

Running title: Tree-grass interactions in savannas

**Tree-grass coexistence in savannas revisited – insights from an examination of  
assumptions and mechanisms invoked in existing models**

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**Abstract**

Several explanations for the persistence of tree-grass mixtures in savannas have been advanced thus far. In general, these either concentrate on competition-based mechanisms, where niche separation with respect to limiting resources such as water lead to tree-grass coexistence, or demographic mechanisms, where factors such as fire, herbivory and rainfall variability promote tree-grass persistence through their dissimilar effects on different life history stages of trees. Tests of these models have been largely site-specific, and although different models find support in empirical data from some savanna sites, enough dissenting evidence exists from others to question their validity as general mechanisms of tree-grass coexistence. This lack of consensus on determinants of savanna structure and function arises because different models: i) focus on different demographic stages of trees, ii) focus on different limiting factors of tree establishment, and iii) emphasize different subsets of the potential interactions between trees and grasses. Furthermore, models differ in terms of the most basic assumptions as to whether trees or grasses are the better competitors. We believe an integration of competition-based and demographic approaches is required if a comprehensive model that explains both coexistence and the relative productivity of the tree and grass components across the diverse savannas of the world is to emerge. As a first step towards this end, we outline a conceptual framework that integrates existing approaches and applies them explicitly to different life-history stage of trees.

**Keywords:** savanna, tree-grass coexistence, resource limitation, competition, disturbance, climatic variability, demographic bottlenecks, models

## **Introduction**

Savanna ecosystems are characterized by the co-dominance of two contrasting plant life forms – trees and grasses. Although the relative representation of these life-forms varies considerably across savanna types, they typically comprise communities with a continuous herbaceous layer and a discontinuous stratum of shrubs and trees (Frost et al. 1986). Savannas occupy an eighth of the global land surface and support a large proportion of the world's human population and a majority of its rangeland and livestock (Scholes & Archer 1997). However, despite their recognized importance to human welfare and economy, the origin, nature and dynamics of savannas are poorly understood (Scholes & Archer 1997, Jeltsch et al. 2000). In particular, mechanisms permitting trees and grasses to coexist without one displacing the other, and factors determining the relative proportions of woody and herbaceous components across different savanna types remain unclear (Scholes & Archer 1997, House et al. 2003).

Many explanations for the persistence of tree-grass mixtures in savannas have been advanced thus far, but perceptions differ on whether the suite of interactions that characterize savanna systems results in a mix of trees and grasses that is 'stable' or 'unstable' (Scholes & Archer 1997). Broadly, proposed explanations for the persistence of both trees and grasses in savannas fall into two categories: those that emphasize the fundamental role of competitive interactions in fostering coexistence (hereafter competition-based models), and those that focus on the limiting roles of demographic bottlenecks to tree establishment and persistence in savannas (demographic-bottleneck models). Competition-based models are predicated on classic niche-separation mechanisms of coexistence, and invoke differences in the resource-acquisition potential

of trees and grasses as the fundamental process structuring savanna communities (Walter 1971, Walker et al. 1981, Walker & Noy-Meir 1982, Eagleson & Segarra 1985, Eagleson 1989, Van Langevelde et al. 2003, Fernandez-Illescas & Rodriguez-Iturbe 2003). In these models, coexistence results because of spatial and/or temporal niche differences between trees and grasses that serve to concentrate intra- relative to inter- life form competition (see Chesson & Huntly 1997, Chesson 2000, Amarasekare 2003).

Demographic-bottleneck models, on the other hand, argue that the critical problem for savanna trees is demographic and not competitive in nature (Higgins et al. 2000). Here, trees and grasses persist in savannas because of climatic variability and/or disturbances such as fire and grazing which limit successful tree seedling germination, establishment and/or transition to mature size classes (Menaut et al. 1990, Hochberg et al. 1994, Jeltsch et al. 1996, 1998, 2000, Higgins et al. 2000, van Wijk & Iturbe 2002). Although disturbances and environmental variability do ultimately create niche opportunities by modifying resource availability or supply rates, it is their proximate density-independent effects on tree germination, establishment and/or mortality, rather than any altered competitive relationships, that are the primary focus of these models. In these models, although both trees and grasses can persist in the system over long time scales, chance events such as protracted droughts or extended periods of above-average rainfall conditions may lead to complete dominance by one or other life form (Pellew 1983, Archer 1989, Jeltsch et al. 2000).

Ecologists continue to debate the validity of these two paradigms in an attempt to resolve the 'savanna question' (Sarmiento 1984, Scholes & Archer 1997, Higgins et al. 2000, Jeltsch et al. 2000). In recent years, demographic-bottleneck models of savannas

have gained favor over traditional competition-based models (Scholes & Archer 1997, Higgins et al. 2000, Jeltsch et al. 2000, van Wijk & Iturbe 2002). Two reasons underlie this shift in focus. First, empirical support for root niche separation in water uptake between trees and grasses, the mainstay of the predominant competition-based model of savanna structure (Walker et al. 1981, Walker & Noy-Meir 1982, Eagleson & Segarra 1985), is equivocal. Second, resource-competition alone has been insufficient to generate long-term tree-grass coexistence in spatially explicit models of savannas parameterized with field data (Jeltsch et al. 1996, 1998, 2000), leading ecologists to seek additional mechanisms for the same (Jeltsch et al. 2000).

Savanna structure is undoubtedly the consequence of several interacting factors including climate, resource-competition, fire and grazing that operate at various spatial and temporal scales (Scholes & Archer 1997). Nevertheless, recognizing whether or not savannas are intrinsically unstable systems maintained by disturbances such as fire and grazing, or stable systems that persist despite these disturbances is critical to their management worldwide. Revisiting the assumptions and predictions of the dominant paradigms in savanna ecology, and attempting to reconcile their differences comprise the dual themes of this paper. For simplicity, we ignore explicit consideration of issues arising from the ‘scale’ of enquiry. Our focus is at the landscape scale where a system is easily recognizable as a savanna, regardless of whether trees are homogeneously or heterogeneously (i.e. clumped) distributed within this area.

