

Interactions among grasses, shrubs, and herbivores in Patagonian grass-shrub steppes

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Abstract. *The Patagonian shrub steppe, as most Patagonian ecosystems, is dominated by tussock grasses and shrubs. Our main objective was to review the ways in which grasses and shrubs interact and how this affects the structure and functioning of the steppe and discuss the impact of grazing on them. Water is the main limiting resource in the Patagonian shrub steppe. Competition and facilitation control grass and shrub density and distribution. Introduction of sheep since the beginning of the century may have affected vegetation and ecosystem structure and functioning and modified the grass-shrub relationships. We use a simple conceptual model to suggest how sheep grazing can modify the result of competition and the grass/shrub balance in ecosystems that show different levels of degradation. Additionally, grazing may disrupt the current two-phase organization of vegetation and therefore may radically affect the ecosystem functioning of the steppe.*

Introduction

Patagonia is a broad region in South America that encompasses different ecosystems, from grasslands to shrub-steppes and semideserts. Tussock grasses and shrubs account for most of the biomass and production in Patagonian ecosystems. The main features of climate, soil, and vegetation as well as plant production of these Patagonian communities have been reviewed recently (Soriano 1983, Ares et al. 1990). However, there has been no review of how grasses and shrubs interact and determine the structure and functioning of these ecosystems. Here we focused mostly on one ecosystem: the Patagonian shrub steppe. This ecosystem is currently co-dominated by tussock grasses and shrubs and corresponds to the Occidental District defined by Soriano (1956).

The grass-shrub balance has been at the core of debates on the functioning of arid ecosystems. Understanding this issue is important for predicting how semiarid systems will respond to human impact and environmental changes (Taush et al. 1993). Patagonia has not escaped this debate. The general idea is that the major ecosystems in Patagonia were originally dominated by grasses, and that since the beginning of the century, grazing by domestic herbivores has promoted a decrease in grass cover and concurrently either an increase or the invasion of shrubs. This phenomenon has occurred in the western mesic communities of the Subandean district (Soriano 1956b, Boelcke 1957, León and Aguiar 1986) but not in the Patagonian shrub steppes (Occidental District) (Perelman et al. 1997). Our review discusses ways in which grasses and shrubs interact and the effect of grazing on them. We finally propose a conceptual model that explain the differential responses of the Occidental and the Subandean district.

We focused on the current structure and functioning of this ecosystem, knowing that there are limitations to the inference of presettlement structure and functioning from current data. We will first compare grasses and shrubs as different plant functional types. Then, we will present information on how they interact and determine energy flux and water balance. In a third section, we will review studies on the dynamics of the community and how grasses and shrubs control it.

Finally, we will return to the issue of how grazing by domestic herbivores may have impacted the balance between grasses and shrubs in Patagonian ecosystems.

Characterization of tussock grasses and shrubs

In the Patagonian-shrub steppe (Occidental district, Soriano 1956a), the dominant tussock grass species are *Stipa speciosa*, *S. humilis*, *Poa ligularis*, *Bromus pictus*, and *S. neai*, whereas the dominant shrub species are *Mulinum spinosum*, *Senecio filaginoides*, *Adesmia campestris*, and *Berberis heterophylla*. After studying several grass and shrub species, Soriano and Sala (1983) concluded that these two life forms represent different plant strategies for the Patagonian shrub steppe. In this steppe, growth is limited in winter by low temperature and in late spring and summer by soil water availability (Soriano and Sala 1983). Grasses are active most of the year, green leaves rapidly expand during spring, and flowering occurs in early summer. Some shrubs are active during winter (*Senecio filaginoides*, *Berberis heterophylla*) and others are not (*Mulinum spinosum*, *Adesmia campestris*). All shrubs flower in late summer. Grasses and shrubs differ in their root systems. Tussock grasses have most of their root biomass (67%) in the upper 20 cm, whereas most of the shrubs species have only 13% in this layer (Paruelo and Sala 1995). Within the shrubs, *Senecio filaginoides* has more root biomass in the upper layer than *Mulinum spinosum* (Fernández and Paruelo 1989). These differences in root system and the higher availability of water in deep soil layers determine a lower leaf water potential in grasses than in shrubs during summer (Soriano and Sala 1983).

