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Interrelationships between plant functional types and soil moisture heterogeneity for semiarid landscapes within the grassland/forest continuum: a unified conceptual model

David D. Breshears[1,*] & Fairley J. Barnes[1,2]
[1]*Environmental Science Group, Mail Stop J495, Los Alamos National Laboratory, Los Alamos, NM 87545, USA;*
[2]*Current address: Atmospheric Science Group, Mail Stop D407, Los Alamos National Laboratory, Los Alamos, NM 87545, USA*
([*]author for correspondence, e-mail: daveb@lanl.gov; fax: +1 505 665 3866)

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Abstract

In semiarid landscapes, the ratio of herbaceous to woody plant biomass is a major determinant of ecosystem properties. This ratio depends to a large extent on the amount and spatial distribution of soil moisture that is available to plants, and these variables, in turn, are determined primarily by climate and land use. Current conceptual models for determining the ratio of herbaceous to woody plant biomass in semiarid plant communities are based either on differences in soil moisture with depth (vertical heterogeneity) from one site to another (Walter's two-layer model) or on differences in soil moisture between canopy and intercanopy patches at the same site (horizontal heterogeneity) that result from disturbances associated with land use (Schlesinger et al.'s model of desertification). We developed a model that unifies these two perspectives by relaxing two assumptions of Walter's two-layer model. First, our model recognizes that soil moisture varies horizontally between canopy and intercanopy patches, not only due to land-use disturbance, a general assumption of the Schlesinger et al. model, but also due to the physical nature of the canopy itself. Second, while retaining the general assumption of Walter that woody plants obtain moisture from deeper soil layers than do herbaceous plants, our model recognizes the existence of two types of woody plants: those that extract a substantial proportion of their moisture from deeper layers and those that extract mainly from shallower layers. By modifying the two-layer hypothesis to include four soil compartments and distinguishing between shallow- and deeper-rooted woody species, our model integrates three key concepts in semiarid ecology: (1) the proportion of woody cover increases as moisture in the deeper soil layers increases (Walter's two-layer hypothesis for coexistence of herbaceous and woody plants); (2) land use practices that cause a reduction in herbaceous vegetation and compaction of intercanopy soils lead to a long-term increase in the proportion of woody plants (Schlesinger et al.'s concept, or more generally, that at a given site multiple variations in the proportions of herbaceous and woody plant biomass are possible); and (3) changes in the ratios of herbaceous to woody plant biomass exhibit complex behavior (changes can happen quickly and are not directly reversible without intensive management). This integration of concepts results because rather than assuming a simple, one-way dependence of plant functional types on soil moisture heterogeneity, our model assumes an interdependence between the two: soil moisture heterogeneity constrains the composition of the plant community, which in turn modifies soil moisture heterogeneity. The four-compartment model that we propose enables, for the first time, an integrated picture of both dimensions of soil moisture heterogeneity – horizontal and vertical – and of the interdependence between soil moisture heterogeneity and the proportions of the plant functional types that make up a given plant community. This unified conceptual model can be applied to provide insight into the individual and the combined effects of climate and land use on semiarid plant communities within the grassland/forest continuum, which vary in the proportions of canopy and intercanopy patches.

Introduction

Plant communities in semiarid regions have exhibited widespread and rapid changes in response to changes in climate and/or land use in the past (Archer et al. 1988; Archer 1989, 1990; Schlesinger et al. 1990; Grover and Musick 1990; Miller and Wigland 1994; Keeley and Mooney 1993; Tausch et al. 1993; Allen and Breshears 1998; Shugart 1998) and are expected to be among the most sensitive to the accelerated climate changes and increasing intensity of land use that future decades are likely to bring (IPCC 1996a, b). An important approach for assessing the complex responses of these communities is to identify plant functional types and characterize the functional response of each type to a suite of environmental conditions (Golluscio and Sala 1993; Steffen 1996; Epstein et al. 1997; Smith et al. 1997).

The plant community in many semiarid landscapes can be viewed as a 'two-phase' mosaic of vegetation – individual or aggregated woody plants (shrubs and trees) on the one hand and the intercanopy locations that separate them on the other (e.g., Milne et al. 1996). A given site will lie somewhere along a continuum, the extremes of which are open grassland (no woody plant canopy) and forest (nearly complete closure of the canopy by woody plants) (Belsky and Canham 1994). The position of a site along this grassland/forest continuum, and the associated relative proportions of the two types of cover, affect many ecosystem properties – including near-ground energy input (Breshears et al. 1997b, 1998), water balance (Aguiar et al. 1996; Schulze et al. 1996), erosion rates (Ludwig and Tongway 1995; Reynolds et al. 1997; Davenport et al. 1998), and nutrient cycling (Padien and Lajtha 1992). In addition, the biomass associated with the two plant types provides key resources (forage and fuel wood).

The ability to predict changes in landscapes that are dominated by a mixture of woody and herbaceous plants is one of the top priorities for global change research (IPCC 1996a, b; Walker 1996). Within the grassland/forest continuum, the composition of a plant community depends in large part on the amount and spatial distribution of soil moisture available to the plants (Walter 1971; Tilman 1988; Belsky 1990; Martens et al. 1997; Medina and Silva 1990; Stephenson 1990; Barton 1993; Coffin and Urban 1993; Lauenroth et al. 1993; Solbrig et al. 1996). The conceptual models developed to date to investigate how a plant community might change are based on one or the other of two fundamentally different concepts: (1) differences between two or more relatively undisturbed sites are a function of differences in climate and/or soil profile; (2) the same site can change over time as a result of disturbance (change in land use).

