

# We are IntechOpen, the world's leading publisher of Open Access books Built by scientists, for scientists

6,900

Open access books available

186,000

International authors and editors

200M

Downloads

Our authors are among the

154

Countries delivered to

TOP 1%

most cited scientists

12.2%

Contributors from top 500 universities



WEB OF SCIENCE™

Selection of our books indexed in the Book Citation Index  
in Web of Science™ Core Collection (BKCI)

Interested in publishing with us?  
Contact [book.department@intechopen.com](mailto:book.department@intechopen.com)

Numbers displayed above are based on latest data collected.  
For more information visit [www.intechopen.com](http://www.intechopen.com)



---

# Ecology of Woody Plants in African Savanna Ecosystems

---

Allan Sebata

Additional information is available at the end of the chapter

<http://dx.doi.org/10.5772/intechopen.69865>

---

## Abstract

Woody plants are key components of African savanna ecosystems as they provide wildlife habitats, offer browsing to ungulates and are also a major source of fuel wood. Disturbance events such as herbivory and fire negatively affect woody plant communities. However, some woody plants respond to disturbance events through resprouting. In savanna ecosystems, woody plants co-occur with grasses and disturbance events such as overgrazing result in the proliferation of woody plants at the expense of the grasses. Therefore, an understanding of the factors that influence woody plants is critical for the better management of African savanna ecosystems. This chapter reviewed our current knowledge of the ecology of woody plants in African savanna ecosystems and examined disturbance events such as herbivory and fire that shape woody plant communities. The role of resprouting as a response to disturbance events and the negative effects of woody plant encroachment on African savannas was also investigated. In addition, the consequences of poor management such as woody plants loss and possible restoration measures were explored. Disturbance events such as herbivory and fire were found to play critical roles in shaping the African savanna ecosystems. Interventions such as restoration have a role to play in restoring the productivity of degraded woody plant communities.

**Keywords:** encroachment, fire, herbivory, resprouting, restoration, savanna

---

## 1. Introduction

In most African savannas, plant communities are influenced by shortage of moisture during the dry season, with growth occurring largely during the wet season. The occurrence of dry seasons and the resultant fires, fuelled by a continuous annual supply of dry fuel, are thought to be the key drivers in the development of African savannas. Savannas occur where rainfall is seasonal and unpredictable. In general, savannas are characterised by a continuous grass layer

which is occasionally interrupted by woody plants, with fires occurring from time to time [1, 2]. Furthermore, plant communities in the savanna evolved under and continue to be increasingly subjected to intense herbivory pressures. African savanna ecosystems are an important wildlife habitat, offer grazing to livestock and are also a major resource for fuel wood and other products. Their structure and productivity are determined by complex and dynamic interactions between climate, soils and disturbances (such as fire and herbivory) [3]. Woody plants in savannas create favourable micro environments (e.g. through deposition of leaf litter and shading) and habitats that can support a great diversity of flora and fauna [4]. Woody plant communities in African savannas are influenced by many factors such as rainfall, soil type, herbivory and fire. The ability of woody plant communities to cope with disturbances is critical for the sustainability of African savanna ecosystems. Resprouting is widely acknowledged as a mechanism through which woody plants respond to disturbance events such as fire and herbivory. The productivity of African savanna ecosystems is negatively affected by the proliferation of woody plants, a phenomenon referred to as woody plant encroachment. An understanding of the factors that favour woody plant encroachment is important for the better management of African savannas. Poor management of woody plant communities in African savannas leads to land degradation with restoration a slow and expensive process.

This chapter was based on a review of the current literature and sought to highlight the state of our knowledge on the ecology of woody plants in African savanna ecosystems. An extensive search for literature on the effects of rainfall, soil type, herbivory and fire on woody plant communities was undertaken. The role of resprouting as a mechanism that enables woody plants to cope with disturbance events such as fire and herbivory was also examined. Additionally, the negative effects of woody plant encroachment on African savanna communities were covered. Finally, land degradation as a consequence of poor woody plant community management together with possible restoration measures was discussed.

## 2. Effect of rainfall on woody plant communities in African savannas

Woody vegetation structure is determined by the amount of precipitation, with many African savannas water-limited [5–7]. Gordijn et al. [8] reported an increase in woody vegetation with increasing mean annual rainfall. Savannas can be classified according to the amount of rainfall, length of dry season and reliability of rainfall as shown in **Table 1**.

Types of savanna	Mean annual rainfall (mm)	Length of dry season (months)	Normal deviation of rainfall from the annual mean (%)
(a) Moist savanna	1000–2000	2.5–5	15–20
(b) Dry savanna	500–1000	5–7.5	20–25
(c) Semi-arid savanna	250–500	7.5–10	25–40

**Table 1.** Classification of savannas according to amount of rainfall received per year, length of dry season and reliability of rainfall.

Rainfall is least predictable in the semi-arid savanna and most predictable in the moist savanna. Water is considered the main resource limiting plant growth in semi-arid savannas [9]. Woody plant biomass, basal cover and height increase with increasing availability of water to the plants [10]. For example, woody plants are usually abundant along drainage lines within semi-arid savannas owing to greater availability of water [11]. There is also greater woody plant species richness and equitability with increasing rainfall [10, 12]. In addition to the 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. The effects of rainfall interact with soil nutrients, fire and herbivory to influence the density of woody plants [13, 14]. In savannas, the extent of woody vegetation cover at a regional scale is determined by precipitation, while at the landscape level it is influenced by geologic substrate, topography, fire and large herbivores, especially elephants. The density of woody plants varies from dense in woodlands to sparse in nearly treeless areas [15]. Woody plant cover is a key determinant of ecosystem function in savannas [6]. Sankaran et al. [6] set a threshold of 650 mm mean annual precipitation as limiting woody plant growth, above which maximum closed woody cover canopy can be achieved. Additionally, the stature of woody plants decreases with declining precipitation to the point where below *ca.* 300 mm most woody plants will be shorter than the arbitrary 2.5 m threshold used to distinguish trees from shrubs. Scholes et al. [10] found that members of the *Mimosaceae* (mainly *Acacia*) to dominate the tree layer in areas with mean annual precipitation (MAP) of up to 400 mm were then replaced by either the *Combretaceae* (*Combretum* or *Terminalia*) or *Colophospermum mopane* of the *Caesalpiniaceae* where MAP was between 400 and 600 mm and by other representatives of the *Caesalpiniaceae* above 600 mm MAP. Although high precipitation results in increased recruitment of woody plants [16], other factors such as fire, herbivory and frost preclude woody vegetation from reaching the maximum woody cover [17]. A combination of frost, fire and herbivory (for example by elephants) are important determinants of the structure and composition of the woody vegetation of some southern African savannas [18, 19].

