

Vegetation dynamics under grazing disturbance. The state-and-transition model for the Patagonian steppes

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Abstract. *Plant communities in Patagonia have a low plant cover (10-60%) and are dominated by two main functional groups: shrubs and perennial grasses. Domestic grazing reduces total plant cover and favors the replacement of species within functional groups (grasses or shrubs) and the replacement of entire functional groups (grasses for shrubs). We assessed the dynamics of vegetation in grazed ecosystems of Patagonia within the conceptual framework of the state-and-transition model, which allowed us to identify and arrange vegetation states induced by grazing along a sequence of physiognomic types. State-and-transition models for different Patagonian ecosystems indicate that changes are greater in the most humid ecosystems. In areas with annual precipitation above 250 mm, grazing induces a high number of stable states (4 to 7) with marked changes in physiognomy, from grass steppes to dwarf shrublands. Conversely, in areas with annual precipitation below 250 mm, grazing induces a low number of stable states (3 to 5) with less marked physiognomical differences, from shrub-grass steppes to dwarf shrub steppes. These changes were associated with specific steps in soil degradation and in the status of the soil seed bank. The intrusion of shrubs (a more xeric plant functional group than grasses) following soil disturbance is a key transition to an alternate stable state with strongly different structural and functional properties. Our results suggest that, the more humid areas possibly deserve special attention because they suffer more drastic changes than arid areas. In the future, stopping degradation and restoring ecosystems will need more intensive interventions than the sole regulation of stocking rates. Other strategies, like manipulating surface soil, adding nutrients or seeds, and planting target species in seasons or years with favorable precipitation and under grazing exclusion, should be designed and experimentally tested.*

Introduction

The Patagonian region extends from south of the Río Negro River (39.5°S) to 55°S (Soriano et al. 1983, Ares et al. 1990). Its climatic heterogeneity results from the combined influence of the latitudinal gradient of temperature, and the west-east gradient of precipitation. The decrease of precipitation from the western mountains towards the east is altered by the influence of the Atlantic Ocean, in a narrow zone along the eastern continental coast (Prohaska 1976, Barros y Rivero 1982). Throughout the area, strong westerly winds and precipitation events occur in a highly variable pattern within and between years.

There are two phytogeographic provinces in the region. Northeastern Patagonia corresponds to the southern extreme of the Monte Phytogeographic Province (mainly shrublands with *Larrea* spp.), while the rest of the territory is covered by the Patagonian Phytogeographic Province represented by the following districts: the Subandean district dominated by grasslands or perennial grass steppes of *Festuca pallenscens* or *F. gracillima*, the Occidental district covered by grass-shrub and shrub steppes of *Stipa* spp. *Mulinum spinosum* and *Senecio* spp., the San Jorge Gulf district with shrublands of *Retanilla patagonica* and *Colliguja integerrima*, the Central district represented by

Table 1. Physiognomic characterization of all the stable states of vegetation in 13 sites of Patagonia. Numbers enclosed in rectangles represent the number of states for each physiognomic category. P: annual precipitation in mm. Modified from Paruelo et al. (1993), Beeskow et al. (1995), and Bisigato and Bertiller (1997).

Site	Phytog. Province	District	Disturbance →						P
			Grass steppe	Grass-shrub steppe	Shrub-grass steppe	Shrub steppe	Dwarf shrub-grass steppe	Dwarf shrub steppe	
P. Leman	Patagonia	Central					1	2	110
Río Mayo	Patagonia	Occidental			3				168
Garayalde	Patagonia	Central				4		1	175
Ea San Luis	Monte				2	1			175
Trelew	Monte				3	1		1	175
Pla. Valdés	Patagonia	Central			1	2			233
Pta. Ninfas	Patagonia	Central	1	1		1		1	254
Río Gallegos	Patagonia	Subandean	1	2			3	1	270
Esperanza	Patagonia	Subandean	2	1	1			1	270
Media Luna	Patagonia	Subandean	3	1	1		1	1	367
Río Grande	Patagonia	Fuegian	4				2	1	379
Río Turbio	Patagonia	Subandean	2	1	1			1	412
Leleque	Patagonia	Subandean		1	2	1			521

shrub steppes of *Chuquiraga avellanadae*, *Nassauvia glomerulosa*, or *Junellia tridens* and the Fuegian district covered by grasslands of *Festuca gracillima* with patches of *Nothofagus* spp. (Soriano 1956, León et al. this issue).