In the past, savanna dynamics have been variously interpreted in the context of equilibrium, non-equilibrium and disequilibrium dynamics (Ellis & Swift 1988, Illius & O’Connor 1999, Higgins et al. 2000, Sullivan & Rohde 2002). To preserve continuity

with the extant savanna literature, we retain use of these terms here. However, to avoid ambiguities arising from semantics (DeAngelis & Waterhouse 1987), we clarify our usage of these terms in the context of their underlying mechanisms below. As in the past, we use the term "equilibrium" in a limited sense to refer to savannas where long-term coexistence of trees and grasses is not dependent on rainfall variation or disturbances such as fire and grazing (Scholes & Archer 1997). For a given mean climate, tree-grass ratios tend to hover around fixed values, but are not conceived of as being fixed. They can fluctuate in response to both variable rainfall and disturbances such as fire and grazing, but, critically from a theoretical perspective, the competitive balance between trees and grasses remains unchanged in the face of these perturbations. In contrast, we use the term "non-equilibrium" to refer to savannas where tree grass coexistence is contingent on inter-annual rainfall variability that temporally switches the competitive balance between trees and grasses and/or provides opportunities for tree germination and establishment. Such variability fosters the coexistence of both life forms in the system and results in more dynamic tree-grass ratios. Finally, we use the term "disequilibrium" to refer to savannas where long-term coexistence is not possible and the system would converge to a wooded or grassy state following the cessation of fires and/or herbivory. Here, disturbances are essential for the persistence of trees and grasses in the system.

In the following sections, we briefly review some of the proposed competition-based and demographic-bottleneck models, highlight some of their limitations, and suggest approaches to integrate these disparate models that can help account for the observed persistence and variety of tree-grass systems. In comparing the different models, we focus our attention, naturally, on the principle mechanisms that distinguish

them. In doing so, it is not our intent to portray different views as being completely polarized; indeed most savanna ecologists would agree that competitive interactions, population demographics, climate and disturbance regimes interact in complex ways to influence savanna structure and function. However, the models emphasize different suites of factors and processes, and these differences have implications for how we perceive and predict savanna dynamics. It is these contrasts that we attempt to bring out below.

## **The models and their predictions**

### **i) Competition-based models**

Traditionally, ecologists have recognized four key variables as being the determinants of savanna structure and function: water, nutrients, fire and herbivory (Frost et al. 1986). In competition-based models, water and nutrients are considered the ‘primary determinants’, with fire and grazing representing ‘modifiers’ (Stott 1991). Trees and grasses coexist in savannas because of their differential ability to acquire and partition limiting resources. For the most part, models have focused on plant-available moisture (PAM), rather than plant-available nutrients (PAN) as the main resource limiting plant growth in savannas (Walter 1971, Walker et al. 1981, Walker & Noy-Meir 1982, Eagleson & Segarra 1985, Eagleson 1989, Van Langevelde et al. 2003, Fernandez-Illescas & Rodriguez-Iturbe 2003).

Four different, but potentially related, competition-based models currently dominate the savanna literature: the root niche separation model, the phenological niche separation model, the balanced competition model and the hydrologically driven

competition-colonization model. The root niche separation model proposed by Walter (1971) is the classic equilibrium model of savannas. It assumes that water is the primary limiting factor and trees and grasses have differential access to this resource due to spatial differences in their rooting profiles. Trees and grasses compete for water in the upper soil profiles, and although grasses are superior competitors for water in the upper horizons, trees are able to persist in the system because of exclusive access to deeper water (Walter 1971). For a given set of environmental conditions, the ratio of trees to grasses is then a function of the vertical distribution of water in the soil profile, with tree biomass increasing as the amount of subsoil water increases (Fig. 1a). The existence of an equilibrium ratio of grass and woody vegetation for a given set of soil and mean climatic conditions has been demonstrated analytically for savannas modeled on these assumptions (Walker et al. 1981, Walker & Noy-Meir 1982, Van Langevelde et al. 2003). Although these models predict a ‘characteristic’ tree-grass ratio for a given set of soil and climatic conditions, factors that alter the ratio of subsoil to topsoil water (e.g. variable rainfall patterns, grazing) can cause realized tree-grass ratios to deviate from this predicted ratio (Walker & Noy-Meir 1982, Van Langevelde et al. 2003).

Niche separation by phenology has also been proposed as a mechanism that can potentially contribute to equilibrium forms of tree-grass coexistence in savannas (Scholes & Archer 1997, Sala et al. 1997, House et al. 2003). Savanna trees are able to store water and nutrients and thereby achieve full leaf expansion either prior to, or within a few weeks following, the onset of the rains (Scholes & Archer 1997). Peak leaf area of grasses is achieved much later. Deciduous savanna trees also tend to retain leaves for several weeks following grass senescence (Scholes & Archer 1997). Thus, trees have

potentially exclusive access to resources early and late in the growing season. For grasses to persist, they would then have to be superior competitors for resources during periods of growth overlap with trees. The implications of such phenological niche-separation for patterns of change in tree-grass ratios across broad gradients of rainfall are not immediately apparent because the eventual outcome is contingent not only on total rainfall but also on the length and predictability of the growing season (Scholes & Archer 1997). To date, the parameter space that favors tree-grass coexistence under scenarios of phenological niche partitioning in savannas has not been investigated in detail.