### 3. Effect of soil type on woody plant communities in African savannas

The spatial heterogeneity of woody vegetation in African savannas is influenced by the physical and chemical properties of soil [20]. For instance, shallow, gravelly soils with a low soil nutrient status will limit the woody plant size. Soil moisture and nutrient content are related to geology [21], implying that geology predetermines the array of vegetation types found in the African savannas [22]. For example, in African savannas, broad-leafed savanna occur on ancient, highly weathered surfaces, whereas the fine-leafed savanna is restricted to recently formed, nutrient-rich soils [14, 23]. The *Combretaceae* (*Terminalia* & *Combretum*) make up about half of the basal area on soils that are free-draining or rocky, whereas soils with an impeded layer (often sodic or calcareous) within the rooting zone are dominated by *Colophospermum mopane* (Kirk ex Benth.) Kirk ex J. Leonard, an ecologically and morphologically atypical member of *Caesalpiniaceae* [10]. Furthermore, sandy soils tend to favour woody over herbaceous (grasses) plants, which could be attributed to their ability to allow water to percolate deeper beyond the rooting zone of grasses [6, 14, 24, 25]. Additionally, woody plant cover

declines as soil clay content increases [26], because the higher water holding capacity of the finer textured clay soils favours the shallow-rooted grasses over the deep-rooted woody vegetation [17]. Scholes [27] also reported nutrient-poor savannas as generally supporting higher woody biomass than nutrient-rich ones.

#### 4. Effect of herbivory on woody plant communities in African savannas

In African savanna ecosystems, large ungulate herbivores are considered to be the major drivers of vegetation dynamics through directly reducing the abundance of the plants they consume and altering the competitive interactions between trees and grasses [28–30]. Intensive grazing by cattle is normally associated with an increase in woody vegetation [31], with wild browsing ungulates, such as elephants having the opposite effect [32]. Woody plants evolved with herbivory and herbivores play a key role in regulating their cover [33, 34]. In African savannas, herbivores include both invertebrates and vertebrates. Vertebrate herbivores range in size from the diks-diks (3–4 kg) to the elephant (6000 kg). The small herbivores tend to be selective concentrate feeders, whereas the large ones are bulk feeders because they cannot meet their daily feed requirements by being very selective [35]. Termites are an important group of herbivores as they can consume between 10 and 80 percent of available forage. The effects of herbivores on savanna ecosystems will vary depending on the vegetation type, the herbivore and the environment. Bond [25] found herbivory together with fire to be key determinants of vegetation structure and other ecosystem functions. Herbivores modify vegetation structure in many savanna ecosystems [36]. For example, browsers prevent woody plants recruitment to higher height strata [17, 32, 37]. This browser limitation of woody plant growth has been attributed either directly to browsing-induced mortality of woody seedlings and saplings or indirectly to fire, when browsing serves to suppress growth and maintain woody vegetation within the flame zone making them more susceptible to fire-induced mortality [29]. On the contrary, increases in woody cover have been attributed to overgrazing [31], which has been found to enhance dispersal of woody seeds, reduce competition from grazed grasses, reduce fire frequency and intensity due to lowered grass-fuel loads and increase water availability for deep-rooted woody plants as a result of lowered uptake by grasses [29, 31]. Sankaran et al. [17] reported higher woody cover in sites without elephants compared to those with high elephant biomass. Herbivory has both negative and positive effects on woody plants. For instance, megaherbivores (especially elephants) negatively affect woody plants [38], while intense herbivory by mesoherbivores increases woody plants density [39]. O'Connor [40] found elephants to kill woody plants mainly through complete uprooting. Additionally, herbivores enhance woody plant seed dispersal and increase germination rates following gut passage of the seeds, increasing the recruitment success of encroaching species [41, 42].

The major impact of herbivory, particularly by elephants, is to alter the structure and composition of vegetation by converting woodlands to shrublands and then to grasslands [32, 43]. Buechner and Dawkins [44] reported the conversion of *Terminalia glaucescens* woodlands, *Cynometra alexandri* rainforests and riparian woodlands to treeless grassland through the combined effects of elephants and fire in the Murchison Falls National Park, Uganda. Similar results have been reported from Tsavo National Park, Kenya, where elephants were shown to be the

major cause of woodland decline and fire maintained the converted vegetation in a grassland state. Timberlake [45] reported that continuous browsing by elephant results in many small- and medium-sized trees being knocked down, effectively forming a shrubland 1.5–2 m high. Elephants break large trees resulting in an increase in shrub density from coppiced growth [46], with continued herbivory on shrubs preventing their recruitment into taller height classes [47]. Additionally, they can fell, push over or uproot trees and trample on seedlings [48, 49]. Elephants can fell as much as 20 percent of trees in an area per year, with the impacts more severe in restricted areas [50]. Woodland damage by elephants has been reported in the Kruger National Park in South Africa [51], the Luagwa Valley in Zambia [48], the Sengwa Wildlife Research area in northern Zimbabwe [52–54] and the savanna woodlands of East Africa [44, 55]. Furthermore, breakage of the main stems of trees results in a multi-stemmed growth form with limited vertical growth, altering woody vegetation structure [56]. The multi-stemmed coppiced tree stems have high survivorship making them resilient to repeated herbivory which over time could lead to the development of a stable vegetation phase with low canopy cover but resistant to conversion into grassland [19, 56]. Eland also prevent recruitment of woody plants to higher height classes while at the same time causing extensive damage at lower height strata [57], while giraffe browsing reduces tree growth rates [58]. High impala densities have also been found to prevent the regeneration of *Acacia* tree populations through intense seedling predation [59]. Herbivory may lead to an increase in fast-growing palatable woody species or in slow-growing, often chemically defended, unpalatable species [60].

Fire and herbivory act synergistically in influencing woody plant density and composition [61]. Repeated herbivory exposes woody plants to fire by preventing their escape from the fire-prone lower height strata [62]. Additionally, elephants break or ring-bark large mature trees opening up their canopy, leading to an increase in herbage production in the woodlands, which in turn, increases the risk of intense annual fires that kill regenerating plants, converting woodland to shrubland or grassland. The interactive effects of elephants and fire have led to a decline of some woodlands and their subsequent replacement by grasslands or open savanna ecosystems [32, 63]. On the contrary, grazing herbivores through consumption of grass, reduce the fuel load, frequency and intensity of fires allowing woody plants to successfully establish [64]. Herbivores can also positively influence woody plant germination and establishment through other direct and indirect impacts such as trampling and seed dispersal [65]. Gordijn et al. [8] reported browsing as reducing the density of microphyllous palatable species which in turn were replaced by unpalatable macrophyllous species. Giraffe browsing has been found to result in extirpation of some deciduous microphyllous palatable species [66].

