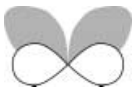
Journal of Biogeography, **30**, 1763–1777



Conundrums in mixed woody–herbaceous plant systems

Joanna I. House[1]*, Steve Archer[2], David D. Breshears[3], Robert J. Scholes[4] and NCEAS Tree–Grass Interactions Participants** [1]*Max Planck Institute of Biogeochemie, Jena, Germany,* [2]*School of Renewable Natural Resources, University of Arizona, Tucson, AZ, USA,* [3]*Earth and Environmental Sciences Division, Los Alamos National Laboratory, Los Alamos, NM, USA, and* [4]*CSIR Forest Science and Technology, Division of Water, Environment and Forest Technology, Ecosystem Management Services Program, Pretoria, South Africa*

Abstract

Aims To identify approaches to improve our understanding of, and predictive capability for, mixed tree–grass systems. Elucidation of the interactions, dynamics and determinants, and identification of robust generalizations that can be broadly applied to tree–grass systems would benefit ecological theory, modelling and land management.

Methods A series of workshops brought together scientific expertise to review theory, data availability, modelling approaches and key questions.

Location Ecosystems characterized by mixtures of herbaceous and woody plant life-forms, often termed 'savannas', range from open grasslands with few woody plants, to woodlands or forests with a grass layer. These ecosystems represent a substantial portion of the terrestrial biosphere, an important wildlife habitat, and a major resource for provision of livestock, fuel wood and other products.

Results Although many concepts and principles developed for grassland and forest systems are relevant to these dual life-form communities, the novel, complex, nonlinear behaviour of mixed tree–grass systems cannot be accounted for by simply studying or modelling woody and herbaceous components independently. A more robust understanding requires addressing three fundamental conundrums: (1) *The 'treeness' conundrum*. What controls the relative abundance of woody and herbaceous plants for a given set of conditions at given site? (2) *The coexistence conundrum*. How do the life-forms interact with each other? Is a given woody–herbaceous ratio dynamically stable and persistent under a particular set of conditions? (3) *The net primary productivity (NPP) conundrum*. How does NPP of the woody vegetation, the herbaceous vegetation, and the total ecosystem (woody + herbaceous) change with changes in the tree–grass ratio? Tests of the theory and conceptual models of determinants of mixed woody–herbaceous systems have been largely site- or region-specific and have seldom been broadly or quantitatively evaluated. Cross-site syntheses based on data and modelling are required to address the conundrums and identify emerging patterns, yet, there are very few data sets for which either biomass or NPP have been quantified for both the woody and the herbaceous components of tree–grass systems. Furthermore, there are few cross-site comparisons spanning the diverse array of woody–herbaceous mixtures. Hence, initial synthesis studies should focus on compiling and standardizing a global data base which could be (1) explored to ascertain if robust generalizations and consistent patterns exist; and (2) used to evaluate the performance of savanna simulation models over a range of woody–herbaceous mixtures. Savanna structure and productivity are the result of complex and dynamic interactions between climate, soils and disturbances, notably fire and herbivory. Such factors are difficult to isolate or experimentally manipulate in order

*Correspondence: Joanna I. House, Max Planck Institute of Biogeochemie, Winzerlaer Strasse 10, 07745 Jena, Germany. E-mail: jo.house@bgc-jena.mpg.de
**NCEAS (National Center for Ecological Analysis and Synthesis) work group on Tree–Grass Interactions: M.B. Coughenour, M.B. Dodd, J. Gignoux, D.O. Hall, N.P. Hanan, R. Joffre, X. Le Roux, J.A. Ludwig, J.-C. Menaut, R. Montes, W.J. Parton, J.J. San Jose, J.C. Scanlan, J.M.O. Scurlock, G. Simioni, B. Thorrold.

to evaluate their impacts at spatial and temporal scales appropriate for assessing ecosystem dynamics. These factors can, however, be evaluated with simulation models. Existing savanna models vary markedly with respect to their conceptual approach, their data requirements and the extent to which they incorporate mechanistic processes. Model intercomparisons can elucidate those approaches most suitable for various research questions and management applications.

Conclusion Theoretical and conceptual advances could be achieved by considering a broad continuum of grass–shrub–tree combinations using data meta-analysis techniques and modelling.

Keyword
Coexistence, competition, facilitation, modelling, primary production, savanna, shrubland, grassland, rangeland, tree–grass ratios.

INTRODUCTION

Ecosystems comprising coexisting herbaceous and woody plants can be viewed as forming a continuum between grasslands with no woody vegetation and forests with nearly complete coverage of woody vegetation (Walker & Noy-Meir, 1982; Belsky & Canham, 1994; Breshears & Barnes, 1999). These systems have been variously referred to as savannas, grasslands, wooded grasslands, shrublands, parklands, bushlands, rangelands and woodlands. Collectively, they represent a substantial portion of the terrestrial biosphere (15–35% depending on classification and inclusion or otherwise of 'grassland' categories: Atjay *et al.*, 1979; De Fries *et al.*, 1995; House & Hall, 2001). They support the majority of the world's livestock and large mammals (White *et al.*, 2000). They are found from hot tropical to cold temperate climates, on a variety of soil types and topography and are subject to major natural and anthropogenic disturbances, in particular fire and herbivory.

Mixed woody–herbaceous systems are diverse, exhibiting differences in the woody plant canopy cover, stature (shrub vs. tree, tall vs. short grass), tree functional form (evergreen vs. deciduous; broad-leaved vs. needle-leaved vs. succulent-leaved; shallow vs. deeply rooted), grass functional form (annual vs. perennial, C3 vs. C4 photosynthetic pathway) and spatial arrangement (random, regular, or clumped trees, bunch vs. rhizomatous grass). The relative abundance of herbaceous and woody plants in these ecosystems can be highly dynamic and change markedly at decadal time-scales (Archer, 1996). Given the high diversity of possible structural combinations, there is little international agreement on how they should be classified and named. For example, the defined upper limit of tree canopy cover of savannas in the published literature ranges from 25% to 80% (Anderson *et al.*, 1999). Inconsistency in classification terminology (Burgess, 1995) and confusion over definitions of terms such as 'savanna' or 'grassland' may have artificially constrained cross-site comparisons and syntheses. A more synthetic and functional understanding might be achieved by examining the broad range of herbaceous–woody assemblages along the grassland–forest continuum. Here we refer to mixed woody–herbaceous systems as 'tree–grass' or 'savanna' systems, where 'tree' is shorthand for woody plants (which vary from fruticose shrubs <2 m tall to arborescents up to 20 m tall, and range from low to high density or canopy cover); and where 'grass' includes grasses, sedges and forbs.

