

Burning and grazing in a bunchgrass páramo ecosystem: Vegetation dynamics described by a transition model

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Abstract. A simulation model is proposed, describing vegetation dynamics in a bunchgrass páramo ecosystem, in relation to cattle grazing and burning. Field-work was conducted in Parque Nacional Natural Los Nevados, Colombia, at elevations of 3900–4200 m. Three successive stages of vegetation development are recognized in relation to grazing: an opening phase of the bunchgrass layer, conditionally followed by an invasion of short grasses, and eventually a degeneration stage of the vegetation where severe erosion may occur. Test runs of the model, based on analysis of data collected in a small pilot area, were executed with an arbitrary set of parameters. These simulations produced realistic results. The proposed model serves as a tool for identification and analysis of processes, significant to the management of bunchgrass páramo ecosystems.

Resumen. Se propone un modelo de simulación que describe la dinámica de un páramo de pajonal en relación al pastoreo de ganado y quemas. El trabajo de campo fue efectuado en el Parque Nacional Natural Los Nevados en la Cordillera Central de Colombia, entre 3900 y 4200 m. En relación al pastoreo, se distinguen tres etapas sucesivas de cambio de la vegetación: una primera fase de abertura de macollas, una fase siguiente de desarrollo de pastos cortos y, eventualmente, una última fase de degeneración caracterizada por una marcada erosión. Se hizo correr el modelo con parámetros fijados arbitrariamente, sobre la base del análisis de datos colectados en un área piloto, habiéndose obtenido resultados satisfactorios. Se considera que el modelo propuesto sirve como instrumento para la identificación y el análisis de los procesos vinculados al manejo del páramo de pajonal.

Introduction

Although natural tropical alpine vegetations are mainly governed by climatic factors and the hydrological regime, nowadays the impact of man represents an important factor causing a highly dynamic environment.

Burning, cattle grazing, and agricultural practices are the main human activities determining the pattern of landscape development in time and space in these tropical alpine ecosystems (Ellenberg, 1979).

Mature specimens of native bunchgrass species, such as *Calamagrostis effusa* and *Festuca sublimis*, consist mainly of dry, tough material. Cattle prefer green shoots to the dead standing crop and it has been found that food selection is related to nitrogen content and digestibility of plants (Schmidt and Verweij, 1992). To improve forage quality, vegetation can be set to fire if sufficient fuel is present in the form of dead material. After some weeks, new, fresh shoots with a higher N-content and digestibility in comparison to mature bunches appear.

Within the framework of a research project concerned with monitoring and modelling human influences on vegetation dynamics of the páramo of Parque Nacional Los Nevados, it was investigated how fire events, combined with cattle grazing, influence floristic composition and vegetation structure (Verweij and Budde, 1992). In the analysis of these vegetation changes, simulation models are used. It was the objective of the present study to develop a simulation model for a small pilot area, describing mechanisms of vegetation dynamics that have led to the present distribution of vegetation types under influences of grazing and burning.

In the literature two kinds of simulation models can be found that deal with plant-herbivore systems: deterministic models (Smith and Williams, 1973; Noy-Meir, 1976, 1978; Innis, 1978; Fetcher, 1981; Walker *et al.*, 1981) and transition models (Swarzman and Singh, 1974; Redetzke and van Dyne, 1976; Runkle, 1981; Usher, 1981; Lippe *et al.*, 1985; Turner, 1987). Deterministic models generally consist of several interrelated differential equations. These equations describe system variables such as, growth of plant biomass, consumption rate, competition between plant species, nutrient flows, or animal (secondary) production. French (1990) defines several classes of deterministic models according to differences in scales of space and time. For grazing studies, the relevant levels of detail are that of ecophysiology, of biotic production, and of vegetation community development. Fetcher (1981) uses ecophysiological concepts in the simulation of a plant-herbivore system. The effect of shoot removal on cold desert shrubs is determined by studying biomass flows among active shoots, active roots, and reserves. At the level of biotic production, Noy-Meir (1978) analyzed stability criteria for several vegetation growth functions combined with different consumption functions. Using parameters such as net relative growth rate, effective grazing rate, and satiated consumption rate, system characteristics and stability criteria can be determined when the shape of the function is known. The model of Smith and Williams (1973) and the ELM-Grassland Simulation Model (Innis, 1978) are examples of grazing models at the same level of detail. Walker *et al.* (1981) propose a simulation model that describes grazing processes at the ecosystem level in a semi-arid savanna. The effects of grazing on the

interaction between woody species and grasses in relation to hydrological factors are simulated. Other deterministic grazing models at the community level are described by Pellew (1983), Van Wijngaarden (1985), and Thalen *et al.* (1987).

The process of grazing, resulting in dynamic ecosystems, where species composition and vegetation structure are subject to change, is more commonly simulated with help of transition models. These models define a number of static states that may develop. A state is defined at the level of single species (Usher, 1966; Runkle, 1981; Lippe *et al.*, 1985) or, on a smaller scale, of vegetation types (Austin and Belbin, 1981; Usher, 1981). During simulation, each state has a certain probability to change into another state. Besides its application for grazing studies, transition models are commonly applied to simulating succession in plant communities subject to fire (Noble and Slatyer, 1981). A Markov transition model is formulated when, during simulation, transition probabilities are kept constant (Hulst, 1979; Usher, 1981; Lippe *et al.*, 1985). Effects of grazing can be studied using different transition matrices for several grazing intensities (Swartzman and Singh, 1974; Redetzke and Van Dyne, 1976). Although cattle range freely over extensive areas, grazing intensity is not equally distributed. This causes a mosaic of heavily used and virtually unused vegetation patches that commonly develop under grazing (Thalen *et al.*, 1987). In Parque Nacional Los Nevados, the mosaic pattern is enhanced by the heterogeneity of the terrain. Therefore, fixed transition probabilities as used in Markov models do not apply. Characteristics of the terrain and the local vegetation influence the attractivity of a particular area for cattle grazing and hence the probability of vegetation change. Moreover, the biotic and abiotic environment is constantly changing and behavior of organisms will reflect these changes (Lippe *et al.*, 1985). Dynamic transition probabilities that incorporate temporal and spatial effects are, therefore, preferred (Turner, 1987).

In order to determine transition probabilities, a long series of field observations is required. Vegetation has to be monitored until sufficient vegetation transitions have occurred. In this way it usually takes years before a transition model can be built that produces any meaningful results, although Swartzman and Singh (1974) described a transition model based on a two-year record. To gain insight into the dynamics of páramo vegetation in relation to burning and grazing, observations over a period of decades would be needed. In this study, an alternative method is used to analyze vegetation dynamics. We assume that present vegetation types are derived from zonal páramo bunchgrass vegetation, transformed by grazing and/or fire events. With the help of ordination techniques (DCA, PCA), transition tables that describe vegetation dynamics in relation to burning, grazing, and recovery are constructed. A forcing function is defined, determining local vegetation transition, if the vegetation does not agree with local grazing pressure.

The present model is based on a survey of vegetation types instead of observed vegetation dynamics. Several methods are used to unravel the processes that have led to the occurrence of the present vegetation. In this way a dynamic transition model is developed, based on several months rather than several years of fieldwork. For this reason the results of simulation should be interpreted carefully.

Methods

Study area and data collection. The Parque Nacional Natural Los Nevados is situated in the central cordillera of Colombia (4°70'N; 75°20'W). The geomorphology of the landscape has been shaped by volcanic eruptions together with the activity of Pleistocene glaciers (Thouret, 1983). Heterogeneous blocklava flows, smooth lateral moraines, glaciated lava fields, and small lakes characterize the area. A more detailed description of the study area is given by Verweij and Budde (1992).

For the present study, data were collected in a pilot area, situated in a region called Loma Bonita (3900–4200 m). The simulation model is based on an area where about 80 head of cattle graze. This area of about 440 hectares belongs to one farmer.