## **5. Effect of fire on woody plant communities in African savannas**

Fire plays an important role in altering woody plant community structure in African savannas [4, 7]. It occurs in all savannas with most of the fires deliberately set by human beings, although there are some incidences of fire caused by lightning. Frequent fires reduce woody cover and maintain woody vegetation in a juvenile state by 'top-killing' seedlings and saplings, retarding transition to adulthood in tree species which can resprout from rootstocks after damage of aboveground structures [5, 22, 67]. In areas where fires have

been suppressed, an increase in woody vegetation cover and density has been reported [8]. Woody cover is determined by tree abundance and size, with fire altering the population and community structure and tree size. Fire reduces the proportion of young trees that reach maturity, leading to a disproportionately large number of small trees [7]. In addition, fire reduces competition among mature trees leading to higher growth and survival rates. Repeated burning may result in bimodal tree size distribution, with small and large tree size classes being predominant. Fire also initiates processes such as coppicing which result in the production of multiple stems [7, 68]. Coppice regrowth is a strong regeneration response of woody species in the savanna [69].

Fire can destroy 50% or more of the annual forage production. Moist savannas produce high plant biomass, which in turn increase the fuel load resulting in intense fires. Conversely, herbivory causes a significant reduction in plant biomass accumulation thereby reducing the fuel load limiting the impacts of fires. However, elephant damage of trees makes them more susceptible to fire. Most tree damage occurs when fires are hot such as during late winter or early wet season as compared to mid-summer or wet seasons, with the hot early season burns damaging new plant growth. The frequency of burning also impacts on the extent of plant damage, with very frequent burns resulting in a reduction of plant biomass build up, thereby reducing the intensities of fire and the resulting damage to trees.

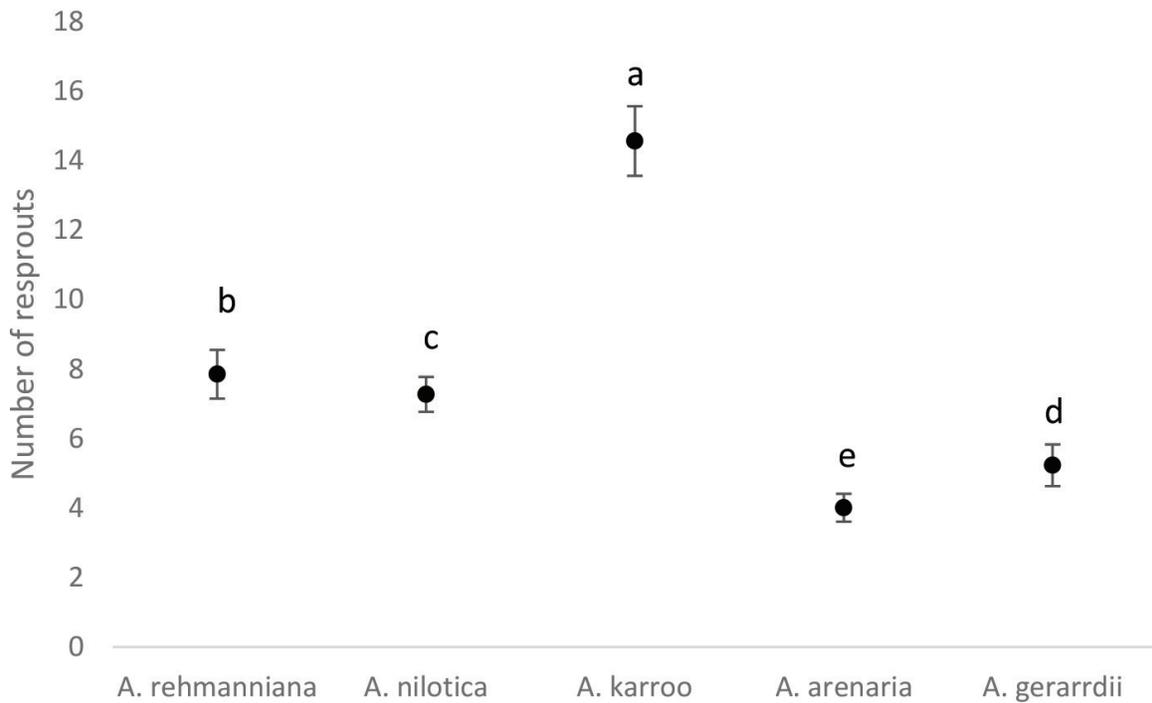
## 6. The role of resprouting in woody plant responses to disturbance

The abundance of woody vegetation in African savanna ecosystems is determined by their ability to respond to disturbance events. Disturbance events widely recognised to influence abundance of woody vegetation include fire [70], herbivory [71] and frost [72]. The ability of woody plants to resprout in response to disturbance events is important in sustaining woody plant populations, particularly in cases where seed production, germination and seedling survival are low [73]. Most woody plants in the savanna have the ability to resprout (coppice) and invest root reserves in rapid growth following a disturbance event [74, 75]. The removal of terminal shoots results in the breaking of apical dominance, allowing lateral meristems to develop into new shoots (hereafter referred to as resprouts) [76, 77]. The development of lateral buds into resprouts enables woody plants to tolerate persistent herbivory, through rapid replacement of lost photosynthetic tissue [78]. Resprouting is considered a strategy for the plant to produce cheap photosynthetic tissue to compensate for lost biomass and to quickly regain a positive carbon and nitrogen balance [77] and can be initiated from a root or stem [79].

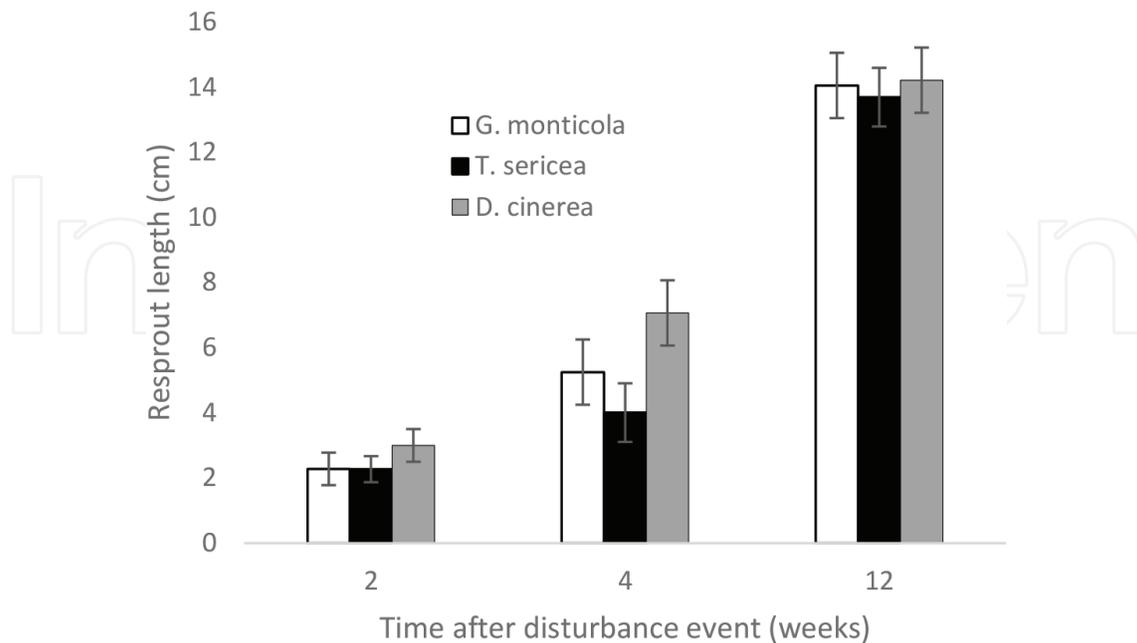
The resprouting responses of woody plants to herbivory vary considerably. Choeni and Sebata [77] compared the resprouting abilities of five *Acacia* species in a semi-arid savanna by determining the number of resprouts following simulated herbivory. *Acacia karroo* was found to be a prolific resprouter, whereas *A. arenaria* produced very few resprouts (**Figure 1**).

