

Ecosystem responses to changes in plant functional type composition: An example from the Patagonian steppe

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Abstract. Grass cover along a grazing intensity gradient in Patagonia decreases, whereas bare soil and shrub cover increases. Our objective was to study the effect of a change in the dominant plant functional type on soil water balance, primary production, herbivore biomass, roughness, and albedo. Using a soil water balance model, we found increases in evaporation and deep drainage, and a decrease in total transpiration along the grazing intensity gradient. Above-ground primary production, estimated from transpiration, decreased along the grazing intensity gradient because shrubs did not fully compensate for the decrease in grass production. Using a statistical model, we calculated herbivore biomass from estimates of above-ground primary production. Estimated herbivore biomass was lowest in the shrub-dominated extreme of the grazing gradient. Roughness increased from the grass-dominated to the shrub-dominated community. Albedo had a maximum at an intermediate position along the gradient.

Our results suggest that changes in plant functional type composition, independent of changes in biomass, affect ecosystem functioning and the exchange of energy and material with the atmosphere. Grasses and shrubs proved to be appropriate plant functional types to link structure and function of ecosystems.

Keywords: Albedo; Ecosystem-atmosphere feedback; Grass; Grazing; Remote sensing; Roughness; Shrub; Water balance.

Nomenclature: Correa (1971-1984).

Introduction

Climate, atmospheric composition and land-use changes are major forces that simultaneously impinge upon ecosystems at a variety of scales ranging from patches to the planet. Ecosystems respond to these forces by changes in function (i.e. primary production, water dynamics, decomposition, nitrogen dynamics, etc.) and changes in structure (i.e. total plant cover, plant functional type composition, carbon and nitrogen storage, etc.). Land-use changes, in particular, directly modify ecosystem structure which in turn affect ecosystem func-

tioning and the exchange of energy and materials with the atmosphere.

At regional to global scales plant functional types (PFTs) are alternatives to species representing ecosystem structure (Smith & Shugart 1996). PFTs based on morphology have the potential to link ecophysiological traits with ecosystem processes relevant at large scales (Chapin 1993). However, the definition of PFTs is not a trivial problem. Which plant traits (i.e. vegetative, regenerative, both, etc) should be used to define PFTs? Are morphological traits related to functional traits? Do functional plant traits represent community and ecosystem functioning? How many PFTs will be required to represent the main aspects of community and ecosystem functioning? Is it possible to define a set of PFTs that represent different major ecosystems in the world? Answering these questions will help us to understand the role that PFTs can play in models representing the responses of ecosystems to global change.

The Patagonian region of Argentina is an excellent location to approach such questions. Here, patterns of both environmental and anthropogenic factors result in abrupt changes in PFT composition (León & Facelli 1981; León & Aguiar 1985; Jobbágy et al. in press). Although we do not completely understand all aspects of ecosystem structure and functioning of the Patagonian steppes, we need to urgently resolve questions related to the potential effects of global change. The western edge of the Patagonian region is occupied by grass steppes. Similar to many other parts of the world, heavy grazing has caused changes in the vegetation of these steppes. Grazing has reduced grass cover, increased bare soil and shrub cover, and increased soil erosion (Fig. 1) (León & Aguiar 1985); such changes are common in arid and semi-arid grasslands and are often referred to as desertification (Schlesinger et al. 1990). We do not yet understand the impact of vegetation changes on ecosystem functioning in this region.

Patagonian grass steppes are typically species-rich, with 40 - 50 forbs and 15 - 25 grasses and shrubs, with

one grass (*Festuca pallelescens*) and one shrub (*Mulinum spinosum*) contributing a large fraction of the total plant cover (Golluscio et al. 1982; León & Aguiar 1985). Plant functional types (PFTs) based on growth-form, e.g. shrubs, grasses and forbs, represent the main aspects of ecosystem functioning in arid and semi-arid regions (Leishman & Westoby 1992; Sala et al. in press).

Here, we summarize current knowledge about PFTs in Patagonia and use it to investigate some effects of changes in PFT composition associated with heavy grazing on ecosystem functioning in the *Festuca* steppe. We emphasize how changes in PFT composition across a gradient of grazing intensity affect:

- (1) Ecosystem water balance;
- (2) Above-ground net primary production and herbivore carrying capacity;
- (3) Surface properties such as albedo and roughness.

We use the results of these analyses to evaluate the degree to which morphologically-based PFTs are useful in characterizing the response of the *Festuca* steppe.

