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What Limits Trees in C$_4$ Grasslands and Savannas?

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Key Words

biome boundaries, fire ecology, mammal herbivory, tree-grass competition, trophic ecology

Abstract

Though the distribution of global vegetation can generally be predicted from climate, grasslands are an exception. C$_4$ grassy biomes cover vast areas that are warm enough and wet enough to support closed forests. The extent of this climate mismatch has been revealed by physiologically based global vegetation simulations and by large empirical data sets. Reasons for the existence of grassy biomes have long been debated, polarized into bottom-up (resources) or top-down (fire, herbivory) arguments. Recent studies indicate that both are important, especially in suppressing woody recruits. Grasses are formidable competitors belowground, create highly flammable fuels, and can support large herbivore densities. The net effect on trees is rare and episodic recruitment of adults in tree-fall gaps. The implication is that ecosystem structure and function depend on demographic transitions. Tree cover is increasing and grass/forest boundaries are changing. These changes can have large feedbacks to the earth-atmosphere system. Though progress has been made, there is still great uncertainty in predicting the future of C$_4$ grassy biomes.

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INTRODUCTION

The relative importance of abiotic and biotic controls on ecosystem structure and function has long been debated in ecology. Finding answers has become essential for predicting how global change will influence ecosystems. Aquatic ecologists have made considerable progress in identifying when and where bottom-up (abiotic) and top-down (predation, herbivory) controls influence ecosystem properties (Carpenter & Kitchell 1994). Top-down control is usually considered of minor importance in terrestrial ecosystems (Polis 1999). At the global scale, this would imply that biome distribution conforms with climate and soils so that future distributions could be predicted from ecosystem physiology. However, grassy biomes are a major exception often occurring in climatic zones that also support forests (Bond 2005, Whittaker 1975). The extent of these grasslands is enormous (30 million km^2 or ~25% of the world's vegetated land surface; Ramankutty & Foley 1999). Grasslands are strongly influenced by herbivores and fire. Fire has many analogies to mammal herbivory in its effects on vegetation (Bond & Keeley 2005). Both herbivores and fire consume vegetation and act as top-down controls on ecosystem structure. C_4 grasses dominate savannas and associated grasslands in the tropics and subtropics. Despite their socioeconomic importance, there is no consensus on what limits tree cover in these ecosystems and why they are not replaced by closed woody ecosystems.

Explanations for the existence of grasslands have been vigorously debated by generations of ecologists generally polarized into supporters of bottom-up (e.g., water, soil nutrients) or top-down (fire, herbivory) control. A particularly pervasive hypothesis is that they are an anthropogenic artifact, "early successional" vegetation created by clearing and burning of forests. But grassy biomes are millions of years old (Jacobs et al. 1999), and tropical grasslands were even more extensive in the last glacial, when human populations were sparse or nonexistent (e.g., Dupont et al. 2000, Mayle et al. 2004). The rich biota endemic to many grassy ecosystems belies their supposedly recent anthropogenic origin (Bond et al. 2005). Studies of evolution of this biota and the conservation of grassy ecosystems have been much neglected relative to forests, partly because of their supposed anthropogenic origins. Here I review recent progress in identifying bottom-up (climatic limits) on trees in grassy regions and quantifying ecological factors (bottom-up and top-down) that contribute to low tree cover. I restrict the review to C_4 grass-dominated ecosystems, but similar arguments may be relevant for temperate grassy ecosystems.

C_4 grassy biomes are particularly interesting to study because the physiology of C_4 grasses has been intensively examined and the history of the biomes can be explored with carbon isotopes. The C_4 photosynthetic pathway differs from C_3 by the addition of a CO_2-concentrating mechanism at the site of carboxylation. This reduces photorespiration, enabling leaves to fix more carbon than C_3 plants in warmer, open environments. C_4 plants are thought to have evolved in hot regions of the world in response to decreasing atmospheric CO_2 through the Tertiary (Ehleringer 2005, Sage 2004). By the middle of this century, CO_2 concentrations will exceed the threshold at which C_4 plants have a photosynthetic advantage over C_3. C_4 grass clades evolved as early as the Oligocene but only formed distinct biomes millions of years later (Jacobs et al. 1999). Carbon isotope analysis of paleosols and vertebrate fossils indicate a geologically abrupt appearance of C_4-dominated ecosystems simultaneously in Asia, Africa, and the Americas between 7 and 8 Mya (Cerling et al. 1997). Spreading very rapidly from their equatorial origins, they formed novel, grassy ecosystems where forested systems had prevailed. Today C_4 grassy ecosystems occur in a latitudinal band ~30° N and S of the equator. They occupy a very broad rainfall range from ~200 mm MAP to ~3000 mm MAP (mean annual precipitation) (Sarmiento 1992, Scholes & Archer 1997). All experience a significant dry season when the grasses dry out and are highly flammable if there is sufficient biomass. They occur on diverse soil types from nutrient-rich clays

to very infertile soils on deeply weathered ancient peneplains (Cole 1986, Scholes & Archer 1997). Savannas support very large mammal biomass in parts of Africa but very low mammal densities in other regions (e.g., Brazilian Cerrado, Australia). Human populations also vary from dense to extremely sparse in different savanna regions. The wide range of environmental, faunal, and anthropogenic conditions among savannas suggests diverse causes for variable tree cover and contributes to the lack of consensus on key determinants.

CLIMATIC LIMITS ON WOODY VEGETATION

Savannas are the most extensive C_4 grassy biome, defined as having a more or less continuous grass cover but discontinuous tree cover (Scholes & Archer 1997). They have been usefully described as patch mosaic landscapes with patches of grasslands, scattered trees, or closed woodlands that vary in their proportions in different places and at different times (Gillson 2004, Scholes & Archer 1997, Wiegand et al. 2005). Most savanna landscapes also contain patches of closed, nongrassy thickets or forests (Bowman 2000, Sarmiento 1992, White 1983). These are alternative ecosystem states with completely different structure, composition, and function. They coalesce to form tropical forests at the wet end of the MAP gradient, and thickets at the dry end (e.g., South American *Chaco* and *Caatinga*, Pennington et al. 2000; African and Madagascan thickets, White 1983). Treeless C_4 grasslands replace savannas in high rainfall areas with cool winters. Examples of the latter include the tallgrass prairies of North America and the highveld of southern Africa (Mills et al. 2006).