Unlike the root niche and phenological niche-separation models, the ‘balanced competition’ model makes no explicit assumptions about the presence of exclusive tree niches resulting from separation in either rooting depths or phenology. Here, equilibrium coexistence arises because the superior competitor (in this case, trees) becomes self-limiting at a biomass insufficient to exclude the inferior competitor, grasses (Scholes & Archer 1997, House et al. 2003). In the absence of external perturbations, this model predicts an abrupt threshold with increasing rainfall above which tree cover should be relatively high and below which grasses dominate (Scholes & Archer 1997, Fig. 1b). At the lower end of the rainfall gradient, water availability is insufficient to support tree growth. Above the critical threshold of rainfall required to permit tree growth, trees, by virtue of being better competitors, should dominate the system. Tree density above this threshold is then limited by tree-on-tree competition for water, and is presumably determined by the rooting volumes required to meet trees’ water demands. The predicted tree density for any level of rainfall above the threshold is fairly high in this model since tree-on-tree competition is unlikely to be a limiting factor at low tree densities (Scholes &

Archer 1997). For low levels of rainfall above the threshold, grasses can persist in this system by surviving in the interspaces between trees. However, as rainfall continues to increase, rooting volumes required to meet the water demands of trees correspondingly decrease, thereby permitting a greater packing of trees within a given area. A further increase in rainfall leads to a closed-canopy scenario where grasses are out-competed, and the system converges to a closed woodland. According to this model, the only equilibrium savanna states are wooded savannas, with open savannas representing disequilibrium states maintained by fire and grazing (Scholes & Archer 1997).

In contrast to the equilibrium models just described, the hydrologically driven competition-colonization model (Fernandez-Illescas & Rodriguez-Iturbe 2003) is a non-equilibrium competition-based model of savannas. In essence, the model invokes the trade-off between competitive ability and colonization potential (Levins & Culver 1971, Levine & Rees 2002, Amarasekare 2003, Kneitel and Chase 2004), with the added caveat that the competitive rankings of trees and grasses and their colonization potential change in response to fluctuations in soil water stress caused by inter-annual rainfall variability (Fernandez-Illescas & Rodriguez-Iturbe 2003). The model predicts long-term coexistence of both life forms in the system, with the balance between trees and grasses sensitive to the magnitude and variance of inter-annual rainfall fluctuations. In terms of broad scale patterns of tree cover across precipitation gradients, the predictions of this model match those of the root niche separation model (Fig. 1a) with average tree cover increasing, albeit displaying more variability, with mean growing season rainfall (Fernandez-Illescas & Rodriguez-Iturbe 2003).

## ii) Demographic-bottleneck models

The basic premise underlying demographic-bottleneck models is that the impacts of climatic variability and disturbances differ between life history stages of trees. Importantly, it is the direct effects of these disturbances on germination, mortality and demographic transition in trees, rather than any post-disturbance competitive interactions, that is the primary focus of these models (Hochberg et al. 1994, Jeltsch et al. 1996, Higgins et al. 2000, van Wijk & Rodriguez-Iturbe 2002). Although most demographic-bottleneck models incorporate the effects of multiple drivers including herbivory, fire and climatic variability, differences exist in the context within which model results have been interpreted. One body of work views savannas as transitional ‘disequilibrium’ systems (Menaut et al. 1990, Hochberg et al. 1994, Jeltsch et al. 1996, 2000). Pure grasslands or forests are believed to be the only equilibrium states (Archer 1989, Jeltsch et al. 2000), with disturbances such as fire and grazing permitting savannas to persist in a disequilibrium state by ‘buffering’ the system against transitions to either of these extremes (Jeltsch et al. 2000). In other words, there are no ‘primary determinants’ of savannas and disturbances like fires and grazing are not just ‘modifiers’ but also ‘maintainers’ of the savanna state.

An alternate viewpoint interprets savanna structure in the context of ‘non-equilibrium’ dynamics driven by variation in rainfall in arid regions (Higgins et al. 2000, van Wijk & Rodriguez-Iturbe 2002) and ‘disequilibrium’ dynamics driven by variation in fire intensity in mesic savannas (Higgins et al. 2000). Trees are assumed to be limited by drought at the seedling stage and by fires at the sapling stage. In arid savannas, temporal variance in tree seedling establishment opportunities caused by stochastic rainfall

patterns, combined with low adult tree mortality, leads to a dynamic scenario where tree recruitment is pulsed in time (Higgins et al. 2000, van Wijk & Rodriguez-Iturbe 2002). Here, recruitment potential is ‘stored’ (*sensu* Warner & Chesson 1985) in the adult tree population and trees persist in arid savannas if there are occasional ‘good’ years for recruitment and/or growth to maturity, and if mature trees live long enough to bridge these events (Higgins et al. 2000). In contrast, in mesic sites, trees are capable of entirely dominating the system, but frequent high-intensity fires limit opportunities for tree seedlings to escape the flame zone into adulthood, thereby allowing both trees and grasses to persist in a ‘disequilibrium’ state (Higgins et al. 2000). Although long-term persistence of trees and grasses is possible in this way, the tree-grass mix is not stable in a theoretical sense (*sensu* Chesson 2000) – because intra- life form interactions are considered weak and trees are capable of displacing grasses, the occurrence of extended periods of favorable or unfavorable conditions for tree recruitment can lead to the system converging to woodland or open grassland, respectively.

These models represent a departure from traditional equilibrium models of savannas in that the emphasis is on demographic, rather than physiological mechanisms (Higgins et al. 2000, van Wijk & Rodriguez-Iturbe 2002). Recurrent droughts in savannas prevent seedling establishment (Harrington 1991, Wilson & Witkowski 1998, Midgley & Bond 2001). Even when seedlings do manage to establish successfully, disturbances such as fires and browsing prevent them from escaping into mature size classes (Pellew 1983, Frost & Robertson 1987, Bond & van Wilgen 1996, Higgins et al. 2000). Under this scenario, across a gradient of increasing rainfall, an abrupt transition from grassland to forest should occur in the absence of external perturbations (Fig. 2).