Seventy relevés were made in the region of Loma Bonita. With the aid of aerial photographs, samples were chosen that represent a wide range of fire regeneration stages (stratified sampling). Data were recorded on floristic composition of the vegetation (cover abundance scale of Braun-Blanquet), vegetation structure (height of structural layers, bunch diameter, dead/alive ratio, total real coverage, basal coverage, and size of erosion spots), geomorphology (terrain form, slope, aspect), soil (color, pH, texture, root density per horizon), cattle grazing (number of cow droppings per area, traces of trampling impact), and fire events (estimation of fire frequency and fire age).

Data analysis. The cluster program TWINSpan (Hill, 1979a) was used to create a vegetation table in which floristic groups were defined. Floristic gradients were studied with a correspondence analysis (DCA-ordination; Hill, 1979b). The DCA technique places each sample on a theoretical gradient reflecting the main variation in the data. The technique is based on a unimodal response curve for the species; abundance values for a particular species increase to a maximum, and subsequently, decrease along the gradient. Since a long gradient in units of standard deviation was found, the use of a unimodal model is preferred (Verweij and Budde, 1992).

Vegetation structure data were clustered, using the Pearson correlation coefficient. A hierarchical tree was created to define structural types. The vegetation structure was ordinated with PCA (Principal Component Analysis). This ordination is based on a linear response model. The PCA-technique was chosen because it was not clear how vegetation structure re-

sponds to grazing and burning. A linear response model is in that case most simple, and therefore, most appropriate.

The groups resulting from the cluster analyses were used to define vegetation types. Each vegetation type is characterized by a specific combination of floristic composition and structural appearance. In order to interpret the ordination axes of both DCA and PCA, correlations were analyzed between these axes and measured environmental variables. The ordination analyses are used to verify whether the main variation in the data set is the effect of grazing and/or fire events. Also, the position of the vegetation types relative to each other and to the gradients is used to define possible paths of vegetation change.

Model development. To define a spatial data base for the model, the Loma Bonita area was subdivided into 195 plots of size 150×150 m (Fig. 1). The

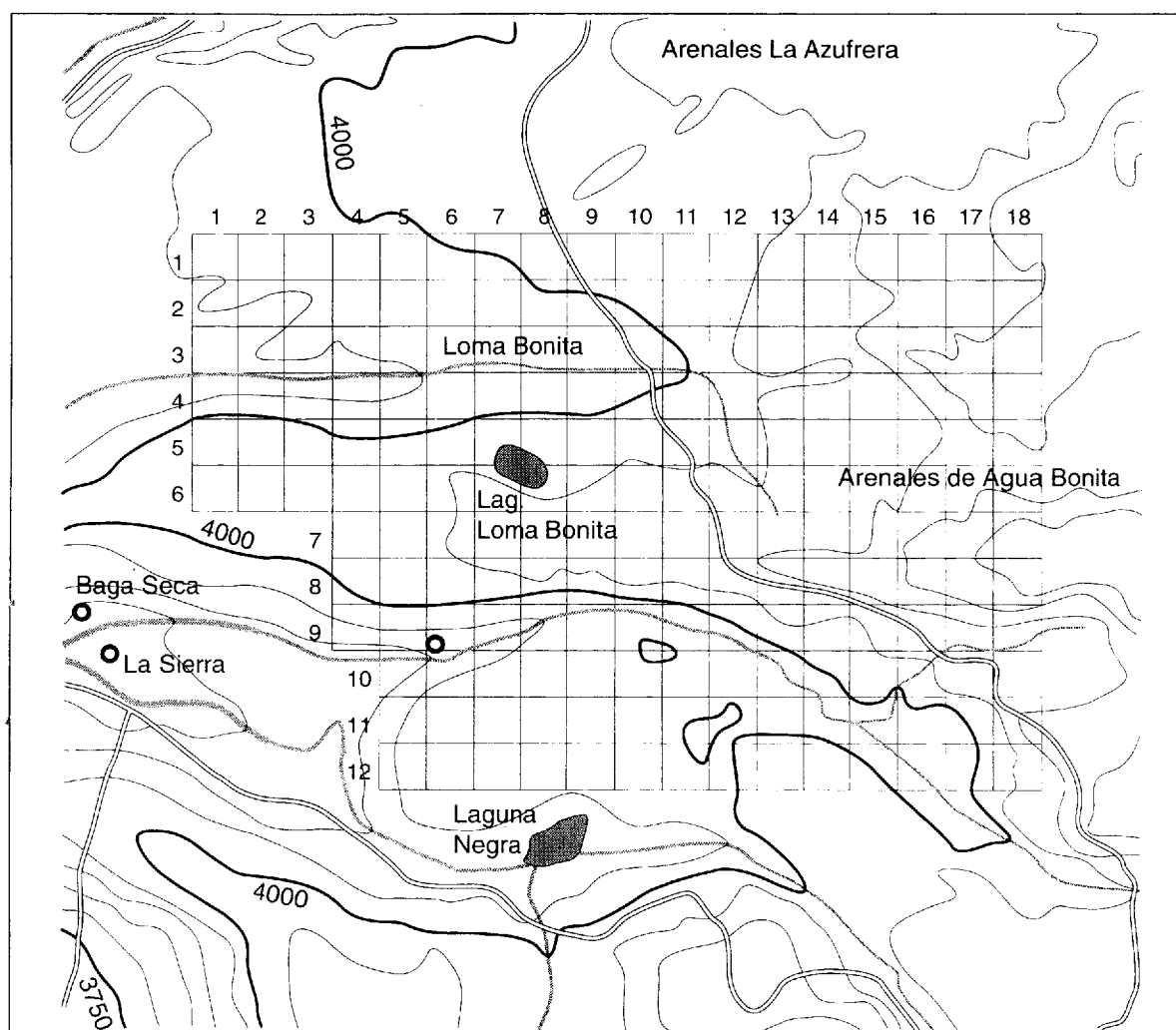


Figure 1. Grid over the Loma Bonita site. Each plot represents an area of 150×150 meters. In this site of 195 plots, about 80 head of cattle of one farmer graze. For the simulation model, data on the terrain and the present vegetation are stored for each plot.

vegetation for each plot is specified and data about terrain characteristics are stored (slope, terrain form). During simulation, vegetation change in response to burning and grazing is followed.

The procedures for simulating vegetation change can be divided into two parts. In the first module it is determined in which direction the vegetation in a plot potentially changes and with what probability. For this purpose some simple algorithms are defined, incorporating the stress that arises in the system in case of overgrazing (positive stress) or undergrazing (negative stress). During the simulation of one time interval, these calculations are made for each plot of the Loma Bonita area.

In the second module of the simulation model, it is determined which vegetation types can replace the current vegetation type in the plot, given the direction and total probability of change. If there is only one alternative vegetation type, the probability calculated in the first module is used to assess (with a random number generator) whether the transition will occur or not. In case more than one path of vegetation change exists, the total probability is shared over these paths, based on the relative distances between the vegetation types in the ordination diagrams. Nearby groups in the ordination diagrams have more species in common, so the chance that a transition occurs between these groups is larger in comparison to transitions to more distant groups (Witte, pers. comm.). Transition vectors in ordination diagrams, in general deduced from observed vegetation dynamics, are commonly applied in succession studies (Austin, 1977; Belsky, 1986; Whisenant and Wagstaff, 1991).

Results from data analyses

Based on floristic data, three main groups can be defined for the Loma Bonita area (Fig. 2). In the first group, f1, high cover values can be found for the bunchgrasses *Calamagrostis effusa*, *C. recta*, and *Festuca sublimis*. In the second group, f2, species with a lower growth form (short grasses) appear. In this group, relatively high abundances occur for such grasses as *Calamagrostis coarctata* and *Trisetum spicatum*. From both the vegetation table and the ordination analysis, it followed that floristic group f2 can be considered a transition state between groups f1 and f3. In the last group, f3, several species from the f1 group have almost disappeared. A low, mostly closed mat is formed by species such as *Lachemilla orbiculata*, *Rumex acetosella*, and *Trifolium repens*. The main variation along the first axis ($\lambda_1 = 0.58$) is explained by grazing variables as observed in the field. Therefore, it was concluded that the transition f1–f2–f3 is correlated with an increase in grazing pressure. The second ordination axis ($\lambda_2 = 0.20$) seems to be most closely related to soil humidity. However, more data are needed to confirm this hypothesis. Fire is not a major component influencing floristic composition in the Loma Bonita area.