Resource conservation and management is challenging in savannas because of their sensitivity to changes in land use. Land use in savannas is intensifying, and the area modified by human use is becoming more extensive (Young & Solbrig, 1993; IPCC, 1996a). The effects of land use are exacerbated by accelerating changes in climate (Serreze *et al.*, 2000), N-deposition (Köchy & Wilson, 2001), and CO_2 (Houghton *et al.*, 2001). Ecosystem properties and dynamics related to changes in the relative proportions of herbaceous and woody components have profound effects on wildlife habitat (e.g. Norton-Griffiths, 1979; Ben-Shaher, 1992), livestock production (e.g. Fisher, 1977; Higgins *et al.*, 1999), and the hydrological cycle (Hoffman & Jackson, 2000), including potential (but controversial) effects on stream flow and ground water recharge (Hibbert, 1983; Greenwood, 1992; Belsky, 1996) and water-table/soil-salinity relationships (Walker *et al.*, 1993). More recently, recognition of the potential for changes in plant abundance to impact atmospheric chemistry and global climate has added incentive for improving our understanding of herbaceous and woody plant interactions (e.g. Scholes & Bailey, 1996; Guenther *et al.*, 1999; Archer *et al.*, 2001). Indeed, savannas appear to have a higher biodiversity (Solbrig *et al.*, 1996), greater productivity (Long *et al.*, 1989, 1992; Scholes & Hall, 1996) and greater impact on the global carbon cycle (Ojima *et al.*, 1993; Hall *et al.*, 1995; IPCC, 1996a,b; Scholes & Hall, 1996; Walker, 1996; Houghton *et al.*, 1999; Schimel *et al.*, 2000, 2001; Tilman *et al.*, 2000; Pacala *et al.*, 2001) than previously appreciated. Therefore, a realistic representation of these mixed and dynamic systems in global models efforts is urgently required.

A robust understanding of savanna systems has yet to emerge, despite several reviews over the last three decades (Bourliere & Hadley, 1970; Huntley & Walker, 1982; Bourliere, 1983; Sarmiento, 1984; Tothill & Mott, 1985; Cole, 1986; Walker, 1987a; Werner, 1991; McPherson, 1997; Scholes & Archer, 1997; Jeltsch *et al.*, 2000; Mistry, 2000). This may reflect the fact that most studies to date have been small-scale, short-term and site-specific, often measuring either the tree or grass component in isolation, and seldom including belowground biomass or productivity (Scholes & Hall, 1996). This is, perhaps, related to site-specific research and management objectives that often focus on one component (e.g. managing grasses for livestock grazing) or the other (e.g. managing woody plants for fuel or timber). Intensively studied savanna sites exist (e.g. Schlesinger *et al.*, 1990; Pandey & Singh, 1992; Scholes & Walker, 1993; Archer, 1995; Breshears *et al.*, 1997; Goutorbe *et al.*, 1997; Hanan *et al.*, 1998; San José *et al.*, 1998; Abbadie *et al.*, in prep.), but they emphasize different suites of variables and do not include the full range of diversity of structural types and bioclimatic conditions found along the grassland–forest continuum.

Analysis of the full range of tree–grass systems, their interactions, dynamics and determinants, may lead to theoretical and conceptual advances, identifying robust generalizations that can be broadly applied. Alternatively, it may be that the full range of mixed tree–grass systems are not ecologically similar, but that nevertheless it is possible to identify certain savanna types that are functionally alike and to develop conceptual models for each of these. Several conceptual models exist to explain the functioning of savanna systems (e.g. Walker, 1987a; Archer, 1989; Belsky, 1990; Sala *et al.*, 1997; Breshears & Barnes, 1999; Jeltsch *et al.*, 2000). They generally have not been rigorously tested or extensively evaluated, and often ignore fundamental interactions among key driving variables (Fig. 1). Mixed tree–grass systems appear to have nonlinear behaviours with respect to primary production and woody plant abundance (McPherson, 1992) and rates of change in tree cover (Archer *et al.*, 1988; Miller & Wigand, 1994; Milne *et al.*, 1996) that cannot be accounted for by simply treating or modelling tree and grass fractions as independent, autonomous entities. Efforts to evaluate tree–grass dynamics have been hampered by the lack of quantitative models that might provide a means for hypothesis testing, identifying key data and knowledge gaps, and prioritizing research agendas. Models explicitly representing savannas are emerging and show great potential (e.g. McKeon *et al.*, 1990; Coughenour, 1992; Scanlan, 1992; Höchberg *et al.*, 1994; Mauchamp *et al.*, 1994; Ludwig & Marsden, 1995; Thiery *et al.*, 1995; Wiegand *et al.*, 1995, 1997, 1998; Moore *et al.*, 1997; Reynolds & Acock, 1997; Jeltsch *et al.*, 1998; Dunkerley, 1999; Klausmeier, 1999; Gambiza *et al.*, 2000; Higgins *et al.*, 2000; Simioni *et al.*, 2000; Ludwig *et al.*, 2001), but are not yet widely used and have not yet been widely evaluated across a range of savanna types.

Here, we present a research agenda arising from a series of international meetings with the aim of improving understanding of woody–herbaceous interactions and dynamics. Three key questions or conundrums were identified, which, when resolved, should lead to a more robust understanding of, and predictive capability for, tree–grass systems. The conundrums can be addressed through data synthesis activities, cross-site experimental and field studies, and model application, intercomparison and advancement.