The current model based on the first concept was developed by Walter (1971, 1973). The assumptions of this model focus on vertical heterogeneity: that two soil layers may be distinguished on the basis of the rooting depths of plants; that herbaceous plants have a denser root distribution in the upper layer than do woody plants and are much more efficient at obtaining available water in the upper layer; and that woody plants have sole access to the lower soil layer. The model postulates, therefore, that the ratio of herbaceous to woody biomass at a site is proportional to the relative amounts of moisture in the two soil layers. (Essentially the same two-layer hypothesis had been advanced earlier by Emerson (1932), who documented differences in root distribution and available soil moisture between semiarid grassland and piñon-juniper woodland.)

Walter's two-layer hypothesis subsequently became the basis for other models (Walker et al. 1981; Eagleson 1982; Walker and Noy-Meir 1982; McMurtrie and Wolf 1983; Eagleson and Segarra 1985; Sala et al. 1997), and its assumptions and predictions have been supported by field studies (Knoop and Walker 1985; Liang et al. 1989; Sala et al. 1989, 1997). The hypothesis was recently proposed as part of a framework for comparing ecosystem dynamics among the study sites that make up the Long-Term Ecological Research Network (Lauenroth et al. 1993), which includes several sites along the grassland/forest continuum; it has also been presented as the basis for quantifying the response of a semiarid ecosystem to changes in climate. (Coffin and Lauenroth 1990; Burgess 1996; Sala et al. 1997).

The shortcoming of Walter's (1971, 1973) model is that it allows for only a single ratio of herbaceous to woody biomass at a site. Yet, at many semiarid sites, the ratio has been observed to change (Johnsen 1962; Schlesinger et al. 1990; Tausch et al. 1993; IPCC 1996b; Schlesinger and Pilmanis 1998) particularly following disturbances that cause soil properties to change, such as heavy grazing or off-road vehicle use. Further, once the ratio of herbaceous to woody biomass has shifted, it does not seem to shift back after the disturbance has ceased.

The conceptual model based on the second concept (Schlesinger et al.'s [1990] model of desertification) takes these observed phenomena into account. The assumptions of this model focus on horizontal heterogeneity: that land-use disturbances cause a reduction in herbaceous vegetation; that in conjunction with the reduction in herbaceous vegetation, intercanopy soils become compacted; that both these phenomena lead to an increase in runoff from intercanopy areas; and that woody plants effectively use the extra water that runs off into canopy areas, as well as the portion remaining in intercanopy areas. (Such redistribution of runoff from intercanopy to canopy areas has been documented in a variety of ecosystems (Cornet et al. 1992; Ludwig et al. 1997)). The focus of this model on horizontal linkages between canopy and intercanopy patches, rather than on the vertical differences in soil moisture or rooting depth that form the basis for Walter's model, yields predictions of alternative plant community compositions at a given site. (See Belsky 1994; Reynolds et al. 1997; and Scholes and Archer 1997, for related discussions.)

Both the concepts on which the two types of models are based relate use of soil moisture by plants to the composition of the plant community, and each is useful for comparisons within a limited set of plant communities. But because each model ignores the important aspects of the other, neither can depict the relative importance of vertical vs. horizontal soil moisture heterogeneities in determining the proportions of different plant functional types.

On the basis of findings of recent studies, we have relaxed some of the simplifying assumptions of Walter's model to construct a conceptual model that unifies the two perspectives. Our objectives in developing this model were to (1) factor in the roles of both the horizontal and vertical components of soil moisture heterogeneity in determining the compositions of semiarid plant communities, and (2) assess the interrelationships between these components both within and across sites for consistency with the models of Walter and of Schlesinger et al.

Table 1. Model assumptions for the relative use of soil moisture available to plants. Assumptions are presented for (1) within each of the four soil compartments, and (2) among the four soil compartments for each of the three plant types. The relative water use by all three plant types totals 1.0 (i.e. 100%) within a soil compartment.

Relative water use within each soil compartment	
Upper Intercanopy (*UI*):	*H* > *S* > *D*
Upper Canopy (*UC*):	*S* > *D* > H
Lower Intercanopy (*LI*):	*D* > *H* > *S*
Lower Canopy (*LC*):	*D* > *S* > *H*
Relative water use by each plant type	
Herbaceous plants (*H*):	*UI* > *LI* > *UC* > *LC*
Shallow-extracting woody plants (*S*):	*UC* > *UI* > *LC* > *LI*
Deeper-extracting woody plants (*D*):	*LC* > *LI* > *UC* > *UI*

Development of a unified model

Our unified model is built on the relaxation of two key assumptions of Walter's two-layer model, namely, (1) that horizontal heterogeneity in soil moisture is not important (an implicit assumption), and (2) that all woody species obtain soil moisture only from deep soil layers (an explicit assumption).

Horizontal heterogeneity in soil moisture can be important

Several recent studies have demonstrated that, in addition to varying with depth, soil moisture varies with type of plant cover, i.e., horizontally – specifically, with respect to the presence or absence of woody plant canopy (Joffre and Rambal 1988, 1993; Belsky et al. 1989, 1993; Dawson 1993; Ryel et al. 1996; Breshears et al. 1997b). Such studies show that the physical structure of woody canopies modifies the environment beneath those canopies in many ways, and that the differences between these microenvironments and those of the intercanopy areas influence the amounts of soil moisture in both patch types.

Differences in soil moisture between canopy and intercanopy locations may be more important in woodlands and shrublands than in either forests or grasslands, because at these intermediate sites along the grassland/forest continuum, canopy and intercanopy areas are both large enough to be major components of the ecosystem. In contrast, in forests the intercanopy component is much smaller than the canopy component, and in grasslands the canopy component is much smaller than the intercanopy component.