Plant functional types in Patagonian steppes

In the Patagonian steppes vascular plant species can be grouped in three growth-form based groups: shrubs, grasses, and forbs (see Soriano 1983; or Paruelo et al. 1991 for maps and descriptions of vegetation units and plant species) (Table 1). Shrubs are woody plants taller than 0.5 m without a well-developed main stem. Some species are evergreen and others deciduous. Grasses are herbaceous and tufted, and have the C_3 photosynthetic pathway. Most grass species have stiff leaves which remain attached to the plant for more than one year; they have green leaves all year round. Forbs comprise a heterogeneous group that includes annual and perennial herbaceous evergreen or deciduous plants that are mostly dicots.

In Patagonia, water is the most frequent constraint for plant growth, and community and ecosystem functioning. Rain falls mostly during winter and early spring; plants use this water during the growing season. The start of the growing season is controlled mainly by temperature, whereas the end is controlled by soil water availability. During the growing season rainfall is infrequent. Shrubs and grasses differ in their strategies to cope with limited water availability. Shrubs use resources mostly from lower soil layers (Soriano & Sala 1983; Fernández & Paruelo 1988). Because of this, shrubs do not make effective use of rainfall that occurs during the growing season and only wets the upper soil layers. Both evergreen and deciduous shrubs rely primarily on winter recharge of deep soil water. By contrast, the tussock grasses use resources mostly from the

upper soil layers because their root systems are located near the surface (Soriano & Sala 1983; Soriano et al. 1987). During the summer growing season, grasses are often under greater water stress than shrubs. Soriano & Sala (1983) reported very little variability within these strategies for either grasses or shrubs. Although there are no equivalent studies for the *Festuca* steppe, measurements of oxygen isotopes support the existence of these two strategies (Schulze et al. unpubl. data).

Grasses, shrubs and forbs differ in their relative importance for community and ecosystem functioning in the Patagonian steppe. Forbs are numerous but have a small share in above-ground biomass and productivity. Grasses and shrubs are less numerous but make up most of the above-ground production, up to 96 % of the net primary production and 97 % of the canopy cover (Golluscio et al. 1982; Fernández et al. 1991). Furthermore, shrubs and grasses play a special role in community functioning by forming patches (Soriano & Sala 1986; Aguiar et al. 1992; Aguiar & Sala 1994) and controlling community dynamics (Sala et al. 1989). In turn, these patches may control ecosystem functioning (Sala & Aguiar in press).

In the *Festuca* steppe, grasses may contribute > 80 % of the total cover (Bertiller 1984; Defossé et al. 1990). When the steppe is heavily grazed, grass cover decreases and shrub cover increases (León & Aguiar 1985) (Fig. 1). Our analyses will concentrate on the two most important PFTs in the *Festuca* steppe, grasses and shrubs, and within these groups on *Festuca pallelescens* and *Mulinum spinosum* to characterize the responses of grasses and shrubs, respectively.

Site description and background information

The *Festuca* steppe is located at the western edge of the Patagonian phytogeographic province in Argentina (Soriano 1983; Paruelo et al. 1991). It extends over 5200 km² between 43° 30' and 46° 00' S and is dominated by the grass *Festuca pallelescens*. Scattered areas of this vegetation type exist both north and south of the geographic boundaries. The *Festuca* steppe is a semi-arid system with mean annual precipitation between 350 and 450 mm, most of which falls during winter and early spring (April - September). Monthly mean temperatures vary between 12 °C in January and -4 °C in July. Soils are coarse-textured (43 % sand) and homogeneous up to 50 cm deep (Anon. 1990; Defossé et al. 1990).

The *Festuca* steppe has been grazed by sheep since the beginning of this century (Ares et al. 1990). Grazing has led to significant changes in the structure of the vegetation (León & Aguiar 1985; Borelli et al. 1985). León & Aguiar (1985) using indirect gradient analysis

identified a gradient of grazing intensity. Along this grazing gradient, the cover of the dominant grass *Festuca pallescens* decreased exponentially, while the cover of a mostly unpalatable shrub *Mulinum spinosum* increased towards the heavily grazed end (Fig. 1). Other species (grasses, forbs, and small shrubs) variously decreased or increased along the gradient, however they accounted for < 15% of total cover (León & Aguiar 1985).

