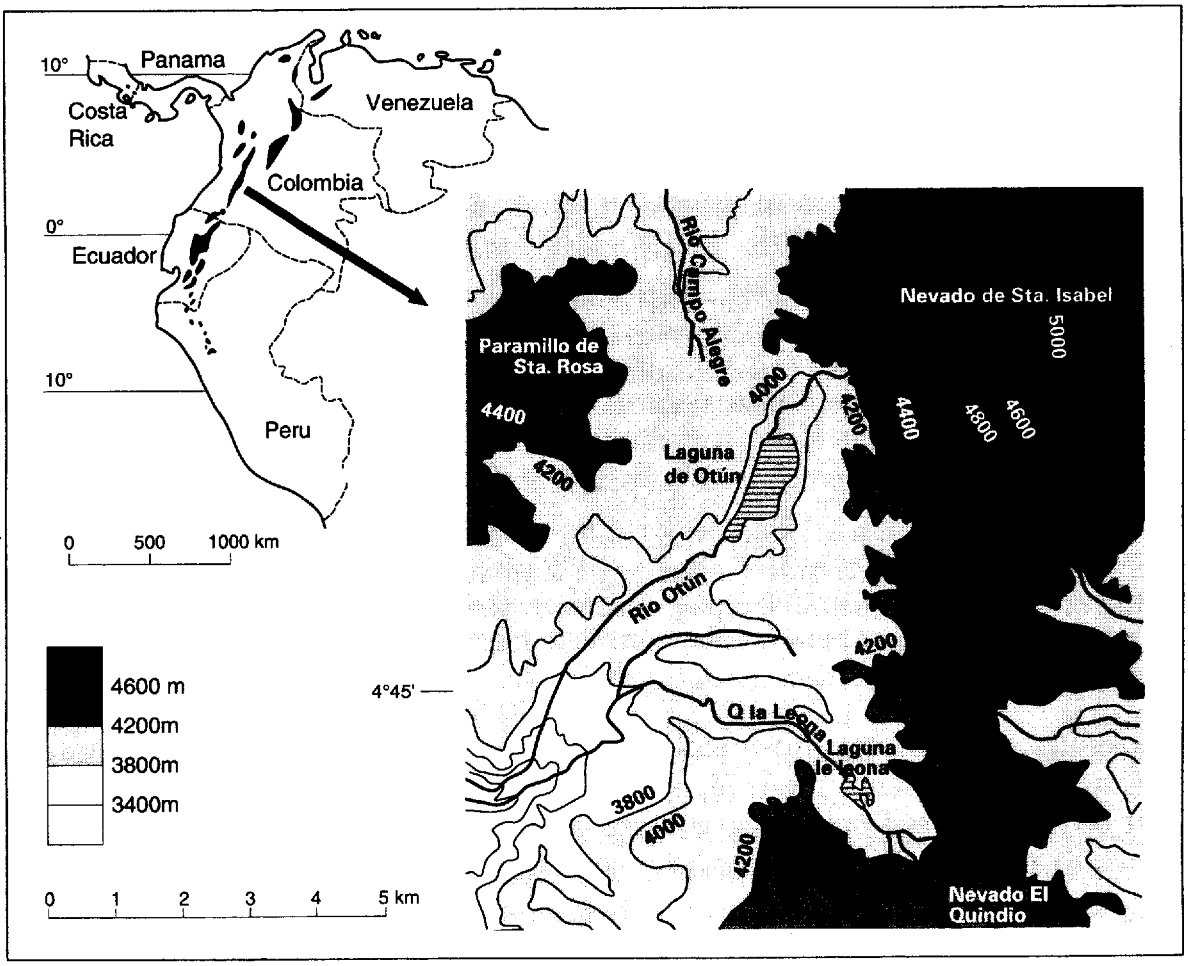

Figure 1. Map of the study area.

Table 1. The plant species mentioned in this paper with an indication of their family and life form.