This horizontal aspect of heterogeneity in soil moisture is not included at all in Walter's (1971, 1973) model, and is included in that of Schlesinger et al. (1990) only as it pertains to land-use disturbances. However, the results of the studies just cited suggest that pronounced horizontal heterogeneity of soil moisture is not restricted to disturbed shrublands and woodlands. In other words, there are intrinsic differences in soil moisture between canopy and intercanopy locations that result simply from the presence of the canopy. Because of the significant limiting effect of water in semiarid ecosystems, even small horizontal differences in volumetric water content may be important biologically – small differences in volumetric water content have large, nonlinear effects on soil water potential, which limits a plant's ability to extract water from the soil (Sala and Lauenroth 1982; Breshears et al. 1997b, 1998).

Different woody-plant functional types extract soil moisture from different soil layers

The conceptual models of both Walter (1971, 1973) and Schlesinger et al. (1990) group all woody plant species into a single category, and a fundamental assumption of Walter's model is that woody plants extract soil moisture from deeper depths than do herbaceous species. However, numerous recent studies have documented that woody species differ with respect to the depths from which they extract water (Flanagan et al. 1992; Evans and Ehleringer et al. 1994; Peléz et al. 1994; Montaña et al. 1995; Breshears et al. 1997a). In general, the roots of shrubs will have a shallower distribution than those of trees (Canadell et al. 1996; Jackson et al. 1996). Several arid and semiarid plant communities include woody species that are able to extract soil moisture from shallow intercanopy locations – which means that in those locations they are likely to be competing for resources with herbaceous plants (Caldwell et al. 1985; Ansley et al. 1991; Peléz et al. 1994; Le Roux et al. 1995; Montaña et al. 1995; Breshears et al. 1997a; Briones et al. 1998).

Our model, therefore, incorporates the differences between woody plant species with respect to where they obtain water – both vertically and horizontally – as well as the heterogeneity of soil moisture – both vertically and horizontally.

Assumptions of the unified conceptual model

Our unified conceptual model, by distinguishing both between canopy and intercanopy patches and between upper and lower soil layers, yields four soil compartments (Figure 1): upper canopy (*UC*), upper intercanopy (*UI*), lower canopy (*LC*), and lower intercanopy (*LI*).

The two upper compartments together constitute the *upper soil layer* (*U*) for both canopy and intercanopy patches, and the two lower compartments together constitute the *lower soil layer* (*L*) for both canopy and intercanopy patches. The upper layer, as distinguished from the lower, is the depth interval that encompasses the predominant rooting depths of herbaceous plants (this assumption is similar to but less stringent than Walter's (1971, 1973)). The upper and lower canopy compartments combined form the canopy column, and the upper and lower intercanopy compartments combined form the intercanopy column (Figure 1).

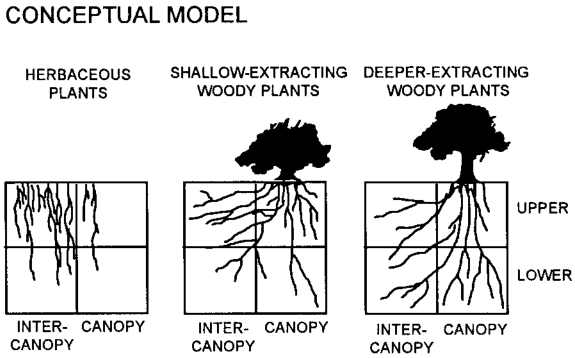

Figure 1. Conceptual model relating soil moisture heterogeneity to differences in plant uptake. Four soil compartments result from distinguishing between an upper vs. lower soil layer and between canopy vs. intercanopy locations.

'Plant-available' moisture from these four soil compartments is that portion of the total amount of moisture that remains in the soil after losses through runoff, soil evaporation, and evaporation of water intercepted by plant foliage.

A second characteristic of the unified model is that it distinguishes three, rather than only two, functional plant types (Figure 1): herbaceous plants (*H*), shallow-extracting woody plants (*S*), and deeper-extracting woody plants (*D*). The model assumes differences among the three types with respect to ability to obtain soil moisture from each of the four soil compartments, as a function of differences in root morphology; and it also assumes differences among the four soil compartments with respect to the proportion of total moisture each loses to each of the three plant functional types. These combined differences are expressed in the following three sets of assumptions:

(1) The ability to obtain moisture from each of the four soil compartments differs for the three plant functional types: herbaceous plants are most able to obtain water from the upper intercanopy and least able from the lower canopy; shallow-extracting woody plants are most able to obtain water from the upper canopy and least able from the lower canopy; and deeper-extracting woody plants are most able to obtain water from the lower canopy and least able from the upper intercanopy (Table 1).

(2) Each of the four soil compartments loses a different proportion of its total moisture to each of the three plant functional types (see Table 1). For ex-

ample, for the upper intercanopy compartment, the greatest proportion is lost to herbaceous plants, the next greatest to shallow-extracting woody plants, and the smallest to deeper-extracting woody plants.

(3) All the available soil moisture from all four soil compartments (i.e. that amount left after losses through runoff, soil evaporation, and evaporation of water intercepted by plant foliage) will be used by the plants and converted into biomass. In terms of soil water potentials, all three plant functional types have equal ability to access soil moisture, and all three convert soil moisture to biomass with equal efficiency.

Table 2 gives a representative set of values that satisfies the three sets of assumptions.

It should be noted that our model does not consider temporal differences in soil moisture availability (see Sala et al. 1997, for related discussion) but rather focuses on the time-integrated relationships for plant water use. Nor does our model consider differences between age/size categories of woody plants; rather it focuses on the size of mature plants of each plant functional type.