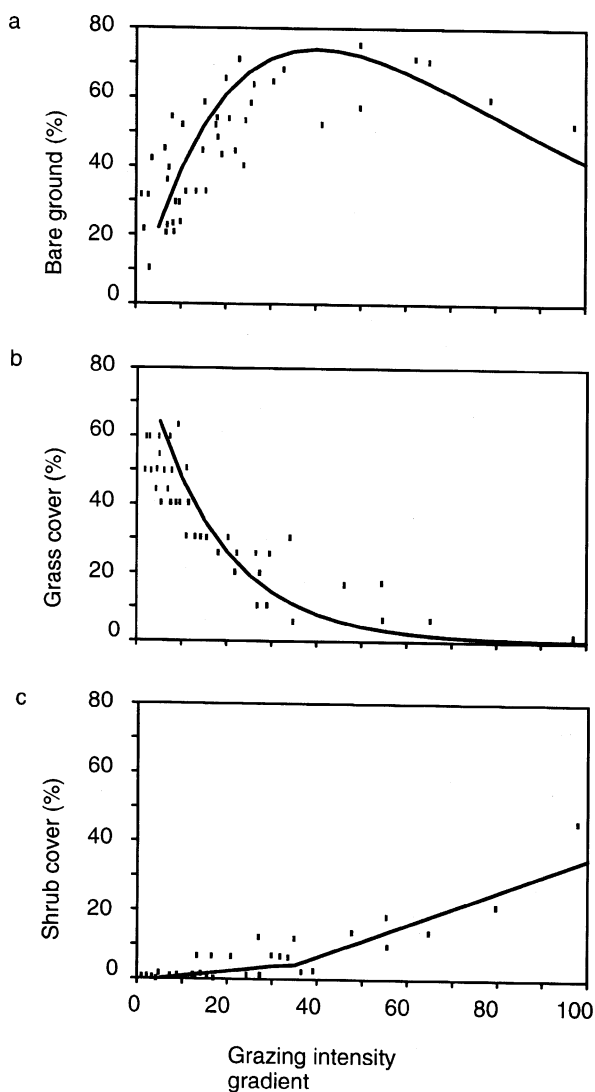


Fig. 1. Changes in the cover (%) of bare ground (a), *Festuca pallescens* (b) and *Mulinum spinosum* (c) along the grazing intensity gradient. The grazing intensity gradient corresponds to the first ordination axis in a multivariate analysis of 43 sites sampled in the *Festuca* steppe in Patagonia (León & Aguiar 1985). Redrawn from León & Aguiar (1985).

Methods

We studied 10 positions, located at equal intervals, along the grazing intensity gradient defined by León & Aguiar (1985). To characterize soil water dynamics along the gradient, we used a soil water balance model (DINAQUA). A full description of the model and an evaluation of its performance in the Patagonian steppe is presented in Paruelo & Sala (1995). We ran the model for 9 yr using daily temperature and rainfall data for a site located in the *Festuca* steppe (Lepá, Chubut province, Argentina, 42° 35' S and 71° 03' W, mean annual precipitation 365 mm). Simulations considered a uniform soil profile corresponding to a representative pedon of the *Festuca* steppe (43 % sand, 18 % clay and 39 % silt) (Anon. 1990). Field capacity for this texture was calculated according to Cosby et al. (1984).

DINAQUA simulates transpiration, soil evaporation, and drainage on a daily time-step. Weather input data are daily values of temperature, global radiation, and precipitation. The model considers saturated water flows between each of six soil layers. The water content of each layer is updated daily after computing evaporation and transpiration. The flow from the last layer downward corresponds to deep drainage. Evaporation is estimated using Ritchie's (1972) algorithm. The model does not simulate surface run-off.

Transpiration is computed for each of the functional types (grasses and shrubs in this case). Daily transpiration is proportional to the maximum transpiration per unit of biomass for each PFT, to the effective soil water content, and to the biomass of the PFTs. DINAQUA simulates the seasonal course of green biomass by linearly interpolating between the minimum and maximum biomass values throughout the year. This calculation requires the dates of the start and end of the growing season, and date of maximum biomass for each functional type. Relative root densities for each layer and for each functional type were derived from Soriano et al. (1987) and Fernández & Paruelo (1988). Maximum biomass was estimated from mean annual precipitation (MAP) (mm) using the equation presented by Sala et al. (1988a), assuming that the peak green biomass and above-ground net primary production (ANPP) ($\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$) were equivalent (Lauenroth et al. 1986; Sala et al. 1988b).

$$\text{ANPP} = -48 + (0.6 \times \text{MAP}). \quad (1)$$

The start and end of the growing season were estimated from phenological data for grasses (Defossé et al. 1990; Bertiller et al. 1990, 1991) and shrubs (Soriano & Sala 1983). Maximum values of transpiration for each functional type were derived from Paruelo & Sala (1995).