Reproduction of both grass and shrub species is predominantly sexual; stolons and rhizomes are not particularly well represented in either group. Exceptions are *Poa lanuginosa* and *Berberis heterophylla*. Grasses and shrubs differ in other characteristics. For example, biomass production per unit of water transpired is higher in grasses than in shrubs (1.1 g/mm vs 0.6 g/mm) (Aguiar et al. 1996). Foliar specific area is higher in grasses than in shrubs (43 vs 28 cm²/g). Nitrogen content, on the other hand, is higher in shrubs than in grasses (10 vs 6 mg/g) (Sala et al. 1989).

Does competition control the grass-shrub balance?

A mechanistic view of competition needs to address both the dynamics of the competing species or plant functional types and the dynamics of the resources for which they compete (Tilman 1987). Overall, water is the main constraint of functioning in the steppes in Patagonia. Soil water dynamics may be summarized as the balance between precipitation (input) and the different losses. Annual precipitation in the steppe (160 mm) is lost through evaporation (56%), transpiration (34%), and deep percolation (10%) (Paruelo and Sala 1995). From a plant perspective, soil water can be divided into two different soil resources: upper soil water and deep soil water (Soriano and Sala 1983). During winter and early spring the entire profile is wet. Later in the season, the probability of high water availability for plants decreases, with the decrease being more accentuated in upper layers than in deep layers (Paruelo and Sala 1995). Upper soil water is lost through evaporation and transpiration; deep soil water is lost to transpiration and deep percolation. The amount of soil water lost to transpiration from one horizon depends on root density. Therefore, upper soil water will be lost through transpiration by grasses and deep soil water will be lost through transpiration by shrubs. On the other hand, the amount of water that enters the soil depends on infiltration. Depth of infiltration of a rainfall event (i.e., refilling of upper and deep soil layer resources) depends on the amount of precipitation and on the soil water content. An analysis of the rainfall events in the steppe indicated that events < 10 mm make up 85% of the total number of events and represent 58% of total annual precipitation (number of years=22). Most of these small events occur during autumn and winter (78%) (Golluscio et al. 1998).

