

# DO WE UNDERSTAND THE CAUSES OF BUSH ENCROACHMENT IN AFRICAN SAVANNAS?

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Bush encroachment affects the agricultural productivity and biodiversity of 10-20 million ha of South Africa. Many people believe that we understand the causes of bush encroachment. We do not. Many people believe that either heavy grazing by domestic livestock or fire is the sole cause of bush encroachment. This is wrong. Bush encroachment occurs in many arid regions where fuel loads are insufficient for fires to be an important causal factor. Belief in grazing as the sole cause of bush encroachment stems from Walter's two-layer model. This model states that grasses typically outcompete trees in open savannas by growing fast and intercepting moisture from the upper soil layers, thereby preventing trees from gaining access to precipitation in the lower soil layers where their roots are mostly found. When heavy grazing occurs, grasses are removed and soil moisture then becomes available to the trees, allowing them to recruit *en masse*. The fact that many bush-encroached areas are heavily grazed means neither that grazing causes encroachment nor that Walter's model is correct. This is the logical fallacy, *post hoc ergo propter hoc* (after the fact, therefore because of the fact). Bush encroachment is widespread in areas where there is a single soil layer and where grazing is infrequent and light. We need to move away from observational studies and these single-factor explanations. If we are to understand the causes of bush encroachment, we need mechanistic models to guide us and multi-factorial experiments to tease out the interactions among causal factors. Variations on David Tilman's resource allocation models, as well as some spatially-explicit models, appear to hold great promise in this regard. Field experiments carried out to date show that support for factors conventionally claimed to cause bush encroachment is underwhelming, and that rainfall amount and frequency, coupled with specific soil nutrient levels, may drive this phenomenon.

## 1. Introduction

Savannas are extensive, socioeconomically important ecosystems with a mixture of two life-forms, trees and grasses (Bourlière, 1970; Belsky, 1990; Scholes and Walker, 1993; Scholes, 1997; Scholes and Archer, 1997). Savannas are the most important ecosystems for raising livestock in Africa (Bourlière, 1970; Lamprey, 1983). In the past 50 years, evidence has accumulated suggesting that savannas throughout the world are being altered by a phenomenon known as 'bush encroachment' (reviewed by Archer *et al.*, 1995). Bush encroachment is the suppression of palatable grasses and herbs by encroaching woody species often unpalatable to domestic livestock. Therefore, bush encroachment reduces the carrying capacity for livestock. The reduction in carrying capacity is of great significance because savannas in southern and central Africa contain a large and rapidly growing proportion of the world's human population, including many pastoralists whose livelihood is threatened by this process (Lamprey, 1983; Scholes, 1997).

Factors causing bush encroachment are poorly understood. The first attempt at a general explanation for bush encroachment was Walter's (1939) two-layer hypothesis for tree-grass coexistence (Walter, 1954; Noy-Meir, 1982). Walter (1939, 1971) explained the coexistence of these two different life forms in terms of root separation, viz. he assumed water to be the major limiting factor for both grassy and woody plants and hypothesized that grasses use only topsoil moisture, while woody plants mostly use subsoil moisture. Under this assumption, removal of grasses, e.g. by heavy grazing, allows more water to percolate into the sub-soil, where it is available for woody plant growth.

Although the two-layer theory is still widely accepted (Skarpe, 1990a), field data and theoretical models have produced conflicting evidence. Several field studies have shown the increase of shrub or tree abundance under heavy grazing (van Vegten, 1983; Skarpe, 1990a,b; Perkins and Thomas, 1993). However, recruitment in honey mesquite (*Prosopis glandulosa*), a bush-encroaching tree in North America, is unrelated to herbaceous biomass or density, indicating that release from competition with grasses is not required for mass tree recruitment to occur (Brown and Archer, 1989; Brown and Archer 1999). Similarly, while some models have shown that the two-layer hypothesis may indeed lead to tree-grass coexistence (Walker *et al.*, 1981; Walker and Noy-Meir, 1982), a spatially-explicit simulation model by Jeltsch *et al.*, (1996) showed that rooting niche separation might not be sufficient to warrant coexistence under a range of climatic situations.

Field studies investigating root distribution and water uptake also produced mixed results. In the different studies, great differences were observed in the degree of niche separation, depending on abiotic factors and the species involved (Hesla *et al.*, 1985, Weltzin and McPherson, 1997; Knoop and Walker, 1985; see also Scholes and Archer, 1997 and Higgins *et al.*, 2000 for further references). Clearly, rooting niche separation cannot be an explanation for the *initiation* of bush encroachment because young trees use the same subsurface soil layer as grasses in the sensitive early stages of growth. Furthermore, heavy grazing is not a sufficient cause of bush encroachment. For example, the naturalist, Charles John Andersson (1856), reported heavy bush encroachment in areas in Namibia that were, according to his and other independent historical records, not heavily grazed. Thus, rooting niche separation cannot be a general mechanism explaining tree-grass coexistence and overgrazing is unlikely to be the most important factor causing bush encroachment. Furthermore, overgrazing in combination with rooting niche separation is not a prerequisite for bush encroachment because bush encroachment sometimes occurs on soils too shallow to allow for root separation (Wiegand *et al.*, 2000). To date, mitigation protocols based on the two-layer theory, e.g. reducing livestock densities in years with below-average rainfall, have failed to reduce bush encroachment, indicating that the causes of the problem are poorly understood (Teague and Smit, 1992; Smit *et al.*, 1996).