Water balance; simulations and assumptions

We ran two simulation experiments for each of the 10 positions along the grazing intensity gradient. The first experiment was designed to analyze the effects of changes in PFT composition and the resulting changes in total biomass on ecosystem water balance. We ran DINAQUA for the 10 positions along the grazing intensity gradient. We estimated biomass by assuming a direct-linear relationship between biomass and cover. First, we calculated total biomass for the first position using Eq. 1 and MAP of the site. We then partitioned this total biomass value according to the relative cover of grasses and shrubs. For the remaining positions, the total biomass was reduced in proportion to the reduction in total cover, and then partitioned between grasses and shrubs. Simulations that resulted from this experiment represent the effects of both changes in PFT composition and changes in total cover-biomass, and represent our best estimate of the effects of land-use on the ecosystem. We will refer to these results as the total effect of land use.

The second simulation experiment was designed to answer questions about the effects of PFT composition on ecosystem responses to heavy grazing, holding total biomass constant. This experiment allowed us to isolate the specific effects of the two PFTs on ecosystem functioning and ecosystem-atmosphere exchange separately from the effects of changes in biomass. We held total biomass constant along the gradient, but partitioned it according to the relative cover of grasses and shrubs. We will refer to these results as the effects of changes in PFT composition.

The response variables of both simulation experiments were annual total transpiration, shrub and grass annual transpiration, annual evaporation, and deep drainage. We also evaluated soil water content for the upper five layers (0–120 cm). We averaged these variables for nine years.

Primary production and herbivore carrying capacity

To analyze the effects of changes in PFT composition on ANPP and herbivore carrying capacity we used annual transpiration for each PFT to estimate ANPP along the grazing intensity gradient. Simulated transpiration accounts for a key difference between the two PFTs, transpiration per unit of biomass. To estimate ANPP, we first calculated transpiration use efficiency for each PFT (TUE; $\text{g}\cdot\text{mm}^{-1}\cdot\text{yr}^{-1}$) using data from the Patagonian steppe:

$$\text{TUE} = \text{PFT production} / \text{PFT transpiration}. \quad (2)$$

Plant functional type production data ($\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$) are

from Fernández et al. (1991) and PFT transpiration (mm/yr) data are from Paruelo & Sala (1995). We then multiplied the TUE for grasses and shrubs by the corresponding values of transpiration from our simulations. To calculate total ANPP we added the estimated production of grasses and shrubs. Herbivore carrying capacity was calculated using the equation for South-American grasslands from Oesterheld et al. (1992).

$$\log_{10} \text{BH} = 1.602 \times \log \text{ANPP} - 3.98. \quad (3)$$

Where BH is the biomass of herbivores in energy units (kJ/m^2) and ANPP is the above-ground primary production also in energy units ($\text{kJ}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$) (Energy-biomass conversions are 9900 kJ per kg livestock fresh weight and 16.76 kJ per gram of ANPP.) We expressed ANPP and herbivore biomass in $\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ and $\text{g}\cdot\text{m}^{-2}$ respectively.

Roughness length and visible albedo

We evaluate the effects of changes in PFT relative abundance on the surface properties of the *Festuca* steppe by estimating roughness of ungrazed (grass-dominated) and heavily grazed (shrub dominated) positions using Szeics's equation (Rosenberg et al. 1983):

$$\log_{10} z_0 = 0.997 \times \log H - 0.883 \quad (4)$$

where z_0 is roughness length and H (cm) is height of the canopy. We measured the height of 20 plants for each PFT and calculated z_0 for each of them.

We estimated visible albedo (Rosenberg et al. 1983) using an empirical relationship between total cover and satellite reflectance (LANDSAT MSS) in the visible and near infrared bands. Several authors have used LANDSAT data to estimate albedo (Courel et al. 1984; Brest & Goward 1987; Duguay & LeDrew 1991). For an area of 1500 km^2 ($41^\circ 12' \text{ S}$, $70^\circ 42' \text{ W}$), Paruelo & Golluscio (1994) found a positive linear relationship between total plant cover and the Normalized Difference Vegetation Index ($\text{NDVI} = (\text{Red band} - \text{Infra red band}) / (\text{Red band} + \text{Infra red band})$). For a portion (8152 pixels, $79 \text{ m} \times 79 \text{ m}$ each) of the LANDSAT-MSS image (January 1986) used by Paruelo & Golluscio (1994), we obtained the visible albedo as the sum of the digital counts of the two visible bands (500–600 nm and 600–700 nm) and related them to total cover values from Paruelo & Golluscio (1994). Visible albedo was linearly related to total plant cover ($\text{Alb} = 57.6 - 0.186 \times \text{plant cover} (\%)$, $r^2 = 0.98$, $F = 320$, $n = 5$). We used this relationship to estimate albedo along the grazing intensity gradient for which we had total cover data from León & Aguiar (1985). We did not address the seasonality of albedo.

