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### Authors

Moustakas, Aristides  
Wiegand, Kerstin  
Meyer, Katrin M.  
[et al.](#)

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## Learning new tricks from old trees: revisiting the savanna question

Aristides Moustakas<sup>1,\*</sup>, Kerstin Wiegand<sup>2</sup>, Katrin M. Meyer<sup>2</sup>, David Ward<sup>3</sup> & Mahesh Sankaran<sup>1,4</sup>

<sup>1</sup>Institute of Integrative & Comparative Biology, Faculty of Biological Sciences, University of Leeds, Leeds LS2 9JT, UK

<sup>2</sup>Ecosystem Modelling, University of Göttingen, Göttingen, Germany

<sup>3</sup>School of Biological and Conservation Sciences, University of KwaZulu-Natal, Scottsville 3209, South Africa

<sup>4</sup>National Centre for Biological Sciences, Tata Institute of Fundamental Research, GKVK, Bellary Road, Bangalore 560065, India

\*Corresponding author. e-mail: [arismoustakas@gmail.com](mailto:arismoustakas@gmail.com); [http://www.fbs.leeds.ac.uk/staff/profile.php?tag=Moustakas\\_A](http://www.fbs.leeds.ac.uk/staff/profile.php?tag=Moustakas_A)

### Introduction

Savannas are ecosystems comprising of a mixture of woody species (trees and bushes), grasses and forbs. They cover about a fifth of the global land surface and about half of the area of Africa, Australia and South America (Scholes and Archer 1997, Sankaran et al. 2004). Savannas are characterized by a continuous grass understorey and a discontinuous tree layer. A savanna, where trees and grasses co-dominate (often referred to as co-existence), may be viewed as an intermediate ecosystem between grassland (grass dominance) and forest (tree dominance). Tree-grass ratios vary widely in savannas, with higher precipitation usually leading to a more continuous tree layer (Sankaran et al. 2005). However, tree canopies in mesic savannas are still discontinuous enough, with significant understorey grass biomass for the system to be characterised as a savanna and not forest. There are several different savanna ecoregions worldwide, each containing different subsets of species and displaying substantial variation in physical and structural attributes (Scholes and Archer 1997, House et al. 2003). In this paper, we focus primarily on tropical and subtropical savannas, although some of the conclusions might be valid for a broader extent of savannas.

Until the early 1990s, it was generally believed that trees and grasses coexist because of a separation of rooting niches (Scholes and Archer 1997). This idea was based on Walter's (1939) two-layer hypothesis, a version of niche separa-

tion theory (Walker et al. 1981). According to this theory, water is the limiting factor for woody species as well as grasses. It was assumed that grasses were the better competitors for topsoil moisture (usually < 30 cm, depending on soil properties), but because woody species could develop deeper roots they were able to persist by exploiting subsoil resources (usually > 30 cm). Topsoil is usually defined by its fast reaction to climatic regimes, getting wet during light rain, drying out with a few days of sunshine (Knoop and Walker 1985). The two-layer theory has been verified by field experiments which reported that in the Nylsvlei savanna (South Africa) grasses reduced the supply of water to the trees (Knoop and Walker 1985). Furthermore, subsoil competition between the trees, probably for water but possibly also for nutrients, was reported (Smith and Goodman 1986). Several studies have concluded that savanna stability is based on the two-layer theory (e.g. Knoop and Walker 1985, Skarpe 1990).

There is a growing body of literature that questions the validity of the two-layer theory. A number of field studies have reported facilitative effects of trees on grass biomass, where grass biomass is greater below tree canopies rather than away from trees (e.g. Belsky et al. 1989). Among others, Ludwig et al. (2004) reported a field experiment where the two-layer theory is inappropriate. More specifically, according to Ludwig et al. (2004) "prevention of tree-grass interactions

through root trenching led to increased soil water content indicating that trees took up more water from the topsoil than they exuded via hydraulic lift. [...] grasses which competed with trees used a greater proportion of deep water compared with grasses in trenched plots. Grasses therefore used hydraulically lifted water provided by trees, or took up deep soil water directly by growing deeper roots when competition with trees occurred". This means that rooting niche separation fails to generally explain savanna tree–grass co-dominance in this system. Further, in ecosystems (e.g. Kalahari and Namibia) where soil was too shallow to allow for a two-soil layer differentiation, trees and grasses coexisted (Hipondoka et al. 2003, Wiegand et al. 2005).