As a consequence of the inadequacy of previous explanations for the occurrence of bush encroachment, several new hypotheses have been put forward to explain tree-grass coexistence. Disturbances have been mooted as major determinants of savanna structure, with savannas being portrayed as inherently unstable ecosystems that oscillate in an intermediate state between those of stable grasslands and forests because they are pushed back into the savanna state by frequent disturbances such as human impact (Scholes and Archer, 1997; Jeltsch *et al.*, 1998a; Jeltsch *et al.*, 2000), fire (Higgins *et al.*, 2000), herbivory, or drought (Scholes and Walker, 1993), and spatial heterogeneities in water, nutrient, and seed distribution (Jeltsch *et al.*, 1996). These disturbance-based hypotheses all suggest that bush encroachment occurs as disturbances shift savannas from the open grassland towards the forest end of the environmental spectrum. All of these hypotheses may be valid for specific situations but may lack generality. None of these purported mechanisms of bush encroachment has been convincingly demonstrated under field conditions.

## 2. Resource allocation models

I believe that we need to return to the drawing board as far as theory is concerned and develop a general theory of *Acacia* savanna function that considers the mechanisms of plant coexistence. David Tilman has developed a general, mechanistic theory for the role of competition and the allocation of resources in plant community ecology (Tilman, 1982; 1988). This is a graphical theory that is neither equilibrational nor non-equibrational (Tilman, 1987).

A brief introduction to Tilman's theory is necessary to introduce it as a general theory, which I will then adapt to consider factors likely to affect bush encroachment. A crucial aspect of Tilman's theory involves the definition of  $R^*$ , which is that value of resource availability at which population biomass neither increases nor decreases.  $R^*$  is reached when growth is

balanced by loss. A population can only be maintained in a habitat if its growth rate > loss rate.  $R^*$  will increase with the loss rate because more resources are required to invest in growth in order to balance loss (Figure 1.).

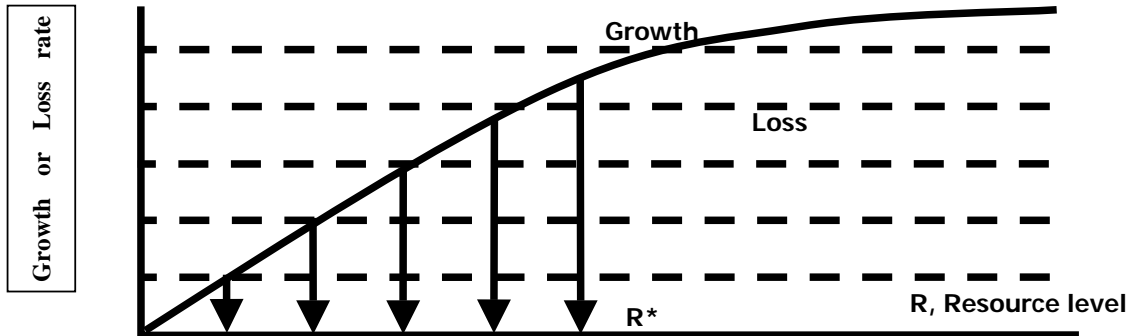


Figure 1. Model of effects of loss on  $R^*$ .  $R^*$  will increase with increasing loss rate. A population can only be maintained in a habitat if its growth rate > loss rate.

The species with the lowest  $R^*$ , that is the species that can maintain its population at the lowest level of resource availability will outcompete any other species (Figure 2).

