



Vegetation patterns, regeneration rates and divergence in an old-field succession of the high tropical Andes

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Received 13 November 2001; accepted in revised form 9 May 2002

Key words: Alpine vegetation, Fallow agriculture, Life forms, Paramo, Species diversity, Species invasions, Vegetation succession, Venezuela

Abstract

Vegetation restoration during old-field succession was studied in an alpine Andean ecosystem (paramo). 123 plots with different fallow times (1 to 12 years) and 8 plots under natural vegetation were sampled. The results indicate that secondary succession in the paramo, like in other extreme environments, can be interpreted as an *autosuccession*: there are mainly changes in species relative abundance and little floristic relay (i.e. species turnover). Only a few herbaceous species, mostly introduced (e.g. *Rumex acetosella*), act as strict pioneers and strongly dominate the early stages. Then, they undergo a progressive decline, while native forbs (e.g. *Lupinus meridanus*) and grasses (e.g. *Vulpia myuros*) have their peak abundance in intermediate stages. The characteristic paramo life forms, sclerophilous shrubs (e.g. *Baccharis prunifolia*, *Hypericum laricifolium*) and giant rosettes (e.g. *Espeletia schultzei*), appear very early and gradually increase in abundance during succession, becoming dominant in the late stages and showing a dual behaviour, both as ruderal and stress tolerant species. The 1st axis of a Detrended Correspondence Analysis arranges the sites according to their fallow time. The 2nd and 3rd axes, associated with diverging pathways of regeneration, are correlated with topographic factors and physio-chemical soil characteristics. Hence, structural divergence between plots increases along succession as community composition starts to reflect the conditions of each site. We found evidence of a constant rate of succession during the first 12 years, contradicting the generally accepted hypothesis in the succession literature of a continuous slow down up to the climax. Regeneration of vegetation physiognomy is relatively fast, questioning the prevailing idea of slow restoration in alpine ecosystems. However, 12 years of fallow are insufficient to attain the species richness of the natural paramo. Under the current trend of fallow length reduction observed in traditional potato cultivation in the Andes, our results raise doubts about the conservationist value of this management strategy.

Introduction

Knowledge of the mechanisms, rates and pathways of secondary succession is crucial for understanding the response of the vegetation to disturbance and to design strategies for ecosystem management and restoration. There are a number of generalizations in the literature on what to expect during plant secondary succession, including a successional increase in evenness, a high degree of predictability in the sequence of different life forms (Bazzaz 1996), a successional

decline of introduced species (Pickett 1982; Vitousek 1986), and a decrease of the rate of succession as the system approaches its mature state (Myster and Pickett 1994). Other aspects, like the successional trend for species diversity, have generated substantial debate. Some authors (e.g. Odum (1969)) support the idea of a continuous increase in diversity, while others suggest there should be a “nearly universal decline” at late stages (e.g. Horn (1974)). Another important area of disagreement has been whether to expect convergence in community structure towards

a single climax (as suggested by the classical ideas of Clements) or divergence along multiple alternative states of ecosystem development.

The study of succession has mostly been developed in temperate ecosystems, and in the case of the tropics, in lowland "old-field to forest" systems. Considerably less information is available on secondary succession in the highland tropics. The unique climate (low temperatures and no thermal seasons) and the treeless nature of tropical highland environments make them ideal for evaluating the generality of the expected trends discussed above. In other treeless ecosystems, like arctic and temperate alpine, attention has mainly been given to the study of primary succession in recently deglaciated areas (Matthews 1992). However, secondary succession proceeds at different rates and implies other mechanisms.

The Paramo is a tropical alpine ecosystem that occupies the upper belt of the Northern Andes (3000 to 4800 m). Giant caulescent rosettes, shrubs and bunch grasses dominate the vegetation. Most of the paramos are located in Venezuela, Colombia and Ecuador, and their flora is among the richest in the high mountains of the world (van der Hammen and Cleef 1986). Recently, the paramo has been subjected to an accelerated process of degradation and transformation, characterised by agricultural intensification and a continuous expansion of the agricultural frontier (Ferweda 1987; Luteyn 1992; Hofstede 1995; Hess 1990; Drost et al. 1999). The increasing human intervention, frequently involving long fallow agriculture, makes the study of secondary succession a priority for the preservation and management of this unique environment.

An important insight from recent theory, which can help in furthering the understanding of paramo succession, is to interpret vegetation development as a "vector", analysing both its rate and its directionality (Bakker et al. 1996). On the one hand, several authors agree that these high altitude ecosystems are fragile, showing slow rates of plant growth and regeneration after disturbances like fire and grazing (Janzen 1973; Horn 1989; Luteyn 1992; Hofstede et al. 1995). On the other hand, the possibility of multiple pathways of vegetation development has been emphasised in the mountain restoration context (Urbanska 1997). Apart from processes like random colonisation and non-linear species interactions, divergence in these highland systems could be due to the spatial heterogeneity of the environment, which would favour differentially the persistence of the ar-

iving species. The high topographic and edaphic heterogeneity that characterises paramo environments (Llambí and Sarmiento 1998) offers a unique opportunity to analyse this issue. Nevertheless, very few detailed studies on vegetation dynamics in paramo old-field succession are available in the literature (but see Ferweda (1987) and Moreno and Mora-Osejo (1994)) and none have measured divergence and regeneration rates.

The objective of this study is to characterise old-field succession in a Venezuelan paramo, analysing the change in species richness and abundance and in the life-forms spectrums of the vegetation. Succession is evaluated in terms of whether it shows convergence or divergence and how this is related to environmental conditions. The rate of succession and the time necessary for the restoration of vegetation structure are also examined, evaluating the possible impact of fallow agriculture on paramo biodiversity.

