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The maintenance of the productivity and value of farmland in savanna through the effective management of bush encroachment: Ecological considerations

Abstract

Due to bush encroachment the grazing capacity of large areas of the Southern African savanna has declined, often to such an extent that many previously economic livestock properties are now no longer economically viable. Causes of bush encroachment include the exclusion of occasional hot fires, the replace-ment of most of the indigenous browsers and grazers by domestic (largely graz-ing) livestock, the restriction of movement of herbivores by the erection of fences, poor grazing management practice and the provision of artificial watering points. 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 results of woody plant removal may differ between vegetation types, with the outcome determined by both negative and positive responses to tree removal. In view of this it can be concluded that any bush control program (chemical, mechanical or biological) should focus on tree thinning rather than clearing of all woody plants. It is important for any land manager to realize that there is no quick solu-tion to the problem of bush encroachment. Effective management of bush encroachment should not be considered a once-off event, but rather a long-term commitment.

Keywords: Savanna, bush encroachment, grazing capacity, herbivore.

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DIE BEHOUD VAN DIE PRODUKTIWITEIT EN WAARDE VAN PLAASGROND IN SAVANNA DEUR DIE EFFEKTIEWE BESTUUR VAN BOSVERDIGTING: DIE EKOLOGIESE OORWEGINGS

As gevolg van bosverdigting het die weidingkapasiteit in groot areas van die Suider-Afrikaanse savanna in der mate afgeneem dat veeboerderyeenhede stagneer wat voorheen ekonomies bedryf is. Oorsake van bosverdigting sluit in: die uitsluiting van sporadiese warm vure; die vervanging van inheemse struik- en grasvreters met gedomestikeerde (hoofsaaklik grasvretende) vee; die beperking van dierebeweging deur heinings; swak weidingbestuurpraktyke; en die voorsiening van kunsmatige waterpunte. Die verwydering van sommige of alle houtagtige plante sal normaalweg tot 'n toename in grasproduksie lei, ook ten opsigte van weidingkapasiteit. Die resultate van boomuitdunning mag egter tussen verskillende plantegroeitipes verskil en die uitkoms bepaal word deur beide negatiewe en positiewe reaksies op boomverwydering. In die lig hiervan kan die gevolgtrekking gemaak word dat enige bosbeheerprogram (chemies, meganies of biologies) eerder op boomuitdunning gefokus moet wees as op totale ontbos-sing. Dit is ook belangrik dat grondeienaars besef dat daar geen kitsoplossing vir die bosvedigtingsprobleem is nie. Die effektiewe bestuur van bosverdigting moet ook nie as 'n eenmalige proses beskou word nie, maar as 'n langtermyn verpligting hanteer word.

Sleutelwoorde: Savanna, bosverdigting, weidingskapasiteit, herbivoor.

1. Introduction

In Southern Africa the phenomenon of increasing woody plant abundance is commonly referred to as bush encroachment. It involves indigenous woody species occurring in their natural environment and is thus mainly associated with the savanna biome. The term savanna (or savannah), once restricted to describe central South American grasslands in Spanish, is now widely accepted as describing vegetation with a herbaceous layer, dominated by graminoids, with an upper layer of woody plants which can vary from widely spaced to a 75% canopy (Edwards, 1983; Rutherford & Westfall, 1994).

The savanna biome extends from north of 22°S into northern Namibia, Botswana, the higher rainfall areas of the Northern Cape, North-West Province, Northern Province, the lower altitude areas of the north-western Free State, Mozambique, central and east Swaziland, and the lower altitude areas of Mpumalanga, KwaZulu-Natal and the Eastern Cape Province. The biome is the largest, comprising about 959 000 km^2 or 46,2% of southern Africa (one third of South Africa) (Rutherford & Westfall, 1994).

Many savanna areas are water-limited ecosystems and bush encroachment is considered a major factor contributing towards the low occur-rence or even total absence of herbaceous plants in severe cases (Smit *et al* 1999). The grazing capacity of large areas of the southern African savanna is reported to have declined due to bush encroachment, often to such an extent that many previously economic livestock properties are now no longer economically viable. Removal of some or all of the woody plants will normally result in an increase of grass production and thus also in the grazing capacity. However, the results of woody plant removal may differ between vegetation types, with the outcome determined by both negative and positive responses to tree removal.

2. The importance of woody plants in the savanna

2.1 Direct uses for woody plants

Woody plants in South African savannas are used for firewood, rough construction timber, the production of charcoal and woodcarving. For many rural communities, wood is still the only source of fuel for cooking and heating. The wood of several savanna woody species is known for its excellent fuel properties, especially species with dense heartwood. These species also yield excellent charcoal. Branches from spiny woody species like *Acacia tortilis* and *A. erubescens* are used for the construction of fencing kraals where livestock can be protected from predators (Smit, 1999a).

With the expansion of the tourism industry the market for woodcarving from indigenous tree species has become very popular. Subsequently, woodcarving has developed into a major industry in many southern African countries and the wood of a wide range of tree species is being used. Of some concern though is the threat of non-sustainable harvesting of trees, brought about by increasing numbers of entrepreneurs who resort to this practice as an only source of income. This is especially true where larger trees are being cut down indiscriminately to produce larger and more spectacular carvings (Smit, 1999a).

In addition, woody plants are an important source of food for browser herbivore species, which includes both domestic stock and game. With the expansion of game ranching the latter aspect is of increasing importance. Game ranching is a recognised agricultural enterprise and is currently one of the fastest growing sectors in the agricultural industry. The Northern Province is a good example, as a recent survey showed that about 2 300 farms have already been fenced with game-proof fences, of which 83% with exemption. This represents an area of approximately 3,6 million ha (26% of the total area of the province) (Van der Waal & Dekker, 2000). The presence of woody plants creates unique habitats that can thus support a greater diversity of herbivore game species than other ecosystems without woody plants.