The growth of resprouts following a disturbance event is very rapid to quickly replace lost photosynthetic plant material. For instance, sixfold resprout length increments within 10

weeks were reported in a study in central Zimbabwe [80]. Interestingly, three different woody species *viz.* *Grewia monticola* Sond., *Terminalia sericea* Burch. ex DC. and *Dichrostachys cinerea* (L.) Wight & Arn. have similar resprouting responses to disturbance (**Figure 2**).



**Figure 1.** Mean ( $\pm$ SE) number of resprouts of *Acacia rehmanniana*, *A. nilotica*, *A. karroo*, *A. arenaria* and *A. gerrardii* in response to simulated herbivory in a semi-arid savanna. Source: Choeni and Sebata [77].



**Figure 2.** Mean ( $\pm$ SE) ( $n = 5$ ) resprout lengths of three woody species following a disturbance event in a savanna ecosystem. Source: Huruba et al. [80].

Fornara and du Toit [78] found shoot growth rates to increase consistently with severity of herbivory. The timing of the disturbance event initiating resprouting will determine the resprout growth rate. For example, resprouting will be rapid when the plant growth conditions are favourable [81]. Sebata et al. [82] found resprout growth rates to be higher during the wet (growth) than the dry season in a southern African savanna. Resprouts benefit from better mobilization of stored energy reserves and higher photosynthetic rates during the growth season. Page and Whitham [83] found resprout growth to depend on the amount of carbohydrates that can be mobilized, by photosynthesis or in carbohydrate reserves.

## 7. Woody plant encroachment in African savannas

In most African ecosystems, open savannas are considered stable and productive because they are less prone to the rapid proliferation of new woody plants. This is due to the positive effect that large trees have on the natural functioning of the ecosystem which suppresses growth of woody plant seedlings and saplings. The open savanna is maintained through a process of system dynamics, which is based on the principle that the distance between a tree and its nearest neighbour of the same species is not determined purely by chance, but that tree spacing is normally distributed [4]. System dynamics predicts that the larger the tree, the greater is the distance between it and the nearest individual of the same species; this is particularly true for *Acacia* species. Reduced tree competition, through mortality, will result in increasing the growth rate of remaining individuals, whereas competition between individuals in a community will result in reduced growth in a tree population [4]. In the event that the system dynamics is upset, such as through loss of the established mature trees, there will be a rapid proliferation of woody plants, leading to an encroachment of the open savanna ecosystem. Woody plant encroachment is a common consequence of disturbance in savannas [84] and is characterised by an increase in density, cover, extent and biomass of trees in grass-dominated ecosystems [85]. It is a growing concern in most African savannas [86], negatively affecting cattle grazing, fuelwood provision, biodiversity conservation and ecosystem resilience [2]. Overgrazing, unsuitable fire regimes, increased carbon dioxide and climate change have been implicated as the key drivers of woody plant encroachment [29, 87, 88]. In African savannas, woody plant encroachment has generally been attributed to trees escaping from competition with grasses and browse pressure where cattle have replaced wildlife as the predominant herbivores [30]. Due to encroachment, an ecosystem transition takes place leading to an increase in shrub and tree cover in grasslands and savannas resulting in states of co-dominance by shrubs and grasses or complete conversion of grasslands to shrublands or tree-dominated woodlands [89]. These ecosystem transitions affect community composition and vegetation structure, ecosystem functions and biodiversity conservation [90]. However, some grasslands generate self-reinforcing mechanisms that promote conditions which prevent invasion by woody plants [89]. For instance, leaving little open space for colonization, producing many fibrous roots in the upper soil layers that can rapidly use water and nutrients and generating large amounts of herbaceous biomass that facilitates frequent and intense fires that kill unprotected woody plant meristems [91–93].

The competitive dynamics between grasses and woody plants changes once the later establish [89]. Woody plant seedlings recruit as single stems susceptible to top kill by fire then rapidly develop into multi-stemmed plants resistant to burning. Woody cover of the multi-stemmed plants increases limiting grass growth by reducing access to light. Eventually, grass cover, grass biomass and the fuel load decreases [94], allowing further woody plant recruitments [95]. Once woody plants establish themselves in grassland, it is difficult to reverse the process.

The most widely accepted theory explaining bush encroachment is the two-layer soil-water hypothesis [87, 96]. In this theory, the assumption is that water is the limiting factor and grasses use only topsoil moisture and nutrients, whereas woody plants use subsoil resources [97]. This separation of rooting niches allows for the coexistence of woody and grass plants [22]. A disruption of this relationship in favour of trees leads to woody plant proliferation. Overgrazing results in the grass roots extracting less water from the top soil layer and allowing more water to percolate into the sub-soil, where it is available for woody plant growth [22, 29]. Thus, overgrazing changes the grass-tree competitive interactions in favour of the woody plants and also reduces the fuel load through grass removal preventing woody plant damage by fire [67]. Grass competition restricts tree recruitment [39], although grasses may also have positive effects on tree establishment by protecting the saplings from mammalian browsers [98]. In open savannas, grasses generally outcompete trees for water and nutrients 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 [87]. Thus, when heavy grazing occurs, grasses are removed and soil moisture then becomes available to the trees, because they are more deeply rooted, allowing them to grow, recruit and expand [22]. Overgrazing of grasses has been identified as the main cause of increased woody plant density in the eastern areas of Botswana. Tree species with shallow roots (e.g. *Acacia mellifera* and *Grewia flava*) have been reported to be responsible for bush encroachment, suggesting that they are favoured by an increase in water availability in the surface soil following overgrazing of the grass layer. Heavy grazing also reduces the fuel load, which makes fires less intense and thus less damaging to trees and, consequently, results in an increase in woody vegetation. Woody plant encroachment in savannas can also be considered as a cyclical succession between open savanna and woody dominance that is driven by rainfall, which is highly variable, and inter-tree competition [22]. This means that savanna landscapes are composed of many patches in different states of transition between grass and woody dominance, that is, savannas are patch-dynamic systems. Alternatively, woody plant encroachment can be viewed as a natural recruitment process for savannas [22]. In recent years, the increasing carbon dioxide levels associated with global warming have been proposed to be favouring woody plant encroachment [73, 99]. Increases in atmospheric carbon dioxide improve water-use efficiency and increased carbon uptake in  $C_3$  (mostly woody) plants favours them over  $C_4$  (mostly grasses) [4, 73, 99]. The elevated carbon dioxide hypothesis is based on observations that most woody plants have the  $C_3$  photosynthetic pathway and many of the grasses have the  $C_4$  photosynthetic pathway. The  $C_3$  photosynthetic pathway is advantageous at higher levels of carbon dioxide. Woody plant encroached areas can be converted back to open savannas through a process of self-thinning [22]. However, the interactive effects of tree growth with fire and herbivory make the process of self-thinning complex and prolonged.