In a given community, then, the proportions of the three plant functional types are a function of the distribution of soil moisture among the four compartments and of the use of water from the four compartments by the three types of plants. The model allows those proportions to be calculated for a given distribution of soil moisture as follows:

All of the plant-available water (value = 1.0) is assumed to be distributed among the four soil compartments:

$$M_{UI} + M_{UC} + M_{LI} + M_{LC} = 1.0$$

(or, considered as the sum of the two layers:

$M_U + M_L = 1.0$)

(or, considered as the sum of the two columns:

$M_I + M_C = 1.0$),

where M = the proportion of total soil moisture (total value = 1.0) that resides in a particular soil compartment; UI = upper intercanopy soil compartment; UC = upper canopy soil compartment; LI = lower intercanopy soil compartment; and LC = lower canopy soil compartment; M_U = the proportion of soil moisture in the upper soil layer (two upper compartments); M_L = the proportion of soil moisture in the lower soil layer (two lower compartments); M_I = the proportion of soil moisture in the intercanopy column (upper and lower layers); and M_C = the proportion of soil moisture in the canopy column (upper and lower layers).

The proportion of soil moisture in each of the four compartments can be determined from the proportions of soil moisture in a row (M_U or M_L) and in a column (M_I or M_C) using matrix algebra. Because the proportion in each compartment is a fraction of the total (total value = 1.0), each can be calculated as the product of the appropriate row fraction times the appropriate column fraction, as follows (we go on to express each equation in terms of only M_U and M_I):

$$\begin{aligned}
M_{UI} &= M_U \cdot M_I, \\
M_{LI} &= M_L \cdot M_I = (1.0 - M_U) \cdot M_I, \\
M_{UC} &= M_U \cdot M_C = M_U \cdot (1.0 - M_I), \\
M_{LC} &= M_L \cdot M_C = (1.0 - M_U) \cdot (1.0 - M_I).
\end{aligned}$$

All of the water in each compartment (total for each compartment = 1.0) is assumed to be divided among the three plant types:

$$\begin{aligned}
&A_{H_{UI}} + A_{S_{UI}} + A_{D_{UI}} = 1.0, \\
&A_{H_{UC}} + A_{S_{UC}} + A_{D_{UC}} = 1.0, \\
&A_{H_{LI}} + A_{S_{LC}} + A_{D_{LC}} = 1.0, \\
&A_{H_{LC}} + A_{S_{LC}} + A_{D_{LC}} = 1.0,
\end{aligned}$$

where A = the relative ability of a specified plant type to obtain soil moisture from a given soil compartment; H = herbaceous plants; S = shallow-extracting woody plants; and D = deeper-extracting woody plants. The abilities reflect root morphology (Figure 1).

Each unit of plant-available water is assumed to yield a unit of biomass. All of the biomass in the plant community is from the three plant functional types:

$$B_H + B_S + B_D = 1.0,$$

where B = fraction of the total plant biomass in the community consisting of a given plant type.

The fraction of plant community biomass for each plant functional type, then, is the product of the proportion of the water in a compartment (relative to the total amount of water in all four soil compartments) and the proportion of water a plant functional type can obtain from that compartment (relative to the three

Table 2. Representative values for the relative use of soil moisture available to plants that meet both sets of criteria for model assumptions presented in Table 1. The relative water use is a fraction of the total soil moisture relative to all of the soil moisture in a given soil compartment that is obtained by a given plant functional type. The relative water use by all three plant types totals 1.0 within each compartment (e.g. for the upper intercanopy compartment, 0.70 for herbaceous plants + 0.25 for shallow-extracting woody plants + 0.05 for deeper-extracting woody plants = 1.0 total for the compartment). Selecting sample values that meet the assumptions in Table 1 changes the maximum possible proportions of each type of plant and the intersections on the predicted surface but does not change the qualitative nature of the model predictions.

	Herbaceous plants (*H*)	Shallow-extracting woody plants (*S*)	Deeper-extracting woody plants (*D*)	Total
Upper Intercanopy (*UI*)	0.70	0.25	0.05	1.00
Upper Canopy (*UC*)	0.10	0.70	0.20	1.00
Lower Intercanopy (*LI*)	0.25	0.15	0.60	1.00
Lower Canopy (*LC*)	0.05	0.20	0.75	1.00

plant functional types for that compartment), summed over the four compartments:

$$\begin{aligned} B_H &= (M_{UI} \cdot A_{H_{UI}}) + (M_{UC} \cdot A_{H_{UC}}) \\ &\quad + (M_{LI} \cdot A_{H_{LI}}) + (M_{LC} \cdot A_{H_{LC}}), \\ B_S &= (M_{UI} \cdot A_{S_{UI}}) + (M_{UC} \cdot A_{S_{UC}}) \\ &\quad + (M_{LI} \cdot A_{S_{LI}}) + (M_{LC} \cdot A_{S_{LC}}), \\ B_D &= (M_{UI} \cdot A_{D_{UI}}) + (M_{UC} \cdot A_{D_{UC}}) \\ &\quad + (M_{LI} \cdot A_{D_{LI}}) + (M_{LC} \cdot A_{D_{LC}}). \end{aligned}$$

Although the proportions of the three types of plants depend on the total *amount* of plant-available moisture, this amount is not explicitly considered in our model. Rather, the model is based on the distribution of plant-available water among the four soil compartments (i.e., the *fraction* of soil moisture in a compartment relative to the total soil moisture in all four compartments).

The distribution of soil moisture itself is a function of the factors that determine vertical and horizontal heterogeneity – climate and soil profile in the case of vertical heterogeneity (upper soil layer M_U vs. lower soil layer M_L) and number of canopy and intercanopy patches, which is a function of the composition of the plant community, and average soil moisture content (amount) of each patch type in the case of horizontal heterogeneity (canopy soil moisture M_C vs. intercanopy soil moisture M_I). In other words, the distribution of soil moisture influences the composition of the plant community and at the same time the composition of the plant community influences the distribution of soil moisture.