Results

When both PFT composition and total biomass were allowed to vary, transpiration, evaporation, and deep drainage changed along the grazing intensity gradient (Fig. 2a). Total transpiration was higher in positions dominated by grasses than in positions dominated by shrubs. Evaporation showed the opposite trend and increased along the gradient. Deep drainage coincided with minimum biomass (position 4). Results from the second simulation experiment to investigate the individual effect of the PFTs yielded similar patterns to the first experiment, evaporation was higher than transpiration as shrubs replaced grasses as the dominant PFT (Fig 2b). Deep drainage did not change along the gradient. These results point to the importance of the individual effects of changes in PFTs for desertification of the *Festuca* steppe.

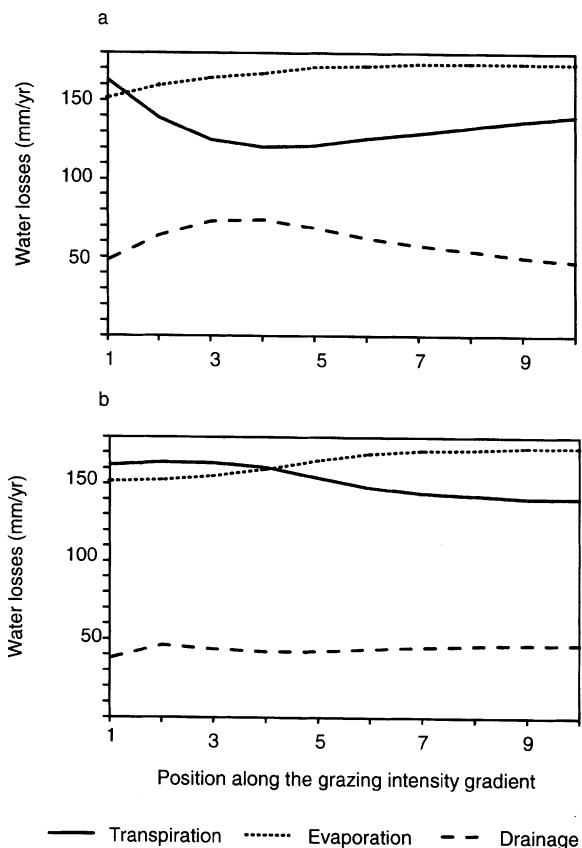


Fig. 2. Transpiration (—), evaporation (····) and deep drainage (---) along the grazing intensity gradient simulated with DINAQUA. **a.** Total effects of the land use on the *Festuca* steppe (changes in PFT composition and biomass); **b.** Effects of changes in PFT composition (no changes in biomass). See Fig. 1 for an explanation of the grazing intensity gradient.

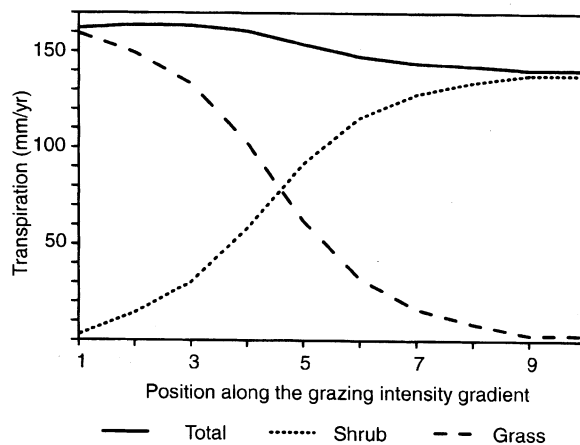


Fig. 3. Grass (---), shrub (····) and total (—) transpiration along the grazing intensity gradient when only the PFT composition changed in the simulations. See Fig. 1 for an explanation of the grazing intensity gradient.