Adiantaceae: *Jamesonia* sp., herb. **Apiaceae:** *Azorella multifida* (Ruiz & Pav.) Pers., cushion; *Myrrhidendron glaucescens* (Benth.) Coult. & Rose, herb; *Niphogeton dissecta* (Benth.) Macbr., ground rosette; *Oreomhyrris andicola* (Kunth) Hook.f., herb. **Asteraceae:** *Aphanactis piloselloides* Cuatrec., ground rosette; *Baccharis rupicola* H.B.K., shrub; *Baccharis tricuneata* (L.f.) Pers., shrub; *Belloa longifolia* (Cuatrec. & Arist.) Sagast. & Dill., ground rosette; *Bidens triplinervia* H.B.K., ground rosette; *Conyza uliginosa* (Benth.) Cuatrec., herb; *Espeletia hartwegiana* ssp. *centro-andina* Cuatrec., stem rosette; *Gnaphalium antennarioides* DC. , ground rosette; *Gnaphalium pellitum* H.B.K., ground rosette; *Gnaphalium lanuginosum* H.B.K., ground rosette; *Hieracium tolimense* Cuatrec., ground rosette; *Hypochoeris sessiliflora* H.B.K., ground rosette; *Oritrophium peruvianum* (Lam.) Cuatrec., ground rosette; *Pentacalia vaccinoides* (H.B.K.) Cuatrec., shrub; *Taraxacum officinale* Weber, ground rosette; *Werneria crassa* Blake, cushion. **Caryophyllaceae:** *Arenaria serpens* H.B.K., creeping species; *Arenaria serpyllifolia* L., herb; *Arenaria* sp., creeping species. **Cyperaceae:** *Carex pichinchensis* H.B.K., sedge; *Carex tristichia* Spruce ex Boott, sedge. **Ericaceae:** *Disterigma empetrifolium* (H.B.K.) Drude, dwarf shrub; *Pernettya prostrata* (Cav.) DC., dwarf shrub. **Fabaceae:** *Lupinus tolimensis* C. P. Smith, herb; *Lupinus microphyllus* Desr., creeping species; *Trifolium repens* L., creeping species. **Grossulariaceae:** *Escallonia myrtilloides* L.f., shrub. **Gentianaceae:** *Gentiana sedifolia* H.B.K., low herb; *Gentianella dasyantha* (Gilg) Fabris, herb. **Geraniaceae:** *Geranium columbianum* R. Knuth, creeping species; *Geranium multipartitum* Benth., creeping species; *Geranium sibbaldioides* Benth., creeping species. **Hypericaceae:** *Hypericum lancioides* Cuatrec., shrub; *Hypericum laricifolium* Juss., shrub. **Juncaceae:** *Luzula racemosa* Desv., herb. **Lamiaceae:** *Satureja nubigena* (Kunth) Briq., creeping species. **Lycopodiaceae:** *Huperzia cruenta* (Spring) Rothm., herb; *Lycopodium clavatum* L., herb. **Poaceae:** *Aciachne pulvinata* Benth., short grass; *Agrostis haenkeana* Hitchc., short grass; *Agrostis tolucensis* H.B.K., short grass; *Anthoxanthum odoratum* L., grass; *Bromus lanatus* Kunth, tall grass; *Calamagrostis coarctata* (H.B.K.) Steudel, short grass; *Calamagrostis effusa* (H.B.K.) Steudel, tussock grass; *Calamagrostis recta* (H.B.K.) Trin. ex Steud., grass; *Cortaderia bifida* Pilger, grass; *Cortaderia nitida* (H.B.K.) Pilger, grass; *Festuca andicola* H.B.K., short grass; *Festuca breviaristata* Pilger, short grass; *Festuca sublimis* Pilger, tussock grass; *Poa subspicata* (Presl) Kunth, short grass; *Poa annua* L., short grass; *Trisetum irazuense* (Kuntze) Hitchc., short grass. **Polygonaceae:** *Muehlenbeckia vulcanica* Endl., dwarf shrub; *Rumex acetosella* L., herb. **Ranunculaceae:** *Ranunculus peruvianus* Pers., herb; *Ranunculus praemorsus* H.B.K., herb. **Rosaceae:** *Lachemilla hispidula* (Perry) Rothm., herb; *Lachemilla holoserica* (Perry) Rothm., creeping species; *Lachemilla mandoniana* (Wedd.) Rothm., creeping species; *Lachemilla orbiculata* (Ruiz & Pav.) Rydb., creeping species; *Potentilla heterosepala* Fritsch, herb. **Rubiaceae:** *Nertera* sp., herb; *Relbunium ciliatum* (Ruiz & Pav.) Hemsl., creeping species; *Relbunium hirsutum* (Ruiz & Pav.) Schum., creeping species. **Scrophulariaceae:** *Castilleja fissifolia* L.f., herb; *Veronica serpyllifolia* L., herb.

insolubilization of organo-metallic complexes (Thouret, 1989). They have a low supply of bases, a low pH, and are rich in organic material. The western part of the national park was selected as study area, being representative for the full range of grazing intensities and fire regimes.

Data collection. In the field, integrated relevés were made in order to describe both natural and human-influenced variation of the main ecosystem components. Sample size was 5 × 5 m or 10 × 10 m, depending on the occurrence of *Espeletia hartwegiana* or shrubs (Cleef *et al.*, 1983). Terrain was described by altitude, landform, slope, slope length, aspect, micro-, and meso-relief. Soil profiles were described after augering up to 120 cm depth, recording for each horizon the corresponding depth, pH, texture, color, and presence of mottles, plant roots, or lapilli. In almost all soil samples a clear 5–10 cm thick layer of lapilli could be distinguished, in general at depths of 60–90 cm. Because this layer impedes penetration of roots and water, its upper boundary was taken as the effective soil depth. Erosion features were included by estimation of the average size (square centimeters) and cover (%) of bare soil spots.

Aspects of vegetation structure included in the relevés were coverage, height, dominant species of the vegetation strata distinguished, and total real coverage. In general, stem rosette, tussock, herb, and ground covering layers were recognized, sometimes with an additional shrub layer. Floristic composition was described by estimation of species coverage according to a modified Braun-Blanquet scale (Mueller-Dombois and Ellenberg, 1974). Above 5% coverage, the percentage was estimated, whereas below this value an abundance rating was given (r= rare, p= few, a= abundant, m= many individuals).

A series of aerial photographs of different years, dating from 1955 to 1989, was used to select sample sites representative for certain changes in vegetation structure. For many sites burning history could be reconstructed by means of identification of clear black spots turning slowly into grey again. Another change was recognized representing the development of light-toned short grass communities under the influence of grazing. Additional information on land management was provided by local farmers and park guards. As a measure of grazing intensity, the number of cow droppings per unit of surface area was taken as an indication. Grazing impact was described by noting the abundance of grazing traces within the vegetation, including traces of scraping by cattle on the stem rosettes, the occurrence of cow paths, micro-terraces, and other trampling impacts such as bare spots induced by cow hoofs. Height of the dead leaf column of regenerating stem rosettes was taken as an estimate of the time since fire, called fire age (Verweij and Kok, 1992). All together 165 relevés were made.