Savannas exist because of factors that favor tree establishment at the low end of the rainfall gradient, and those that prevent canopy closure at the high end (Fig. 2). For example, in arid savannas, the primary demographic bottleneck for trees is thought to be at the germination and seedling establishment stage (Jeltsch et al. 1998, Higgins et al. 2000, van Wijk & Rodriguez-Iturbe 2002). This bottleneck is removed only in rare wet years during which seedling establishment occurs, and when establishment does occur it usually results in recruitment to the adult classes (Higgins et al. 2000, van Wijk & Rodriguez-Iturbe 2002). Additionally, in arid savannas, tree persistence can also be facilitated by factors such as localized deposition of tree seeds in herbivore dung and underground seed caches that provide more suitable conditions for tree-seedling germination and establishment, locally eliminating the bottleneck and permitting trees to persist in the system (Jeltsch et al. 1998). In both these cases, climatic variability and disturbances (e.g., high rainfall years and herbivores, respectively) maintain savannas by removing a prevailing bottleneck.

On the other hand, in more mesic sites, disturbances such as fire serve to maintain, rather than remove, bottlenecks (Jeltsch et al. 2000, Higgins et al. 2000). The bottleneck in these savannas is presumably at the transition stage to adulthood. Although seedling germination and establishment is high at these sites because of less frequent droughts, frequent fires prevent recruitment to adulthood by ‘topkilling’ saplings, resulting in direct mortality or causing saplings to resprout from rootstocks (Higgins et al. 2000).

### **Empirical evidence for and against the different models**

Tests of these models have been largely site-specific, and although different models find support in empirical data from some savanna sites, enough dissenting evidence exists from others to preclude a consensus (House et al. 2003). For example, although empirical evidence exists for rooting niche differentiation between adult trees and grasses in some systems (Soriano & Sala 1983, Helsa et al. 1985, Knoop & Walker 1985, Sala et al. 1989, Pelaez et al. 1994, Weltzin & McPherson 1997), data from others indicate an overlap rather than separation in rooting profiles of adult trees and grasses (Johns 1984, Richards & Caldwell 1987, Belsky 1990, 1994, Le Roux et al. 1995, Seghieri 1995, Mordelet et al. 1997, Smit & Rethman 2000, Hipondoka et al. 2003). In general, spatial niche separation in root distributions appears to be more prevalent in arid systems where the bulk of precipitation falls during the non-growing season (Schenk & Jackson 2002). In such systems, the absence of plant uptake during the rainy season allows water to percolate down the soil profile and the potential therefore exists for trees to tap water from deeper regions of the soil profile. In contrast, there is no particular reason to expect root partitioning between trees and grasses in more mesic sites or even in arid systems where rainfall occurs during the growing season but where individual rainfall events tend to be small. In mesic systems, availability of sufficient water in the upper soil profiles precludes the need for trees to invest in deep roots. In arid systems with growing season rainfall, investment in deep roots is unlikely to be a fruitful strategy if the depth of average rainfall events only suffices to wet the upper layers of the soil profile (Scholes & Archer 1997). Significant root partitioning between trees and grasses is, therefore, likely to be prevalent, and thereby contribute to tree-grass coexistence, only under a limited set of environmental conditions. A caveat here is that theoretically,

coexistence may be possible even when root profiles overlap if there is variation in water distribution across the soil profile, if root distributions vary in relation to this pattern and/or there are differences in the relative water use efficiencies of trees and grasses (Walker et al. 1981, Walker & Noy-Meir 1982, Scholes & Archer 1997).

There is ample observational evidence to indicate niche separation by phenology between trees and grasses in savannas (Trapnell 1959, Scholes & Archer 1997). However, as previously mentioned, whether or not this contributes to coexistence of the two life-forms has not been investigated in detail. With regards to the balanced competition model, some evidence exists to indicate tree-on-tree competition in savannas. For a southern African savanna, using neighbor removal experiments, Smith and Goodman (1986) clearly demonstrated intra- life form competition between trees that increased with decreasing nearest neighbor distances. Further, the strength of this competition was influenced by both water and nutrient availability in the soil. Spacing patterns of trees in a *Burkea-Terminalia* savanna were similarly suggestive of tree-on-tree competition (Smith & Grant 1986). In both these cases, as is likely in most savannas, competition was attributable to below-ground resources rather than light. What remains unknown, however, is how the strength, and the neighborhood space over which this competition occurs, varies across broad environmental gradients. If water is the primary limiting resource for savanna trees, we might expect increases in precipitation to correspond to decreases in the neighborhood space over which individuals compete, since rooting volumes required to meet the water demand of trees should decrease. However, in a global analysis of plant rooting patterns across precipitation gradients, Schenk & Jackson (2002) found that lateral spread of tree and shrub roots did not appear to be well

correlated with rainfall. Thus, while some data do demonstrate tree-on-tree competition, the resources that cause this competition and the ecophysiological responses of trees to such competition (which ultimately bear on savanna structure in terms of tree-grass ratios) remain unclear and call for further investigation.

There is little doubt that the individual and interactive effects of disturbances such as fire, drought, grazing and browsing play important roles in influencing savanna structure and function (Trollope 1982, Menaut & Cesar 1982, Frost et al. 1986, Frost & Robertson 1987, Harrington 1991, McNaughton 1992, Skarpe 1992, Scholes & Walker 1993, Scholes & Archer 1997, Gignoux et al. 1997, Wilson & Witkowski 1998, Higgins et al. 2000, Jeltsch et al. 2000, Midgley & Bond 2001), and the available empirical evidence suggests that demographic bottlenecks imposed by such disturbances are a reality in many savannas. Data from long-term fire exclusion plots from diverse savanna localities around the world indicate a consistent trend toward increased woody cover with long-term fire exclusion (25-50 yrs), particularly for sites receiving >650 mm rainfall annually (Trapnell 1959, Peterson & Reich 2001, Bond et al. 2003). These data establish a strong role for fire in the suppression of trees in mesic savannas (Bond et al. 2003). Arid and semi-arid savannas (<650 mm), in contrast, appear to remain in a fairly open state despite long-term fire suppression, suggesting that factors other than fire limit tree cover in these regions (Bond et al. 2003). Although the data are insufficient to preclude other possibilities at this time, available data suggest that wet-season droughts, which are frequent in arid areas, can impose mortality on tree seedlings in these regions (Medina and Silva 1990, Harrington 1991, Hoffman 1996). While these data indicate that the relative importance of different disturbances varies across broad environmental gradients

(Skarpe 1992, Scholes & Archer 1997), robust generalizations are yet to emerge that illustrate how the relative importance of competitive versus demographic processes correspondingly change. Addressing this issue requires manipulative experiments, coupled with the synthesis of long-term data from fire and herbivore exclusion plots, replicated across diverse environmental gradients (House et al. 2003).