Transpiration of grasses and shrubs showed opposite patterns along the gradient (Fig. 3). Shrubs did not compensate for the reduction in grass transpiration when they were dominant. Total transpiration in shrub dominated positions was 21 mm less than in grass-dominated positions in simulations accounting for the individual effects of the PFTs. When the total effect of land use change was evaluated, the difference rose to only 23 mm. In other words, 93% (21/23 mm) of the difference

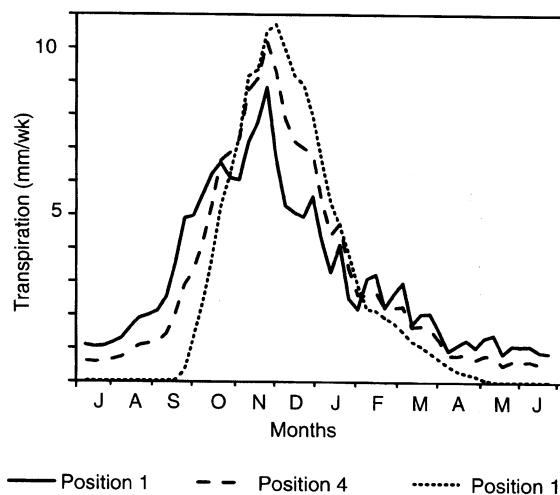


Fig. 4. Total transpiration through time for three communities along the grazing intensity gradient: position 1 (grass dominated) (—), position 4 (mix of grasses and shrubs) (---), and position 10 (shrub dominated) (····). These are results from simulations where only PFT composition varied along the grazing intensity gradient.

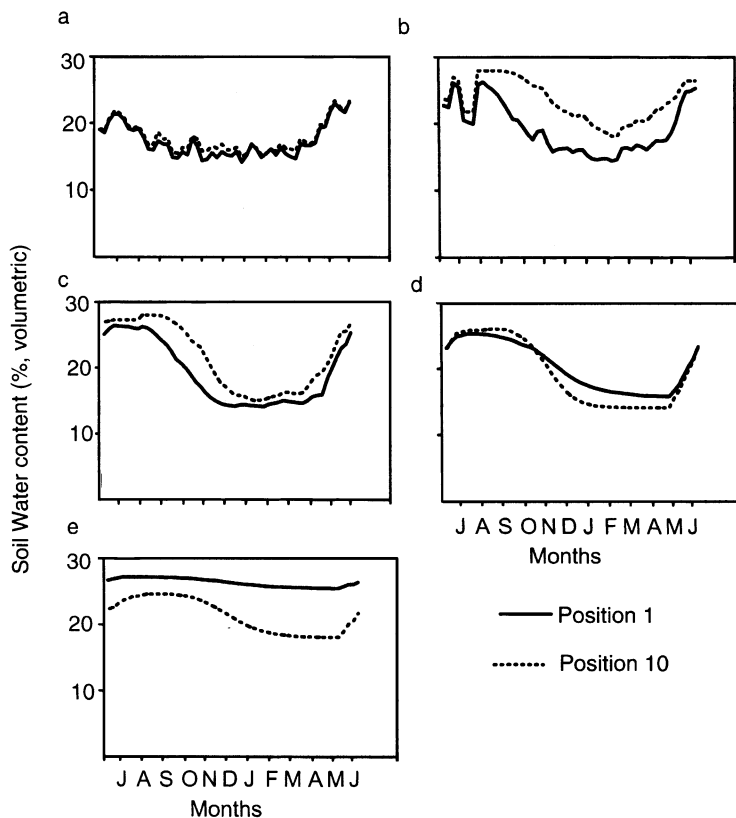


Fig. 5. Soil water content through time for five layers: (a) 0-10; (b) 10-20; (c) 20-40; (d) 40-80 and (e) 80-120 cm representing the original community dominated by grasses (position 1 along the gradient) (—), and a shrub-dominated community (position 10) (····). Results correspond to changes only in PFT composition.

