

A patch-dynamics approach to savanna dynamics and woody plant encroachment – Insights from an arid savanna

Kerstin Wiegand^{a,b,*}, David Saltz^{b,c}, David Ward^{b,d,1}

^a*Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544, USA*

^b*Mitrani Department for Desert Ecology, Jacob Blaustein Institute for Desert Research, Ben-Gurion University of the Negev, Sede Boqer 84990, Israel*

^c*Israel Nature and Parks Authority, 3 Olam vaOlamo Street, 95463 Jerusalem, Israel*

^d*Ramon Science Center, Jacob Blaustein Institute for Desert Research, Ben-Gurion University of the Negev, Sede Boqer 84990, Israel*

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Abstract

The coexistence of woody and grassy plants in savannas has often been attributed to a rooting-niche separation (two-layer hypothesis). Water was assumed to be the limiting resource for both growth forms and grasses were assumed to extract water from the upper soil layer and trees and bushes from the lower layers. Woody plant encroachment (i.e. an increase in density of woody plants often unpalatable to domestic livestock) is a serious problem in many savannas and is believed to be the result of overgrazing in ‘two-layer systems’. Recent research has questioned the universality of both the two-layer hypothesis and the hypothesis that overgrazing is the cause of woody plant encroachment.

We present an alternative hypothesis explaining both tree–grass coexistence and woody plant encroachment in arid savannas. We propose that woody plant encroachment is part of a cyclical succession between open savanna and woody dominance and is driven by two factors: rainfall that is highly variable in space and time, and inter-tree competition. In this case, savanna landscapes are composed of many patches (a few hectares in size) in different states of transition between grassy and woody dominance, i.e. we hypothesize that arid savannas are patch-dynamic systems. We summarize patterns of tree distribution observed in an arid savanna in Namibia and show that these patterns are in agreement with the patch-dynamic savanna hypothesis. We discuss the applicability of this hypothesis to fire-dominated savannas, in which rainfall variability is low and fire drives spatial heterogeneity.

We conclude that field studies are more likely to contribute to a general understanding of tree–grass coexistence and woody plant encroachment if they consider both primary (rain and nutrients) and secondary (fire and grazing) determinants of patch properties across different savannas.

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*Corresponding author. Present address: Institute of Ecology, University of Jena, 07737 Jena, Germany.

E-mail address: mail@kerstin-wiegand.de (K. Wiegand).

¹Present address: School of Biological and Conservation Sciences, University of KwaZulu-Natal, Scottsville, 3209, Republic of South Africa.

Introduction

Savannas are ecosystems dominated by trees and grasses. They are geographically extensive and socio-economically important in both tropical and temperate regions (Scholes and Walker, 1993; Scholes and Archer, 1997). All tropical and sub-tropical savannas occur in hot regions with a highly seasonal rainfall distribution with summer rain (Scholes and Walker, 1993), indicating that water stress is a common phenomenon in these savannas. Until recently, the coexistence of woody and grassy plants (hereafter in short ‘tree–grass coexistence’) was believed possible due to a separation of rooting niches. According to Walter’s two-layer hypothesis (Walter, 1971; Walker et al., 1981), water is the limiting factor for both grassy and woody plants. Grasses use only topsoil moisture, while woody plants use sub-soil moisture. Several non-spatially explicit models have shown that this hypothesis may indeed lead to tree–grass coexistence (Walker et al., 1981; Walker and Noy-Meir, 1982; Eagleson and Segarra, 1985). However, a spatially explicit simulation model by Jeltsch et al. (1996) showed that rooting-niche separation might be insufficient to warrant coexistence under a range of climatic situations. Field studies investigating root distribution and water uptake also produced mixed results. In these studies, great differences were observed in the degree of niche separation, depending on abiotic factors and the species involved (e.g. Hesla et al., 1985; Knoop and Walker, 1985; Mordelet et al., 1997; Weltzin and McPherson, 1997; Hipondoka et al., 2003). Thus, rooting-niche separation is unlikely to be a general mechanism explaining tree–grass coexistence.

Several new hypotheses have been put forward to explain tree–grass coexistence (for a recent review see Sankaran et al., 2004). One hypothesis is that disturbances are key determinants of savannas. According to this hypothesis, savannas are inherently unstable ecosystems that do not transform into stable grasslands or forests because they are pushed back into the (unstable) savanna state by relatively frequent disturbances (called ‘ecological buffers’ by Jeltsch et al., 2000) such as fire, human impact, or grazing (Scholes and Archer, 1997; Jeltsch et al., 1998a, 2000). For example, trees could invade grassland if the grass cover is reduced by herbivores or, inversely, an increasing tree cover could be reduced by fire, allowing grass to grow in the open areas. Disturbances also play a central role in the hypothesis that trees and grasses coexist due to a storage effect that levels out temporal fluctuations in tree recruitment success (Higgins et al., 2000). According to this hypothesis, temporal variations in fire intensity and rainfall lead to temporal variations in seedling establishment and tree recruitment. However, once established, trees persist in such an environment because their longevity is great enough to ensure reproduction in

favourable years. These hypotheses are not mutually exclusive and have a common focus on temporal stochasticity. Though many savanna models are spatial, a focus on spatial processes to explain tree–grass coexistence is uncommon. However, Jeltsch et al. (1998b) point out that spatial heterogeneities, e.g. in the distribution of seeds or safe sites for tree seedling establishment, in combination with low overall tree recruitment probabilities, could explain the widespread existence and persistence of savannas. Also, Rodriguez-Iturbe et al. (1999) focus on space. They yield a stable equilibrium of tree–grass coexistence in a spatial model considering local spatial competition for soil moisture in combination with temporal (daily) patterns of water use (Rodriguez-Iturbe et al., 1999).