Data analysis. As a first step, a vegetation table was produced, using TWINSPAN (Hill, 1979). This clustering program constructs an ordered two-way table from a sites-by-species matrix. Samples corresponding to the superpáramo belt as described by Cleef *et al.* (1983), the azonal cushion bogs, and the regeneration stage after potato cultivation could be identified and excluded from further analysis. The remaining samples, representing the relatively dry bunchgrass community and its derived succession stages, were studied. For this data set, a new TWINSPAN table was produced.

Initially, the full data set was likewise taken as starting point for analyses using the CANOCO program, that consists of different ordination techniques (Ter Braak, 1987a). All environmental and management variables were included in the set of environmental variables to be related to vegetation parameters. For the above excluded samples, the factors explaining the irrelevant variation were confirmed. An iterative process of exclusion of irrelevant samples and subsequent analysis of results led to a final smaller data set of 122 samples, where only management factors account for the main variation in vegetation characteristics. This final data set corresponds to the zonal bunchgrass páramo, like the TWINSPAN vegetation table. In the CANOCO analyses, however, only samples containing stem rosettes (66 relevés) were included in order to have a reliable assessment of fire age.

Vegetation structure. The variation in coverage of vegetation structure layers among samples of the final data set was analyzed using a linear response model. Principal component analysis, or PCA, is the ordination technique that constructs the theoretical variable that minimizes the total residual sum of squares after fitting straight lines to the coverage data. PCA was carried out to select the best explanatory variables out of 20 available. Of some variables, their natural logarithm (ln) was also included as a possible variable. From the intra-set correlations of environmental variables with the axes, the following variables were selected: 1) the ln of cow droppings (n per 100 square meters), 2) trampling impact, on an ordinal scale from 0.0 to 2.0, with intervals of 0.5, 3) the ln of regrowth of *Espeletia* leaf column as an estimate of fire age (cm), 4) % alive, *i.e.*, the percentage of live tussock biomass, and 5) slope, in degrees.

Subsequently, an overall redundancy analysis (RDA) was performed to relate vegetation structure to these five active variables. RDA is the canonical form of PCA and selects linear combinations of environmental variables to construct the ordination axes, minimizing the total residual sum of squares. The resulting ordination clusters are described. Statistical significance of the first axis was tested with a Monte Carlo permutation test, a standard option of CANOCO. After 99 random permutations, Eigen values did not change ($P < 0.01$).

As it proved difficult to analyze the influences of grazing and burning separately, three detailed RDA-ordinations were carried out to describe the pure influence of grazing on the structure variables. For this purpose, samples were divided into three different classes of regeneration time after fire: 0–10 cm, 10–40 cm, and >40 cm *Espeletia* regrowth. Ordinations were carried out for each fire age class.

Species composition. For species occurring more than twice in the data set, both direct and indirect gradient analyses were carried out, based on their cover values in each sample. First, a linear response model was tested