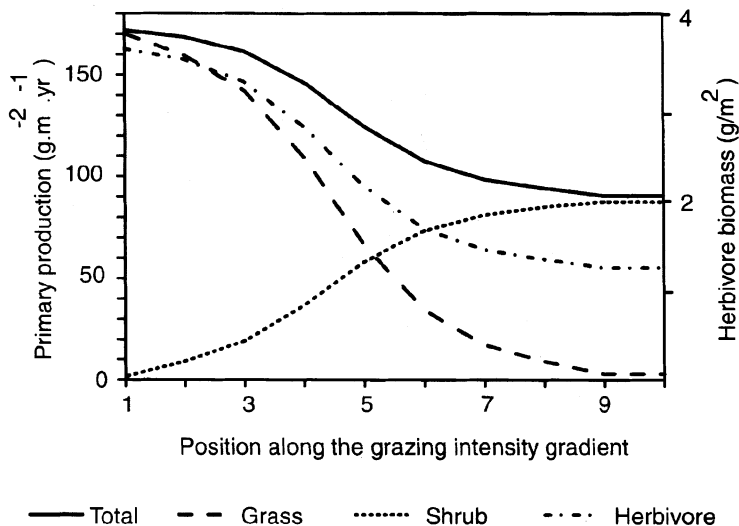


Fig. 6. Above-ground net primary production and herbivore biomass along the grazing intensity gradient; total above-ground primary production (—); grass production (- -); shrub production (····) and herbivore biomass (-.-.-). Results correspond to changes only in PFT composition. See Fig. 1 for an explanation of the grazing intensity gradient.

in transpiration between the extremes of the gradient was explained by the individual effects of the PFTs. Change in relative abundance of PFTs also modified the seasonal pattern of transpiration (Fig. 4). Communities where shrubs were dominant had high transpiration in late spring and early summer at the start of the drought season. Transpiration of shrub dominated communities was negligible during winter months. In contrast, positions dominated by grasses showed some transpiration throughout the year and the peak occurred earlier than in shrub dominated positions. The transition from one community to the other follows the proportion of grasses and shrubs in the community.

Shrub-dominated communities showed higher soil water content (SWC) in the upper three layers (0 - 10, 10-20, 20 - 40) than grass dominated communities (Fig. 5). In contrast, in the 40 - 80 cm layer, shrub dominated communities had higher SWC during winter and early spring, and lower SWC in summer than in the grass dominated position. The bottom layer always had lower SWC in shrub dominated positions than in grass dominated positions.

Grasses produce an average of 1.07 g biomass per mm³ water transpired (SE = 0.09, n = 5) and shrubs produce 0.6 g biomass per mm³ water transpired (SE = 0.07, n = 5) (Fernández et al. 1991; Paruelo & Sala 1995). Using these coefficients, we transformed our transpiration estimates into production of grasses and shrubs (Fig. 6). Total community production (grass production plus shrub production) decreased along the grazing intensity gradient because shrubs did not compensate completely for the decrease in grass production. Estimated biomass of domestic herbivores also decreased from 3.7 g·m⁻² in the grass dominated position (position 1) to 1.3 g·m⁻² in the shrub dominated position (position 10) (Fig. 6).

Grasses and shrubs differed in height by 52 cm (Table 1). The grass-dominated community had lower roughness length than the shrub-dominated community: 0.02 m against 0.09 m (F = 350, 1, 38, P < 0.05). Vis-

Table 1. Ecological characterization of grasses and shrubs of the Patagonian steppe.

Trait	Grass	Shrub
Specific LAI (cm ² /g) ¹	43	28
Leaf N content (mg/g) ²	6.2 ± 0.3	9.9 ± 0.3
Roots in 0-20 cm layer (%) ^{3,4}	67	13
Winter dormancy ^{5,7}	none	most
Height (m) ⁶	0.17 ± 0.009	0.69 ± 0.025
Rhizomes, stolons, etc. ⁶	few	none

¹Paruelo (1991); ²Sala et al. (1989); ³Fernández & Paruelo (1988); ⁴Fernández unpubl. data; ⁵Soriano & Sala (1983); ⁶Paruelo & Golluscio unpubl.; ⁷Bertiller et al. (1990, 1991).

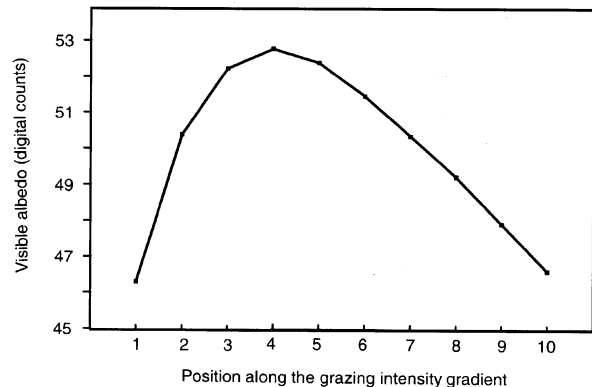


Fig. 7. Estimated visible albedo for the different positions along the grazing intensity gradient using the equation, where $Alb = 57.6 - 0.186 \times \text{plant cover } (\%)$, $r^2 = 0.98$. This equation was obtained from a relationship between plant cover and NDVI (LANDSAT MSS). See Fig. 1 for an explanation of the grazing intensity gradient.

ible albedo closely followed total plant cover. At the fourth position, visible albedo was 14 % higher than in the grass dominated community. In the shrub dominated position the albedo was only 0.8 % higher than in the grass dominated position (Fig. 7).