According to Rutherford (1979) it is important to have a clear understanding of what is meant by browse and available browse. He defined browse as the sum total of that material on woody species that is potentially edible to a specific set of animals, and that browse is most commonly regarded as the current season's growth of both leaves and twigs. Available browse, on the other hand, is usually a more restricted quantity than browse, and in most studies available browse is simply determined on the basis of the maximum height above ground to which a specific animal can utilise browse. The availability of browse below a specified browse height may be reduced by obstruction of browse material towards the centre of the plant by dense branch entanglements (Rutherford, 1979), while the leaf senescence of winter deciduous species will lower available browse during certain periods (Styles, 1993; Smit, 1994). In savanna areas dominated by leguminous woody species, pods are important as forage, especially during the win-ter months (Fagg & Stewart, 1994).

Browsers select among plant species as markedly as grazers do (Grunow, 1980). A preferred food species is defined as one which is proportionally more frequent in the diet of an animal than it is in the available environment; and 'food preference' as the extent to which food is consumed in relation to its availability (Petrides, 1975). A principal food species is described as one making a large contribution to the diet (Grunow, 1980). Barnes (1976) concluded that a proper understanding of animal-plant relationships in terms of intake would depend on knowledge of the diet of the animals, the amount of the different species on offer and their distribution and availability. In addition, chemical defences of woody plants may influence the actual intake of available browse (Van Hoven, 1984; Bryant *et al* 1992), as well as nutritional characteristics of leaves in different phenological stages (Hall-Martin & Basson, 1975; Cooper, 1982; Owen-Smith & Cooper, 1987; Cooper *et al* 1988; Styles, 1993; Van der Waal, 2001).

Chemical defences of plants may include chemical substances, which may be poisonous (Smith, 1992; Taylor & Ralphs, 1992) or reduce palatability (Robbins *et al* 1987; Bryant *et al* 1992). A diverse array of secondary metabolites deters feeding by mammals on woody plants. Condensed tannins are especially important as a defence mechanism in woody plants (Haslam, 1974; Van Hoven, 1984; Martin *et al* 1985; Hagerman *et al* 1992). Tannins are a diverse group of compounds, widespread among dicotyledonous forbs and trees, which precipitate protein (Asquith & Butler 1985; Robbins *et al* 1987) and sometimes act as a toxin rather than as a digestion inhibitor (Hagerman *et al* 1992). Regarding structural defences, Cooper (1982) observed that the presence of straight spines or thorns has little effect on the feeding of goats and impalas, while hooked thorns are more effective deterrents. In some species the physical defences of juvenile and mature trees differ. Juvenile *A. nilotica* trees were found to be physically more heavily defended than mature plants (Brooks & Owen-Smith, 1994).

Integrated quantitative data on total browse, available browse, its seasonal nutritional and phenological characteristics and the way in which it is influenced by bush encroachment or tree thinning, are poorly reported in the literature. Some quantitative data of aboveground peak biomass of *Burkea africana-Ochna pulchra* savanna has been reported by Rutherford (1982). He estimated the mean aerial biomass to be 16 273 kg ha^{-1}, of which 236 kg ha^{-1} comprised the current season's twigs and 1100 kg ha^{-1} the leaves. Of the potential browse, only 3,8% was estimated to be within reach of impala, 5,1% within reach of kudu and 67% within reach of giraffe. Aboveground standing crop of *Colophospermum mopane* in the Klaserie Private Nature Reserve, at peak biomass, has been estimated at 20 840 kg ha^{-1} of wood and 801 kg ha^{-1} of leaves (Scholes, 1987). Kelly and Walker (1976) estimated the mean standing crop of *C. mopane* in Zimbabwe to be 19 940 kg ha^{-1}, of which 1506 kg ha^{-1} comprised the current season's shoots.

2.2 Soil enrichment

Nutrients, such as nitrates, phosphorus, a series of anions and cations and various trace elements, are essential to the nutrition of plants (Bel,l 1982), and act as determinants of the composition, structure and productivity of vegetation. While the base-richness of the parent material is initially important in determining soil fertility, biological activities are important in the creation and maintenance of localised areas of enhanced soil fertility, often on base-poor substrates (Scholes, 1991). Trees may act as such a biological agent, creating islands that differ from those in the open. Ample evidence in support of soil enrichment under tree canopies exists (Bosch & Van Wyk, 1970; Kennard & Walker, 1973; Tiedemann & Klemmedson, 1973; Kellman, 1979; Bernhard-Reversat, 1982; Belsky *et al* 1989; Young, 1989; Smit, 1994, Smit & Swart, 1994; Hagos, 2001).

In the North West Province, Bosch and Van Wyk (1970) found a higher content of N, P, K, Mg and Ca in soil from under *Boscia albitrunca, Combretum apiculatum*, *Acacia tortilis* and *A. senegal* in comparison with soil from the open areas. They also reported a higher pH and lower electrical resistance for under canopy soils. Kennard and Walker (1973) conducted an investigation in Zimbabwe, which compared the nutrient status from soils under *Combretum molle*, *Terminalia sericea* and *Albizzia spp*. with the nutrient status in open areas. In accordance with the results of Bosch and Van Wyk (1970), they established a higher content of organic C and exchangeable Mg, Ca and K, as well as a higher pH, in soil from under tree canopies in comparison with soil from the open, but found little difference in P or mineral N. While Kennard and Walker (1973) reported no differences in soil depth and texture under trees and in the open, Tiedemann and Klemmedson (1973) found that the bulk density was lower in soil under *Prosopis juliflora* trees, but increased with depth in that location. They also reported higher contents of organic C, total N, K and total soluble salts in soils under *P. juliflora* trees, but observed no significant difference in P or pH. Differences with increasing soil depth were also recorded by them.