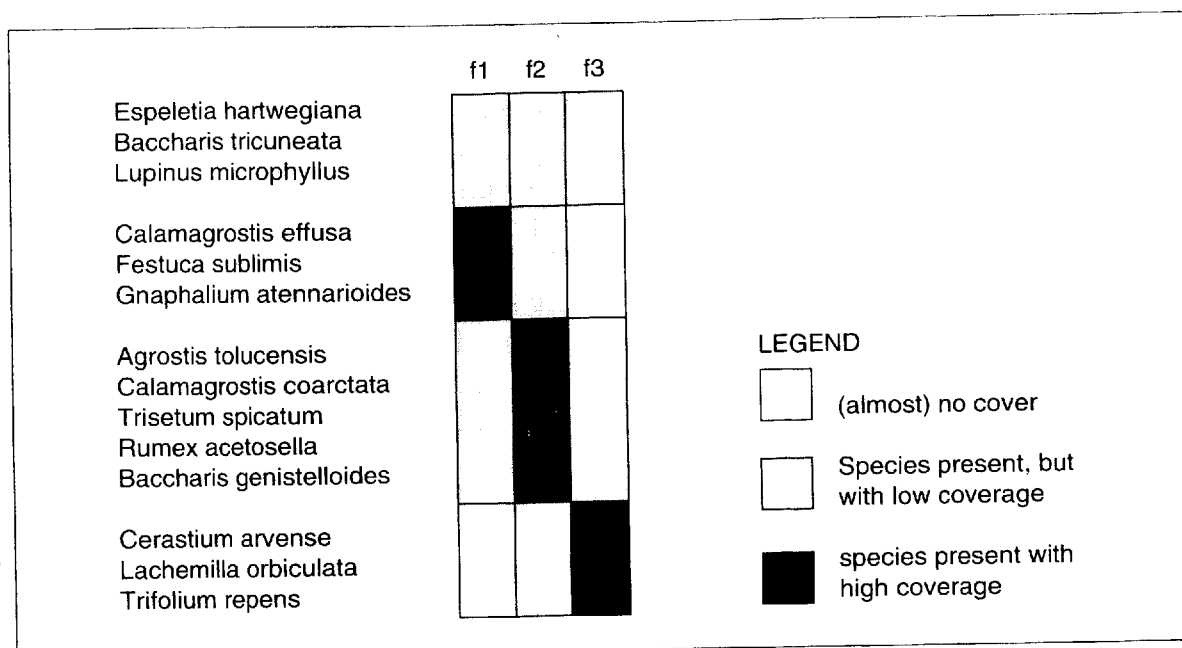


Figure 2. Bar diagram of the three floristic groups based on a TWINSpan cluster analysis. Only the most common species that characterize these groups are given.

The structural data set was divided into five main groups. The division into the first four groups, s1–s4, is mainly based on vegetation height, bunch diameter, and dead/alive ratio. Group s1 describes the high, mature bunchgrass vegetation, while from s1 to s4 vegetation gets lower and bunch diameter decreases. The PCA ordination diagram (Fig. 3) shows this main division along the first axis, while the second axis describes a (sub)-division based on total real coverage. Relatively closed structure types (a-types) were separated from more open vegetation (b- and c-types). Finally, a group is defined (sB), describing the vegetation structure that appears shortly after a fire event.

If all combinations of three floristic groups and nine vegetation structures would be possible, maximally 27 different vegetation types could be defined. In the data set only 15 combinations are present. Since for modelling purposes three more theoretical combinations are used, all together 18 vegetation types were defined (Fig. 4).

The simulation model

Transition probabilities. In the first module of the simulation model, it is evaluated in which direction and with which probability a vegetation transition might occur in a particular area. As an example, a plot is considered that has been grazed for several years with a moderate grazing intensity. It is assumed that in this plot the vegetation has developed in equilibrium with the local grazing activities. If the course of vegetation development is

followed using the simulation model, one of the following events can take place during the next simulation interval:

- 1) Local grazing pressure remains constant. Since the local vegetation is in equilibrium with local grazing pressure, no changes will occur;
- 2) Local grazing pressure increases compared to the previous situation. In this case more biomass is grazed from the vegetation than is supplied by the current vegetation type. Consequently, the vegetation translates to another type. Although this translation is inevitable over a longer time span, the velocity of transition (*i.e.*, transition probability) depends on the amount of local stress in the plot. Local stress is a function both of the grazed yield and of the yield that can be supplied by the vegetation present in the plot. It is clear that at moderately grazed sites, plants develop that are lower in height and diameter than plants at ungrazed sites. In the model, it is assumed that this difference lasts as long as grazing continues. Small bunchgrasses and short grasses require a certain grazing intensity in order to persist. This implies that if a transition occurs due to overgrazing of the

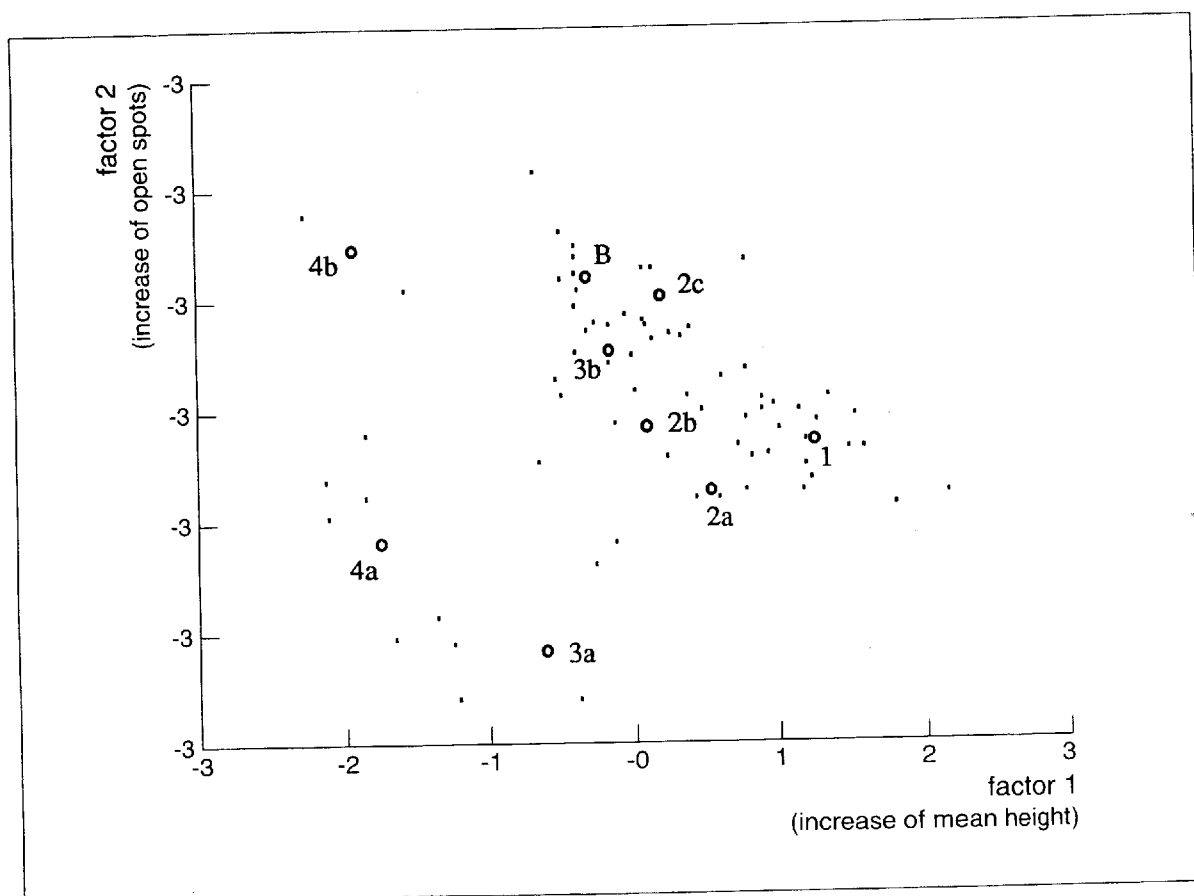


Figure 3. PCA ordination diagram of the structural data set. The first factor, explaining 46% of the variance, is correlated with vegetation height, dead/alive ratio, and bunch diameter. The second factor, explaining 28% of the variance, is correlated with total real coverage. The open circles are the centroids of the distinguished structural groups. Relevés are indicated by a small dot.

	sB	s1	s2a	s2b	s2c	s3a	s3b	s4a	s4b
f1	●	●		●	●		●		
f2	●	●	●	●	●	○	●	○	
f3			●	○		●		●	●

Figure 4. Defined combinations of floristic and structural types. Closed circles (●) represent 15 combinations that have been found in the data set. Three more theoretical vegetation types are used in the model (open circles ○).

current vegetation, the successive vegetation offers more yield for cattle grazing. This holds only for the non-degenerated states (Fig. 5); or

3) Local grazing pressure is lower compared to the previous situation. Since less biomass is grazed and trampling frequency is lower, recovery can occur. If the vegetation gets higher, the process can be compared with a transition to the right-hand side in the structural ordination diagram.

