The grassland–forest continuum: trends in ecosystem properties for woody plant mosaics?

David D Breshears

Many ecosystems can be viewed as lying within a continuum between grassland and forest, where ground coverage by woody plants (trees and shrubs) ranges from non-existent to complete. Patterns of energy, water, and biogeochemistry are often heterogeneous between canopy patches beneath woody plants and the intercanopy patches that separate them. Notably, connectivity between patch types is produced by processes such as shading, root uptake of resources, and redistribution of runoff. Patch-scale connectivity is hypothesized to influence trends in energy, water, and biogeochemistry as a function of woody plant canopy coverage. When connectivity is strong, the mean for an ecosystem property is expected to change in a more curvilinear than linear fashion along the continuum. Associated variance is expected to be greatest not midway along the continuum, as might be expected, but rather at a site with substantially less than 50% canopy coverage. These hypotheses collectively provide a framework for future research and are directly applicable to numerous, seemingly disparate environmental issues associated with encroachment, xerification (desertification), deforestation, die-off, fire, and restoration.

Front Ecol Environ 2006; 4(2): 96–104

From an airplane, we often look out the window and survey the landscape as we begin our final descent. As we get closer to the ground, our focus changes from an initial broad survey of the topography to an increasingly detailed picture of vegetation patterns. Perhaps the first thing we notice is the extent to which the land is covered by trees or shrubs (Figure 1). If the location is devoid of woody plants, we might be landing in a grassland, and if it is completely covered by trees, we are landing amidst forest with a closed canopy. These two states represent the extremes of a continuum of coverage by woody plants (Belsky and Canham 1994; Breshears and Barnes 1999). Much of the terrestrial biosphere has an intermediate level of coverage by woody plants and therefore lies between the two extremes – within a "grassland–forest continuum" (Figure 2). Examples of such systems include savannas, shrublands, and woodlands, as well as grasslands with a few woody plants, and forests with nearly complete canopy closure. Each of these types is fundamentally differentiated on the basis of coverage by woody plants, even though the percentages of canopy coverage used to distinguish them are highly variable (Anderson *et al.* 1999).

The amount of coverage, as well as the associated stature and spatial patterns seen in the woody plants, forms a mosaic within an ecosystem. This woody plant mosaic not only represents a first-order descriptor of major vegetation types, but is also a fundamental determinant of many key ecosystem processes and associated abiotic patterns (Scholes and Archer 1997; Aguiar and Sala 1999; Martens *et al.* 2000; Sankaran *et al.* 2005). It is well known that woody plants modify the environment beneath them – the canopy patches – quite dramatically. They intercept incoming precipitation and solar radiation, thereby creating patterns that are heterogeneous between the canopy patches and the adjacent intercanopy patches. Because woody plants have major effects on the ecosystem properties of the patches beneath their canopies, and because these effects can provide feedbacks to woody and herbaceous plants (Scholes and Archer 1997; Breshears and Barnes 1999), it is important to understand and quantify these effects for individual sites as well as for sites along the grassland–forest continuum.

Understanding trends in ecosystem properties along the grassland–forest continuum is not simply of esoteric interest, but rather is highly applicable to a diverse and apparently disparate set of environmental issues (Figure 2). For

In a nutshell:

- Many terrestrial ecosystems lie within a continuum between grassland and forest
- Ecosystem properties along the continuum are thought to depend on differences and connections between patches that are beneath woody plants and patches that are not
- Diverse environmental problems such as woody plant encroachment, deforestation, and restoration require an improved understanding of ecosystem properties along the grassland–forest continuum

School of Natural Resources, Institute for the Study of Planet Earth, and Department of Ecology and Evolutionary Biology, 1311 E Fourth Street, Biosciences East 325, University of Arizona, Tucson, AZ 85721–0043 (daveb@email.arizona.edu)

 © The Ecological Society of America

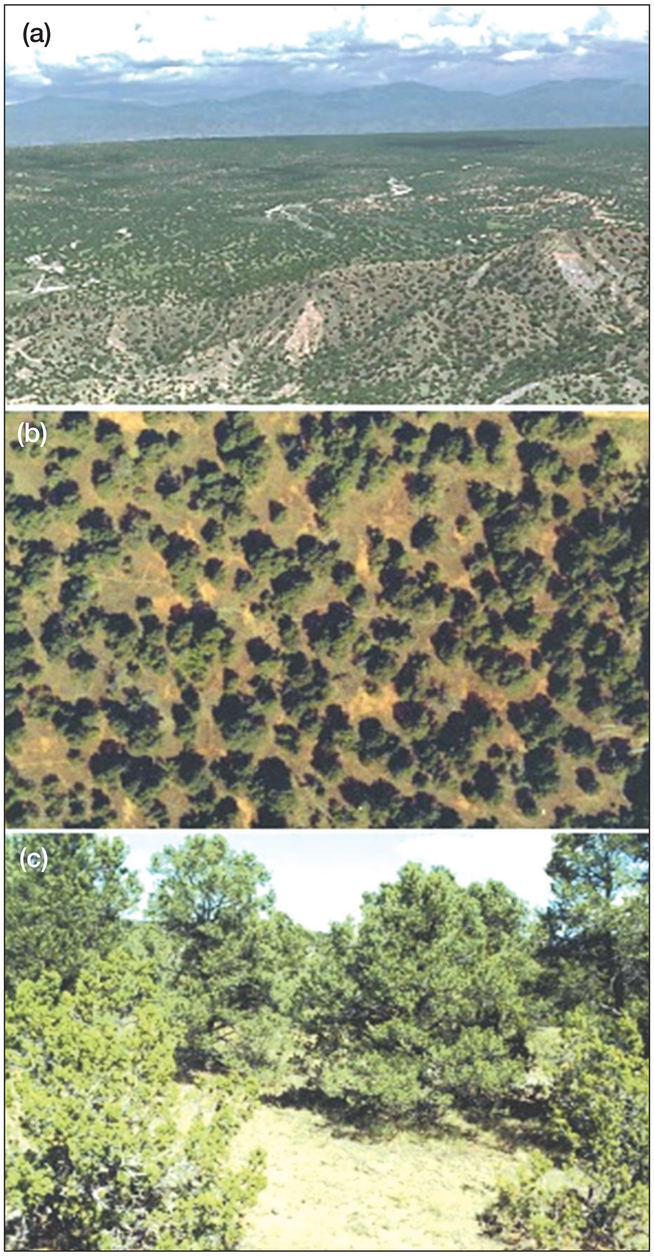

Figure 1. Mosaic patterns of canopy and intercanopy patches in piñon–juniper woodlands from (a) afar, across topographic gradients; (b) directly overhead; and (c) within a woodland.

example, woody plant encroachment, forest die-off, fire management, and associated restoration all require an understanding of how changes in the relative proportion of woody plants influences key ecological processes (Archer and Stokes 2000; Van Auken 2000; Allen *et al.* 2002; Breshears *et al.* 2005). Addressing these issues requires a better understanding of how ecosystem properties related to energy, water, and biogeochemistry vary as a function of woody plant coverage.