As the niche separation theory was inappropriate in several cases, new theories were proposed to explain savanna stability and wood plant–grass co-dominance. One such influential theory is the demographic bottleneck theory which suggests that savannas are unstable systems that are constantly perturbed by disturbances such as fire, herbivory and climatic variability (Jeltsch et al. 2000, Higgins et al. 2000). Ideally, in the absence of such disturbances, a savanna would turn into woodland (forest) or into grassland (Scholes and Archer 1997, Jeltsch et al. 2000). Demographic bottleneck models take life stages explicitly into account and emphasize the role of disturbances and climatic variability in limiting tree establishment and growth in arid areas, and preventing tree dominance in mesic areas (Jeltsch et al. 2000, Higgins et al. 2000, Sankaran et al. 2004). Fire is typically considered to be the most important driver limiting tree dominance in mesic areas, thereby maintaining the system as a savanna (Jeltsch et al. 2000, Higgins et al. 2000, Sankaran et al. 2004, Bond 2008). In contrast, in arid savannas, the primary demographic bottlenecks for woody species are germination and seedling establishment (Higgins et al. 2000). Here, tree recruitment is pulsed in time following stochastic rainfall patterns. The fact that trees are long-lived enables them to persist, and 'store' reproductive potential, over periods when precipitation is sufficient only for grass and not for tree

germination (Higgins et al. 2000). There are several savanna ecosystems where there are many gaps in tree canopy cover but no germination; in such places the lack of germination is due to the absence of consecutive days with sufficient soil moisture rather than to the absence of gaps. Fewer consecutive days and lower soil moisture appears sufficient for grass persistence but not bush or tree germination (Noe 2002).

### Bush encroachment

A common phenomenon in savannas is the increased dominance of woody species, often referred to as bush encroachment (Ward 2009). In Africa, the phenomenon is often associated with bushes such as *Acacia mellifera*, *A. karroo*, *A. nilotica*, *Dichrostachys cinerea* and *Grewia flava* which suppress grasses (Ward 2009). While the problem may be more acute in arid savannas with heavy grazing, the increase of savanna woody species is a more "global" savanna phenomenon observed in African (e.g. Hudak and Wessman 2001, Britz and Ward 2007), American (e.g. Archer 1989), and Australian (e.g. Burrows et al. 1990) savannas. This increase of woody species is a serious problem in savannas because many herbaceous plants are suppressed or lost, and as a result, biodiversity is decreased. Furthermore, domestic livestock is unable to pass through such places (Scholes and Archer 1997).

There have been attempts to explain the causes of bush encroachment. Experimental studies carried out in savannas at higher rainfall found evidence that competition from relatively shallow-rooted grasses for water reduced the growth of relatively deep-rooted trees (Kraaij and Ward 2006 for seedlings; Knoop and Walker 1985 for adult trees), and evidence that trees competed with each other, plausibly for water (Smith and Goodman 1986). It has also been reported that the cover of some shrub species was increased only in the most heavily grazed areas (Skarpe 1990). There was evidence that the species which did increase (*Acacia mellifera* and *Grewia flava*) had a lot of shallow roots, which must suffer direct competition from grasses in an ungrazed system. The conclusion drawn was that in a mini-