Discussion

In many arid and semi-arid communities, shrub density is increasing (Glendenning 1952; West 1979; Walker et al. 1981; Schlesinger et al. 1990). This change in the vegetation structure is often caused by grazing (human made change) and/or drought (climate driven change) (Breman & de Wit 1983; Graetz 1991). In the *Festuca* steppe of Patagonia, grazing has been suggested as the cause of the change in the relative abundance of grasses and shrubs and the decrease in total cover (León & Aguiar 1985). Our study has shown that these changes can modify ecosystem functioning and surface characteristics, and therefore may affect energy and material exchanges with the atmosphere.

Decreases in grass cover accompanied by increases in shrub cover and bare ground increased water losses through evaporation and deep drainage and reduced transpiration. Most of the reduction in transpiration was due to the individual effects of the PFTs. Shrubs transpired less water per unit of biomass than grasses. Because the production per mm³ of water transpired is also lower in shrubs than in grasses, we estimated a 43% reduction in ANPP along the grazing intensity gradient. This result agrees with the data reported by Sala et al. (1989) that showed that shrubs were not able to use all

the water released when grasses were experimentally removed. Herbivore biomass also decreased (64%) with the change in PFT composition. A larger effect on herbivore biomass was expected since the relationship between primary production and herbivore biomass is non-linear (Oosterheld et al. 1992). These estimates only consider the individual effects of the PFTs. The total land use effect was larger because of the lower total cover at the shrub dominated end of the grazing gradient. We are aware that our estimates may be affected by accumulation of errors as a result of combining data from several models. However, aside from questions that may arise about the quantitative accuracy of our results, qualitatively the major issue is that differences in the transpiration per unit of biomass and production per unit of water transpired are key attributes for defining PFTs in arid and semi-arid regions. Efforts should be directed to study these attributes in plants.

Land use changes modify surface characteristics and therefore ecosystem-atmosphere exchanges. Our preliminary estimates of roughness length (z_0) agree with values currently used in global climate models for grasslands and shrublands (Claussen 1994). In our case, z_0 for shrublands was $4 \times$ greater than for grasslands. From a global perspective, this change in vegetation roughness may not be significant because of the much greater influence of the orographic component of roughness (Claussen 1994). Nevertheless, on a regional scale and because of the gentle topography of the *Festuca* steppe we suggest that our estimate of the change in z_0 may have an impact on ecosystem-atmosphere interactions. Transformation of grassland into cropland has been reported to change surface characteristics and mesoclimate (Segal et al. 1988, 1989).

Albedo increased 14 % between the ungrazed steppe and the fourth position, where total plant cover was minimum. A comparison across the U.S.-Mexico border showed that as a result of heavy grazing on the Mexican side, plant cover was lower and albedo was higher which resulted in an increase in average daily maximum temperature of 3.8 °C (Balling 1988, 1989; Bryant et al. 1990). Our estimate of albedo does not take into account some of the effects of replacement of grasses by shrubs, such as changes in seasonality or canopy reflectance. For this reason, our results underestimate the difference between the grass and shrub-dominated communities. Ongoing measurements also support this assertion (Jobbágy unpubl. data).

Our results provide further support for the use of growth-form based PFTs in arid and semi-arid regions. In the case of Patagonia, grass and shrub growth forms are related to functional traits and represent alternative strategies to deal with the most frequent constraint on plant growth and survival, water scarcity. Because grasses

and shrubs account for a major proportion of plant cover and production, these two groups provide a good representation of the aspects of ecosystem functioning that we explored. While forbs were excluded from our analysis, we recognize that they may play an important role in other aspects of ecosystem functioning (e.g. mineral nutrition of herbivores).

Ecosystems in arid and semi-arid regions of the world differ substantially in species composition but not in the types of growth forms. A PFT definition based on grasses, shrubs, forbs and succulents is simple, intuitive and supported by a variety of field data (Leishman & Westoby 1992; Sala et al. 1996). This is the reason why studies of relationships between plant growth form and plant and ecosystem functioning are of great importance. Systems such as the *Festuca* steppe where the species and PFT approaches are identical are ideally suited for such studies. They represent a unique opportunity to study the attributes in which the species/functional types differ.

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