In the simulation model, cattle need a fixed amount of yield during each time interval. Yield is defined as a value for each vegetation type, according to both quantity and quality of available forage (Fig. 6). The forage is grazed from some of the defined 150 × 150 m plots in the Loma Bonita site each time interval, where one time interval corresponds with a period of about one year. The amount of forage collected from a particular plot depends on the local grazing pressure present in the plot. The sum of locally grazed forage represents the total amount of yield that is consumed by cattle each time interval. It is assumed that at low stocking rates, total yield grazed is not limited by forage availability. Total yield grazed depends exclusively on the number of cows present in the area.

Depending on the vegetation present locally (floristic composition and vegetation structure), a plot can offer a certain amount of forage during each time interval, without vegetation change being enforced (Fig. 6). The quantity of forage that is actually grazed from the vegetation depends on the local grazing pressure (PlotPress). A linear relationship is assumed between the forage locally grazed and the local grazing intensity:

$$\text{PlotYieldGrazed}_{pq} = \gamma \text{PlotPress}_{pq} \quad (1)$$

where PlotYieldGrazed is the locally grazed forage [yield per plot per time unit], PlotPress is the local grazing intensity [cow per plot per time unit], and γ represents a conversion parameter [yield per cow]. The subscript pq is used to specify one particular plot.

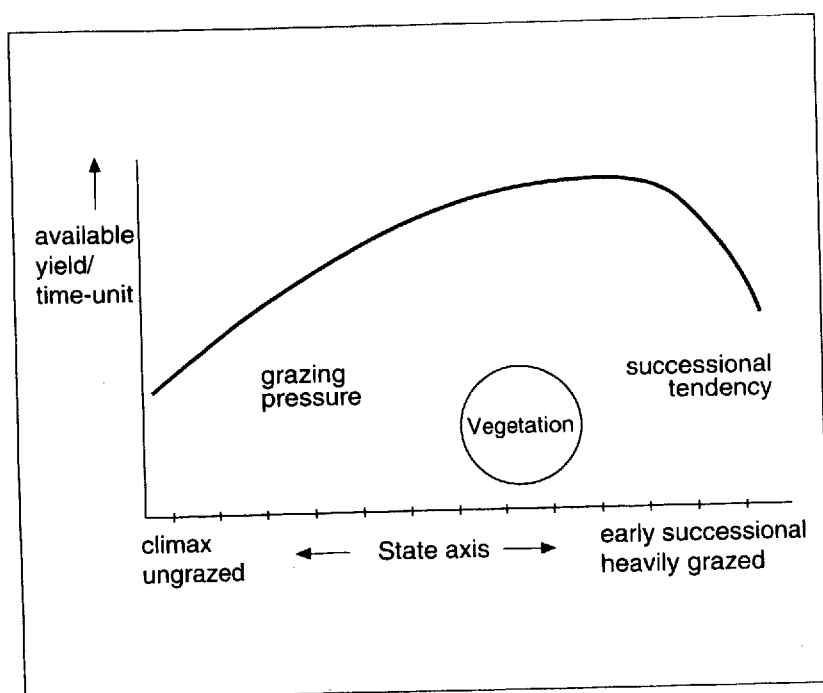


Figure 5. General scheme of the transition model (modified from Westoby *et. al*, 1989). The yield, offered by a vegetation per time unit, is plotted against the position of the vegetation on a succession axis. If grazing events occur more frequently, yield increases. As a result, the vegetation translates to another type. Only in the degeneration phase, does the amount of available forage decrease.

The grazing pressure for each particular plot is determined by a regional measure of grazing pressure (RG_Press) and a local measure, representing the attractivity of the plot for grazing (PlotAttract):

$$\text{PlotPress}_{pq} = \text{RG_Press} \times \text{PlotAttract}_{pq} \quad (2)$$

In the model, the attractivity of a plot for grazing is determined by the weighted sum of four factors: attractivity of the terrain, attractivity of the current vegetation, attractivity of the vegetation adjacent to the current plot, and inverted distance to special places like drinking holes or a farm.

If local grazing pressure would depend only on attractivity of a plot for grazing, total yield grazed would become variable. However, on the condition that the stocking rate remains the same, total yield grazed is assumed to be constant. As a consequence, if a plot becomes more attractive for grazing, other plots are grazed less intensively. Because attractivity of

	sB	s1	s2	s3	s4
f1	0.5	0.3	0.5	0.7	
f2	0.7	0.5	0.7	0.9	0.6
f3		0.6	0.6	1.0	0.7

Figure 6. Relative yield values (estimated) for the defined vegetation types. Both floristic composition and vegetation structure determine the available yield.

plots does not change if cows are grazing at other locations, local grazing pressure must be controlled by more factors than the attractivity of a plot only. For this reason, another variable is included, namely, the Regional Grazing Pressure (RG_Press), which determines the grazing pressure for each plot together with the local attractivity.

The value of RG_Press is determined by repeated adjustments in the following way. Each vegetation type offers a certain amount of yield per time interval without vegetation change (Fig. 6). The summation of the yields of all plots gives a measure of total yield present in the area:

$$\text{TotalYieldPresent} = \sum \text{PlotYieldPresent}_{pq} \quad (3)$$

The sum of locally grazed forage in terms of quantity and quality, TotalYieldGrazed, is assumed to be constant for a fixed stocking rate. If the system is in equilibrium, TotalYieldPresent in (3) should be equal to TotalYieldGrazed. The system is in stress if there is a difference between these two measures. During each time step, RG_Press is adjusted by adding a fraction of the difference between TotalYieldGrazed and TotalYieldPresent to the value of RG_Press from the last time step. If, for instance, TotalYieldPresent is lower than TotalYieldGrazed, RG_Press is increased a little. This means that the local grazing pressure in all plots increases (equation 2). In this way, the regional stress in the system is transformed to local stress in the plots which enforces local vegetation transition. As a result TotalYieldPresent increases. Eventually, a stage is reached where TotalYieldPresent is equal to TotalYieldGrazed. In that situation, there is no stress in the system, which implies that RG_Press remains constant.

Simple functions are defined to calculate transition probabilities for the vegetation in a particular plot. In Figure 7, these functions are plotted in relation to RG_Press. Depending on the present vegetation, the value of RG_Press, and the attractivity of the plot, transitions can take place towards more affected states of the vegetation in the case of positive stress (over-grazing), or towards more natural states of the vegetation in the case of negative stress (under-grazing).

Structure of the transition matrix. In the second module of the simulation model, it is determined which vegetation will appear in a plot on the condition that a transition occurs. Alternative vegetation types are mainly deduced from the ordination diagrams, which are considered a reflection of the different paths of vegetation change in response to grazing or recovery. Transitions between the floristic groups are straight forward. If grazing occurs, species composition translates from group f1 to group f2. A further increase of grazing activities may cause the disappearance of several species. In this way, floristic group f2 evolves to group f3.