Woody plant encroachment

‘Woody plant encroachment’ is an increase in woody plant density typically resulting in impenetrable thickets, suppressing palatable grasses and herbs. The encroaching woody plants are often unpalatable to domestic livestock. Therefore, woody plant encroachment reduces the carrying capacity for domestic livestock in savannas. Woody plant encroachment is common in savannas and a reduction of the carrying capacity of savannas is of great significance because savannas contain a large and rapidly growing proportion of the world’s human population, including many pastoralists (Lamprey, 1983; Scholes and Archer, 1997). Attempts to explain woody plant encroachment begin with Walter’s two-layer hypothesis (Walter, 1954; Noy-Meir, 1982). It is assumed that if grasses are removed, e.g. by heavy grazing, grass roots extract less water from the top soil layer, allowing more water to percolate into the sub-soil, where it is available for woody plant growth. Even though it has become evident that rooting-niche separation is not an ubiquitous pattern (see above), it is still generally believed that overgrazing is the cause for woody plant encroachment due to changed grass–tree competitive interactions, but also due to loss of fuel leading to a disrupted fire regime (Midgley and Bond, 2001). Several studies have shown the increase of woody plant abundance under heavy grazing (Van Vegten, 1983; Skarpe, 1990a, b; Perkins and Thomas, 1993). However, other studies do not support this theory. Recruitment in honey mesquite (*Prosopis glandulosa*) is not regulated by herbaceous biomass or density (Brown and Archer, 1989, 1999), establishment of *Acacia karoo* seedlings is not influenced by several treatments influencing herbaceous density (du Toit, 1972), and germination of the heavily encroaching species *Acacia mellifera* is much more sensitive to rainfall than to grazing (Kraaij and Ward, in press). Furthermore, Andersson (1856) reported woody plant encroachment

in areas in Namibia that had not, according to historical records, been heavily grazed. Therefore, overgrazing is unlikely to be ubiquitously the most important factor causing woody plant encroachment. Furthermore, overgrazing in combination with rooting-niche separation is not a prerequisite for woody plant encroachment because encroachment may occur on soils too shallow to allow for root separation (Wiegand et al., 2005). An alternative hypothesis that increases in global CO₂ levels have led to a proliferation of woody plants, and the mechanisms causing this possible proliferation are still being debated (Archer et al., 1995; Polley et al., 1997; Bond and Midgley, 2000). Archer et al. (1995) argue for wooded grasslands in the USA that positive correlations between the spread of woody plants and atmospheric CO₂ are not cause and effect. However, several mechanisms have been proposed, which may explain a positive influence of atmospheric CO₂ concentrations on woody plant abundance: (i) Rising CO₂ levels favour C₃ relative to C₄ synthesis, thus increasing the quantum yield and thus growth of C₃, but not C₄ plants. (ii) Elevated CO₂ may reduce transpiration rates of grasses causing deeper percolation of water and thereby favouring woody species (Bond and Midgley, 2000; Polley et al., 2003). Furthermore, an increased amount of carbon may become available for (iii) a faster escape of seedlings from the zone of influence of grass fires (Bond and Midgley, 2000), or for (iv) investments in carbon-based defence compounds, such as tannins, which are the main defence compounds of many encroaching trees but not of grasses (Ward and Young, 2002).

Both savannas and woody plant encroachment are widely distributed and have been intensively studied. Nevertheless, they are not well understood (Midgley and Bond, 2001; Sankaran et al., 2004; Ward, 2005). Especially for woody plant encroachment, the poor results of woody plant control measures support the notion that the causes of woody plant encroachment are poorly known (Teague and Smit, 1992; Smit et al., 1996). Furthermore, tree–grass coexistence and woody plant encroachment have mostly been investigated as separate phenomena even though there is no evidence that this should be the case. In the following, we present an alternative hypothesis explaining both tree–grass coexistence and woody plant encroachment in arid savannas based on patch-dynamic systems and stochastic rainfall patterns. For the purpose of this paper we distinguish between arid savannas and fire-driven savannas depending on whether fuel production is large enough to make fire an important factor. Rather than trying to uniquely sort savannas into two groups, the idea behind this distinction is to gain new insights by temporarily viewing savannas from a different angle. After introducing our patch-dynamic savanna hypothesis, we summarize multi-scale patterns of tree distribu-

tion from an arid savanna in Namibia (Wiegand et al., 2005), which are in agreement with our hypothesis. Thereafter, we attempt to extend our hypothesis to fire-driven savannas. Our focus is on tropical and subtropical savannas that are water-limited (by high evaporation rates) even though rainfall may be as high as 1800 mm per year (Johnson and Tohill, 1985).

Patch-dynamic arid savanna hypothesis

Two reviews of savanna dynamics (Skarpe, 1992; Scholes and Archer, 1997), reviewing large numbers of detailed field studies, made an interesting attempt to integrate the array of observations reported in the literature. For example, Scholes and Archer (1997) ask the question: ‘Is the tree–grass mix in savannas stable or unstable?’ Scholes and Archer (1997) and Skarpe (1992) argue that savannas are both stable and unstable depending on the scale of observation. Competition experiments are typically conducted at a small spatial scale and show that mature trees are competitively superior to grasses, while grasses tend to outcompete immature trees (e.g. Moore et al., 1988). However, weakening the suppressive effect of the grass layer on young trees in a patch of a few hectares for a few years by overgrazing and/or fire can lead to an open savanna patch being converted to a tree-dominated thicket (woody plant encroachment). Once established, the thicket may take decades to revert to an open savanna (Scholes and Archer, 1997). At the scale of the whole landscape, savannas can be in a stable equilibrium, persisting over millennia due to the fact that the landscape consists of a shifting mosaic of many patches in different states of transition between grassy and woody dominance (Watt, 1947; Remmert, 1991; Turner et al., 1993; Scholes and Archer, 1997). The scarcity of field data on multi-scale patterns in savanna might be the reason why recent reviews of tree–grass coexistence in savannas discuss the stability of savannas without explicit reference to spatio-temporal scales (Jeltsch et al., 2000; House et al., 2003; Sankaran et al., 2004). Motivated by characteristic multi-scale patterns of tree distribution in an arid savanna (summarized in the section ‘Pattern of tree distribution in an arid savanna’ below) and the advances in our understanding of the role of space and the nature of equilibrium in other fields of ecology (Perry, 2002), we further develop the hypothesis of savannas as patch-dynamic systems.

Arid savannas are water-limited. In these systems, woody vegetation needs above-average precipitation for germination and subsequent establishment (e.g. O’Connor, 1995). To keep the soil moist for a period sufficient for germination, several rain events are necessary (Obeid and Seif El Din, 1971; Wilson and Witkowski, 1998).