Many studies have focused on how differences among sites and along gradients within the grassland–forest continuum result from interactions between climatic, ecological, and management factors (Walter 1971; House *et al.* 2003; Sankaran *et al.* 2004, 2005). These studies highlight the need for caution when generalizing across different ecosystem types. Nonetheless, many of the effects of woody plants on the patches beneath them result from fundamental physical processes, such as interception of light and precipitation (McPherson 1997; Scholes and Archer 1997). Previous efforts to differentiate between diverse systems within gradients of woody vegetation may have caused researchers to overlook the similarities between them (Belsky and Canham 1994; Breshears and Barnes 1999; House *et al.* 2003; see also Lauenroth *et al.* 1993). General insights about ecological properties along the grassland–forest continuum have been hampered by the narrow scope of most field studies, which usually focus on a single site (House *et al.* 2003).

A few recent papers have explicitly or implicitly developed synthetic hypotheses about how key ecosystem attributes related to energy, water, and biogeochemistry vary systematically with increasing woody plant coverage (Klopatek *et al.* 1998; Breshears and Barnes 1999; Martens *et al.* 2000; Muñoz-Erickson *et al.* 2004; Huxman *et al.* 2005). These hypotheses have yet to be integrated with one another. They share a focus on the fundamental importance of spatial heterogeneity in determining means and associated variances in ecosystem properties, which is a theme of landscape ecology (Pickett and Cadenasso 1995). Understanding ecological processes in ecosystems within the grassland–forest continuum requires consideration not only of how woody plants modify the areas directly beneath them, but also of the processes that provide modes of connectivity between canopy and intercanopy patches. For example, trees shade the areas around them, not just beneath them, and can obtain belowground resources from adjacent intercanopy patches through root uptake. Although modes of connectivity between canopy and intercanopy patches are generally recognized, their importance in determining ecosystem properties along the grassland–forest continuum has been underappreciated.

Can scientists, land managers, and policy makers gain useful insights by focusing on the general effects of woody plants on ecological properties at individual sites, as well as in the broader context of gradients of increasing coverage? This paper provides an overview of the many types of ecosystems and vegetation gradients that can be encompassed within the general perspective of the "grassland–forest continuum", focusing on how trends in ecosystem properties, both within and among sites, result from the patch-scale heterogeneity and connectivity associated with woody plants. Key ecosystem properties related to energy, water, and biogeochemistry that differ between canopy and intercanopy patches are summarized, as are modes of connectivity between the two patch types. Based on recent field studies, model simulations, and proposed conceptual models, the effects of canopy–intercanopy heterogeneity and connectivity along these gradients are suggested, with a particular focus on the effects of patch-scale connectivity.

Examples presented here focus on piñon–juniper ecosystems, which are particularly well characterized with

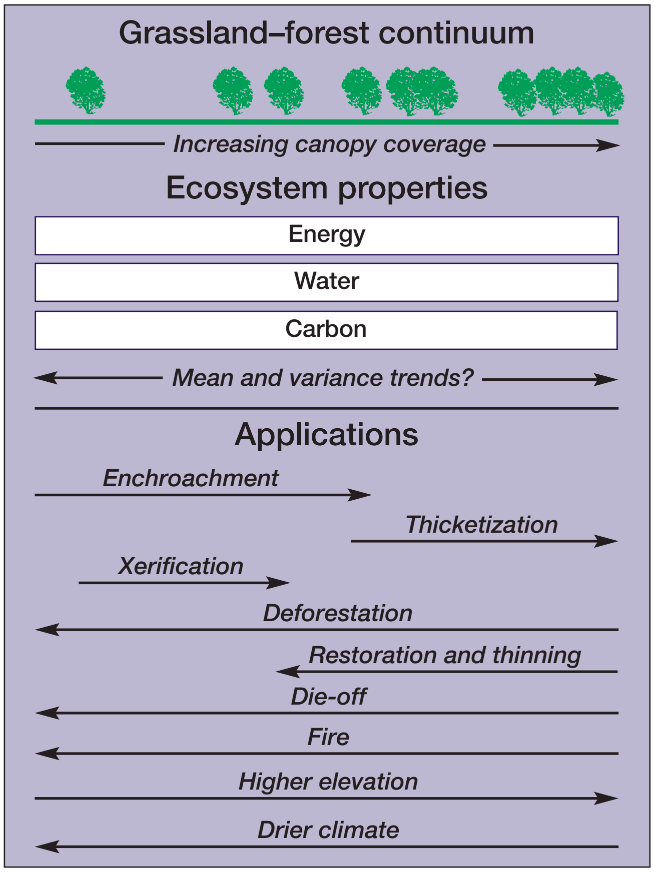

Figure 2. *Ecosystem properties for which trends in mean and variance are needed as a function of canopy coverage along the grassland–forest continuum. Insights gained from studies along the grassland–forest continuum are needed for a variety of ecological applications, as highlighted by the lower set of arrows.*

respect to canopy–intercanopy properties, especially at the Mesita del Buey piñon–juniper woodland in northern New Mexico. Piñon–juniper woodlands are also regionally extensive (McPherson 1997; Anderson *et al.* 1999) and are sensitive to the effects of both climate (Betancourt *et al.* 1990; Breshears *et al.* 2005) and land management (McPherson 1997; Davenport *et al.* 1998; Anderson *et al.* 1999). Additional important ecosystem patterns and processes can occur at finer scales of spatial heterogeneity (Wilcox and Breshears 1995), such as bare versus vegetated patches within intercanopies (eg Wilcox *et al.* 2003a) or bare soil locations as opposed to those covered with biotic soil crust (Loik *et al.* 2004; Belnap *et al.* 2005). However, this finer-scale heterogeneity is often less important than woody plant canopy–intercanopy heterogeneity and is beyond the scope of this paper. The general trends discussed here highlight the importance of patch-scale connectivity and the potential for nonlinear changes in ecosystem properties as a function of changes in woody plant coverage. These trends are applicable to numerous, seemingly disparate environmental issues associated with encroachment, xerification (sometimes referred to as desertification), deforestation, die-off, fire, and restoration, all of which are related to the amount of woody plant coverage at a site.