Note, however, that the model does not operate in a 'circular' fashion; that is, a given plant community composition is determined by a given soil moisture distribution, but a given soil moisture distribution is not determined solely by plant community composition – rather, it is a function of both the plant community composition (more specifically, the number of canopy and intercanopy patches) and the average soil moisture content of the two patch types.

Evaluation of the unified conceptual model

Our evaluation of the model included three areas of investigation. First, we investigated how the overall composition of the plant community would change as the distribution of soil moisture changes. Second, we investigated how the composition of the plant community would change with changes in only the vertical distribution of soil moisture (i.e., we compared our model with that of Walter (1971, 1973), holding the horizontal component of soil moisture constant). And third, we investigated how the composition of the plant community would change with changes in only the horizontal distribution of soil moisture (i.e., we compared our model with that of Schlesinger et al. (1990), holding the vertical component of soil moisture constant). In each case, we calculated the proportions of biomass that each of the three plant types would have under various distributions of soil moisture among the four compartments and then summarized the results in terms of two values – a row total and a column total, from which all of the individual compartment values are derivable: (1) the total proportion of soil moisture in the two upper compartments (M_U – row total) and (2) the total proportion in the two intercanopy compartments (M_I – column total).

Overall interrelationships between plant community composition and soil moisture distribution

The proportion of herbaceous plants, of shallow-extracting woody plants, and of deeper-extracting woody plants in a given community is each related curvilinearly to the distribution of available soil moisture (Figure 2, A–C). Which of the three plant functional types will dominate at a site, therefore, is a function of that distribution (Figure 2, D and E) as follows: dominance by herbaceous plants corresponds with high levels of soil moisture in the upper intercanopy compartment (Figure 2A); dominance by shallow-extracting woody plants corresponds with high levels of soil moisture in the upper canopy compartment (Figure 2B); and dominance by deeper-extracting woody plants corresponds with high levels of soil moisture in the lower canopy and intercanopy compartments (Figure 2C).

Our model considers all possible distributions of soil moisture among the four soil compartments, but some of these distributions are unlikely conditions. In particular, it is unlikely that most of the available soil moisture would ever reside in the lower intercanopy compartment because when the plant community is composed of predominantly deeper extracting woody plants, only a small proportion of the area is intercanopy (this is the predicted surface near the corner corresponding to all of the water in the upper layer and all of the water in the intercanopy soil column – Figure 2, D and E). Other interrelationships between soil moisture distribution and plant functional types are reasonable.

Interrelationships between plant community composition and vertical distribution of soil moisture

In semiarid regions, a transition from grassland to forest generally corresponds with an increase in soil moisture, in which several factors change simultaneously: as total soil moisture increases, the proportion in the lower layer increases relative to that in the upper layer (Emerson 1932; Walter 1971, 1973; Grover and Musick 1990; Lauenroth et al. 1993; Aguiar et al. 1996; Sala et al. 1997); and as the proportion of soil moisture in the lower layer increases, the proportion of deeper-extracting woody plants increases – which, in turn, causes the proportion of water in canopy areas to increase. Therefore, along a gradient of increasing total soil moisture, changes in the distribution of soil moisture among the four compartments produce changes in plant community composition. As shown in Figure 3, these changes are represented by vectors that are somewhat diagonal along the predicted surface (running between the corner corresponding to all of the water in the upper intercanopy and that corresponding to all of the water in the lower canopy). When horizontal heterogeneity in soil moisture is not large, then, the plant community composition will lie on or near the diagonal.

For the diagonal cross section corresponding to a grassland/forest gradient, our model indeed shows that the ratio of herbaceous to woody plant biomass increases as soil moisture in the lower layer increases. Therefore, even with the assumptions of Walter relaxed to allow for horizontal heterogeneity and for differences between woody plants with respect to the depths at which they extract moisture, the results yielded by our model are consistent with Walter's (1971, 1973) two-layer hypothesis. But our model goes further than that of Walter, allowing for different ratios of herbaceous to woody biomass to exist at a site.

Interrelationships between plant community composition and horizontal distribution of soil moisture

The proportion of total moisture located in the upper soil layer, as noted previously, is largely determined by climate and soil conditions; hence, within a given site, vertical heterogeneity is relatively constant. Our model allows for horizontal as well as vertical heterogeneity in soil moisture and therefore it depicts various combinations of the three plant functional types as possible at a given site where vertical heterogeneity is held constant. For example, Figure 4 shows three possible scenarios, for three different (constant) levels of moisture in the top soil layer: 80% (Figure 4B), 60% (Figure 4C), and 40% (Figure 4D). For each of these constant vertical distributions, several different overall distributions of soil moisture can exist, as a result of variances in horizontal heterogeneity.

As noted above, when differences in the average soil moisture content between canopy and intercanopy are small, a plot of the composition of the plant community will tend to fall along the center diago-