Plant communities in Patagonia are characterized by a low vegetation cover which may range from 60% or higher to less than 10% in the most arid areas. Shrubs and perennial grasses are the dominant plant functional groups in all environments. Their relative abundance or cover is closely related to the environmental conditions, included anthropomorphic disturbance. Patagonian ecosystems have been used since the beginning of this century as grazing areas. As reported for other ecosystems, grazing causes an overall reduction of plant cover through the decrease in abundance, or eventually the extinction, of palatable species, mainly grasses (Soriano et al. 1983, Ares et al. 1990, Defossé et al. 1990, Schlesinger et al. 1990, Soriano et al. 1995, Bertiller 1996). Deflation and deposition processes, as well as organic matter and nutrient losses, are triggered by wind and precipitation after grazing disturbance thus creating large areas of bare soil (Rostagno and

del Valle 1988, Rostagno 1989, Ares et al. 1990, Mazzarino et al. 1996, 1998). These processes seriously limit the potential of vegetation reestablishment (Soriano and Movia 1986, Ares et al. 1990, del Valle 1998).

Local managerial strategies to revert these changes have so far largely been based on the reduction of stocking rates (Borrelli et al. 1984, Nakamatsu et al. 1989a, 1989b), in accordance with the postulates of the range succession model (Dyksterhuis 1949). However, observations of vegetation dynamics in areas where domestic herbivores have been intentionally excluded during several years or decades are not consistent with this model. In most cases, the release from grazing pressures did not result in a reversal of vegetation changes and did not arrest land degradation (Soriano 1959, Soriano et al. 1980, Paruelo et al. 1993, Bertiller 1994, 1996, del Valle 1998). Consequently, both scientists and managers have recently agreed that alternative and more reliable models, such as the state-and-transition model (Westoby et al. 1989), should be developed to describe rangeland dynamics in Patagonia (Paruelo et al. 1993, Bertiller 1994, Laycock 1995). For the time being, however, a general management model which would organize the prevailing hypotheses about ecosystem structure and functioning in Patagonia is not available. In most cases, range management decisions are based on the principles of the traditional succession model, on empirical trial and error actions by ranchers or on local studies of limited geographical scope (but see Golluscio et al. this issue). Thus, it is necessary to organize the available knowledge on Patagonian rangelands and to identify gaps of knowledge, which may be the target of further research.

The objective of the present contribution is to analyze vegetation dynamics under grazing disturbance in Patagonia, within the conceptual framework of the state-and-transition model (Westoby et al. 1989). We also identify thematic or geographic areas for further research.

The state-and-transition model in Patagonia

Paruelo et al. (1993), Bertiller (1994), Beeskow et al. (1995), Laycock (1995), and Bisigato and Bertiller (1997) presented and discussed thirteen state and transition models for different rangelands of Patagonia, based on floristic and structural descriptions of vegetation under different grazing regimes and disturbance intensities. Most state-and-transition models refer to grasslands in northern Patagonia, covering the south extreme of the Monte province and the majority of phytogeographic districts of the Patagonian province (Subandean, Occidental, and Central-Chubut). Conversely, they are scarce in south Patagonia where only the grasslands in the Subandean and the Fuegian districts are represented. An important area of the vast Central district (the Santa Cruz subdistrict) has not been described.

There are also few ecosystems where long-term studies on structure and functioning were carried out. The largest data series are in Río Mayo (45°25'S, 70°20'W, 500 m.a.s.l) and Media Luna (45°35'S, 71°25'W, 600-950 m.a.s.l) sites (44 years and 15 years, respectively), while in the other sites (Pampa de Lemman: 45°26'S, 69°50'W, 400 m.a.s.l; Ea. San Luis: 42°39'S, 65°23'W, 115 m.a.s.l; and Punta Ninfas: 42°59'S, 64°34'W, 90 m.a.s.l) they range from 3 to 5 years. However, the study sites are representative of large homogeneous areas covering a wide range of climatic variation, a fact that allows the use of this knowledge to make some generalizations about the factors involved in vegetation dynamics under grazing in Patagonia.

All the rangelands described show that vegetation changes caused by grazing induce different stable vegetation states that may be clearly recognized in the field. A general pattern of changes in botanical composition and physiognomy of the community may be identified in the diagrams (Table 1, Figure 1). The results indicate that vegetation states in all sites shift along different physiognomic types and more diverse changes may occur in the most humid ecosystems. In areas with more than 250 mm, vegetation may be shifted by grazing along a high number of stable states (4 to 7) from grass steppes to dwarf shrublands. Conversely, in areas with less than 250 mm annual precipitation, changes in vegetation are less marked from shrub-grass steppes to dwarf shrub steppes (3 to 5 stable

states). These changes involve different plant processes, such as the overall reduction of plant cover and deletion and replacement of species within or between functional groups.