Kellman (1979) supplied more evidence of soil enrichment under tree canopies was supplied by. Higher concentrations of Ca, Mg, K, sodium (SO_4), total N and P under the canopies of 5 broad-leaved tree species of the genera *Quercus*, *Clethra* and *Miconia* were found by him. Bernhard-Reversat (1982) reported that organic C and N content of soils of savanna in north Senegal were concentrated in the first few centimetres of soil and increased under tree canopies (*Acacia senegal* and *Balanites aegyptiaca*). In the Valley Bushveld of the Eastern Cape, it was found by Palmer *et al* (1988) that soils of the grasslands were poorer in

Ca, Mg, Na and organic material than those of bush clumps, while grassland soils had lower conductivity and pH values. In a semi-arid savanna in Kenya, Belsky *et al* (1989) established that soil organic matter, extractable P, K and Ca were highest adjacent to trunks of both *Acacia tortilis* and *Adansonia digitata*, but declined away from the trunk, being considerably higher under the tree canopies than in the open grassland. Calcium declined more rapidly further from the trunk of *A. digitata* than under *A. tortilis*, while the soil under *A. digitata* contained significantly more Mg than the soil under *A. tortilis*. Invasion of coastal fynbos by the alien *Acacia cyclops*, resulted in elevated N sta-tus of the fynbos and strandveld ecosystems (Witkowski, 1991).

Contrary to reports of a higher pH under tree canopies (Bosch & Van Wyk, 1970; Kennard & Walker, 1973; Palmer *et al* 1988; Young, 1989), Belsky *et al* (1989) and Hagos (2001) recorded a lower pH at the base of *Acacia* trees than further from the trunk. Similarly, Falkengren-Grerup (1989) claimed that stem flow appeared to have decreased pH and base saturation in the topsoil of Swedish forests. However, based on the positive association between increases in exchangeable cations and soil-pH (higher base saturation) (Barnard & Fölscher, 1972; Kennard & Walker, 1973; Hatton & Smart, 1984), a higher pH under canopies of savanna trees conforms more logically with the higher content of exchangeable cations in this subhabitat. Corresponding with the report by Tiedemann and Klemmedson (1973), Belsky *et al* (1989) reported a lower soil bulk density under tree canopies than in open grassland.

Soil enrichment can differ between tree species that grow in the same environment. Smit and Swart (1994) demonstrated that soil under both leguminous trees (mainly *Acacia erubescens*) and non-leguminous trees (mainly *Combretum apiculatum*) was richer in % total N, % organic C, Ca and Mg, while nutrients like K and Mg differed in soil from under the two tree species. They also reported a higher pH from soil under both leguminous and non-leguminous trees, whilst electrical resistance was the lowest (i.e. brackish conditions) under tree canopies. Evidence exists that soil enrichment under tree canopies is a slow process. This is demonstrated by correlations between total C and N in soil under tree canopies and tree girth, an index of age (Bernhard-Reversat, 1982; Hagos, 2001).

The question of source and mechanism of soil enrichment under tree canopies remains largely unexplained. Many theories have been pre-sented. Leaf litter from leaf fall has been mentioned as a possible source (Bosch & Van Wyk, 1970; Stuart-Hill *et al* 1987; Belsky *et al* 1989). A a litterbag experiment by Schroth *et al* (1992) showed that within 6-7 weeks leaching and decomposition resulted in the release of 90% of the main nutrients from leaves and branches. Ola-Adams and Egunjobi (1992) estimated that in the case of *Terminalia superba*, leaf litter contributed over 97% of the nutrients returned to the soil surface. They ranked the relative nutrient contents of litter from *Tectona grandis* and *T. superba* as Ca>N>K>Mg>P. Structural differences in leaves of micro-phyllous and broad leafed trees present a possible source of difference in the amount of leaves reaching the soil under tree canopies, the latter being more subject to further dispersion by wind (Smit & Swart, 1994). In a temperate mixed forest the pattern of leaf litter was found to correspond with the distribution of the canopy structure (Hirabuki, 1991).

Stemflow and throughfall represent a source of mineral input to soil (Kellman, 1979; Williams *et al* 1987; Potter, 1992). Kellman (1979) con-cluded that mineral nutrients concentrated beneath neotropical savan-na trees could not have been derived from weathering at depth and that they must have been derived from the capture of precipitation inputs. From an investigation by Williams *et al* (1987) in Britain, through fall and stem flow chemistry under bracken (*Pteridium aquilinum*) was shown to be significantly different from that of precipitation above the bracken canopy. Potassium (K) was found to be the most important cation, related to high levels of K release during senescence of brack-en. Potter (1992) identified K , SO_4 and PO_4 ions to be the most easily leached ions from stems of young forest trees. Alcock and Morton (1981) concluded that the pH of through fall under the canopies of pine (*Pinus sylvestris*) and birch (*Betula pendula*) was reduced to below that of rainfall.

Nitrogen is one of the key elements in ecosystem functioning and productivity (Du Preez *et al* 1983; Tietema *et al* 1992). The occurrence of N-fixation due to microbial activities under leguminous trees is a possible source of N enrichment (Felker & Clark 1982; Högberg & Kvarn-ström 1982; Virginia & Delwiche 1982; Shearer *et al* 1983; Högberg 1986). The annual N fixation by *Leucaena leucocephala* in a semi-arid site in Tanzania was estimated at 110 kg ha-1 (Högberg & Kvarnström 1982). In the *Burkea*-savanna of Nylsvley, Zietsman *et al* (1988) established that dinitrogen fixation was almost exclusively due to activity of legume-*Rhizobium* symbiotic systems, and they could find no evidence of dinitrogen fixation by symbiotic systems involving grasses. The review by Chalk (1991), however, indicated that *Panicum maximum* is distinctive as a non-legume capable of natural inputs of significant amounts of biologically fixed N_2. According to Miranda and Boddey (1987) potential N inputs by *P. maximum* from associated N_2 fixation, in the order of

30-40 kg N ha^{-1}y^{-1} are possible. It was shown by Högberg (1986) that the Nconcentration in leaves was substantially higher in potentially N_2-fixing woody species of Tanzania than in non-N_2-fixing woody species$_2$ while there were no differences in the concentrations of K, Mg, Ca, S, Mn and B.