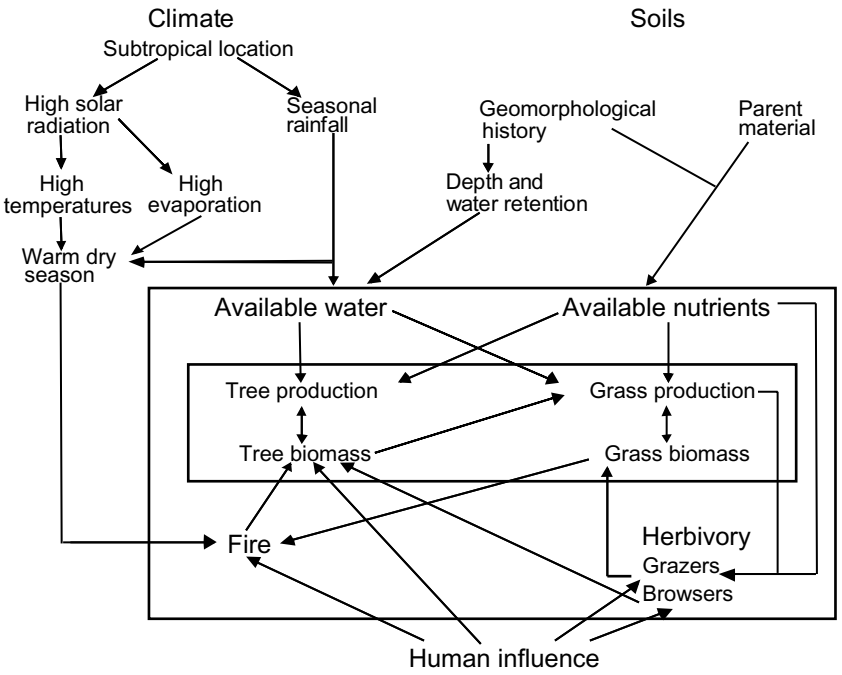


Figure 1 Key driving variables for mixed tree–grass systems. Numerous factors interact to affect the abundance of grasses and woody vegetation in drylands (from Scholes & Walker, 1993). The balance between trees and grasses (innermost level) is affected by determinants of structure and function (water, nutrients, fire and herbivory). The outermost level contains the factors that give the determinants their characteristics.

THREE KEY CONUNDRUMS

The 'treeness' conundrum

What controls the relative abundance of woody and herbaceous plants for a given set of conditions at given site?

Savannas experience a wide range of bioclimatic factors related to water and nutrient availability, herbivory and fire (Fig. 1). It would be useful to identify if a given woody plant abundance and tree–grass ratio can be predicted from a particular set of key determinants, and whether there are ranges or envelopes within which certain life-form mixtures consistently occur. Further, it would be revealing to ascertain the maximum possible woody plant abundance at a given site under, for example, different biophysical conditions or management regimes. There is widespread evidence that the herbaceous plant abundance at a savanna site is strongly controlled by the woody plant abundance, therefore, prediction of the latter could enable prediction of the former.

There are numerous indices for quantifying woody plant abundance in mixed tree–grass systems (hereafter referred to simply as 'treeness'), including leaf area index (LAI), canopy cover, plant density, basal area and biomass. These indices vary with respect to ease and accuracy of measurement. They are often produced by different methodologies (e.g. biomass from allometric relationships between tree basal area and shape, canopy cover from line transects or aerial photography, and LAI from fish-eye photography or satellite imagery), and each provides different representations of functional ecosystem attributes appropriate for different analyses. Use of different indices of treeness across studies has hampered cross-site comparisons. There is a need to (1) improve methodologies for converting between different treeness indices to facilitate cross-site comparisons; and (2) relate readily obtained structural measurements of treeness (e.g. LAI or canopy cover) to system function [photosynthetically active radiation (PAR) absorption, evapostranspiration, net primary productivity (NPP)].

Recent advances in fundamental scaling relationships in biology, as constrained by biophysics, may have important implications for addressing the treeness conundrum (West *et al.*, 1997, 1999; Enquist *et al.*, 1998, 1999a,b). These scaling relationships determine how some properties of biological systems change with size. Of particular relevance here, are predictions of how the number of trees might scale with basal stem diameter (Enquist & Niklas, 2001). The theoretical framework underlying these recent advances describes how variation in population density as a function of organism size (e.g. the thinning law in plant ecology) can be explained in terms of size-based resource utilization by individuals. This would provide the basis for a new approach relating tree–grass ratios to site resource availability.

The coexistence conundrum

How do woody and herbaceous life-forms interact with each other?

Our ability to understand tree–grass ratios and their trends through time is dependent on knowledge of how the contrasting life-forms interact with each other in the context of resource availability and disturbance. There are several corollary questions associated with this conundrum. Is a given tree–grass ratio dynamically stable and persistent under a particular set of conditions? How do the woody and herbaceous components coexist without one becoming dominant? Over what range of bioclimatic conditions does the coexistence phenomenon occur? Explanations of tree–grass interactions fall into four classes of alternative hypotheses that in turn lead to different conceptual models of equilibrium and persistence: niche separation, balanced competition, competitive exclusion and alternate states.