However, rainfall in arid regions is often very patchily distributed, both in time and space with rain cells as small as 1 km² in diameter (Green, 1969; Sharon, 1972, 1981; Bell, 1979; Prins and Loth, 1988; Ward et al., 2004). Therefore, the spatial overlap of several rainfall events keeping the soil moist (say, for several weeks) is a rare occurrence that, when it occurs, provides the opportunity for germination and subsequent survival of woody plants. In addition to local seed availability, spatial overlap of several rainfall events within a short time frame is a necessary condition to create a recruitment event, which will result in a patch of woody plant encroachment. Depending on the woody and grassy species involved, other conditions such as appropriate temperature, or nutrient availability may have to be met to facilitate germination. The patchiness of rainfall leads to patchy vegetation patterns (several hectares in size; cf. below) within a range of intermediate long-term rainfall levels only. If average rainfall is too low, there is insufficient soil moisture to support tree growth, while above a certain amount of rainfall and if fire is suppressed, savannas or dense woodlands with mixed age distribution develop (K. Wiegand, pers. observ.; Belsky, 1990). The classification of long-term rainfall as ‘intermediate’ depends on local conditions (e.g. soil water holding capacity; topography affecting lateral flow) that translate precipitation events into water available to individual plants (Wilcox et al., 2003; Kirkham, 2005).

New woody plant encroachment will occur in patches of open savanna for the following reasons. (i) As already mentioned, in arid systems, rainfall sufficient for germination is a rare event compared to the longevity of woody plants. And (ii) many woody savanna plants including the very common genus *Acacia* (Schulze et al., 1991) are ‘canopy intolerant’ (e.g. Smith and Goodman, 1986). Thus, in many savanna systems, competition between adult trees and seedlings will prevent establishment of new trees when the adult trees are still vigorous, i.e. in non-open savanna (Smith and Goodman, 1986; Milton, 1995). These considerations show that the size of tree-encroached patches is determined by the size of the area within which the rainfall was sufficient for germination and the availability of open savanna within this area. All these factors (as well as local seed availability, nutrient availability, and microclimate, as discussed above) have to be coincident in space to create a tree-encroached patch. Consequently, tree-encroached patches will always be smaller than individual rain patches. Thus, given the spottiness of rainfall, tree-encroached patches will be in the order of several hectares or smaller (cf. below, Wiegand et al., 2005). Note that there is also patchiness at finer spatial scales such as at the scale of single trees, which is not addressed in this paper (e.g. Belsky and Canham, 1994; Wiegand et al., 2005).

With time, growth and inter-tree competition will convert the tree-encroached patch to an open savanna. Similar processes have often been reported in the literature, typically at the stand level, i.e. not spatially explicit (e.g. Watt, 1947; Bugmann, 2001). At the plant level, this spatially explicit self-thinning process might appear as follows: Assume that the tree seedlings are all of equal size and spatially distributed in a hexagonal pattern with crowns touching each other. If one of the seedlings has a competitive advantage over the others (Fig. 1a), this seedling is able to draw more resources (water and nutrients) than its immediate neighbours and thereby kills these neighbours and grows noticeably in size (Fig. 1b). This gives seedlings in the second circle around the ‘centre’ seedling the opportunity to access more resources, to grow and to use even more water and nutrients (Fig. 1c). Distances from the focal seedling to the seedlings in the circle of surviving plants are not identical. Therefore, every second plant along this circle has a disadvantage, which, with time, leads to mortality of every second seedling in the ring (Fig. 1c). Furthermore, the increased size of the surviving seedlings leads to suppression and finally the death of the seedlings in the third row (Fig. 1d). The death of these seedlings gives seedlings in the fourth row access to more water and nutrients, leading to their growth (Fig. 1e) and the death of the next ring and so on. Thus, one somewhat competitively superior seedling in a patch of densely packed seedlings can lead to a ‘honeycomb-rippling effect’ of mortality and growth of individuals. As seedlings continue to grow, they reach a dense hexagonal pattern again (Fig. 1f), and the process may start all over again, continuing many times until the final tree size has been reached. Of course, in nature, seedlings are unlikely to be evenly spaced. However, due to the successive thinning, the arrangement of trees becomes more and more regular. Thus, we predict increasing evenness of inter-tree distances with increasing size. In addition, inter-tree distances should increase with increasing tree size due to root competition. This is because the horizontal extent of savanna tree roots is about 10 times the extent of their canopy (Smit, 2004), and thus, for larger trees, the hexagonals in Fig. 1 represent root extent rather than canopy size. Accordingly, the final outcome predicted by the honeycomb rippling model is an open savanna. An explicit consideration of this self-thinning process in models of savanna dynamics can facilitate estimates of the temporal duration of the transition from tree-encroached patches to open savanna (Wiegand et al., in revision); information that, due to the long time scales involved, cannot easily be measured in the field and that cannot be derived from spatially implicit gap models (Bugmann, 2001).

The honeycomb rippling model is supported by size and spatial distributions in *Acacia reficiens* in arid