Microbial C, N and P may also be influenced by other determinants. Singh *et al* (1991) concluded that the maximum amounts of available nutrients and microbial biomass in a dry tropical Indian savanna occurred in the dry period and a minimum in the wet period. They also established that grazing and burning increased inorganic N, bicarbon-ate-extractable inorganic P and microbial C. In contrast, Holt and Coventry (1991), who emphasised the role played by microorganisms in the decomposition of organic matter and cycling of nutrients in savannas, claimed that their activity is restricted to the wet season.

The contributions of bird droppings and dung of large mammals spending time under trees have also been mentioned as a source of soil enrichment (Belsky *et al* 1989; Teague & Smit, 1992). This is an example of what Scholes (1991) termed "nutrient import".

2.3 Positive influences of trees on the herbaceous layer

Trees may have positive effects on grass growth and Stuart-Hill *et al* (1987) have argued that the net result of the negative and positive inter-actions on grass production is dependent on tree density. As stated before, established trees create sub-habitats, which differ from the open habitat and which exert different influences on the herbaceous layer (Kennard & Walker, 1973; Tiedemann & Klemmedson, 1973; Kellman, 1979; Grossman *et al* 1980; Yavitt & Smith, 1983; Stuart-Hill *et al* 1987; Belsky *et al* 1989; Smit & Rethman, 1989; Smit, 1994; Smit & Swart, 1994; Smit & Rethman, 1999; Hagos, 2001). Stuart-Hill *et al* (1987) demonstrated a consistent pattern of grass production around isolated *Acacia karroo* trees in the false thornveld of the Eastern Cape. High yields were recorded under and immediately to the south of the tree canopy, and low yields to the immediate north of the canopy. They attributed the for-mer to the favourable influence of the trees on the micro-environment (e g deposition of leaf litter, shading) and the latter to the reduced water input associated with the physical redistribution of rainfall by the trees.

In Kenya, Belsky *et al* (1989) recorded significantly higher production of herbaceous plants under the canopies of both *Acacia tortilis* and *Adansonia digitata* than outside their canopies. In Mixed Bushveld of the Northern Province, higher DM yields have been recorded under the canopies of leguminous trees (*A. erubescens*) in comparison with yields under either nonleguminous trees (*Combretum apiculatum*) or between the tree canopies, mainly due to the occurrence of *Panicum maximum* under tree canopies (Smit & Swart, 1994). Smit and Swart (1994) con-cluded that contrary to most other grass species, the yield of *Panicum maximum* increased with an increase in tree density, up to a point where after the yield of *P. maximum* was also suppressed through com-petition from the trees. In contrast, Grossman *et al* (1980) measured sig-nificantly greater biomass in open veld than under *Burkea africana* and *Ochna pulchra* trees, although the canopied habitats did yield better quality forage.

The relatively high nutrient status of soil under, compared to between, tree canopies, would be expected to lead to a relatively higher nutrient content of the grass growing under the tree canopy. However, reported results are variable. Grossman *et al* (1980) reported no difference in the *in vitro* digestible organic matter content but a higher protein content of forage growing under *Burkea africana* trees that are growing in open savanna. In Mopane savanna, Smit (1994) reported that subhabitat dif-ferentiation by Mopane trees did provide some qualitative benefits. Some good forage grass species, which typically have high crude protein and *in vitro* digestibility values, prefer the canopied sub-habitat to the open sub-habitat and would probably be lost with the removal of all the Mopane trees. Pieterse and Grunow (1985) reported, however, that clearing all woody plants in *Combretum* veld in the northern Transvaal had no effect on forage quality. In addition, Moughalu and Isichei (1991) could find no significant difference between the crude protein, lignin and fibre content of forb species growing in the open and under tree canopies in Nigerian savanna.

A possible contributory factor to the higher production of forage from under-canopy sub habitats in many southern African savannas is the well documented association between *Panicum maximum*, a palat-able and potentially very productive species (Jordaan, 1991; Smit & Rethman, 1 992) and the under-canopy subhabitat of the larger trees in particular (Bosch & Van Wyk, 1970; Kennard & Walker, 1973; Belsky *et al* 1989; Smit & Rethman, 1992; Smit & Van Romburg, 1993; Smit & Swart, 1994). This species may develop into pure stands under, for example, *Acacia tortilis*, *A. karroo* and *Dichrostachys cinerea* trees taller than 2,0, 4,0 and 4,5 m respectively (Smit & Van Romburg, 1993).

3. Causes of bush encroachment

Two processes primarily bring about an increase in woody plant abundance. The first is by an increase in the biomass of already established plants (vegetative growth) and the second is by an increase in tree density, mainly from the establishment of seedlings (reproduction). Some influences may inhibit vegetative growth and/or reproduction, resulting in the decreased biomass of woody plants. The reasons for an increase in the abundance of woody plants in any vegetation type are diverse and complex. In most situations man modified the determinants of savanna systems, either directly or indirectly. These determinants may either be primary (such as climate and soil) or secondary (such as fire and the impact of herbivores) (Teague & Smit, 1992). The latter are of particular interest since, although they act within the constraints imposed by the primary determinants, management can often directly modify them. Examples are the exclusion of occasional hot fires, the replacement of most of the indigenous browsers and grazers by domes-tic (largely grazing) livestock often at extremely high stocking rates, the restriction of movement of herbivores by the erection of fences, poor grazing management practice, and the provision of artificial watering points (Smit *et al* 1999).

