11 Plant functional types in temperate semi-arid regions

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Introduction

Grouping plants into categories as a way of simplifying some of the complexities of nature has been one of the aims of biology and ecology since the very beginning. Alexander von Humboldt (1806), early in the nineteenth century, distinguished 16 groups of plants. Subsequently, many authors have attempted different classifications of plants (see Barkman (1988) for a thorough review of this topic). These classifications have varied in their scope, in the characters taken into account, and in the methods used. Some classifications have been broad, attempting to include all plant types, such as Raunkiaer's (1907) or Grime's (1988); others have been narrow and, for example, directed only at aquatic plants. Some classifications use only morphological characters and others include functional characters, such as phenology or bud height. Barkman (1988) made the distinction between growth forms, which were groups based only upon morphological characteristics, and life forms, which were based upon morphological and/or physiological adaptations to a certain ecological factor. The techniques authors have used to arrive at groups have also changed through time. Early groupings were often the result of the author's experience, whereas at present objective multivariate methods are preferred (Leishman & Westoby 1992; Golluscio & Sala 1993).

In order to model the response of ecosystems to global change, and to assess their contribution to present changes in the composition of the atmosphere and in the climate, it will be necessary to reduce the number of elements in the models. It will not be possible to model every species nor every ecosystem. The units that aggregate several species with a common behaviour in the ecosystem are the functional types (FTs). Species within each FT should have a similar function in the ecosystem, and they should play a common ecological role. Functional types will be a critical hierarchical level at which to develop global change models.

This chápter describes research that involved defining and testing hypotheses about the relationships among FTs in the Patagonian steppe and extrapolating results to a regional scale. The objective of this chapter is to present (1) a set of hypotheses about the partitioning of water among FTs in the Patagonian steppe; (2) a test through manipulative experiments of these hypotheses; (3) a set of regional-scale hypotheses about the distribution of FTs and the occurrence of vegetation units, based upon the results of previous items; and (4) a test of these regional-scale hypotheses.

Functional types of arid regions

The functional types were defined *a priori* based upon morphological and phenological characteristics. We tested specific hypotheses relating to the kind of resources used by each FT, which in turn have major implications about their competitive interactions and their role in arid ecosystems.

The functional types of arid regions are grasses, shrubs, forbs and succulents. The conceptual model that relates these four FTs focuses on water relations because water is the critical resource explaining both the structure and the dynamics of these ecosystems. Water is partitioned among the four FTs along two axes: the depth from which each FT is able to absorb water, and the residence time of water in the soil. Residence time is the period of time during which water remains within the range of water potential available for plants (Fig. 11.1).

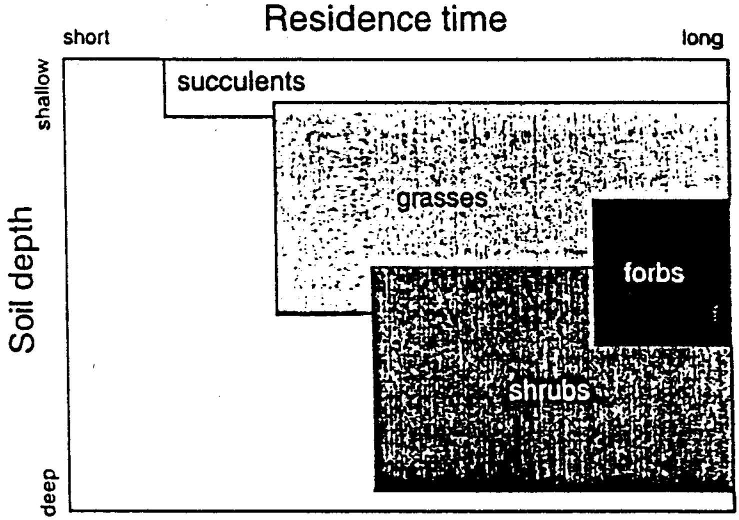

Figure 11.1 *Conceptual model of the partitioning of water resources among the four functional types of the Patagonian steppe: grasses, shrubs, succulents and forbs. The axes of the model are the depth from which each functional type is able to absorb water, and the residence time of water, which is the period of time during which water remains within the range of water potential available for plants.*

The model is based upon the following hypotheses:

1. Grasses absorb most of the water from the upper layers of the soil. They utilize frequent and short-duration pulses of water availability.
2. Shrubs absorb most of the water from the lower layers of the soil. They utilize infrequent and long-duration pulses of water availability.
3. Succulents absorb water from the shallowest layers of the soil. They utilize pulses of the shortest duration.
4. Forbs overlap with grasses and shrubs regarding the region of the soil where they absorb water. They utilize pulses of the longest duration. These pulses are infrequent, but they usually yield a quantity of water sufficient to complete a growth cycle of the forbs.