Methodology

Study area

The study was carried out in the Páramo de Gavidia, located in the Sierra Nevada National Park, in the state of Mérida, at an altitude of 3200 to 3800 m a.s.l. The area is a narrow glacial valley, with well-drained inceptisols (*Ustic Humitropept*) of a sandy-loam texture, low pH (4.25 to 5.5), high organic matter levels (up to 20%) but low mineral nutrient contents (Llambí and Sarmiento 1998). Agriculture is practised on steep slopes and also on small colluvial and alluvial deposits in the valley bottom. The precipitation regime is unimodal, with a dry season between December and March and a peak of rainfall between June and July. The mean temperature ranges between 9 and 5 °C (with a higher frost frequency during the dry season) and the mean annual precipitation is 1300 mm. The land use system practised in the area is long fallow agriculture. Potatoes are grown during an agricultural phase lasting between 1 to 3 years. Agricultural practices include the incorporation of the successional vegetation as a green manure, mineral fertilisation with an average dose of 1.8 t ha⁻¹ year⁻¹ of NPK and two to three ploughs per year. After the cultivation period, the fields are abandoned and the succession-restoration phase begins (Sarmiento et al. 1993). The current average fallow length is 4.6 years, but there is 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 cattle and horse grazing.

Plot selection

In mountain ecosystems, the study of secondary succession using synchronic methods (space for time substitution) is especially difficult due to the inherent heterogeneity of the environment. A large number of plots were selected in this study to attempt to differentiate the effects of time and spatial heterogeneity. We used a spatial database (Smith (1995), updated to the year 2000) which contains information on the fallow lengths of 1200 fields. This database also contains information for all the plots of attributes such as slope, area, aspect, elevation and distance to the valley bottom. 123 plots, between 1 and 12 years of fallow (repetitions per year: 12, 11, 12, 15, 16, 11, 10, 9, 7, 5, 4, 3), and 8 areas of never cultivated paramo (NCP) were selected. Fewer late successional plots were included as the database has no information on the exact fallow time for the oldest plots.

Sampling and data analysis

In each selected plot, the point-quadrat method was used to sample the vegetation (Greig-Smith 1983). A pin was placed vertically 100 times at random positions and the contacts with all species in 10 cm height intervals were recorded. All the vegetation relevés were carried out between 1996 and 1999, during the last part of the rainy season (September to November), when most of the species are in flower. This information was used to construct a matrix of species versus relevés.

A composite soil sample (0–20 cm) of each plot was collected from 10 random points and analysed for texture (Bouyocos method), total carbon (Walkley-Black), nitrogen (micro Kjeldahl), pH (measured in 1/1 soil water mixture using a pH meter) and CEC (measured after extraction with 1 M NH₄OAc at pH 7). An environmental matrix was constructed using the soil parameters and the other plot attributes extracted from the spatial database.

Richness was estimated as the total number of species recorded in each plot. Species abundance was calculated as the total number of contacts of each particular species by plot. Rank abundance diagrams were plotted for contrasting stages of succession as originally suggested by Whittaker (1972). The distri-

bution of the abundance between the different life-forms was also analysed. Additionally, species were classified as native or introduced.

We performed a Detrended Correspondence Analysis (DCA) on the species vs. relevés matrix, using the CANOCO 4.02 software (Ter Braak and Smilauer 1999). The “detrending” was done by segments as suggested by Hill and Gauch (1980). To interpret the ordination we calculated Spearman’s rank correlations of each axis with successional time and environmental variables.

The rate of succession has been understood in two ways in ecology: as the time it takes community structure to reach its climax stage, or as the year to year rate of change in the vegetation structure (Prach 1993). The first interpretation faces the difficulty of clearly defining what is considered to be the terminal stage. For the second interpretation, two main approaches have been proposed (Pickett 1982; Prach 1993; Myster and Pickett 1994; Donnegan and Rebertus 1999): 1) calculating an index of species turn-over (e.g. Sorensen’s) between consecutive years, ignoring changes in species abundance or 2) calculating an index of community dissimilarity (e.g. Euclidean distance). The second approach was deemed the most promising in the case of the paramo, since our results indicate that succession is characterised by changes in species abundance more than species turnover. For the calculation we used two different methodologies, both based on calculating dissimilarity between all the plots of each fallow time and 1st year plots (called by Bakker et al. (1996) the *net rate of succession*). In one method we used chord distance (i.e. Euclidean distance on the normalized matrix, Orloci (1978)) as our dissimilarity index. For the other method, we used the distance in the DCA 1st axis scores, as this axis is strongly correlated to successional time (see results). A regression analysis was then carried out having time as the independent variable and our dissimilarity index as the predicted variable. The slope of the adjusted curve corresponds to the succession rate. To obtain an estimate of the time required for the system to reach a community structure similar to that of the never cultivated paramo an extrapolation of the adjusted function was performed, using the average distance between the 1st year plots and the NCP plots.

Successional divergence in species composition was analysed by comparing dissimilarity between all plots of a particular age (Christensen and Peet 1984). We used chord distance as our dissimilarity measure.