Niche separation If woody and herbaceous plants occupy distinct niches of resource use, a 'characteristic' equilibrium tree–grass ratio should occur at a given site with a given soil and climate (Fig. 2a). Woody and herbaceous plants might

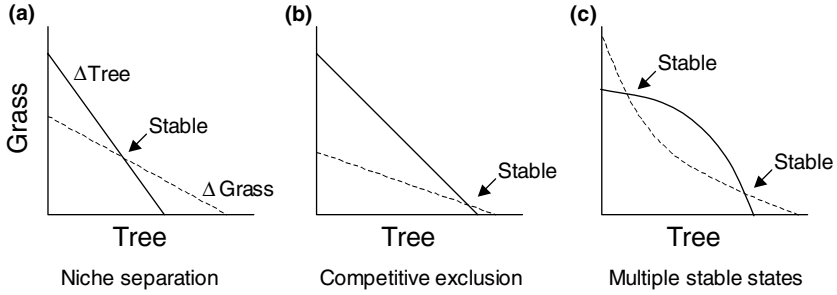


Figure 2 Theories of coexistence of trees and grasses. These figures highlight different theories of the way trees and grasses may coexist (based on Walker & Noy-Meir, 1982). Dashed lines represent the effects of changes in 'treeness' (biomass/NPP/density) on grasses (biomass/NPP); solid lines represent the effects of changes in grasses on trees. In each case the system would tend towards a 'stable' equilibrium point where the lines cross. (a) Niche separation where woody and herbaceous plants use different resources (or balanced competition where intraspecific competition is greater than interspecific competition) would lead to a mixture of trees and grasses. (b) Competitive exclusion where one life-form is more competitive than the other would result in one or the other component monopolizing resources and becoming dominant. (c) It is more likely in nonlinear systems that multiple stable states exist. Different environmental conditions, including disturbances, would result in different slopes of the curves.

coexist by partitioning resources in space, e.g. preferential access to deep soil water by woody plants vs. more effective use of shallow soil water by grasses (e.g. Walter, 1971), or time, e.g. phenological displacement of physiological activity (Sala *et al.*, 1997). To date, spatial partitioning for soil water has been observed in some savanna ecosystems (Knoop & Walker, 1985; Sala *et al.*, 1989; Brown & Archer, 1990; Dodd *et al.*, 1998; Midwood *et al.*, 1998), but such a partitioning is not necessarily a general rule (Scholes & Walker, 1993; Le Roux *et al.*, 1995). Interannual variability may also contribute to coexistence, if factors favouring herbaceous vegetation occur in some years (e.g. frequent small rainfall events, shift to summer rainfall) and factors benefiting woody vegetation occur in other years (e.g. infrequent large rainfall events that give deep recharge, winter rainfall), such that neither life-form maintains a consistent advantage (e.g. Soriano & Sala, 1983; Knoop & Walker, 1985; Lauenroth *et al.*, 1993).

Balanced competition The balanced competition concept argues that woody and herbaceous plants compete for rather than partition resources, and intraspecific competition (e.g. grass-on-grass and tree-on-tree) predominates over interspecific (e.g. tree-on-grass) competition. If the competitively superior life-form becomes self-limiting at a biomass or density insufficient to exclude the competitively inferior life-form, then a stable coexistence could be achieved. The resulting equilibrium tree–grass ratio would vary, depending on soil and climate.

Competitive exclusion Niche separation and balanced competition lead to a *stable equilibrium* that may be 'dynamic' if the determinants of the equilibrium fluctuate. Competitive exclusion, on the other hand, would tend to drive the system away from an *unstable equilibrium*, i.e. the system will tend towards a forest or pure grassland. Competitive exclusion is predicated on the assumption that over time, one life-form sufficiently pre-empts and monopolizes resources so as to virtually eliminate the other (Fig. 2b). Disturbances, which have a greater effect on the competitively superior life-form, may prevent those plants from achieving or maintaining dominance. According to this model, herbaceous vegetation may competitively exclude woody seedlings and reduce their growth rates, thus keeping woody plants in the 'flame zone' and hence more susceptible to fire. The result would be a stable grassland with few woody plants, unless selective grazing for example, reduces the ability of grasses to exclude woody plants. On the other hand, if woody plants are able to out-compete grasses, their establishment would lead to the formation of a shrubland or woodland with little grass, unless disturbance (such as periodic fire) prevented trees from achieving dominance.

Multiple stable states Incorporating spatial and temporal heterogeneity of resource availability and disturbance into equilibrium models leads to the concept of *non-equilibrium dynamics* resulting in *multiple stable states*, whereby contrasting tree–grass ratios might exist for a given site at various times. Changes in resource availability or disturbance would alter life-form interactions and displace the tree–grass ratio from one equilibrium point to another (e.g. Walker & Noy-Meir, 1982; Ellis & Swift, 1988; Archer, 1989; Schlesinger *et al.*, 1990; Skarpe, 1992; Behnke *et al.*, 1993; Sullivan, 1996; Breshears & Barnes, 1999; Miller *et al.*, 2000; Skarpe, 2000) (Fig. 2c). Given the inherent climatic variability and the frequency of disturbances such as fire, grazing and browsing in savannas, a non-equilibrium perspective seems plausible, especially over decadal time frames. The existence of alternate states at decadal time-scales is predicated on the existence of transition thresholds, whereby a given tree–grass configuration may be dynamically stable and persistent over a range of resource availability or disturbance frequency/intensity, then rapidly change to an alternate dynamically stable, persistent state once that range is exceeded (Archer, 1989; Westoby *et al.*, 1989a,b; Friedel, 1991; Laycock, 1991; NRCS, 1994; Breshears & Barnes, 1999; Archer & Stokes, 2000). Once such a transition has occurred, relaxation of the stress, disturbance or environmental conditions that triggered the change will not necessarily enable a return to the previous state (Rapport & Whitford, 1999).

In tree–grass systems, transitions that cross boundaries into other biome types are buffered by mechanisms that prevent the transition to closed woodland or forest (e.g. fire, tree clearing, browsing) and mechanisms that prevent the transition to treeless grassland (e.g. grazing, fire suppression, availability of microsites for tree establishment). Thus, the emphasis switches from mechanisms responsible for promoting a certain state, to those that may prevent transition to other states (Jeltsch *et al.*, 2000). Transitions to alternate states may be accelerated if 'keystone species' establish and alter resource or disturbance regimes (D'Antonio & Vitousek, 1992) or if geophysical forces (e.g. wind, water erosion) initiate positive feedbacks (Schlesinger *et al.*, 1990; Archer & Stokes, 2000). The occurrence of transition thresholds thus leads to the question, 'How far can a given tree–grass mixture be pushed before crossing the line of ecological function that separates it from an alternate configuration?' This question is the essence of the concept of ecosystem resilience.