Reduction of plant cover

This is one of the most conspicuous processes in grazed ecosystems of Patagonia that includes all edible species (Soriano et al. 1983, Ares et al. 1990, Paruelo et al. 1993, Bertiller 1994, Bertiller 1996, Bisigato and Bertiller 1997). Although this process has continuously occurred since the introduction of sheep, Soriano et al. (1983) reported that it is highly probable that the most drastic reduction of plant cover occurred at the beginning of this century, when rangelands supported their highest historical stocking rates. Changes in plant cover may be extremely severe in the most humid ecosystems, such as the grasslands of the Subandean district (350 to 500 mm annual precipitation), in which plant cover may range from more than 90% to less than 20% (Borelli et al. 1984, Bertiller and Defossé 1993, Bertiller 1994). In the more arid environments, the reduction of plant cover is less: i.e., 23% reduction in Pta. Ninfas rangelands of the Central district (254 mm annual precipitation), 12-18% in the Patagonian Monte (175 mm annual precipitation), c.a 20% in the Occidental district (170 mm annual precipitation), 12% in the Pampa de Leman rangelands of the Central district (110 mm annual precipitation) (Bertiller 1993, Beeskow et al. 1995, Bisigato and Bertiller 1997, Perelman et al. 1997).

Changes in vegetation cover may be produced by the direct effect of removal of tissues (Sala 1988), which may lead to plant death in extreme cases or by indirect effects following cover reduction, such as erosion and losses of soil organic matter, nutrients, and seeds that limit plant establishment (Soriano and Sala 1986, Ares et al. 1990, Bertiller and Coronato 1994, Aguiar and Sala 1994, 1997, Bertiller 1996, 1998, Defossé et al. 1997a, b).

Changes in botanical composition within functional groups

The replacement of plant species of the same functional group is one of the first steps in the degradation processes of grazed ecosystems of Patagonia. In the grasslands of the Subandean district, the first effect of grazing disturbance is the reduction of perennial grass diversity (Figure 1a). In the less disturbed areas (State I), the most abundant perennial grasses are *Festuca pallescens*, *Hordeum comosum*, *Bromus setifolius*, *Rytidosperma virescens*, and *Koeleria vurilochensis*, while in the State II *Festuca pallescens* is practically the only species present (León and Aguiar 1985, Defossé et al. 1990, Bertiller 1994, 1996). In the Patagonian Monte (Figure 1b), species replacement occurs within the group of tall shrubs (*Chuquiraga hystrix*, *Lycium chilense*, *Atriplex lampa* and *Larrea divaricata*) (States I and II, respectively, Bisigato and Bertiller 1997). In the Occidental district (Figure 1c), grazing leads to species replacement within the group of the perennial grasses. The cover of the most palatable species (*Bromus setifolius*, *Poa ligularis*, and *Hordeum comosum*) decreases, while the cover of a non-palatable grass (*Stipa humilis*) increases (Soriano et al. 1980, Fernández and Paruelo 1993). These changes of species are probably triggered by different factors related to the reduction of seed and microsite availability for seedling emergence and establishment (Soriano and Sala 1986, Aguiar and Sala 1994, 1997, Bertiller and Coronato 1994, Bertiller 1996, Defossé et al. 1997a, b, Bertiller 1998). In this ecosystem, replacements occur also within shrubs. Under grazing, the cover of *Mulinum spinosum* decreases, while the cover of *Senecio filaginoides* increases. These changes are probably due to the great competitive ability of *Senecio* to capture available resources released in grazed areas and to the reduction of the *Mulinum spinosum* seed bank, since fruits are consumed by sheep (Fernández et al. 1992).

Replacement of functional groups

The increase of shrub cover (relative or absolute) and the decrease of the absolute cover of perennial grasses occur as an extended process in grazed rangelands of Patagonia (Paruelo et al. 1993, Bertiller and Defossé 1993, Bertiller 1994, Bisigato and Bertiller 1997, Perelman et al. 1997). These replacements lead to changes in the physiognomy of the plant community (see Table 1). In the case of *Festuca pallescens* grasslands (Table 1, Figure 1a), perennial grasses are replaced by *Mulinum spinosum* or *Senecio* spp., and in the more disturbed sites by dwarf shrubs (different