## 8. Effect of land degradation on woody plant communities and opportunities for restoration

Rangeland degradation starts with the formation of small bare patches which then expand to form large denuded areas [100], leading to the reduction or loss of biodiversity and woody plant productivity [101]. The recovery of woody vegetation in severely degraded areas through natural succession processes is very slow, necessitating active intervention in the form of restoration efforts [102]. Restoration efforts are aimed at returning ecosystems to their previously stable states through the re-establishment of lost vegetation. Cairns [103] argued that restoration must be firmly rooted in ecology and the connection between ecological succession and ecological restoration. The presence of large trees in an African savanna represents a structured stable ecosystem that is productive because of the benefits of the presence of woody plants such as soil enrichment, favourable sub-habitats for the maintenance of positive grass-tree associations and increased stability as large trees may suppress the establishment and development of woody seedlings under their canopies or in their close proximity [4]. The presence of large trees plays a critical role in the restoration of degraded rangelands, particularly the suppression of bush encroachment. Smit [4] suggested that restoring savanna structure requires a highly selective approach where woody plants are thinned in such a way that the remaining trees will benefit from the reduced competition from other woody plants, resulting in increased growth and thus an increasing sphere of influence on newly establishing seedlings.

In most African savannas, woody plant recovery is facilitated through the initial development of pioneer woody species, usually xerophytic spinescent microphyllous species, which are then replaced by a more stable savanna consisting of long-lived broad-leaved species [4]. The broad-leaved woody species are able to germinate and develop under the canopies of spinescent species like some *Acacia* species. The spinescent species later succumb to natural causes, enabling the broad-leaved species to predominate, as the former are unable to establish under the canopies of established trees [4].

The vegetation structure of African savannas is being altered by expansion of human settlements into previously undisturbed areas [104], with fuelwood harvesting as the key driver [105]. Preventing loss of plant communities is more cost-effective than attempts to restore degraded ecosystems, because restoration processes will require costly inputs, such as woody plant establishment. Nonetheless, restoration of degraded savanna systems is inevitable to increase rangeland productivity. Restoration measures include the re-introduction of desired grass species or other investments to improve rangeland quality from both an ecological and an economic perspective.

Attempts at restoring encroached areas by the removal of some or all of the woody plants will normally result in an increase of grass production and thus also the grazing capacity. However, the rapid establishment of tree seedlings after the removal of some or all of the mature woody plants may reduce the effective time span of restoration measures. In many cases, the resultant re-establishment of new woody seedling may in time develop into a state that is worse than the original state. To counter this, a more stable environment can be created by maintaining or restoring savanna structure (large trees). In a structured savanna, large

trees are able to suppress the establishment of new seedlings, while maintaining the other benefits of woody plants like soil enrichment and the provision of food to browsing herbivore species. The loss of large trees from savanna ecosystems through indiscriminate, non-selective bush control measures results in failure to successfully restore encroached areas. Restoration should involve a highly selective process where woody plants are thinned in such a way that the remaining trees will benefit from the reduced competition from other woody plants. Direct competition between grasses and woody seedlings and saplings for soil water can suppress the recruitment of woody species.

## 9. Future perspective

Woody plants in African savanna ecosystems are increasingly being cleared to make way for cropping or being harvested as poles for construction of houses as human population increases. The loss of woody plants alters the ecology of African savanna ecosystems affecting the goods and services offered. A better understanding of the ecology of woody plants is essential in managing these ecosystems in addition to attempts to restore severely degraded areas. Further research to better understand the interactions between the woody and herbaceous components of the African savannas is required. The phenomenon of bush encroachment remains poorly understood necessitating further research to gain better insights.

## 10. Conclusion

A better understanding of the ecology of woody plants is a key to the sustainable management of African savannas because they stabilize these ecosystems. Rainfall, soil, herbivory and fire play important roles in shaping African savanna ecosystems. The resilience and persistence of woody plants in African savannas are determined by their ability to resprout quickly after a disturbance event. Woody plant encroachment disrupts the balance between woody and herbaceous plants resulting in the replacement of the more productive open savannas with less productive densely vegetated ecosystems. Land degradation, mainly due to overgrazing, accelerates woody plant encroachment. Successful restoration of degraded savanna ecosystems requires a good understanding of their ecology.

## Author details

Allan Sebata

Address all correspondence to: [allan.sebata@nust.ac.zw](mailto:allan.sebata@nust.ac.zw)

Department of Forest Resources and Wildlife Management, Faculty of Applied Sciences, National University of Science and Technology, Zimbabwe