Each of the conceptual models described above has merit, but none of them on their own can fully account for the observed variety and persistence of tree–grass systems. Interacting factors occurring at various spatial and temporal scales preclude simple models from predicting the outcome of tree–grass interactions (Scholes & Archer, 1997). There is likely to be a combination of niche separation, interspecific competition, intraspecific competition (particularly at the extremes of dominance), buffering mechanisms and changes in climate or disturbance operating simultaneously (Jeltsch *et al.*, 1999). A comprehensive model would ideally incorporate elements of all (e.g. Walker, 1987b; Teague & Smit, 1992) and help prioritize the conditions under which each is most important.

Progress in addressing the coexistence conundrum has been hampered for several reasons:

(1) Most studies have looked at woody and herbaceous components in isolation from each other. The majority of studies have focused on woody plant effects on herbaceous vegetation; relatively few have explicitly examined the direct effects of herbaceous vegetation on woody plants. Of those that have, some suggest herbaceous plants may reduce woody plant resource acquisition (e.g. Caldwell *et al.*, 1987; Sala *et al.*, 1989) and growth (e.g. Knoop & Walker, 1985; Stuart-Hill & Tainton, 1989), and affect woody plant recruitment by adversely affecting seed production (McPherson & Wright, 1987) and seeding establishment (Van Auken, 2000).
(2) Few studies have examined interactions among woody plants, hence we know little of how density-dependent mortality, self-thinning and tree-on-tree competition might regulate woody plant abundance and distribution. Regular woody plant spacing in some systems suggests that intra-life-form competition may be strong, whereas in other systems, woody plants may be highly aggregated, the result of patchy disturbance (Jeltsch *et al.*, 1996, 1999) and neutral or positive tree–tree interactions (e.g. Archer *et al.*, 1988; Höchberg *et al.*, 1994).
(3) It is widely assumed that tree–grass interactions are based either on competition for light, or competition for water. It is entirely consistent with observations, however, that competition (and facilitation) between trees and grasses may be mainly for nutrients (nitrogen in particular) (Fig. 1), with water uptake simply a proxy for nitrogen uptake (Scholes & Hall, 1996). Savanna structure and function may thus be a function of water–nutrient interactions (Medina, 1987; Walker & Langridge, 1997) with co-limitation and the relative importance of nutrients perhaps varying with annual rainfall (Hooper & Johnson, 1999).
(4) Few studies have been sufficiently long-term to capture the important effects of interannual variation in climate and disturbance.

Given the high temporal and spatial heterogeneity, even over short periods and distances, extrapolation based on short-term, patch-scale studies of life-form interactions to the landscape scale over the long-term would probably be erroneous. A given savanna physiognomy, dynamically stable at the landscape scale, may consist of patches in various states of transition between woody and herbaceous dominance (Scholes & Archer, 1997). Savannas may thus exhibit non-equilibrium dynamics over the short-term and small-scale, but maintain some characteristic tree–grass ratio over the long-term and large scales (Jeltsch *et al.*, 1999).

It is imperative that perspectives on the deterministic role of niche separation and competition be evaluated within the broader context of long-term dynamic changes. For example, grasses may competitively suppress tree seedlings and foster conditions conducive to frequent fire that would suppress or eliminate woody plants. When grasses are preferentially grazed, their competitive suppression may be relaxed and fire frequency simultaneously reduced, allowing trees to establish and develop. These woody plants may initially facilitate grass production by improving microclimate and soil and nutrients; however, when tree size/density gets to a certain point, they may negatively affect grasses. In this scenario, life-form interactions proceed from asymmetric competition (grass-on-tree) to facilitation (tree-on-grass) to asymmetric competition in the other direction (tree-on-grass). Disturbances such as fire, grazing and browsing may interrupt this progression and cause it to stall at a certain tree–grass ratio or to revert to another ratio. Climatic and edaphic factors would influence rates and dynamics of transitions among various tree–grass states and constrain the types of tree–grass ratios that might be possible. These structuring forces, which operate over a range of spatial and temporal scales, are not amenable to evaluation via small-scale, short-term field experiments.

The NPP conundrum

How does NPP of the woody plant component, the herbaceous plant component, and the total ecosystem (both components) vary with changes in the tree–grass ratio? This fundamental, unresolved question encompasses a series of corollary questions. Can tree–grass systems be adequately represented with respect to their productivity and influence on soil C and N pools by simply modelling life-forms in a highly aggregated fashion (e.g. 'woody plants' and 'grasses')? Or, must differences among growth forms, functional types or species of woody plants (e.g. conifers vs. broad-leaved deciduous vs. broad-leaved evergreen; N-fixing vs. non-N fixing, shrub vs. tree) and herbaceous groups (e.g. C_3 vs. C_4 grasses) be taken into account? Are woody plants more productive than herbaceous plants when site factors are held equal (substrate, climate, and disturbance)? If so, is this due to greater leaf area, higher photosynthetic rates, greater leaf area duration, better access to soil resources, or more efficient use of resources? How do spatial patterns affect NPP (i.e. does NPP for a given woody plant basal area vary if trees are clumped or dispersed)?

Four contrasting relationships describing NPP in tree–grass systems are presented in Fig. 3. The zero sum models (Fig 3, panel a and b) predict that a change in the NPP of one life-form results in a directly proportional, inverse change in the NPP of the other life-form with no change in whole system NPP. The inverse relationship between herbaceous aboveground NPP and woody plant abundance may be linear (Fig. 3a) or nonlinear (Fig. 3b; Walker *et al.*, 1972; McPherson, 1992). The facilitation optimum model (Fig. 3c) predicts that whole system NPP peaks at an intermediate tree–grass ratio (Scifres *et al.*, 1982; Teague & Smit, 1992) because life-forms benefit each other at an intermediate density. For example, woody plants may enhance soil nutrient availability and ameliorate environmental stress immediately below their canopy, thus stimulating herbaceous NPP under or near woody plant canopies with no ill-effects on tree or shrub NPP. However, as woody plant size and density increase, stand-level effects adversely