The grassland–forest continuum defined

The grassland–forest continuum is a simple framework for viewing ecosystems as gradients of increasing coverage by woody plants (Belsky and Canham 1994; Breshears and Barnes 1999; Martens *et al.* 2000; House *et al.* 2003). Numerous factors determine ecosystem properties at sites with varying levels of canopy coverage. Focusing on how trees modify the patches beneath their canopies relative to the intercanopy patches that separate them may yield important but previously overlooked trends in ecosystem properties. Ecosystem types that can be placed within the framework of the grassland–forest continuum include not only shrublands, woodlands, and savannas, but also systems with banded or striped patterns of vegetation, as well as grasslands with some woody vegetation and forests with a few canopy gaps.

The grassland–forest continuum encompasses several types of ecological gradient. The first is a climatic gradient, in which precipitation, temperature, and associated evaporative requirements vary among sites (eg Kerkhoff *et al.* 2004). One particularly common and important form of climatic gradient is an elevational gradient, in which major elevation changes over short distances produce climatic gradients, with associated effects on vegetation (eg Whittaker and Niering 1975; Padien and Lajtha 1992; Klopatek *et al.* 1998; Martens *et al.* 2001). Another type is known as an establishment gradient, where woody plants are establishing within a grassland, sometimes referred to as "encroachment", or are increasing in coverage in a savanna or woodland, sometimes referred to as "thicketization" (Archer *et al.* 1988, 2001; Archer and Stokes 2000; Van Auken 2000). The most dramatic of these types of gradients is a sharp boundary at a grassland–forest edge, producing a discrete change from grassland to forest (eg an old field that has re-established grasses and is adjacent to a closed-canopy forest; Longman and Jenik 1992; Bonan 2002). As discussed below, many site-specific changes associated with disturbance or management can also be viewed within the context of the grassland–forest continuum.

Canopy versus intercanopy: patch-scale heterogeneity

The physical and biological effects of woody plant canopies on the environment can create substantial heterogeneity in several ecological properties between canopy and intercanopy patches (Figure 1c). Differences between these two patch types occur in key aspects of energy, water, and biogeochemistry (Veetas 1992; McPherson 1997; Scholes and Archer 1997). Canopy patches usually have more biomass and a higher leaf-area index than adjacent intercanopy patches. Consequently, incoming solar radiation and precipitation are subject to direct physical effects. In addition, the greater biomass associated with canopy patches generates greater amounts of litter beneath the woody plant. These direct effects can lead to several indirect effects also related to energy, water,

 © The Ecological Society of America

or biogeochemistry. For example, at the Mesita del Buey woodland, energy inputs of near-ground solar radiation were 40% lower beneath woody canopies than in adjacent intercanopy patches (Figure 3). Corresponding soil temperatures were as much as 10°C lower beneath woody canopies, which can substantially reduce soil evaporation (Breshears *et al.* 1998). Similarly, precipitation inputs are substantially reduced as a result of interception by the canopy (Wilcox *et al.* 2003b), which can lead to differences in runoff and associated erosion. In the Mesita del Buey piñon–juniper woodland, intercanopy patches generated approximately an order of magnitude more runoff and roughly 17 times more erosion than canopy patches. This difference is also due, in part, to the higher infiltration rates of soils under canopy patches (Reid *et al.* 1999; Wilcox *et al.* 2003a,c). The greater aboveground biomass and litter inputs associated with canopies are also associated with belowground biogeochemical properties. At the Mesita del Buey woodland, canopy patches had more belowground root mass and soil carbon (Davenport *et al.* 1996) and faster rates of nitrification and mineralization (Padien and Lajtha 1992).

The differences between canopy and intercanopy patches related to incoming water, light, and soil properties (eg organic content) can act collectively to produce patch-scale differences in the amount of water available to plants. This is reflected in measures of soil water potential (Figure 3; more negative values indicate that water is more difficult to obtain). The amount of water available to plants is a key driver of ecological processes in many of the water-limited ecosystems that lie within the grassland–forest continuum (Dawson 1993; Breshears *et al.* 1997a; Tongway *et al.* 2001). At the Mesita del Buey woodland, the difference in soil water potential between canopy and intercanopy patches varies temporally and can be greater in either patch type, depending on recent environmental conditions (Breshears *et al.* 1997b). Horizontal heterogeneity in plant-available water may be as important as the vertical variation in terms of vegetation dynamics (Breshears and Barnes 1999). Additional studies of horizontal heterogeneity in available soil water are therefore required (Loik *et al.* 2004).

■ Patch-scale connectivity

Accounting for the differences between canopy and intercanopy patches may be insufficient when trying to understand, predict, and manage ecosystem dynamics; the ways in which the two patch types are connected must also be taken into account. Some processes provide important modes of connectivity between canopy and intercanopy patches. Thus, abiotic properties are transferred from one patch type to the other or are attenuated by one patch type before they reach the other. These modes of connectivity include shading of intercanopy patches by trees and shrubs, uptake of intercanopy resources by these plants, and redistribution of runoff and associated nutrients from one patch type to the other, most commonly from inter-

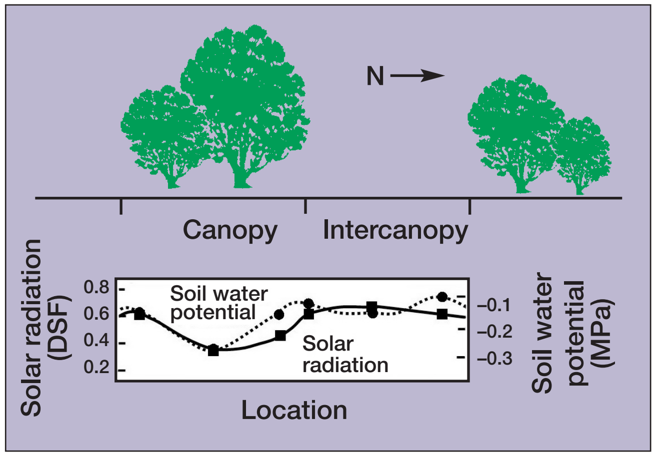

Figure 3. *Patch-scale heterogeneity in near-ground solar radiation and soil water potential within a piñon–juniper woodland (modified from Breshears* et al. *1997b). Near-ground solar radiation is estimated as a direct site factor (DSF), the fraction of annual solar radiation that could potentially reach 1 m above the ground. Soil water potential is estimated from 3 years of soil water content data. More negative values indicate that soil water is less available to plants.*

canopy to canopy patches (Figure 4). Shading represents connectivity as a result of attenuation, whereas both redistribution of runoff and plant root uptake of resources represent connectivity resulting from the transfer of resources from one patch type to another.