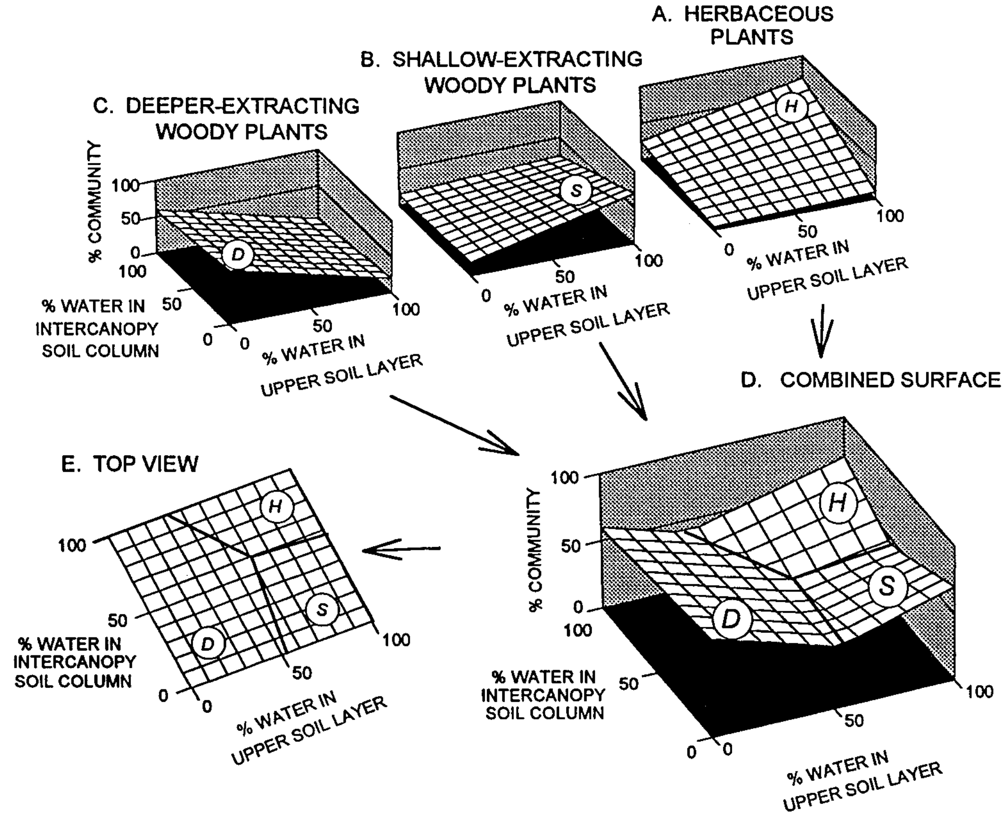

Figure 2. Model predictions for percent of community biomass for three plant types based on location of soil moisture. Soil moisture heterogeneity was varied by specifying the percent of the total plant-available moisture in the upper horizon and in the intercanopy column. Parameter values are presented in Table 1. Predictions are presented for each plant type individually for A) herbaceous plants (*H*), B) shallow-rooted woody plants (*S*), and C) deeper-rooted woody plants (*D*) and D) for the dominant plant type as a function of spatial distribution of available soil moisture; shown as a top view in E).

nal (Figure 4A); changes in the differences between canopy and intercanopy soil moisture (i.e., in horizontal heterogeneity), then, are represented as movement away from the diagonal, in one direction or another.

For the first scenario (Figure 4B), most of the soil moisture is in the upper layer and herbaceous plants dominate when there are no large differences in average soil moisture content between canopy and intercanopy patches (i.e., the plant community lies on or near the diagonal). Plant community composition can be altered in conjunction with changes in the ratio of canopy to intercanopy soil moisture, but a change of considerable magnitude would be needed to affect a shift in the dominant plant functional type.

For the second scenario (Figure 4C), the proportion of soil moisture in the upper layer is only slightly higher than the proportion in the lower layer, and shallow-extracting woody plants are dominant when there are not large differences in average soil moisture between canopy and intercanopy patches (again, in this case the plant community lies along the diagonal). However, in this scenario a small change in the ratio of canopy to intercanopy water produces a shift in the dominant plant functional type. That is, a small shift away from the diagonal leads to shallow-extracting woody plants becoming dominant rather than herbaceous plants.

For the third scenario (Figure 4D), most of the soil moisture is in the lower layer and deeper-extracting woody plants will dominate. For this scenario, the degree of change in the ratio of canopy to intercanopy water must be extreme for any change in the dominant plant type to be affected, although the proportions of biomass for herbaceous and shallow-extracting woody plants can still vary with horizontal heterogeneity in soil moisture.

From these different scenarios, it is apparent that a change from dominance of one plant type to that of

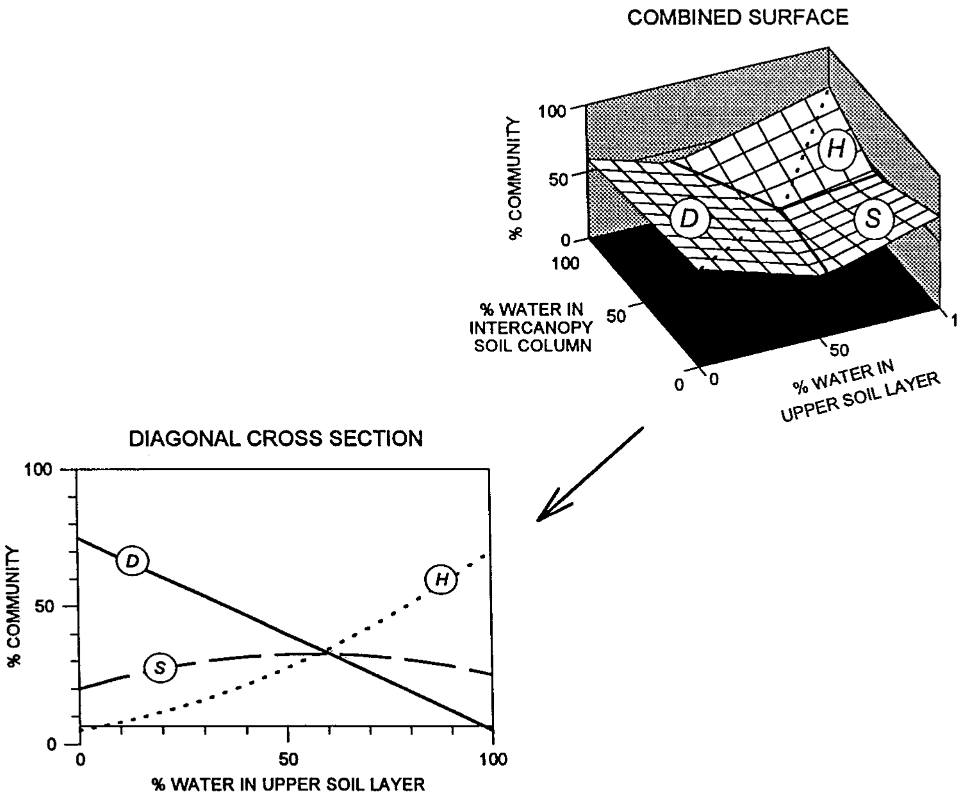

Figure 3. Model predictions for percent of community biomass for three plant types based on location of soil moisture: the diagonal of the surface represents a cross section along a moisture gradient. Along the diagonal, the % of water in the upper layer is equal to the % of water in the intercanopy soil column. Parameter values are as presented in Table 1.