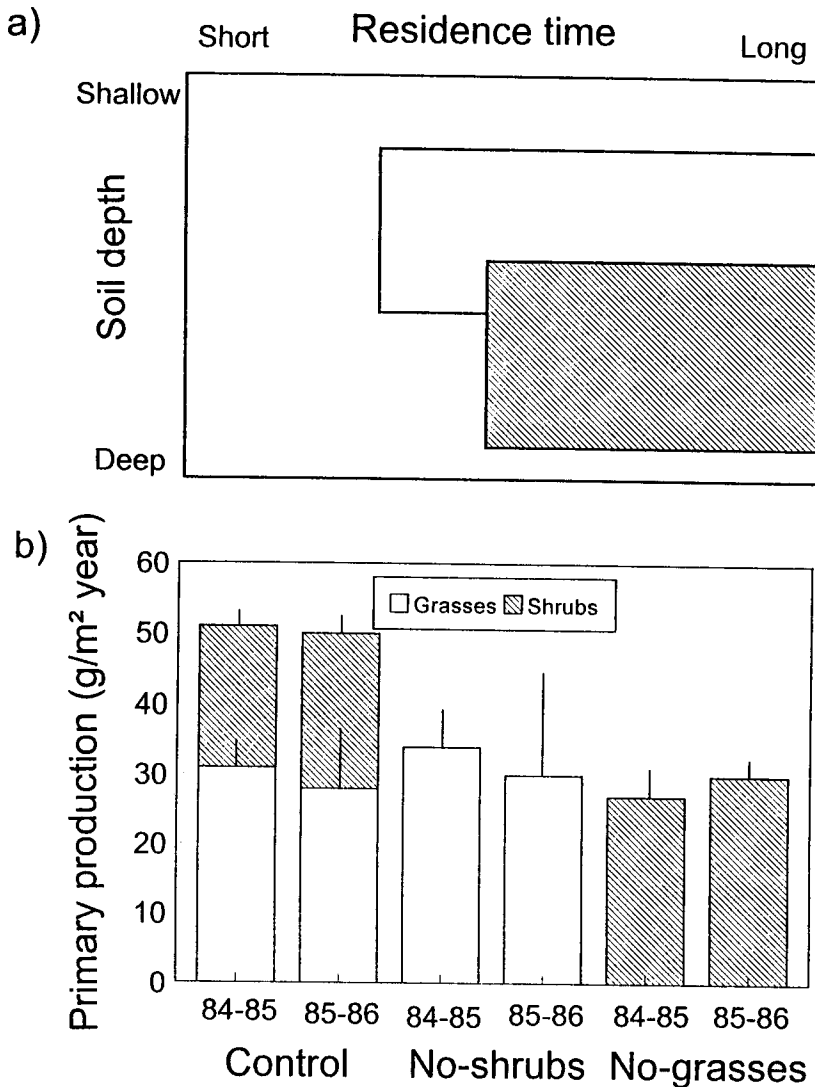


Figure 1. a. Conceptual model of the utilization of water by grasses and shrubs in the hypothetical space defined by residence time and soil depth. Rectangles indicate the space exploited by each plant functional type. Modified from Sala et al. 1997. b. Production of grasses and shrubs in two consecutive years. From left to right, the first two bars indicate the production of the two plant functional types in the control treatment. The following two bars correspond to the production in plots where shrubs were removed. The last two bars correspond to the production in plots where grasses were removed. Modified from Sala et. 1989.

Sala et al. (1997) proposed and tested in field experiments a conceptual framework for the interaction between grasses and shrubs in the Patagonian steppe (Figure 1a). In this framework, the soil water resource was characterized by its location in the soil and its residence time. Residence time is the period during which water is available to plants. Grasses utilized most of the water from the upper soil layers from both small and large precipitation events -water with a short to long residence time. Shrubs utilized mostly deep soil water and infrequent large precipitation events; i.e., water with a long residence time. In the experiments, Sala et al. (1989) selectively removed all tussock grasses or shrubs from 20 x 20 m plots, and compared primary production relative to control plots. In two consecutive years, they measured no increase in grass production in shrub-removed plots compared with the controls. In contrast, shrubs increased their production when grasses were removed, but only with an efficiency of 25%. Efficiency was calculated as the ratio between the increment of production when the grasses were removed over production of the grasses

in the control. This increment in shrub production when grasses were removed was associated with an increase in soil water potential in deep soil layers. In other words, grasses, by using mostly water from upper layers, kept this layer dry and reduced water infiltration into deep soil layers. In plots where shrubs were removed, a small reduction in soil water potential of deep soil water was observed, suggesting that grasses may use a portion of the deep soil water.

Golluscio et al. (1998) presented data on the use of large rainfall events by grasses and shrubs. They watered plots with 30 mm in order to simulate a large precipitation event in three consecutive summers. Their hypothesis was that grass response to water addition would not change with shrub-removal, but the response of shrubs would increase with the removal of grasses. They found that grasses responded to the experimental water addition, but shrubs only responded during the dry year and showed no response to the presence or absence of grasses. Additionally, water supplementation was effective in changing the soil water potential in deep soil layers only during a dry year.