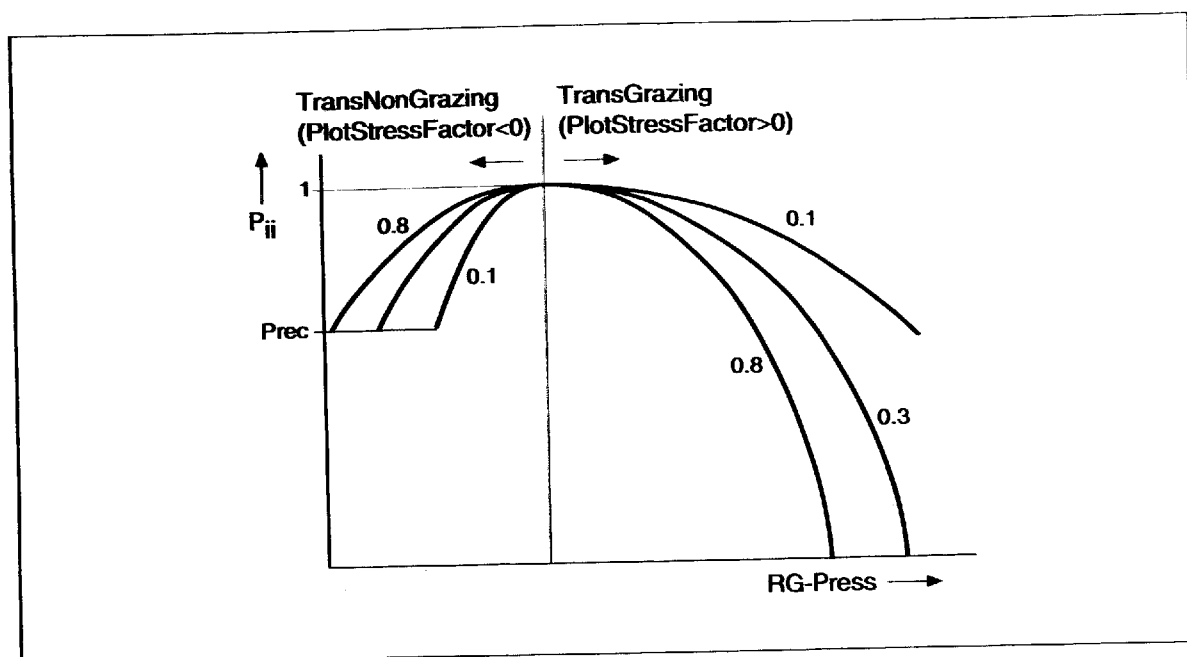


Figure 7. Probability functions of the vegetation in one particular plot. If the probability of no transition (P_{ii}) is plotted in relation to the Regional Grazing Pressure for several values of Plot-Attractivity, distinct curves are obtained. The vertical dotted line indicates the situation where the vegetation is in equilibrium with the local grazing pressure. At the right-hand side of this line, transitions can take place in response to overgrazing of the current vegetation type. Since P_{ii} decreases faster for more attractive plots, transitions will occur earlier in these plots. At the left-hand side of the dotted line, transitions can take place in response to recovery. Less attractive plots have a higher probability to recover compared with the more attractive plots. Maximal probability of recovery is defined (Prec).

A more complex transition scheme is defined for the structural groups. From the PCA ordination diagram, three successive phases can be recognized as a response to grazing (Fig. 8):

1) Opening phase. As a result of grazing of the bunches, average height, and diameter decrease. Consequently, the structural appearance of the vegetation is pushed left-wards along the first PCA ordination axis. Since the native páramo species are sensitive to trampling, open spots are formed around fragmented bunches, and total real coverage decreases;

2) Closing phase. After the opening phase, more light reaches the ground surface. Probably together with increased nutrient availability, favorable conditions are created for the invasion of short grasses into the system. In general, these grasses possess higher resistance against trampling which gives them a competitive advantage. Although average height of the vegetation decreases in this phase, total real coverage reaches higher values compared to the ungrazed state; and

3) Degeneration phase. If grazing activities pass a certain critical level, severe damage occurs due to frequent trampling. This results in areas where only a sparse vegetation persists or even in bare soil.

From the combinations shown in Figure 3, the floristic DCA diagram, and the structural PCA diagram, five transition tables are defined: grazing and recovery at slopes (Fig. 9A,B), grazing and recovery at level areas (not included), and transitions caused by fire events (Fig. 9C). For constructing these tables it was decided to define three more combinations of floristic composition and vegetation structure in addition to the combinations actually found in the data set. By including these (theoretical) vegetation types, the interpretation of the transition tables is made easier, whereas the simulation model is hardly altered. Exclusion of these types would lead to the same simulation results.

The following assumptions have been incorporated in the transition diagrams:

1) If grazing occurs at slopes, the vegetation will become more open compared to level areas. Open vegetation structures (*i.e.*, low total real coverage, large erosion spots) were found more frequently at moderate slopes than at level areas as a result of trampling impact (Verweij and Budde, 1992);

2) When floristic composition changes from f1 to f2 to f3, there is a tendency of the vegetation to form a more closed mat, especially in level

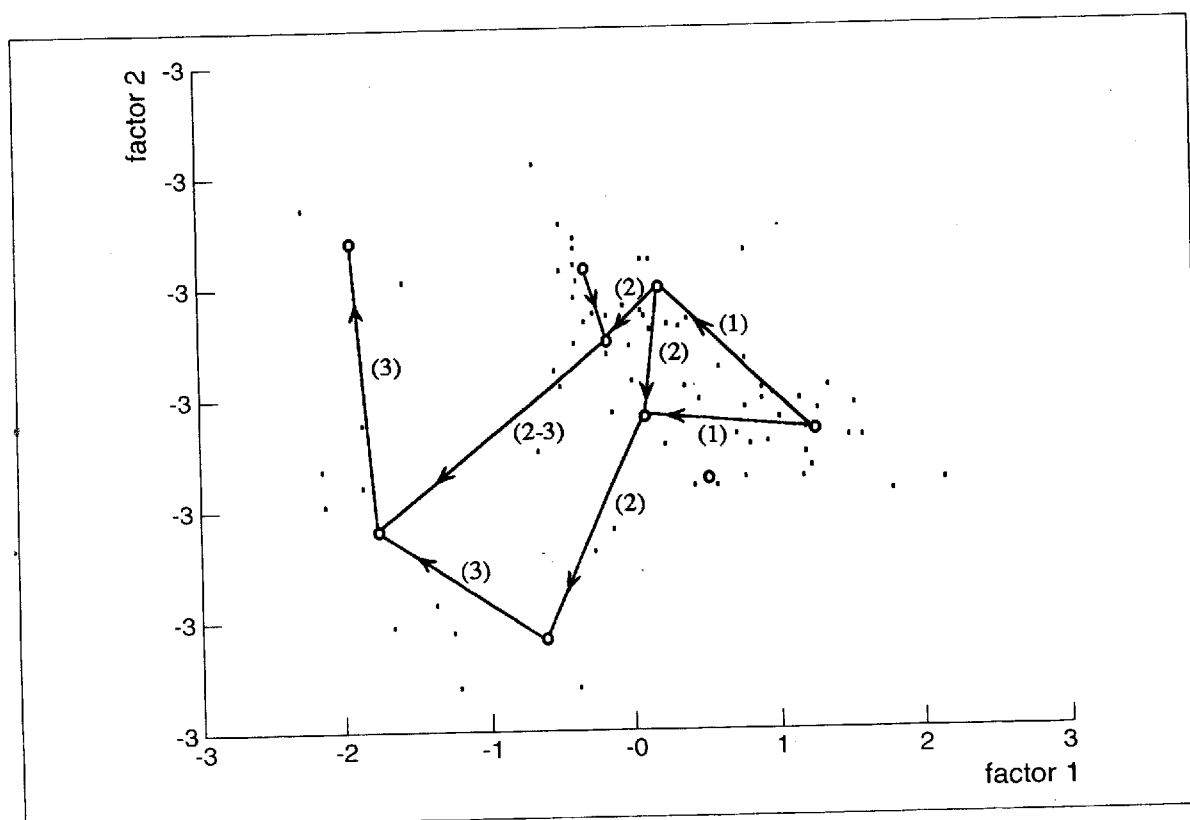


Figure 8. Distinction of three successive phases in the PCA ordination diagram as responses to increased grazing intensity: 1) opening phase, 2) closing phase, and 3) degeneration phase. Only transition vectors of slopes are indicated. Since group s2a was not found at slopes, it was not included in a succession path.

areas. Floristic groups f2 and f3 consist mainly of low species, apparently relatively resistant to grazing and trampling. These species are, for example, *Calamagrostis coarctata*, *Agrostis tolucensis*, *Pernettya prostrata*, and *Lachemilla orbiculata*. Also ground-rosette species such as *Taraxacum officinale* and *Oritrophium peruvianum* have high abundances in the f2 and f3 groups;

3) There is a tendency of species to remain in the vegetation. In this way, secondary species invade when the structure is low and open, but they can still be found when vegetation becomes higher in case of recovery;

4) When a plot is burned, only the structure of the vegetation is affected. In the model, fire will not change the floristic composition directly.