another plant type occurs most readily when conditions are such that both are obtaining approximately the same amount of water from the upper soil layer, as in the case of herbaceous plants and shallow-extracting woody plants when the proportion of soil moisture in the upper soil layer is at intermediate values (Figure 4C).

Consequently, our model shows that even with no variation in the vertical distribution of soil moisture, horizontal heterogeneities can produce a variety of plant community compositions at a given site. This result is consistent with the model of Schlesinger et al.'s (1990), which shows that the ratio of herbaceous to woody biomass at a site can vary with changes in land use.

Some types of land use, such as those leading to desertification as described by Schlesinger et al. (1990), may actually change the vertical distribution of soil moisture in conjunction with changes in the horizontal distribution. Compaction of intercanopy soils in conjunction with depletion of intercanopy herbaceous plants (e.g., by grazing animals) can reduce the amount of plant-available water in intercanopy locations by causing a redistribution of runoff from intercanopy areas (where infiltration rates have been reduced) to canopy areas, thereby altering the horizontal distribution of soil moisture. Compaction of intercanopy soils probably also results in an increased evaporative loss from intercanopy patches (Schlesinger et al. 1990; Davenport et al. 1998); this would result in less plant-available water overall, and an increase in the proportion of that water in the upper soil layer. Such a change in both the horizontal and vertical distribution of soil moisture results in a vector somewhat perpendicular to the diagonal, as illustrated, for example, by the arrow in Figure 5.

Our model illustrates why these types of changes in the composition of the plant community associated with desertification or other types of land degradation cannot readily be reversed. Such reversal would require management intervention that not only reduces the woody biomass but that also increases the proportion of soil moisture in the intercanopy patches. One of the few means of accomplishing both requires

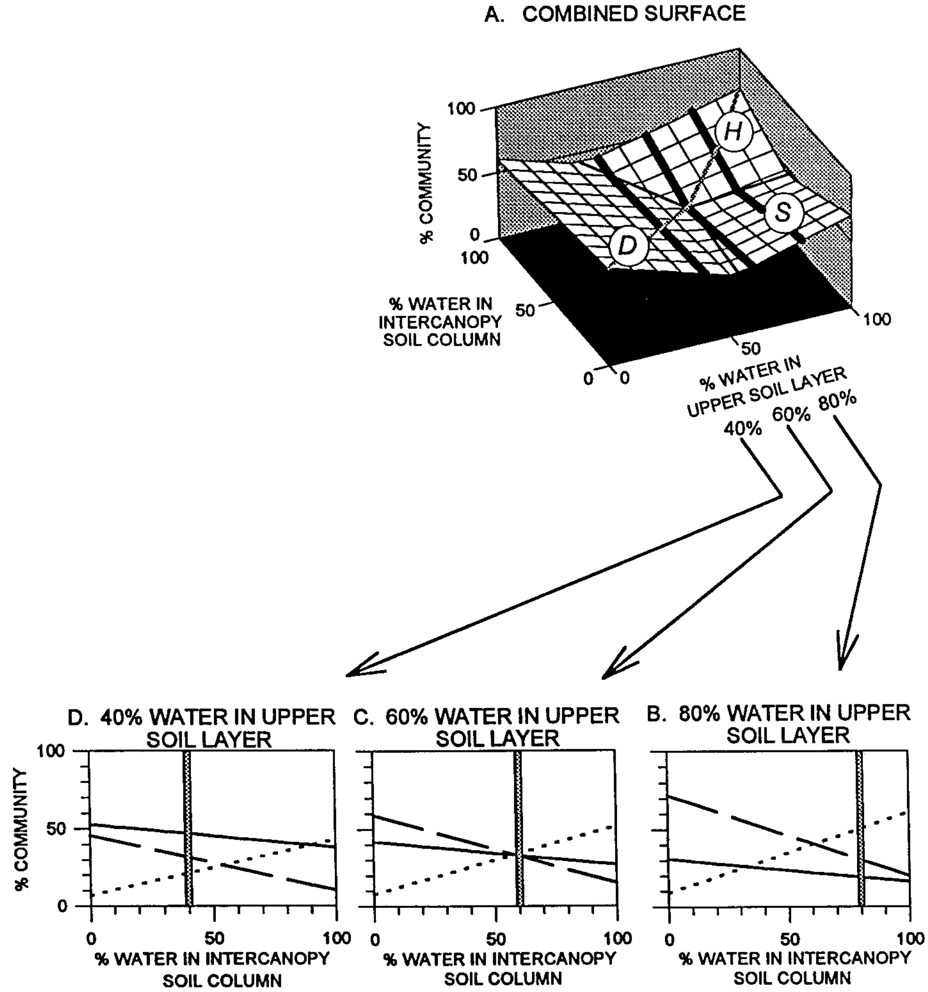

Figure 4. Model predictions for percent of community biomass for three plant types based on location of soil moisture (A). Cross sections are presented where the amount of soil moisture in the upper layer is held constant at (B) 40%, (C) 60%, and (D) 80%. The black bar in each cross section indicates where the cross section intersects the diagonal (shown in A) where the percent of water in the upper soil compartment equals the percent of water in the intercanopy soil column. Paramer values are as presented in Table 1.

intensive range management: thinning of the woody vegetation and application of the thinned material as a mulch increases the ground cover on the intercanopy patches, reducing soil temperature (and thereby soil evaporation rates – Breshears et al. 1998) as well as runoff (Wischmeier and Smith 1978). Such manipulation has been used successfully to reestablish herbaceous cover in eroding semiarid piñon-juniper woodlands (Chong 1994), but is very labor-intensive. The simultaneous reduction of woody biomass and increases in the proportion of plant-available water in intercanopy patches produces a vector leading back towards the center diagonal of the predicted response surface (i.e., in the opposite direction of the arrow in Figure 5).

