

See discussions, stats, and author profiles for this publication at: <http://www.researchgate.net/publication/228401923>

The woody weed encroachment puzzle: gathering pieces

ARTICLE *in* ECOHYDROLOGY · DECEMBER 2008

Impact Factor: 2.63 · DOI: 10.1002/eco.28

CITATIONS

13

DOWNLOADS

29

VIEWS

100

1 AUTHOR:



[Friedrich Patrick Graz](#)

Federation University Australia

31 PUBLICATIONS 66 CITATIONS

SEE PROFILE

The woody weed encroachment puzzle: gathering pieces

F. Patrick Graz*

Science and Engineering, University of Ballarat, Ballarat, VIC 3353, Australia

ABSTRACT

Increases in woody plant densities in savanna grazing lands worldwide have resulted in a decline in the grazing capacity of these rangelands. At present, the actual cause of the problem is unknown although a vast body of literature deals with various aspects relevant to the issue.

It is generally assumed, however, that the changes in the tree : grass ratio are a response to changes in soil-water development brought about by rangeland utilization. These utilization patterns differ from those under which the savanna system evolved. While changes in physiognomy are very prominent, these are generally preceded by changes in grass species assemblage.

The development of species composition has been used as an indicator of rangeland condition for many years; the increase or decrease of individual species is considered in this context. Thus far, however, the shift from perennial to annual grasses has not been evaluated for its effect on soil moisture development, and subsequent implications for woody plant establishment and growth.

The review presented here consolidates the existing information in order to provide a basis for understanding the woody weed encroachment problem. Copyright © 2008 John Wiley & Sons, Ltd.

KEY WORDS bush encroachment; savanna ecology; model; vegetation composition

Received 24 October 2007; Accepted 17 April 2008

INTRODUCTION AND BACKGROUND

The terms *bush encroachment* or *woody weed encroachment* in the savanna system are used to describe a change in the physiognomy of the general vegetation. Within the affected areas, the woody plant component shows a substantial increase in density resulting in a decrease in rangeland productivity. Most notable is the decline in grass production (Scholes and Archer, 1997), with a concomitant reduction in livestock carrying capacity (Molele *et al.*, 2002). Harrington *et al.* (1984) estimate that carrying capacity of sheep in mulga (*Acacia aneura*) woodland declined from 1 sheep to 4 ha to 1 in 10, while de Klerk (2004) reports a complete loss in grazing capacity for parts of Namibia. The phenomenon has been recorded from most areas where savanna vegetation is used as the rangeland to graze domestic stock, i.e. in Australia (Werner, 1991), Africa (Molele *et al.*, 2002; de Klerk, 2004; Ward, 2005), USA (Archer, 1991; Jeltsch *et al.*, 2000) and India (Roques *et al.*, 2001). Despite the fact that the problem was already recorded by Dyksterhuis (1949), Molele *et al.* (2002) and Ward (2005) emphasize that the cause has not been fully explained thus far. This review therefore attempts to consolidate existing information to provide a basis for such an explanation.

Any explanation of the cause is based on an underlying conceptual idea or model of the system, particularly the relationship between grasses and trees. Current models may be divided into two groups based on the part of the

system they address. On the one hand we consider models describing how the system works. This group includes, amongst others, the two-layer model after Walter (1971) and the temporal separation suggested by Harrington *et al.* (1984) and Scholes and Walker (1993).

The second group of models considers the reaction of the vegetation to utilization and/or disturbance. These include the *range succession* model of Dyksterhuis (1949) and *state-and-transition* models such as that of Westoby *et al.* (1989).

The *two-layer* theory, discussed by Walter (1971) and Walker and Noi-Meir (1982), separates the soil into two consecutive layers that support different components of the savanna system; the herbaceous layer extracts its resources primarily from the upper few centimetres, while the lower soil layers primarily support the woody vegetation component. In line with the theory, water would only become available to the woody plant component once infiltration and drainage exceed the requirements of the herbaceous plants. As will be discussed in more detail later, it is not only the quantity of water that enters the soil, but also the rate of infiltration and drainage that need to be considered. Despite the criticisms that have been levelled at the two-layer model it has had by far the most influence on directing research.

The second approach considers a temporal rather than spatial separation in resource uptake by trees and grasses. Harrington *et al.* (1984) had shown differences in the timing of establishment (for annuals) and growth were not only between grasses and trees but also between perennial and ephemeral herbaceous plants and perennial woody plants. Temporal separation was also discussed

* Correspondence to: F. Patrick Graz, Science and Engineering, University of Ballarat, Ballarat, VIC 3353, Australia.
E-mail: p.graz@ballarat.edu.au

by Scholes and Walker (1993) and supported by much corroborating evidence. It is somewhat surprising that temporal separation has not received more attention in the literature thus far, although support seems to be growing (Rodriguez-Iturbe *et al.*, 1999; Hipondoka *et al.*, 2003).

The *range succession* model described by Dyksterhuis (1949) is perhaps the oldest approach used to describe the development of the savanna system, although it focuses on rangeland productivity rather than the coexistence of trees and grasses. This model identifies potential climax states for different rangeland types. Grazing and other range management activities are assumed to direct rangeland development towards or away from the envisaged climax state. Dyksterhuis (1949) supported the monitoring of annual grasses and woody plants to assess range development. While the method has been used extensively, the prerequisite knowledge of a climax state might be regarded as a serious shortcoming.

A further approach considered different states of vegetation that would be reached under various management scenarios. Such *state-and-transition* models include those of Westoby *et al.* (1989) and Joubert & Rothauge (cited in Zimmermann *et al.*, 2001). This approach recognizes various possible stable states of vegetation coexistence and provides for the inclusion of equilibrium and non-equilibrium dynamics. Rather than attempting to identify a single, most important factor, the approach recognizes that different limiting factors may act on the system at different stages of its development (see the frame-based models of Starfield *et al.* (1993) and Graz (1996)).

While state-and-transition models represent a significant, fundamental improvement on the range succession model, Briske *et al.* (2003) point out that the different stable states of the vegetation need to be known, as well as the nature, causes and thresholds of the transitions between them, before the model may be implemented. We must also consider that these models describe conditions, i.e. states, that are static in time, i.e. they do not consider processes within each state. Briske *et al.* (2003) therefore suggest a combination of the range succession and state-and-transition models.