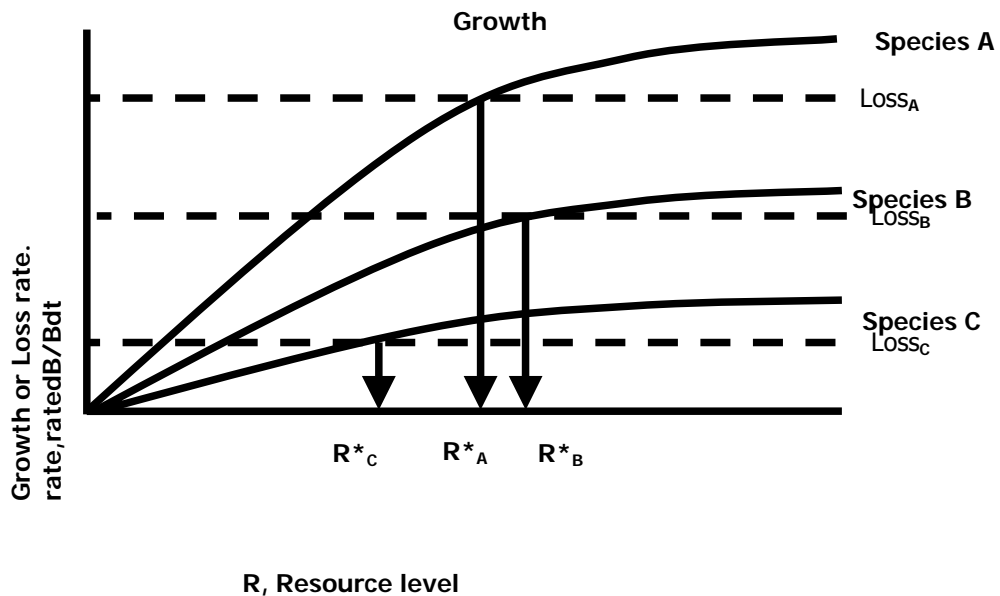
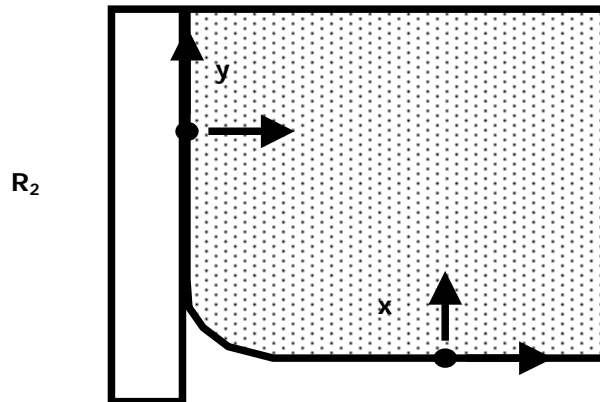


Figure 2. Effects of  $R^*$  on outcome of competition. Species C will exclude the other 2 species in competition because it has the lowest  $R^*$ .

We can represent the position of a particular habitat in a two-dimensional graphical space. The dimensions (axes) are defined by the resources that limit growth. Conventionally, these axes have been represented as light and nutrients (in the case of forests and grasslands) or nitrogen and phosphorus in the case of lakes. However, there is no need to restrict resource definition in any particular way.  $R^*$  for the two resources are drawn as a zero net growth isocline (ZNGI) (Figure 3).

### Perfectly essential resources



**Figure 3. ZNGI for a single species with perfectly essential resources. Population size decreases for resource levels in the unshaded region and increases in the dotted region. If a habitat is at point  $x$ , an increase in  $R_1$  will not affect population size. However, any increase in  $R_2$  will cause an increase in population size (and *vice versa* for habitat at  $y$ ).**

Typically, limiting resources used by plants are perfectly essential (Tilman, 1988). That is, if a habitat is at point  $x$ , an increase in  $R_1$  will not affect population size. However, any increase in  $R_2$  will cause an increase in population size (& vice versa for habitat at  $y$ ). The isocline does not have a perfect right-angled corner but is curved because the resource-dependent growth isocline is a summary curve for an entire size-structured population (or at least one with a range of resource-extraction abilities). Some individuals are better at extracting resources than others. At intermediate resource supply rates, some individuals are limited more than others. Thus, shorter individuals could be more light limited than tall ones in the same habitat in which the tall plants are simultaneously nutrient-limited. The total effect of this dual limitation is a curved isocline. We can superimpose the ZNGI of two or more species on the same axes. If a species has a ZNGI closer to the origin on both axes (i.e. has a lower  $R^*$  for both resources) than that of another species, it will win in competition. When the ZNGI cross, each species will have a range of  $R^*$  for the 2 resources where it will dominate, i.e. the species with the lower  $R^*$  on a particular axis will outcompete the other when the habitat falls within that range of resource availability (Figure 4).

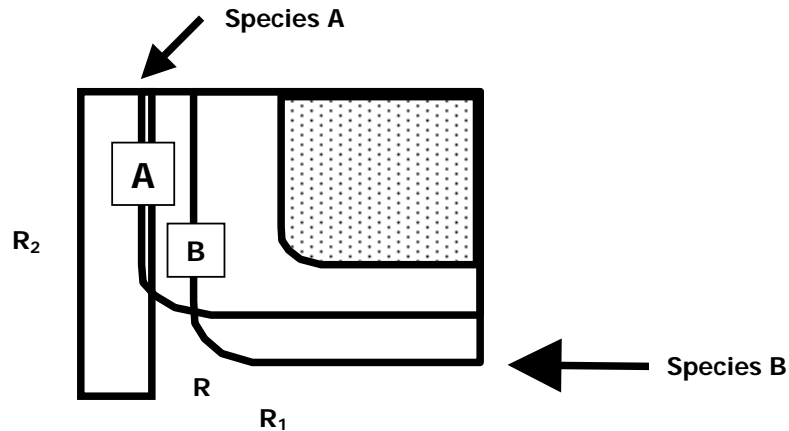


Figure 4. ZNGI for two species. When the ZNGI cross, each species will have a range of  $R^*$  for the two resources where it will dominate.

Thus far, we have considered resource availability. Consumption also needs to be considered because it affects subsequent availability (Figure 5).