African savannas have an evolutionary history of high levels of browsing ungulate herbivore, capable of significantly modifying the structure and composition of woody plants (Owen-Smith, 1989). Browsing herbivores may include small herbivores (Belsky, 1984) and mega-herbivores, notably elephants (Jarman, 1971; Anderson & Walker, 1974; Guy, 1981; Barnes, 1985; Okula & Sise, 1986; Lewis, 1987; Kalemera, 1989; Ben-Shahar, 1991a; Lewis, 1991; Styles, 1993). Lewis (1991) found that although ele-phants in Zambia browsed a high percentage of coppiced *Colophospermum mopane* trees, a mean mortality of only 0,5% was recorded. However, an incident of intense browsing followed by a below-average rainfall reportedly led to a 100% mortality of damaged trees. Removal of browsing ungulate game species may have con-tributed to the bush encroachment problem.

The impact of poor grazing practices would seem to be particularly severe during dry seasons because of the greater negative effect of such management on grass growth than on the tree growth during peri-ods of severe water stress (Britton & Sneva, 1991). The warmer and drier climate, which is reported to have been experienced over the past 1 00 or so years may also have favoured the woody component of the savannas over the grass component (Smeims, 1983). Biological interactions may be further complicating factors since they can modify the impact of the various determinants.

It is generally conceded that high grazing pressure reduces the growth rate and reproductive potential of individual plants and in so doing influences the competitive relationships among the different species. Van Vegten (1983) identified overgrazing of grasses as the main cause of the increased woody plant density in the eastern areas of Botswana. Skarpe (1990) showed that in non-grazed and moderately grazed areas, shrub densities showed no consistent trend, but increased where grazing was heavy. The tree species whose abundance increased were shallow rooted (*Acacia mellifera* and *Grewia flava*) which, according to

Skarpe (1990), suggests that they were favoured by an increase in water availability in the surface soil following overgrazing of the grass layer. It is generally conceded, however, that trees are able to make more effective use of deep water than can the grasses (Walker & Noy-Meir 1979; Stuart-Hill 1985) so that any management actions which increase water penetration to depth in the soil profile should stimulate growth in already established trees.

Knoop (1982) observed that on a site dominated by Acacia species, large numbers of seedlings germinated and survived in an area cleared of vegetation, but few were to be found in an uncleared area. Thompson (1960) reported that *Colophospermum mopane* seedlings could not take root where the grass cover was dense. In contrast to these reports, Brown and Archer (1989) recorded high rates of emergence and establishment of *Prosopis* on long-term protected plots, which carried a good grass cover. Similarly, in the eastern Cape, sparing veld did not prevent the establishment of *Acacia karroo* seedlings after the eradication of mature trees (Du Toit, 1972).

These reports are therefore at variance with the widespread and general view that long-term or heavy grazing is a requisite for increased rates of woody plant establishment. However, Smit and Rethman (1992) have reported that while woody plants increased in sourish Mixed Bushveld, which had been leniently grazed over a period of 52 years, they increased much more rapidly in veld, which had been severely grazed during the growing season.

Smit and Rethman (1992) indicate that woody plants correlate positively with Increaser IIb herbaceous species (species that increase under moderate overgrazing) and the latter correlate negatively with grass production. While representing the same amount of animal unit grazing days ha^{-1} (stocking density x period of occupation during growing season), a relatively high stocking density and occupation for part of the growing season had a less severe long-term effect on the increase of woody plants than a relatively low stocking density and occupation for the whole growing season.

In the same study the number of Tree Equivalents (1 TE = a single stemmed tree 1,5 m high) per hectare and the percentage canopy cover of woody plants were found to be positively correlated with the number of Animal Unit (AU)-grazing days per hectare (total and growing season) (Smit & Rethman, 1997). They concluded that the longer the period that severe grazing reduces the competitive ability of the grasses, the better the chances of woody seedling survival, hence an increased rate of woody plant establishment in response to an increase in the severity of the grazing treatment.

The role of fire as a determinant of woody plant density has received considerable attention in the literature (Trollope, 1 980; Rutherford, 1981; Belsky, 1984; Sweet & Mphinyane, 1986; Trollope & Tainton, 1986; Sabiiti & Wein, 1988). Fire is widely used, ostensibly to control woody plants, in spite of it now having been repeatedly established that fire alone is not effective in killing woody components of the savannas of southern Africa (Rutherford, 1981; Belsky, 1984; Sweet & Mphinyane, 1986; Trollope & Tainton, 1986). This is, indeed, not surprising since the vegetation of Africa has for long been subjected to regular fires and the woody species which now occupy these regions are well able to survive in its presence. Veld fires may, however, be used to modify the structure of the woody layer and it is for this purpose that they are most useful.

The following fire regime (season and frequency of burning) is considered to have the greatest effect on the woody plants and is recommended for the prevention of bush encroachment (Trollope 1980):

(i) high intensity fire (>2 000 KJ s^{-1} m^{-1}) is required. This can be achieved with a fuel load of 2 000-4 000 kg dry matter ha^{-1}

(ii) The relative humidity must be low (<30%)

(iii) Air temperature should be above 25°C

(iv) Burn with the wind (head fire), but the wind speed should not exceed 20 km/hour

(v) Time of burning is also important and the best time is during spring when the woody plants have already started to grow but the grasses are still dormant (usually just before the first rains)

(vi) The frequency of burning is not fixed. In wetter savanna areas a fire every 3 tot 4 years may be possible, while in drier areas it should be undertaken opportunely depending on the rainfall and the presence of small woody plants that need to be controlled.

The total exclusion of fire or, conversely, the frequent occurrence of fire under conditions different from the above mentioned fire regime, may benefit the establishment of woody plants (Smit *et al* 1999).