In summary, soil water in the Patagonian steppe may be divided into two resources: upper soil water, used almost exclusively by grasses, and deep soil water, preferentially consumed by shrubs. However, grasses may affect deep soil water through root uptake and interception of water that would otherwise reach these layers. Deep percolation is frequent in Patagonia because most precipitation occurs during winter when plant growth is low (Paruelo and Sala 1995). Competition between grasses and shrubs mostly occurs for deep soil water; grasses may directly consume that water or reduce the infiltration to deep layers, suggesting that competition may play an important role in determining the grass-shrub balance. The fact that most rain falls in winter, when evaporation and transpiration are low, determines that, in general, the growing season starts with the entire soil profile wet. In other ecosystems where precipitation is more evenly distributed during the year, such as the Monte region in northern Patagonia, removal of grasses may determine a higher increment of shrubs.

Interactions between grasses and shrubs and the origin of patches

Competition is not the only way in which grasses and shrubs interact. The steppe presents a two-phase mosaic formed by two types of patches. Individual shrubs are encircled by a ring of grasses forming a patch with high plant cover. This patch type is dispersed in a low-cover matrix formed by scattered tussocks (Soriano et al. 1994). These two patch types form a two-phase mosaic structure. A global review of plant communities in different continents support the hypothesis that this type of two-phase mosaic structure is common in arid and semiarid ecosystems and may be the result of the interactions between grasses and shrubs (Sala and Aguiar 1996, Aguiar and Sala, in press).

Establishment of new individuals of grasses is controlled by seed distribution, as well as by competition and facilitation between adult grasses and shrubs and new seedlings (Soriano and Sala 1986, Aguiar et al. 1992, Aguiar and Sala 1994). In general, seed density of the main tussock grasses is higher near vegetation than in bare soil because of wind dispersal (Aguiar and Sala 1997). Competition and facilitation in the vegetation patches co-occur and their effects vary in time because balance between them shifts over the life stages of the interacting species (Callaway and Walker 1997). In the Patagonian shrub steppe we assumed that competition intensity is directly related to the ring of grasses completeness, however it runs behind it (Figure 2). We also assumed that facilitation depends linearly on shrub size (here represented by the radius). We separated two stages in the development of the vegetation patch. In the first stage, facilitation dominates because the shrub reduces both wind velocity and atmospheric water demand compared with open space, promoting establishment of seedlings. Competition at this stage is not intense because the ring of grasses is not complete. In the second stage, competition dominates because of the high density of grasses growing in the ring. At this stage the establishment of seedlings decreases -compared with stage 1- because facilitation does not disappear but competition overshadows its effect (Aguiar and Sala 1994). Competition and facilitation alternate in importance and it is possible to separate two stages in the development of the vegetation patch (Figure 2). Competition depends on the ring