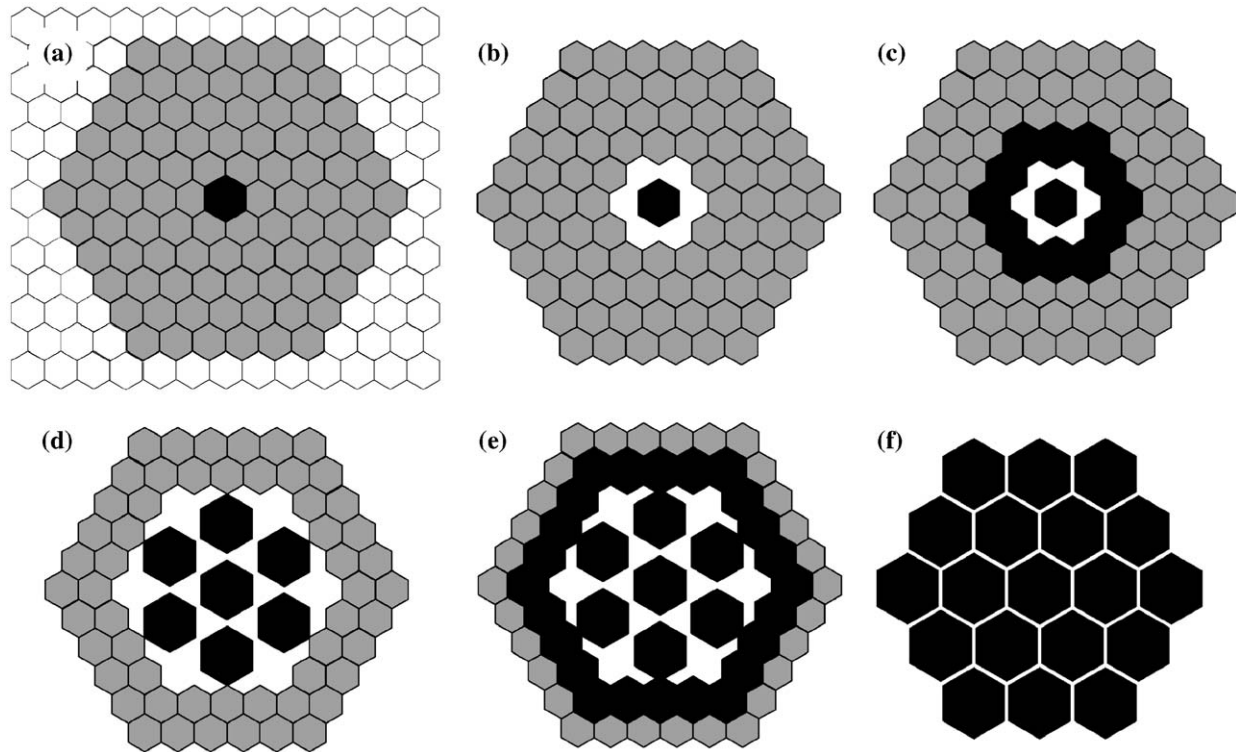


Fig. 1. Honeycomb rippling model. Figures show a time series of hexagonal sub-sets of a larger patch. Each (small) hexagonal represents a tree, the relative sizes of the hexagonals represent relative tree sizes. Black filling of the hexagonals indicates trees acquiring sufficient resources to survive the competition with their neighbours. See text for further explanations.

Namibia (trees are spaced further apart and with more even inter-tree distances with increasing size; Ward, 2005) and by patterns of growth and mortality observed in long-term experiments of red alder *Alnus rubra* and loblolly pine *Pinus taeda* (DeBell and Harrington, 2002; K.M. Meyer et al., unpubl. results). Interestingly, the honeycomb-rippling model shows that woody plant encroachment can be a natural recruitment process for savannas. Further research is necessary on water balance and the physiological mechanisms required by plants to survive in the highly seasonal savanna environment. Water balance studies are needed to understand the mechanisms by which encroaching trees survive the first dry season and how competition for water between adult trees affects differential survival. Such studies will add the physiological mechanisms to the honeycomb rippling model in specific cases and the local cycles between open savanna and bush encroachment in general. From woody plant encroachment being a natural recruitment process, it follows that encroachment is a phenomenon that can occur without fire (e.g. in our study area described below) and without over-grazing (because savannas were already widespread in pre-settlement times).

Why is the patchiness of arid savannas sustained over long time periods? – If mature stands are the results of

past woody plant encroachment, these stands would be even-aged. Because the occurrence of several rainfall events in a single patch is very rare, chances are high that most trees in a mature stand will die before a new series of suitable rainfall within that stand occurs. Moreover, cohort senescence is a predisposing cause of mortality (Young and Lindsay, 1988), resulting in synchronized mortality during extended drought periods (Fensham and Holman, 1999; Sharp and Bowman, 2004) or other common stress factors. For example, newly encroaching trees growing in the inter-canopy spaces may enhance the death of aging trees. Complete dieback of a tree stand before new woody plant encroachment occurs would not interrupt the cycle because there will be a seed influx from trees in adjacent patches. In absence of persistent seed banks, years without seed production may result in a delay of the new recruitment event. In any case, synchronized aging and mortality of tree patches reinforces the patchiness of savannas caused by rain that is stochastic in space and time. Importantly, under this hypothesis, woody plant encroachment, mature stands and open savanna are three states of the same system, a patch-dynamic system co-dominated by woody and grassy plants. Within this idea, patches of woody plant encroachment are an integral part of savanna dynamics.

Pattern of tree distribution in an arid savanna

In Wiegand et al. (2005), we investigated the patterns of tree, grass and soil nutrient distribution on several scales along a rainfall gradient, from about 100 to 200 mm year⁻¹ in the western edge of the Khomas Hochland, Namibia. At the study site, monthly rainfall measured in 14 rain gauges (average nearest-neighbour distance: 3.6 km, min 1.7 km, max 5.2 km) for 3 years was not spatially correlated (Ward et al., 2004). Here, we summarize the results of a survey of tree size distributions along 53 line transects, each including up to 60 trees, totalling to 2825 trees (Wiegand et al., 2005). Transects are much shorter (average length 300 m; average nearest-neighbour distance between transects 700 m) than the extent of the study area along the rainfall gradient (about 15 km). Therefore, average rainfall conditions are virtually identical within each transect, but differ between transects. The study site is characterized by a shallow layer of sandy soil (<5–15 cm deep) overlying vertically oriented schist. Thus, roots of both woody and grassy plants are confined to a thin soil layer, which means that Walter's two-layer hypothesis cannot explain woody plant encroachment and savanna dynamics in our study area. Furthermore, due to the arid climate, grass biomass is rarely great enough to fuel fire, meaning that fire is virtually absent. Nevertheless, throughout this rainfall gradient, we found both tree–grass coexistence (i.e. grass-dominated areas with interspersed trees) and woody plant encroachment (i.e. impenetrable woody thickets, which – following our hypothesis – constitute a recent local increase in woody plant density). The predominant woody species is *A. reficiens*, a thorny tree. Virtually all of the size–frequency distributions observed on single transects are bimodal (62%) or unimodal (34%). Both bi- and unimodality occur and are equally frequent across the entire rainfall gradient investigated (Wiegand et al., 2005). In other words, the chance of finding a bimodal or unimodal tree stand is independent of the rainfall gradient. Furthermore, mean transect-tree heights are spread across the entire range of tree sizes, independent of local rainfall intensity. Tree density drops drastically with increasing mean tree size in the transects (Wiegand et al., 2005). Thus, transect-tree size–frequency distributions with a mode at small tree sizes (e.g. Fig. 2a,c,d) come from tree-encroached patches while modes at large tree sizes (e.g. Fig. 2b) represent open savanna. Bimodal size distributions (such as Fig. 2c) can be explained by a transition, i.e. new woody plant encroachment within previously open savanna. Bimodality can also arise due to noise in the pattern caused by small or large trees being interspersed in a patch of open savanna or bush-encroachment, respectively (cf. Fig. 2b and d). A qualitative estimate from a slow-moving vehicle

showed that the spatial extent of these patches is on average about 280 m in length (min 50 m, max 600 m; Wiegand et al., 2005).