Further non-equilibrium ecological approaches were considered by the disturbance models discussed by Scholes and Archer (1997) and Jeltsch *et al.* (2000), and the patch-dynamic model of Wiegand *et al.* (2005). None of these models have received the general acceptance of the first two, however.

Both the two-layer and temporal separation models have some validity and the two are readily combined. This combination may be augmented, however, if additional physiological differences between grasses and trees are included.

Most applicable studies seem to agree that soil moisture uptake and competition for moisture and nutrients are determining factors in the tree–grass interaction (see the discussions by Rodriguez-Iturbe *et al.* (1999) and Kerkhoff *et al.* (2004)).

Most authors also seem to agree that bush encroachment is a result of changes in the tree–grass balance brought about by modifications in grazing regimes (Skarpe, 1991; Scholes and Archer, 1997; Jeltsch *et al.*, 2000; van Langenvelde *et al.*, 2003).

A number of authors consider changes to the fire regime, particularly changes in frequency and intensity as a further promotion of bush encroachment (see for instance Jeltsch *et al.*, 2000 and van Langenvelde *et al.*, 2003). Accumulating empirical evidence (Archer *et al.*, 1988; Hoffmann, 1998; Meyer *et al.*, 2005) suggests, however, that the seedlings of woody plants are not as susceptible to fire induced mortality as had previously been assumed.

Changes in the rangeland composition and their effect on the soil moisture balance have received limited attention in the literature. This does not imply that there have been no studies relating to different parts of this aspect. For instance, Garnier (1992) compared growth parameters between annual and congeneric perennial grasses; Heng *et al.* (2001) compared the soil–water dynamics between perennial and annual pastures.

This review uses the available literature to integrate the effects of grazing and soil moisture regime, and to assess the implications for the development of rangelands. The information reviewed here is necessarily taken from a wide range of investigations from arid and semi-arid areas, as no single system has been studied in all of the aspects considered here.

Soil-water and savanna plants

Soil moisture is primarily recharged by rain (Schwinning *et al.*, 2002). In the savannas of southern Africa, South America and Australia, precipitation is seasonal and highly variable in terms of its intensity, as well as its temporal and spatial distribution. For any given site, this results in distinct wet and dry periods of irregular length, giving rise to substantial variation in moisture supply and soil-water recharge.

The soil surface, as the entry point for any rainfall, affects the rate at which moisture may infiltrate the soil. The condition of the soil surface, in terms of soil texture and structure, the presence or absence of crusts (Belnap, 2006) and the accumulated litter (Kelly and Walker, 1976; Murphy *et al.*, 2004) therefore plays a significant role in soil moisture development; Walker *et al.* (1981) report ten times the infiltration rate under grass-litter than is found on bare soils. Once water has infiltrated it may drain to lower soil layers or be removed through evapotranspiration.

For a given soil type infiltration, and subsequent drainage, are not only a function of the amount and intensity of rainfall events but are also affected by the prevailing moisture contents of the soil—with an increase in soil moisture contents there is a concomitant increase in the rate of infiltration and drainage (Foth, 1990; D'Odorico and Porporato, 2006). This is, in turn, a function of prior rainfall events; the relationship is highly

non-linear, with decreases in conductivity of four to five orders of magnitude with changes in soil-water contents (Hopmans, 2006).

Paradoxically, therefore, water will not readily infiltrate very dry soils (Foth, 1990). This may be observed in the field; after longer dry periods the raindrops of the first shower form small domes of moisture on the surface before infiltrating. Depending on continuing conditions the water will evaporate.

According to the two-layer theory, moisture from light rains will only drain into a relatively shallow depth thus becoming available to plants with their roots close to the soil surface, primarily grasses (Knoop and Walker, 1985; Frost *et al.*, 1986; Schwinning *et al.*, 2002; Hipondoka *et al.*, 2003).

More generally, we must assume that moisture will only become available to the plants with deeper roots when the rate of infiltration and drainage exceeds the rate of direct evaporation from the top-soil and water uptake by shallow rooted plants. Apart from rainfall patterns and intensity, moisture recharge of the lower lying soils is therefore a function of the condition of the soil surface, and water use by vegetation utilizing the top-soil.

Yet, not all shallow rooted plants, specifically grasses, have the same effect on soil moisture development. Annual and perennial grasses not only differ in their response to the stochastic nature of rainfall (Frost *et al.*, 1986) or grazing (see later) but also differ in their effect on soil moisture accumulation (Kelly and Walker, 1976) and with respect to water use. (Kelly and Walker, 1976) report that water may funnel down perennial tussock grasses towards their roots, resulting in reduced runoff from the areas dominated by such grasses; annual grasses were unable to do so. Walker *et al.* (1981) thus hypothesize an asymptotic relationship between total grass biomass and water infiltration.

Differences with respect to water use are particularly apparent from studies comparing annual and perennial planted pastures as reported by Ridley *et al.* (1997); White *et al.* (2000); Heng *et al.* (2001) and Bird *et al.* (2004), and covering a range of species, soils and climatic conditions. These authors determined higher rates of deep drainage under annual grasses than under perennials, given like conditions. White *et al.* (2000), for instance, reported higher deep drainage rates of 38–40 mm under annual pastures. Similar observations were also reported by Walker *et al.* (1981); White *et al.* (2000) and Virgona and Southwell (2006) under rangeland conditions.

In addition, Virgona and Southwell (2006) report higher rates of evapotranspiration on perennial grasses, particularly when these were assigned longer periods of rest. These findings show that changes in rangeland composition will be accompanied by changes in soil-water utilization.

Further differences in soil-water use occur between woody and herbaceous plants. To study the interactions of these plants, some authors have simplified the system by studying plants in pot experiments or by manipulating the herbaceous plant cover (Knoop and Walker, 1985;

Ward, 2005). In doing so, Knoop and Walker (1985) were able to determine that sites cleared of herbaceous material had a higher soil moisture content than those dominated by the prevalent perennial grass, *Cenchrus ciliaris*, despite lower rates of water infiltration on the cleared sites. Similar findings had been reported by Kelly and Walker, (1976) who compared intensively utilized and unutilized grazing areas. On the basis of their findings Knoop and Walker (1985) considered the competition for water between woody and herbaceous vegetation to be most severe during years of intermediate rainfall.

