

# ECOLOGICAL DYNAMICS OF CENTRAL NAMIBIA'S SAVANNAS: PART 2 – BUSH ECOLOGY

AXEL ROTHAUGE

AGRA (Co-operative) Limited, Private Bag 12011, Windhoek, Namibia  
axelr@agra.com.na

## ABSTRACT

Bush encroachment by *Acacia mellifera* is initiated by a wet spell of sufficient duration (three years) to allow this woody species to set viable seeds, followed by successful establishment of the seedlings. It is a rare, sporadic event in Namibia and in the arid zones of southern Africa. Bush encroachment follows a “sleep, then leap” mode of action rather than a steady and continuous “creep” mode. Bush seedling establishment is facilitated hugely by the exclusion of fierce veld fires, a grass sward weakened by grazing and by reduced browsing pressure. Hence, the most obvious manner to prevent bush encroachment from occurring in the first place is to set a fierce fire whenever rainfall was above the average for three years in a row, but only in those areas that are threatened by bush encroachment. Since the seed of *Acacia mellifera* is not long-lived, not mobile and not distributed in the dung of herbivores, there is little need to burn areas that do not contain a large proportion of mature *Acacia mellifera* bushes.

If this sporadic opportunity to prevent bush encroachment was missed and the savanna changes from a grassy to a bushy state, fire is no longer an effective means of control. Chemical and mechanical control mechanisms are the best option to thin (rather than eradicate) the population of invasive *Acacia mellifera*, failing which they will mature over many decades to old age. Only when senescent do they again become vulnerable to stressors and natural control. Control presents an ideal opportunity to improve the grass sward and thus recover the production potential of Namibia's savanna rangelands, but has to be followed by aftercare.

## SUMMARY OF THE ECOLOGICAL MODEL

The savannas found in central Namibia, the Highland, Thornbush and Camelthorn savanna (Giess, 1971), can occur in a grassy or a bush-encroached (bushy, woody) state (Figure 1). Within these two major states, climax and pioneer states exist (Joubert, Rothauge & Smit, 2008). Various forces and events change the state of a savanna (a “transition”). The degraded grassy (pioneer) state can degrade further to full-scale desertification which is, for all practical purposes, irreversible. A crucial stage for the land manager is when a grassy turns to a bushy state. In such a case the grass – bush balance is severely disrupted and the characteristics of the savanna change completely

(Rothauge, 2007a). Bush encroachment is a problem of national significance and is further elucidated in this, the second part of the article.

In the savannas of central Namibia, the major invasive woody species is *Acacia mellifera* subsp. *detinens* (Bester, 1998). Over these vast areas, the abundance and density of *Acacia mellifera* bushes have exploded until far exceeding its probable natural density. Unfortunately, there is no scientific norm of what this plant's “natural density” should be. De Klerk (2004), based on recommendations by Prof G.N. Smit, theorised that the probable “natural density” of woody plants (expressed in evapo-transpiration tree equivalents, ETTE, per hectare) in Namibian savannas is twice the average annual rainfall received (in millimetre). An ETTE is the amount of water required by a woody plant of 1,5 m height. The number of ETTE/ha gives an indication of how much soil moisture is extracted from the soil by woody plants (Smit, 1989). If an area receives on average 350 mm per year, the probable natural density of all woody plant species is about 700 ETTE/ha, i.e. 700 bushes of 1,5 m height per hectare. However, considering that the statistical variability of rainfall in Namibia exceeds 40 %, bush density in a 350 mm rainfall area should not be uniform, but vary from as little as 420 ETTE/ha to, in patches, 980 ETTE/ha to achieve a diverse mosaic effect. In bush-encroached rangelands, the density of *Acacia mellifera* alone can often reach 6 000 and sometimes even 16 000 bush per hectare (Bester, 1998). Such thorny thickets form monostands that are impenetrable to large herbivores and starve the herbaceous component of water.

## THE TRANSITIONAL STATE OF BUSH SEEDLING ESTABLISHMENT

Bush seedlings are easily overlooked and therefore, this state is not often recognised in the field. In this transitional state, the still-dominant grass sward conceals a high number of *Acacia mellifera* saplings which are still below grass-emergent height. At superficial inspection, this state is virtually indistinguishable from the grassy states, masking the progression towards a bushy state. A savanna may persist in this state for a variable length of time, depending on the competitiveness of the grass sward, rainfall, soil fertility, herbivory and especially the frequency and severity of fire. Even after six years, *Acacia mellifera* saplings may be no taller than year-old seedlings and are only distinguishable by their branches and thicker