The honeycomb-rippling model leads to the prediction that trees in patches with even-sized stands will exhibit increasing nearest-neighbour distances with increasing tree size. To test this idea, the canopy diameter and the distance to the nearest neighbour was measured in 16 even-sized stands (Wiegand et al., 2005). Distance to nearest neighbour increases significantly with canopy diameter (Ward, 2005). We also predicted that successive thinning will convert an initial random spatial distribution of seedlings to a regular pattern of tree distribution. Consistent with this, the coefficient of variation in nearest-neighbour distance decreases with tree size (Ward, 2005), i.e. the trees become more evenly dispersed as they become larger.

To sum up, we discuss these patterns with respect to the patch-dynamic savanna hypothesis. Typical tree size–frequency distributions observed by us are depicted in Fig. 3a–d. Replacing time by location and assuming that tree size and age are at least weakly correlated, we can interpret these four graphs as snapshots of a local vegetation cycle. Starting from a unimodal distribution representing a cohort of relatively small trees (Fig. 3a), trees grow with time and the distribution shifts towards greater tree sizes (Fig. 3b). During this transition, inter-plant distances become increasingly even (Ward, 2005). This is also evident from the range of nearest-neighbour distances divided by canopy size of individual trees, which is much larger for small (7.2) than for large (2.0) trees (Wiegand et al., 2005, see also Skarpe, 1991). By the time the large trees become larger and almost die out, a woody plant encroachment event takes place (Fig. 3c). With time, the mode of the small trees moves towards larger tree sizes and the second mode becomes smaller and smaller (Fig. 3d), eventually leading back to a unimodal distribution (Fig. 3a). This cycle is principally the same across the entire rainfall gradient. Obviously, our savanna is composed of many patches at different stages of this cycle. The observed changes in tree size–frequency distributions may be indicative of natural birth and death cycles as well as of the process of bush encroachment; i.e. bush encroachment is a natural part of birth and death cycles of this species. In other words, if our interpretation is correct, this savanna is a patch-dynamic system locally cycling between woody plant encroachment and open savanna. If the decrease in tree density during the transition from woody plant encroachment to open savanna was due to tree mortality independent of the location of neighbours, nearest-neighbour distances would span a large range of values. However, nearest-neighbour distances increase significantly with increasing tree size (Gutierrez and Fuentes, 1979; Smith and Walker, 1983; Smith and Goodman, 1986, 1987; Ward, 2005; but see Couteron and Kokou,

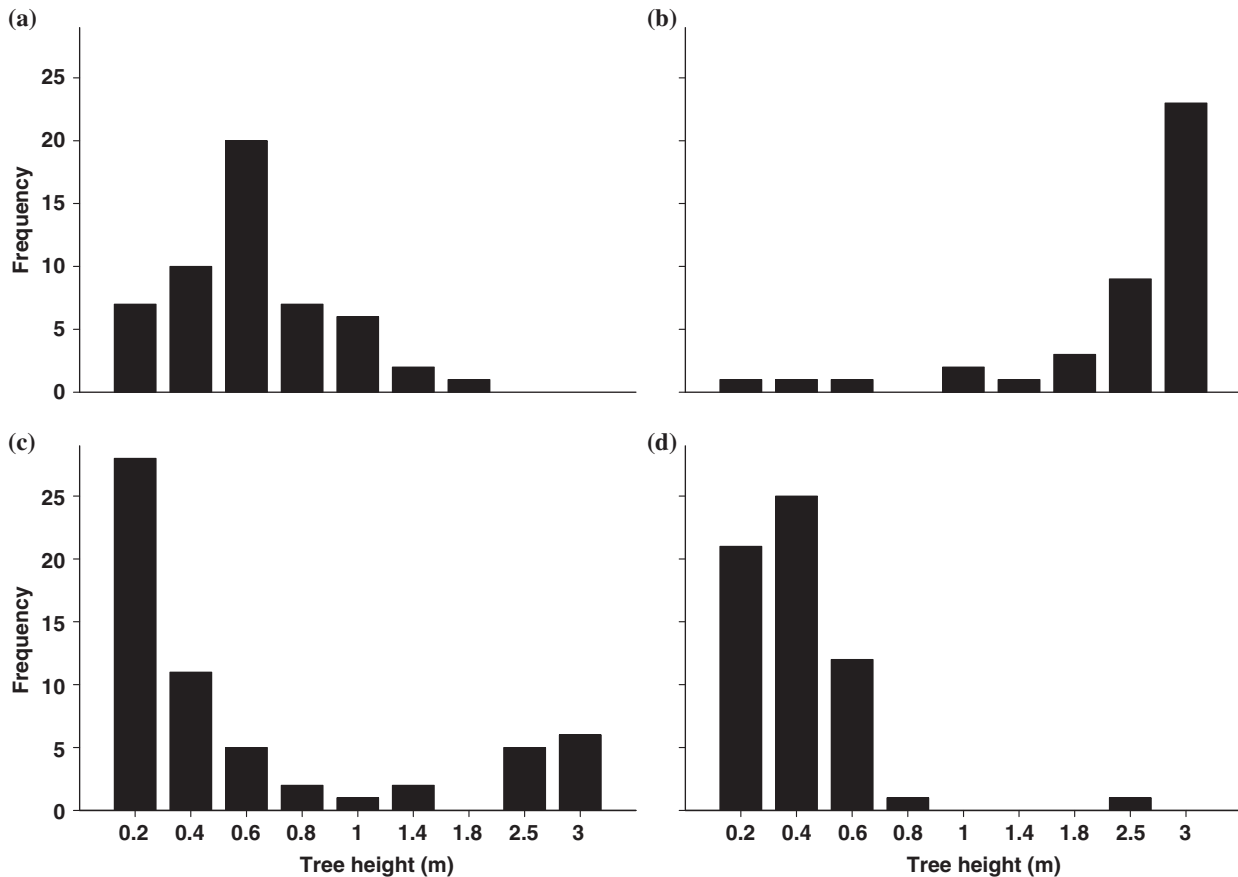


Fig. 2. Representative tree size–frequency distribution observed within line transects (Wiegand et al., 2005). Transects shown contain 53 (a), 41 (b), 60 (c) and 60 (d) trees.

1997) indicating that competition is a major determinant of spatial tree distribution at all life stages.