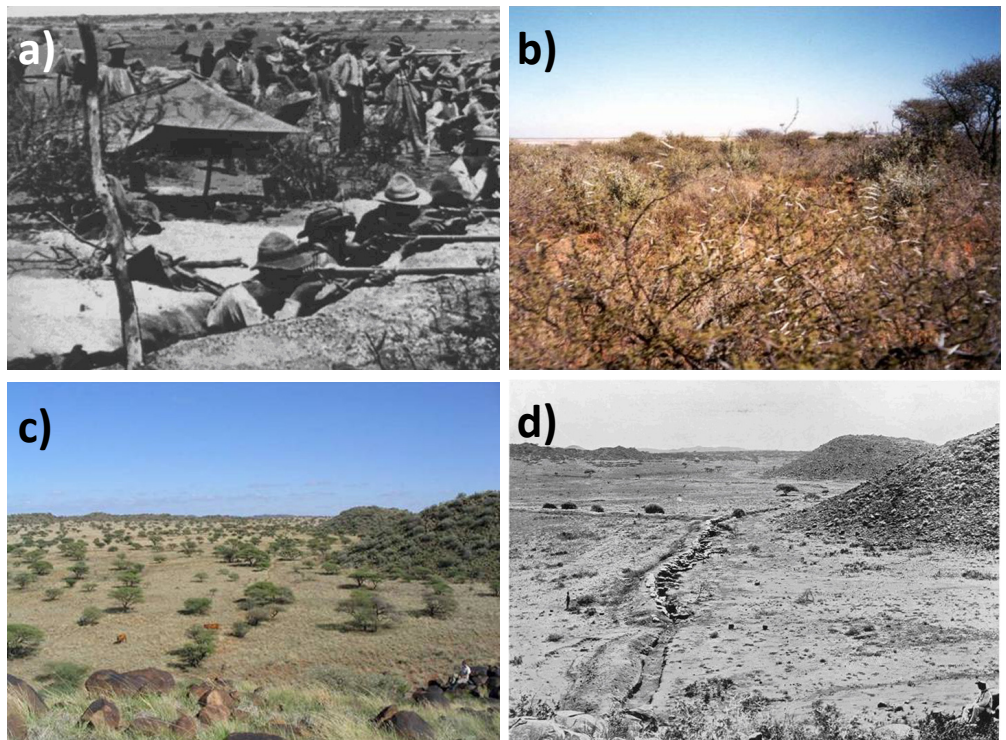
mally grazed system these shrubs and the grasses can coexist despite having most of their roots in the upper soil (Skarpe 1990). That has led to the conclusion that the increase in cover of certain relatively shallow-rooted shrub species seen in heavily grazed dry savannas on both deeper and shallower soils is primarily a result of an increase in soil water content that is due to the absence of competition with grass roots. However, the co-dominance of tall shrubs with grasses on shallow soils shows that, with certain combinations of species, co-dominance is not dependent on root stratification and thus grasses are not better competitors in shallow soil layers. While this does not mean that when root stratification occurs it makes no contribution to the maintenance of co-dominance, the validity of this explanation is limited because it fails to explain the increase of woody species in areas with shallow soils (Hipondoka et al. 2003, Wiegand et al. 2005), or in areas with little grazing (Hipondoka et al. 2003).

A second alternative theory attempting to explain the increase of woody thorny species was based on the evidence that increasing levels of global CO<sub>2</sub> favour the growth of trees and bushes which are C<sub>3</sub> species rather than grasses which are mainly C<sub>4</sub> species (Knapp 1993, Ward 2010). Spe-

cifically, it was found that different responses in stomatal conductance between C<sub>3</sub> and C<sub>4</sub> species during periods of sunlight variability resulted in a twice as rapid rate of change in the C<sub>3</sub> species (Knapp 1993). C<sub>3</sub> plants have a metabolic pathway which is more energy efficient, and if water is plentiful, the stomata can stay open and let in more CO<sub>2</sub>. However, carbon losses through photorespiration are high. Thus, elevated levels of CO<sub>2</sub> would be expected to increase the abundance of C<sub>3</sub> species as carbon availability levels would increase. However, the validity of this theory was significantly reduced by the findings of Archer et al. (1995), reporting an autogenic succession of an open savanna to an encroached one (Fig. 1). Nonetheless, there is expected to be a greater increase in the net photosynthetic rate of C<sub>3</sub> plants (which are usually trees) than C<sub>4</sub> plants (Wolfe and Erickson 1993). An additional factor that may be important is that higher levels of CO<sub>2</sub> may reduce transpiration rates of grasses, which results in deeper percolation of water and, consequently, greater growth rates of trees.

Other theories combining fire with low atmospheric CO<sub>2</sub> (Bond et al. 2003) and resource ratios have been proposed (Ward 2010). However, they have not been verified with field studies.

**Figure 1.** Photographs taken at Magersfontein battlefield, South Africa in (a) 1899 and (b) 2001. The Boer soldiers massacred the British, but today they would not have been able to do so because of *Acacia tortilis* encroachment. (c) Panoramic view of the battlefield. The trees in the foreground are *Acacia tortilis*. The hillside in the distance is covered with the encroaching *Tarchonanthus camphoratus* in 2005 (d) but was not in 1899. The area is now bush encroached in spite of the absence of heavy grazing. This is an example of autogenic succession of an open savanna to an encroached one (see also Archer et al. 1995).