For energy, woody canopies shade adjacent intercanopy patches; the degree of shading depends on factors such as sun angle, leaf area, and, particularly, density and height of woody plants (Martens *et al.* 2000). Therefore, the distribution of near-ground energy (ie beneath the canopy, just above the ground surface), which is an important driver of ecosystem processes, requires an understanding and quantification of how canopy and intercanopy patches differ in near-ground solar radiation, as well as how canopy patches shade intercanopy patches. At the Mesita del Buey woodland, which has roughly 50% canopy coverage, intercanopy patches receive about three times more near-ground (below-canopy) solar radiation than canopy patches. However, intercanopy patches still receive only about 60% of the potential amount of radiation because of shading by tree canopies (Martens *et al.* 2000).

Uptake of intercanopy resources by woody plants is another mode of patch-scale connectivity. Woody plants often obtain resources in adjacent intercanopy patches, while the converse seems to occur to a much lesser extent (Schenk and Jackson 2002). At the Mesita del Buey woodland, trees are able to obtain shallow soil moisture from 0–30 cm depths in adjacent intercanopy patches (Breshears *et al.* 1997a). This may be particularly important when there is a high level of patch-scale heterogeneity of a limiting resource such as water (Breshears and Barnes 1999; Loik *et al.* 2004).

Redistribution of runoff from intercanopy to canopy patches is clearly important in some systems, perhaps most

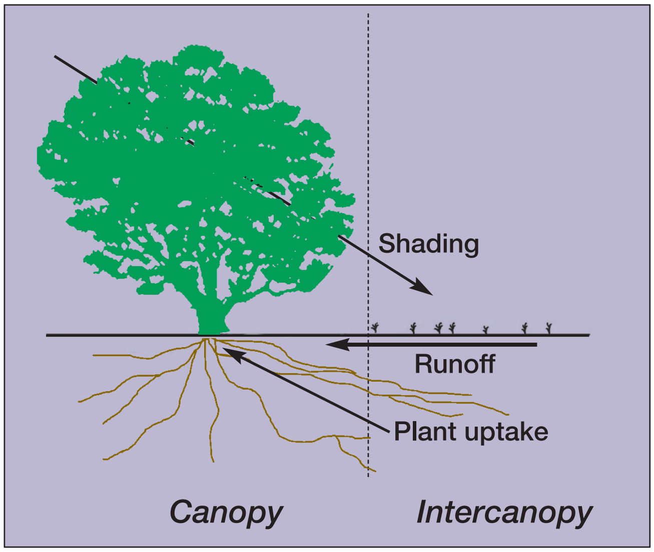

***Figure 4.** Heterogeneous patch types of canopy (beneath the canopy of a woody plant) and intercanopy (between woody plants) and processes that represent connectivity between patches (arrows): shading of adjacent intercanopy patches by woody plant canopies; redistribution of runoff, often from intercanopy to canopy patches; and uptake of resources from intercanopy patches by woody plant roots*

dramatically in ecosystems with low slopes and banded or striped vegetation patterns (Tongway *et al.* 2001). In the Mesita del Buey woodland, redistribution of runoff appears to occur largely within intercanopy patches from bare to grassy locations, rather than from intercanopy to canopy patches (Wilcox *et al.* 2003a). Understanding runoff connectivity is important for evaluating the amount of water leaving an area and the amount that is reconcentrated and stored within it (Wilcox *et al.* 2003a).

■ Gradients of woody vegetation

Both patch-scale heterogeneity and connectivity need to be considered in concert when assessing trends in the properties of energy, water, and biogeochemistry along gradients associated with the grassland–forest continuum. Several hypotheses related to such gradients have recently been proposed, explicitly or implicitly, for mean and variance in properties across sites. Trends in incoming energy as a function of canopy coverage may be most generalizable. Recent model simulations along a gradient that included the Mesita del Buey woodland provide a basis for generating broad hypotheses (Martens *et al.* 2000). These simulations show that an increase in the percentage area covered by woody plants of as little as 20% can produce dramatic changes in the distribution of near-ground, incoming solar radiation (Figure 5). Changes in the distribution of near-ground incoming solar radiation can be particularly large and nonlinear for intercanopy patches. For example, at 21% tree coverage, more than a third of the total area is unaffected by the trees and receives the maximum amount of incoming solar radiation, whereas at 43%, all of the area is shaded to some degree by the trees, even though 57% of the area is still categorized as intercanopy (Figure 5). The mean near-ground solar radiation should decrease in a predominantly linear fashion with increasing coverage, assuming that the height of the woody plants remains constant (Figure 6). Taller woody plants produce more intercanopy shading, which represents stronger connectivity between patch types. Mean near-ground solar radiation changes in a more curvilinear manner as canopy coverage increases if the woody plants are consistently taller. If the woody plants change in height over the gradient – as is common for an elevational gradient (in which height often increases with woody plant density; Martens *et al.* 2000) – then mean near-ground solar radiation decreases more rapidly and in a curvilinear fashion as coverage increases. Plot-scale variance in near-ground, incoming solar radiation peaks at an intermediate value of canopy coverage that is substantially less than 50%. The

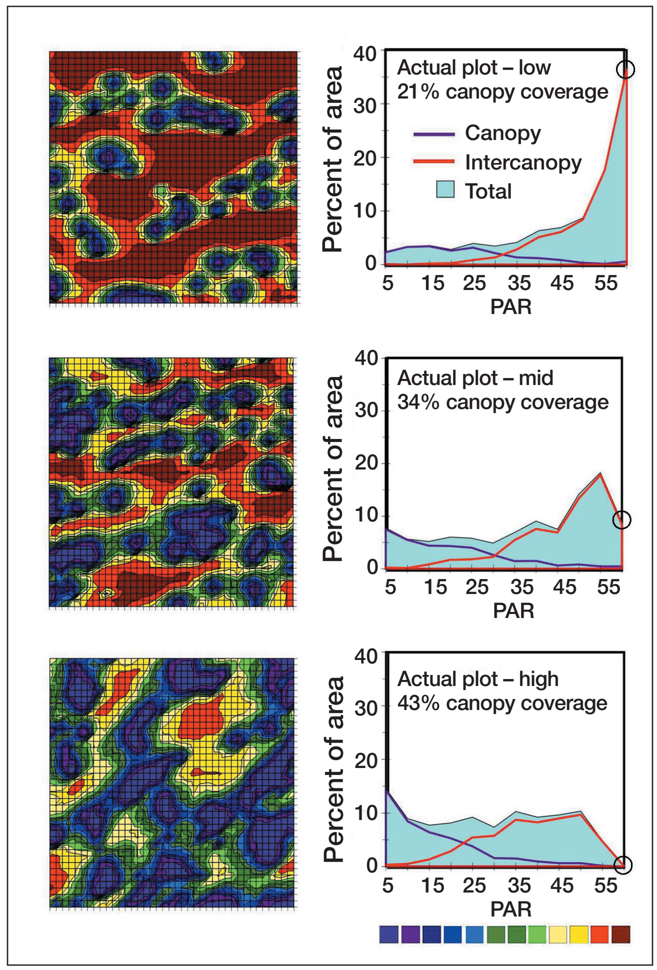

***Figure 5.** Patterns of normalized, near-ground solar radiation below woody plant canopies for plots (40 x 40 m) with varying amounts of canopy coverage (left panel) and associated histograms for canopy and intercanopy locations (right panel; index is mean photosynthetically active radiation [PAR] for April 1 – October 31 in mol m^{-2} normalized to a daily basis). Circles in right panels indicate percent of area that is unaffected by shading from woody plants. (Modified from Martens* et al. *2000.)*