## References

- [1] Frost PG, Medina E, Menaut JC, Solbrig O, Swift M, Walker BH. Response of Savannas to Stress and Disturbance. *Biology International Special Issue 10*, Paris: IUBS; 1986
- [2] Fisher JT, Witkowski ETF, Erasmus BFN, Mograbi PJ, Asner GP, van Aardt JAN, Wessels KJ, Mathieu R. What lies beneath: Detecting sub-canopy changes in savanna woodlands using a three-dimensional classification method. *Applied Vegetation Science*. 2015;**18**:528-540
- [3] House JI, Archer S, Breshears DD, Scholes RJ. Conundrums in mixed woody-herbaceous plant systems. *Journal of Biogeography*. 2003;**30**:1763-1777
- [4] Smit GN. An approach to tree thinning to structure southern African savannas for long-term restoration from bush encroachment. *Journal of Environmental Management*. 2004;**71**:179-191
- [5] Bond WJ, Woodward FI, Midgley GF. The global distribution of ecosystems in a world without fire. *New Phytologist*. 2005;**165**:525-537
- [6] Sankaran M, Hanan NP, Scholes RJ, Ratnam J, Augustine DJ, Cade BS, Gignoux J, Higgins SI, Le Roux X, Ludwig F, Ardo J, Banyikwa F, Bronn A, Bucini G, Caylor KK, Coughenour MB, Diouf A, Ekaya W, Feral CJ, February EC, Frost PGH, Hiernaux P, Hrabar H, Metzger KL, Prins HHT, Ringrose S, Sea W, Tews J, Worden J, Zambatis N. Determinants of woody cover in African Savannas. *Nature*. 2005;**438**:846-849
- [7] Devine AP, Stott I, McDonald RA, Maclean IMD. Woody cover in wet and dry African savannas after six decades of experimental fires. *Journal of Ecology*. 2015;**103**:473-478
- [8] Gordijn PJ, Rice E, Ward D. The effects of fire on woody plant encroachment are exacerbated by succession of trees of decreased palatability. *Perspectives in Plant Ecology, Evolution and Systematics*. 2012;**14**:411-422
- [9] Scholes RJ, Bond WJ, Eckhardt HC. Vegetation dynamics in the Kruger ecosystem. In: du Toit JT, Rogers KH, Biggs HC, editors. *The Kruger Experience*. Washington: Island Press; 2003. pp. 242-262
- [10] Scholes R, Dowty PR, Caylor K, Parsons DAB, Frost PGH, Shugart HH. Trends in savanna structure and composition along an aridity gradient in the Kalahari. *Journal of Vegetation Science*. 2002;**13**:419-428
- [11] Mucina L, Rutherford MC. *The Vegetation of South Africa, Lesotho and Swaziland*. Strelitzia 19. Pretoria: South African National Biodiversity Institute; 2006
- [12] O'Brien EM. Climatic gradients in woody plant species richness: Towards an explanation based on an analysis of southern Africa's woody flora. *Journal of Biogeography*. 1993;**20**:181-198
- [13] Huntley BJ, Walker BH, editors. *Ecology of tropical savannas*. Berlin, DE: Springer-Verlag; 1982

- [14] Scholes RJ, Walker BH. *An African Savanna: Synthesis of the Nylsvley Study*. Cambridge: Cambridge University Press; 1993
- [15] Mills AJ, Milewski AV, Fey MV, Gröngroft A, Petersen A, Sirami C. Constraint on woody cover in relation to nutrient content of soils in western southern Africa. *Oikos*. 2013;**122**:136-148
- [16] Kraaij T, Ward D. Effects of rain, nitrogen, fire and grazing on tree recruitment and early survival in bush-encroached savanna, South Africa. *Plant Ecology*. 2006;**86**:235-246
- [17] Sankaran M, Ratnam J, Hanan N. Woody cover in African savannas: The role of resources, fire and herbivory. *Global Ecology and Biogeography*. 2008;**17**:236-245
- [18] Childes SL, Walker BH. Ecology and dynamics of the woody vegetation on the Kalahari sands in Hwange National Park, Zimbabwe. *Vegetation*. 1987;**72**:111-128
- [19] Holdo RM. Elephant herbivory, frost damage and topkill in Kalahari sand woodland savanna trees. *Journal of Vegetation Science*. 2006;**17**:509-518
- [20] Campbell BM, Cunliffe RN, Gambiza J. Vegetation structure and small-scale pattern in Miombo woodland, Marondera, Zimbabwe. *Bothalia*. 1995;**25**:121-126
- [21] Cole MM. The influence of soils, geomorphology and geology on the distribution of plant communities in savanna ecosystems. In: Huntley BJ, Walker BH. editors, *Ecology of Tropical Savannas*. Ecological Studies. Berlin: Springer; 1982. Vol. 24. pp. 145-174
- [22] Wiegand K, Saltz D, Ward D. A patch-dynamics approach to savanna dynamics and woody plant encroachment – Insights from an arid savanna. *Perspectives in Plant Ecology, Evolution and Systematics*. 2006;**7**:229-242
- [23] Scholes RJ. Savanna. In: Cowling RM, Richardson DM, Pierce SM. editors, *Vegetation of Southern Africa*. Cambridge, MA: Cambridge University Press; 1997. pp. 258-277
- [24] Walker BH, Langridge JL. Predicting savanna vegetation structure on the basis of plant available moisture and plant available nutrients: A case study from Australia. *Journal of Biogeography*. 1997;**24**:813-825
- [25] Bond WJ. What limits trees in C<sub>4</sub> grasslands and savannas? *Annual Review of Ecology, Evolution, and Systematics*. 2008;**39**:641-659
- [26] Williams RJ, Duff GA, Bowman DMJS, Cook GD. Variation in the composition and structure of tropical savannas as a function of rainfall and soil texture along a large scale climatic gradient in the Northern Territory, Australia. *Journal of Biogeography*. 1996;**23**:747-756
- [27] Scholes RJ, 1990. The influence of soil fertility on the ecology of southern African dry savannas. *Journal of Biogeography*. 1990;**17**:415-419
- [28] Skarpe C. Dynamics of savanna ecosystems. *Journal of Vegetation Science*. 1992;**3**:293-300
- [29] Scholes RJ, Archer SR. Tree-Grass Interactions in Savannas. *Annual Review of Ecology and Systematics*. 1997;**28**:517-544

- [30] Riginos C, Young TP. Positive and negative effects of grass, cattle, and wild herbivores on Acacia saplings in an East African savanna. *Oecologia*. 2007;**153**:985-995
- [31] Roques KG, O'Connor TG, Watkinson AR. Dynamics of shrub encroachment in an African savanna: Relative influences of fire, herbivory, rainfall and density dependence. *Journal of Applied Ecology*. 2001;**38**:268-280
- [32] Dublin HT, Sinclair ARE, Mcglade J. Elephants and fire as causes of multiple stable states in the Serengeti-Mara woodlands. *Journal of Animal Ecology*. 1990;**59**:1147-1164
- [33] Cumming DHM. The influence of large herbivores on savanna structure in Africa. In: Huntley BJ and Walker BH, editors. *Ecology of Tropical Savannas*. Springer-Verlag, Berlin, Germany; 1982. pp. 217-245
- [34] Holdo RM, Holt RD, Fryxell JM. Herbivore-vegetation feedbacks can expand the range of savanna persistence: Insights from a simple theoretical model. *Oikos*. 2013;**122**:441-453
- [35] Hofmann RR. Evolutionary steps of ecophysiological adaptation and diversification of ruminants: A comparative view of their digestive system. *Oecologia*. 1989;**78**:443-457
- [36] Staver AC, Bond WJ, Stock WD, Van Rensburg SJ, Waldram MS. Browsing and fire interact to suppress tree density in an African savanna. *Ecological Applications*. 2009;**19**:1909-1919
- [37] Augustine DJ, McNaughton SJ. Regulation of shrub dynamics by native browsing ungulates on East African rangeland. *Journal of Applied Ecology*. 2004;**41**:45-58
- [38] Owen-Smith N. Pleistocene extinctions: The pivotal role of megaherbivores. *Paleobiology*. 1987;**13**:351-362
- [39] Goheen JR, Palmer TM, Keesing F, Riginos C, Young TP. Large herbivores facilitate savanna tree establishment via diverse and indirect pathways. *Journal of Animal Ecology*. 2010;**79**:372-382
- [40] O'Connor TG. Demography of woody species in a semi-arid African savanna reserve following the re-introduction of elephants. *Acta Oecologica*. 2017;**78**:61-70
- [41] Miller MF. Acacia seed survival, seed-germination and seedling growth following pod consumption by large herbivores and seed chewing by rodents. *African Journal of Ecology*. 1995;**33**:194-210
- [42] Tews J, Schurr F, Jeltsch F. Seed dispersal by cattle may cause shrub encroachment of *Grewia lava* on southern Kalahari rangelands. *Applied Vegetation Science*. 2004;**7**:89-102
- [43] Ben-Shahar R. Changes in structure of savanna woodlands in northern Botswana following the impacts of elephants and fire. *Plant Ecology*. 1998;**136**:189-194
- [44] Buechner HK, Dawkins HC. Vegetation change induced by elephants and fire in Murchison Falls National Park, Uganda. *Ecology*. 1961;**42**:752-766
- [45] Timberlake JR. *Colophospermum mopane*, Annotated Bibliography and Review. Harare: The Zimbabwe Bulletin of Forestry Research No. 11, Forestry Commission; 1995