### **Limitations of different approaches**

By focusing on different life history stages and different factors limiting tree establishment and competitive interactions, different models emphasize different subsets of the potential interactions between trees and grasses (Fig. 3). In general, competition-based models do not differentiate between life-history stages of trees (Fig. 3a). For example, the focus of the root niche-separation model is largely limited to adult trees, or to be more precise, those life-history stages of trees that have access to soil water below grass rooting profiles. In doing so, it ignores the critical, and often most limiting stage in tree life-history, namely the seedling establishment stage. What models of this type predict, therefore, is a theoretical maximum tree-grass ratio for a given set of environmental conditions in the absence of disturbances, when water is the limiting factor and where the number of adults is not limited by availability of seedlings and saplings. From a theoretical perspective, it is not surprising that the existence of exclusive tree niches can foster tree-grass coexistence even if grasses are better competitors for surface soil water. What is critical, therefore, is whether and under what conditions, individual trees achieve this exclusive niche in a given savanna environment. There is some evidence to indicate that savanna tree species with rapid root development achieve this

exclusive niche fairly early in their life cycle (Bragg et al. 1993, Brown & Archer 1990, Scholes & Archer 1997). Furthermore, there is also evidence to suggest that spatial root niche partitioning exists even between very young seedlings and grasses, with seedlings utilizing water in the uppermost regions of the soil profile, even shallower than the exploitation zone of grasses (Weltzin & McPherson 1997). Savanna tree seedlings, therefore, appear to be decoupled from the grass system at the earliest stages in their lives; a fact that potentially serves to enhance their establishment success (Weltzin & McPherson 1997). Nonetheless, there remains a period of root overlap between older tree seedlings and grasses, representing a potentially critical limiting phase in tree establishment, which has largely been ignored in root niche-separation models (Jurena & Archer 2003).

The balanced competition model, likewise, ignores explicit consideration of tree life-history stages by implicitly assuming that the competitive balance between trees and grasses remains unchanged across all life-history stages of trees. This is unlikely to be strictly true in all cases, and there is evidence to indicate that grasses can reduce emergence and survival of tree seedlings, both directly through competition and indirectly via their effects on fire regimes (see Scholes & Archer 1997, House et al. 2003). Central to the issue of tree persistence in savannas is whether, and under what conditions, this suppression is sufficient to cause complete exclusion of trees (Scholes & Archer 1997).

Unlike competition-based models, demographic-bottleneck models specifically take into account life history-disturbance interactions of savanna components, often in a spatially explicit context (Menaut et al. 1990, Hochberg et al. 1994, Jetsch et al. 1996,

1998, Higgins et al. 2000, van Wijk & Rodriguez-Iturbe 2002). However, in these models competition between trees and grasses for resources is either not explicitly incorporated (Fig. 3b; Higgins et al. 2000, van Wijk & Rodriguez-Iturbe 2002), or has only been semi-quantitatively modeled (Jeltsch et al. 1996, 1998; but see Menaut et al. 1990). Interestingly, demographic models that do not explicitly incorporate competition for soil water predict persistence of both trees and grasses for a wide range of environmental conditions (Higgins et al. 2000, van Wijk & Rodriguez-Iturbe 2002), whereas models that do include competition for water predict persistence only under an extremely limited set of conditions (Jeltsch et al. 1996, Menaut et al. 1990). In this instance, coexistence was achieved only at the more arid end of the rainfall gradient under assumptions of strict niche separation of water use between trees and grasses (Jeltsch et al. 1996). In the models where competition is not invoked, coexistence results either from a stress tolerance-colonization tradeoff (van Wijk & Rodriguez-Iturbe 2002) or is achieved essentially by default, since the inability of one life-form to maximally reproduce in the face of disturbances allows for the persistence of the other (Higgins et al. 2000).

That competition, both inter- and intra- life form is important in savanna ecosystems has been well documented (Smith & Goodman 1986, Smith & Grant 1986, Mordelet & Menaut 1995, Scholes & Archer 1997, Brown et al. 1998, McPherson & Weltzin 1998). Incorporation of competitive effects into demographic-bottleneck models in the form of a covariance between the environment and competition (i.e. strong intra-life form competition during periods favorable to that particular life form, and strong inter- life form competition otherwise), can potentially serve to stabilize the tree-grass

system by preventing competitive exclusion (Chesson & Huntly 1997, Chesson 2000). Nevertheless, the fact that demographic-bottleneck models have been successful at faithfully reproducing certain aspects of tree-grass dynamics for some savanna types (Higgins et al. 2000) attests to the importance of these processes in savannas.

### **Integrating competition-based and demographic approaches**

It is not surprising that ecologists are yet to agree on a comprehensive model of savannas that explains both coexistence and the relative productivity and cover of the tree and grass components across the range of tree-grass systems observed in nature (House et al. 2003). Although both competition-based and demographic-bottleneck models have contributed significantly to our understanding of savanna dynamics, existing implementations tend to focus their attention on particular life history stages or environmental drivers and processes important for a given site or region. This has been primarily for logistic reasons, since plenty of evidence suggests that all of the processes invoked in the different models are important to some degree in any savanna. However, models differ in terms of basic assumptions regarding who the better competitor is. In the root niche separation model, grasses are the better competitors for water, but trees persist because they have exclusive access to deep water. In contrast, in the balanced-competition model, trees are the better competitors but become self-limiting at a stage prior to the exclusion of the poorer competitor, i.e. grasses. In demographic-bottleneck models trees are once again assumed to be better competitors, capable of out-competing grasses once seedlings establish, but limitations to establishment and/or recruitment into adult classes determine tree-grass ratios. The ecological reality of tree-grass competition

is more likely to lie somewhere in between, with the competitive dominance of trees with respect to grasses changing with life-history stage, over time and across environmental gradients.