 © The Ecological Society of America

coverage value at which peak variance occurs is highly dependent on the height of the woody plants, with taller plants shifting the peak to lower values of coverage (Figure 6). More generally, as woody plants of a particular shape become taller (retaining the same foliar density), the patch-scale connectivity due to shading increases and peak variance for a plot shifts to a lower value of coverage (Figure 7).

Trends in ecosystem properties associated with water budget or biogeochemical patterns along the grassland–forest continuum are more complicated than those for incoming energy alone. Nonetheless, some trends can be hypothesized, based on canopy–intercanopy patterns of heterogeneity and connectivity (Figure 7). In most systems, the vast majority of the water budget leaves via evapotranspiration – more than 95% in most water-limited ecosystems (Wilcox *et al.* 2003b). Yet "evapotranspiration" includes both the evaporative portion that was not used directly by biota and the transpiration portion that was. Therefore, the partitioning of evapotranspiration into transpiration and evaporation may be more important than the total amount of evapotranspiration in determining ecological–hydrological interrelationships (Loik *et al.* 2004; Huxman *et al.* 2005). Building on recently proposed hypotheses that are consistent with the limited available data (Huxman *et al.* 2005), the ratio of transpiration to total evapotranspiration is expected to vary with coverage. If other factors, such as soil texture and climate, are held constant, the ratio of transpiration to total evapotranspiration is expected to increase with woody plant coverage, due to the increase in leaf area and the reduced soil evaporation resulting from the greater level of shading. As canopy coverage increases, the rate of change in the ratio of transpiration to total evapotranspiration may be particularly sensitive at intermediate levels, due to increased levels of competition among woody plants for resources and reduced inputs of water as a result of interception. Variation in the ratio of transpiration to total evapotranspiration is expected to behave similarly to that for near-ground solar radiation, such that the variance peaks at an intermediate site that has less than 50% coverage (Figure 7). The shifting of the peak to a lower value of coverage is due to patch-scale connectivity associated with uptake of resources within intercanopy patches. These hypotheses, relating the amount of canopy coverage to the ratio of transpiration to total evapotranspiration, are consistent with observations to date but require more rigorous testing.

Biogeochemical patterns for several key properties (eg total ecosystem carbon, C) might also be expected to vary in predictable ways if other factors, such as soils and climate, are held constant (Figure 7). For systems within the grassland–forest continuum, most of the C in the biota is associated with woody plants (eg Pieper 1990). Soil within canopy patches often contains substantially more C than adjacent intercanopy patches, as seen along elevational gradients spanning piñon–juniper woodlands (Klopatek *et al.* 1998). Where this is the case, total ecosystem C would be expected to increase with expanding canopy coverage if other factors are held constant, and even in some cases where they are not. Similar gradients in C trends have been documented in other systems where variations in coverage are associated with encroachment and disturbance history (Reich *et al.* 2001; but see also Archer *et al.* 2001; Jackson *et al.* 2002). Erosional processes, which can affect site biogeochemistry, are also hypothesized to vary systematically along the grassland–forest continuum, with wind-driven erosion and associated transport being considerably greater than water-driven erosion and transport for systems that are intermediate along the continuum (eg shrublands; Breshears *et al.* 2003).

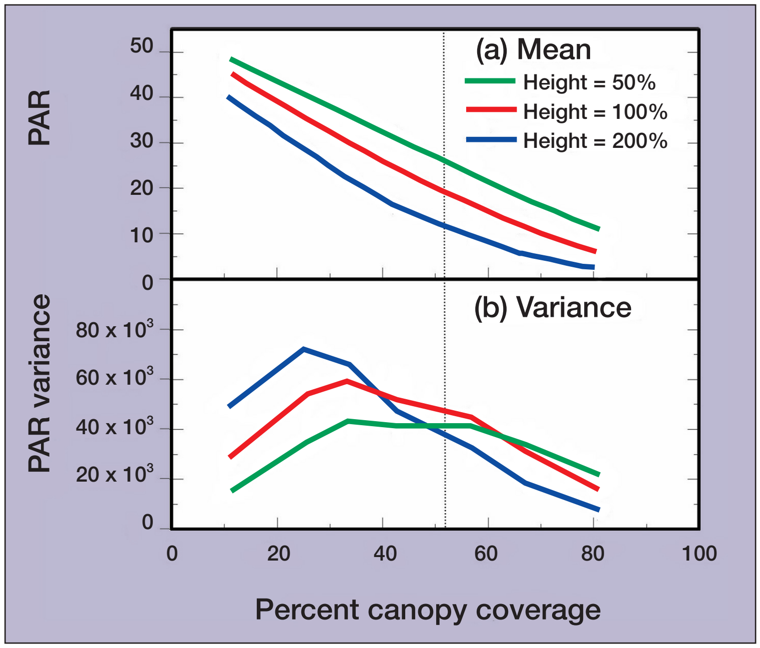

Figure 6. *Patterns of normalized near-ground solar radiation below woody plant canopies of varying coverage, summarized for (a) plot mean and (b) plot variance, for trees of three heights: 100% = mean height of 3.8 m, 200% = 7.6 m, and 50% = 1.9 m actual (foliar density is constant for all three heights; index is mean photosynthetically active radiation [PAR] for April 1 – October 31 in mol m^{-2} normalized to a daily basis. Modified from* Martens et al. *2000).*

The aforementioned gradient-based studies and associated hypotheses, related to energy, water, and biogeochemistry, could collectively represent a more integrated framework of hypotheses about trends along the grassland–forest continuum (Breshears and Barnes 1998; Klopatek *et al.* 1998; Martens *et al.* 2000; Muñoz-Erickson *et al.* 2004; Huxman *et al.* 2005;). The hypothesized trends in gradients collectively suggest that if there is relatively weak connectivity between canopy and intercanopy patches for a given ecological property, the mean values of that property may change relatively linearly with changes in canopy coverage (Figure 8). However, as patch-scale connectivity