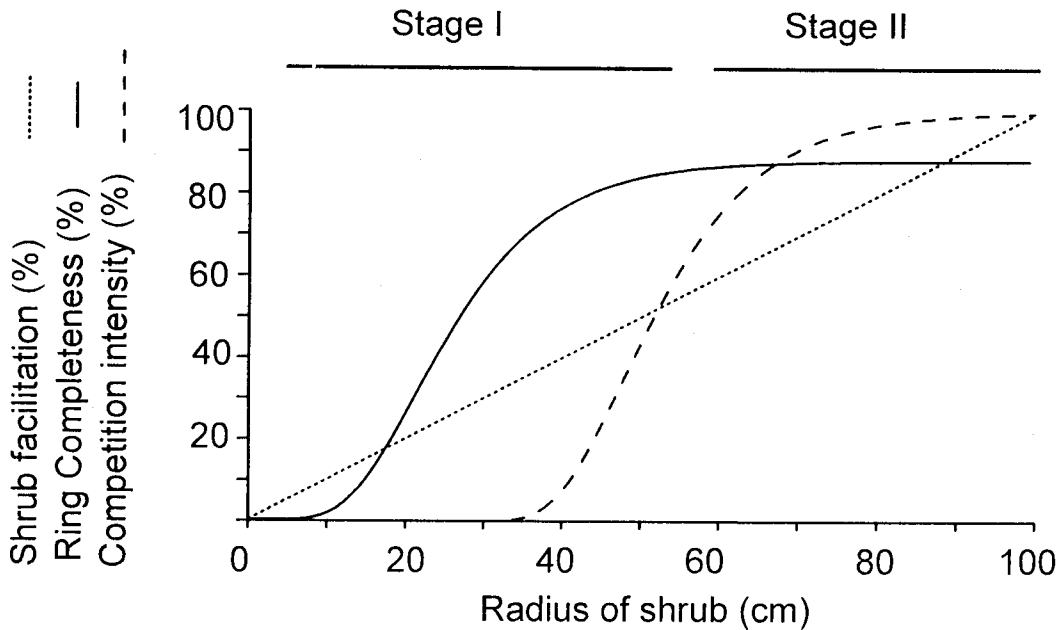


Figure 2. Conceptual model of the variation in relative importance of competition and facilitation during the building of the vegetation patch formed by a shrub and a ring of grasses. Shrub facilitation depends on the size of the shrub. Competition intensity depends on the completeness of the ring of grasses that surrounds the shrub. Stage I is dominated by facilitation and stage II by competition. Modified from Aguiar and Sala 1994.

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Soriano et al. (1994) proposed a cyclical dynamics that link the two vegetation patch types and proposed an explanation of what happens after shrubs die (Figure 3). According to this, shrubs afford aerial protection to the adult grasses in the rings allowing a rather high density of plants. The scattered tussock matrix may result from the mortality of the shrub and the disappearance of the aerial protection. Higher atmospheric water demand determines high water consumption and high competition for water among grasses in the ring. Because grasses are not the same age and size, competition drives differential mortality of plants and consequently the ring fragments. Eventually, a fragmented ring will have a plant density similar to the scattered tussock matrix.