Grasses have a higher transpiration rate than woody plants and are able to use soil moisture almost until it reaches wilting point (Frost *et al.*, 1986, p. 20) with the wilting point of grasses lower than that of woody plants (Scholes and Walker, 1993; Rodriguez-Iturbe *et al.*, 1999). This may be a compensatory response to the drying of the soil; recalling that the soils also dry out from the top downwards, we must assume that shallow rooted plants are subject to low soil water before more deeply rooted plants, and need access to sufficient moisture until the next effective rainfall event. Importantly, this ability to extract more water from the soil will provide grasses with a competitive advantage over woody plants in the upper soil layers.

The extraction of soil moisture by grasses also has important implications for further soil moisture development since drainage decreases with the reduced soil moisture contents. Because intervals between rainfall events increase in length, more and more water is extracted by grass plants. The first rainfall events after a longer dry spell will, therefore, initially benefit the plants rooted in the upper-most soil layers.

The transpiration rates of woody plants seem to be more regulated by actual soil moisture availability (Frost *et al.*, 1986, p. 20). At the same time woody plants effectively modify the spatial distribution of moisture through stem-flow and through fall (Pressland, 1973; du Toit de Villiers and de Jager, 1981). These are dependent on the rainfall intensity and total amount (Belsky *et al.*, 1989), and differ between species and growth habits.

In addition to the horizontal redistribution of rainfall, woody plants may also redistribute soil moisture vertically within the soil profile through hydraulic lift and reverse flow (D'Odorico and Porporato, 2006). In periods of low rainfall, hydraulic lift may cause some plants to release water obtained from moister layers in the higher-lying, dryer soil layers. This phenomenon has the advantage that more water is available in the upper soil layers to assist with nutrient uptake. At the same time, the water is made available to other plants that root higher in the soil profile. Reverse flow, on the other hand, releases water in the lower soil profile.

The combination of hydraulic lift and stem-flow effectively concentrates the moisture around the base of the tree, thus also facilitating drainage to the lower soils. Evaporation from the soil surface below the canopy is also reduced as a result of shading (Dean *et al.*, 1999). The grasses that establish under the trees are generally

C3 grasses with a lower water use efficiency than the C4 grasses that predominate in the open areas between canopies.

Grasses and grazing

The composition of rangelands is not only a function of short-term or long-term climatic variation, but, importantly, a result of past grazing regimes. Effects of grazing regimes have been studied and reported repeatedly (see, for example, Dyksterhuis, 1949; Harrington *et al.*, 1984; Westoby *et al.*, 1989; Tainton, 1999 and Rothauge, 2006). Generally, different species of grass also differ in their response to grazing; while grazing may be detrimental to some species, others will disappear if they are underutilized (McNaughton, 1993; Ryerson and Parmenter, 2001; Rothauge, 2006). Similarly, not all grasses are equally acceptable to grazers; while some are preferentially selected (Rothauge, 2006), others seem to be avoided.

The degree to which individual species may cope with defoliation regimes, as indicated by changes in their abundance in the rangelands, has been used to classify grasses as being *increasers* or *decreasers* (Dyksterhuis, 1949; Hardy *et al.*, 1999; Vesk and Westoby, 2001). The presence or absence of species, and the rate at which their abundances change within the rangeland may thus be used to assess the impact of management regimes (Dyksterhuis, 1949; Westoby *et al.*, 1989; Hardy *et al.*, 1999).

Let us consider the effects of grazing in more general terms. The reduction in leaf area, and the rate at which it is reduced as a result of grazing, has a number of implications in the short, medium and long term. Most notable is the immediate reduction of photosynthetic tissue with a concomitant lowering of the productivity of the plant immediately after grazing. Depending on the severity of the defoliation, this leads to an immediate reduction in transpiration and therefore a reduction in the rate at which soil moisture is used.

However, grazing not only affects the above-ground biomass, but also results in a decline and even complete cessation of root growth, depending on the rate of defoliation. Where grasses are heavily defoliated, root activity may not resume for several days (Crider, 1955; Wolfson, 1999). Other studies have shown that grazing results in a shift in root production to the higher-lying soil layers (Schuster, 1964).

In the medium term light and moderate grazing induce the plant to produce additional tillers, and may therefore increase the productivity of individual plants (See the review by Wolfson (1999)).

Longer term change in rangeland composition is not only reflected in the present composition of the herbaceous plant component but also in the development of the soil seed bank. For instance, O'Connor (1994) and Milton and Dean (1994) found a reduction in seed production of perennial grass species as a result of grazing or overgrazing; Peart (1989) found annual grasses to have a higher overall seed production than perennials in general.

The seed bank is further affected, as cattle remove the inflorescences of some grasses under sustained grazing (O'Connor and Pickett, 1992). The inflorescences of other grasses, i.e. those with sticky infructescences are generally avoided by cattle when they ripen (Ernst *et al.*, 1992).

The development of the soil seed bank has long-term implications for rangeland composition through recruitment. O'Connor and Pickett (1992) showed, for instance, that seeds of perennial grasses had a limited longevity (3 years in their study), as opposed to those of annuals.

Woody plants and browsing

Flowering and fruiting of most woody savanna plants occur in the dry season. In Australian and South American savanna the fruit ripen and are dispersed in the subsequent wet season, while those in southern Africa only ripen during the subsequent wet season to be dispersed in the following dry season (Frost *et al.*, 1986).

The development of the accumulated seed bank may be substantially affected by predation. Setterfield (2002), for instance, found a high degree of predation by insects, particularly ants. The presence of the ants was significantly affected by burning regimes (see later) with most species of seed harvesting ants occurring in areas more frequently burnt.

Wilson and Witkowski (1998) and Joubert (pers. comm.) showed that recruitment of seedlings was episodic. Wilson and Witkowski (1998) determined that seeds needed a critical amount of soil moisture for 10–14 days before emergence. While seed may germinate, seedlings may not become established as they are desiccated in the absence of further rain (Wilson and Witkowski, 1998; Setterfield, 2002).

Once established, woody seedlings and young plants may be suppressed by competition or herbivory (reminiscent of the bonsai process) for a number of years before they emerge from the grass layer (Higgins *et al.*, 2000). At the same time Shaw *et al.* (2002) and Goheen *et al.* (2004) report significant seedling mortality attributed to herbivory by small mammals and insects. Goheen *et al.* (2004) showed that seedling mortality was significantly higher (exceeding 75%) in areas from which large mammals were excluded, with little actual damage attributed to herbivory or trampling by the larger mammals.