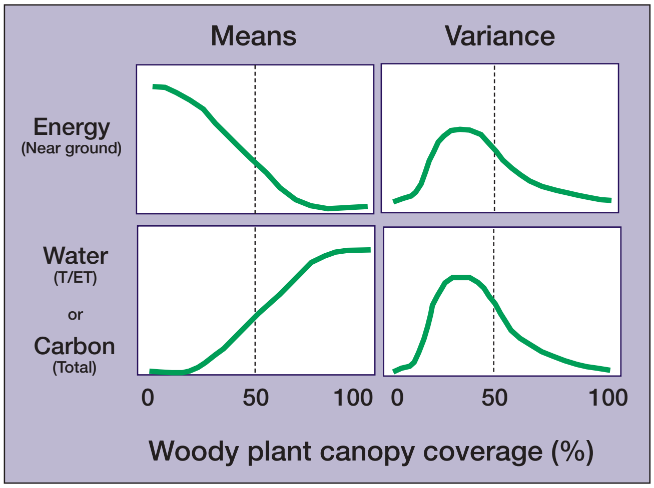

Figure 7. *Hypothesized trends for energy as incoming solar radiation (based on Martens* et al. *2000), transpiration of water as a fraction of total evapotranspiration (building on Huxman* et al. *2005), and biogeochemistry (total carbon) as a function of canopy coverage (building on Klopatek* et al. *1998) for plot means and variances.*

becomes stronger, the relationship between the mean value of the ecosystem property can change more curvilinearly with varying amounts of canopy coverage (Figure 8), as seen in the modeling study of solar radiation (Figure 6).

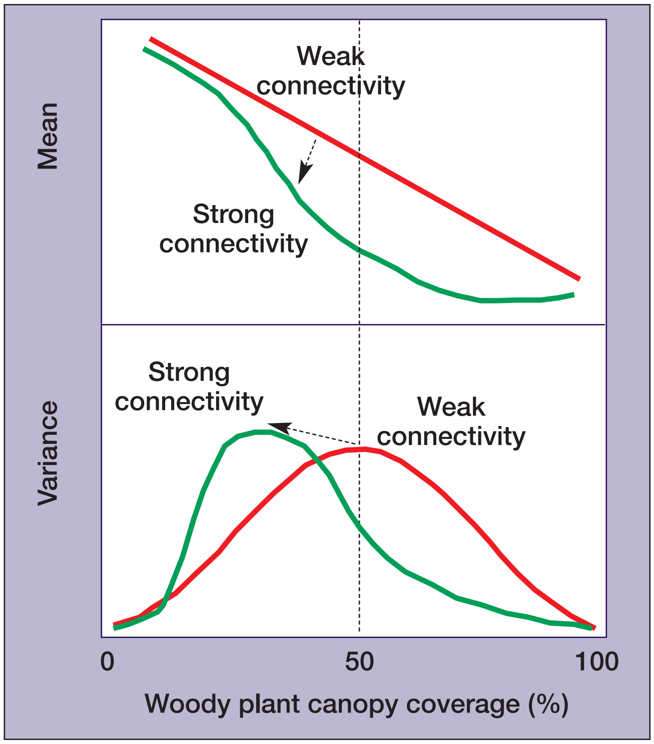

Figure 8. *Patterns of variance along the grassland–forest continuum. For properties with high heterogeneity and weak connectivity, maximal variance occurs midway along the continuum. For properties with strong patch-scale connectivity, the variance shifts away from the middle of the continuum and towards lower values of canopy coverage. The magnitude of the shift is dependent on the degree of patch-scale connectivity.*

Consequently, when connectivity is strong, there may be a greater rate of change in the mean for an ecosystem property along intermediate portions of the continuum compared to that at either end.

Although it seems obvious that spatial variance in ecosystem properties should be greatest at some intermediate value of canopy coverage, these recently proposed hypotheses indicate how maximal variance could occur at a site with substantially less than 50% canopy coverage, if there is strong patch-scale connectivity in that property (Figure 8). If there is no connectivity between patches, then variance should be greatest at 50% canopy coverage; however, as patch-scale connectivity increases, the peak in variance shifts toward lower values of canopy coverage (Figure 8; unless the connectivity becomes so strong that it obliterates patch-scale heterogeneity in that ecological property).

In general, therefore, if other factors are held constant, changes in site means for properties of energy, water, and biogeochemistry for sites along the grassland–forest continuum might be expected to vary curvilinearly with increasing canopy coverage (Figure 7). For example, near-ground solar radiation, an energy metric, should decrease with increasing coverage, whereas the ratio of transpiration to evapotranspiration, a water metric, and total ecosystem C, a biogeochemical metric, should increase with coverage. Variance for all three should peak at a value of canopy coverage of < 50% and is dependent on the strength of patch-scale connectivity for a particular property.

Of course, along many gradients and under many management scenarios, factors other than those considered here can vary, thereby complicating the trends along gradients. Nonetheless, because woody plants modify the environment beneath and around them in physical ways and provide physical as well as biological connectivity between patch types through their root distributions, the relationships between key ecosystem properties and woody plant density may underlie more complex patterns for sites along the grassland–forest continuum. An improved understanding of these relationships may yield important insights for a diverse set of ecosystems and is directly applicable to several environmental issues.

■ Applying the grassland-forest continuum perspective to environmental issues

The observed and hypothesized trends described above have important implications for numerous, disparate environmental issues. An understanding of how the proportion of woody plants at a site affects key ecosystem properties and how this, in turn, affects feedbacks to alter vegetation is key to the assessment, and/or management of many pressing environmental problems (Figure 2). These include encroachment of woody plants into grasslands (Archer *et al.* 1988; Van Auken 2000); xerification (or desertification), wherein arid grasslands transition into shrublands (Archer and Stokes 2000); deforestation, in which canopy coverage is severely and rapidly reduced;

 © The Ecological Society of America

die-off of woody plants triggered by drought (Breshears *et al.* 2005); risk of fire and subsequent hydrological changes (Johansen *et al.* 2001), as well as associated forest thinning practices (Allen *et al.* 2002); and restoration issues associated with several of these problems (Hobbs and Norton 1996). Woody plant encroachment in the southwestern US and northern Mexico has shifted at many sites from low to high coverage over the past 150 years, posing key challenges for managing these systems (Archer and Stokes 2000; Van Auken 2000). Much effort has focused on restoring these sites by reducing tree coverage, but restoration may not be economically or logistically feasible (Van Auken 2000). Deforestation shifts a system towards lower levels of coverage by planned management or less-planned exploitation, whereas drought and fire do so as a result of disturbance. Drought-induced mortality can change canopy structure dramatically in a year or two (Breshears *et al.* 2005). The probability of fire spread in systems that have intermediate coverage is greatly dependent on the connectivity of fuel structure among patches of the same type and between the two patch types (Peters *et al.* 2004). Thinning trees as a management strategy for reducing fire risk also hinges on the central concept of reducing connectivity for fire among tree crowns. Management related to all such environmental issues requires an improved understanding of how key ecosystem properties vary with changes in canopy coverage. In addition, assessments of potential climate change impacts require evaluation of how elevational gradients of vegetation may shift in response to climate (Kerkhoff *et al.* 2004; Breshears *et al.* 2005) and how ecologically related sites in disparate regions might change.