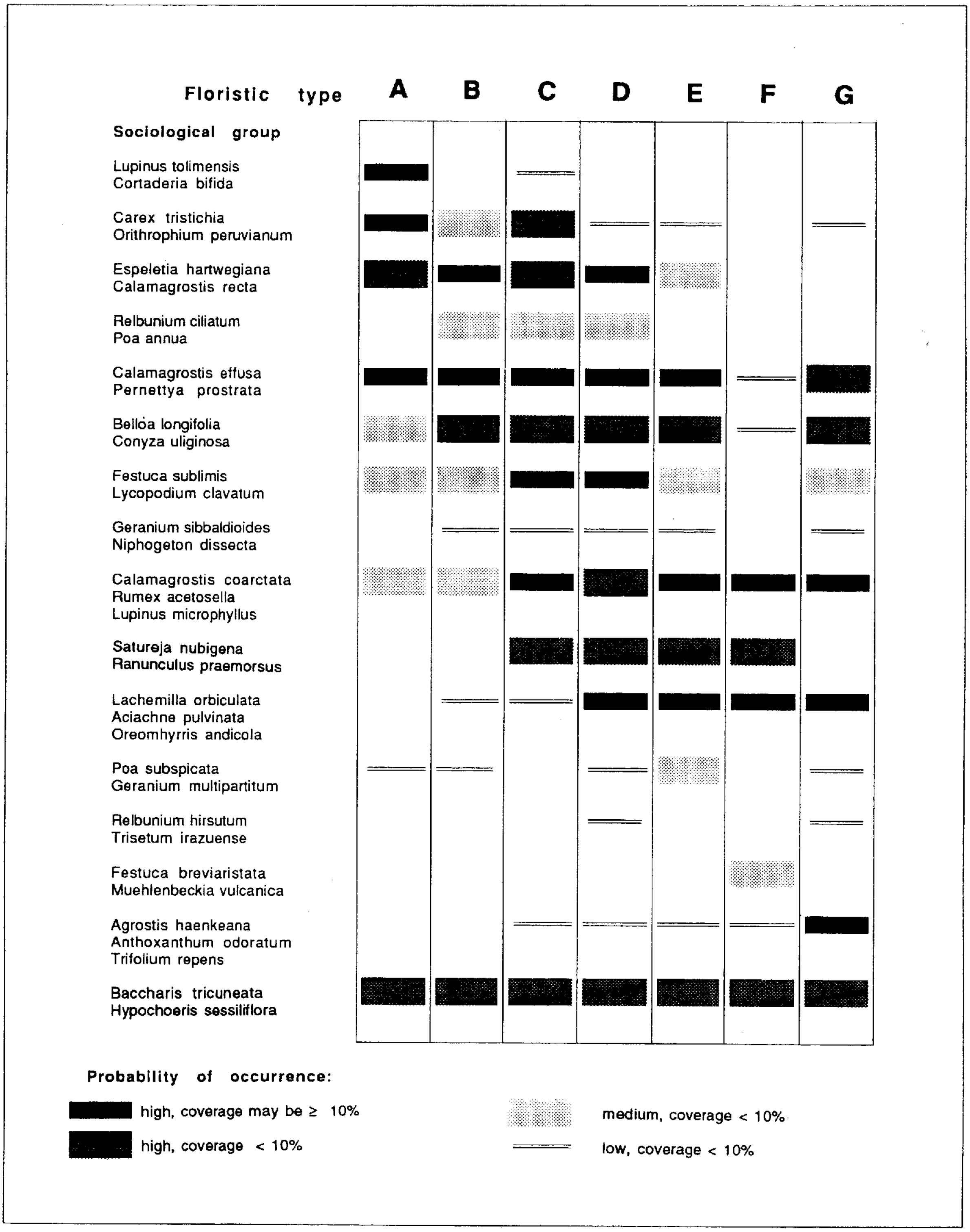

Figure 2. Bar diagram of the vegetation table based on TWINSPAN, representing the zonal tussock grasslands (3900–4200 m) of the western part of Parque Nacional Natural Los Nevados. The probabilities of occurrence of species of a sociological group in a certain vegetation type are expressed as follows: high = occurrence > 50 %, medium = occurrence 25–50 %, and low = occurrence 5–25 %.

against a unimodal response model, by using a Principal Component Analysis (PCA) and a Correspondence Analysis (CA), respectively. CA is a technique that constructs theoretical variables that best explain the variation in species scores; it is based on a unimodal response curve. CA gave a good separation of the species. The length of the first axis was 3.8 standard deviation units, which implied that the use of a unimodal response curve was more appropriate (Jongman *et al.*, 1987). On the basis of the CA, best explanatory variables were selected. Subsequently, direct gradient analyses were carried out with the selected variables, using the technique of Canonical Correspondence Analysis (CCA). What distinguishes CCA from CA is that it constructs ordination axes directly out of linear combinations of the environmental variables. The separate influence of burning and grazing on species composition still could not be seen very clearly in the prepared biplots due to the large number of both species and management variables. Therefore, three biplots were produced with CCA in which the first axis was kept constrained for only one variable and the other axes unconstrained. In this case, the constrained axis was constructed in each analysis out of one determined variable. These variables were number of cow droppings, trampling impact, and regrowth of *Espeletia* combined with percent living biomass. By this method, species reaction to one variable was revealed.

Results

A summary of the vegetation table prepared with the aid of TWINSPAN is given in the form of a bar diagram presented in Figure 2. Seven floristic types were defined, coinciding with the first three levels of division of

Table 2. Averages of management variables of grazing and burning in relation to recognized vegetation types of the zonal bunchgrass páramo.

Floristic types	**A**	**B**	**C**	**D**	**E**	**F**	**G**
No. of cow droppings (per 100 square meters)	4	–	7	11	42	4	32
Distance to farm (m)	4000	2900	2240	1810	1640	2140	910
Micro-terraces (ordinal scale, from 0 to 1)	0.08	0.00	0.56	0.63	0.00	0.57	0.64
Slope (°)	25	30	21	20	11	14	13
Fire age (years)	1.5	9.0	3.1	6.7	> 20	> 20	–
n	13	8	35	24	18	7	13