Results

In the 123 studied plots, 122 species of vascular plants were recorded. The best represented families were: Asteraceae, Poaceae and Rosaceae, with 32, 27 and 6 species respectively. In Table 1 the 44 most abundant species are ordered according to their relative abundance in succession (the same species included in the DCA diagrams). The following groups of species can be identified: a) Pioneers, such as *Rumex acetosella*, which is the most abundant species during the first 9 years of succession, showing a maximum of relative abundance during the 2nd year and a continuous decrease thereafter. Other species as *Erodium cicutarium*, also act as pioneers but show a faster decline. b) Mid-successionals, having their peak of abundance at intermediate stages (e.g. *Lupinus meridanus*). c) Late-successionals, showing their peak at the end of the study interval (e.g. *Baccharis prunifolia*). d) Dominant paramo species, a group that appears during the succession but has its maximum in the NCP (e.g. *Espeletia schultzei*). e) Exclusive paramo species, which do not appear during succession (e.g. *Calamagrostis effusa*).

It can be seen in Table 1 that most of the successional species can also be found in the NCP, with the exception of a few pioneers. Moreover, the majority of the species are present during the whole studied interval. Succession appears as a continuous process of change in species abundance more than as a sequence of well defined successional stages.

Species richness doubles during the first four years of succession, passing from an average of 10 to 20 species per plot (Figure 1). Hereafter, the number of species stabilises, without any clear successional trend. After 12 years of succession, richness stays significantly lower than the average of 36 species measured for the NCP.

The rank abundance curves showed a tendency to flatten out as succession proceeds, reflecting the increase in the number of recorded species and the decrease in their relative dominance (Figure 2). Although the difference between the extremes (first year fallow and NCP) was clear, there were no clear differences between the rank abundance patterns for the intermediate years. This agrees with the asymptotic behaviour of richness seen in Figure 1.

The average relative abundance of the main life forms showed clear successional trends (Figure 3). Forbs presented a progressive decline, beginning with 80% of the total abundance in the first year of suc-

cession and attaining 33% by the 12th year. Simultaneously, shrubs and giant rosettes increased their abundance from less than 2% in the first year to 42% and 10% after 12 years respectively. Grasses did not show any successional tendency, representing on average 20% of the total plant abundance. After 12 years of succession the life form spectrum of the vegetation was very similar to that of the NCP, suggesting a relatively effective restoration of vegetation physiognomy.

There was a sharp decrease in the abundance of introduced species during succession, from 70% in the first year to 5.5% in year 12 (Figure 4). The most abundant of the introduced species was, by a large margin, *Rumex acetosella* (Table 1).

A clear successional progression can be seen in the ordination of the plots along the 1st DCA axis, with the early successional plots occupying the extreme left of the diagram and the NCP plots the right (Figure 5). A strong positive correlation between time and the scores on this 1st axis was found ($r = 0.85$, $p < 0.001$, Table 2). Nevertheless, an important overlap between plots of different ages occurred, indicating again the difficulty of defining discrete successional stages and suggesting that the rate of succession is not the same for all the plots.

The ordination scores of the species on the 1st axis were indicative of their changes in abundance in the successional sequence and corresponded very closely with the results in Table 1. The analysis of the 2nd axis indicated that there was a clear successional divergence, with a progressively greater dispersion of the sites from the left to the right extreme of the 1st axis. The 2nd axis was negatively correlated with the distance to the valley bottom and less significantly to the clay content (Table 2). The distance to the valley bottom can be related both to geomorphologic position and to grazing intensity, which is greater in lower areas due to the proximity of farmer houses. *Acaena elongata* is an example of a species that prefers the valley bottom, while species such as *Luzula racemosa* show a strong preference for the more distant zones.

Divergence along the 3rd axis showed the opposite trend, with maximal dispersion in early successional stages (Figure 5). This axis was significantly correlated with many environmental variables as soil texture, pH, C and N content, absolute altitude above sea level and slope (Table 2) and can be interpreted as the more subtle response of plant species to the specific environmental conditions of the plots. In the 3rd axis *Lupinus meridanus* and *Senecio formosus* are

Table 1. Abbreviation of the 44 more abundant species names and their origin (N = native, I = introduced), life form and relative abundance along the succession and in the never cultivated paramo (NCP).