Higgins *et al.* (2000) assume that the eventual emergence of seedlings from the herbaceous vegetation is triggered by above-average rainfall, to produce cohorts of even aged stems.

Browsing often stimulates the growth of new shoots or facilitates coppicing as apical dominance is removed with a terminal bud. Skarpe *et al.* (2000) assume such regrowth to have a higher palatability, as the authors observed an increased probability that a bush was browsed if it had been browsed previously. This is further supported by the findings of Du Toit *et al.* (1990) who report increased nutrient contents and a reduction

in defensive chemicals in the new foliage as a result of browsing.

No literature was found on the development of the root system of woody seedlings in response to browsing. It must be assumed, however, that root development is slowed. This would imply that browsing contributes to a delay in woody plant development and the maintenance of the savanna system, and would highlight the importance of herbivore composition.

Most savanna plants are able to coppice allowing the individual species to persist without having to re-establish from seed. The regrowth does not have to outcompete the herbaceous layer for water and nutrients, but is able to use an established root system. Individual plants may thus survive within the system for a longer period. Considering the lower apparent recruitment rates of woody plants in a healthy savanna system, it seems necessary for a tree or shrub to live through a number of cycles of favourable conditions to ensure a certain number of offspring.

Jeltsch *et al.* (2000) suggest that the absence of mega-herbivores, such as elephant, are a major cause of change in the physiognomy of African savanna. This suggestion may have been prompted by elephant damage to woody plants that may be readily observed in areas where these animals occur. However, the significance of their impact in maintaining the savanna vegetation structure should not be over-emphasized as these animals are absent from other continents where the vegetation type occurs, and where they have no functional equivalent.

Plant interactions

Studies regarding competition in savannas have thus far focused on the interaction between perennial grass plants and woody plants. Those studies dealing with comparisons of competition between annual and perennial grasses focus on the invasion of rangelands by exotic annuals as, for instance, the studies reported by Huffaker and Cooper (1995) and Corbin and Antonio (2004), although Milton and Dean (2000) compared recruitment of annuals and perennials in relation to herbivory and rainfall.

In their study, Corbin and Antonio (2004) found annuals to respond more readily to exploit available resources and space. These authors, as well as Milton and Dean (2000) noted, however, that annuals were excluded by perennial grasses as the latter start utilization resources earlier in the growing season; seedlings of annuals are disadvantaged by the time they require for establishment before they may compete for resources.

The effect of the grass cover on the recruitment of woody seedlings also seems to require further investigation as the results from various field and pot trials are variable. For instance Brown and Archer (1989) showed that seedling recruitment of *Prosopis glandulosa* was not related to herbaceous biomass, while Harrington (1991) reported that the recruitment of *Dodonaea attenuata* was significantly affected. Harrington (1991) attributed the

differences in these findings to be a result of differences in the rooting habits between the two woody species under study.

There seems to be similar variation in the findings regarding the recruitment patterns of seedlings. For instance, Brown and Archer (1999) report low levels of continuous recruitment of *P. glandulosa*, while Joubert (pers. comm.) found recruitment of *Acacia mellifera* in the highland savanna of Namibia only after two successive years of high rainfall.

Westoby *et al.* (1989) suggest that overgrazing, coupled with long dry spells/drought, may create suitable conditions for recruitment events for woody plants. With the removal of the perennial grasses and the delayed water use of annuals, woody seedlings will be less subject to competition. This is contradicted to some degree by Higgins *et al.* (2000) who emphasize the inability of seedlings of woody savanna plants to tolerate drought. Soil moisture availability therefore seems to be a key issue.

The ability of grasses to reduce water availability to levels below the wilting point of woody plants suggests that the woody seedlings will desiccate in the presence of grasses under normal conditions. As soil moisture availability increases either through favourable rainfall regimes or as a result of changes in the condition of the grass component seedling establishment is likely to be affected.

Vegetation and fire

Various authors have identified fire as an important control agent mitigating against the establishment of woody plants (see Frost and Robertson, 1982; Jankowitz, 1983; Jeltsch *et al.*, 1996, 2000). By implication a change in fire regime in terms of changes in frequency, season and intensity may benefit the establishment of woody plants. Such changes may result from reduced fuel loads caused by increased grazing pressure, as suggested by van Langenvelde *et al.* (2003). Exclusion of fire may also be due to a conscious decision by land managers not to burn. Graziers may, for instance, consider the temporary loss of grazing undesirable, particularly under poor economic circumstances. In Namibia, for example, management burning was actively discouraged by government policy for a number of years, and the administrative input that are currently required by government to prepare a management burn are time consuming.

Despite the importance that is attached to fire as a control agent there is a gradual accumulation of empirical evidence of high seedling survival rates after fire. Archer *et al.* (1988) found, for instance, that most (80%) seedlings of *P. glandulosa* were able to survive hot burns while Meyer *et al.* (2005) reported over 90% seedling survival for *A. mellifera* after a moderate to hot burn. Hoffmann (1998) considers the seedlings of *Periandra meiterrania* and *Rourea induta* to be rather fire tolerant, while, despite the implementation of a burning regime on the Waterberg Plateau Park, Namibia,

Terminalia sericea has reached substantial densities. These findings support the reports by Hodgkinson (1991) and Trollope (1999) who noted an increase in woody plant density in areas subject to annual burning, when compared to their control plots. Low intensity burns are less likely to damage woody plants, but may benefit existing plants through the ash-bed effect, and encourage woody plant growth.

Simulation studies using the FLAMES model (Liedloff *et al.*, 2005) indicate that fire is less likely to affect the total woody biomass produced but rather modifies the age and size structure of tree populations. The authors concluded that single burns were less important than regular, repeated fires in the elimination of woody plants.

While the effect of fire on the establishment and development of woody seedlings appears to vary according to circumstances, fire is clearly able to reduce the amount of viable propagules that are produced. Consider, for instance, that the woody plant *Acacia mellifera* flowers and fruits towards the end of the dry season, rather than during the wet season (Frost *et al.*, 1986). A fire that occurs at this stage may reduce the number of flowers or fruit substantially (Hoffmann, 1998; Setterfield, 2002). While Joubert (pers. comm.) recorded higher fruit production of *A. mellifera* in the dry season following seasons of particularly high rainfall, the same conditions are also associated with a higher grass production (O'Connor, 1994; Higgins *et al.*, 2000) and incidence of fire under natural conditions (Siegfried, 1981). It is therefore likely that fewer viable seeds will become available in the event of a fire under such conditions.