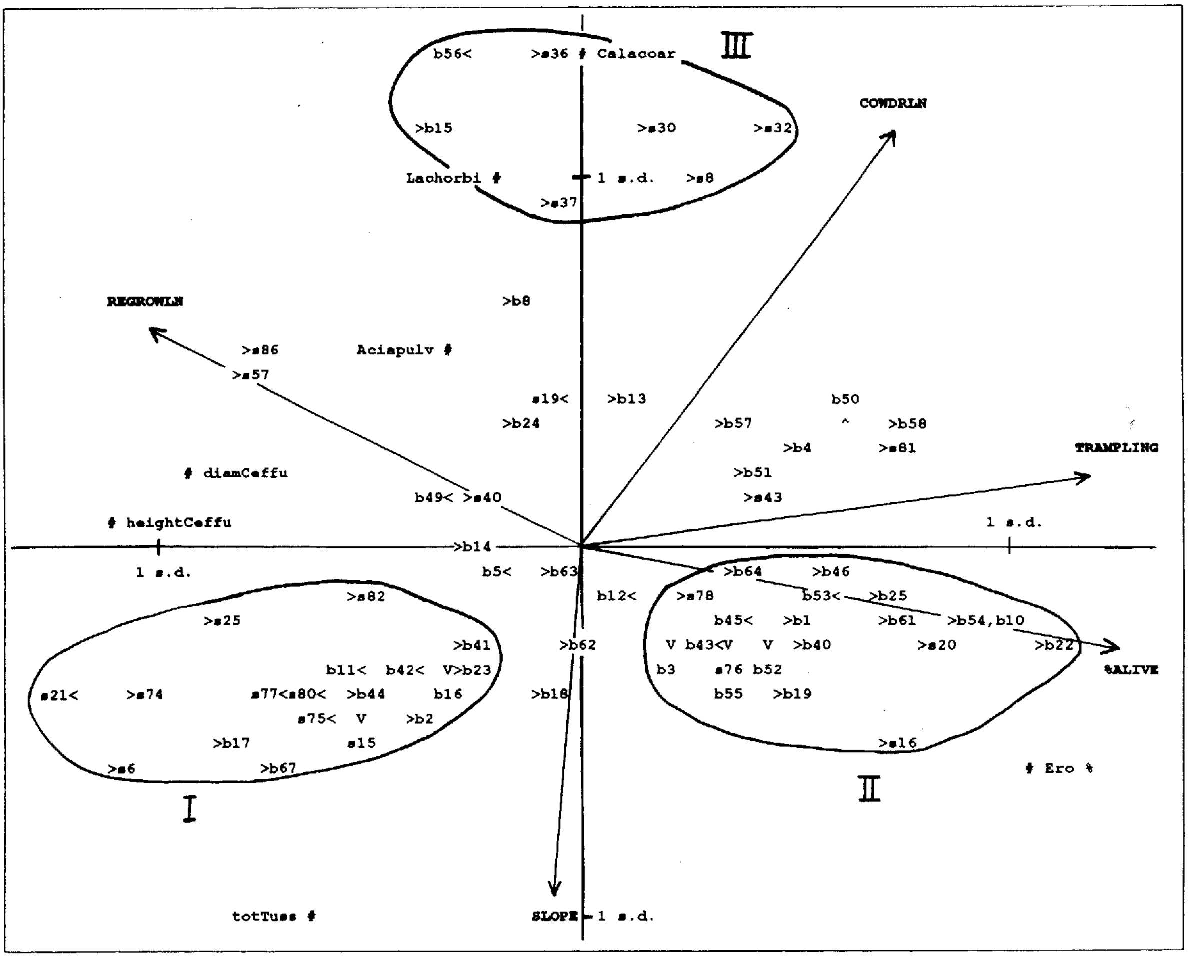

Figure 3. Biplot of the overall structure analysis resulting from RDA ordination. Sample numbers: numbers beginning with s or b. >, <, ^, and V indicate the position of the corresponding sample numbers. Structure variables: total tussock coverage, *Calamagrostis effusa* height, *Calamagrostis effusa* diameter, *Calamagrostis coarctata* coverage, *Aciachne pulvinata* coverage, *Lachemilla orbiculata* coverage, and erosion percentage. Management variables: ln (regrowth of *Espeletia* in cm) as fire age variable, ln (number of cow droppings per 100 square meters), trampling impact in classes, percentage alive tussock biomass, and slope in degrees. Scale of the diagram: 1 unit in the plot corresponds to 1 standard deviation unit for sample scores, to 3.45 units for the structure variables, and to 0.29 units for the management variables.

TWINSPAN. In Table 2, the average values of relevant management variables are given for each floristic type. The first and thus most important division was made between floristic type D and E, and corresponds with samples on moderate slopes on one hand (A–D) and the more gentle slopes (11–14° on average of types E–G) on the other. From type A–D, certain differences in grazing intensity and fire age were observed. Type A corresponds to recently burned situations (fire age 1.5 years on average) and is not yet intensively grazed. Type B is not grazed at all, which is probably because of the long time since burning (9 years on average) which makes the bunchgrasses less palatable (Schmidt and Verweij, 1992). Types C and D are recovering from burning and are moderately grazed.

The flatter parts are in general most intensively grazed, and it is particularly at those places that the short grass species and matted herbs develop, *e.g.*, the group of *Lachemilla orbiculata* and *Aciachne pulvinata*, and the group of *Calamagrostis coarctata* and *Lupinus microphyllus*. Floristic type G is intensively and is located a short distance from the farms. This type is characterized by species such as *Agrostis haenkeana*, *Lachemilla orbiculata*, and *Trifolium repens*; probably it corresponds to the *Agrostio breviculmis – Lachemilletum orbiculatae* (Cleef, 1981). Type E and F are similar to the *Aciachnetum pulvinatae* (Vareschi, 1953); type F is a product of grazing in the past, maintained by an actual low grazing pressure.

Vegetation structure. Of the RDA ordination, a biplot is given in Figure 3. The drawn clusters were made visually to gain insight into the variation of relevant variables. They were drawn around small groups of samples along or just in between arrows of management variables, and with some distance from the origin. Table 3 presents the average values of the structural variables and the management variables of the distinguished clusters of Figure 3. Fire age and percent of living tussock biomass (% alive) are best correlated to the first axis, whereas the amount of cow droppings (ln) and slope steepness are best correlated to the second axis. The RDA output showed the following figures for eigen values and species-environment

Table 3. Average values and standard deviations of structure variables and management variables of clusters I–III in the overall RDA structure analysis.

Variable	I (n=18)	II (n=20)	III (n=7)
Total tussock coverage (%)	63 ± 14	29 ± 8	5 ± 6
Calamagrostis effusa height (cm)	44 ± 08	18 ± 7	30 ± 16
Calamagrostis effusa diameter (cm)	16 ± 05	4 ± 2	13 ± 7
Calamagrostis coarctata coverage (%)	1 ± 1	1 ± 1	38 ± 20
Aciachne pulvinata coverage (%)	0 ± 0	0 ± 0	10 ± 10
Lachemilla orbiculata coverage (%)	0 ± 0	0 ± 0	27 ± 23
Erosion spots (%)	7 ± 5	30 ± 9	4 ± 3
Espeletia regrowth (cm)	59 ± 73	12 ± 12	136 ± 85
Cow droppings (n/100 m^2)	0 ± 0	8 ± 8	46 ± 30
Alive tussock biomass (%)	34 ± 13	73 ± 20	39 ± 11
Slope (^{o})	28 ± 05	25 ± 7	11 ± 13
Trampling impact (ordinal scale from 0 to 2)	0.3 ± 0.4	0.9 ± 0.6	0.5 ± 0.4