Species name	Abbreviation	Origin	Life form	Years in succession												NCP
				1	2	3	4	5	6	7	8	9	10	11	12	
<i>Poa annua</i> L.	Poa ann	I	Grass	2.8	1.6	2.2	0.2	0.6	0.7	1.2	2.2	1.3	0.1	0.4	0.2	0.0
<i>Erodium cicutarium</i> L. Hér.	Ero cic	I	Forb	1.3	1.9	0.3	0.2	0.1	0.1	0.0	0.2	0.2	0.0	0.0	0.2	0.0
<i>Gnaphalium antennarioides</i> D.C.	Gna ant	N	Forb	0.0	1.6	1.2	0.0	0.0	0.0	0.2	0.1	0.1	0.3	0.0	0.0	0.0
<i>Rumex acetosella</i> L.	Rum ace	I	Forb	52.8	54.4	45.3	30.9	21.0	22.1	19.6	19.3	15.7	12.6	14.8	7.2	1.1
<i>Lachemilla moritziana</i> Damm	Lac mor	N	Forb	8.7	10.1	8.0	6.1	5.6	5.2	5.6	5.2	2.8	3.6	5.8	1.2	0.3
<i>Senecio formosus</i> H.B.K.	Sen for	N	Forb	1.8	3.2	7.8	6.4	4.0	1.4	1.8	0.3	0.2	0.0	0.3	0.2	0.4
<i>Conyza mima</i> S.F. Blake	Con mim	N	Forb	0.5	0.8	1.5	0.3	0.6	0.4	0.3	0.5	0.2	0.2	2.2	0.0	0.2
<i>Gnaphalium elegans</i> Kunth	Gna ele	N	Forb	0.6	1.6	1.9	2.7	0.7	0.0	0.1	0.5	0.0	0.0	0.5	0.0	1.0
<i>Gnaphalium meridanum</i> Aristeg.	Gna mer	N	Forb	0.3	0.4	1.2	1.7	0.8	0.8	0.2	0.1	0.1	0.9	0.2	0.6	0.4
<i>Bidens triplinervia</i> H.B.K.	Bid tri	N	Forb	0.1	0.6	0.7	0.7	0.7	0.1	0.1	0.3	0.1	0.0	0.0	0.2	1.4
<i>Gamochaeta americana</i> (Mill.) Wedd.	Gam ame	N	Forb	1.8	0.6	0.4	2.8	2.6	2.2	1.1	2.1	0.2	2.1	0.5	0.5	0.3
<i>Lupinus meridanus</i> Moritz	Lup mer	N	Forb	4.6	3.1	1.4	2.2	8.8	4.6	1.7	0.3	0.5	2.5	3.2	0.3	0.6
<i>Agrostis jahnii</i> Luces	Agr jah	N	Grass	1.4	0.8	1.1	1.3	2.7	2.4	0.9	0.7	0.1	0.0	0.2	0.5	0.2
<i>Calamagrostis pittieri</i> Hack	Cal pit	I	Grass	0.2	0.0	0.5	1.1	1.2	0.0	0.3	0.0	0.3	0.4	0.4	0.0	1.1
<i>Vulpia myuros</i> (L.) C.C.Gmel.	Vul myu	N	Grass	9.9	11.3	10.5	15.5	17.1	11.4	12.8	13.3	12.8	14.1	7.1	2.6	0.4
<i>Luzula racemosa</i> Desv.	Luz rac	N	Grass	0.0	0.0	0.3	0.9	0.5	1.4	0.1	0.0	0.1	0.0	0.0	0.0	0.6
<i>Acaena cylindristachya</i> Ruiz & Pav.	Aca cyl	N	Forb	0.0	0.0	0.1	0.5	0.4	0.6	0.1	0.1	0.5	0.2	0.1	0.0	1.5
<i>Geranium chamaense</i> pittier.	Ger cha	N	Forb	0.9	0.4	1.4	1.3	2.2	3.5	2.0	2.0	0.9	0.5	0.1	2.3	0.0
<i>Nassella mexicana</i> (Hitche.) R. W. Pohl	Nas mex	N	Grass	0.6	0.0	0.4	0.9	0.9	1.8	1.0	0.0	0.1	0.9	0.6	0.3	2.7
<i>Stevia elatior</i> H.B.K.	Ste ela	N	Forb	1.9	0.6	0.6	1.0	1.0	2.3	5.3	4.5	2.8	3.4	4.4	3.3	1.2
<i>Oxalis</i> sp.	Oxa sp.	N	Forb	0.0	0.5	0.1	0.4	0.0	0.1	0.4	0.9	0.2	0.1	0.3	0.2	0.3
<i>Acaena elongata</i> L.	Aca elo	N	Shrub	0.9	1.3	1.1	2.0	2.9	3.0	4.1	7.7	4.3	3.6	3.7	2.6	2.6
<i>Agrostis trichodes</i> (H.B.K.) Roem. & Schult.	Agr tri	N	Grass	0.3	0.2	0.5	0.9	0.9	0.4	1.5	2.0	2.4	0.1	0.7	0.3	0.2
<i>Oenothera epilobifolia</i> H.B.K.	Oen epi	N	Forb	0.1	0.4	1.3	1.5	1.9	1.3	1.4	1.8	1.4	2.6	0.8	0.8	0.4
<i>Stevia lucida</i> Lag.	Ste luc	N	Shrub	0.0	0.3	0.6	1.2	0.9	1.3	2.9	2.2	3.1	6.6	5.8	4.4	1.6
<i>Sisyrinchium tinctorum</i> Kunth	Sis tin	N	Forb	1.0	0.3	2.0	2.2	2.9	4.9	3.4	3.8	3.4	3.9	6.7	1.4	0.6
<i>Baccharis prunifolia</i> H.B.K.	Bac pru	N	Shrub	1.4	0.4	0.2	1.0	1.7	4.8	5.7	4.1	14.6	11.5	14.0	23.5	3.7
<i>Noticastrum marginatum</i> (Kunth) Cuatrec.	Not mar	N	Forb	0.2	0.0	0.0	0.5	0.6	0.8	0.3	1.3	1.9	5.7	6.8	14.3	1.2
<i>Trisetum irazuense</i> (Kuntze) Hitche.	Tri ira	N	Grass	0.2	0.0	0.5	0.5	1.2	1.7	1.9	1.2	2.4	3.9	3.2	8.6	1.3
<i>Ruilopezia floccose</i> (Standl.) Cuatrec.	Rui flo	N	Rosette	0.0	0.0	0.0	0.1	0.0	0.1	0.4	0.5	0.0	0.2	0.0	0.0	1.7
<i>Hypericum laricifolium</i> Juss.	Hyp lar	N	Shrub	0.1	1.3	1.8	3.5	3.2	6.2	8.1	5.0	6.2	6.5	4.7	7.6	9.9
<i>Orthoanthus chimboracensis</i> (Kunth)	Ort chi	N	Forb	0.7	0.2	0.1	0.3	0.4	1.2	1.8	2.0	1.6	0.7	0.1	1.1	2.1
<i>Bartsia laniflora</i> Benth.	Bar lan	N	Forb	0.0	0.1	0.1	0.5	0.5	0.3	0.0	0.0	0.2	0.0	0.0	0.0	2.4
<i>Hesperomeles obtusifolia</i> (Pers.) Lindl.	Hes obt	N	Shrub	0.1	0.0	0.0	0.0	0.1	0.1	0.5	0.7	0.4	0.0	0.3	0.0	1.4
<i>Espeletia schultzii</i> Wedd.	Esp sch	N	Rosette	0.8	0.6	2.1	2.4	5.1	8.7	8.4	9.3	8.5	7.2	7.0	9.3	11.7
<i>Agrostis subpatens</i> (Hitche)	Agr sub	N	Grass	0.0	0.0	0.0	0.5	0.1	0.0	0.1	0.0	0.4	1.2	0.3	0.5	4.6
<i>Pernettya prostrata</i> (Cav.) DC	Per pro	N	Shrub	0.2	0.0	0.1	0.2	0.0	0.0	1.3	0.7	3.7	0.9	0.3	1.4	8.7
<i>Nassella linerifolia</i> (Fourn.) Pohl	Nas lin	N	Grass	0.2	0.0	0.0	0.3	0.9	0.8	0.0	0.1	0.3	0.1	0.5	1.6	2.5
<i>Arcytophyllum nitidum</i> (H.B.K.) Schldl.	Arc nit	N	Shrub	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.6
<i>Calamagrostis effusa</i> (H.B.K.) Steud	Cal eff	N	Grass	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.3
<i>Brachypodium mexicanum</i> (Roem. & Schult.)	Bra mex	N	Grass	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0
<i>Hypericum juniperinum</i> Kunth	Hyp jun	N	Shrub	0.0	0.0	0.0	0.1	1.5	0.0	0.4	0.2	0.0	0.0	0.0	0.0	0.7
<i>Conyza lasseriana</i> Aristeg.	Con las	N	Forb	0.0	0.0	0.7	0.3	0.6	0.3	0.0	0.0	0.2	0.7	0.9	0.2	0.8
<i>Bromus carinatus</i> Hook & Arn	Bro car	N	Grass	0.9	0.2	0.4	0.0	0.8	0.0	0.0	0.3	0.6	0.9	0.9	0.3	0.0