There is clearly enormous variation in tree abundance within C_4 grassy biomes and between them and adjacent nongrassy ecosystems. How well does climate, modified by soils, explain this variation? Until recently, answers have been sought by correlations between climate and vegetation. For example, Whittaker (1975) ordinated major biomes on a temperature–precipitation plane. C_4 grassy biomes fitted into a climate envelope of "uncertain ecosystems" where woodiness could not be predicted. Correlations cannot reveal potential vegetation—the forests that should replace "early successional" grasslands. However, potential vegetation should theoretically be predictable from ecosystem physiology. Dynamic global vegetation models (DGVMs) have taken up the challenge of predicting vegetation from physiological principles (Woodward & Lomas 2004). Like global climate models, they aim to provide mechanistic, rather than correlative, predictions of vegetation using only climate and soil inputs. DGVMs allow us to generate potential vegetation at global scales, providing a test of just how much of the world can be explained by ecosystem physiology and bottom-up control.

Bond et al. (2003a, 2005) used DGVMs to compare potential to realized vegetation. They used a daily climate data set for the twentieth century and global soil depth and texture databases to simulate potential, climate-limited vegetation. They found massive discrepancies between simulated climate potential and actual vegetation, especially in C_4 grassy biomes. For example, forests should occupy at least double their current extent if limited only by climate. In southern Africa, a DGVM including a fire module produced a far better match to the dominant grassy vegetation than simulations with fire switched off, which produced forests. Bond et al. (2005) concluded that much of the global mismatch between actual and potential vegetation could be explained by fire. Thus ecosystem physiology does not predict the vast spatial extent of C_4 grassy biomes. Other factors, of which fire is a major candidate, have to be considered.

Empirical Data Sets

DGVM simulations provide a first global assessment of climate-limited potential vegetation. Analyses of determinants of real vegetation are complicated by the patch mosaic structure of savannas
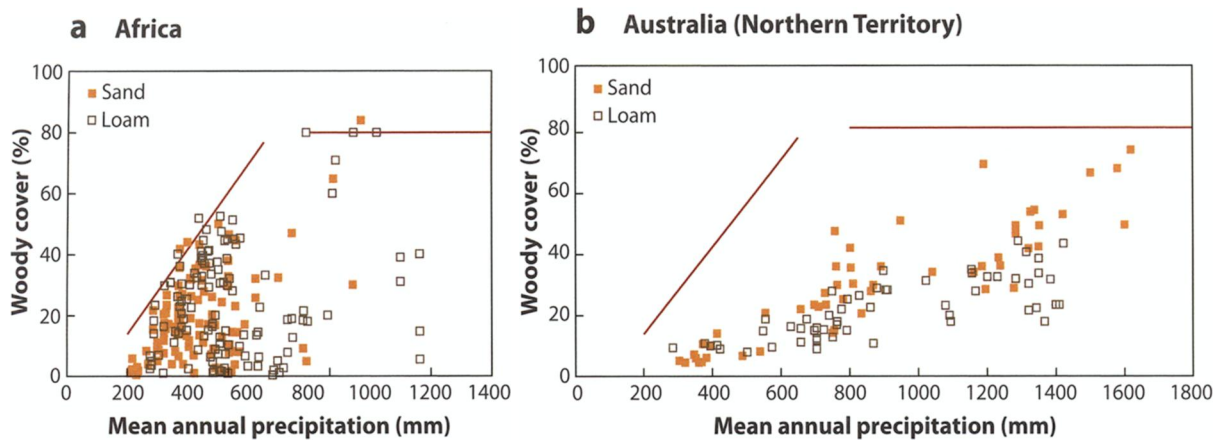
a   Africa

b   Australia (Northern Territory)

Figure 1

Changes in woody cover as a function of mean annual precipitation and soil texture in (*a*) African savannas and (*b*) Australian savannas in the Northern Territory. Lines indicate maximum tree cover fitted by 99th quantile regression for Africa (Sankaran et al. 2005). Data for Africa redrawn from Sankaran et al. (2005) and from data provided by R.J. Williams for Australia (see Williams et al. 1996).

(Gillson 2004, Scholes & Archer 1997, Wiegand et al. 2005). For example, the density of large trees may be limited by competition for resources in woodland patches and by fire in grassy patches. Local studies on what limits trees would come up with different results depending on the patch type studied (Wiegand et al. 2005). Large unbiased data sets are required to identify both potential woody biomass and variance in biomass ("patchiness") along environmental gradients. Sankaran et al. (2005) analyzed tree cover for 850 field locations in African savannas along a gradient of increasing MAP. They found that maximum tree cover increased linearly along the gradient until ~650 mm MAP above which closed woodlands (>80% cover) could develop. However, very few sites reached the maximum. Most locations, across the entire rainfall gradient, had less than half the maximum cover (**Figure 1*a***). Their data indicate that MAP limits maximum tree cover but that other factors prevent most of the landscape mosaic from reaching this maximum. Satellite imagery provides a convenient new source of data for analyzing variation in tree cover at very large scales. MODIS (Moderate Resolution Imaging Spectroradiometer) imagery has been used to explore correlates of tree cover in African savannas (Bucini & Hanan 2007). Results showed that potential tree cover increased asymptotically with MAP but, as in Sankaran et al. (2005), with very high variance in tree cover over the entire precipitation gradient. The main variables reducing tree cover from its potential were fire frequency, the density of human populations, and cattle densities.