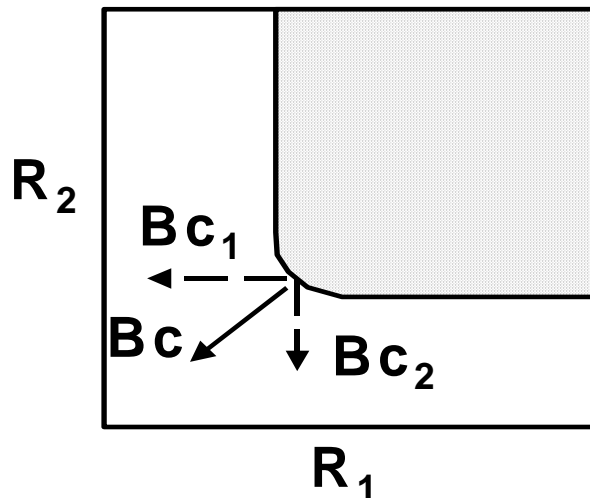
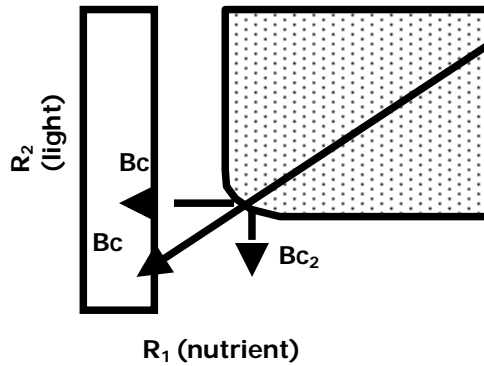


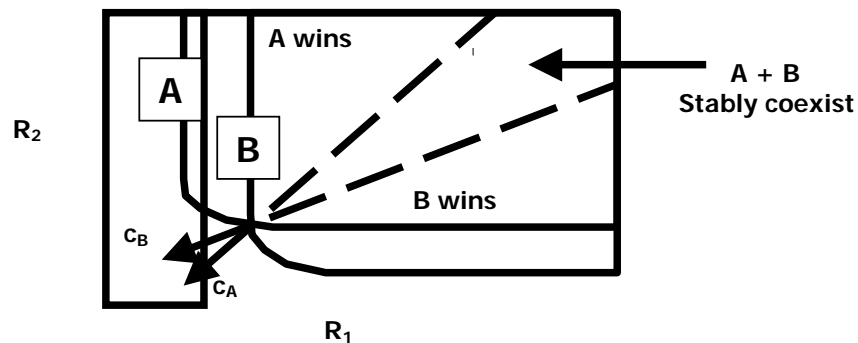
Figure 5. Consumption vectors superimposed on ZNGI. Consumption also needs to be considered because it affects subsequent availability. The consumption vector,  $Bc$ , has 2 components:  $c_1$  = amount of resource 1 consumed per unit biomass per unit time and  $c_2$  ( $\simeq$  for  $R_2$ ).

The consumption vector,  $Bc$ , has 2 components:  $c_1$  = amount of resource 1 consumed per unit biomass per unit time and  $c_2$  ( $\simeq$  for  $R_2$ ). The consumption vectors are determined in large part by the plasticity of plant growth, e.g. if  $R_1$  = a nutrient and  $R_2$  = light, the plant must allocate resources to above-ground growth (towards the light) and to below-ground growth (towards the nutrients) (Figure 6).



**Figure 6. The consumption vectors are determined in large part by the plasticity of plant growth. e.g. If  $R_1$  = a nutrient and  $R_2$  = light, the plant must allocate resources to above-ground growth (towards the light) and to below-ground growth (towards the nutrients).**

When there are perfectly essential resources, the optimal strategy for a plant is to grow so that the two resources are consumed in a way that they equally limit growth. In this case, its consumption vector will be closest to the ZNGI for the resource for which it has the lowest  $R^*$  (Figure. 7). When this occurs, a species will win out in competition with another species in the region of state space between its consumption vector and the isocline for the resource for which it has a lower  $R^*$  (Figure 7).



**Figure 7. When there are perfectly essential resources, the optimal strategy for a plant is to grow so that the 2 resources are consumed in a way that they equally limit growth (see text for explanation).**

In the intermediate region of resource availability between the consumption vectors of the two species, stable coexistence is possible. Coexistence is stable because each species consumes more of the resource that more limits it at equilibrium. It is also possible to construe this outcome as: intraspecific competition is stronger than interspecific competition, and coexistence results (Tilman, 1988). Unstable coexistence will occur when a species consumes excess amounts of a resource that is not limiting. In this case, its consumption vector will be closest to the ZNGI for the resource for which the other species has the lowest  $R^*$ . The outcome of competition will be determined by initial conditions (Tilman, 1988).