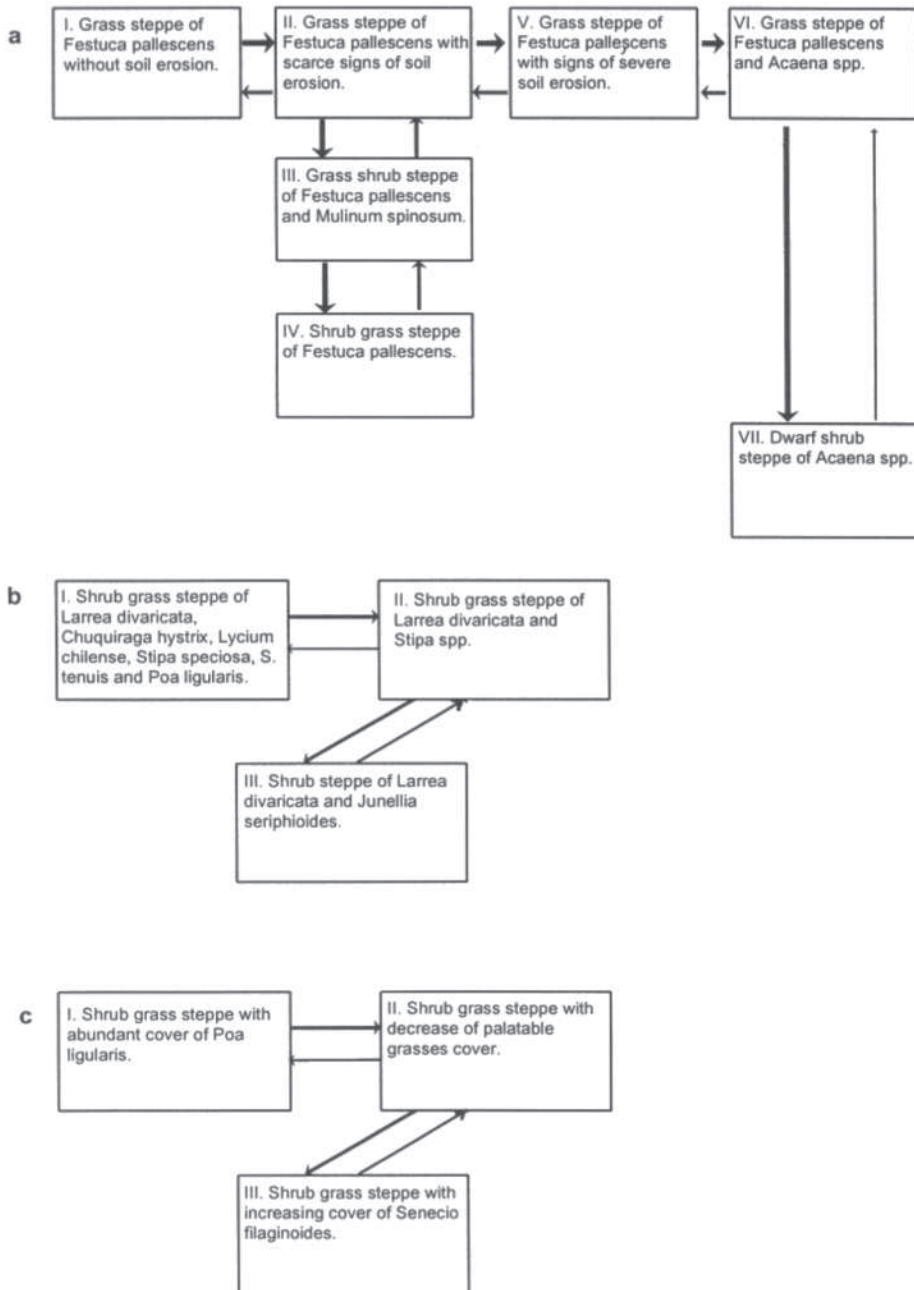


Figure 1. State-and-transition diagrams from: a. Media Luna site (10), b. Estancia San Luis site (4) and c. Rio Mayo site (2).

species of the genus *Acaena*). In the Patagonian Monte (Figure 1b), grazing reduces total plant cover through reduction of perennial grasses and some tall shrubs. The cover of dwarf shrubs (*Junellia seriphioides* and *Nassauvia fuegiana*) increases, although this does not compensate for the effect on the decreasing species. These changes in specific cover are reflected in the patch structure. Patches dominated by grasses disappear in areas with high grazing pressure, and are replaced by dwarf shrub patches. The patches dominated by tall shrubs are smaller, less diverse, and with less grass cover in areas more intensely grazed. In this form, each vegetation state induced by grazing

disturbance may be described by a discrete array of types of vegetation patches (Bisigato and Bertiller 1997). In the Occidental district, grasses are also partially replaced by shrubs such as *Mulinum spinosum*, *Senecio* spp. (Figure 1c) and eventually by dwarf shrubs (Bonvissuto et al. 1983, Fernández and Paruelo 1993, Perelman et al. 1997).