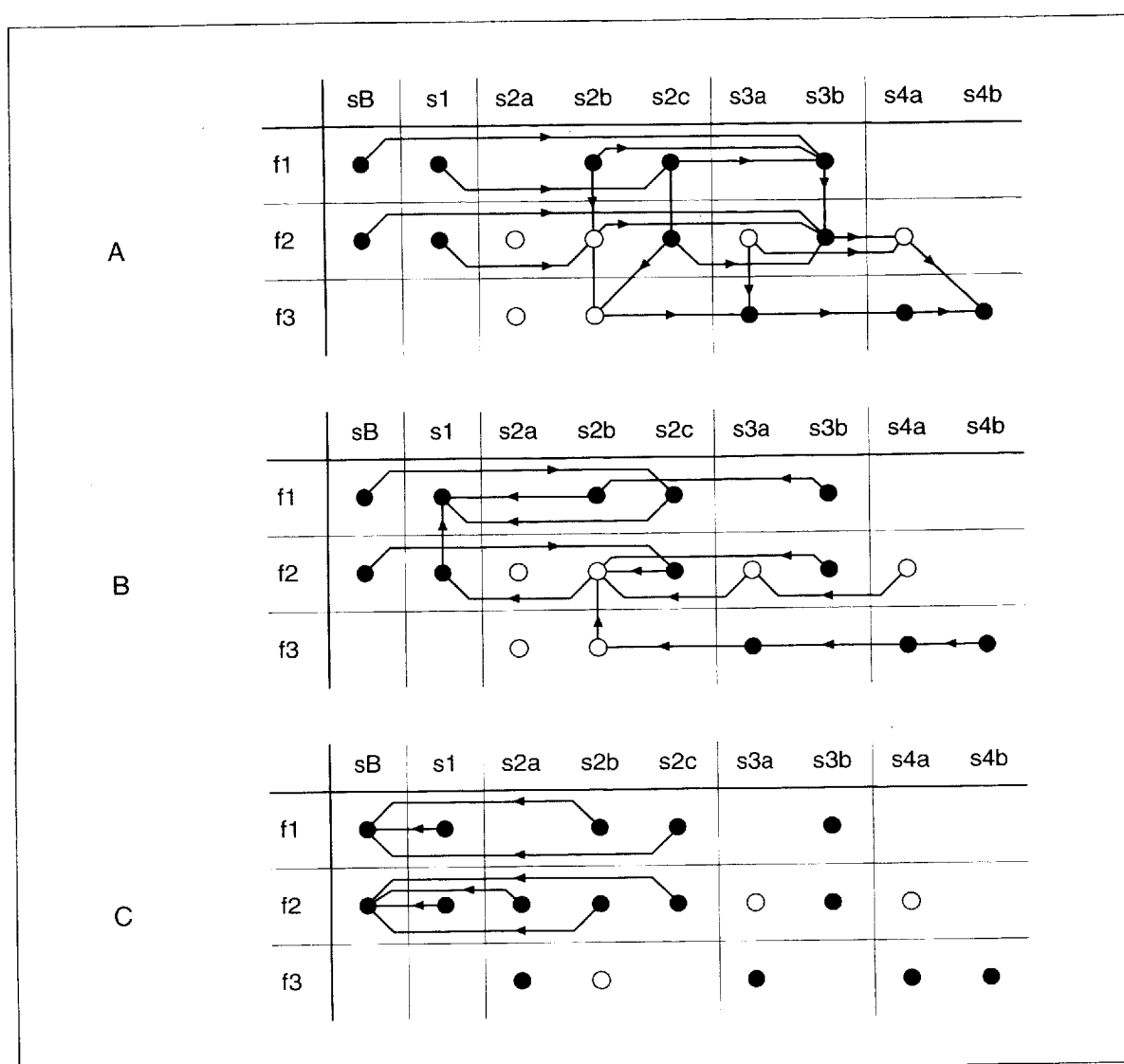


Figure 9. Hypothetical transitions for slope sites as responses to grazing (A), recovery (B), and fire events (C). Closed circles indicate vegetation types actually found in these sites. Open circles represent theoretical combinations of floristic composition and vegetation structure.

From the gradient analysis of the floristic data set, it was concluded that fire is not an important factor in determining the floristic composition in the pilot area. Apparently, a fire regime of repeated fires has controlled the pattern of species that are currently present or absent; mainly fire tolerant species have survived. Verweij and Budde (1992) discuss responses to fire in other parts of the Parque Nacional Los Nevados; and

5) Since no data are available concerning the effects of different types of fires in the páramo ecosystem (*e.g.*, head or back fire, intensity, and seasonal effects), no differentiation is made for fire types.

If from module I it follows that the vegetation in a particular plot changes due to overgrazing, the model uses the transition schemes of module II to evaluate alternative vegetation types. If there is only one alternative vegetation type that can replace the current vegetation in the plot, the probability calculated in module I is used as a measure for the chance that in the next time interval the alternative vegetation appears in the plot. However, a number of bifurcations are present in the transition diagrams. A bifurcation means that more than one vegetation type can replace the current vegetation. In that case, it is assumed that the relative distances between the defined groups in the ordination diagrams can serve as a distribution key for the total transition probability. In this study, it is assumed that vegetation change is easier if the centroids of the defined groups are situated near each other in the ordination diagram, provided that single relevés can be found between them.

During the simulation of one time-step, there is the probability in each plot that a transition takes place towards a more grazed vegetation type if the current vegetation in the plot is over-grazed, or towards a more natural vegetation type if the current vegetation in the plot is under-grazed. During each time-step, the vegetation will change locally as long as there is stress in the system. Eventually, a stage is reached where *TotalYieldGrazed* equals *TotalYieldPresent*. In that situation, the distribution of the grazed plots agrees with the attractivity of these plots for grazing (Fig. 10).

Since the simulation model is based on data from the Loma Bonita area itself, independent test runs of the model cannot be made. A rough verification of the defined procedures was obtained by starting a simulation of grazing for a mature páramo bunchgrass vegetation. In the beginning of the simulation the vegetation in all plots was set to f1/s1. Grazing was introduced by setting parameter *TotalYieldGrazed* to 100 (this value agrees with the current stocking rate in the Loma Bonita area if relative yield values from Figure 6 are used). Vegetation transitions occurred until the system reached its equilibrium (about 60 time-steps). In this stage, the distribution of simulated grazed plots could be compared to the distribution of actually grazed plots in the Loma Bonita area. It was concluded that in general the distribution of simulated grazed plots corresponds rather well with the real situation.