Based on the hypothesized trends (Figure 7), we might expect ecosystem properties for areas with an intermediate proportion of coverage to be among the most sensitive to ecosystem change. In systems with intermediate coverage, not only is the variance high, but there is also a transition in the dominant type of vegetation coverage (eg woody compared to herbaceous vegetation) and in associated ecosystem processes. That is, there are rapid changes in the degree to which patches of one type or the other form dominant, contiguous clusters across the landscape (Milne *et al.* 1996). There is a threshold of intermediate coverage at which a system transforms from domination by contiguous clusters of one patch type to domination by contiguous clusters of the other type. This threshold-like response is related to the connectivity of patches and can be quantified using percolation theory (Milne *et al.* 1996; Davenport *et al.* 1998). Effective management to address the environmental issues mentioned above will need to take these trends into account, particularly noting that variance may be greatest at low values of canopy coverage if patch-scale connectivity is strong.

Conclusions

Despite numerous studies associated with vegetation gradients over the past several decades, few have evaluated large portions of the grassland–forest continuum and asked how variation in woody plant coverage alone might impact different ecosystem properties. The few studies that have focused on this area of research have suggested that variance in an ecosystem property is likely to be greatest at an intermediate level of woody plant coverage, the value of which is dependent on the degree of patch-scale connectivity. Consequently, ecosystem properties are expected to be most sensitive to changes in canopy coverage along the intermediate portion of the continuum (particularly where the value of canopy coverage shows the greatest variance in a particular property). The hypotheses associated with the grassland–forest continuum provide a framework for future research that is directly applicable to a wide range of environmental issues, all of which center on how changes in woody plant coverage affect ecosystem properties.

Acknowledgements

I thank previous collaborators and coauthors and new colleague CB Zou for their contributions to the development of grassland–forest continuum concepts. This synthesis was supported by Los Alamos National Laboratory through Laboratory Directed Research and Development.

References

Aguiar MR and Sala OE. 1999. Patch structure, dynamics, and implications for the functioning of ecosystems. *Trends Ecol Evol* **14**: 273–77.

Allen CD, Savage M, Falk DA, *et al.* 2002. Ecological restoration of Southwestern ponderosa pine ecosystems: a broad perspective. *Ecol Appl* **12**: 1418–33.

Anderson RC, Fralish JS, and Baskin JM (Eds). 1999. Savannas, barrens, and rock outcrop plant communities of North America. Cambridge, UK: Cambridge University Press.

Archer S, Boutton TW, and Hibbard KA. 2001. Trees in grasslands: biogeochemical consequences of woody plant expansion. In: Schulze E-D, Heimann M, Harrison S, *et al.* (Eds). Global biogeochemical cycles in the climate system. San Diego, CA: Academic Press.

Archer S, Scifres CJ, Bassham CR, and Maggio R. 1988. Autogenic succession in a subtropical savanna: conversion of grassland to thorn woodland. *Ecol Monogr* **58**: 111–27.

Archer S and Stokes C. 2000. Stress, disturbance and change in rangeland ecosystems. In: Arnalds O and Archer S (Eds). Rangeland desertification. Boston, MA: Kluwer Academic Publishers.

Belnap J, Welter JR, Grimm NB, *et al.* 2005. Linkages between microbial and hydrologic processes in arid and semiarid watersheds. *Ecology* **86**: 298–307.

Belsky AJ and Canham CD. 1994. Forest gaps and isolated savanna trees. *BioScience* **44**: 77–84.

Betancourt JL, Van Devener TR, and Martin PS (Eds). 1990. Packrat middens: the last 40 000 years of biotic change. Tucson, AZ: University of Arizona Press.

Bonan G. 2002. Ecological climatology. New York, NY: Cambridge University Press.

Breshears DD and Barnes FJ. 1999. Interrelationships between plant functional types and soil moisture heterogeneity for semiarid landscapes within the grassland/forest continuum: a unified conceptual model. *Landscape Ecol* **14**: 465–78.

Breshears DD, Cobb NS, Rich PM, *et al.* 2005. Regional vegetation die-off in response to global-change type-drought. *P Natl Acad Sci USA* **102**: 15144–48.

Breshears DD, Myers OB, Johnson SR, *et al.* 1997a. Differential use of spatially heterogeneous soil moisture by two semiarid woody species: *Pinus edulis* and *Juniperus monosperma*. *J Ecol* **85**: 289–99.

Breshears DD, Nyhan JW, Heil CE, and Wilcox BP. 1998. Effects of woody plants on microclimate in a semiarid woodland: soil temperature and evaporation in canopy and intercanopy patches. *Int J Plant Sci* **159**: 1010–17.

Breshears DD, Rich PM, Barnes FJ, and Campbell K. 1997b. Overstory-imposed heterogeneity in solar radiation and soil moisture in a semiarid woodland. *Ecol Appl* **7**: 1201–15.

Breshears DD, Whicker JJ, Johansen MP, and Pinder III JE. 2003. Wind and water erosion and transport in semiarid shrubland, grassland, and forest ecosystems: quantifying dominance of horizontal wind-driven transport. *Earth Surf Proc Land* **28**: 1189–1209.

Dawson TE. 1993. Woodland water balance. *Trends Ecol Evol* **8**: 120–21.

Davenport DW, Breshears DD, Wilcox BP, and Allen CD. 1998. Viewpoint. Sustainability of piñon–juniper woodlands – a unifying perspective of soil erosion thresholds. *J Range Manage* **51**: 231–40.

Davenport DW, Wilcox BP, and Breshears DD. 1996. Soil morphology of canopy and intercanopy sites in a piñon–juniper woodland. *Soil Sci Soc Am J* **60**: 1881–87.