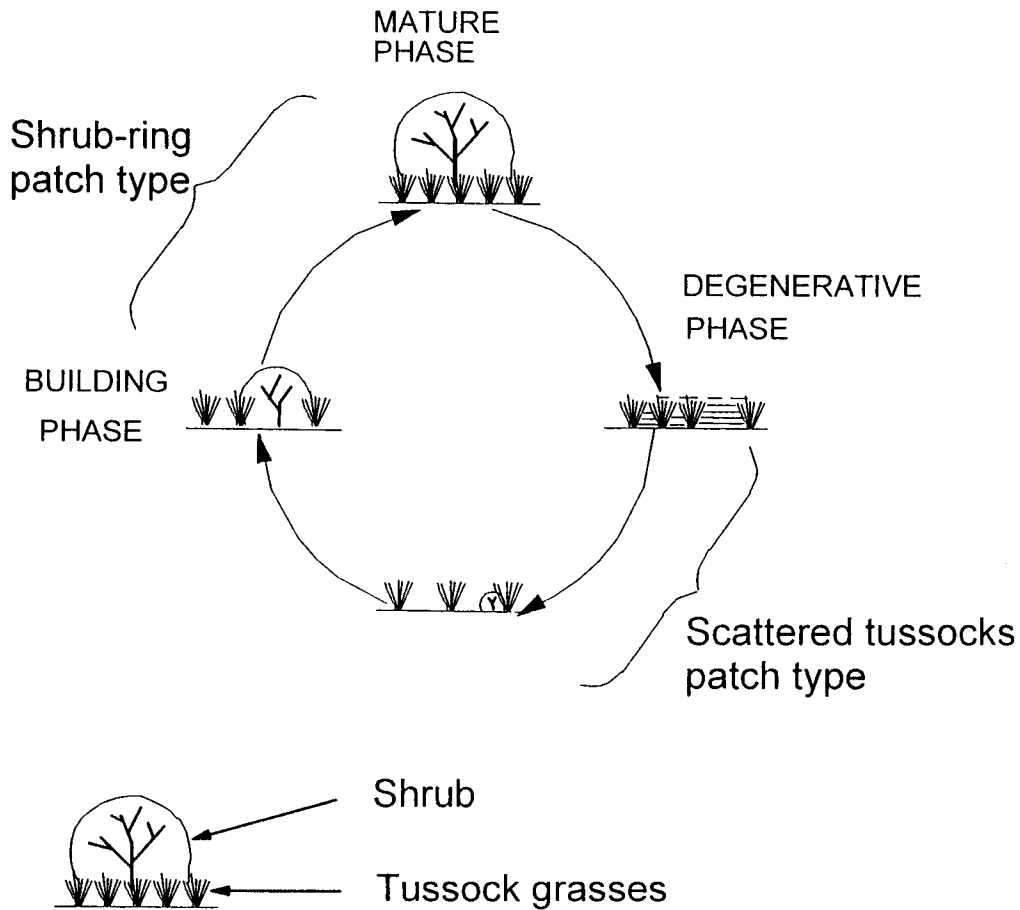


Figure 3. Hypothetical model of the cyclical patch dynamics in the Patagonian shrub steppe. Vegetation patch types are the shrub-ring and the scattered tussocks. Two dynamics have connected the two patch types been proposed, the building and the degenerative dynamics. Adapted from Soriano et al. 1994.

Herbivores and interactions between grasses and shrubs

Guanacos (*Lama guanicoe*) and lesser rheas (*Pterocnemia pennata*) are the largest native herbivores, and probably were the main herbivores before grazing by sheep started in Patagonia (Bucher 1987) (see Lauenroth 1998 for a discussion on this). Presently, it is accepted that the change from wild herbivores to domestic herbivores may have promoted a decrease in the grass-shrub ratio of the Patagonian ecosystems and that this may have impacted ecosystem functioning. Because there is no reliable data on the ecosystems before settlement, this hypothesis is difficult to test. In this section, we will discuss the effects of grazing on current structure and functioning of the Patagonian shrub steppe. We review the evidence from both the perspective of the herbivore and the plant.

Current diet of guanacos and sheep in Patagonia differ and support process of change in the grass-shrub ratio (Prodesar 1997). For example, for the Patagonian shrub steppe in the Occidental District, the diet of guanacos is composed mainly (55-80%) of woody species (*Senecio* spp.,

Mulinum spp., and *Berberis* spp.). Sheep diet includes mostly tussock grasses (80-100%) (*Stipa* spp., *Poa* spp.) and herbs; only during winter do they integrate shrubs into their diet (10-20%).

Vegetation data offer contrasting evidence about the effect of overgrazing on the structure of two major vegetation types in Patagonia such as the *Festuca* grassland in the Subandean District and the Patagonian shrub steppe in the Occidental District. In the former, overgrazing may have promoted a replacement of the highly dominant and palatable tussock grass *Festuca pallescens* by the spiny shrub *Mulinum spinosum* (León and Aguiar 1985, Aguiar et al. 1996, but see Bertiller et al. 1993). This change caused a shift in the structure and physiognomy of vegetation from grass-steppe to shrubland. In the Occidental district, the same type of gradient analysis indicated that in the shrub-steppe there is a change in the dominant species but the overall structure and physiognomy of vegetation does not change (Perelman et al. 1997). The grass-shrub ratio does not change as significantly as in the *Festuca* grassland.

The response of *Festuca* grasslands to overgrazing agrees with conventional wisdom and it is explained by the effect of both grasses and shrubs to water availability (Figure 1). Sheep may have promoted a decrease in the grass-shrub ratio because sheep grazing have a direct negative effect on the biomass of grasses and to a lesser extent on shrub biomass. Furthermore, the change in water dynamics derived from the replacement of plant functional type may reinforce the tendency for shrub dominance (Aguiar et al. 1996) (Figure 4a). Because grasses use mainly upper soil water, overgrazing on grasses may increase upper soil water availability and therefore more water may infiltrate into deep layers and increase shrub cover, which will eventually reduce sheep biomass (Aguiar et al. 1996).