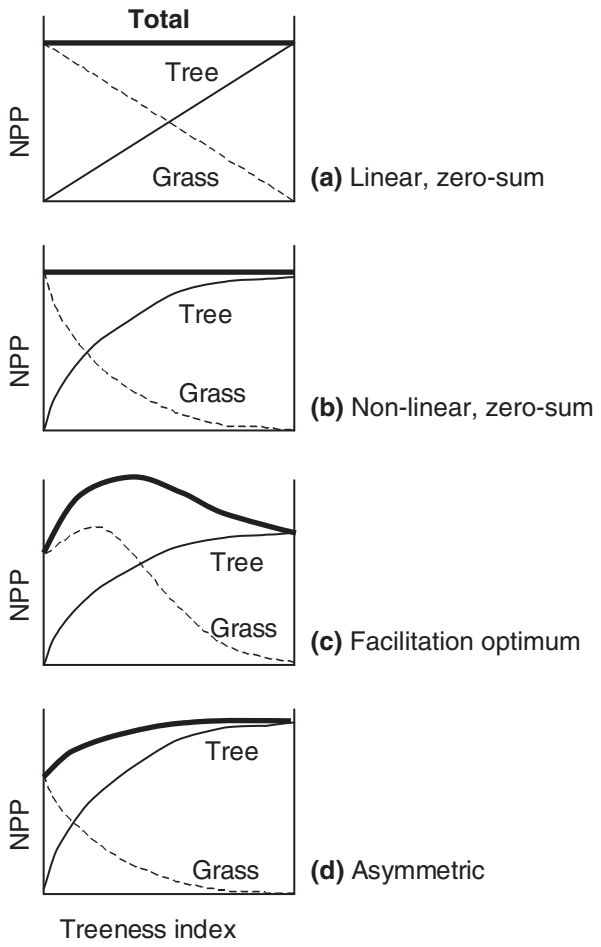


Figure 3 Possible relationships of tree, grass and total NPP in tree–grass systems. (a) Linear, zero-sum: change in NPP of one life-form results in a linear inverse change in the other such that there is no change in NPP of the whole system. (b) Non-linear, zero-sum: As in (a), but the inverse relationship is non-linear. (c) Facilitation optimum: may occur with a peak in whole system NPP at some intermediate tree-grass ratio when one lifeform benefits the other at an intermediate density, or if life-form access different resources. (d) Assymetric: Maximum NPP may occur when one life-form is competitively superior at utilising available resources.

affecting herbaceous aboveground NPP (ANPP) (such as competition for soil water, rainfall interception (Stuart-Hill *et al.*, 1987) and shading (Archer, 1995; Martens *et al.*, 2000) begin to predominate over positive canopy-level effects. Peak NPP might also occur at intermediate tree–grass ratios if life-forms access different resources (e.g. a mixture of C_3 woody plants and C_4 grasses may be able to exploit the seasonal cycle more effectively, with more water-use efficient C_4 grasses able to respond to small rainfall events in the dry season, and C_3 trees able to use more of the available water in the wet season). An asymmetric woody maximum model would apply if woody plants have an immediate, negative impact on herbaceous NPP and if woody plants are more productive than herbaceous plants (e.g. better access to deep stores of soil moisture, higher LAI, higher photosynthetic rates and extended leaf area duration) (Fig. 3d). Conversely, maximum system NPP might be realized with C_4 grass domination (for example in arid areas, where the superior water-use efficiency of C_4 plants could be an important factor), with increasing C_3 woody plant abundance causing a decline in system NPP.

Experimental manipulations and limited site comparisons have examined the effects of changing treeness on grass NPP (or biomass) and have generally found declining grass NPP with increasing treeness. This negative relationship may be linear or curvilinear depending on site and environmental conditions (reviewed in Scholes & Archer, 1997). Tests of the effects of treeness on total ecosystem NPP remain elusive, as few studies have simultaneously considered NPP of both the woody and herbaceous components. Of particular note is the recent study by Reich *et al.* (2001), in which temperate oak savannas stands on comparable soils were compared across a wide range of tree canopy cover. As woody cover increased, ANPP, which ranged from 2 to 12 Mg ha^{-1} $year^{-1}$, increased exponentially and grass ANPP decreased linearly.

It should be noted that estimates of NPP are subject to great uncertainty, particularly when there are mixtures of woody and herbaceous life-forms. Methodologies for measuring NPP depend upon how above- and belowground biomass and turnover are handled over an annual cycle. For example, accounting for monthly gain/loss increments can result in NPP estimates that are two to five times higher than those obtained using standard International Biological Program methods (Milner & Hughes, 1968) which ignore biomass mortality, and two to ten times higher than estimates based on annual aboveground maximum standing crop (Long *et al.*, 1992). Accounting for root biomass and turnover is particularly difficult and there is evidence to suggest that grass roots may turn over more slowly (Milchunas & Lauenroth, 1992) and tree roots more rapidly (Hendrick & Pregitzer, 1992; Eissenstat & Yanai, 1997; Reich *et al.*, 2001) than has been generally assumed.

ADDRESSING THE TREE–GRASS CONUNDRUMS

Addressing the conundrums identified above and developing a more robust understanding of tree–grass systems requires, we believe, fundamental advances in two areas. First, cross-site comparisons and syntheses based on existing data are needed. The emergence of robust generalizations from cross-site comparisons will be enhanced as additional data, particularly on biomass and NPP of the combined woody and the herbaceous components, become available from diverse sites. Secondly, models that explicitly deal with the interactions of woody and herbaceous plants, as opposed to models developed for either grasslands or forests, are needed to represent key assumptions, to conduct broad multi-factor cross-site comparisons, and to provide a basis for experimentally testing field observations. Several models have recently been developed, but further testing and development is needed.