Our model is related to those proposed by Walker *et al.* (1981) and Walker & Noy-Meir (1982) in that it is based upon ideas first put forward by Walter (1971) as an explanation for the existence of savannas in tropical regions. Walter suggested that 'only in the tropics where both summer rain and a deep, loamy sand coincide, are they [grasses and woody plants] found existing in a state of ecological equilibrium'.

Walter (1971) suggested in his two-layer hypothesis for savannas that woody plants and grasses compete for water in the surface layers of the soil, but woody plants have exclusive access to a source of water relatively deep underground. Knoop & Walker (1985) tested this hypothesis for southern African savannas through removal experiments.

Based upon our hypothetical model we can make deductions, which may be tested in the field. The deductions are: (1) that the removal of shrubs will not increase the water status or productivity of grasses and will increase the availability of deep soil water; and (2) that the removal of grasses will not increase the water status or the productivity of shrubs and will increase the availability of water in the upper layers of the soil. The experiments consisted of removing grasses or shrubs and monitoring primary production, plant water status and soil water potential at different locations in the soil profile. Production was measured by using a harvest technique, plant water status by the pressure chamber technique (Scholander *et al.* 1965), and soil water potential with themocouple hygrometers (Spanner 1951). A complete description of the experimental design and the methods is given by Sala *et al.* (1989).

The experiments were carried out in the Occidental District of the Patagonian steppe (Soriano 1956). The five-year average above-ground net primary production (ANPP) of this ecosystem was 60 $g\,m^{-2}\,a^{-1}$; total canopy cover was 49% (Golluscio *et al.* 1982; Fernández-A. *et al.* 1991). Grasses, shrubs and forbs account, respectively, for 64%, 33% and 3% of canopy cover and 53%, 43% and 4% of ANPP. Temperatures range between 1 °C in July and 15 °C in January. The annual precipitation average, over a period of 37 years, was 136 mm. It was concentrated during the winter months, resulting in a recharge of the profile at this time.

The experimental results showed that the removal of shrubs did not result in an increase in the productivity of grasses (Fig. 11.2). Removal of grasses resulted in a small increase in the productivity of shrubs. The increase in shrub productivity was much smaller than the decrease in total productivity (grass productivity) that resulted from grass removal. The removal of grasses freed resources, which were used by shrubs. The efficiency with which one FT used the resources, water and nutrients liberated by removal of the other FT was calculated as

$$\text{Efficiency} = \Delta \text{FT}_1/\text{ANPP FT}_2 \tag{11.1}$$

where ΔFT_1 is the change in the productivity of FT_1 as the result of removing FT_2, and ANPP FT_2 is the production of the experimentally removed FT in the control plots. The efficiency ranged between 0 for the removal of shrubs and 25% for the removal of grasses. These results partly support the overall hypothesis that these FTs use different resources.

Removal of shrubs did not result in any change in the water status of grasses (Fig. 11.3A). The lack of response in leaf water potential agreed with

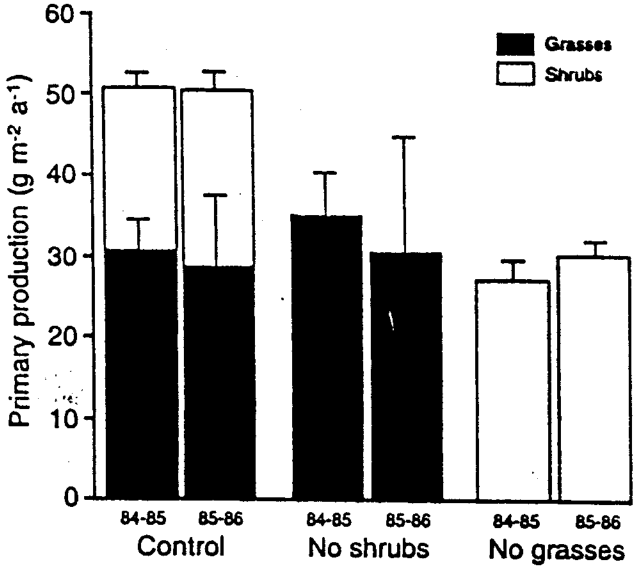

Figure 11.2 *Above-ground net primary production (+ standard error) of grasses and shrubs in the Patagonian steppe for treatments in which grasses or shrubs were selectively removed, and the control where both functional types were present (after Sala* et al. *1989).*

the lack of response observed in the production of grasses as a result of the removal of shrubs. By contrast, removal of grasses resulted in an increase in leaf water potential of shrubs. This increase occurred on only a few sample dates: two during the first year, one during the second year, and never during the last year (Fig. 11.3B). These infrequent and small increases in the shrub water status may account for the small increase in production observed as a result of grass removal.