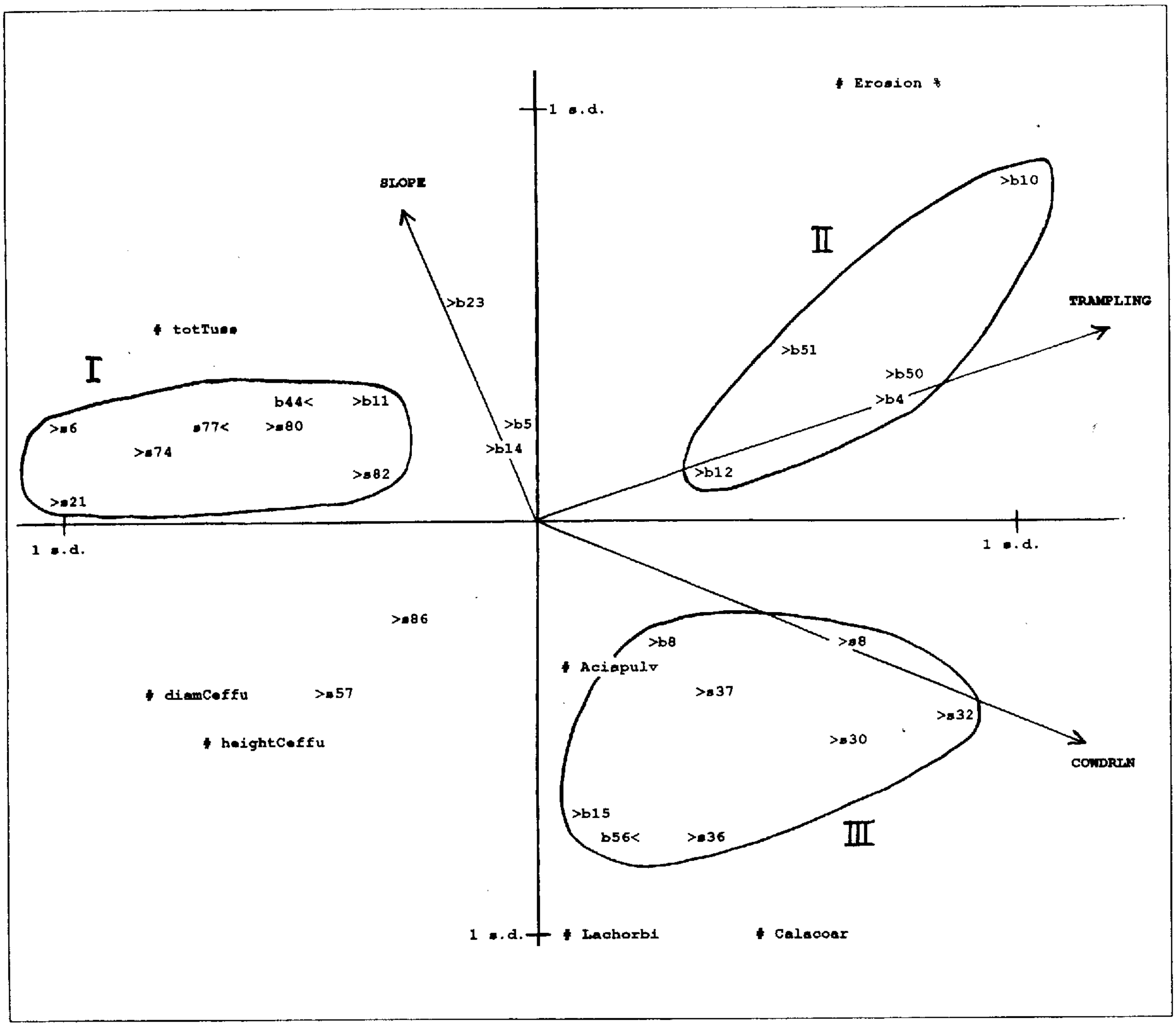

Figure 4. Biplot of a RDA structure analysis in which only samples with an *Espeletia* regrowth of 40–300 cm were analyzed to show the influence of grazing in this time interval. Sample numbers: numbers beginning with s or b. Position of the corresponding sample is indicated by >, <, ^, and V. Structure variables: total tussock coverage, *Calamagrostis effusa* height, *Calamagrostis effusa* diameter, *Calamagrostis coarctata* coverage, *Aciachne pulvinata* coverage, *Lachemilla orbiculata* coverage and erosion percentage. Management variables: ln (number of cow droppings per 100 square meters), trampling impact in classes, and slope in degrees. Scale of the diagram: 1 unit of standard deviation in the plot corresponds to 1 unit for samples, to 2.76 units for the structure variables and to 0.39 units for the management variables.

correlations:

1st axis	$\lambda = 0.23$	$R = 0.85$
2nd axis	$\lambda = 0.14$	$R = 0.77$

The first two axes account for 87% of the variance in the weighted averages of the species with respect to the environmental variables. This percentage is calculated as in principal components analysis by taking $100 \times (\lambda_1 + \lambda_2)/$

($\lambda_1 + ... + \lambda_p$) (Ter Braak, 1987b). In the biplot of Figure 3, scores of structural variables, sample scores according to these structural variables, and biplot scores of environmental values are plotted. The first axis describes how a decrease of tussock height and diameter and an increase of erosion (bare soil) are positively correlated to recent burning (low values of ln regrowth, high values of percent alive). The second axis represents the positive correlation between a decrease of tussock cover and an increase of matted herb cover on the one hand and a higher number of cow droppings on the more gentle slopes on the other hand.