It is particularly with respect to this problem that an approach that explicitly considers demographic and competitive effects at each life-history stage of the tree is most likely to further our understanding of savanna dynamics (Fig. 4). Such a framework is the logical, indeed, self-evident outcome of comparing different schools of thought in savanna ecology. Here, demography is included in the form of four recruitment rates that express transitions across relevant life-history stages of the tree: from adult tree to seed progeny ( $r_{tp}$ ), seed progeny to seedling ( $r_{pj}$ ), seedling to sapling ( $r_{js}$ ) and sapling to adult tree stages ( $r_{st}$ ). Both tree-on-tree and tree-grass competition occur at each life-history stage (competition coefficients are indicated by indices  $c_{xx}$  in Fig. 4), and the balance between these forms of competition at each stage influences recruitment into subsequent life-history stages. Processes characteristic of savanna systems, such as rainfall variability, fires and grazing, may now be considered in terms of their influences on these coefficients. Both fires and rainfall variability can affect recruitment rates both through direct mortality (primarily on tree seedlings) and through changes they impose on the competitive balance between trees and grasses. Grazers shift the competitive balance in favor of the tree component by removing grass, and potentially reducing the probability of fires. Browsers may do the opposite, shifting the competitive balance in favor of grass by removing seedlings. Finally, all of these interactions are embedded within an environmental context (soil moisture, soil texture, nutrient status, spatial and temporal

variability in the environment), which ultimately regulates the recruitment and competitive indices shown.

The above framework can be utilized as a conceptual tool to develop synthetic models of savanna systems. Ideally, comparable spatial and non-spatial models should be developed under this common framework. Presently, most spatial models of savannas focus on demography, while most non-spatial ones focus on competition. One obvious way forward is to build on existing spatial and non-spatial models to include missing elements from the above framework. Significant progress on the issue of tree-grass coexistence may come from drawing on recent theoretical advances on spatial mechanisms of coexistence (Amarasekare 2003, Murrell and Law 2003, Snyder and Chesson 2003, Kneitel and Chase 2004). In spatially homogenous competitive environments, i.e., where species' competitive rankings do not change in space (as is the case for many savanna models), theory predicts that inter-specific trade-offs between life-history traits that influence competitive ability (e.g., fecundity, longevity) and those that allow species to escape or minimize competition (e.g. dispersal) are likely to be important for coexistence (Amarasekare 2003). Such trade-offs have been rarely invoked in spatial models of savannas (e.g., Van Wijk & Rodriguez-Iturbe 2002), but may nevertheless be important despite the contrasting growth forms of trees and grasses. Similarly, coexistence in such environments can also be fostered by 'heteromyopia', a relatively new concept where species differ in the spatial scale of intra-versus inter-specific competition (Murrell and Law 2003). Heteromyopia may well be a feature of the interaction between trees and grasses, and its inclusion in spatial models of savannas may be a promising venue for exploration.

A consideration of Figure 4 also helps us to identify the kinds of empirical data that are needed, both for the validation and testing of models, as also for the eventual resolution of the 'savanna problem'. Although some empirical evidence exists for all mechanisms invoked for tree-grass coexistence thus far (e.g., niche separation, tree-tree competition, demographic limitations), little is known about how these mechanisms vary across diverse savannas. In this regard, studies that synthesize existing data from savannas across the world are urgently needed (House et al 2003). Such syntheses will enable us to identify how savanna structure varies across broad environmental gradients, and in turn, to infer something about the relative contributions of different mechanisms that contribute to tree-grass coexistence. At the same time, empirical studies that directly measure competitive and demographic effects in different savannas are also needed. Recent techniques for assessing uptake of marked elements from the soil by surrounding biota (Casper et al. 2003) provide a means for quantitative assessment of the zones of uptake by trees and grasses, and thereby the strength of inter- and intra-life form competition for soil moisture and nutrients. Simultaneous measurements of the demographic structure of the tree community can help identify prevalent bottlenecks and the particular life-history stage where they occur. Combining these data with the rainfall and fire histories of sites to infer the strength of temporal storage effects will then allow evaluation of the effects of competitive and demographic processes in a given savanna.

Identifying the specific mechanism that fosters coexistence and defines tree cover in savannas is also critical from an applied perspective. Such knowledge bears directly on our ability to predict savanna responses to changing environmental drivers, and in turn design appropriate management strategies to counteract these changes. For example,

woody encroachment into savannas has been identified as a problematic issue in many of the world's arid and semi-arid rangelands where it reduces available pasture (Archer 1989). Woody encroachment is often discussed in the context of overgrazing (Archer 1989, Skarpe 1992); a view consistent with root niche separation models where tree cover is limited by subsoil water (Walker & Noy-Meir 1982). By reducing grass cover and subsequent water uptake by grasses, grazing increases subsoil moisture and simultaneously releases tree seedlings from competition, thereby favoring the woody component. However, this explanation is not wholly consistent with demographic-bottleneck models of savannas. If, as argued by these models, woody cover in arid savannas is limited by seedling establishment during droughts rather than by grass competition, then increased grazing, by itself, should not result in encroachment by woody plants. In these models, woody encroachment in arid savannas is more likely to result from extended periods of wet years (and should be characterized by even-aged stands of woody plants). In mesic savannas, where fire is assumed to suppress tree saplings, encroachment should result from fire suppression (either through direct human intervention or indirectly through reduced fuel load). Finally, woody encroachment is less likely to be a problem in savannas structured by adult tree-on-tree competition, since it is neither extended droughts nor disturbances that are assumed to limit tree cover in these systems.