On the landscape level, the overall size–frequency distribution of all transects combined declines monotonically. For a range of sizes, the distribution follows almost perfectly a negative exponential distribution. Negative exponentially declining size–frequency distributions are characteristic of stable (model) systems that are in equilibrium with constant birth and death rates (Adler, 1998). Although local recruitment and mortality are clearly not constant through time, on average across the landscape they may well approximate constant birth and death rates. Thus, the overall size–frequency distribution is in agreement with the idea that the studied savanna system is in equilibrium at a landscape scale (Wiegand et al., 2005).

Patch-dynamic fire-driven savannas

Similar to arid savannas, tree recruitment (i.e. seedling germination, establishment and/or transition to mature size classes) is a bottleneck in tree dynamics of

fire-driven savannas (Sankaran et al., 2004). There are several causes for this bottleneck. Due to high evapotranspiration during the hot growing season, periods of inadequate soil moisture during the growing season are frequent even in moist savannas and limit tree recruitment (Medina and Silva, 1990; Harrington, 1991; O'Connor, 1995; Hoffmann, 1996; Wilson and Witkowski, 1998; Barnes, 2001). In addition, the spatio-temporal distribution of soil moisture affects tree recruitment indirectly via its positive influence on grass biomass (fuel load) and its negative influence on grass moisture (flammability), i.e. by its influence on the fire regime. Fire is an important factor for tree recruitment in fire-driven savannas because seed mortality, seedling mortality and topkill increase with fuel load and flammability. However, mortality and topkill decrease with seedling size (Danthu et al., 2003; Hoffmann and Solbrig, 2003; but see Meyer et al., 2005). Thus, the direct effects of fire reduce tree regeneration in all tree species and retards transition to adulthood in tree species which can resprout from rootstocks after damage of aboveground structures (Gignoux et al., 1997; Midgley and Bond, 2001). Even though grasses are probably not able to control tree establishment,

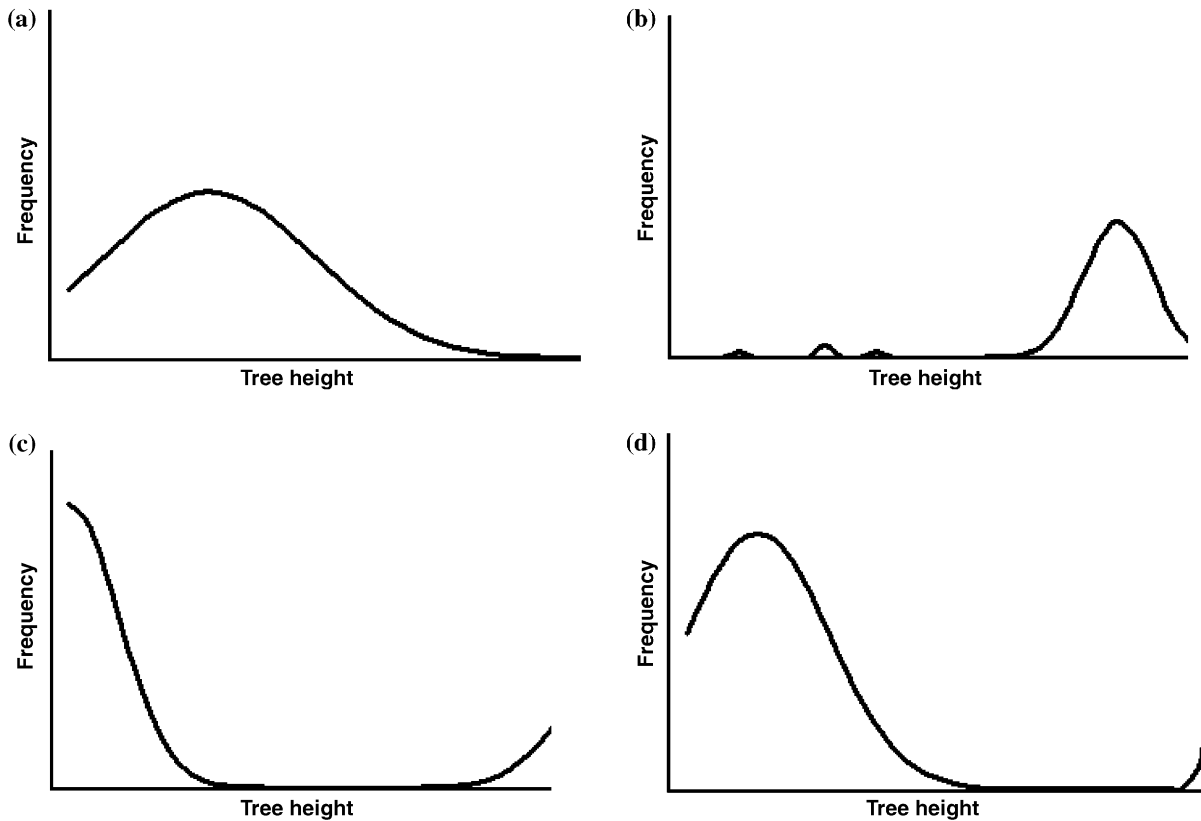


Fig. 3. Conceptual model of the development of tree size–frequency distribution over time in patches. The graphs are idealized sketches of the size–frequency distributions observed along a total of 53 line transects, which are described in Wiegand et al. (2005). Each transect contains up to 60 trees. The four cases represent 19 (a), 5 (b), 5 (c) and 23 (d) transects.

grass biomass may also directly add to the recruitment bottleneck via competition with tree seedlings (Moore et al., 1988; Scholes and Archer, 1997), but the negative effect of grass can be reduced by fire reducing the grass biomass (i.e. an indirect, positive effect of fire on tree regeneration). Finally, tree recruitment is also affected by animals via seed distribution as well as grazing and browsing. Grazing has two indirect effects on the tree recruitment bottleneck by reducing grass biomass and thereby (i) reducing competition from grasses, and (ii) altering the fire regime, while browsing may retard transition to mature size classes (Bergström, 1992; Augustine and McNaughton, 2004).

Similar to arid savannas, tree recruitment in fire-driven savannas is not only a temporal bottleneck in savanna tree dynamics, but also spatially highly variable. In contrast to arid savannas, patchiness in tree recruitment is not primarily caused by rainfall (high spatio-temporal variability of rainfall is characteristic of arid areas; Bell, 1979), but by existing patchiness in vegetation, patchy grazing and browsing, patchiness in fire, as well as interactions among these factors. By existing patchiness in vegetation we refer to tree clumps (Hochberg et al., 1994; Belsky, 1995; Jeltsch et al., 1996), and mosaic patterns in the grass layer (Belsky, 1995;

Augustine, 2003). The effect of grazing on spatial heterogeneity depends on the interaction between the spatial pattern of grazing and the pre-existing spatial pattern of vegetation (Adler et al., 2001). Elephants are the best-known example of browsers influencing the spatial distribution of woody vegetation (Belsky, 1995; Augustine and McNaughton, 2004). Fires burn patchily as a result of varying wind speeds, topography and fuel loads, and thereby create and maintain patchiness (Frost and Robertson, 1987; Hochberg et al., 1994; Jeltsch et al., 1996; Getzin, 2002).