Soil water potential showed a clear seasonal pattern (Fig. 11.4). The entire soil profile was wet by the end of the winter or beginning of the spring and dried out throughout the spring and summer, when all layers attained very low soil water potential values. The differences among treatments were only evident during the drying period. In the upper layers, removal of grasses resulted in an increase in soil water potential, but the

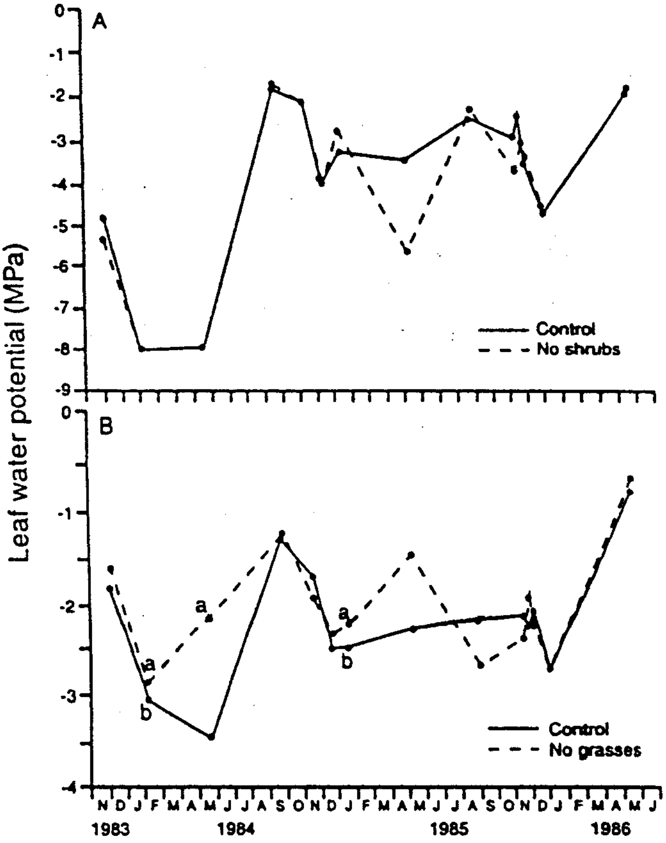

Figure 11.3 *Midday leaf water potential of grasses and shrubs in the Patagonian steppe for the control, and treatments in which grasses or shrubs were selectively removed. Different letters indicate significant differences* ($p<0.05$) *between treatment and the control. Absence of letter for a date indicates that differences were not significant (after Sala* et al. *1989).*