Open savannas may be stable over long periods (Skarpe, 1992; Scholes and Archer, 1997). Hence, we will consider a modelling scenario in which both trees and grasses grow so that the two resources equally limit growth and stable coexistence is possible (Figure 8). As indicated above, it is widely accepted that water is a major limiting factor to plant growth in savannas. Moreover, its use clearly differs between the tree and grass strata of a savanna. Grasses are smaller plants and can maintain population biomass (i.e.  $R^*$ ) on lower amounts

of water than can trees. Another feature that clearly differentiates trees and grasses in systems where bush encroachment characteristically occurs is that the encroaching species are nitrogen fixers while the grasses are not. Hence, I choose to model water and nitrogen as the primary limiting factors (Figure 8). How do grazing, fire, and other disturbances enter this scenario? As sources of loss. Following this theory, the cause of loss is of no particular interest. It is only important that more loss means that a higher level of resources is required to maintain population biomass (i.e.  $R^*$  increases). If loss by grazing, for example, is slight then  $R^*$  of the grasses will increase. If this loss is extreme, the ZNGI of trees and grasses will no longer cross and trees will outcompete grasses, resulting in bush encroachment (Figure 9).

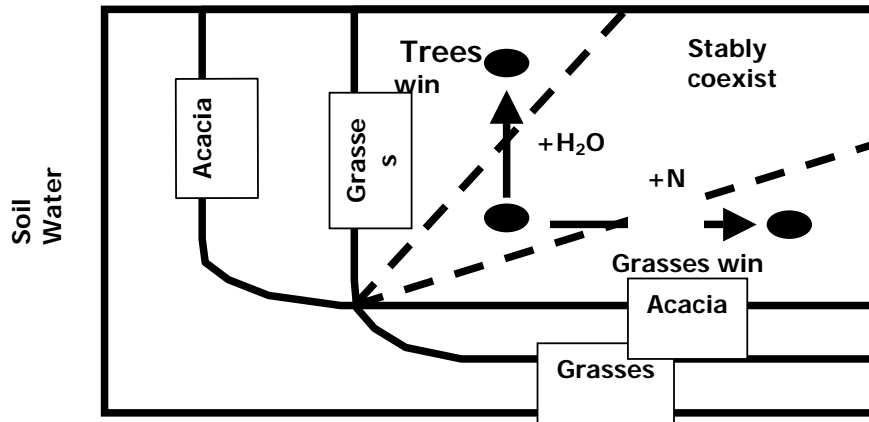


Figure 8. In South African savannas, the axes of the resource allocation model may be modeled as water and soil nitrogen availability. A habitat may shift from stable coexistence (open savanna) to either bush encroachment (with an increase in water availability – e.g. through unique rainfall amount or frequency) or to grassland (through increase in soil nitrogen availability).

Fig. 9a

Fig. 9b

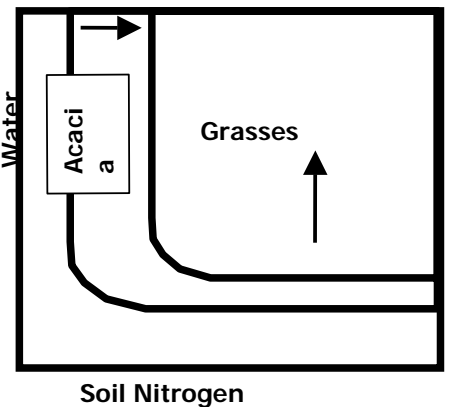
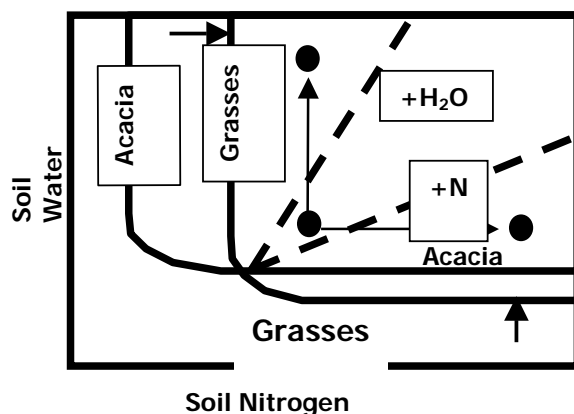


Figure 9. Grazing and fire are seen as factors affecting loss in the resource allocation models. Increasing fire or grazing will lead to increased loss. Slight changes in loss will not affect the experimental outcome. Extreme changes in loss will make the ZNGI for trees closer to the origin for both factors, in which case trees will outcompete grasses. Either of these scenarios is possible.

Interestingly, global climate change may also create bush encroachment: Atmospheric CO<sub>2</sub> is increasing exponentially and will likely double (to 700 parts per million (ppm)) within the next century (Wolfe and Erickson, 1993). This will have a potential beneficial effect on plant life because plants take up CO<sub>2</sub> via photosynthesis and use it to produce sugars and to grow. If this CO<sub>2</sub> fertilization effect is large, it could significantly increase the capacity of plants to absorb and temporarily store excess carbon. This is likely to have an effect on tree-grass dynamics in savannas because savanna trees and grasses have different photosynthetic pathways, which will respond differently to changes in atmospheric CO<sub>2</sub> levels. *Acacia* trees have the C<sub>3</sub> photosynthetic pathway, which is less efficient (lower net photosynthetic rate) at current atmospheric CO<sub>2</sub> levels than the C<sub>4</sub> pathway used by most savanna grasses (Wolfe and Erickson, 1993). However, at higher atmospheric CO<sub>2</sub> levels than currently experienced, C<sub>3</sub> plants will have a higher net photosynthetic rate than C<sub>4</sub> plants (Wolfe and Erickson, 1993). Consequently, C<sub>3</sub> plants should show increases in yield of 20-35% with a doubling of atmospheric CO<sub>2</sub>, while C<sub>4</sub> plants such as grasses should only experience a 10% increase in yield (Wolfe and Erickson 1993). Additionally, *Acacia* trees will have more carbon to invest in carbon-based defences such as condensed tannins (Rohner & Ward, 1997; Ward & Young, 2002). Thus, these trees should be better defended and loss will consequently decrease. Hence, R\* will decline. The consequence of a decline in R\* for trees is that the ZNGIs of trees and grasses will not cross and ZNGI for trees will be lower (closer to the origin) than that of grasses. Trees will outcompete grasses and bush encroachment will result. This prediction is consistent with Idso's (1992) assertion that current trends in atmospheric CO<sub>2</sub> enrichment may exacerbate shifts from grass to woody plant domination (although see Archer *et al.*, 1995 for a counter-argument).