4. Negative aspects associated with bush encroachment

The botanical composition and productivity of any mature stand of vegetation is largely determined by competition (Wilson, 1988). Competitive interactions between the woody and herbaceous components of savannas, involving mainly available soil water as the primary determinant of production, have been reported world-wide (Australia: Walker *et al* 1986a; Winter *et al* 1989; Harrington & Johns, 1990; Scanlan & Burrows, 1990; North America: Scifres *et al* 1982; Scifres ,1987 ; Archer *et al* 1988; Bozzo *et al* 1992; Haworth & McPherson, 1994; southern and east Africa: Donaldson & Kelk, 1970; Dye & Spear, 1982; Scholes, 1987; Belsky *et al* 1989; Smit, 1994; Smit & Swart, 1994; Smit & Rethman, 1999; 2000; Richter *et al* 2001).

The roots of woody plants are fundamental in their competitive interactions with herbaceous plants and other woody plants. Roots determine the spatial distribution of water and nutrient uptake and can cause an increase or a decrease in resource availability (Wu *et al* 1985).

The roots of savanna woody plants extend well beyond their projected crown radius (Wu *et al* 1985). In *Burkea savanna*, for example, the lateral roots of some species commonly extend linearly up to seven times the extent of the canopy (Rutherford, 1980). Roots of *Colophospermum mopane* trees have been shown by Smit (1994) to extend horizontally to a distance of approximately 7,6 times their height and 12,5 times the extent of their canopies, thus, the larger the tree, the larger the area of resource depletion and the greater its competitive effect on its neighbours. In addition, a large proportion of the roots are concentrated at a shallow depth (Ellis, 1950; Kellman, 1979; Muthana & Amora, 1980; Rutherford, 1983; Knoop & Walker, 1985; Castellanos *et al* 1991; Smit & Rethman, 1998b), where they would actively compete with the shallow rooted herbaceous plants.

The competitive advantage of drought adapted woody species over herbaceous plants is evident from a study by Smit and Rethman (1998a) in mopane savanna. They found that the total root biomass of *Colophospermum mopane* ranged from 9 760 kg ha^{-1} to 29 790 kg ha^{1} (mean: 17 354 kg ha^{-1}). Of these a mean of 19% was in the 0-1,0 mm diameter class, and 20,3%, 16,2% and 44,5% in the >1,0-5,0 mm, >5,0-10,0 mm and >10 mm diameter classes respectively. A mean of 66,1% of all fine roots (<5,0 mm) was found within the first 400 mm of the soil. The coarse roots (>5,0 mm) were virtually absent within the 0-200 mm soil layer, with the highest concentration between 200-600 mm. Leaf biomass was found to be significantly lower than the root biomass.

In a subsequent study Smit and Rethman (2000) presented evidence that the roots of the *C. mopane* trees are able to utilise soil water at a matric potential lower than that of grasses (ψ < -1 500 kPa). This feature, combined with high rainwater runoff losses due to a lack of an herbaceous cover, resulted in a dramatic reduction in the amount of plant available water with an increase in tree density. This enables the *C. mopane* trees to compete successfully with herbaceous plants and to prevent their establishment at high tree densities.

Moore *et al* (1985) reported reduced production of the herbaceous layer with increasing tree abundance in Kalahari Thornveld and Shrub Bushveld of the Molopo area. They recorded increased grass production of between 220% and 740% following aerial applications of an arborocide (Tebuthiuron), which caused woody plant mortality. In another study Moore and Odendaal (1987) found no reduction in grass production up to a density of 200 tree equivalents (TE) per hectare in the Molopo area but grass production declined linearly with further increases in tree density. A density of 2 000 TE ha^{-1} almost completely suppressed grass growth. They estimated that the grazing capacity was reduced from 8,7 ha AU^{-1} (I 200 kg grass DM ha^{-1}) to 45,8 ha LSU^{-1} (230 kg grass DM ha^{-1}) over the 200 to 2 000 TE ha^{-1} density gradient. Richter (1991) and Richter *et al* (2001) reported similar results from other parts of the Molopo area of the Northern Cape. However, clearing woody plants in mixed savanna dominated by *Combretum apiculatum* and *A. tortilis* resulted in only a small improvement in grazing capacity (from 9,1 ha AU^{-1} to 7,3 ha AU^{-1}) (Donaldson, 1978).

Notwithstanding the references to higher grass DM production at low tree densities than in open veld, much work has shown that the complete removal of trees leads to substantial increases in grass production (Donaldson & Kelk, 1970; Louw & Van der Merwe, 1973; Dye & Spear, 1982; Walker *et al* 1986a; Harrington & Johns, 1990; Scanlan & Burrows, 1990; Richter, 1991). Donaldson and Kelk (1970) found that grass yields did not decline linearly with increasing tree density. Yields declined rapidly as tree density increased to 350 mature *A. mellifera* trees per hectare, after which yields declined more slowly. Similar results were recorded in the Northern Cape (Richter, 1991; Richter *et al* 2001) and in the Mopane savanna of the Northern Province (Smit, 1994). The negative relationship between tree basal area and herbaceous production has also been found to be curvilinear in the *Eucalyptus* savannas of Australia (Scanlan & Burrows, 1990) and similar to that described by Donaldson and Kelk (1970). However, the relationship between tree biomass and herbaceous biomass in a *Eucalyptus* savanna in Australia has been reported to be linear (Walker *et al* 1986a; Harrington & Johns, 1990).

These differences in the response to tree thinning or clearing may be ascribed to differences in soil type and soil fertility, both of which are important determinants of the magnitude of the response to tree thinning (Dye & Spear, 1982). In years of high rainfall, higher yield responses have been attained in thornveld on relatively fertile clay soils than on nutrient poor sandveld. Scholes (1987) estimated an absolute increase in herbaceous production with clearing of 300-500 kg ha^{-1} in *Combretum* veld, 300-2 500 kg ha^{-1} in *Acacia* veld and 300-350 kg ha^{-1} in Mopane savanna. During a period of prolonged water stress he noted increased grass tuft mortality in uncleared plots, especially on soils with a fine texture (*Acacia* and Mopane sites). Different components of the herbaceous layer may also react differently to tree thinning. Smit (1994) demonstrated, for example, that in Mopane savanna the DM yield of the grass component reacted positively to thinning but that the yield of forbs declined.