As previously described for other ecosystems (Friedel 1991, Laycock 1995), plant cover reduction, species replacement within the same functional group, and functional group replacement may be associated with three thresholds in soil degradation and in the status of the soil seed bank (Rostagno and del Valle 1988, Rostagno 1989, Rostagno et al. 1991, Bertiller et al. 1995, Bertiller 1996, 1998). In a first step, plant removal by grazing reduces plant cover, opening small gaps in the canopy. However, these gaps are not large enough to expose the upper soil to erosion forces, which would also reduce the soil seed bank. In a second step, the reduction of plant cover is followed by soil erosion, and incipient and isolated signs of erosion may be recognized (Rostagno and del Valle 1988, Ares et al. 1990, Bertiller et al. 1995). This produces a loss of seeds of grasses and a likely decrease of suitable microsites for the emergence and establishment of grasses. Under these conditions, plant establishment may occur in the undisturbed patches of bare soil (Bertiller 1996, Defossé et al. 1997a, 1997b, Bertiller 1998). In a third stage, the removal of plant tissue is more intense, and the overgrazed plants begin to die, increasing the proportion of bare soil exposed to wind and water erosion. Organic matter, nutrients, and seeds are lost from the upper soil, and erosion appears in all patches of bare soil (Rostagno et al. 1991, Bertiller 1992, 1996, 1998, Bertiller and Coronato 1994, Mazzarino et al. 1996, 1998, Bertiller and Aloia 1997, Bouza et al. 1993). At this stage, shrubs are probably the only functional group that can colonize the bare patches and restore plant cover (Collantes et al. 1989, Bertiller 1996, Bisigato and Bertiller 1997). As in other arid ecosystems (Fisher and Turner 1978, Walker et al. 1981, Caldwell 1985, Nilsen et al. 1987), the relative advantage of shrubs over grasses, when resources are limiting, can be explained by their extensive root systems, which are able to utilize water and some nutrients stored deep in the soil profile. Shallow-rooted perennial grasses, conversely, depend largely on the water and nutrients stored in the upper soil, limiting their fitness in environments where the upper soil compartment is degraded (Sala et al. 1989, Bertiller et al. 1991, 1996, Bisigato and Bertiller 1997, Defossé et al. 1997a, 1997b).

Conclusions

Disturbance of Patagonian rangelands has largely been initiated during the early part of this century by sheep grazing. In many rangelands, vegetation changes imposed by grazing cannot be reverted by a reduction or cessation of grazing. The intrusion of shrubs (a more xeric plant functional group than grasses) results in a state difficult to reverse, because of the loss of a significant amount of nutrient-rich top soil. Except for the sites mentioned in Table 1 and some others for which data are unpublished, no complete floristic lists are available for the different stable vegetation states found in ecosystems of Patagonia. This limits the identification of the effects of grazing on some aspects of plant structure, such as plant diversity at different scales, species additions and deletions, etc. Also, the scarce available knowledge on ecosystem functioning does not allow the identification of the environmental scenarios in which transitions may occur, or to predict the likelihood of their occurrence. However, an approach using the state-and-transition models provide an important conceptual framework to organize the available knowledge on Patagonian ecosystems and support the design of future research. The transitions proposed by Paruelo et al. (1993), Bertiller (1994), Laycock (1995), and Beeskow et al. (1995) for different rangelands of Patagonia are functional hypotheses that can be tested in order to give further insights into the process of degradation/recovery. In doing this, the criteria for the selection of areas for intensive future studies is an important step. Extent, homogeneity, and level of disturbance, and social and economic value, among others, are aspects that should be considered in such selection. In this context, more humid areas possibly deserve special attention because they provide scenarios where changes are more

drastic than in arid areas. In the future, more intensive interventions than the regulation of stocking rates will probably be needed to stop degradation and to restore disturbed areas. Strategies like surface soil manipulation, nutrient and seed addition, or planting of target species in seasons or years with favorable precipitation and under grazing exclusion should be identified, and experiments should be conducted as a basis for future management tools. Recommendations should be based on an adequate knowledge of the main processes involved in ecosystem functioning, and on the quantification of the effects of each management strategy on vegetation dynamics.

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