Highly variable tree densities along precipitation gradients seem characteristic of most savannas (Sarmiento 1992, Scholes & Archer 1997). Australian savannas may be an exception. A large data set for northern Australian eucalypt savannas showed that tree basal area increased linearly along an MAP gradient, with soil texture having an additional influence (Williams et al. 1996) (**Figure 1*b***). In contrast to Africa, there was much less variance in savanna structure, with vast expanses of homogenous woodlands. Open grassy patches were very rare and usually associated with clay soils. Neither the African nor the Australian studies included closed forests, the alternative ecosystem state, in their analysis. Fire exclusion experiments in humid savannas have shown that forests support considerably more tree biomass and cover than the savannas that they replace (e.g., Louppe et al. 1995, Woinarski et al. 2004). Therefore, top-down controls on ecosystem structure are even more pervasive than these studies have indicated.

ATTRIBUTES OF GRASS

Why should grasses limit trees? How does a low herbaceous growth form prevent exclusion by tall trees? Grasses have traits that influence both direct (bottom-up) and indirect (top-down) interactions with woody plants. Grasses have dense fibrous root systems tending to explore soil more intensively than tree roots (Partel & Wilson 2002) and outcompeting trees for a nutrient supply where their roots occur together. However, trees can sample the soils more extensively to find high-resource patches not occupied by grasses. Grass growth is more responsive than are trees to resource pulses, such as nitrogen released by mineralization after a rainfall event (Scholes & Walker 1993). Plasticity of resource use is reflected in savanna phenology. Grasses in an African savanna showed much greater inter- and intraseasonal variation related to rainfall events than trees (Archibald & Scholes 2007). In general, grasses seem to be formidable competitors where they share the same belowground rooting space with, and grow at the same time as, woody seedlings and saplings.

Grasses are better protected than trees from fire and herbivory and have faster regrowth rates. C_4 grasses dry out rapidly in the dry season forming highly flammable fuels (d'Antonio & Vitousek 1992). Because nitrogen is concentrated in the bundle sheaths, C_4 grasses generally have higher C:N ratios than C_3 plants with slower decomposition rates (Ehleringer & Monson 1993). Undecomposed litter can accumulate over several growing seasons, contributing to highly flammable fuel loads (Knapp & Seastedt 1986). Grass productivity can be very high in humid savannas, regularly producing fuel loads in excess of 5 Mg ha^{-1} and up to 15 Mg ha^{-1} for an invasive African grass in Australian savannas (Rossiter et al. 2003). Because of the high NUE (nitrogen use efficiency), especially in Andropogoneae (Ehleringer & Monson 1993), large quantities of biomass can be produced on nutrient-poor soils (Gignoux et al. 2005). The C_4 combination of high productivity, rapid curing in the dry season, and low decomposition rates contributes to the very high fire frequencies in these ecosystems, the most frequent fires on Earth (Mouillot & Field 2005). C_4 fire regimes are a formidable obstacle for tree recruitment. The surface fires do much less damage to established trees.

Grasses also differ fundamentally from trees as food for herbivores. Suitable browse is patchily distributed in forests and mostly beyond the reach of ground-based vertebrate herbivores. Grasslands, in contrast, provide large quantities of easily accessible, albeit low-quality, food. Grazers dominate grassland assemblages and, by removing fuel, can reduce the extent of fires, thereby promoting fire-sensitive trees (van Langevelde et al. 2003). However, heavy grazing can also produce grazing lawns, which seldom burn yet have very low tree densities. They support high densities of grazers, including mixed feeders, whose browsing activities suppress tree growth (e.g., Prins & van der Jeugd 1993).

Without the need to grow woody stems and the root systems to support them, grasses are quick responders to pulsed resources, fire, and herbivory. Consequently they are able to directly or indirectly suppress juvenile woody plants. The relative importance of competition, fire and herbivory varies along resource gradients and in different geographic regions. For example, native mammal herbivores are abundant in Africa but very rare in Australia and South America. Thus, whether grasses limit trees primarily by bottom-up or top-down interactions will vary along environmental gradients and in different regions because of historical contingencies.

FACTORS LIMITING TREES

Bottom-Up Control: Water

Earlier explanations for both inter- and intrabiome variation in trees generally emphasized single factors, either bottom-up (climate, soils) or top-down (fire, herbivory), with bottom-up hypotheses

usually assuming that trees were at equilibrium with resources. Schimper (1903) believed that the long dry season characteristic of savanna landscapes accounted for the absence of forests. Palaeoecologists still widely interpret abundant grass pollen as indicating aridity. However, aridity is a poor predictor of grassy biome distribution since closed woody vegetation, forests or thickets occur as alternative ecosystem states from arid to humid climates (Bond et al. 2005, Bowman 2000, Pennington et al. 2000, Sarmiento 1992). Water supply has also long been considered the key determinant of tree biomass within savannas. The root niche differentiation hypothesis of Walter (1971) argued that tree cover is determined by the amount of water percolating beyond grass roots to deeper soil layers where trees have exclusive access. The root niche assumption is not empirically supported in many savannas (Higgins et al. 2000, Sankaran et al. 2004, Scholes & Archer 1997). A major problem with the hypothesis is that tree seedlings compete directly with grasses. The root niche hypothesis predicts that tree cover should increase more or less smoothly with increasing precipitation as more water percolates to deeper soil layers. This prediction is clearly at variance with the highly variable tree cover observed along MAP gradients in Africa, but perhaps not in northern Australia (**Figure 1**). The Walter hypothesis is no longer tenable as a general explanation for varying tree cover in savannas.