- [46] Richardson-Kageler SJ. Large mammalian herbivores and woody plant species diversity in Zimbabwe. *Biodiversity and Conservation*. 2003;**12**:703-715
- [47] Gadd ME. The impact of elephants on the marula tree (*Sclerocarya birrea*). *African Journal of Ecology*. 2002;**40**:328-336
- [48] Caughley G. The elephant problem—An alternative hypothesis. *East African Wildlife Journal*. 1976;**14**:265-283
- [49] Mapaire I, Mhlanga L. Elephants and woodlands: The impact of elephant damage on *Colophospermum mopane* on Namembere Island, Lake Kariba, Zimbabwe. *Zimbabwe Science News*. 1998;**32**:15-19
- [50] Conybeare AM. Elephant occupancy and vegetation change in relation to artificial water points in Kalahari sand area of Hwange National Park. Unpublished MSc thesis, Department of Biological Sciences, University of Zimbabwe. Harare, Zimbabwe; 1991
- [51] van Wyk P, Fairall N. The influence of the African elephant on the vegetation of Kruger National Park. *Koedoe*. 1969;**9**:57-95
- [52] Anderson GD, Walker BH. Vegetation composition and elephant damage in the Sengwa Research Area, Rhodesia. *Journal of South African Wildlife Research Management Association*. 1974;**4**:1-14
- [53] Guy PR. The feeding behaviour of elephant (*Loxodonta africana*) in the Sengwe area, Rhodesia. *South African Journal of Wildlife*. 1976;**6**:55-63
- [54] Guy PR. The influence of elephants and fire on a *Brachystegia-Julbernardia* woodland in Zimbabwe. *Journal of Tropical Ecology*. 1989;**5**:215-226
- [55] Pellew RAP. The impacts of elephant, giraffe and fire upon the *Acacia-Tortilis* woodlands of the Serengeti. *African Journal of Ecology*. 1983;**21**:41-74
- [56] Holdo RM. Woody plant damage by African elephants in relation to leaf nutrients in western Zimbabwe. *Journal of Tropical Ecology*. 2003;**19**:189-196
- [57] Nyengera R, Sebata A. Effect of eland density and foraging on *Combretum apiculatum* physiognomy in a semi-arid savanna. *African Journal of Ecology*. 2009;**48**:45-50
- [58] Birkett A, Stevens-Wood B. Effects of low rainfall and browsing by large herbivores on an enclosed savanna habitat in Kenya. *African Journal of Ecology*. 2005;**43**:123-130
- [59] Prins HHT, van der Jeugd HP. Herbivore population crashes and woodland structure in East Africa. *Journal of Ecology*. 1993;**81**:305-314
- [60] Skarpe C, Aarrestad PA, Andreassen HP, Dhillion SS, Dimakatso T, du Toit JT, Halley DJ, Hytteborn H, Makhabu S, Mari M, Marokane W, Masunga G, Modise D, Moe SR, Mojaphoko R, Mosugelo D, Motsumi S, Neo-Mahupeleng G, Ramotadima M, Rutina, L, Sechele L, Sejoe TB, Stokke S, Swenson JE, Taolo C, Vandewalle M, Wegge P. The return of the giants: Ecological effects of an increasing elephant population. *Ambio*. 2004;**33**:276-282

- [61] Midgley JJ, Lawes MJ, Chamailé-Jammes S. Savanna woody plant dynamics: The role of fire and herbivory, separately and synergistically. *Australian Journal of Botany*. 2010;**58**:1-11
- [62] Jachmann H, Bell RHV. Utilization by elephants of the *Brachystegia* woodlands of the Kasungu National Park, Malawi. *African Journal of Ecology*. 1985;**23**:245-258
- [63] Laws RM. Elephants as agents of habitat and landscape change in East Africa. *Oikos*. 1970;**21**:1-15
- [64] van Langevelde F, van de Vijver CADM, Kumar L, van de Koppel J, de Ridder N, van Andel J, Skidmore AK, Hearne JW, Stroosnijder L, Bond WJ, Prins HHT, Rietkerk M. Effects of fire and herbivory on the stability of savanna ecosystems. *Ecology*. 2003;**84**:337-350
- [65] Danell K, Duncan P, Bergström R, Pastor J. *Large Herbivore Ecology, Ecosystem Dynamics and Conservation*. Cambridge, UK: Cambridge University Press; 2006
- [66] Bond WJ, Loffell D. Introduction of giraffe changes acacia distribution in a South African savanna. *African Journal of Ecology*. 2001;**39**:286-294
- [67] Midgley JJ, Bond WJ. A synthesis of the demography of African acacias. *Journal of Tropical Ecology*. 2001;**17**:871-886
- [68] Chidumayo EN. Growth responses of an African savanna tree, *Bauhinia thonningii* Schumacher, to defoliation, fire and climate. *Trees*. 2007;**21**:231-238
- [69] Kaschula S, Twine W, Scholes M. The effect of catena position and stump characteristics on the coppice response of three savannah fuelwood species. *Environmental Conservation*. 2005;**32**:76-84
- [70] Bond WJ. Fire. In: Cowling RM, Richardson DM, Pierce SM, editors. *Vegetation of Southern Africa*. Cambridge: Cambridge University Press; 1997
- [71] O'Connor TG, Puttick JR, Hoffman MT. Bush encroachment in southern Africa: Changes and causes. *African Journal of Range and Forage Science*. 2014;**31**:67-88
- [72] Muller K, O'Connor TG, Henschel JR. Impact of a severe frost event in 2014 on woody vegetation within the Nama-Karoo and semi-arid savanna biomes of South Africa. *Journal of Arid Environments*. 2016;**133**:112-121
- [73] Bond WJ, Midgley GF. A proposed CO<sub>2</sub>-controlled mechanism of woody plant invasion in grasslands and savannas. *Global Change Biology*. 2000;**6**:865-869
- [74] Bergström R. Browse characteristics and impact of browsing on trees and shrubs in African savannas. *Journal of Vegetation Science*. 1992;**3**:315-324
- [75] Whitecross MA, Archibald S, Witkowski ETF. Do freeze events create a demographic bottleneck for *Colophospermum mopane*? *South African Journal of Botany*. 2012;**83**:9-18
- [76] Aarssen LW. Hypothesis for the evolution of apical dominance in plants: Implications for the interpretation of overcompensation. *Oikos*. 1995;**74**:149-156