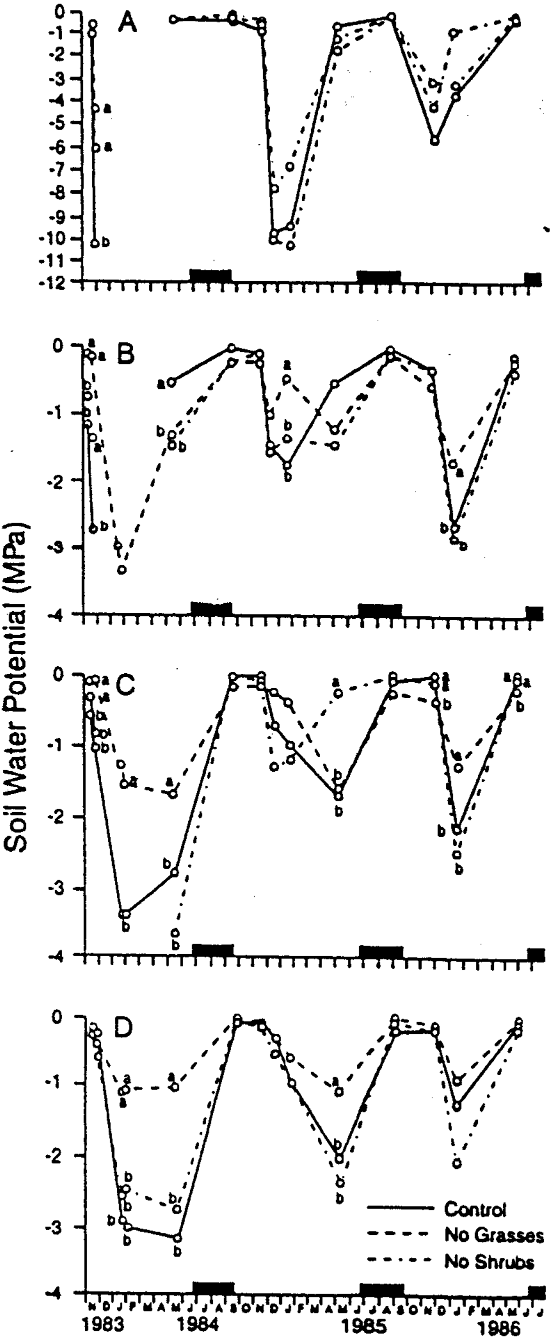

Figure 11.4 *Soil water potential at (A) 5, (B) 15, (C) 30 and (D) 60 cm depth in the Patagonian steppe for the control, and treatments in which grasses or shrubs were selectively removed. Different letters indicate significant differences* ($p<0.05$) *among treatments for a given date. Absence of letter for a date indicates that differences were not significant (after Sala* et al. *1989).*

removal of shrubs did not result in any changes in soil water. In lower layers, removal of grasses also resulted in an increase in soil water potential but removal of shrubs did not result in the hypothesized increase in soil water availability, suggesting that they absorb from even deeper layers.

These experimental data support the overall hypothesis that shrubs and grasses in the Patagonian steppe use different water resources. Shrubs absorb water exclusively from the lower layers. Grasses indeed take up most of the water from the upper layers of the soil. However, grass removal resulted in a small increase in soil water in deeper layers, in shrub leaf water status and in shrub production. This may indicate that grasses influence the input of water to lower layers and/or that they are also able to absorb from lower soil layers.

These results have important implications for the nutrient economy of both FTs. A characteristic of arid and semi-arid regions is that soil organic matter and nutrient availability are concentrated in the layers very near the soil surface (Clark 1977; Cole *et al.* 1977; Schimel & Parton 1986). Therefore, if shrubs and grasses absorb their nutrients from the same location from which they absorb water, shrubs will be at a competitive disadvantage since they will be absorbing from a nutrient-poor layer. By contrast, grasses will have the advantage of absorbing from the richest layer of the soil. How do shrubs cope with these circumstances? Do they have lower requirements than grasses? Do they meet a larger fraction of their requirements via internal retranslocation?

Biogeographical model of the distribution of arid functional types

The objective of this section is to develop a biogeographical model of the distribution of temperate grasslands and shrublands. The model is based upon our current understanding about the functioning of grasses and shrubs, and about the resources used by each of these FTs. This is an attempt to extrapolate our experimental results about FTs to the scale of vegetation units. The approach is to match abiotic requirements of FTs with resource availability to estimate the probability of occurrence of grasslands, shrublands or a mixture. Finally we will discuss the influence of biotic factors, which range from competition to human intervention.

Generalizing the results obtained for the Patagonian steppe and for the southern African savannas, we will propose the potential conditions for temperate semi-arid sites to support grasses, woody plants or a mixture. These conditions can be assessed with information about the seasonality of precipitation and the texture of the soil.

If grasses have an advantage at locations where soil water is stored near the surface, two easily assessed characteristics can be used to evaluate the potential of that location to support grasses. First, soil texture will have a large influence on the location at which water is stored. In general, fine-textured soils will store more water near the surface than coarse-textured soils (Fig. 11.5). Given an identical precipitation regime, a site with a silty soil will have a larger proportion of its total water storage in the surface layers (0–30 cm) than will a sandy or gravelly soil. This occurs because the storage capacity (cm^3 cm^{-1}) is higher for silty soils.