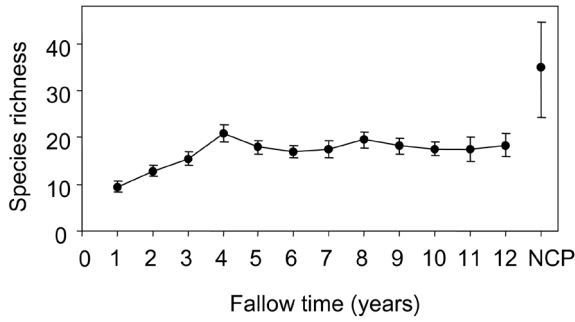


Figure 1. Species richness by plot during the first 12 years of succession and in the never cultivated paramo (NCP). Mean \pm standard error.

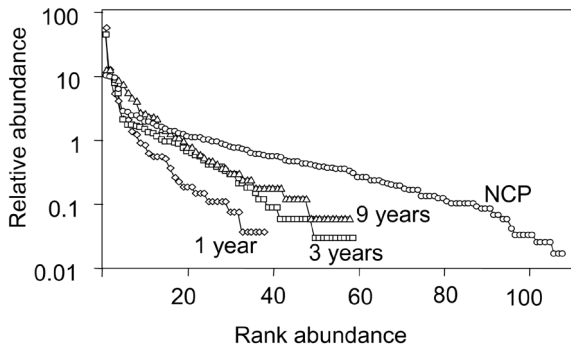


Figure 2. Rank abundance diagrams for 1, 3 and 9 years of succession and for the never cultivated paramo (NCP). For each fallow age the average abundance of the species in all the sampled plots was considered. The y axis is on a logarithmic scale.

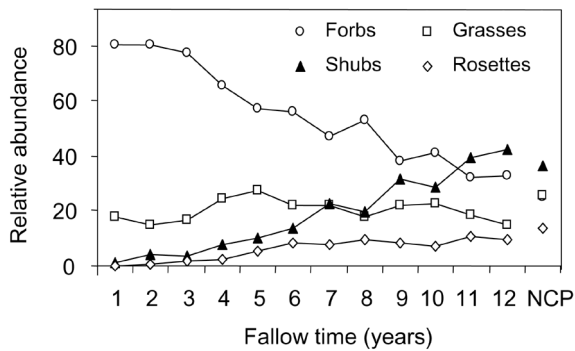


Figure 3. Relative abundance of the different life forms along succession.

examples of intermediate species in opposite extremes, with *L. meridanus* preferring sites with high pH, C, N and clay content.

The quantification of the successional rate is presented in Figure 6. The two methods used indicated the same trend: a linear regression provided a very good fit to the floristic distance between the first year plots and subsequent years, indicating a constant rate

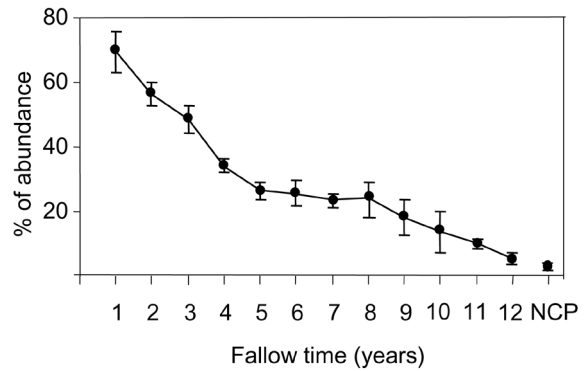


Figure 4. Percent of the total abundance represented by introduced species along the succession and in the never cultivated paramo (NCP). Mean \pm standard error.