Burning not only affects woody plant populations, but also impacts the grass component. Different combinations of grasses predominate under various rangeland management regimes or burning regimes (Trollope, 1999; Howe, 2000). Trollope (1982) reports that dry season burns break the dormancy of perennial grass plants, stimulating them to out-of-season growth.

This response to fire has been traditionally used as a hunting tool. While some animals may only reluctantly move in direct response to fire, game animals are readily attracted to the early growth in the burnt areas (Vedder, 1923; Lusepani *et al.*, 1998), making them easier to find and hunt. The out-of-season flush requires the grasses to use reserves that would otherwise have been used at the start of the next wet season. The reduced availability in reserves at the start of the next wet season results in a less vigorous flushing and growth, and a concomitant reduction in water uptake.

At this stage it is uncertain what role the formation of hydrophobic layers will play in the maintenance of savanna systems. Such layers may form under moderate fire intensities (DeBano, 2000) and reduce infiltration or drainage. Most studies dealing with hydrophobic layers were conducted under woodland vegetation or under brush piles in arid areas (Adams *et al.*, 1970), i.e. under heavier fuel loads. DeBano (2000) indicated that water repellency is formed under 175–200 °C. Scotter (1970) assumes, however, that temperatures under light grass

fuels do not rise significantly above 100 °C. At higher fuel loads, such as found after heavier rainfall, hydrophobic layers may well be formed periodically.

Temporal separation

In addition to the spatial separation of water use reported above, water use by plants may be partitioned by temporal differences in physiological activities (Harrington *et al.*, 1984; Fowler, 1986; Scholes and Walker, 1993).

The discussions of Harrington *et al.* (1984) are particularly useful in this regard. The authors compare the commencement and duration of different growth stages between annual and perennial grasses, as well as woody plants. Resource use is therefore partitioned by time as effectively as by the rooting habits of plants. At the same time, there are indications that grasses will respond faster to the availability of moisture than do woody plants (Schwinning *et al.*, 2002).

Rodriguez-Iturbe *et al.* (1999) warn that emphasis on a temporal separation between the grass and tree components accepts an inherent instability of the system. The authors do not support this approach.

DISCUSSION: ASSEMBLING THE PIECES

The interaction between grasses and trees within the savanna system evolved in response to a number of prevailing factors. Grasses and trees have established separate responses in order to cope with variable rainfall patterns and soil moisture availability. Importantly, the grass component also developed under the influence of grazing, as no doubt the shrubs evolved in response to browsing. While changes in rainfall patterns are currently much under discussion, their effects are uncertain. Rather, bush encroachment is assumed here to be in response to changes in the spatial and temporal grazing patterns.

In the following discussion, a number of differences between grazing regimes that prevailed in the evolutionary past, and those occurring now are identified to form the framework within which the bush encroachment puzzle is assembled here.

From the review above we can conclude that the effect of grazing on rangelands is determined by the interaction of the herbivores involved (Rothauge, 2006), the rate at which material is removed (Vesk and Westoby, 2001), the timing of the defoliation and the degree to which it is able to recover between grazing events (Savory and Butterfield, 1999; Vesk and Westoby, 2001). A change in any one of these components must therefore, in view of the discussions above, modify the effect of grazing and subsequently results in a change in rangeland condition. The latter would, in turn, alter the soil moisture regime and the tree: grass balance.

Prior to European settlement in the arid and semi-arid areas of Africa and Australia most surface water was ephemeral (James *et al.*, 1999). It is assumed that animal movement through the savanna system was prompted by the availability of water rather than by the available

forage. While water requirements differ between herbivores, most mammals were induced to migrate once water became limiting.

Low rainfall that resulted in only limited growth and development of the grass plants, also limited the amount of surface water that would accumulate. Grass, and particularly the available drinking water, would typically have been consumed relatively quickly when compared to consumption in periods of higher rainfall. Herbivores were thus induced to migrate earlier in the season to areas where the resources were more readily available.

The faster movement of animals through an area effectively shortened the grazing period and reduced the rate at which the available grass biomass was reduced, permitting the grass component to retain a more extensive below ground biomass. At the same time, the earlier migration of herbivores provided the grass component more time to recover.

Lower primary productivity would also have been reflected in reduced fecundity and higher mortality of natural grazers, leading to reduced population pressure in subsequent seasons. The amount of time required for herbivore populations to recover to a given level would also have extended the time of reduced grazing pressure.

With the onset of European settlement, however, surface water becomes available throughout the year (James *et al.*, 1999). At the same time, the land was subdivided into farms/ranches and fenced to facilitate the management of domestic herbivores. Grazing regimes were therefore no longer regulated by the available water or grazing, and the movement of herbivores was restricted. Rather, stocking rates became regulated by considerations such as the economics of the individual farming enterprise. Economic viability, for instance, dictates a minimum number of livestock for the farming enterprise to break even under a given set of market conditions. At the same time, market forces may prevent graziers from destocking their range in response to decreased fodder availability, but may rather encourage supplementary feeding.

European graziers responded to changes in range condition by implementing rotational grazing systems such as those described by Tainton (1999) or Savory and Butterfield (1999). While this seemed to address the rate at which rangelands declined, the area within which herds are rotated is small when compared to open grazing systems.

The repeated defoliation that subsequently occurs under unfavourable environmental conditions not only affects the plant growth but also reduces the amount of water removed from the soil through evapotranspiration.

Overutilization of the grass component may develop in a number of ways: (1) animals are retained on a piece of land for too long, thus preventing the individual grass plants from recovering; (2) too many animals utilize the grasslands for the time allocated, thus resulting in heavy utilization and, subsequently, in retarded or curtailed root growth; (3) while rest periods are implemented, animals are returned to a given area before the grasses and their

roots have fully recovered. Time indications such as 'too long' or 'too soon' are relative to rangeland productivity rates at the time in question, and vary seasonally and annually.

Under such grazing practices there is a decline in perennial grasses and a shift towards annual species as reported by Harrington *et al.* (1984); O'Connor and Pickett (1992); Milton and Dean (1994); Huffaker and Cooper (1995); Milton and Dean (2000) and Bird *et al.* (2004). This should thus not be unexpected, and the subsequent increase in soil moisture availability should be inevitable.