Although soil texture is important in determining the location of water stored in the soil, the seasonality of precipitation must also be taken into account. We propose to account for the effects of seasonality of precipitation by evaluating the overlap between the wet season and the warm season. Because grass roots densely occupy the top soil layers, we assume

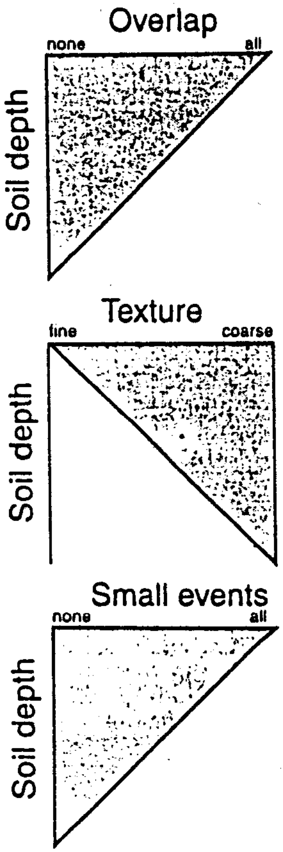

Figure 11.5 *Conceptual model of the effects of the overlap between the warm and wet seasons, soil texture, and the proportion of precipitation received as small events on the depths in the soil at which water is available to plants.*

that precipitation that occurs during the time of year when air temperatures are favourable for plant growth will favour grasses. Precipitation falling during the cold portion of the year will have a higher probability of being stored in deep layers, where grasses are less effective, and therefore should favour woody plants.

Two independent soil water modelling exercises support the idea that seasonality controls the distribution of available water in the soil profile. In the North American shortgrass steppe, where most of the precipitation occurs during the warm season, water availability is skewed towards the upper layers (Sala *et al.* 1992). The 4–15 cm soil layer was the layer that had the highest frequency of being wet (soil water potential > −1 MPa) over a 33 year period (Fig. 11.6). By contrast, in the South American Patagonian steppe, where 70% of the precipitation occurs during the cold months, the layer with the highest probability of being wet is the deepest layer (Paruelo & Sala 1995).

The combination of the soil texture and precipitation seasonality variable results in an explanation of grass–woody plant relationships (Fig. 11.7). Areas with maximum precipitation during the warmest portion of the year should support grasslands on all sites except those with very coarse-textured soils. Areas with maximum precipitation during the coldest portion of the

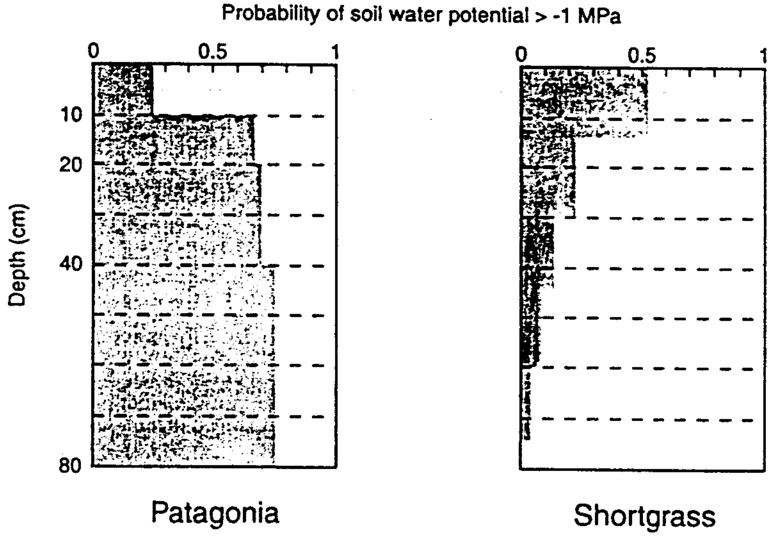

Figure 11.6 *Probability of soil water potential being greater than −1 MPa for different soil layers for the South American Patagonian steppe, which has mainly winter precipitation, and for the North American shortgrass steppe, which has predominantly summer precipitation. Results were obtained using two daily simulation models run for periods of 19 (Patagonia) and 33 years (shortgrass) (after Sala* et al. *1992; Paruelo & Sala 1995).*

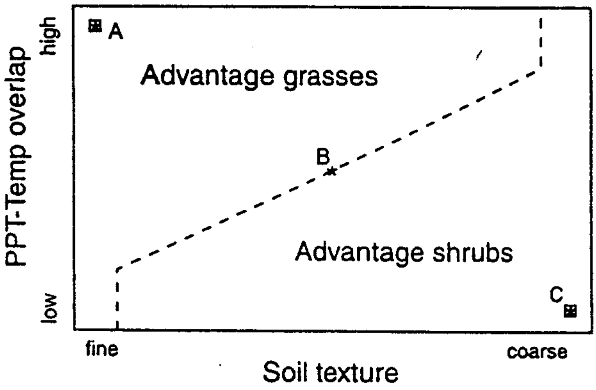

Figure 11.7 *Conceptual model of the effects of soil texture, and the overlap between the warm and wet seasons, upon the relative importance of grasses and shrubs. The model based exclusively on abiotic variables suggests that vegetation is composed exclusively of either grasses or woody plants only close to points A and C. Other points are mixtures of grasses and shrubs. The influence of biotic factors will be maximum near point B.*