Cluster I (Fig. 2) corresponds to samples with high tussock cover (63%) and high values of tussock height and diameter. Matted herbs are not important, erosion is low. Both trampling impact and number of cow droppings are close to zero, and regrowth of *Espeletia* indicates that fire age is at least five years. This cluster can thus be characterized as relatively undisturbed. Cluster II represents recently burned samples with an average regrowth of 12 cm, which corresponds to a fire age of 1–2 years. It is therefore not surprising that tussock cover, height, and diameter are small and that a high percentage of green tussock biomass is present (73% in comparison to 34% of cluster I). The bare soil percentage is important (30%). Finally, cluster III is characterized by high cover of matted grasses and forbs, whereas tussocks are almost absent with a cover value of 5%. If tussocks are present, the size of the bunches is rather large, which indicates that cattle apparently prefer to graze on the short grasses or young bunchgrasses. The number of cow droppings shows a high grazing pressure and such samples occur on the more level terrains. The few stem rosettes remaining possess high dead leaf columns, corresponding to a long regeneration time after fire or no burning at all. Probably the absence of sufficient fuel prevents these sites from being burned.

Of the detailed RDA-ordinations carried out for each fire age class separately, one example is presented. In Figure 4, the ordination diagram of sites burned at least four years ago (regrowth stem rosettes 40–300 cm) is given. As a consequence of this separate analysis, the sample number became smaller, but tendencies are nevertheless clear. Eigen values and species-environment correlations were:

1st axis	$\lambda = 0.27$	$R = 0.88$
2nd axis	$\lambda = 0.13$	$R = 0.87$

where % variance accounted for by the first two axes equals 84%.

The environmental variables best correlated to the first axis are trampling and cow droppings (ln), which means that the first axis is a grazing gradient. The biplot of Figure 4 shows three clear groups at the outer parts of the diagram. Corresponding values of structure and environmental variables are presented in Table 4. Cluster I is the relatively undisturbed situation on moderate slopes, similar to the first cluster of the overall ordination (Fig. 2). If clusters II and III are compared, the effect of slope steepness becomes clear. Both groups are more intensively grazed, which at the steeper slopes of cluster II clearly leads to a more pronounced trampling impact and higher cover of bare soil than on the gentle slopes and flat terrain of cluster III.

It can be concluded that grazing on slopes leads to a decrease of bunchgrass cover, diameter, and height, and simultaneously to an increase of the percentage of bare soil and trampling impact. In the valley bottoms and on flat parts, grazing is related to the development of a closed mat of short grasses and ground-covering forbs.

Species composition. Three separate analyses were performed in which only one variable determined the first constrained axis. Three joint representations of species scores and biplot scores of environmental variables were prepared, analyzing response to number of cow droppings, trampling impact, and *Espeletia* regrowth combined with percent alive tussock biomass. Eigen values of the first axes were 0.21, 0.09, and 0.13, respectively. The corresponding species-environment correlations for each of these first axes were 0.78 (R for cow droppings), 0.83 (R for trampling impact), and 0.68 (R for *Espeletia* regrowth combined with % alive), respectively. Species

Table 4. Average values and standard deviations of structure variables and management variables of RDA ordination groups in a structure analysis in which only samples with an *Espeletia* regrowth of 40–300 cm were analyzed to show the influence of grazing in this time interval.

Variable	**I (n=18)**	**II (n=5)**	**III (n=8)**
Total tussock coverage (%)	63 ± 10	21 ± 16	7 ± 8
Calamagrostis effusa height (cm)	50 ± 9	21 ± 12	31 ± 15
Calamagrostis effusa diameter (cm)	24 ± 6	7 ± 3	14 ± 7
Calamagrostis coarctata coverage (%)	1 ± 1	6 ± 10	36 ± 20
Aciachne pulvinata coverage (%)	0 ± 0	0 ± 0	9 ± 10
Lachemilla orbiculata coverage (%)	0 ± 0	1 ± 1	25 ± 22
Erosion spots (%)	4 ± 4	20 ± 11	4 ± 3
Espeletia regrowth (cm)	145 ± 79	96 ± 87	127 ± 84
Cow droppings (n/100 m^2)	2 ± 3	18 ± 8	41 ± 31
Alive tussock biomass (%)	33 ± 12	58 ± 12	36 ± 12
Slope (°)	27 ± 11	25 ± 13	10 ± 12
Trampling impact (ordinal scale from 0 to 2)	0.1 ± 0.2	1.6 ± 0.4	0.6 ± 0.4

Table 5. Results of three species analyses in which each time the first axis was kept constrained with one (or two) management variables. In the first analysis the number of cow droppings was the active management variable on the first axis, in the second analysis trampling impact, and in the third analysis fire age as indicated by ln (regrowth of *Espeletia* in cm) combined with % alive tussock biomass. The distance from the origin of the species is given in standard deviation units. The species mentioned lie at least 1.2 units from the origin.

COW DROPPINGS		*TRAMPLING IMPACT*		*FIRE AGE AND % ALIVE*	
Negative reaction (s.d.)		**Negative reaction (s.d.)**		**Recent burning and high % alive tussock biomass**	
Cortaderia bifida -	1.5	*Cortaderia bifida* -	4.0	*Relbunium hirsutum* -	2.5
Myrrhidendron glaucescens -	1.5	*Myrrhidendron glaucescens* -	3.6	*Carex tristichia* -	2.4
Werneria crassa -	1.5	*Werneria crassa* -	3.1	*Carex pichinchensis* -	2.4
Cortaderia nitida -	1.3	*Huperzia cruenta* -	2.8	*Disterigma empetrifolium* -	2.0
Gnaphalium pellitum -	1.3	*Jamesonia sp.* -	2.7	*Oritrophium peruvianum* -	1.8
Hieracium tolimense -	1.3	*Lupinus tolimensis* -	2.3	*Arenaria serpens* -	1.8
Nertera sp. -	1.3	*Gnaphalium pellitum* -	2.0	*Zorella multifida* -	1.7
Relbunium hirutum -	1.3	*Lachemilla hispidula* -	1.9	*Nertera sp.* -	1.6
Jamesonia sp. -	1.2	*Hypericum lancioides* -	1.8	*Lupinus tolimensis* -	1.5
		Hieracium tolimense -	1.8	*Cortaderia bifida* -	1.4
		Bromus lanatus -	1.8	*Gnaphalium antennarioides* -	1.2
		Castilleja fissfolia -	1.7		