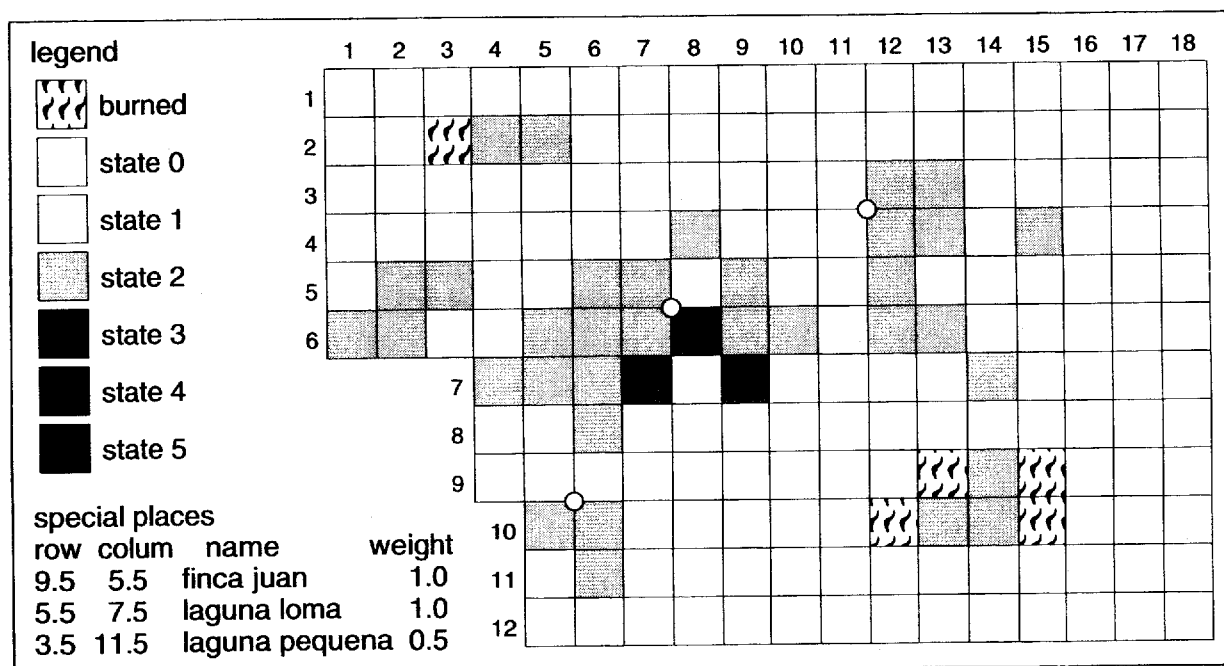


Figure 10. Distribution of the grazed plots. For each plot a rough indication is given for the grazed state of the vegetation. More affected vegetations can be found surrounding drinking sites and the farm (indicated by small circles).

At this stage of the research, it is not possible to indicate which weight and parameter settings are relevant for the real situation. Test runs of the model were made with rather arbitrary values for these parameters. The time-step in the model may be changed as soon as additional data become available which prove a different timescale of the processes. Since invasion and exclusion of species can occur within one time-step and seasonal influences are preferably excluded, a period of one year is taken as a basis. Sensitivity analyses were carried out in order to determine the effect of varying the parameter settings on simulation results. It appeared that *RG_Press* is one of the most sensitive variables in its reaction to parameter changes. The distribution of the grazed plots in the equilibrium stage is rather consistent.

Discussion

Since almost no independent data are available for the present simulation model, conclusions cannot at present be drawn concerning its usefulness to predict future vegetation changes. Test runs show satisfactory results if the distribution of grazed plots in the equilibrium stage is considered, but this does not prove that vegetation changes shown by the model agree with the real situation. Moreover, parameter settings of the test runs were arbitrarily chosen and not based on field experiments. Although the simulation model cannot be used at this time for predicting future vegetation

change, the formulation of the model brought out some interesting questions.

In the model, stability of a vegetation type depends on the balance between vegetation yield and local grazing pressure. In the work of Westoby *et al.* (1989), a different approach with respect to stability is presented. States are defined which are relatively stable under grazing activities and/or climatic fluctuations. However, certain events may occur which bring the vegetation into a so-called "transitional state." This state is more sensitive to external forces. Depending on the forces, the vegetation can return to the previous stable state, or a new stable state is established at the site (State-and-Transition Model). If the ideas of the State-and-Transition Model are applied to the current simulation model, it can be argued that the opening phase results in unstable states. In the open spots, secondary species can invade and cause new transitions. After the establishment of these species, the vegetation in the plot is brought to a new stable state, where local grazing intensity can fluctuate somewhat without forcing new vegetation transitions. In this concept, the degree of stability has to be emphasized. Vegetation types that appear only for a short period must then be recognized.

In the present simulation model, the same forcing function is used for all transitions which are defined in the transition matrices. No distinction is made between transitions caused by a shift of floristic composition and those caused by a change of vegetation structure. For the real situation, the time scales of both types of changes are expected to be different. The principle that species remain in the vegetation if the vegetation structure gets higher in case of recovery, is incorporated in the transition diagrams (Fig. 11). In spite of this, the different time scales of the replacement series are not taken into account in the probability calculations. To improve the transition procedures, the time spans required for establishment and exclusion of species should be determined. In the literature, recovery times for

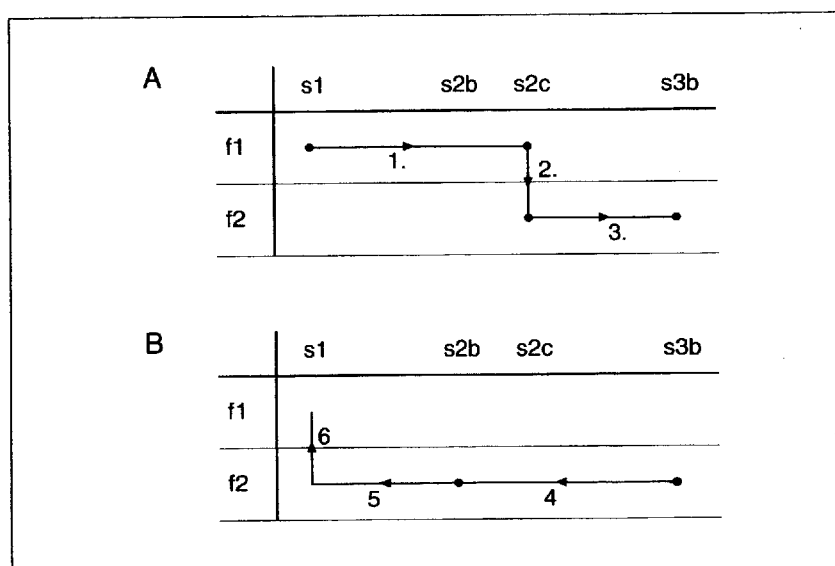


Figure 11. Example of a transition path under grazing (A) and recovery (B). In the first transition (1), the vegetation is opened. Secondary species can invade causing a new transition (2). A ground layer develops which closes the vegetation (3). In case of recovery, vegetation structure first gets higher (4, 5). Only in the last transition (6), are secondary species excluded.

grasslands are found to be highly variable, ranging from two years to more than 100 years (Belsky, 1986).

The interaction between primary production and consumption processes, as dealt with in the model, needs more attention. Depending on the stress made up by the difference between yield needed for the current stocking rate and yield available in the current vegetation, transitions take place towards more grazed or more recovered vegetation. Eventually, a stage is reached where the vegetation offers the yield which is required for the cattle. In this concept, the amount of yield which is grazed during each time interval (in the model the parameter TotalYieldGrazed) depends only on the number of cows grazing on the site. In most deterministic grazing models, total consumption depends on both stocking rate and plant biomass. The consumption per animal becomes a function of the biomass present in the system. Noy-Meir (1978) mentions four such functions, which generally are saturation curves. At the current stocking rate in the Loma Bonita area, consumption rate is thought to be maximal and not limited by available biomass. Forage quality was found to be the most important factor that determines food intake (Schmidt and Verweij, 1992). From other studies it is known that grazing stimulates plant growth (McNaughton, 1979, 1985), but in almost all deterministic growth-consumption models the quality aspect is neglected (but see Edelstein-Keshet, 1986). If the response of the system to grazing activities is a shift of the floristic composition, both plant biomass and plant quality will undergo changes (McNaughton, 1985). Most deterministic grazing models, however, deal only with one plant species or at least with only one vegetation type. Walker *et al.* (1981) discuss a situation where palatable, leafy perennials are partly replaced by resistant, early successional species under intense grazing, but the dynamics of invasion and exclusion of these species is not considered explicitly.