year should support shrublands except on those sites with very fine-textured soils. Are mixtures of grasses and woody plants possible with this explanation? Yes: we would expect a vegetation composed exclusively of either grasses or woody plants only in very close proximity to either points A and C. Other points in the space represent mixtures of grasses and shrubs. As an interesting side issue we suggest that the ease with which one can manipulate a vegetation type decreases as one moves from the dividing line towards either A or C.

The remainder of this chapter is concerned with relations between grasslands and shrublands, why they occur where they do, and how humankind's uses of grasslands and shrublands change their structure and FT composition.

Consider the following ordinary non-linear differential equations:

$$dG/dt = r_g\, G(1 - G/G_{\max}) \tag{11.2}$$

$$dS/dt = r_s\, S(1 - S/S_{\max}) \tag{11.3}$$

for the case in which the dynamics of the vegetation is determined entirely by climatic and soil variables. The maximum biomass of each FT ($S_{\max}$ or $G_{\max}$) is an expression of the suitability of the site. Taking grasses as an example, we can write

$$G_{\max} = f(PPT, T, ST, Bg_{\max}) \tag{11.4}$$

where PPT is monthly precipitation, T is monthly temperature, ST is soil texture and $Bg_{\max}$ is the maximum standing crop of grasses to be expected per unit of annual precipitation. If we assume a linear decline in the suitability of a site to support grasses as one moves from point A to point C in Fig. 11.7, the following equation applies:

$$G_{max} = (0.1 + 0.45X_1, + 0.45X_2)Bg_{max} \qquad (11.5)$$

We can ignore the scale factor Bg_{max} by considering G_{max} to be a proportion of the maximum biomass. The variable X_1 in Eqn 11.5 is an expression of overlap between the wet and the warm seasons based upon monthly data of precipitation and temperature. We use the product moment correlation coefficient expression:

$$X_1 = \frac{CORR(PPT, T) + 1}{2} \qquad (11.6)$$

$CORR(PPT, T)$ is the correlation coefficient between monthly average precipitation and monthly average air temperature. X_1 has a range from zero, when PPT and T are perfectly negatively correlated, to 1 when PPT and T are perfectly positively correlated.

The variable X_2 in Eqn 11.5 is an effect of soil texture. The function has the same shape as the function relating the effect of soil texture to water-holding capacity

$$X_2 = (2 - e^{KST}) \qquad (11.7)$$

where K is a scaling factor and ST is a soil texture variable. X_2 has a range from 1 for very fine-textured soils to zero for very coarse-textured soils.

The parameters r_g and r_s in Eqns 11.1 and 11.2 are the intrinsic rates of increase of either grass or shrub biomass. They are taken to be constants in this analysis, although one could argue for their dependence upon information similar to that used to calculate the maximum standing crop parameters. In that case, variable r values may be interpreted as changes in species composition, within FTs, as sites become more or less favourable for the particular FT.

The behaviour of this simple model over time will result in $G = G_{max}$ and $S = S_{max}$, assuming the simulation is carried out for a sufficient period of time and that the seasonal distributions of precipitation and temperature do not change. The interesting aspects of the analysis of the model revolve around the calculations of G_{max} and S_{max} and the associated equilibrium solutions G^* and S^*. How well does the model predict climatically controlled steady-state biomass? This is a question of how good are G_{max} and S_{max}.

Sims *et al.* (1978) presented soil, climate and FT composition data to which the calculations of G_{max} and S_{max} can be compared (Table 11.1). It is important to note that the model predicts the relative contribution of

Table 11.1. *Comparison of predictions from our model with data from ten North American sites*