Table 5. CONTINUED —

COW DROPPINGS		*TRAMPLING IMPACT*		*FIRE AGE AND % ALIVE*	
Positive reaction (s.d.)		**Positive reaction (s.d.)**		**Old/no fire and low % alive tussock biomass**	
Taraxacum officinale -	4.5	*Arenaria serpens* -	3.4	*Aciachne pulvinata* -	4.3
Poa subspicata -	3.8	*Poa annua* -	3.1	*Potentilla hetrosepala* -	3.2
Aphanactis piloselloides -	3.6	*Veronica serpyllifolia* -	3.1	*Werneria crassa* -	3.2
Calamagrostis coarctata -	3.3	*Lachemilla mandoniana* -	3.0	*Aphanactis piloselloides* -	3.1
Lachemilla orbiculata -	2.5	*Geranium columbianum* -	2.3	*Agrostis haenkeana* -	2.9
Festuca andicola -	2.3	*Rumex acetosella* -	2.2	*Poa subspicata* -	2.9
Geranium multipartitum -	2.1	*Agrostis tolucensis* -	1.9	*Hieracium tolimense* -	2.4
Veronica serpyllifolia -	1.8	*Gnaphalium lanuginosum* -	1.9	*Escallonia myrtilloides* -	2.2
Aciachne pulvinata -	1.5	*Agrostis haenkeana* -	1.7	*Hypericum lancioides* -	2.1
Ranunculus peruvianus -	1.2	*Arenaria sp. 1* -	1.7	*Geranium sibbaldioides* -	2.0
		Ranunculus praemorsus -	1.6	*Lachemilla orbiculata* -	1.9
		Luzula racemosa -	1.5	*Satureja nubigena* -	1.7
		Lachemilla holoserica -	1.5	*Bromus lanatus* -	1.6
		Bidens triplinervia -	1.4	*Gentianella dasyantha* -	1.6
		Lupinus microphyllus -	1.4	*Geranium multipartitum* -	1.5
		Gentiana sedifolia -	1.3		

located at a distance of at least 1.2 units of standard deviation from the origin (distance as projected on the first axis) were regarded as showing a positive or negative reaction to the management variables concerned. Results are summarized in Table 5, listing the species that show either a positive or negative reaction to grazing intensity, trampling impact, and fire regeneration time.

Some species, such as *Cortaderia bifida, Jamesonia* sp., *Myrrhidendron glaucescens*, and *Werneria crassa* demonstrate a negative response to both trampling impact and number of cow droppings as a measure of grazing intensity. There is a group of species, consisting of *Lachemilla orbiculata, Taraxacum officinale, Festuca andicola, Poa subspicata*, and *Aphanactis piloselloides*, that shows a positive reaction to grazing intensity but neutral or negative to trampling impact. *Arenaria serpyllifolia* and *Poa annua* are two examples of species reacting positively to trampling impact only.

Carex tristichia, Lupinus tolimensis, and *Cortaderia bifida* are species related to recent burning. This confirms the relation of vegetation type A, where these last species are characteristic, with recent burning (Fig. 2). These species are also related to more humid conditions, as appeared from earlier TWINSPAN and CANOCO analyses. *Aciachne pulvinata* only occurs at places that were burned a long time ago or at unburned sites. Shrubs showing a positive reaction to a long regeneration time after fire are *Escallonia myrtilloides* and *Hypericum lancioides*. Other shrub species such as *Hypericum laricifolium, Pentacalia vaccinoides*, and *Pernettya prostrata* were found to be related to the average fire age.

The ordinations are useful in confirming the characterization of certain processes, but do not prove direct causal relationships. In this sense, the obtained results need to be interpreted with utmost care. Besides, an aspect requiring further attention is the rate of the observed changes. For modelling purposes, the key variables that we assume steer the replacement of one community by another can be selected on the basis of the described ordinations, but possible transitions and the velocity of these processes still need to be studied. A start has been made with the development of a model for a small pilot area (Pels and Verweij, 1992).

Another interesting aspect that merits further study is the influence of fire frequency on vegetation dynamics. In a study of mortality and regeneration of woody perennials in a Costa Rican páramo vegetation, Williamson *et al.* (1986) concluded that frequent fires possibly maintain a dominance by graminoids at the expense of woody species. A fire frequency of once a decade may be sufficient to preclude dominance by shrubs in these ecosystems. In the case of the páramo of Los Nevados, the cover by shrubs in frequently burned areas is indeed low. Little is known so far concerning the interaction between *Espeletia* plants and tussock grasses. Apparently fire is an important factor in determining the outcome of the dynamics among the different plant groups.

Acknowledgments

We thank the División de Parques Nacionales of INDERENA, in particular C. Castaño, G. Sánchez, and park guards for the continuous logistic support. During the identification of plant species, the help of O. Rangel, S. Díaz, and J. Uribe of the Herbario Nacional of Bogotá was highly appreciated. We further thank the cooperation by the Instituto Geográfico Agustín Codazzi, Bogotá, and by the Herbarium of the State University of Utrecht. Special thanks are due to W. van Wijngaarden and A. M. Cleef for stimulating guidance and to the local farmers from whom we also learned a lot.

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