### Patch dynamics

The driving forces of savanna ecology are mainly unknown. Furthermore, the reported increase in density of woody species in savannas is not well understood. Scientists writing about co-dominance in savannas prior to the 1990s did not write specifically about the issue of scale. However they might have had a scale at which they worked, e.g. the scale of the individual tree or tall shrub or tussock grass, and that scale was taken for granted. It was recorded that many tall shrub species in savanna have many of their roots in the same layer as the grasses, and are thus differentiated from the taller *Acacia* tree species such as *A. tortilis* and *A. erioloba* (Smith and Goodman 1986, 1987). Moreover, it was established that an analogy existed for gap-demanding and shade-tolerant tree species in forest; dominant *Acacia* species were found not to be able to recruit under themselves, but various broad-leaved shrubs (both deciduous and evergreen) did so, and thus self-thinning would occur (Smith and Goodman 1986, 1987). The work on bottlenecks summarized by Higgins et al. (2000) represented the next logical stage in analysis.

Currently, researchers are thinking about dynamics at larger scales, facilitated by models, palaeoecological research (see also Gavin 2010), and technological advances of remote-sensing which allow encapsulating a larger temporal and spatial extent of savannas. There are some field studies that have already suggested that, over large spatial scales, savannas may undergo cycles between grassland and woodland (e.g. Dublin et al. 1990), but the phenomenon of cyclical transitions was not examined across several spatial scales. Using simulation models alternative stable states have been reported as well (e.g. Rietkerk and van de Koppel 1997). With the aid of remote sensing, vegetation patches have been increasingly reported in several ecosystems including savannas (Rietkerk and van de Koppel 2008).

Recently, Gillson (2004a, 2004b) and Wiegand et al. (2005, 2006) developed the idea that savannas are hierarchical patch dynamic systems. Scale is a fundamental problem in ecology because different processes occur at different scales

and are linked to patterns at other larger scales (Levin 1992). In patch dynamics, it is assumed that the landscape consists of distinct patches of variable size and that in every patch the same cyclical succession progresses (Meyer et al. 2007). Successional states may vary in duration and occur spatially asynchronously. The proportion of each state is approximately constant at a landscape scale. As a result, at large spatial scales an equilibrium can persist, although at smaller scales non-equilibrium dynamics occur (Levin 1992, Meyer et al. 2007). Most theories trying to explain savanna tree–grass co-dominance did not explicitly state the scale of their applicability (Gillson 2004a).

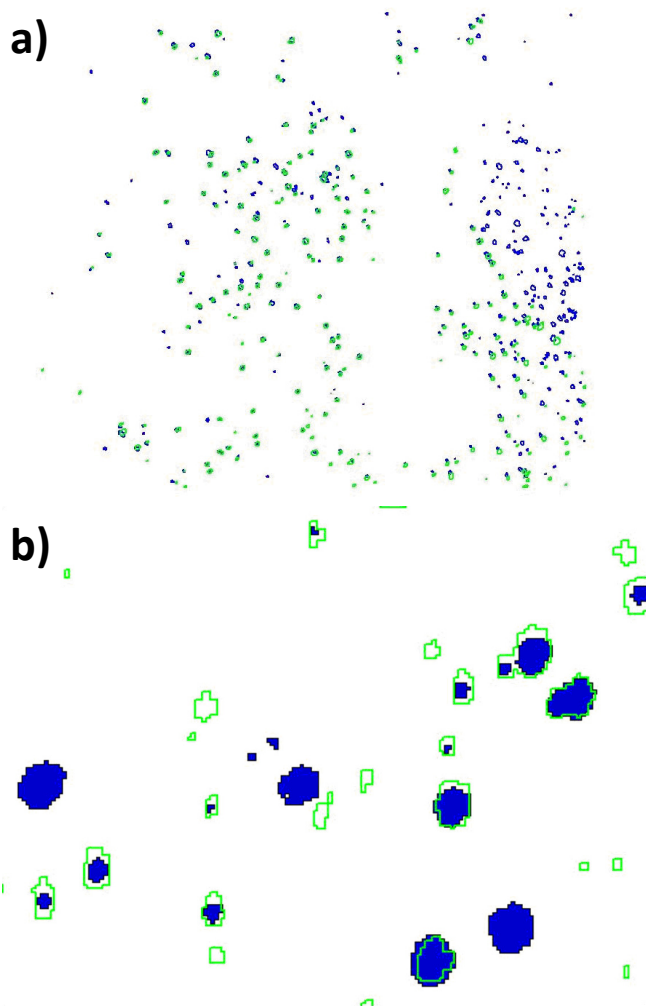
According to the patch dynamics theory, savannas are patch-dynamic systems composed of many patches in different states of transition between grassy and woody dominance. In arid savannas, key factors for patches are rainfall, which is highly variable in space and time, and intra-specific tree competition. According to the savanna patch dynamics theory, bush encroachment is part of a cyclical succession between open savanna and woody dominance (Wiegand et al. 2006). The conversion from a patch of open savanna to a bush-encroached area is initiated by the spatial and temporal overlap of several (localized) rainfall events sufficient for germination and establishment of woody species (trees and bushes). With time, growth and self-thinning of the species that are present will transform the bush-encroached area into a mature woody species stand (of the same species identity) and eventually into open savanna again (Wiegand et al. 2006). Patchiness is sustained because of the local rarity (and patchiness) of rainfall sufficient for germination of woody plants, as well as by plant–soil interactions. According to this theory, there is spatial and temporal variation in savannas. Temporally, a specific patch will pass through an encroached phase and sequentially to a more open savanna, until it is encroached again. Spatially, when a savanna is viewed at a specific time step, there are some encroached patches, while some other patches comprise of an open savanna (for a detailed description, see Wiegand et al. 2006).