### 3. Experimental support for use of resource allocation models

We have been running field and pot experiments on the factors causing bush encroachment by *Acacia mellifera* in a semi-arid savanna north of Kimberley (Northern Cape) for the past two years (see e.g. Kraaij and Ward, submitted). In the pot experiment (large (100 l) garbage bins were used), we planted grasses growing naturally in our study area and allowed them to reach maturity and cover the surface of the bins entirely. Then we added 100 *Acacia mellifera* seeds per bin. In a replicated, balanced, completely crossed experimental design, we used the following experimental factors: rainfall frequency (water supplied to saturation once every 3 days and once every 10 days), clipping (clipped all grass to the surface once every 3 weeks, and unclipped) and nutrients (nitrogen added [equivalent of 30 g/m<sup>2</sup>] and control)(see Kraaij and Ward, submitted; for more details). Rainfall frequency was the most important factor affecting germination and survival of *Acacia* seedlings (Figure 10).

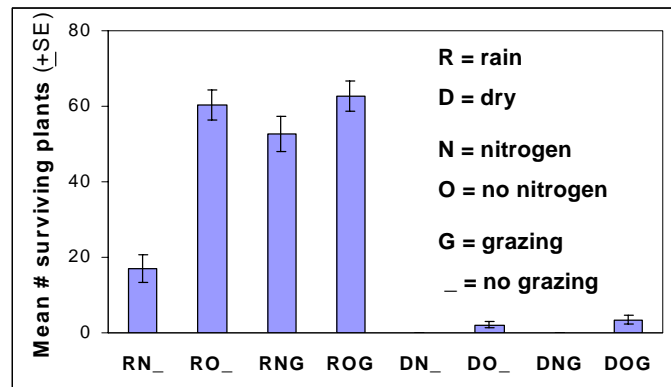


Figure 10. In the pot experiment, rainfall frequency (high frequency = R) was overwhelmingly more important than the other factors (from Kraaij and Ward, submitted).



There was also a significant difference between nitrogen addition and control treatments (Figure 10); nitrogen addition increased grass growth, suppressing tree germination and survival. In the field experiment, in 48 5 m X 5 m plots, with a completely-crossed randomized block design with the same factors and the addition of fire, we found that rainfall addition increased *Acacia* germination and survival (Figure 11a), while nitrogen addition decreased *Acacia* germination and survival (Figure 11b). Fire and grazing (and seed addition in the 2<sup>nd</sup> year of the experiment) did not affect tree seedling germination and survival. Thus, the results of these experiments lend credence to the use of the resource allocation model I outlined above. I stress that, in both the pot and field experiments, high rainfall frequency rather than rainfall amount that resulted in germination and survival of Acacias. Doubling the annual mean rainfall (800 mm as opposed to 400 mm) did not lead to bush encroachment in the field when added twice per month over the growing season, while applying the same amount every two days led to significant germination.

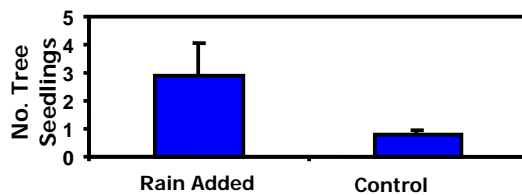


Figure 11a.

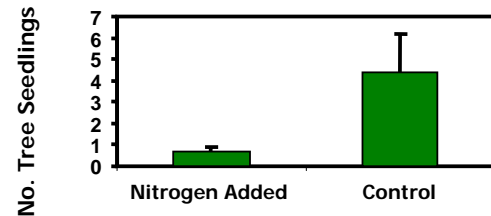


Figure 11b.

Figure 11. In the field experiment, (a) rainfall addition increased *Acacia mellifera* germination and survival. (b) Nitrogen addition decreased *Acacia* germination & survival.