The contrasting pattern of overgrazing effect on the shrub steppe may be explained by a more complex conceptual model (Figure 4b). Perelman et al. (1997) found that overgrazing promoted a decrease in some grass species (*Poa ligularis*, *Bromus setifolius*, *Hordeum comosum*, *Poa lanuginosa*) as well as an increase in other grass species (*Stipa humilis*, *S. neai*). We propose that, in order to explain the lack of change in the grass-shrub ratio, the grass plant functional type must be divided into two, according to sheep preference. In this way, we now have grasses that are preferentially consumed or avoided. Under such conditions, the reduction in the biomass of palatable grasses will not only benefit shrubs but also non-palatable grasses. Therefore, we expect a lower change in the grass/shrub ratio. We do not have data on competition between palatable and unpalatable grasses, but overgrazing certainly may be proposed as a control of the relative importance of these two groups. Together, the increase in unpalatable grasses and shrubs may negatively impact herbivores.

Sheep grazing may also affect the two-phase mosaic structure. Some shrub species such as *Mulinum spinosum* are negatively affected by grazing (Fernández et al. 1992). Sheep eat flowers and fruit thereby reducing recruitment of new individuals. In northern Patagonia, Bisigato and Bertiller (1998) reported that when both the grass and shrub components are negatively affected by grazing, vegetation patches changed from being dominated by tall shrubs to be dominated by small and medium sized shrubs. Soil in vegetation patches in Patagonian -as in other arid ecosystems in the world- has higher nutrient content than the low cover matrix (García-Moya and McKell 1970, Mazzarino et al. 1996, Sala unpubl.). A reduction in plant cover in the two-phase mosaic may also impact nutrient dynamics. Data from Australia (Ludwig and Tongway 1995) support the idea that degradation of vegetation is accompanied by the degradation of the two-phase mosaic structure and this degradation reduces water conservation and production. In the Patagonian shrub steppe, the vegetation patch formed by shrub and grasses represents 18% of the entire plant community but it may explain 44% of production (Soriano et al. 1994). These calculations point to the importance of these patches for the ecosystem functioning of the steppe.