Bottom-Up Control: Nutrients

Low nutrient availability is another widely cited hypothesis for the presence of grassy biomes where the climate can support forests (Cole 1986, Ruggiero et al. 2002, Sarmiento 1992). Large areas of savannas occur on deeply weathered, nutrient-poor, ancient land surfaces in South America, Africa, and Australia (Cole 1986). Though forests often have nutrient-enriched soils relative to savannas (e.g., Bowman 2000), it is far from clear whether this is because they require a larger nutrient pool than savannas or just redistribute the same nutrient pool in different ways from grass. There seem to have been few attempts to predict absolute nutrient constraints on the amount of wood a soil can support. Nutrient concentrations in wood are low and, because closed rainforests occur on nutrient-poor soils in the tropics (Bowman 2000, Sarmiento 1992), it is unlikely that absolute nutrient content of soils generally limits forest distribution. A more likely explanation for soil correlates of forest/grass boundaries is that nutrient supply affects growth and productivity, which in turn influence rates of succession. Slow recovery rates of trees after periodic disturbance, such as fire or hurricanes, would promote savannas at the expense of forests on nutrient-poor soils (Kellman 1984).

Top-Down Control: Fire

Frequent fires have long been proposed as an alternative to climate and nutrient constraints on forest distribution. Fire exclusion experiments became popular from the first half of the twentieth century to test the fire vs resource hypotheses. In Africa, these experiments often consisted of three unreplicated treatments: annual burns early or late in the dry season and fire exclusion (e.g., Louppe et al. 1995, Trapnell 1959). Many were maintained for decades and some, such as the experiments at Kruger National Park in South Africa, are among the longest running field experiments in tropical ecology. The results provide unequivocal evidence that tree densities, biomass, and species composition in many savannas are not at equilibrium with resources but rather depend on the fire regime (Higgins et al. 2007, Russell-Smith et al. 2003). Moreover, fire exclusion often resulted in a complete biome switch, from humid savanna to closed forest, with examples from Africa (e.g., Louppe et al. 1995, Trapnell 1959), North America (Peterson & Reich 2001), and Australia (Woinarski et al. 2004). As in predator exclusion experiments in aquatic

systems (Carpenter & Kitchell 1994), fire exclusion triggers cascading changes in woody species composition. Rates of change from grassy to forested ecosystems varied on the order of a decade to half a century with slower rates on nutrient-poor or seasonally waterlogged soils (Kellman 1984, Louppe et al. 1995). Fire exclusion studies can indicate where, along a precipitation gradient, fire is the primary determinant of grassy biomes. In South Africa, shifts to forest have occurred at locations with >750 mm MAP, but more arid sites have maintained their grassy state, even after 50 years of fire exclusion (Bond et al. 2003a, Higgins et al. 2007).

A major problem with the fire hypothesis is explaining grass/forest boundaries. Though some boundaries coincide with topographic barriers to fire, such as lakes and rivers, others occur at soil boundaries with no obstacles to fire spread. The challenge is to predict boundary location from purely mechanistic models of fire behavior. Perhaps the biggest challenge is to explain why rain-forests exist at all, given that grass-fueled fires carry fire into forests (Cochrane & Laurance 2002).

Top-Down Control: Herbivory

Owen-Smith (1987) suggested that megaherbivores maintained open grassy ecosystems in many parts of the world before Pleistocene extinctions. In parts of Africa, elephants are major agents of adult tree mortality and may even structure biome distribution. When poaching reduced elephant populations in East Tsavo in Kenya, thorny savannas supporting a grazing fauna were replaced by *Commiphora* thickets (nongrassy) and the loss of grazers (Inamdar 1996). The influence of large mammals on opening forests and maintaining open grassy ecosystems needs more study, especially where the megafauna still exists. But in most savannas, livestock are now the major herbivores, and their effect on trees is complex, with strong interactions with fire.

MULTIFACTOR INTERACTIONS: DEMOGRAPHIC STUDIES

Single factor explanations, whether bottom-up or top-down, fail to explain inter- and intrabiome variation in tree biomass. The best evidence for multifactor interactions comes from demographic studies of trees. These show that recruitment is particularly difficult in grassy ecosystems. Unlike forests, a tree-fall gap in a savanna is not filled by continuous growth from juvenile plants. Grasses compete with seedlings and saplings, reducing their growth rate, whereas frequent fires and/or intense herbivory prevent saplings from escaping the grass layer. Consequently, replacement of a savanna tree can be delayed for decades. The long time lags in recruiting adult trees help explain the large difference between realized and potential woody biomass in grassy biomes. The implication is that ecosystem structure and biogeochemistry depend on the demography of trees. To understand ecosystem dynamics in grassy biomes requires that the demography of trees be incorporated. Plant traits important for demography, such as sprouting ability, are quite different from traits important for biogeochemical cycling, such as leaf traits that affect productivity and nutrient turnover (Díaz et al. 2004, Wright et al. 2004).

There is a vast literature on demographic studies of tree-grass interactions (see reviews by Scholes & Archer 1997, Van Auken 2000). There is also a rapidly growing literature on models that explore tree demography, often in the context of tree-grass coexistence (see Sankaran et al. 2004, Scheiter & Higgins 2007), or as a basis for savanna management (Liedloff & Cook 2007). The emphases here are on why demography matters in grassy biomes, why grassy biomes exist, and why trees within savannas seldom reach their resource potential. I also emphasize those aspects of tree demography that select for different traits in grassy ecosystems, especially where these differ from traits linked to ecosystem function.

Models have been important in synthesizing demographic information and thus helping to identify key processes (bottom-up and top-down) and key demographic stages (e.g., Higgins et al.

2000, Jeltsch et al. 2000, Sankaran et al. 2004). For example, Higgins et al. (2000) set out to explore conditions under which trees and grasses can coexist based on nonequilibrium mechanisms. Using a simulation model based on parameter values of South African savannas, they showed that tree-grass coexistence was possible over a wide rainfall gradient, given variable conditions for recruitment, and storage of successful recruitment events in long-lived adults. The results are consistent with the storage effect, a coexistence mechanism identified in theoretical models (Chesson & Huntly 1989). Simulated adult tree densities were most limited by seedling establishment in arid savannas and by sapling escape in frequently burned savannas. Sensitivity analyses showed that the latter was strongly influenced by fire responses and by sapling growth rates between fires. Adult survival rates also had major effects on adult densities in all savanna types. The model explicitly points to demographic bottlenecks as a major constraint on adult tree densities in savannas. The nature of these bottlenecks changes along environmental gradients.