Hobbs RJ and Norton DA. 1996. Towards a conceptual framework for restoration ecology. *Restor Ecol* **4**: 93–110.

House J, Archer S, Breshears DD, *et al.* 2003. Conundrums in mixed woody–herbaceous plant systems. *J Biogeogr* **30**: 1763–77.

Huxman TE, Wilcox BP, Breshears DD, *et al.* 2005. Woody plant encroachment and the water cycle: an ecohydrological framework. *Ecology* **86**: 308–19.

Jackson RB, Banner JL, Jobbágy EG, *et al.* 2002. Ecosystem carbon loss with woody plant invasion of grasslands. *Nature* **418**: 623–26.

Johansen, MP, Hakonson TE, and Breshears DD. 2001. Post-fire runoff and erosion from rainfall simulation: contrasting forests with shrublands and grasslands. *Hydrol Process* **15**: 2953–65.

Kerkhoff AJ, Martens SN, Shore GA, and Milne BT. 2004. Contingent effects of water balance variation on tree cover density in semiarid woodlands. *Global Ecol Biogeogr* **13**: 237–46.

Klopatek JM, Conant RT, Francis JM, *et al.* 1998. Implications of patterns of carbon pools and fluxes across a semiarid environmental gradient. *Landscape Urban Plan* **39**: 309–17.

Lauenroth WK, Urban DL, Coffin DP, *et al.* 1993. Modeling vegetation structure–ecosystem process interactions across sites and ecosystems. *Ecol Model* **67**: 49–80.

Loik ME, Breshears DD, Lauenroth WK, and Belnap J. 2004. A multi-scale perspective of water pulses in dryland ecosystems: climatology and ecohydrology of the western USA. *Oecologia* **141**: 269–81.

Longman KA and Jenik J. 1992. Forest–savanna boundaries: general considerations. In: Furley PA, Proctor J, and Ratter JA (Eds). Nature and dynamics of forest–savanna boundaries. New York, NY: Chapman and Hall.

Martens SN, Breshears DD, and Barnes FJ. 2001. Development of species dominance along an elevational gradient: population dynamics of *Pinus edulis* and *Juniperus monosperma*. *Int J Plant Sci* **162**: 777–83.

Martens SN, Breshears DD, and Meyer CW. 2000. Spatial distributions of understory light along the grassland/forest continuum: effects of cover, height, and spatial pattern of tree canopies. *Ecol Model* **126**: 79–93.

McPherson GR. 1997. Ecology and management of North American savannas. Tucson, AZ: University of Arizona Press.

Milne BT, Johnson AR, Keitt TH, *et al.* 1996. Detection of critical densities associated with piñon–juniper woodland ecotones. *Ecology* **77**: 805–21.

Muñoz-Erickson TA, Loeser MR, and Aguilar-González BJ. 2004. Identifying indicators of ecosystem health for a semiarid ecosystem: a conceptual approach. In: Van Riper III C and Cole KL (Eds). The Colorado Plateau: cultural, biological, and physical research. Tucson, AZ: University of Arizona Press.

Padien DJ and Lajtha K. 1992. Plant spatial pattern and nutrient distribution in pinyon–juniper woodlands along an elevational gradient in northern New Mexico. *Int J Plant Sci* **153**: 425–33.

Peters DPC, Pielke RA, Bestelmeyer BT, *et al.* 2004. Cross-scale interactions, nonlinearities, and forecasting catastrophic events. *P Natl Acad Sci USA* **101**: 15130–35.

Pickett STA and Cadenasso ML. 1995. Landscape ecology: spatial heterogeneity in ecological systems. *Science* **269**: 331–34.

Pieper RD. 1990. Overstory–understory relations in pinyon–juniper woodlands in New Mexico. *J Range Manage* **43**: 413–15.

Reich PB, Peterson DW, Wedin DA, and Wrage K. 2001. Fire and vegetation effects on productivity and nitrogen cycling across a forest–grassland continuum. *Ecology* **82**: 1703–19.

Reid KD, Wilcox BP, Breshears DD, and MacDonald L. 1999. Runoff and erosion for vegetation patch types in a piñon–juniper woodland. *Soil Sci Soc Am J* **63**: 1869–79.

Sankaran M, Hanan NP, Scholes RJ, *et al.* 2005. Determinants of woody cover in African savannas. *Nature* **438**: doi: 10.1038.

Sankaran M, Ratnam J, and Hanan NP. 2004. Tree–grass coexistence in savannas revisited – insights from an examination of assumptions and mechanisms invoked in existing models. *Ecol Lett* **7**: 480–90.

Schenk HJ and Jackson RB. 2002. Rooting depths, lateral root spreads and below-ground/above-ground allometries of plants in water-limited ecosystems. *J Ecol* **90**: 480–94.

Scholes RJ and Archer SR. 1997. Tree–grass interactions in savannas. *Annu Rev Ecol Syst* **28**: 517–44.

Tongway DJ, Valentin C, and Seghieri J (Eds). 2001. Banded vegetation patterning in arid and semiarid environments: ecological processes and consequences for management. Ecological Studies 149. New York, NY: Springer.

Van Auken OW. 2000. Shrub invasions of North American semiarid grasslands. *Annu Rev Ecol Syst* **31**: 197–215.

Vetaas OR. 1992. Micro-site effects of trees and shrubs in dry savannas. *J Veg Sci* **3**: 337–44

Walter H. 1971. Ecology of tropical and subtropical vegetation. Edinburgh, UK: Oliver and Boyd.

Whittaker RH and Niering WA. 1975. Vegetation of Santa Catalina Mountains, Arizona. 5. Biomass, production, and diversity along the elevation gradient. *Ecology* **56**: 771–90.

Wilcox BP and Breshears DD. 1995. Hydrology and ecology of pinyon–juniper woodlands: conceptual framework and filed studies. In: Shaw DW, Aldon EF, and LoSapio C (Tech Co-ords). Desired future conditions in pinyon–juniper ecosystems. Flagstaff, AZ: USDA Forest Service, Rocky Mountain Forest and Range Experimental Station.

Wilcox BP, Breshears DD, and Allen CD. 2003a. Ecohydrology of a resource-conserving semiarid woodland: effects of scale and disturbance. *Ecol Monogr* **73**: 223–39.

Wilcox BP, Breshears DD, and Seyfried MS. 2003b. Water balance on rangelands. In: Stewart BA and Howell T (Eds). Encyclopedia of water science. New York, NY: Marcel Dekker.

Wilcox BP, Breshears DD, and Turin HJ. 2003c. Hydraulic conductivity in a piñon–juniper woodland: influence of vegetation. *Soil Sci Soc Am J* **67**: 1243–49.

 © The Ecological Society of America