- [77] Choeni H, Sebata A. Interspecific variation in the resprouting responses of *Acacia* species following simulated herbivory in a semi-arid southern African savannah. *African Journal of Ecology*. 2014;**52**:479-483
- [78] Fornara DA, du Toit JT. Browsing lawns? Responses of *Acacia nigrescens* to ungulate browsing in an African savanna. *Ecology*. 2007;**88**:200-209
- [79] Bond WJ, Midgley JJ. The evolutionary ecology of sprouting in woody plants. *International Journal of Plant Sciences*. 2003;**164**:S103-S114
- [80] Huruba R, Mundy PJ, Sebata A, Purchase GK, MacFadyen DN. Impala, *Aepyceros melampus*: does browse quality influence their use of sites originally utilised as short-duration kraals in a southern African savanna? *The Rangeland Journal*. 2017;**39**:113-121; in press. <http://dx.doi.org/10.1071/RJ16016>
- [81] Strauss SY, Agrawal AA. The ecology and evolution of plant tolerance to herbivory. *Trends in Ecological Evolution*. 1999;**14**:179-185
- [82] Sebata A, Nyathi P, Mlambo D. Growth responses of *Grewia flavescens* Juss. (Sandpaper Raisin) and *Grewia monticola* Sond. (Grey Grewia) (Tiliaceae) to shoot clipping in a semi-arid Southern African savanna. *African Journal of Ecology*. 2009;**47**:794-796
- [83] Page KN, Whitham TG. Overcompensation in response to mammalian herbivory: The advantage of being eaten. *American Naturalist*. 1987;**129**:407-416
- [84] Vadigi S, Ward D. Herbivory effects on saplings are influenced by nutrients and grass competition in a humid South African savanna. *Perspectives in Plant Ecology, Evolution and Systematics*. 2014;**16**:11-20
- [85] Archer S, Scifres C, Bassham CR, Maggio R. Succession in a subtropical savanna: Conversion of grassland to thorn woodland. *Ecological Society of America*. 1988;**58**: 111-127
- [86] Archer S, Schimel DS, Holland EA. Mechanisms of shrubland expansion: Land use, climate or CO<sub>2</sub>? *Climatic Change*. 1995;**29**:91-99
- [87] Walker BH, Ludwig D, Holling CS, Peterman RM. Stability of semi-arid savanna grazing systems. *Journal of Ecology*. 1981;**69**:473-498
- [88] Bond WJ, Midgley GF. Carbon dioxide and the uneasy interactions of trees and savannah grasses. *Philosophical Transactions of the Royal Society*. 2012;**367**:601-612
- [89] Ratajczak Z, Nippert JB, Briggs JM, Blair JM. Fire dynamics distinguish grasslands, shrublands and woodlands as alternative attractors in the Central Great Plains of North America. *Journal of Ecology*. 2014;**102**:1374-1385
- [90] Ratajczak Z, Nippert JB, Collins SL. Woody encroachment decreases diversity across North American grasslands and savannas. *Ecology*. 2012;**93**:697-703
- [91] Briggs JM, Knapp AK. Determinants of C<sub>3</sub> forb growth and production in a C<sub>4</sub> dominated grassland. *Plant Ecology*. 2001;**152**:93-100

- [92] Nippert JB, Knapp AK. Linking water uptake with rooting patterns in grassland species. *Oecologia*. 2007;**153**:261-272
- [93] van Wilgen BW, Trollope WSW, Biggs HC, Potgieter ALF, Brockett BH. Fire as a driver of ecosystems variability. The Kruger Experience. In: Du Toit JT, Rogers KH, Biggs HC, editors. *Ecology and Management of Savanna Heterogeneity*. Washington, DC: Island Press; 2002. pp. 149-170
- [94] Heisler JL, Briggs JM, Knapp AK, Blair JM, Seery A. Direct and indirect effects of fire on shrub density and above-ground diversity in a mesic grassland. *Ecology*. 2004;**85**:2245-2257
- [95] Ratajczak Z, Nippert JB, Hartman JC, Ocheltree TW. Positive feedbacks amplify rates of woody encroachment in mesic tallgrass prairie. *Ecosphere*. 2011;**2**:1-14
- [96] Walter H. *Ecology of Tropical and Subtropical Vegetation*. Edinburgh: Oliver and Boyd; 1971
- [97] Knoop WT, Walker BH. Interactions of woody and herbaceous vegetation in a southern African savanna. *Journal of Ecology*. 1985;**73**:235-253
- [98] Seymour C. Grass, rainfall and herbivores as determinants of *Acacia erioloba* (Meyer) recruitment in an African savanna. *Plant Ecology*. 2008;**197**:131-138
- [99] Ward D. A resource ratio model of the effects of changes in CO<sub>2</sub> on woody plant invasion. *Plant Ecology*. 2010;**209**:147-152
- [100] Kellner K, Bosch OJH. Influence of patch formation in determining the stocking rate for southern African grasslands. *Journal of Arid Environments*. 1992;**22**:99-105
- [101] Okin G. Desertification: Monitoring and Forecasting, Desertification—Introduction; 2002. website: [http://www.planetary.caltech.edu/\\_arid/desert/desert.html](http://www.planetary.caltech.edu/_arid/desert/desert.html)
- [102] van den Berg L, Kellner K. Restoring degraded patches in a semi-arid rangeland of South Africa. *Journal of Arid Environments*. 2005;**61**:497-511
- [103] Cairns J. *Rehabilitating Damaged Ecosystems*. 2nd ed. Boca Raton: Lewis Publishers; 1995
- [104] Coetzer KL, Erasmus BFN, Witkowski ETF, Bachoo AK. Land cover change in the Kruger to Canyons Biosphere Reserve (1993-2006): A first step towards creating a conservation plan for the subregion. *South African Journal of Science*. 2010;**106**:26-35
- [105] Matsika R, Erasmus BFN, Twine W. A tale of two villages: Assessing the dynamics of fuelwood supply in communal landscapes in South Africa. *Environmental Conservation*. 2013;**40**:71-83