Seedling Establishment

Wet season droughts are the most common cause of germinant mortality, with or without competition from grass. Since these are more likely in arid regions, the establishment phase is probably the critical demographic bottleneck in arid savannas (Higgins et al. 2000, Wiegand et al. 2006). Many, but not all, experimental studies have shown increased survival and growth of woody seedlings with grass removal. Few, if any, have shown complete seedling failure due to grass competition. As Van Auken (2000) pointed out, even low establishment rates would be sufficient to fill a grassland with woody plants over long time spans. Grass competition appears to be primarily belowground. The heterogeneity of grass root occupation of the soils may therefore be critical for seedling establishment (Partel & Wilson 2002). Jurena & Archer (2003) quantified heterogeneity of root biomass in a *Prosopis* savanna and the effect of different belowground gap size on *Prosopis* seedling growth and survival. Seedling performance was markedly affected by gap size, especially its vertical dimensions. However, the distribution of roots was sufficiently heterogeneous in this savanna to permit seedling establishment in the gaps. If grass roots occupy the soil more completely with increasing rainfall, such as in treeless mesic C_4 grasslands, woody seedlings may be completely excluded by root competition (Mills et al. 2006).

Fire has often been cited as a key factor in preventing establishment. Yet species vary greatly in seedling tolerance to burning. In frequently burnt savannas, seedlings can acquire the ability to resprout within their first growing season (Hoffmann 1999, Midgley & Bond 2001). Clonal propagation from root suckers is also common, reducing dependence on seedlings (Chidumayo & Frost 1996, Hoffmann 1999, Lacey & Johnston 1990). Seedlings are less tolerant of burning in more arid savannas and can be killed by fire years after establishment. Reduced fire frequencies allowing increased seedling establishment are thought to be a major cause of shrub invasions in North American grasslands (Van Auken 2000). Biome boundaries between forests and savannas may be maintained by frequent fires that prevent forest seedling establishment. In Brazil, experimental studies have shown that forest seedlings were killed by fire, whereas savanna seedlings survived fires (Hoffmann 2000). Seed and seedling predation, especially by small mammals, has significant effects on establishment in some savannas (e.g., Weltzin et al. 1997). However, few, if any, studies have shown that the effects of herbivore browsing on seedlings ultimately reduce adult tree populations.

Sapling Escape

Sapling banks are common in many frequently burnt savannas yet adult tree densities are low. Here sapling escape from the flame zone is the major demographic hurdle, and top-down control by fire
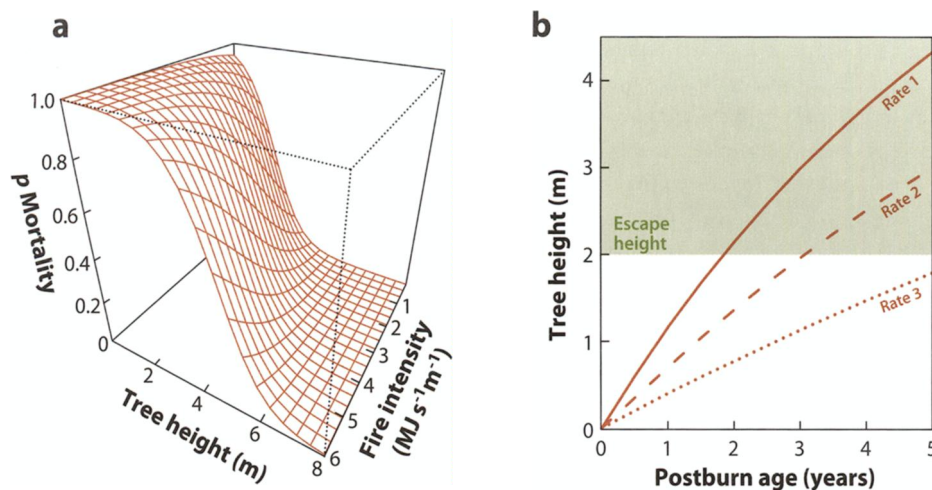
Figure 2

The probability of a sapling growing into a tree in frequently burned savannas depends on topkill of stems and the rate of postburn growth. (*a*) The relationship between topkill (p mortality), stem height, and fire intensity for an African savanna tree. The probability of topkill decreases sharply once plants reach escape height, 2–4 m in this example. (*b*) How sapling growth rates determine the period needed to reach escape height between topkilling fires. This period varies from a minimum of two, three, and more than five years for the three growth rates illustrated. Growth rate varies among species and is influenced by resource supply, which is influenced by competition with grasses. The interaction between the fire regime and sapling growth rates determines juvenile recruitment to adult size classes. Figures are drawn from unpublished data of E. February, S. Higgins, and W. Bond.

limits adult tree densities. Bond & van Wilgen (1996) coined the name "gulliver" for saplings that are trapped in the grass (Lilliputian) flame zone but that are largely unaffected by fire if they grow tall enough to escape the flames. They are very tolerant of fire, resprouting from fire-protected roots and lignotubers. Saplings can be trapped in the flame zone for decades. The probability of gulliver escape is determined by the frequency and intensity of fires causing stem death ("topkill"), and growth rates to escape height, above which stems survive fires (**Figure 2**). Several studies have focussed on topkill and how it varies with plant size, bark thickness and fire intensity (Gignoux et al. 1997, Hoffman & Solbrig 2003, Trollope 1984, Williams et al. 1999). Plant size is the most important predictor with a steep reduction in topkill in plants that have grown above a threshold size ("escape height"; **Figure 2**). High fire intensities increase this threshold, and bark properties account for relatively small interspecific differences.