#### 4. Patch-dynamic hypotheses

Wiegand *et al.* (2002) have hypothesized that bush encroachment in many semi-arid and arid environments is a natural phenomenon occurring in ecological systems governed by patch-dynamic processes. They based their hypothesis on field observations gained on the spatial distribution of *Acacia reficiens* trees in arid central Namibia. Bush encroachment in *A. reficiens* along a rainfall gradient increases with increasing rainfall in spite of a relatively constant level of grazing. Wiegand *et al.* (2002) hypothesized that any form of disturbance (e.g. grazing or, rarely, fire) can create space, making water and nutrients available for tree germination. Under low soil nitrogen conditions, the nitrogen-fixing trees have a competitive advantage over other plants and, given enough rainfall, may germinate *en masse* in these patches created by the disturbances. In the following, I describe the mechanism underlying this hypothesis and demonstrate how it may be used to explain both tree-grass coexistence and bush encroachment in a patch-dynamic system with stochastic rainfall patterns.

In arid and semi-arid savanna ecosystems, woody vegetation needs above-average precipitation for germination and subsequent establishment (e.g. O'Connor, 1995). Moreover, to keep the soil moist for a period sufficient for germination and survival through the sensitive early stages of seedling development, several rain events close in succession are necessary (Obeid and Seif El Din, 1971; Wilson and Witkowski, 1998). However, rainfall in savanna regions is often patchily distributed, both in time and space (Green, 1969; Sharon, 1972; Bell, 1979; Sharon, 1981; Prins and Loth, 1988; Ward *et al.*, 2000). Therefore, the spatial overlap of several rainfall events of high frequency in a single year is a rare occurrence in semi-arid and arid ecosystems. In addition to local seed availability, this rainfall frequency is a necessary condition for the creation of a bush encroachment patch. The patchiness of rainfall leads to patchy vegetation patterns (often only several hectares in size) within an intermediate range of 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, dense woodlands with mixed age distribution develop (see also Belsky, 1990).

Competition experiments have shown that mature trees are competitively superior to grasses while grasses tend to outcompete immature trees (Moore *et al.*, 1988). This asymmetry of competitive effects creates instability in the interactions between trees and grasses. Grazing effectively weakens the suppressive effect of the grass layer on young trees in a patch of a few hectares, leading to the conversion of an open savanna patch into a tree-dominated thicket (=bush 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 stable, persisting over millennia due to the fact that the landscape consists of many patches in different states of transition between a grassy and a woody dominance. According to this concept, bush encroachment is an integral part of savanna dynamics.

The set of factors that can lead to a patch-dynamic savanna will overlap with, but will not be identical to, the set of factors sustaining a more or less homogeneous mixture of trees and grasses. Therefore, clarifying the nature of coexistence between woody and grassy plants is a crucial prerequisite to understanding savanna dynamics.

Due to two reasons, new bush encroachment will occur in patches of open savanna as opposed to patches currently quite densely vegetated by woody plants: (1) As already mentioned, in (semi-) arid systems, rainfall sufficient for germination is a rare event relative to the longevity of woody plants. (2) *Acacias* and other woody savanna plants are 'canopy intolerant'. Thus, competition between adult bushes and seedlings will prevent establishment of new bushes when the adult bushes are still alive in a closed (bush-encroached) savanna (Smith and Goodman, 1986; Milton, 1995). These considerations show that the size of bush-encroached patches is determined by the size of the area within which the rainfall was sufficient for germination and seedling survival and the distribution of open savanna within this area.

With time, tree growth and inter-tree competition will convert the bush-encroached patch to an open savanna. This process has been modelled by Wiegand *et al.* (2002) 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 is stronger than all the others (Figure 12A); this seedling is able to draw more resources (water and nutrients) than its immediate neighbours and thereby outcompetes and ultimately kills these neighbours and grows in size (Figure 12B). This gives seedlings in the second circle around the central seedling the opportunity to access more resources, to grow and to use even more water and nutrients (Figure 12C). Distances from the focal seedling to the seedlings in the circle of surviving plants are not identical. Therefore, every second plant has a disadvantage, which, with time, leads to mortality of every second seedling in the ring (Figure 12C). Furthermore, the increased size of the surviving seedlings leads to suppression and finally the death of the seedlings in the third row (Figure 12D). The death of these seedlings gives seedlings in the fourth row access to more water and nutrients, leading to their growth (Figure 12E) and the death of the next ring and so on. Thus, one somewhat stronger tree 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 (Figure 12F), 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 (weak trees too close to another stronger trees will be eliminated, resulting in more even inter-tree distances with time). Thus, the honeycomb-rippling model is consistent with our field data showing increasing inter-tree distances and increasing evenness of inter-tree distances with increasing size (Wiegand *et al.*, 2002). Furthermore, the honeycomb-rippling model shows that bush encroachment can be a natural recruitment process for savannas that is independent of the source of disturbance that creates space for tree germination under ideal rainfall conditions.