Cross-site synthesis

Advances in ecology are increasingly relying on cross-site data synthesis activities (Jackson *et al.*, 1996; Williams *et al.*, 1996; Walker & Langridge, 1997; O'Brien, 1998; Hooper & Johnson, 1999). Additional examples of these advances include continental-scale transects (Koch *et al.*, 1995), comparisons within the USA Long-Term Ecological Research Network (e.g. Knapp & Smith, 2001) and use of meta-analysis of large numbers of data sets at workshops such as those coordinated through the National Center for Ecological Analysis and Synthesis (NCEAS; http://www.nceas.ucsb.edu). Such activities are particularly relevant for addressing the three conundrums outlined earlier and for advancing our perspective on mixed tree–grass systems. For example, a data base could be compiled to test the hypothesis that the tree–grass coexistence domain occupies a predictable space in the plane of fire return frequency and grazing intensity.

An initial survey of relevant data through a NCEAS-coordinated workshop on tree–grass interactions leads to the following assessment of available data (Parton *et al.*, 2000): (1) data on mixed tree–grass systems are globally extensive, but the number of sites for which the biomass of both the woody and herbaceous components has been quantified is extremely limited; (2) there have been few cross-site comparisons or controlled studies across the grassland–forest continuum; and (3) there are only a few sites for which data sets are robust enough to conduct modelling experiments addressing the coexistence and NPP conundrums. Thus, there is a clear need to develop more comprehensive data sets. In the meantime, valuable insights may emerge from meta-analyses of an extensive, comprehensive data base compiled from existing data. Further advances could be realized by coupling such data with models developed for tree–grass systems.

Modelling

The appropriate representation of mixed tree–grass systems is fundamental to the performance of global vegetation models (e.g. Neilson, 1995; Daly *et al.*, 2000). Models explicitly incorporating tree–grass interactions and dynamics vary widely with respect to their approach, their complexity and their data requirements. They span a continuum of detail, from highly validated empirical formulations to mechanistic, spatially explicit treatment of individual plants and vary with respect to (1) the extent to which they incorporate plant physiological and population processes; (2) their fundamental assumptions of how and to what extent woody and herbaceous plants access, utilize, and redistribute resources; (3) their spatial and temporal resolution; (4) the extent to which they incorporate the determinants in Fig. 1; and (5) their treatment of competition or facilitation interactions. Tree-grass models have generally not been extensively tested outside of the regions for which they were developed. Nor have they been exercised to see if they can reproduce key emergent features of tree–grass systems: the nonlinearity of the effects of trees on grasses and the fundamental instability of tree–grass mixtures.

Four models representing a range of complexity and approaches are summarized in Table 1. One approach for predicting biomass and NPP in savannas, represented by the GRASP model, has been to develop site-specific empirical relationships of life-form water use (Moore *et al.*, 1997). In GRASP, treeness is prescribed (although it can also be modelled independently) and has a small preferential access over grasses to soil water. A second approach, represented by CENTURY-Savanna, is to model the herbaceous and woody components simultaneously using pre-existing and well-tested grassland and forest modules (Parton *et al.*, 1993). In CENTURY, competition is a function of tree basal area (concave curvilinear relationship of decreasing grass access to nutrients with increasing tree basal area) and site nutrient availability (the higher the nutrient availability, the more competitive the grass system). The SAVANNA model utilizes mechanistic tree and grass physiological and population processes to control plant abundance in a spatially explicit fashion across landscapes (Coughenour, 1992; Ludwig *et al.*, 2001). Spatial units in SAVANNA are defined in the context of belowground 'cover' rather than aboveground cover because, in contrast to forest systems where light is a key limiting resource, competition in tree–grass systems is regarded as being primarily for belowground resources. The MUSE-TREEGRASS model employs a complex, data intensive, spatially explicit approach (Simioni *et al.*, 2000), which represents root and foliage crowns of individual trees in space, enabling study of the effect of vegetation structure (e.g. crown shape, density and spatial distribution) on ecosystem function. These four models thus represent approaches for modelling tree–grass systems ranging from coarse to fine-grain in space and time, from empirical to highly mechanistic and from aggregated representations of trees and grasses to explicit spatial representation of different tree and grass growth forms or species.

Model development is typically based on *a priori* knowledge of select processes, and researched at a limited number of sites, in concert with specific objectives research. Therefore, a given modelling approach may be more relevant or appropriate for some situations and research questions than others. Performance of a given model should be evaluated over a wide range of environmental characteristics (arid to moist, infertile to fertile, sandy to clayey and cool to hot) and disturbance regimes (including fire, grazing and tree harvesting). Model-data intercomparisons can be applied either across a wide range of sites which may have limited, but minimally sufficient data sets, or to a smaller set of sites for which more detailed process-oriented data bases exist. Intercomparisons of the performance of different models under different circumstances could generate a more robust understanding of tree–grass systems, and could help to identify and prioritize areas for model development and data requirements needed to address the tree–grass conundrums. At the same time, such model experiments would help both the research and land management communities ascertain what level of modelling detail and complexity might be

Table 1 Features of four savanna models

Model	Temporal/spatial resolution	Processes	Features	Disturbance	Specific data needs	Output parameters
GRASP (McKeon *et al.*, 1990; Moore *et al.*, 1997)	Day Uniform patch (*c.* 0.5 ha as smallest)	Water budget; simple N budget; grazing impact on pasture; erosion	Pasture growth model based on transpiration-use efficiency and nutrient availability. Grass production simulated, trees prescribed or simulated. Growth and N uptake function of transpiration which is a function of cover and pan evaporation. Trees and pasture compete for water and nutrients in top three layers; trees have preferential access	Grazing Fire Irrigation Mowing		Grass biomass, NPP and quality; tree numbers and basal area; animal production; soil water balance including runoff and drainage
CENTURY-Savanna (Parton *et al.*, 1993)	Day–month Patch-regional	Water budget; C, N and P cycling; disturbance impacts	Generalized ecosystem model. Competition for water, nutrients and shade effects, but mostly controlled by nutrients, trees have preferential access to N depending on basal area and site fertility	Grazing Fire Harvest Ploughing Fertilization		Tree and grass biomass and NPP; soil carbon; nutrients
SAVANNA (Coughenour, 1992)	Week-month Patch-landscape (100 km) Semi-spatially explicit	Water budget; nutrients; light; recruitment; mortality; demography	Process-orientated mechanistic model. Each patch in landscape divided into vegetation patches, proportions change dynamically. Cover defined by rooting area. Water and nutrients allocated equally to trees and grasses in proportional to demand in different patches and rooting zones. Can be linked to GIS	Grazing Fire Harvest	Topography	Plant production; recruitment; mortality; population changes; animal production
MUSE-TREEGRASS (Simioni *et al.*, 2000)	Hours–Day Patch (1 ha, 1000 trees) 3D spatially explicit, individual plants	Water; light and energy balance; demography; structure	Process-oriented mechanistic model. Individual radiation absorption, production, and transpiration Two versions: full carbon assimilation processes (including leaf nitrogen effects) or simple light use efficiency. Competition for water and light in different layers driven by shape and spatial distribution of roots and canopy. Nutrients prescribed	Fire	Typically needs initial tree location and geometry	Soil water balance; tree and grass biomass, LAI and NPP