In the model described in this study, both vegetation structure and species composition determine available yield (Fig. 6). The assumption that secondary production in extensive grazing systems is independent of the present vegetation, implies that the appearance of a small area with high-quality vegetation means that a larger area with low-quality vegetation is no longer grazed. Since fire improves plant quality (young bunchgrass shoots contain a lower C/N ratio; Van Groen, 1987), the existence of recently burned areas allows other areas to recover. Although simulation runs of the model showed that relatively unattractive areas are grazed more intensively after a fire, this shift of grazing activities occurs during a short period only. Repeated fires are necessary to stimulate cattle grazing in formerly unattractive areas. If, in these areas, the occurrence of fires is prevented, level regions remain preferred in the simulation model. It should be realized that recurrent fires also have negative effects on the long term, such as loss of nutrients due to volatilization and lixiviation (Medina and Sarmiento, 1979). These impacts are not included in our model.

For the improvement of the model, more data are required for quality and quantity aspects of the defined vegetation types in relation to grazing behavior. The research of Schmidt and Verweij (1992) is an initial step to obtain these data.

In general, simulation models are considered the final stage of an ecological research project. Only then are sufficient data available to calibrate the model and to verify the results of simulation runs. For this project, a simulation model has been developed in a very early stage. The formulation of the model appeared to be helpful for indicating which important factors or processes are insufficiently known. Since (ecological) modeling forces one to think about a specific problem in a fundamental way, a simulation model can serve as a tool rather than an objective.

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Literature cited

- Austin, M. P. (1977). "Use of ordination and other multivariate descriptive methods to study succession." *Vegetatio* 35, 165–175.
- Austin, M. P. and Belbin, L. (1981). "An analysis of succession along an environmental gradient using data from a lawn." *Vegetatio* 46, 19–30.
- Belsky, A. J. (1986). "Revegetation of artificial disturbances in grasslands of the Serengeti National Park, Tanzania. II. Five years of successional change." *J. Ecology* 74, 937–951.
- Edelstein-Keshet, L. (1986). "Mathematical theory of plant-herbivore systems." *J. Math. Biol.* 24, 25–58.
- Ellenberg, H. (1979). "Man's influence on tropical mountain ecosystems in South America." *J. Ecology* 67, 401–416.
- Fetcher, N. (1981). "Effects of grazing on cold desert shrubs: A simulation model based on relative growth rate." *Ecol. Model.* 13, 49–86.
- French, N. R. (1990). "The utility of models in the study of mountain development and transformation." *Mountain Research and Development* 10, 141–149.

- Hill, M. O. (1979a). "TWINSPAN – a FORTRAN program for arranging multivariate data in an ordered two-way table by classification of individuals and attributes." *Cornell University Press, Ithaca*.
- Hill, M. O. (1979b). "DECORANA – a FORTRAN program for detrended correspondence analysis and reciprocal averaging." *Cornell University Press, Ithaca*.
- Hulst, R. van (1979). "On the dynamics of vegetation: Markov chain as models of succession." *Vegetatio* **40**, 3–14.
- Innis, G. S. (ed.). (1978). "Grassland simulation model." *Ecological Studies* **26**. Springer-Verlag, New York.
- Lippe, E., de Smidt, J. T. and Glenn-Lewin, D. C. (1985). "Markov models and succession: A test from a heathland in The Netherlands." *J. Ecology* **73**, 775–791.
- McNaughton, S. J. (1979). "Grazing as an optimization process: Grass-ungulate relationships in the Serengeti." *Amer. Naturalist* **113**, 691–703.
- McNaughton, S. J. (1985). "Ecology of a grazing ecosystem: The Serengeti." *Ecol. Monogr.* **55**, 259–294.
- Medina, E. and Sarmiento, G. (1979). "Tropical grazing land ecosystems of Venezuela. I. Ecophysiological studies in the *Trachypogon* savanna (Central Llanos)." Pp. 612–619 in "Tropical grazing land ecosystems." *Natural Resources Research* **16**. UNESCO, Paris.
- Noble, I. R. and Slatyer, R. O. (1981). "Concepts and models of succession in vascular plant communities subject to recurrent fire." Pp. 311–335 in Gill, A. M., Groves, R. H., and Noble, I. R. (eds.), "Fire and the Australian biota." *Australian Academy of Science, Canberra*.
- Noy-Meir, I. (1976). "Rotational grazing in a continuously growing pasture: A simple model." *Agricultural Systems* **1**, 87–112.
- Noy-Meir, I. (1978). "Stability in simple grazing models: Effects of explicit functions." *J. Theor. Biol.* **71**, 347–380.
- Pellew, R. A. P. (1983). "The impacts of elephant, giraffe and fire upon the *Acacia tortilis* woodlands of the Serengeti." *Afr. J. Ecol.* **21**, 41–74.
- Redetzke, K. A. and Van Dyne, G. M. (1976). "A matrix model of a rangeland grazing system." *J. Range Manag.* **29**, 425–430.
- Runkle, J. R. (1981). "Gap regeneration in some old-growth forests of the eastern United States." *Ecology* **62**, 1041–1051.
- Schmidt, A. M. and Verweij, P. A. (1992). "Forage intake and secondary production in extensive livestock systems in páramo." Pp. 197–210 in Balslev, H. and Luteyn, J. L. (eds.), "Páramo: An Andean ecosystem under human influence." *Academic Press, London*.
- Smith, R. C. G. and Williams, W. A. (1973). "Model development for a deferred-grazing system." *J. Range Manag.* **26**, 454–460.
- Swartzman, G. L. and Singh, J. S. (1974). "A dynamic programming approach to optimal grazing strategies using a succession model for a tropical grassland." *J. Appl. Ecol.* **11**, 537–548.

- Thalen, D. C. P., Poorter, H., Lotz, L. A. P. and Oosterveld, P. (1987). "Modelling the structural changes in vegetation under different grazing regimes." Pp. 167–183 in Van Andel, J., Bakker, J. P., and Snaydon, R. W. (eds.), "Disturbance in grasslands: Causes, effects and processes." Dr. W. Junk Publ., Dordrecht.
- Thouret, J. C. (1983). "Presentación geológica y geomorfoestructural." Pp. 48–55 in van der Hammen, T., Pérez P., A. and Pinto E., P. (eds.), "Studies on tropical Andean ecosystems 1. La Cordillera Central Colombiana. Transecto Parque Los Nevados (introducción y datos iniciales)." Cramer, Vaduz.
- Turner, M. G. (1987). "Spatial simulation of landscape changes in Georgia: A comparison of three transition models." *Landscape Ecology* 1, 29–36.
- Usher, M. B. (1966). "A matrix approach to the management of renewable resources, with special reference to selection forests." *J. Appl. Ecol.* 3, 355–367.
- Usher, M. B. (1981). "Modelling ecological succession with particular reference to Markovian models." *Vegetatio* 46, 11–18.
- Van Groen, F. (1987). "Effects of fires on structure, composition, and nutrient status in two bunchgrass páramos near Bogotá, Colombia." M.Sc. dissertation, Hugo de Vries Laboratory, University of Amsterdam.
- Van Wijngaarden, W. (1985). "Elephants-Trees-Grass-Grazers. Relationships between climate, soils, vegetation and large herbivores in a semi-arid savanna ecosystem (Tsavo, Kenya)." *ITC Publication 4*, Enschede, The Netherlands.
- Verweij, P. A. and Budde, P. E. (1992). "Burning and grazing gradients in páramo vegetation: Initial ordination analyses." Pp. 177–195 in Balslev, H. and Luteyn, J. L. (eds.), "Páramo: An Andean ecosystem under human influence." Academic Press, London.
- Walker, B. H., Ludwig, D., Holling, C. S. and Peterman, R. M. (1981). "Stability of semi-arid savanna grazing systems." *J. Ecol.* 69, 473–498.
- Westoby, M., Walker, B. and Noy-Meir, I. (1989). "Opportunistic management for rangelands not at equilibrium." *J. Range Manag.* 42, 266–274.
- Whisenant, S. G. and Wagstaff, F. J. (1991). "Successional trajectories of a grazed salt desert shrubland." *Vegetatio* 94, 133–140.