This process is, to an extent, similar to the gap-generation phase in forests: in some forests, both temperate and tropical, most turnover is through the replacement of single adults which either fall and make gaps or die *in situ* and do not make canopy gaps. The analogy to savanna dynamics at the scale of individual trees was observed by Belsky and Canham (1994). In other forests the predominant pattern is for groups of trees (regardless of size) to die and be replaced at a given time. The patch dynamic approach at larger scales as described by Wiegand et al. (2006) is similar to the second option: individual trees and tall shrubs in patches defined at the scale of a group of adult trees pass through the various stages of regeneration at the same time because of the precipitation-driven germination of several seedlings in the same year and low seedling germination during several drier years. However, it is important to note that in savannas the key bottleneck is not gaps, as it is in forests, because savanna tree canopies tend not to overlap.

### Synthesis

Thus, there are now three types of theories for tree–grass co-dominance in savannas: niche separation (Walter’s two-layer hypothesis, Walter 1939), demographic bottlenecks (Higgins et al. 2000, Jeltsch et al. 2000), and patch dynamics (Gillson 2004a, Gillson 2004b, Wiegand et al. 2006). All of these vary in terms of the mechanisms and the scales over which they predict tree–grass co-dominance or persistence. The theories also differ in terms of the conditions under which they predict bush encroachment should occur. The niche separation theory (Walter’s two-layer theory), even if the evidence for and against root partitioning is equivocal, does in fact predict encroachment under heavy grazing. Higgins et al. (2000) model suggests that it is the occurrence of unusually wet years which allows trees to escape the demographic bottleneck and establish in arid and semi-arid sites, i.e. bush encroachment is driven by climatic variability in the form of wet years. Finally, the patch dynamics theory suggests that it is a natural cyclic phenomenon in space and time, and thus bush encroachment is a standard

part of patch dynamics rather than a special case. In some ways, the patch dynamics theory can be seen as a spatial extension of the Higgins et al. (2000) model, again invoking rainfall characteristics to explain bush encroachment and persistence of both life forms in space. Ultimately, in order to differentiate between these alternative theories, there is a need for long-term data on savanna plant demography. Long-term remotely-sensed images (Fig. 2) provide a promising approach for understanding tree demography over long time frames.



**Figure 2.** (a) Example of processed aerial photos of a savanna near Kimberley, South Africa. All objects are trees and their X,Y coordinates and projected canopy surface area are known. (b) Detail of processing of a time series of aerial photos. Trees as seen in the 1940 aerial photo are in blue while trees present in the 1964 aerial photo are in green. Trees are individually followed through time and recruitment, death, and canopy growth increments can be detected, c.f. Moustakas et al. (2006).

The next logical step in future analysis after patches have been detected will then be 'How do the patches arise?' If they can be shown not to depend on patchiness in the soil layer, or limited dispersal capabilities or systematic patchiness in the incidence of factors causing death of trees (e.g. fungi or insect herbivores), then it becomes a question of building a bridge between self-organized patchiness, catastrophic shifts that are due to grazing, fire or climate (Rietkerk and van de Koppel 1997, Rietkerk and van de Koppel 2008, Beckage et al. 2009) and patch dynamics using field data. In that case the limits of irreversible vegetation changes due to grazing, fire, and climatic change need to be assessed.

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Edited by Dan Gavin

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