The reaction of the herbaceous component to tree removal will, however, depend on rainfall. Harrington and Johns (1990) concluded that increased herbaceous biomass following clearing of all trees of a *Eucalyptus* savanna in Australia would be obtained in any month only if rainfall exceeded 10 days' potential evapotranspiration and that herbaceous biomass would accrue at a rate of 0,5 g m^{-2} for each mm of monthly rainfall over this threshold. The total clearing of all woody plants resulted in a herbaceous biomass increase of 430% to 670%. In Mopane savanna, grass yields of thinned plots were considerably higher than those of densely wooded plots, especially during years of below average rainfall, while grass yields at high tree densities differed little between seasons of varying rainfall (Smit, 1994).

The aim of tree thinning or tree clearing is usually to achieve increased herbaceous production, but the species composition of herbaceous plants is also important as species may vary significantly in their acceptability to grazing herbivores. Other considerations include long-term stability as influenced by the state of plant succession (e g predominance of climax grasses, mainly perennials, as opposed to the predominance of pioneer grasses, mainly annuals), ground cover for prevention of soil erosion and water runoff (Snyman & Van Rensburg, 1986), and the main-tenance of soil fertility (Hook *et al* 1991).

The effect of bush encroachment on herbaceous cover differs between mesic and arid savannas. In mesic savannas herbaceous plants still coexist with relatively high tree densities. Under these conditions changes in the composition of the herbaceous layer may occur following tree thinning as a result of changing regimes like shade, soil temperatures, soil water and soil nutrients. Depending on the situation, the advantage of increased production of herbaceous plants following tree thinning may, from an agricultural point of view, be offset by unfavourable species changes (e.g. whereby palatable, low fibre 'sweet' grasses are being out-competed and replaced by more unpalatable, high fibre 'sour' grasses) (Smit & Rethman, 1999).

In arid savannas the herbaceous layer largely disappears under high tree densities, leaving large areas of bare ground. The spatial and temporal pattern of herbaceous species establishment (succession) is of relevance under these conditions. Plant succession has been defined as a progressive development of vegetation in an area through a series of different plant communities, finally terminating in a climax community (Trollope *et al* 1990). In this case the establishment of herbaceous plants can be considered as secondary succession, which is defined as succession that occurs after the destruction of part or all of the original vegetation on a site (Trollope *et al* 1990). Crust formations are known to reduce infiltration and cause substantial losses due to rainfall runoff (Hillel & Gardner, 1970; Agassi *et al* 1981; Ralph ,1989; Harmse & Nel, 1990).

Contrary to common belief that bush encroachment is detrimental to grazers, but not browsers, there are indications that bush encroachment may also be detrimental to some browsers. In mopane savanna a study by Smit (2001) showed that tree thinning reduced the available browse at peak biomass, but that trees from the low tree density plots displayed a better distribution of browse, having leaves in comparatively younger phenological states over an extended period. This would shorten the leafless period of the *C. mopane* trees in early spring and might even eliminate it. High-density stands may therefore not only be poorly suited to grazers because of reduced growth of herbaceous plants, but also to browsers because of their relatively poor browse supplying characteristics.

5. Will thinning or clearing of the woody plant solve the problem?

Where tree densities are very high the first operation which may be required will be the thinning of trees to some predetermined density, after which a post-thinning management programme will be required to keep an area open (Smit, 1994). Tree thinning or clearing by means of mechanical or chemical methods will result in immediate changes in competition between woody and herbaceous plants, which often determines the growth and structure of savannas. The resulting gaps will lead either to increased growth of neighbouring individuals or to the establishment of new individuals (Teague & Smit, 1992).

Thinning *Colophospermum mopane* stands has been shown to stimulate vegetative growth, flowering and seed bearing in the remaining trees (Smit, 1994; Smit & Rethman, 1998). Over a three-year period the leaf DM yield of the trees increased by 64, 9% in plots cleared to 10% of the original density, compared to an increase of 22,2% in uncleared plots. Scholes (1990) estimated that, through seedling establishment, recovery of cleared *C. mopane* thicket in the eastern lowveld to its precleared competitive ability would occur within 1 4 years. This recovery period would be shortened by high rainfall and lengthened by drought. He estimated that the *C. mopane* trees would grow to their original precleared state within 40 years.

In Botswana, stem basal area increased by 11 to 21% and tree height by 1,2 to 3,9% in thinned plots compared to increases of 3,5 and 1, 1%, respectively, in uncleared plots (Coe, 1991). Smith & Goodman (1986) found a significant increase in both stem diameter and shoot extension of *Acacia nilotica* trees whose neighbours had been removed within a radius of 5 m. In time, therefore, the competitive ability of the remaining trees will gradually increase and so reduce the impact of the initial thinning, even without seedling establishment.

An important determinant of woody seedling establishment is competition from other plants, either from other woody plants or herbaceous plants (Smith & Walker, 1983; Smith & Goodman, 1986; Schmitt *et al* 1987; Smith & Goodman, 1987; Smith & Shackleton, 1988; Ben-Shahar, 1991b; Grundy *et al* 1994). Ben-Shahar (1991b) has demonstrated that tree species of communities dominated by *Acacia senegal — A. tortilis and Euclea divinorum — A. nilotica* have characteristic dispersal strategies. These were manifested through intra- and inter-specific competition among the dominant tree species. Acacia senegal became dominant in areas previously dominated by *A. tortilis*, while *E. divinorum* was replacing previous dominance by *A. nilotica*.