Creation of a new patch of woody seedlings in a fire-driven savanna may proceed as follows. If in a patch of open savanna the grass layer is reduced by a hot fire, by a series of dry years, or by heavy grazing reducing both competition and fuel load, mass recruitment of tree seedlings is possible if a period of good rains follows (Frost and Robertson, 1987; Danthu et al., 2003). This patch of trees may become even denser in the subsequent years because the weaker grass layer cannot sustain intense fire within the tree patches and tree seedlings can now escape fire in these patches (Frost and Robertson, 1987; Menaut et al., 1990). Also, canopy intolerance is not as pervasive a pattern as in arid savannas (Hoffmann, 1996; Hoffmann et al., 2004).

However, inter-tree competition should level out most size differences, leading to a dominant tree size class; e.g. shrubs and small trees (<8 m) dominating clumps consisting of shrubs and tall trees (12–15 m) in Lamto, Côte-d'Ivoire (Menaut et al., 1990). Conversion to a patch of predominantly mature trees due to growth and self-thinning as described by the honeycomb-rippling model is principally similar to arid savannas, but initially it will be delayed by fires and browsing. Eventually, facilitated by fire, synchronized mortality of a majority of the woody plants within the patch, which are weakened by competition, will break apart the patch, remove fire protection and convert this patch back to open savanna with few trees left. Thus, fire and destruction of seeds and seedlings return in this patch (Young and Lindsay, 1988; Menaut et al., 1990; Danthu et al., 2003).

Discussion

In their overview of African savannas, Scholes and Walker (1993) describe four key determinants of savanna structure and function: water supply, nutrient supply, fire and herbivory. They differentiate between primary determinants (water and nutrients) and secondary determinants (fire and herbivory) of savanna structure (see also Hills, 1965). Water and nutrient supply are partly related to geology (Cole, 1982). This means that geology predetermines the array of vegetation types that can grow within a certain area. In addition to the average amount of moisture available to plants, the spatio-temporal distribution of water will determine the actual species present and how they are distributed in space. In this way, the potential geographic distribution of savannas is determined by the primary determinants, water and nutrients as they are determined by geology and climate. For example, in African savannas, broad-leafed savanna occurs on ancient, highly weathered surfaces while the fine-leafed savanna is restricted to recently formed, nutrient-rich soils (Scholes and Walker, 1993; Scholes, 1997). However, savanna distribution is influenced by both primary and secondary determinants. Apart from historical influences, fire and herbivory will enlarge and in some cases reduce the geographic extent of savannas. This is because herbivores can regulate grass biomass which itself has an influence on fire intensity and, finally, fire intensity may regulate woody plant growth and regeneration (Scholes and Archer, 1997; Jeltsch et al., 2000; Ward, 2004). These considerations show that disturbances, spatial heterogeneities other than patchiness of rainfall, and the long lifespan of trees favour tree–grass coexistence. However, they are secondary determinants of savannas, and for a full understanding of tree–grass coexistence in arid savannas it seems necessary to

acknowledge the patchiness of savannas driven by patchy rainfall.

If our hypothesis is correct, research in savanna ecology and on woody plant encroachment has focused on secondary determinants and overlooked primary determinants. Field studies typically investigate detailed aspects of savanna dynamics, often not paying attention to the overall picture (see also Davis et al., 2005). The homogeneity of our Namibian study area enabled us to ascertain the patch-dynamic aspect of savannas. Even though the idea of patchiness in vegetation dynamics is long-established (Watt, 1947) and even though there is virtually no mention of patches dominated by woody or by grassy plants in the savanna literature (but see Menaut et al., 1990; San José and Fariñas, 1991; San José et al., 1991; Skarpe, 1991), two relatively recent reviews of savanna dynamics (Skarpe, 1992; Scholes and Archer, 1997) and a recent paleoecological study (Gillson, 2004) suggested that savannas are patch-dynamic systems. This indicates that our observations in Namibia might be of general importance.

The usefulness of a patch-dynamic view of savannas will depend on the ability to predict tree–grass ratios as a function of environmental conditions. The tree and grass species that may live in a given environment are influenced by the primary and secondary determinants as outlined above. Additionally, the tree–grass ratio in patch-dynamic savannas depends on the duration of the different stages of the cycle including the probability of formation of a new tree-encroached patch. However, as will be explained below, the size of the patches is usually not important for estimating tree–grass ratios. For the sake of simplicity, we will consider two patch stages only, viz. woody plant encroachment and open savanna. The duration of patches of open savanna depends on the probability of formation of new woody plant encroachment in a patch of open savanna. This probability is a combined function of the factors contributing to the recruitment bottleneck. For example, in arid savannas, this probability can be estimated by combining knowledge on water requirements for germination with models of soil moisture dynamics, driven by models of daily rainfall and knowledge on soil properties (Zucchini et al., 1992; Wilson and Witkowski, 1998; Rodriguez-Iturbe et al., 1999). In fire-driven savannas, fire probabilities and browsing need to enter the calculation as well. Details depend on the system under study. Once formed, the duration of the tree-encroached stage depends on the duration of the self-thinning process from woody plant encroachment to open savanna. In arid savannas this duration can be estimated from plant growth data. For example, for our study site and based on short-term growth data applied to a spatially explicit model of plant growth and competition, we estimated that trees 20 cm in canopy diameter may take 200 years to grow to a size of 100 cm, which is still well below their maximum canopy

diameter of about 500 cm (K. Wiegand, D. Saltz and D. Ward, unpubl. data). For fire-driven savannas, self-thinning is a more complicated process because of the interaction of tree growth with fire and possibly with severe browsing (e.g. by elephants).