Much less is known about sapling growth rates and their response to manipulation of resources or grass competition. Height growth in African miombo species was greatest in the first year after a burn, declining with postburn age (Chidumayo & Frost 1996). Saplings would require a six-year gap between topkilling fires to reach minimum escape heights, a rare event in these savannas. Maximum growth rates may be much higher in some savanna trees. Fensham & Bowman (1992) reported a record "breakaway" eucalypt sapling that grew 8 m in 3 years despite two successive burns. However, eucalypt growth rates are very sensitive to competition from adults and high growth rates have been recorded only in large canopy gaps. Changes in sapling growth rate may account for major changes in tree cover in the past and in the future. Bond et al. (2003b) used a DGVM to simulate growth responses to CO_2 (Woodward & Lomas 2004) and a demographic model to explore the consequences (Higgins et al. 2000) for adult tree densities in southern African savannas. Simulated sapling growth rates were so slow at low CO_2 that trees

would have been eliminated by grass fires in the last glacial. Simulated growth increases over the past century in response to large increases in atmospheric CO_2 caused large increases in tree densities. Experimental studies are urgently needed to establish the sensitivity of growth rates to local and global changes in bottom-up controls. The escape model is a simple way of evaluating their ecological significance under different fire regimes (**Figure 2**).

Browsing is analogous to fire in that, once saplings have grown beyond a height of 2–3 m, they are beyond the reach of most mammal herbivores. Chronic browsing would be needed to prevent saplings from growing to escape height in areas of high herbivore density. Periodic reductions in browser populations, equivalent to fire-free periods, provide escape opportunities. Prins & van der Jeugd (1993) have described such a situation in an African savanna where impala (*Aepyceros melampus*), a mixed grazer/browser that occurs in high densities, were reduced by disease to low densities, thereby allowing a cohort of acacias to escape. Using exclosures, Augustine & McNaughton (2004) showed that browsing by a small African antelope reduced the rate of shrub increase in an African rangeland from 137 to 7 shrubs ha^{-1} year^{-1}. Elephants altered shrub height-class distributions and relative species composition in this study but did not influence shrub densities. Weltzin et al. (1997) showed that black-tailed prairie dogs (*Cynomys ludovicianus*) in a North American savanna suppressed *Prosopis* saplings by heavy browsing on their colony sites. Eradication of a colony led to a doubling of canopy cover to densities comparable to off-colony stands within a 23-year period. Browsing may also interact with fire in preventing sapling escape. Browsing of postburn coppice regrowth suppressed acacia saplings more effectively than topkill by fire alone (Trollope 1980).

Adult Mortality

Whereas recruitment may depend on rare, brief opportunities, adults can persist for decades to centuries. Adult mortality is important in savanna demography because it affects the longevity of woodland patches. Background mortality rates of savanna trees range from 0.01 to 0.05 per annum (Higgins et al. 2000). Adult trees are not immune from fire damage, and species vary in their ability to repair damaged bark causing variation in death rates. Northern Australian adult eucalypts seldom survive more than a century because fires chimney up termite-hollowed stems (Williams et al. 1999). Some African acacias have intrinsically short adult life spans (Midgley & Bond 2001, Wiegand et al. 2006), little longer than their life as suppressed saplings. Major reductions in tree biomass may be caused by large, infrequent disturbances (LIDs) (Gillson 2006). For example, severe droughts, occurring at multidecadal intervals, caused extensive adult tree deaths in semiarid savannas in Queensland, Australia (Fensham et al. 2005). Fensham et al. (2005) showed that these LIDs are the primary reason why tree cover is lower than its "climate potential" in these savannas. They suggest that what matters is high variance at the arid end of the precipitation gradient, and not low mean annual rainfall. Climate change resulting in more frequent severe droughts would have major repercussions for tree cover. The drought hypothesis provides an alternative to recruitment bottlenecks for tree-grass coexistence in more arid savannas (Fernandez-Illescas & Rodriguez-Iturbe 2003, Van Wijk & Rodriguez-Iturbe 2002). Recruitment limitations may or may not influence the rate of postdrought recovery. A challenge for the drought hypothesis is to explain why, in arid regions, tree densities are lower in savannas than in adjoining dry deciduous forest and thickets.

Demographic Transitions and Environmental Variability

The circumstances leading to transitions from one demographic stage to the next (e.g., sapling to adult) vary in different types of savannas. They depend on rare temporal and spatial contingencies.

Interannual variability in rainfall often triggers transitions. High rainfall periods increase grass productivity, promoting fires and suppressing sapling escape in mesic savannas. In arid savannas, high rainfall periods have the opposite effect, promoting tree increases because moisture usually limits establishment and sapling growth. Droughts also have opposite effects in wetter and drier savannas. In mesic savannas, drought reduces grass competition and fire, thereby promoting sapling escape and thus causing an increase in tree biomass. In arid savannas, droughts kill saplings and adults, thereby reducing tree biomass.

Grazing intensity varies greatly in space and time. Heavy grazing generally promotes woody plants by reducing grass competition and fuel for fires in semiarid to mesic savannas. But heavy grazing, often coupled with heavy browsing, can also maintain sparsely wooded grazing lawns. Long intervals between fires promote sapling escape in wetter savannas. These may be caused by local spatial variation in fire intensity due to the vagaries of fire behavior or to landscape-scale effects of drought, or grazing, or both on fuel loads.

The demographic perspective emphasizes the dynamic nature of tree-grass interactions and the difficult combination of temporal scales. Grasses respond very rapidly to resource pulses, and recover rapidly from fire and herbivory. Woody seedlings and saplings are intrinsically slower responders to these factors, whereas a cohort of trees can persist for decades to centuries. Tree populations are regulated by a combination of bottom-up and top-down controls that are highly variable at different temporal and spatial scales. The complex hierarchy of timescales needs to be considered in the design of studies intended to quantify and compare the effects of different processes on tree-grass ecosystems. For example, contingent effects of a drought, reduced fire, and reduced browsing may trigger sapling escape over a period of three or four years. The resultant cohort of trees might persist for a century or more. Experiments of sufficient duration can reveal the necessary conditions for an escape event. Repeat photos or correlative analyses of determinants of tree cover will seldom have a temporal resolution.