Higher soil moisture levels not only cause an increase in infiltration of soil moisture to lower soil layers where the roots of woody plants may dominate, but also cause soil moisture to remain at depths where woody plants may more readily extract it.

The continuous availability of drinking water and the economic considerations that affect farming enterprises have therefore effectively led to a modification of the grazing regime in all of the aspects identified above. These are the amount of material removed (grazing pressure), the timing of defoliation and the time available for recovery. The choice of livestock modifies the last of the factors previously identified, and can, strictly speaking, also be attributed to economic considerations such as the marketability of the associated animal products.

CONCLUSION

There are many gaps in our knowledge of the savanna system, particularly with regard to bush/woody weed encroachment. This review highlights that not only the condition, but also the composition of the grass component of the system, plays an important role through its influence over the soil-water balance.

Current rangeland conditions within the savanna system are attributed to grazing and resting patterns. Management is imposed by economic considerations and differs from those under which the system evolved. As a result, management regimes have effectively reduced the competitive ability of the grass sward, causing the vegetation to develop towards a bush-dominated physiognomy.

Future investigations should approach the bush encroachment problem from two avenues. On the one hand it is necessary to verify the magnitude of the physiological differences of grass plants and their effects on the soil moisture differences. These investigations should particularly focus on differences in the osmotic potential and the temporal differences in water uptake of annual and perennial grass, as well as of woody plants.

On the other hand, the implications of this framework need to be considered for current management initiatives, and for the restoration of degraded rangelands. Here it is important to develop management regimes that consider the economic sustainability of grazing enterprises, with the assumption that sustainability is only achieved if the resource base continues to exhibit good condition. It is

equally important to consider the future development of the rangelands that are already encroached to assess the possibility that the problem might 'solve itself' given time, or to identify possible remedial interventions.