Patch size is not important for estimating tree–grass ratios under the condition that the landscape for which we are trying to estimate the tree–grass ratio is large enough to assure that landscape properties are ‘ergodic’ (i.e. statistical properties are independent of the exact location and stage of single patches). A useful property of such ergodic landscapes is the proportionality between the duration of the different stages of the cycle and the number of patches in the corresponding stages. Thus, the relative duration of a stage can be estimated by the proportion of patches in this stage. Mapping of entire landscapes at a resolution sufficient to identify small trees may become possible in the near future with improved remote sensing techniques (Mistry, 2000). As soon as data on the primary and secondary determinants as well as maps of a number of savannas are available, it will be possible to statistically analyse the influence of the primary and secondary determinants on relative patch duration. This will be a considerable progress in understanding the influence of these determinants on tree–grass ratios.

It takes very little to create patchiness in spatially explicit simulation models of savanna dynamics (van Wijk and Rodriguez-Iturbe, 2002). However, even if future research should show that not all savannas are patch-dynamic, the patch-dynamic perspective will still be valuable. This is because information on the absence of patch dynamics should mean that such a system is more prone to conversion to a grass- or tree-dominated system.

Given constant environmental conditions, the tree–grass ratio of a patch-dynamic savanna is independent of the absolute duration of a typical patch cycle. However, for understanding possible effects of global change we may need to estimate average patch cycle duration as well. Understanding the influence of global change on patch-dynamic savannas in terms of increased global CO₂ levels poses further challenges. This influence depends on the mechanisms causing a proliferation of woody plants and how these mechanisms interact. For example, if increasing CO₂ levels decrease soil water depletion via reduced transpiration rates (Polley et al., 1997), in patch-dynamic savannas, we would expect two contrasting effects on the transition from open savanna to woody plant encroachment. Reduced soil water depletion would slow down this transition by increasing deep percolation and thereby possibly prolonging tree longevity. However, reduced soil water depletion would also accelerate this transition by facilitating woody plant germination.

Walter’s two-layer hypothesis has dominated savanna research for many years. However, because this hypoth-

esis is clearly not widely applicable, research will have to shift to a new paradigm if we wish to increase our understanding of savanna systems. In the Introduction, we presented two examples of alternative theories proposed to explain tree–grass coexistence, the storage effect and ecological buffers (Higgins et al., 2000; Jeltsch et al., 2000). Most savanna ecologists would agree that both storage of reproductive potential in trees and frequent disturbances contribute to tree–grass coexistence. The question is whether they will suffice to explain tree–grass coexistence. One reason why they may not suffice are parameterization problems of savanna models due to the paucity of data on the demography of savanna plants (Scholes and Archer, 1997; Midgley and Bond, 2001). For example, Higgins et al. (2000) discuss the paucity of data on growth, a very sensitive parameter in their model (see Fig. 5 in Higgins et al., 2000). For arid savanna, Higgins et al. (2000) used a maximum stem growth rate of 35 cm per year. This parameter value is at odds with new data showing an average canopy diameter-growth rate of about 3 cm per year over 3 years observed for 18 *A. reficiens* trees that were initially about 24 cm in canopy diameter (cf. Wiegand et al., 2005). This marked deviation provides motivation for collecting further tree growth data in a range of savannas and calls for a subsequent re-analysis of the model results. A further reason why current theories are unlikely to suffice to explain tree–grass coexistence, is the observation that not all ecological buffers in Jeltsch et al. (2000) are buffers in the strict physical sense, which should make buffering disturbances more likely as the system converges towards dominance by either grasses or trees. An exception is, e.g. the buffer example of increasing tree density leading to fire reduction but also to increased browse availability, which attracts elephants. The browsing activity and destruction by the elephants facilitate the penetration of fire, and the savanna is maintained (Jeltsch et al., 2000).

We hypothesize that a combination of storage effect and ecological buffers in a patch-dynamic context can explain tree–grass coexistence in a wide range of savanna ecosystems. Patch dynamics greatly improves the explanatory power of the storage effect because seeds do not need to be produced at the same rate across the entire landscape. Local shortcomings in seed production can be balanced by seed dispersal. Higgins et al. (2000) provide no spatial analysis of their model. However, it is quite likely that patch-dynamics will develop in their simulations of fire-driven savannas because they model spread and intensity of fire as a function of spatially varying grass standing crop and fuel moisture. Thus, patch-dynamics may have contributed to tree–grass-coexistence in this model. Similarly, patch dynamics greatly improves the explanatory power of the ecological buffers because they do not need to prevent an entire landscape from shifting towards woody or grassy dominance. Localized woody or grassy

dominance is not the end of this savanna but inherent to the savanna system. This perspective makes the savanna question less puzzling because conversion of a savanna to grassland or forest requires the more or less simultaneous conversion of many patches to dominance of just grassy or just woody plants, which seems rather unlikely (but has been observed in some savannas; Belsky, 1995). This view is supported in Jeltsch et al. (2000) by their reference to the role of microsites for tree establishment and survival in savannas with a low tree–grass ratio.

The number of plausible theories addressing the savanna question keeps increasing (Sankaran et al., 2004). As noted by Gillson (2004), most of these theories are scale-free. Given the high scale dependence of both primary and secondary determinants of savanna dynamics (see Fig. 1 in Gillson, 2004), this is surprising. Also, the term ‘tree–grass coexistence’ in the context of the savanna question implies an idea of the spatial and temporal scales at which trees and grasses coexist (e.g. 10 km² and 1000 years), which is usually not addressed. We believe that savannas are hierarchical patch-dynamic systems with patchiness at many scales (Wiegand et al., 2005), and that the hierarchical patch-dynamics paradigm (O’Neill et al., 1986) may provide a framework to explicitly link current theories of tree–grass coexistence to spatial and temporal scales, to combine the theories (e.g. in simulation models), to evaluate the relative contribution of the different theories, and to determine when each is most important.

For a full understanding of the globally observed increase in tree–grass ratios (Archer et al., 2001), it will be crucial to gain a better understanding of both natural (e.g. patch dynamics) and allochthonous (e.g. increasing CO₂ levels) causes of woody plant encroachment in savannas, although it is generally agreed that global CO₂ levels have not yet reached the point that net photosynthetic efficiency of C₃ trees exceeds that of C₄ grasses. If savannas are patch-dynamic systems, natural woody plant encroachment will be a part of their dynamics, i.e. bush encroachment is a natural part of birth and death cycles of these encroaching species. In that case, we will have to accept that there will always be some woody plant encroachment and that management measures will not be able to eradicate woody plant encroachment unless we want to destroy savanna systems. Instead, management measures will have to be developed that constrain woody plant encroachment to its natural level that is appropriate to the scale of the patchiness of the system.

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