PLANT FUNCTIONAL TRAITS

Plant trait variation between savannas and forests and within savannas is a useful indicator of what limits trees in grassy ecosystems. Forest/savanna comparisons show that juvenile sprouting is a key trait difference. In frequently burnt savannas, all trees resprout as juveniles, whereas forest species are weak or nonsprouters. Hoffmann et al. (2004) compared the growth and physiological responses of congeneric pairs of Brazilian forest and savanna tree seedlings. Savanna seedlings had higher root-shoot ratios and higher root TNC (total nonstructural carbohydrate) concentrations than forest species. They coped better with seasonal drought but also had sevenfold larger root reserves to support postburn sprouting. Hoffmann et al. (2004) concluded that, whereas seasonal drought would reduce establishment of forest seedlings, fire was the absolute constraint to success of forest species in savannas. In Australia, Fensham et al. (2003) compared the responses of forest and savanna species to a series of fires in savannas protected from burning for more than a century. Both forest and savanna species suffered high initial postburn mortality after the first fire, but many resprouted. Forest species were eliminated after repeated fires, whereas savanna species continued to resprout. Mature forest trees are also less tolerant of surface fire than savanna trees, usually attributed to thinner bark in forests (Cochrane & Laurance 2002). Many savanna trees replace the canopy after leaf scorch by epicormic sprouting and may differ in this respect from forest trees. Though there are surprisingly few rigorous studies comparing forest versus savanna traits, I found none that compare dry forest and thicket traits with arid savannas. We do not know how the demography or physiology of trees in arid savannas differs from adjacent nongrassy thickets. Comparative studies would be useful for exploring

physiological mechanisms of drought death and how competition with grasses might affect canopy cover.

Intrabiome variation in traits along environmental gradients has received some attention. Within African savannas, trees differ along nutrient gradients with microphyllous structurally defended trees dominating on nutrient-rich soils (or arid areas), and broad-leaved chemically defended trees dominating in nutrient-poor (and high-rainfall) regions (Scholes & Walker 1993). Woody traits also differ with different types of top-down control. African acacias can be classified into browse-tolerant or fire-tolerant groups. Saplings with densely ramified cage-like architectures predominate in heavily grazed savannas, whereas sparsely branched "pole" architectures prevail in frequently burned savannas, typically with large swollen roots containing high starch concentrations. Intraspecific architectural differences occur in the widespread *Acacia karroo*, with cage-like saplings in heavily browsed arid savannas and forest gaps and pole-like saplings in frequently burned savannas (Archibald & Bond 2003). The combination of a sparsely branched pole and swollen roots and storage organs seems to be a common feature of saplings in frequently burned savannas worldwide, facilitating sapling escape from the fire trap. Cage-like saplings may only occur where herbivore pressures are intense such as in some African savannas.

SUMMARY OF DEMOGRAPHIC STUDIES

Demographic studies indicate that grasses, directly or indirectly, have major effects on ecosystem structure by suppressing woody recruitment. Tree abundance cannot be predicted from ecosystem physiology alone–the vagaries of tree demography have to be considered. Both bottom-up and top-down controls influence the frequency of tree deaths and particularly the chances of juveniles escaping to replace them. The demographic perspective on what limits woody biomass is radically different from the resource partitioning hypothesis (Walter 1971) that has long dominated the savanna literature. It opens up new questions and different predictions on what structures communities, ecosystems, and biome distributions.

At the community scale, tree species assemblages would be structured by juvenile responses to top-down control. Where fires are frequent, canopy dominants would owe their success to differences in topkill and sapling growth rates and not to the ability of adults to compete for resources. Where the type of top-down control can switch between fire and herbivory, there should also be switches in tree species composition because fire and browsing select for different sapling traits (Archibald & Bond 2003). The escape hypothesis implies highly variable tree species composition where herbivores and fire can alternate as top-down controls.

The demographic perspective also has implications for global vegetation modeling. Current DGVMs use a small set of generic plant functional types (PFTs) defined by physiological attributes (e.g., broad-leaved deciduous, broad-leaved evergreen). These generic trees would be eliminated under realistic simulations of C_4 fire regimes in humid grasslands because sprouting is not included in the definition of any PFT. If demographic bottlenecks limit tree populations, then tree biomass in grassy biomes cannot be predicted unless DGVMs can simulate juvenile size classes. The importance of demography is open to testing by comparing simulated variation in savanna tree biomass to realized variation, with and without demographic controls.

GLOBAL CHANGE AND TREE COVER: THE BUSH ENCROACHMENT PHENOMENON

Increases of woody plants in grassy ecosystems have been observed in many parts of the world over the past century (e.g., Archer et al. 1995, Asner et al. 2003). The causes are much debated, with

some arguing for the importance of changes in land use (top-down control, especially increased grazing and decreased use of fire; Archer et al. 1995) and others for global drivers, particularly the effects of increasing atmospheric CO_2 on the tree/grass balance. Two distinct effects of CO_2 have been suggested, emerging from bottom-up consideration of changes in soil moisture, or top-down control on juvenile escape. The first argues that reduced transpiration with increasing CO_2 would indirectly favor trees by allowing deeper percolation of moisture into soils (Polley et al. 1999). This would favor woody plant establishment because of their deeper roots. Morgan et al. (2007) reported a five-year CO_2 enrichment study showing a 40-fold increase in aboveground biomass of a woody shrub in short grass prairie consistent with this argument. The second argues that woody plants would be able to escape fire and herbivory more readily owing to the direct effects of CO_2 fertilization on growth rates, resprouting ability (Hoffmann et al. 2000), and herbivore defense in seedlings and saplings (Bond & Midgley 2000). Although changes in land use are undoubtedly major drivers of woody invasion of grassy biomes, increases in atmospheric CO_2 might be an additional global driver tipping the balance to trees. For example, fire regimes that excluded trees in the past may no longer do so today because of CO_2 fertilization effects on recruitment.