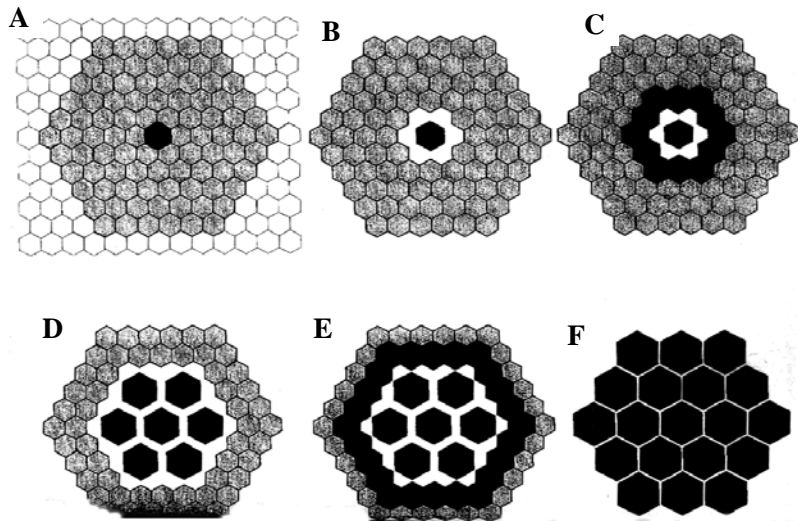


Figure 12. Honeycomb rippling model of patch dynamics. Figures show a time series (A-F) of hexagonal subsets of a larger patch. Each (small) hexagonal represents a bush, the relative sizes of the hexagonals represent relative bush sizes. Black filling of the hexagonals indicates 'strong' bushes/trees acquiring sufficient resources to survive the competition with their neighbors (from Wiegand et al. 2002).

## 5. Management implications

I believe that these results will dramatically alter the way we approach the problem of bush encroachment, i.e. as a problem initiated by unique rainfall conditions that may or may not be exacerbated by certain types of grazing or fire conditions. We can model the management implications of rainfall effects on the initiation of bush encroachment as follows: Without grazing, both grass and tree biomass increase linearly with increasing rainfall. In an open savanna, grass biomass always exceeds tree biomass (Figure 13a). When heavy grazing occurs, grass biomass per unit rainfall is reduced, reducing competition with trees (Figure 13b). This releases water and nutrient resources for trees to germinate *en masse*. Because there is a greater probability that trees will recruit when rainfall is higher, the difference between tree and grass biomass increases with increasing rainfall. The management consequence thereof in areas prone to bush encroachment is that farmers should limit stock in *wet* years and not in dry years (because trees cannot germinate) as is usually the case.

Figure 13A.

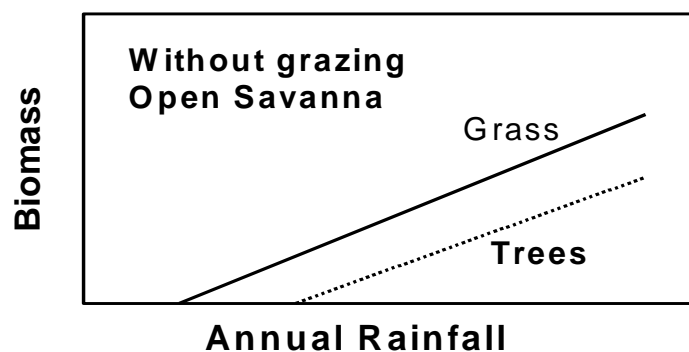
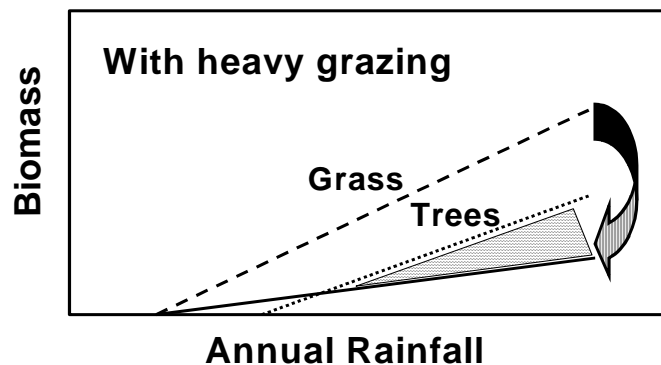


Figure 13B.

Figure 13. The relationship between grass/tree biomass and rainfall. a) Without grazing, both grass and tree biomass increase linearly with increasing rainfall. In an open savanna, grass biomass always exceeds tree biomass. b) When heavy grazing occurs, grass biomass per unit rainfall is reduced, reducing competition with trees. This releases water and nutrient resources for trees to germinate *en masse*. Because the probability of tree recruitment increases with increasing rainfall, the difference (=shaded area) between tree and grass biomass increases with increasing rainfall.

Thus, the mitigation protocol for bush encroachment under this hypothesis differs considerably from those under the two-layer competition hypothesis.

Under the conventional two-layer competition hypothesis, grazing during years with less than average precipitation should be reduced to a minimum so as not to give the



trees a competitive advantage. By contrast, under both the Tilman resource allocation model and the patch dynamics theory, bush encroachment does not occur when water is limited and consequently such a management protocol would be futile. Under the patch dynamic hypothesis, mass germination of acacias is expected in years with greater than average rainfall, especially in open pastures where intra-specific tree competition is minimal. Thus, if tree-grass competition occurs, grazing should be reduced in years with greater than average rainfall especially in open pastures. If tree germination is independent of grass density, then measures should be taken during years with good rainfall to identify open patches susceptible to bush encroachment and steps taken to prevent the establishment of tree seedlings.

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