Table 2. Spearman rank correlations between environmental variables and the DCA axis scores of the sites. Significant correlations ($p < 0.05$) are indicated with an asterisk.

	1st Axis	2nd Axis	3rd Axis
Time ¹	0,85*	0,15	0,17
Sand	-0,12	0,13	-0,44*
Clay	0,24*	-0,25*	0,48*
Silt	-0,03	0,03	0,15
pH	0,18	-0,15	0,46*
%C	0,12	-0,01	-0,58*
%N	0,12	-0,04	-0,51*
C/N	0,10	0,12	-0,46*
CEC	0,09	0,12	-0,37*
Altitude	-0,12	-0,06	-0,54*
Slope	0,04	0,07	0,34*
Aspect	-0,1	-0,00	0,04
Dist. to the Valley bottom	0,03	-0,41*	-0,04

¹ Correlations with time were calculated excluding the natural paramo in the DCA ordination.

of succession (represented by the slope of the line). Assuming that the rate remains constant after 12 years, and extrapolating to the differences in community structure observed between first year plots and the NCP, the time necessary to reach the community structure of the NCP is estimated to be 30 years.

The analysis of divergence using chord distance showed a moderate increase in community heterogeneity along succession. The chord distance at the end of the studied interval attained levels similar to those found in the NCP (Figure 7). The high standard error of chord distances in plots with 11 and 12 years was the result of the lower number of plots included in these late stages of succession.

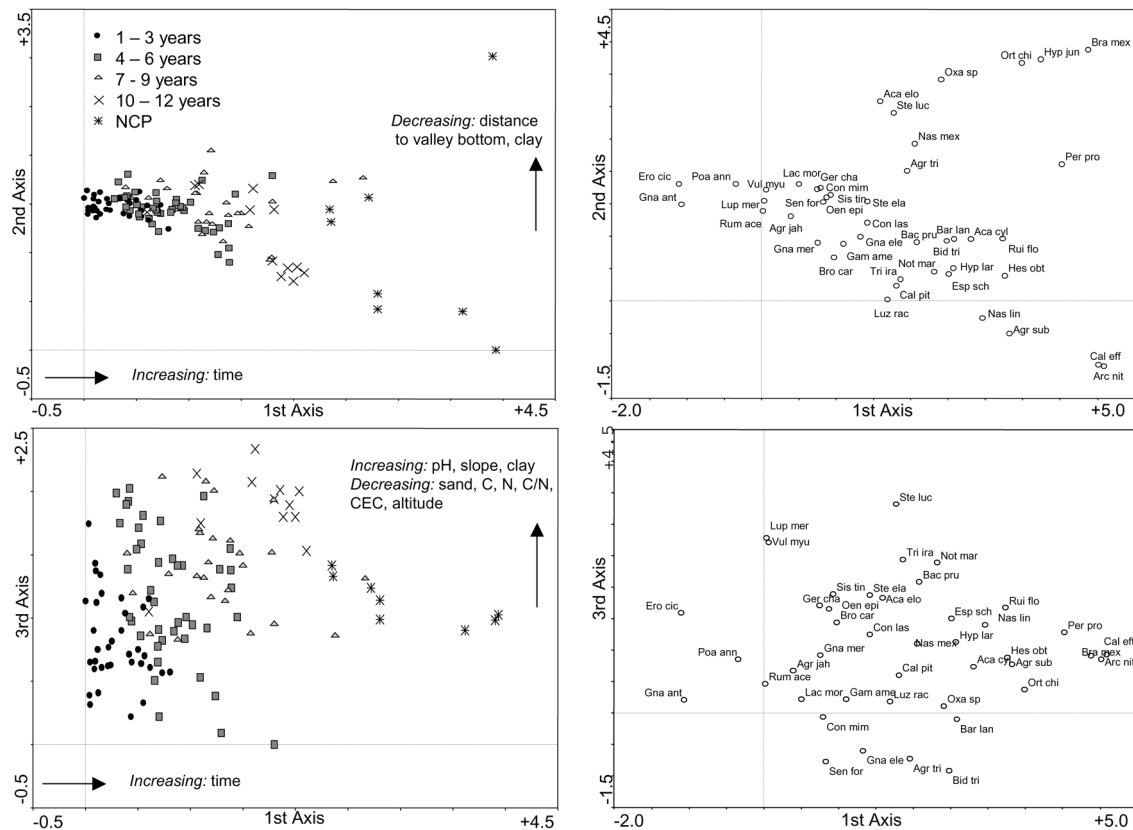


Figure 5. DCA ordination diagrams of sites and species using the 1st vs. the 2nd axis and the 1st vs. the 3rd axis. Only the 44 more abundant species are shown for greater clarity. The eigenvalues for the three first axes were 0.587, 0.348 and 0.217 respectively. For species abbreviations see Table 1.

Discussion

Based on the results of this and other studies on long fallow agriculture in the paramo (Ferweda 1987; Moreno and Mora-Osejo 1994; Jaimes 2000), we can identify a set of common patterns for vegetation change during succession: a) an early increase of richness and diversity; b) a predictable sequence of life forms, with annual and perennial herbs (e.g. *R. acetosella*) dominating the early stages and then progressively being displaced by sclerophilous shrubs (such as *Baccharis* and *Hypericum*), caulescent giant rosettes (mainly of the *Espeletia* genus) and tussock grasses (e.g. *Calamagrostis effusa*); c) a decline in the abundance of introduced species; d) a clear successional pattern in the abundance of the dominant species but without a true floristic relay and e) the existence of divergent pathways in vegetation development.