NPP, net primary productivity; LAI, leaf area index; GIS, geographical information system.

required to achieve a robust and realistic representation of tree–grass interactions for a given research question or management issue.

There are likely to be trade-offs in the advantages of or need for model complexity depending on the questions being addressed. For example, less complex models such as GRASP and CENTURY-Savanna may be appropriate for straightforward hypothesis testing and predictions of treeness and NPP conundrums. As these models are relatively less data-intensive than others, they may be readily deployed on a large number of sites spanning a wide range of bioclimatic conditions. On the other hand, more complex, mechanistically based models such as SAVANNA and MUSE-TREEGRASS may be needed to understand and elucidate processes that generate observed plant distributions and primary production dynamics, and to predict changes in tree–grass mixtures with disturbance and environmental variation. However, because these types of models are parameter-intensive, their use may be limited to a small, select number of well-studied sites. Even so, knowledge gained from using complex models at selected sites could facilitate development of simpler models. Indeed, this premeditated, iterative linkage between simple and complex ecosystem models is a means whereby global impacts of management and climate change might be effectively assessed in tree–grass systems.

CONCLUSION

Elucidation of the determinants, life-form interactions, dynamics and productivity of tree–grass systems has proven to be a major challenge. Over the past three decades, these issues have been addressed using simple, qualitative conceptual models, partial data sets, and site-specific studies. Such approaches have proven insufficient to capture the complex behaviour inherent in savannas. A perspective that embraces the rich array of possible tree–grass mixtures across the entire grassland–forest continuum may yield novel insights and a more robust understanding and predictive capability. It may be possible to develop a broad set of generalizations that determine the ecological outcome of mixed tree–grass systems under a range of site conditions, or it may emerge that such systems are so diverse functionally that no common rules exist.

Data assimilation exercises undertaken so far have highlighted the fact that even the most basic data on woody and herbaceous productivity is lacking on most sites (Scholes & Hall, 1996; House & Hall, 2001). This NPP data shortfall is especially acute for belowground biomass, for woody plants, and for multiple years encompassing a range of climatic variability.

The simulation models available to explore the organization, dynamics and productivity of tree–grass ecosystems are in their infancy and vary widely with respect to their approach, their complexity and their data requirements. Model-data intercomparisons across a range of tree–grass mixtures and sites are needed in order to explicitly identify the strengths and weaknesses of the various approaches and to ascertain the degree of complexity needed to represent tree–grass interactions realistically and robustly for a given research question or management application. Performance testing of these models across a wide range of conditions is currently constrained by lack of suitable data.

Savannas occupy a large fraction of the terrestrial biosphere. They have a significant influence on global biogeochemical cycles and will be highly sensitive to anticipated changes in land use and climate. Addressing conundrums that focus on predicting the tree–grass ratio, understanding what controls it, and assessing the implications for ecosystem productivity, are thus deemed a priority undertaking. It is not sufficient to simply use what we know about grasses and what we know about woody plants to predict what happens where the two life-forms co-occur. Future progress in improving our understanding of and predictive capability for mixed woody–herbaceous systems requires (1) addressing the treeness, coexistence and NPP conundrums via cross-site data synthesis and modelling; and (2) adopting a broad perspective wherein woody–herbaceous mixtures are viewed in the dynamic context of a grassland–forest continuum rather than as static or narrowly defined local or regional physiognomic entities.

ACKNOWLEDGMENTS

This paper resulted from two workshops on 'Interactions in Mixed Tree–Grass Systems' conducted at the National Center for Ecological Analysis and Synthesis (a Center funded by NSF Grant No. DEB-0072909, the University of California, and UC Santa Barbara; http://www.nceas.ucsb.edu/), two meetings of the SCOPE Tree–Grass Dynamics Project (D.O. Hall, J.-C. Menaut, and R.J. Scholes, organizers) and a series of meetings sponsored by the International Union of Biological Sciences/Man and the Biosphere program on 'Responses of Savannas to Stress and Disturbance' (B. Walker, O. Solbrig, J.C. Menaut, E. Medina, and P. Frost, organizers). D.D. Breshears received additional support from Los Alamos National Laboratory (LDRD Program). Charles Moyo, Chad McMurtry, and Nancy Kiang also participated in some of the NCEAS workshops. We dedicate this paper to Prof. David Hall who passed away in August 1999. His great knowledge and love of savannas was equalled by his commitment and enthusiasm for furthering that knowledge and passing it on to others.

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BIOSKETCHES

The Scientific Committee on Problems of the Environment (SCOPE) tree–grass group is a multidisciplinary team of international scientists, representing a broad range of perspectives on tree–grass ecosystems, including data-holders and modellers, collaborating with the aim of improving understanding of woody–herbaceous interactions and dynamics. Their work is based on a series of meetings initiated by SCOPE and continued at the National Centre for Ecological Analysis (NCEAS, Santa Barbara, California, see tree–grass web site at http://www.nceas.ucsb.edu/). They have developed a tree–grass site data base, to be made publicly available once data meta-analyses are published, and have carried out initial model intercomparison activities. Continued expansion of the data base and modelling activities are anticipated.