REFERENCES

- Adams S, Strain BR, Adams MS. 1970. Water-repellent soils, fire, and annual plant cover in a desert scrub community of southeastern California. *Ecology* **51**: 696–700.
- Archer SR. 1991. Development and stability of grass/woody mosaics in a subtropical savanna parkland, Texas, USA. In *Savanna Ecology and Management: Australian Perspectives and Intercontinental Comparisons*, Werner PA (ed.). Blackwell Scientific Publications: London.
- Archer SR, Seifres C, Basham CR, Maggio R. 1988. Autogenic succession in a subtropical savanna: conversion of grassland to thorn woodland. *Ecological Monographs* **58**: 111–127.
- Belnap J. 2006. The potential roles of biological soil crusts in dryland hydrologic cycles. *Hydrological Processes* **20**: 3159–3178.
- Belsky AJ, Amundson RG, Duxbury JM, Rira SJ, Ali AR, Mwonga SM. 1989. The effects of trees on their physical, chemical and biological environments in a semi-arid savanna in Kenya. *Journal of Applied Ecology* **26**: 1005–1024.
- Bird PR, Jackson TT, Kearney GA, Saul GR, Waller RA, Whipp G. 2004. The effect of improved pastures and grazing management on soil water storage on a basaltic plains site in south-west Victoria. *Australian Journal of Experimental Agriculture* **44**: 559–569.
- Briske DD, Fuhlendorf SD, Smeins FE. 2003. Vegetation dynamics on rangelands: a critique of the current paradigms. *Journal of Applied Ecology* **40**: 601–614.
- Brown JR, Archer S. 1989. Woody plant invasion of grasslands: establishment of honey mesquite (*Prosopis glandulosa* var. *glandulosa*) on sites differing in herbaceous biomass and grazing history. *Oecologia* **80**: 19–26.
- Brown JR, Archer S. 1999. Shrub invasion of grassland: recruitment is continuous and not regulated by herbaceous biomass or density. *Ecology* **80**: 2385–2396.
- Childes SL. 1984. *The population dynamics of some woody species in the Kalahari sand vegetation of the Hwange National Park*. MSc thesis, University of the Witwatersrand.
- Corbin JD, Antonio CM. 2004. Competition between native perennial and exotic annual grasses: implications for an historical invasion. *Ecology* **85**: 1273–1283.
- Crider FJ. 1955. *Root growth stoppage resulting from defoliation of grass*, United States Department of Agriculture 1102, 23.
- Dean WRJ, Milton SJ, Jeltsch F. 1999. Large trees, fertile islands, and birds in arid savanna. *Journal of Arid Environments* **41**: 61–78.
- DeBano LF. 2000. The role of fire and soil heating on water repellency in wildland environments: a review. *Journal of Hydrology* **231/232**: 195–206.
- de Klerk JN. 2004. *Bush Encroachment in Namibia*. John Meinert Printing: Windhoek.
- D'Odorico P, Porporato A. 2006. Soil moisture dynamics in water-limited ecosystems. In *Dryland Ecohydrology*, D'Odorico P, Porporato A (eds). Springer: Dordrecht; 31–46.
- Du Toit JT, Bryant JP, Frisby K. 1990. Regrowth and palatability of Acacia shoots following pruning by african savanna browsers. *Ecology* **71**: 149–154.
- du Toit de Villiers G, de Jager JM. 1981. Net rainfall and interception losses in a *Burkea africana*-*Ochna pulchra* tree savanna. *Water SA* **7**: 249–254.
- Dyksterhuis EJ. 1949. Condition and management of range land based on quantitative ecology. *Journal of Range Management* **2**: 104–115.
- Ernst WHO, Veenendaal EM, Kebakile MM. 1992. Possibilities for dispersal in annual and perennial grasses in a savanna in Botswana. *Vegetatio* **102**: 1–11.
- Foth HD. 1990. *Fundamentals of Soil Science*. John Wiley and Sons: New York.
- Fowler N. 1986. The role of competition in plant communities in arid and semiarid regions. *Annual Review of Ecology and Systematics* **17**: 89–110.
- Frost P, Medina E, Menaut JC, Solbrig O, Swift M, Walker BH. 1986. *Responses of Savannas to Stress and Disturbance*, Biology International Special Issue 10. IUBS: Paris.
- Frost PGH, Robertson F. 1982. The ecological effect of fire in savannas. In *Determinants of Tropical Savannas*, Walker BH (ed.). ICSU Press: Miami, FL; 93–140.
- Garnier E. 1992. Growth analysis of congeneric annual and perennial grass species. *Journal of Ecology* **80**: 665–675.
- Goheen JR, Keesing F, Allan BF, Ogada D, Ostfeld RS. 2004. Net effects of large mammals on Acacia seedling survival in an African savanna. *Ecology* **85**: 1555–1561.
- Graz FP. 1996. *The management of a Pterocarpus angolensis population under the influence of land use and fire*. MSc thesis, University of Stellenbosch.
- Graz FP. 2004. Description and Ecology of *Pterocarpus angolensis* in Namibia. *Dinteria* **29**: 27–39.
- Hardy MB, Hurt CR, Bosch JH. 1999. Veld condition assessment. In *Veld Management in South Africa*, Tainton N (ed.). University of Natal Press: Pietermaritzburg; 194–206.
- Harrington GN. 1991. Effects of soil moisture on shrub seedling survival in semi-arid grassland. *Ecology* **72**: 1138–1149.
- Harrington GN, Friedel MH, Hodgkinson KC, Noble JC. 1984. Vegetation ecology and management. In *Management of Australia's Rangelands*, Harrington GN, Wilson AD, Young MD (eds). CSIRO: Melbourne.
- Heng LK, White RE, Helyar KR, Fisher R, Chen D. 2001. Seasonal differences in the soil water balance under perennial and annual pastures on an acid Sodosol in southeastern Australia. *European Journal of Soil Science* **52**: 227–236.
- Higgins SI, Bond WJ, Trollope WSW. 2000. Fire, resprouting and variability: a recipe for grass-tree coexistence in savanna. *Journal of Ecology* **88**: 213–229.
- Hipondoka MHT, Aranibar JN, Chirara C, Lihavha M, Macko SA. 2003. Vertical distribution of grass and tree roots in arid ecosystems of southern Africa: niche differentiation or competition? *Journal of Arid Environments* **54**: 319–325.
- Hodgkinson KC. 1991. Shrub recruitment response to intensity and season of fire in a semi-arid woodland. *Journal of Applied Ecology* **28**: 60–70.
- Hoffmann WA. 1998. Post-burn reproduction of woody plants in a neotropical savanna: the relative importance of sexual and vegetative reproduction. *Journal of Applied Ecology* **35**: 422–433.
- Hopmans JW. 2006. Soil physical properties, processes, and associated root-soil interactions. In *Dryland Ecohydrology*, D'Odorico P, Porporato A (eds). Springer: Dordrecht; 13–30, 31–46.
- Howe HF. 2000. Grass response to seasonal burns in experimental plantings. *Journal of Range Management* **53**: 437–441.
- Huffaker R, Cooper K. 1995. Plant succession as a natural range restoration factor in private livestock enterprises. *American Journal of Agricultural Economics* **77**: 901–913.
- James CD, Landsberg J, Morton SR. 1999. Provision of watering points in the Australian arid zone: a review of effects on biota. *Journal of Arid Environments* **41**: 87–121.
- Jankowitz WJ. 1983. *Die plantekologie van die Waterberg Platopark*. PhD thesis, University of the Orange Free State.
- Jeltsch F, Milton SJ, Dean WRJ, van Rooyen N. 1996. Tree spacing and coexistence in semiarid savannas. *Journal of Ecology* **84**: 583–959.
- Jeltsch F, Weber GE, Grimm V. 2000. Ecological buffering mechanisms in savannas: A unifying theory of long-term tree-grass coexistence. *Plant Ecology* **161**: 161–171.
- Kelly RD, Walker BH. 1976. The effects of different forms of land use on the ecology of a semi-arid region in South-Eastern Rhodesia. *Journal of Ecology* **64**: 553–576.
- Kerkhoff AJ, Martens SN, Milne BT. 2004. An ecological evaluation of Eagleson's optimality hypotheses. *Functional Ecology* **18**: 404–413.
- Knoop WT, Walker BH. 1985. Interactions of woody and herbaceous vegetation in a southern African savanna. *Journal of Ecology* **73**: 235–253.
- Liedloff AC, Ludwig JA, Bartley R, Coughenour MB. 2005. Modelling tropical landscapes for ecological management: what can we learn from preliminary Savanna.au simulations? In *International Congress on Modelling and Simulation: Advances and Applications for Management and Decision Making*, Zerger A, Argent RM (eds). Modelling and Simulation Society of Australia and New Zealand: Melbourne; 170–176, MODSIM 2005.
- Lusepani E, Tjaveondja L, Tuomasjukka T. 1998. *Bushmanland Forest Conservation Workshop*, Unpublished Report, Directorate of Forestry, Windhoek.
- McNaughton SJ. 1993. Grasses and grazers, science and management. *Ecological Applications* **3**: 17–20.