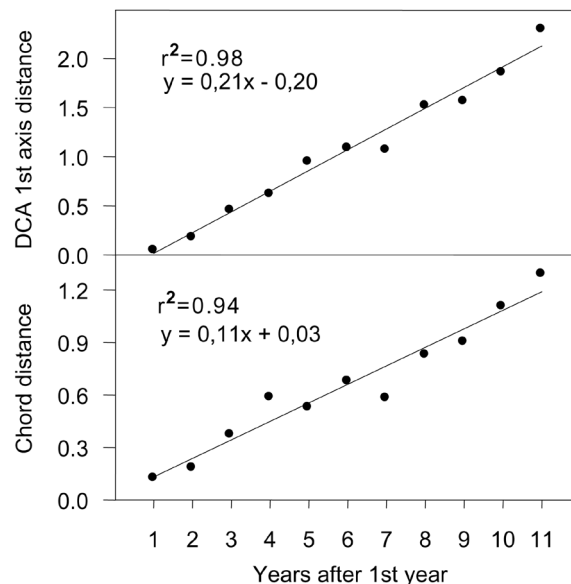


Figure 6. Successional rate calculated as a) the difference between average 1st year DCA scores for the 1st axis and subsequent years and b) average chord distance between 1st and subsequent years.

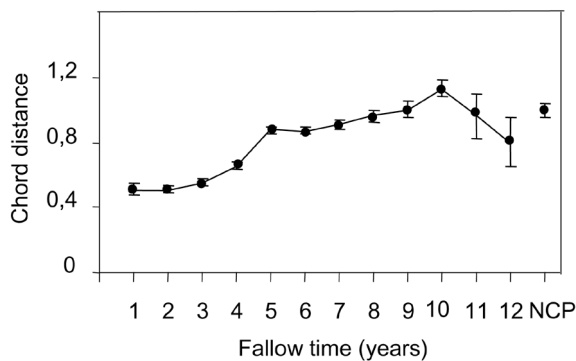


Figure 7. Successional divergence calculated as the dissimilarity between plots of the same fallow age using chord distance as a dissimilarity index. Mean \pm standard error.

Patterns of diversity and the conservation value of the fallow strategy

The asymptotic behaviour showed by species richness early in the succession, with a stabilisation in a number of species far below that of the never cultivated paramo, questions the value of long fallow agriculture as a strategy for the conservation of paramo diversity (Sarmiento et al. 2002). This is especially true considering that the dominant species during early succession are all foreign invaders. The asymptotic behaviour of richness makes it difficult to assess the fallow time that would be necessary for a complete restoration (if it is ever achieved).

Our results contradict the generalisation of a higher diversity at intermediate successional stages linked to the intermediate disturbance hypothesis (Collins et al. 1995). The complete competitive exclusion of early species from late successional stages which is behind these predictions, does not occur in the paramo. Moreover, many of the rare mature paramo species are slow in re-colonizing the fallow areas.

Our results support the general tendency for early succession to show relatively vertical rank abundance patterns, which reflect low evenness (Bazzaz 1996; Wilson et al. 1996).

Life forms dynamics and their life history underpinning

In the context of the alpine tropics, a unique set of adaptations confer competitive advantage to life forms like the giant rosette and the sclerophilous shrub, which show a remarkable degree of conver-

gence between the Andes and the mountains of East Africa (Hedberg and Hedberg 1979; Hedberg 1992). These life forms present morphological and ecophysiological adaptations to low temperature, extreme daily temperature fluctuations, water stress and nutrient deficit (Goldstein et al. 1984; Monasterio and Sarmiento 1991; Squeo et al. 1991; Rada 1993; Meinzer et al. 1994). Our results show that dominant shrub and rosette species are able to colonise from early stages of succession, presenting characteristics of *ruderal* and *stress tolerant* species (*sensu* Grime (1987)). However, as a result of trade-offs with their adaptations to the extreme conditions of the paramo, these species show relatively low photosynthesis and growth rates (Rada 1993). Hence, their abundance increases slowly in succession.

The decline of the introduced species

The colonisation ability of the introduced herb *R. acetosella*, has been related (among other factors) to its dual clonal and sexual reproductive strategy (Escarre and Houssard 1989). This species was introduced in the Venezuelan paramos as a weed of wheat by the Spanish Conquerors (Salgado-Labouriau and Schubert 1977). The clear successional decline of the introduced species could be related to the strong environmental filters of the paramo environment. In the climatically more extreme case of the Venezuelan super-paramo (above 4100 m) permanent plot studies have not found re-colonization by *R. acetosella* after disturbance (Smith and Young 1987). Interestingly, endemic fast growing forbs that are able to show explosive colonization, like *L. meridanus*, only have their abundance peaks after 4 or 5 years.

Patterns of species abundance: paramo regeneration as an autosuccession

Successional dynamics in which changes in abundance more than species replacement are the driving force have been termed *autosuccession* by Muller (1952) and *demographic succession* by Urbanska (1997). These and other authors (e.g. MacMahon (1981) and Svoboda and Henry (1987)) have proposed that in extreme environments (e.g. tundra and deserts), where few adaptive strategies are possible, succession is characterised by the progressive colonisation by the climax species without a real species replacement. Muller (1952) classified autosuccession as selective or non-selective, depending on the exist-

ence of a particular order in species colonisation. Paramo succession can be considered as a selective autosuccession, with the exception of the foreign species that act as colonisers and disappear during succession. Late species become established from early stages and increase in relative importance by virtue of *vital attributes* (*sensu* Noble and Slatyer (1980), see Vargas-Rios (1997) application of the approach to paramo post-fire succession) that allow them to *tolerate* as juveniles (*sensu* Connell and Slatyer (1977)) the high abundance of early ruderal species and to competitively displace them as they grow later in succession. The importance of competition as a mechanism explaining the decline of early species is suggested by their long persistence tails, since the alternative hypothesis of a decline caused by changes in environmental conditions is less compatible with this kind of incomplete exclusion (see Pickett (1982)).