Our model, then, is consistent with the concept that the effects of land degradation in semiarid landscapes are not directly reversible (Schlesinger et al. 1990; IPCC 1996b) – that is, they are not reversed without intensive management intervention. Further, it is consistent with the hypotheses of other researchers, that the changes in the proportions of herbaceous and woody plants observed in semiarid ecosystems are best described by complex behavior (e.g., catastrophe theory: Clary and Jensen 1981; Jameson 1987; Gosz and Sharpe 1989; Lockwood and Lockwood 1993; Tausch et al. 1993).

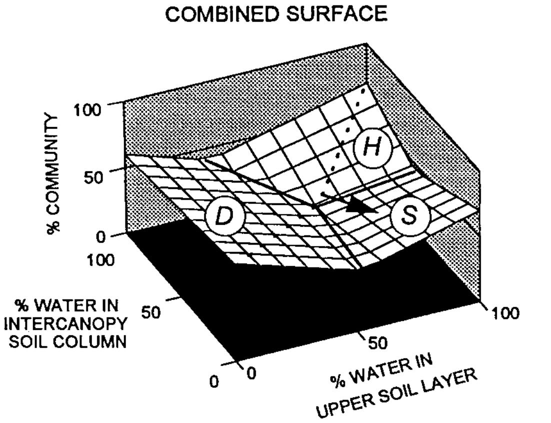

Figure 5. Model predictions for percent of community biomass for three plant types based on location of soil moisture: the trajectory is for loss of herbaceous biomass and decrease in the relative proportion of intercanopy soil moisture (moving away from the diagonal in the direction of the arrow), and, in reverse, is for remediation producing a reduction in woody biomass and an increase in the relative proportion of intercanopy soil moisture, producing an increase in herbaceous biomass.

Discussion

By modifying the two-layer hypothesis to include four soil compartments and distinguishing between shallow- and deeper-rooted woody species, our model integrates three key concepts in semiarid ecology: (1) the proportion of woody cover increases as moisture in the deeper soil layers increases (Walter's two-layer hypothesis for coexistence of herbaceous and woody plants); (2) land use practices that cause a reduction in herbaceous vegetation and compaction of intercanopy soils lead to a long-term increase in the proportion of woody plants (Schlesinger et al.'s concept, or more generally, that multiple variations are possible in the proportions of herbaceous and woody plant biomass at a given site); and (3) changes in the ratios of herbaceous to woody plant biomass exhibit complex behavior (changes can happen quickly and are not directly reversible). This integration of concepts results because rather than assuming a simple, one-way dependence of plant functional types on soil-moisture heterogeneity, our model assumes an interdependence between the two: soil moisture heterogeneity constrains the composition of the plant community, which in turn modifies soil moisture heterogeneity.

Our four-compartment model is, of course, a simplification with respect to soil moisture heterogeneity and variation in plant types. Even so, because it can encompass the more complex behavior documented in recent studies of semiarid ecosystems (behavior consistent with the conceptual models of both Walter and Schlesinger et al.), it is a useful tool (1) for comparing plant functional types across sites, (2) for identifying the different plant community compositions that are possible at a given site (as well as assessing if a shift in composition is readily reversible), and (3) generating testable hypotheses about the relative roles of horizontal and vertical heterogeneity in determining plant community composition.

Our model is also relevant to assessments of the effects of climate change. Horizontal heterogeneity in soil moisture results from differences between canopy and intercanopy patches in interception, runoff, evaporation, and plant water use (Breshears et al. 1997b, 1998), all of which are dependent on climate. Hence, climate changes are expected to alter the horizontal as well as the vertical heterogeneity in soil moisture. Our conceptual model provides a means for considering the interrelationships of these changes in soil moisture heterogeneity with plant community composition.

Heterogeneity in soil moisture, of course, is not the sole factor that determines the distribution of plant types in semiarid regions. Other important factors include nutrients, (Clary and Jensen 1981; Medina 1987; Belsky 1990; Scholes and Walker 1993), fire (Walker 1987; Belsky 1990; Barton 1993; Jeltsch et al. 1996), and grazing (Scholes and Walker 1993; McPherson 1997; Scholes and Archer 1997). In addition, differences among plant functional types in germination and establishment rates (Coffin and Lauenroth 1990) and differences in physiological response to changes in CO_2 (IPCC 1996a) can alter the ratio of herbaceous to woody vegetation. Nonetheless, plant functional types in semiarid ecosystems are largely affected by the distribution of plant available water. Our model provides a conceptual framework for the underlying interrelationships between soil moisture heterogeneity and plant community composition. It can be used as a basis for developing more predictive models of the interrelationships between hydrologic processes and vegetation dynamics across semiarid landscapes.

In summary, the four-compartment model that we propose enables, for the first time, an integrated picture of both dimensions of soil moisture heterogeneity – horizontal and vertical – and of the interdependence between soil moisture heterogeneity and the proportions of the plant functional types that make up a given plant community. This unified conceptual model can be applied to provide insight into the individual and the combined effects of climate and land use on semiarid plant communities within the grassland/forest continuum.

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