The most commonly reported examples of bush encroachment are increases in savanna shrubs and trees. However there are also reports of complete biome switches from grassy ecosystems to closed forest and thicket. Brook & Bowman (2006) reported a landscape-wide expansion of forest (42% increase) in the Australian monsoon tropics over the past five decades, while Russell-Smith et al. (2004) reported a near doubling of forest patches in savannas in northeast Queensland from 1943 to 1991. In Kansas prairies, gallery forest increased in area by 69% from 1939 to 2002, fragmenting the prairie landscape (Briggs et al. 2005). In South Africa, scrub forest has invaded savannas in conservation, commercial ranching and communally farmed areas, with increases from 12% to 68%, 5% to 55%, and 3% to 27%, respectively, from 1937 to 2000 (B. Wigley. W.J. Bond & T. Hoffmann unpublished). The reverse pattern of rapid loss of tropical forest due to frequent intense fires has also been reported (Cochrane & Laurance 2002). Biome switches have cascading consequences for biodiversity and ecosystem function. We need a much better understanding of the dynamics of grass-forest boundaries to be able to predict which parts of the world have the potential for rapid biome shifts and what may trigger them.

ECOSYSTEM CONSEQUENCES OF CHANGES IN TREE COVER

Changes in tree cover can have important ecosystem consequences with feedbacks to the earth-atmosphere system. Even small increases in woody biomass in savannas represent a substantial carbon sink because of their large spatial extent (Asner et al. 2003, Houghton et al. 1999, Williams et al. 2005). Grasslands differ from forests not only in carbon stocks but also in their energy budget and hydrology (Hayden 1998). They typically have a higher albedo than forests, partly because they retain dead, reflective leaves over the dry season. Trees generally transpire more water than grasses because of their more extensive root system, greater leaf area, and greater canopy roughness. Consequently, reduction in trees reduces evapotranspiration and increases runoff with feedbacks to the regional climate (Hayden 1998). Extensive grass-fueled fires also have feedbacks to climate (Hoffmann et al. 2002). Black aerosols alter energy budgets and reduce the size of cloud droplets causing precipitation to be less frequent but more intense (Andreae et al. 2004, Koren et al. 2004), while savanna fires are important sources of NOx which influences tropospheric ozone formation (Hobbs et al. 2003). Evaluating the multiple atmospheric effects of large-scale shifts in tree abundance and/or grass-fueled fire frequencies on the earth-atmosphere system poses a major challenge for earth system scientists.

ORIGIN OF SAVANNAS

Palaeoecological evidence indicates that the distribution and extent of C_4 grassy biomes have varied at multiple temporal scales, from the recent past (Gillson 2004), through glacial-interglacial cycles (DuPont et al. 2000), and since their origin in the late Miocene (Cerling et al. 1997). The causes of the latter are also contentious and controversial. C_4 grassy biomes appeared abruptly in geological time, more or less simultaneously on different continents, and spread rapidly from their equatorial origins. Explanations for the abrupt origin and rapid spread of C_4 grass biomes have variously emphasized direct (bottom-up) and indirect (top-down) controls including decreasing atmospheric CO_2 through the Tertiary (Ehleringer et al. 1997) and increased seasonality of precipitation and more frequent fires associated with the onset of monsoonal climates in the Miocene (Keeley & Rundel 2005). Charcoal records in marine sediments increased exponentially from the late Miocene, closely tracking the spread of C_4 grasslands (Beerling & Osborne 2006, Keeley & Rundel 2005). Beerling & Osborne (2006) have made an intriguing qualitative analysis of the multiple earth-atmosphere feedbacks that may have promoted the spread of C_4 grassy biomes. This analysis demonstrates strong positive feedbacks of grasslands on climate that, in a low CO_2 world, would promote flammable C_4 grasslands at the expense of forests. In contrast to fire, mammals do not seem to be implicated in the early spread of C_4 grassy biomes. The diversity of grazing mammals declined as C_4 grasslands spread, a result attributed to their poor grazing quality (Cerling et al. 1997). Attempts to explain the grassland puzzle in contemporary landscapes need to take cognizance of the historical puzzle of what triggered the abrupt origin and rapid spread of these biomes in the past.

CONCLUSIONS

Vast areas of savannas occur under climates that can support forests. The lack of consensus on the major determinants of this widespread vegetation formation is embarrassing to the community of ecologists. Long-entrenched beliefs in single factor explanations (climate, fire, soils) are no longer tenable. Grasslands differ strikingly from woody ecosystems in the regeneration niche. Growth in tree populations can be suppressed for decades by the varying effects of grass competition, fire, and herbivory on recruitment. The very different temporal scales at which grass, saplings, and trees respond to environmental variability produces an intrinsically complex dynamic that varies in space, time, and along environmental gradients. Trees are increasing in many grasslands and grass-forest boundaries are shifting, with significant effects on ecosystem function and cascading consequences for biodiversity. Effective prediction and management of changes in C_4 grassy biomes will require a rare integration of traditionally separate disciplines, including ecosystem physiology, fire and herbivore ecology, and demography, working at diverse scales from local to global.

FUTURE ISSUES

1. Still needed are experimental studies on tree recruitment linking physiology and disturbance within and across grass/forest biome boundaries.

2. New insights are needed on what maintains grass/forest boundaries and the potential mechanisms, rates, and extent of rapid biome switches.

3. Palaeoecological studies are required to extend the historical record of changes in tree cover within grassy biomes and to document shifts from grassy to closed woody biomes.

4. Evolutionary origins and assembly of C$_4$ grassy biota has been neglected in the literature and in this review.

5. The role of C$_4$ grassy biomes in the earth-atmosphere system has been neglected relative to forests. Future progress requires integration of the complex feedbacks between fire, changes in tree cover or biome distribution, and climate.

6. Intercontinental contrasts will help test the generality of mechanisms thought to control tree cover and the manner in which different biotas affect the outcome.

DISCLOSURE STATEMENT

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