More recently, woody expansion in savannas has been discussed in the context of increasing global levels of atmospheric CO<sub>2</sub> (Polley et al 1997, Bond and Midgley 2000, Bond et al 2003). Some authors assume competition-based models of savannas and posit that decreased transpiration rates under elevated CO<sub>2</sub> increases subsoil moisture, and

thereby increases woody cover (Polley et al. 1997). Others hypothesize that increased woody cover results from increased belowground carbohydrate storage of trees that allows for rapid post-fire recovery of saplings and hastens their escape from the flame zone, a view that assumes demographic constraints (Bond and Midgley 2000, Bond et al 2003). Although tree cover increases in both cases, management strategies to counter such changes through controlled fire regimes will differ depending on the underlying operational mechanism.

Our aim here has been to highlight the fundamental assumptions and focal processes of different schools of thought on savanna ecology, to enquire whether the assumptions hold true under all conditions and to determine whether the different mechanisms that have been advanced in the past are mutually exclusive. It is our hope that this exercise may enable novel insights into savanna dynamics, and provide specific directions for future theoretical and empirical enquiry into savanna ecology.

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### Figure legends

Figure 1. Predicted tree-grass ratios across rainfall gradients as per the different competition-based models: a) root niche and hydrologically driven competition-colonization models and b) the balanced competition model. Solid lines show expected tree cover in the absence of external perturbations. Arrows indicate potential effects of disturbances on tree cover.

Figure 2. Predicted tree-grass ratios across rainfall gradients as per the different demographic-bottleneck models. Solid lines show expected tree cover in the absence of external perturbations. Arrows indicate potential effects of disturbances on tree cover.

Figure 3. Differences in the focus of (a) competition-based models and (b) demographic-bottleneck models with respect to tree life-history stages and interactions between tree and grass components. Bold arrows represent transitions between tree life history components, open arrows represent competitive effects. For simplicity, only the primary transitions / interactions that different models focus on have been depicted and potential cascading effects arising from this ignored.

Figure 4. Framework that integrates demographic and competitive approaches to tree-grass coexistence issues in savannas. Demography is included in the form of four recruitment rates  $r_{xx}$  that express transitions between relevant life-history stages of trees. Both inter- and intra- lifeform competition occur at each stage and are indicated by competitive indices  $c_{xx}$ . All interactions are embedded within a local environmental

context (soil moisture, soil texture, nutrient status) which regulates the recruitment and competitive indices shown. Finally, this environment varies in both space and time.