- Meyer KM, Ward D, Moustakas A, Wiegand K. 2005. Big is not better: small *Acacia mellifera* shrubs are more vital after fire. *African Journal of Ecology* **43**: 131–136.
- Milton SJ, Dean WRJ. 1994. A conceptual model of arid rangeland degradation. *Bioscience* **44**: 70–77.
- Milton SJ, Dean WRJ. 2000. Disturbance, drought and dynamics of desert dune grassland, south Africa. *Plant Ecology* **150**: 37–51.
- Molele NM, Ringrose S, Matheson W, Vanderpost C. 2002. More woody plants? The status of bush encroachment in Botswana's grazing areas. *Journal of Environmental Management* **64**: 3–11.
- Murphy SR, Lodge GM, Harden S. 2004. Surface soil water dynamics in pastures in northern New South Wales. 3. Evapotranspiration. *Australian Journal of Experimental Agriculture* **44**: 571–583.
- O'Connor TG. 1994. Composition and population responses of an African savanna grassland to rainfall and grazing. *Journal of Applied Ecology* **31**: 115–171.
- O'Connor TG, Pickett GA. 1992. The influence of grazing on seed production and seed banks of some African savanna grasslands. *Journal of Applied Ecology* **29**: 247–260.
- Pear DR. 1989. Species interactions in a successional grassland. I. Seed rain and seedling recruitment. *Journal of Ecology* **77**: 236–251.
- Pressland AJ. 1973. Rainfall partitioning by an arid woodland (*Acacia aneura* F. Muell.) In south-western Queensland. *Australian Journal of Botany* **21**: 235–245.
- Ridley AM, White RE, Simpson RJ, Callinan L. 1997. Water use and drainage under phalaris, cocksfoot, and annual ryegrass pastures. *Australian Journal of Agricultural Research* **48**: 1011–1023.
- Rodriguez-Iturbe I, D'Odorico P, Porporato A, Ridolfi L. 1999. On the spatial and temporal links between vegetation, climate, and soil moisture. *Water Resources Research* **35**: 3709–3722.
- Rothauge A. 2006. *The effect of frame size and stocking rate on diet selection of cattle and range condition in the camelthorn savanna of East-central Namibia*. PhD thesis, University of Namibia.
- Roques KG, O'Connor TG, Watkinson AR. 2001. Dynamics of shrub encroachment in an African savanna: relative influences of fire, herbivory, rainfall and density dependence. *Journal of Environmental Management* **38**: 268–280.
- Ryerson DE, Parmenter RR. 2001. Vegetation change following removal of keystone herbivores from desert grasslands in New Mexico. *Journal of Vegetation Science* **12**: 167–180.
- Savory A, Butterfield J. 1999. *Holistic Management, A New Framework for Decision Making*. Island Press: Washington, DC.
- Scholes RJ, Archer SR. 1997. Tree-grass interactions in savannas. *Annual Review of Ecology and Systematics* **28**: 517–544.
- Scholes RJ, Walker BH. 1993. *An African Savanna: Synthesis of the Nylsvley Study*. Cambridge University Press: Cambridge.
- Schuster JL. 1964. Root development of native plants under three grazing intensities. *Ecology* **45**: 63–70.
- Schwinning S, Davis K, Richardson L, Ehleringer JR. 2002. Deuterium enriched irrigation indicates different forms of rain use in shrub/grass species of the Colorado Plateau. *Oecologia* **130**: 345–355.
- Scotter DR. 1970. Soil temperatures under grass fires. *Australian Journal of Soil Research* **8**: 273–279.
- Setterfield SA. 2002. Seedling establishment in an Australian tropical savanna: effects of seed supply, soil disturbance and fire. *Journal of Applied Ecology* **39**: 949–959.
- Shaw MT, Keesing F, Ostfeld RS. 2002. Herbivory on *Acacia* seedlings in an East African savanna. *Oikos* **98**: 385–392.
- Siegfried WR. 1981. The incidence of veld fire in the Etosha National Park, 1970–1979. *Madoqua* **12**: 225–230.
- Skarpe C. 1991. Spatial patterns and dynamics of woody vegetation in an arid savanna. *Journal of Vegetation Science* **2**: 565–572.
- Skarpe C, Bergström R, Bråten AL, Danell K. 2000. Browsing in a heterogeneous savanna. *Ecography* **23**: 632–631.
- Starfield AM, Cumming DHM, Taylor RD, Qadling MS. 1993. A frame-based paradigm for dynamic ecosystem models. *AI Applications* **7**: 1–13.
- Tainton N. 1999. *Veld Management in South Africa*. University of Natal Press: Pietermaritzburg.
- Trollope WSW. 1982. Ecological effects of fire in South African savannas. In *Ecology of Tropical Savannas*, Huntley BJ, Walker BH (eds). Springer Verlag: Berlin.
- Trollope WSW. 1999. Veld burning. In *Veld Management in South Africa*, Tainton N (ed.). University of Natal Press: Pietermaritzburg; 217–245.
- van Langenvelde F, van de Vijver CADM, Kumar L, van de Koppel J, de Ridder N, van Andel J, Skidmore AK, Hearne JW, Stroonsnijder L, Bond WJ, Prins HHT, Rietkerk M. 2003. Effects of fire and herbivory on the stability of savanna ecosystems. *Ecology* **84**: 337–350.
- Vedder H. 1923. *Die Bergdama, Part 1. Völkerkunde, Kulturgeschichte und Sprachenn.*, 7. University of Hamburg.
- Vesk PA, Westoby M. 2001. Predicting plant species' responses to grazing. *Ecology* **38**: 897–909.
- Virgona JM, Southwell A. 2006. The influence of grazing interval and perennial grass species on soil moisture. In "Ground-breaking stuff", *Proceedings of the 13th Australian Agronomy Conference*, Turner NC, Acuna T, Johnson RC (eds). The Regional Institute: Perth.
- Walker BH, Ludwig D, Holling CS, Perman RM. 1981. Stability of semi-arid savanna grazing systems. *Journal of Ecology* **69**: 473–498.
- Walker BH, Noi-Meir I. 1982. Aspects of the stability and resilience of savanna ecosystems. In *Ecology of Tropical Savannas*, Huntley BJ, Walker BH (eds). Springer Verlag: Berlin.
- Walter H. 1971. *Ecology of Tropical and Subtropical Vegetation*. Oliver and Boyd: Edinburgh.
- Ward D. 2005. Do we understand the causes of bush encroachment in African savannas? *African Journal of Range and Forage Science* **22**: 101–105.
- Werner PA. 1991. *Savanna Ecology and Management: Australian Perspectives and Intercontinental Comparisons*. Blackwell Scientific Publications: London.
- Westoby M, Walker BH, Noy-Meir I. 1989. Opportunistic management for rangeland not at equilibrium. *Journal of Rangeland Management* **42**: 266–274.
- White RE, Helyar KR, Ridley AM, Chen D, Heng LK, Evans J, Fisher R, Hirth JR, Mele PM, Morrison GR, Cresswell HP, Paydar Z, Dunin FX, Dove H, Simpson RJ. 2000. Soil factors affecting the sustainability and productivity of perennial and annual pastures in the high rainfall zone of south-eastern Australia. *Australian Journal of Experimental Agriculture* **40**: 267–283.
- Wiegand K, Ward D, Saltz D. 2005. Multi-scale patterns and bush encroachment in an arid savanna with a shallow soil layer. *Journal of Vegetation Science* **16**: 311–320.
- Wilson TB, Witkowski ETF. 1998. Water requirements for germination and early seedling establishment in four African savanna woody plant species. *Journal of Arid Environments* **38**: 541–550.
- Wolfson T. 1999. The response of forage plants to defoliation. In *Veld Management in South Africa*, Tainton N (ed.). University of Natal Press: Pietermaritzburg; 91–115.
- Zimmermann I, Joubert DF, Graz FP. 2001. *Proposed Monitoring of Bush Encroachment in Namibia*. NAPCOD, Ministry of Agriculture, Water & Forestry: Windhoek.