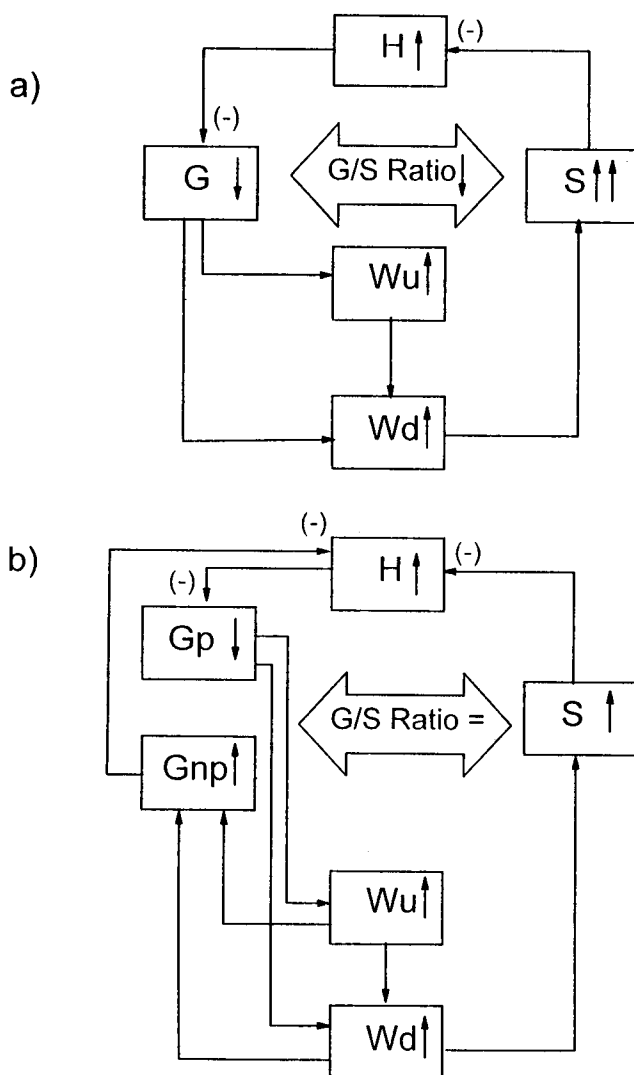


Figure 4. Conceptual model of the interaction between sheep (H), tussock grasses (G), and shrubs (S) in the Patagonian steppes. Soil water has been divided in two different resources: upper soil water (Wu) and deeper soil water (Wd). Arrows indicate positive effect of one compartment on another, when the effect is negative the sign (-) is added. In the compartments arrows indicate the increase (↑) or decrease (↓) in the abundance of the population or resource; magnitude of change is represented with the number of arrows; = indicates no change. a. Model for the *Festuca pallescens* grasslands. b. Model for the Patagonian shrub steppe. This model includes two different type of grasses: palatable (Gp) and non-palatable (Gnp).

Concluding remarks

Patagonia is a region where land use changes have been extensive. The next decades offer the possibility for new challenges for land managers, land planners, and researchers. For land managers, our review may be indicative of the complexity of ecosystem functioning in the Patagonian shrub steppe. The functioning of ecosystems can be described in terms of energy and nutrient fluxes and the ecological regulation due to interactions among organisms and their environment. Noy-Meir (1979/80) proposed that functioning of arid ecosystems is unique. His "autoecological" hypothesis states that the extreme physical environment determines that interaction between organisms and feedbacks of organisms to the environment are negligible. In this context,

plant and animal population dynamics are driven by the physical environment rather than by interactions such as competition, facilitation, or predation. In other words, the autoecological hypothesis proposes that in arid ecosystems "there is a low connectedness, weak or intermittent interactions among populations, and few if any regulatory feedbacks (Graetz 1991)." Our review indicates that the Patagonian shrub steppe is far from being a case of an autoecological ecosystem. Interactions among their components and the feedbacks of organisms to the environment are strong and numerous. Therefore, the extinction of species or alteration of a resource pool may represent a major change in ecosystem functioning. New management needs to include as a general background this notion of complex functioning.

The fact that this Patagonian ecosystem has complex functioning opens various and interesting questions for new experimentation. For example, as nitrogen is a resource with dynamics tied to the upper soil layers, what is the response of grasses and shrub to these dynamics? Does grazing change the relative importance of competition and facilitation and in turn change the total effect of grazing on the grass-shrub ratio? How common is the two-phase mosaic in other Patagonian ecosystems and what is its role in ecosystem functioning? Can the two-phase mosaic be considered another dimension of biodiversity and therefore play a role in the production-diversity relationship? Why the Subandean district dominated by *Festuca pallescens* has not non-palatable grasses? Is it because of the temperature regime? What is the impact of other herbivores such as granivores on the current functioning of this ecosystem?

Acknowledgements. This paper is dedicated to the memory of Alberto Soriano who was an inspiration for scientific research in Patagonia. We wish to acknowledge helpful comments by Rodolfo Golluscio, Bill Lauenroth, Mónica Bertiller, José Paruelo, Amy T. Austin, Martín Oesterheld, and an anonymous reviewer. Funding was provided by CONICET, UBA, FONCYT, and the Inter-American Institute for the Study of Global Change Research.

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Received: September 25, 1998

Accepted: March 12, 1999