Figure 1

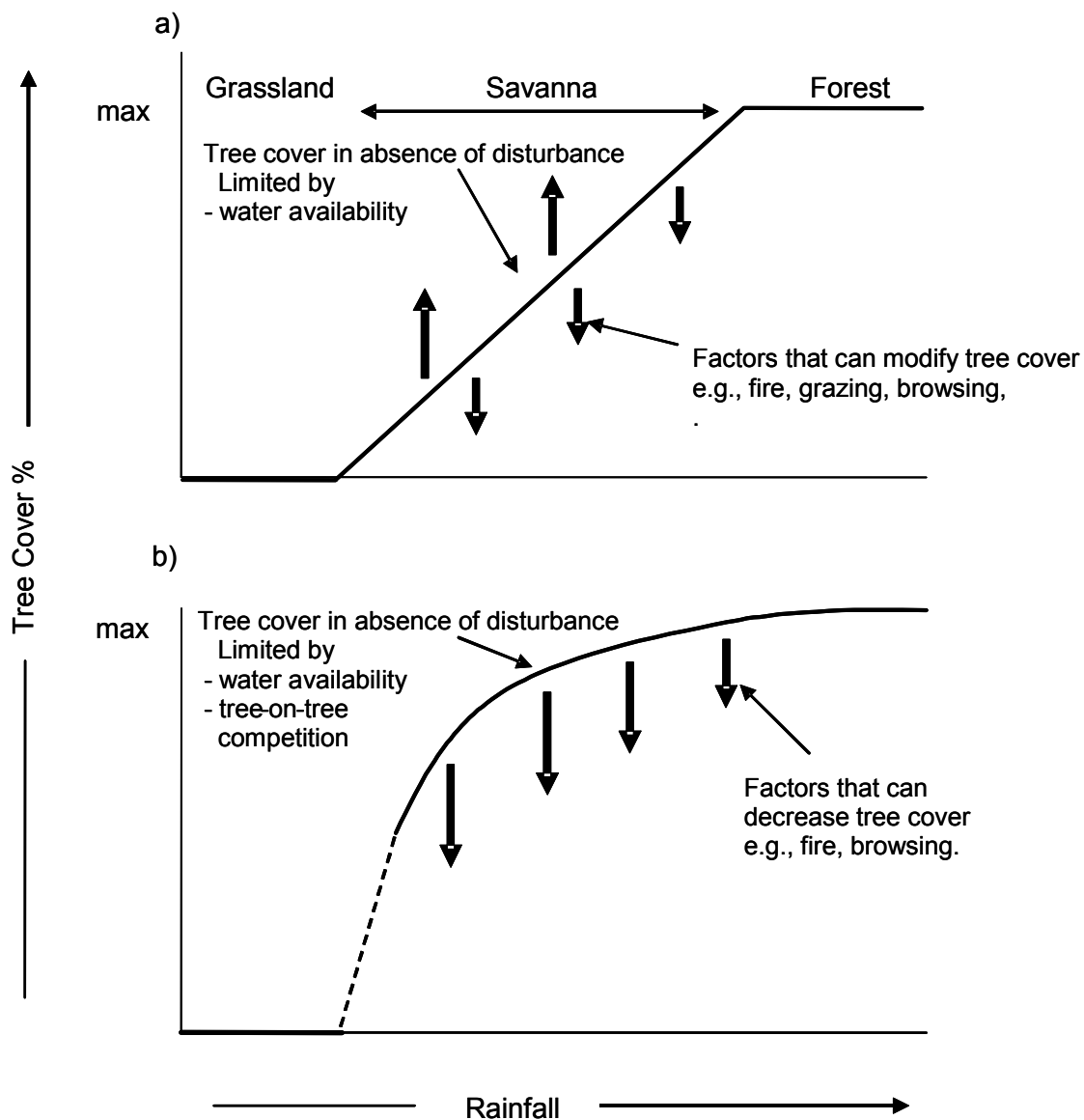


Figure 2

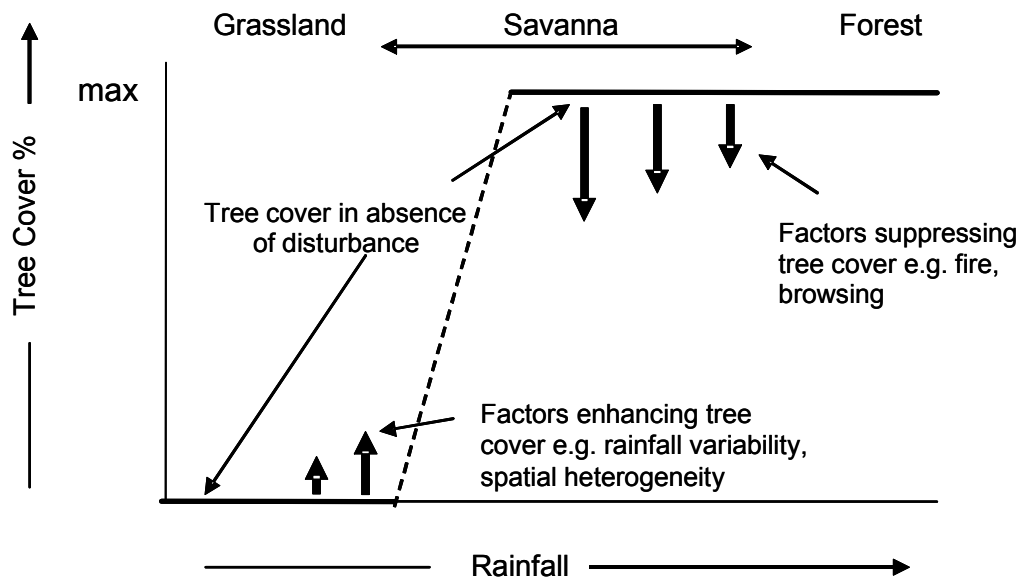


Figure 3

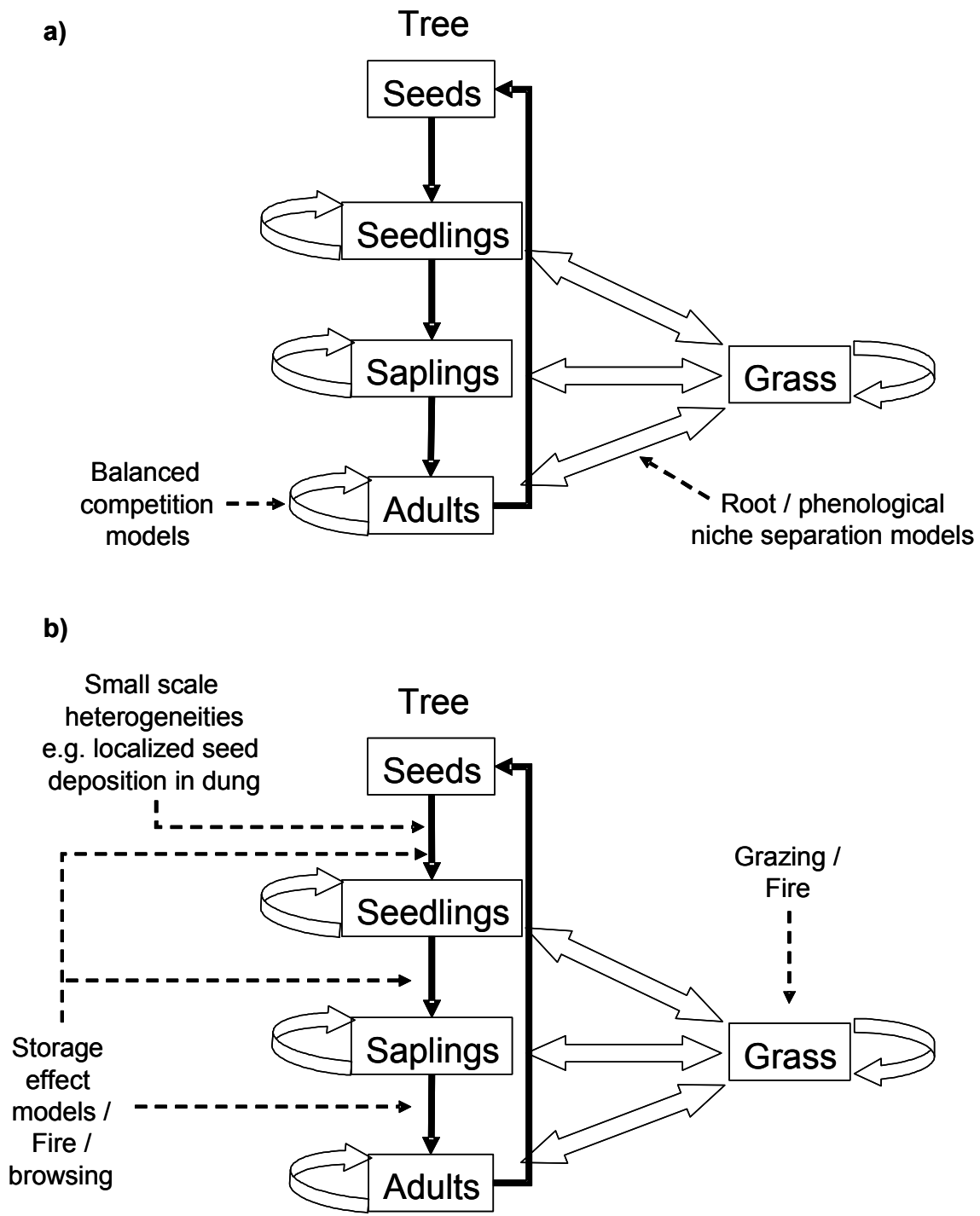


Figure 4

## Spatially and temporally variable environment