Site	Soil texture	Per cent grasses	Per cent shrubs	X_1	X_2	G_{max}	S_{max}
Richland, WA (Ale)	Silt loam	65	29	0.09	0.91	0.55	0.45
National Bison Range, MT (Bridger)	Cobbly silt loam	75	0	0.74	0.91	0.84	0.16
Bangtail Ridge, MT (Bridger)	Silt loam	56	0	0.84	0.91	0.89	0.11
Cottonwood, SD (Cottonwood)	Silty clay loam	97	<1	0.88	0.99	0.94	0.06
Dickinson, ND (Dickinson)	Loamy fine sand	75	<1	0.92	0.57	0.77	0.23
Hays, KS (Hays)	Loam	85	1	0.95	0.68	0.83	0.17
Jornada Exp. Range, NM (Jornada)	Loamy fine sand	44	14	0.83	0.57	0.73	0.27
Pawhuska, OK (Osage)	Silty clay	96	0	0.89	0.99	0.95	0.05
Amarillo, TX (Pantex)	Silty clay loam	80	0	0.94	0.99	0.97	0.03
Central Plains Exp. Range, CO (Pawnee)	Fine sandy loam	52	11	0.92	0.57	0.77	0.23

Source: Sims *et al.* (1978).

grasses and shrubs to total cover ($G_{max} + S_{max} = 1$), whereas the observed data represent percentage cover of each FT and do not add up to 1 because bare soil cover is not presented. Model predictions for shrubs were highest for the sites with the largest shrub components; predictions for grasses were highest for sites with the largest proportions of grasses (Fig. 11.8 and 11.9). The model predicts the shrub contribution better than the grass contribution. The grass predictions are approximately related to the observed cover values except for the Ale site in Washington where predictions were much lower than the observations. This cannot be considered a stringent test of the model, since it contains information only about climatic and soils variables and ignores biotic interactions, management and historical information. The reason for carrying out this comparison is to show general correspondence.

Our analysis recognizes the potential for competition between grasses and shrubs as one of several biotic interactions that influence the balance between the two FTs rather than the dominant interaction. The degree to

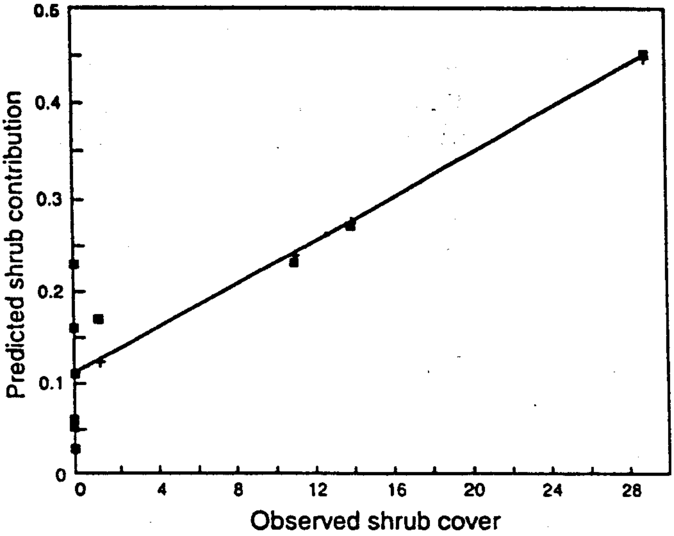

Figure 11.8 *Comparison between predicted and observed shrub cover for ten North American sites. Predictions are the result of the model presented here and represent the fraction of plant cover accounted for by shrubs. The observed values represent ten independent measurements of shrub cover from Sims* et al. *(1978). Observed cover values represent the fraction of soil area covered by shrubs; since total plant cover in most arid and semi-arid regions is not 100% the sum of shrub plus grass cover is less than 100%.*

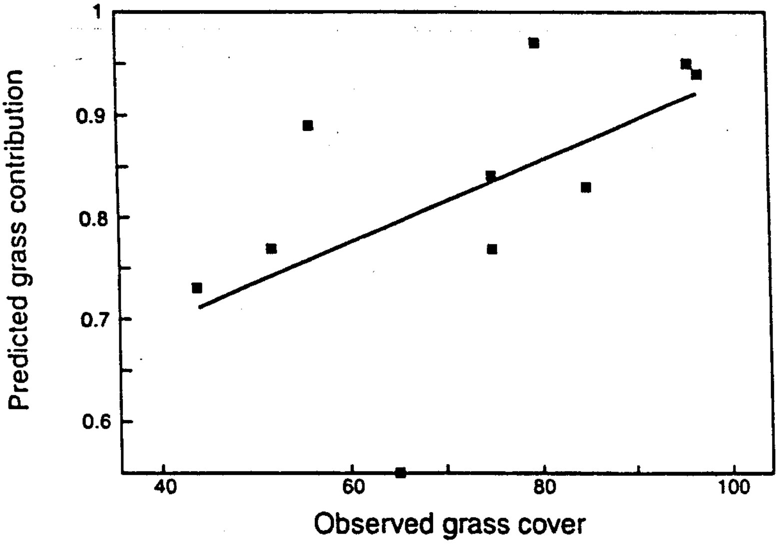

Figure 11.9 *Comparison between predicted and observed grass cover for ten North American sites. Predictions are the result of the model described here; observed values are those reported by Sims* et al. *(1978).*

which competition between FTs will determine the balance between grasses and shrubs in semi-arid regions is related to the local environment. In terms of Figure 11.7, the importance of competition between shrubs and grasses in determining whether a site will be occupied predominantly by grasses or by shrubs will be least for sites located near points A and C. The importance of competition will be greatest for sites near B.