Successional divergence and environmental heterogeneity

The pattern of successional divergence found in this study could be linked to the heterogeneity that is characteristic of these mountain environments. Divergence can be partially explained by the distance of the plots to the valley bottom, a variable that could be related to grazing pressure. The role of grazing intensity is supported by the fact that *Acaena elongata*, a species dispersed by cattle (Molinillo and Bremen 1993), is associated with small distances to the valley bottom on the 2nd axis of the ordination. Absolute altitude as an explanatory factor for divergence is probably linked to the identity of the natural vegetation surrounding the plots. The importance of surrounding vegetation in determining alternative succession pathways has been shown by del Moral (1995) and Tsuyuzaki (1995) in primary mountain succession. In our case, a more dense shrub matrix, dominated by species like *B. prunifolia* and *S. lucida*, is found at low altitudes, coinciding with a higher abundance of these species in the low fallow plots.

The lower heterogeneity in community structure in the early succession stages is linked to the strong dominance of *R. acetosella*. Its ruderal habit ensures a universal presence at this stage, probably making its colonisation less dependent on local abundance.

In the mountain context, Rikhari et al. (1993) have associated divergent pathways of succession with differences in slope and soil depth between plots.

Moreno and Mora-Osejo (1994) were able to link different pathways to fire and grazing intensity, while Ferweda (1987) associated them with differences in slope and altitude. Herben et al. (1993) suggested that this kind of individualistic or multiple pathway response could be the result of non-linearities linked with processes such as small scale spatial interactions between species.

Succession rates: slow and slowing down?

Our results of a constant rate of succession contradict the generally accepted hypothesis of a continuous slow down from initial stages to the "climax" (Shugart and Hett 1973; Armesto et al. 1991; Myster and Pickett 1994). While Brown and Southwood (1987) found a constant rate of species turnover, other authors have found a non-monotonic decrease in the rate of succession (Prach 1993) or a cyclic behaviour (Donnegan and Rebertus 1999).

The early rate of succession in our system seems to be determined by the constant decline of introduced species and the increase in abundance of the dominant paramo species as individuals slowly gain biomass. However, we could expect that later in succession, as community composition approaches a stable climax state (if it ever does), there could be a lower rate of succession. Hence, our figure of about 30 years for the regeneration of the paramo structure, assuming a constant rate, could be an underestimate.

Nevertheless, if we compare this estimation with physiognomic regeneration times calculated for forest ecosystems, which range from hundreds to thousands of years (MacMahon 1981), paramo succession seems relatively fast (partially as a result of the longer mean generation time for most trees compared to paramo species). This suggests we should be cautious about the accepted wisdom that vegetation regeneration in alpine environments is a very slow process (e.g. Billings (1973)), which has also found its echo in the paramo literature (e.g. Janzen (1973) and Smith and Young (1987), Horn (1989), Vargas-Rios (1997), Luteyn (1992)).

However, it is important to consider that the fast regeneration of paramo physiognomy does not imply a fast restoration of plant diversity or other ecosystem properties like soil organic matter (see Llambí and Sarmiento (1998)). Hence, our perception of the conservation value of the fallow strategy will depend on the importance we attach to these different properties of the ecosystem and their roles in the mainte-

nance of the environmental services that we expect the paramo to provide.

Alternatives for management

Some alternative management practices emphasizing the conservation of paramo biodiversity can be suggested. Fallow agriculture, under the current trend of a reduction in fallow times, appears to be an inappropriate strategy from this perspective: it maintains large areas in successional stages that are less diverse than the mature ecosystem. This could contribute to the loss of a number of rare paramo species that are slow in recolonizing fallow areas. A possibility to speed up restoration would be to increase the abundance in early succession of some of the late or intermediate species. For example, the active planting of the fast growing *Lupinus meridanus* (a nitrogen fixer) in the first years of succession could improve the soil nitrogen status and accelerate the reinvasion of other species, a possibility that is being tested at the moment. Nevertheless, the intensification of agriculture seems to be the best alternative to reduce the total area under cultivation while maintaining production levels and improving biodiversity, given that representative natural areas are set aside for protection (Sarmiento et al. 2002). The selection of the areas to be protected must consider the high heterogeneity of paramo vegetation and the divergence in vegetation structure and composition associated with this heterogeneity. Another factor to be evaluated is the impact of grazing practices, which is likely to have a pronounced effect on vegetation structure and on successional patterns, pathways and rates.

Acknowledgements

This research was supported by the European Union within the INCO-DC TROPANDES project (N° IC18-CT98-0263) and by the International Foundation for Science (grant No. C/2668-1). We wish to thank T. Carballas and M. Monasterio, the international and Venezuelan co-ordinators of TROPANDES. J.K. Smith was of great help in plots selection and their characterisation using GIS. Discussions with her, M. Fariñas, D. Acevedo, P. Alvizu, I. Suarez and R. Law provided important insights. A. Olivo was extremely helpful in fieldwork.

A. Berg, B. Briceño, G. Murillo and P. Yañez made most botanical identifications. Special thanks to the community of Gavidia, particularly to Sra. Rosa who many times kindly invited us to dry and warm ourselves in her magical fireplace.

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