Tree-on-tree competition appears to be species specific (Smith & Goodman, 1986) or related to the shade tolerance of the seedlings (Story, 1952; Smith & Shackleton, 1988; O'Connor, 1995). In some, seedling establishment is unaffected by a tree canopy while in others, establishment is limited to between-canopy environments (Smith & Goodman, 1986; Grundy *et al* 1994). In the eastern Cape, shading increased the density of surviving *A. karroo* seedlings (O'Connor 1995), while at Nylsvley in the Northern Province shading decreased the density of surviving *A. tortilis* seedlings (Smith & Shackleton 1988). In another study it was established that *Euclea divinorum* does have the ability to establish under canopies, while seedlings of several *Acacia* species are distinctive as they fail to establish under the canopy of any established individual, regardless of species (Smith & Goodman, 1986). Both *A. nilotica* and *E. divinorum* were found to be regularly dispersed, but there was no significant correlation between nearest-neighbour distance and combined size for mixed-species nearest-neighbour pairs of *A. nilotica* and *E. divinorum* (Smith & Goodman, 1987).

Significant positive correlations between the size of a tree and the distance to its nearest neighbour were reported for large individuals of *Brachystegia spiciformis* and *Julbernardia globiflora* in Zimbabwe (Grundy *et al* 1994). However, they did not observe the same regular dispersion pattern in stands of immature trees. They ascribe this to the fact that young plants often grow in under-canopy environments and that positive correlations between tree size and distance to nearest neighbour only develop through a thinning process as the trees mature.

6. Conclusion

From this review it is clear that the presence of woody plants in savanna is associated with both positive and negative aspects, which are closely related to tree density or tree abundance. In view of this it can be concluded that any bush control program (chemical, mechanical or biological) should focus on tree thinning rather than on clearing of all woody plants. In making decisions on the intensity of tree thinning, the sizes of the trees, which should be removed, and the species to be thinned, cognisance should thus be taken of the balance between the need to reduce the competitive effect of the trees on the herbaceous layer and the positive influences, which the trees may have.

The aridity of the area also needs to be borne in mind since more woody plants can be retained at wet than at dry sites without materially affecting herbaceous yields. It is also important to realise that there is no single optimum tree density and that even within a vegetation type, the optimum density falls within a range rather than being represented by a single value. 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 bush control measures. In many cases the resultant re-establishment of new seedlings may in time develop into a state that is in fact worse than the original state. It is hypothesized that a more stable environment can be created, which is not as prone to the rapid regeneration of new woody plants, by making use of system dynamics (Smit *et al* 1999). Here the natural functioning of the savanna system is allowed to stimulate the development of an open savanna comprised mainly of large trees. It 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. The larger the individual, the greater is the distance between it and the nearest individual of the same species. This is particularly noticeable with *Acacia* species (Smith & Goodman, 1986; 1987).

It is known that if a tree is killed, the reduced competition afforded to the remaining individuals results in an increase in their growth rate (Smith & Goodman, 1986; Coe, 1991; Smit, 2001). Competition between individuals in a community can result in the stagnation of growth in a tree population. If, in such a community, low intensity thinning is applied, the growth rate of individuals adjacent to the thinned individuals will increase and this will lead to a suppression of the growth of other woody species within the area thinned. The key here is low intensity thinning. If thinning is too intensive, the remaining trees will provide insufficient competition to prevent woody plants from regenerating in the cleared area. In time this approach can assist in the creation of a more stable and structured savanna that is more resistant to bush encroachment, especially in areas where all the larger trees were lost through previous non-selective control measures.

It is important for any land manager to realize that there is no quick solution to the problem of bush encroachment. Effective management of bush encroachment should not be considered a once-off event, but rather a long-term commitment. This may involve alternative approaches that are not necessarily the simplest or cheapest. It has been proven time and time again that the least expensive method of killing trees may not be the most economical approach in the long term. Once the established matured trees are lost from the ecosystem, land owners may discover that they now have to manage a much more unstable system that requires frequent and repeated efforts in dealing with a high rate of re-encroachment, often from other, more threatening woody species. It is also important to avoid or minimize other direct or indirect causes of bush encroachment. Of these, sound grazing management practices, which will ensure a vigorous and competitive herbaceous layer, are of critical importance.

The cost of bush control measures is extremely high, especially when chemical arboricides are being used. The cost can vary from R120,00 to R1 000,00 or more per hectare, depending on the degree of encroachment and the control methods used. Unfortunately the extent of bush encroachment on farmland is not always reflected in the value of such land. This is mainly due to adequate buyers, mostly professional people, who acquire farms without proper knowledge of the ecological factors influencing the productivity of farmland. Such buyers often acquire farms for recreational purposes and are not dependent on the farm for an income. The consequence of this is that there is very little incentive to apply substantial sums of money for bush control measures, which will not increase the value of the property.

For full time stock farmers who depend on their farms for an income, the only benefit from the application of bush control lies in increased animal production. Due to the low profit margins on meat production the high cost of chemical bush control measures is often difficult to justify. Such landowners often experience a situation where they cannot economically continue their stock farming because of the reduced gracing capacity of their natural pastures, and cannot afford the high cost of bush control measures. With the increased popularity of game ranching, a practice whereby capital (often borrowed money) is invested in fencing the property with a game proof fence is becoming popular. Such a fenced farm is subsequently being sold as a 'game ranch' at highly inflated prices, despite the low production potential due to its encroached status. The new owners are often hugely disappointed in their investment after they discover the true potential of their 'bushveld farm' through stock or game losses during the dry months of the year.

A possible solution for this undesirable situation is education and an increased awareness of the ecological factors that influence the productivity of farmland in savanna. Investors should always consult with an expert to evaluate the true potential of a property before buying it. Once such a practice becomes well established the incentive to apply sensible, ecologically correct bush control measures will become stronger. This will benefit the potential investor and contribute towards the maintenance of our scarce and valuable natural resources.

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