The outcome of competition will be difficult to predict near point B because here all of the biotic influences will have their maximum impact. To understand why this is so we need to examine the characteristics implied in Figure 11.7. A simplified view of this model reveals an explanation of the behaviour of grasslands and shrublands near points A, B and C.

The significance of the points A and C is clear from this perspective. Point A represents a site with very fine-textured soils and a perfect correlation between the warmest and wettest months. According to our model, this is the epitome of a grassland site. By contrast, point C is located on a coarse-textured soil at a site that receives essentially all of its precipitation during the coldest months. This is a site that we would expect to be dominated by shrubs. How will the vegetation at sites A and C be influenced by biotic factors, including manipulation by humankind?

To answer this question, we need to use the concept of substitution efficiency developed in Eqn 11.1. This is the number of units of one FT that can be supported at a particular site as a result of removing a unit of the other FT. This is both FT- and site-dependent. According to the model, point C represents a very unfavourable site for grasses and consequently we would expect a small substitution efficiency. The probability of replacement of one FT by the other or the replacement rate is related to the distance of the site from point B in Figure 11.7. The further the site is from point B, the lower will be the efficiency of substitution and, therefore, the probability of replacement.

Let us now return to the question of the importance of biotic factors in determining the structure of the vegetation. Because the substitution efficiency of grasses for shrubs at point C or shrubs for grasses at point A is low, we would expect these two sites to show a maximum degree of independence from biotic factors. For instance, heavy herbivory on a site such as A would be expected to produce a vegetation composed of unpalatable grasses rather than one dominated by shrubs. In this case the effect of applying a force to the existing vegetation may result in a shift in species composition within the grass FT (or perhaps a shift in the relative frequency of tolerant genotypes). An analogous response may be expected for a shrubland represented by point C. Herbivory or perhaps herbicide treatment to control shrubs will result in either a change in species composition among shrubs or a short-lived vegetation dominated by grasses or other forbs. In addition to their degree of independence from biotic effects, sites represented by points A and C should be expected to show a minimum of year-to-year fluctuation in FT composition.

Previously we suggested that sites near point B should have behaviour quite different from those represented by points A and C. These sites occupy the boundary between the grassland and shrubland regions. Rather than a sharp edge separating the two, we suggest that there is a region in parameter space with a degree of indeterminacy for vegetation structure. It is here that biotic and other non-climatic influences should have their maximum impact. Sites in this region will be characterized by alternative vegetation structures depending upon their recent history. This is the region for which bifurcation models with bimodal behaviour are applicable.

Such sites have contributed to the idea that past heavy use by domestic herbivores has resulted in the conversion of many grasslands into shrublands. While this explanation may be exactly correct for sites in the vicinity of point B, it is clear that our model does not support such a deduction in the general case. The generality from the model is that the further the site is from the dividing line (point B), the smaller will be the difference between the alternative states of the system. In other words, the greater the distance from point B, the more similar the alternative steady states will be. Our previous discussion makes clear the notion that at point A or C the alternative states will have converged to a point.

Conclusion

Grasses are better suited to utilizing water stored in the upper layers of the soil than shrubs, which are more effective at utilizing water stored in the deep layers of the soil. Location of soil water determines the proportion of FTs, shrubs and grasses. Characteristics of the environment such as soil texture and seasonality of precipitation are the major controls of the distribution of water in the soil profile. Sites that have fine-textured soils and in which the wet season occurs in synchrony with the warm season represent the most favourable conditions for grasses. By contrast, shrubs dominate on coarse-textured soils and in regions in which precipitation does not occur during the warm season.

The probability of replacement of one FT (grasses) by the other (shrubs) increases as conditions become more different from the optimum. The model suggests that the boundary between grassland and shrubland regions is not sharp but implies a degree of indetermination for vegetation structure. It is in these regions, where the probability of replacement is high, that biotic factors have their maximum impact.

Acknowledgements

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