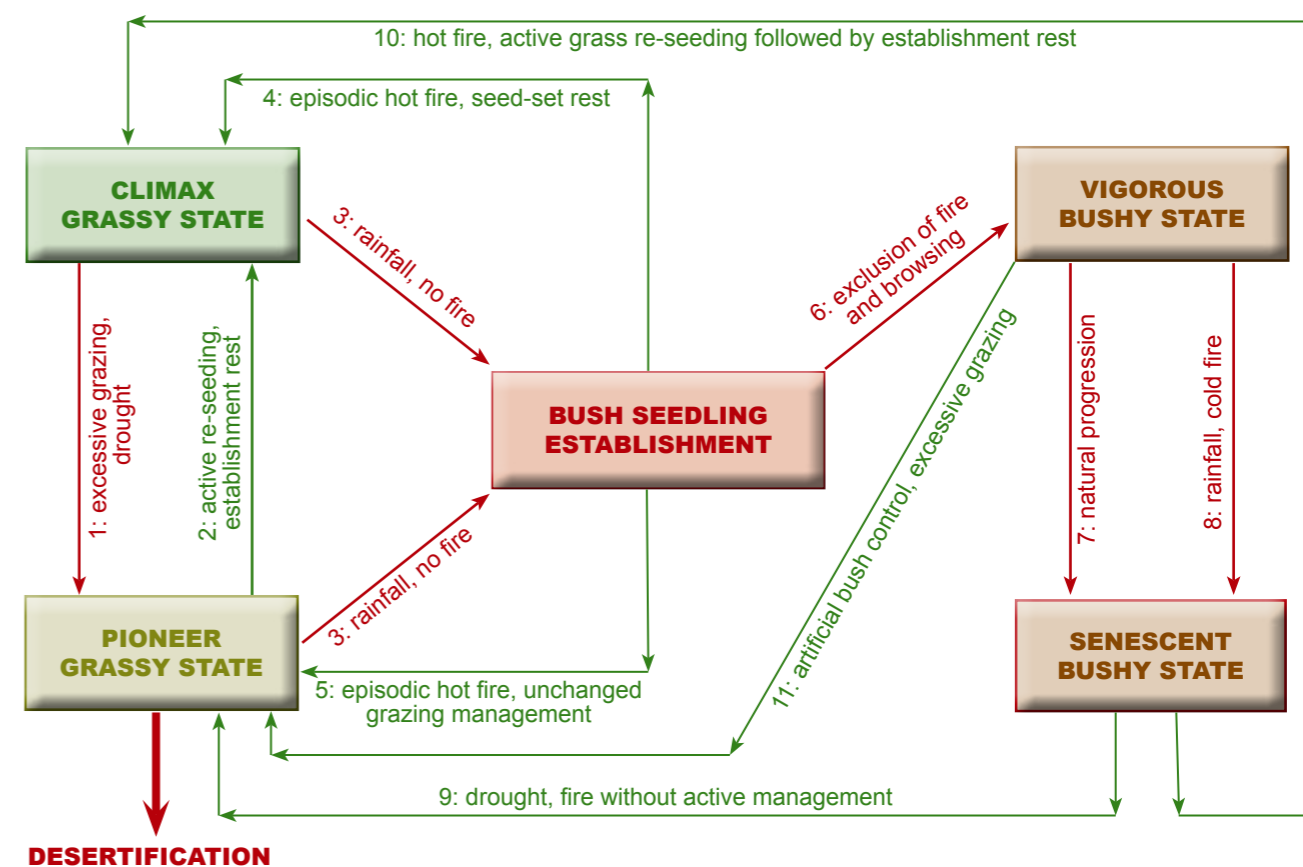


Figure 1. Complete schematic presentation of the five states of the Highland savanna and the eleven transitions between states (red = degradation and green = rehabilitation transitions).

stems that bear the abscission scars of previous years' growth (Rothauge, 2007b), so-called gullivers (Bond & Van Wilgen, 1996). As the seedlings mature, they become more easily visible and the savanna apparently changes “quickly” to the bush-encroached state. However, it had been in transition already for some years.

The transitional state of bush seedling establishment represents a critical time period for management intervention to prevent the initiation of bush encroachment, because *Acacia mellifera* seeds and saplings are extremely prone to fire, frost, predation and competition. These events, if utilised properly, could affect the restorative Transitions 4 and 5 back towards the grassy states. In their absence, Transition 6 is initiated and a bushy state will develop.

## TRANSITION 3 TOWARDS THE ESTABLISHMENT OF BUSH SEEDLINGS

The transition from the grassy state towards establishment of *Acacia mellifera* seedlings needs three consecutive years of above-average rainfall to be initiated and is facilitated by secondary conditions, especially by a grass sward that has been weakened by over- or selective grazing, the complete suppression of fire and reduced browsing pressure. Successful recruitment of *Acacia mellifera* in the Highland savanna is rare and probably occurred on only five occasions in the past 95 years (Figure 2). This is in

agreement with findings in another semi-arid savanna in eastern Australia, where six widespread *Dodonaea attenuata* establishment events were estimated to have occurred in 97 years (Harrington, 1991). In the past century, there were only five occasions of three consecutive years of above-average rainfall at Neudamm, viz. 1917 to 1921, in the early fifties, in the mid fifties, in the late seventies and in the late eighties/early nineties (Figure 2, circled in green). During these wet spells, *Acacia mellifera* could have been established only if fires were totally excluded, the grass sward was weakened and browsing pressure was greatly reduced. These secondary conditions would probably only have been satisfied from the 1970s onward, when many farmers acquired mechanised fire fighting equipment. It is thus postulated that much of the landscape-level *Acacia mellifera* encroachment of the Highland savanna occurred sporadically in the late seventies and again in the late eighties/early nineties; 30 and 15 years ago, respectively.

Why are three successive, above-average rainfall years required to initiate bush encroachment by *Acacia mellifera* in the central savannas of Namibia? A first good rainy season is required for this woody species to produce viable seed. The bush flowers and sets seed before the advent of the rains, using carbohydrate energy reserves accumulated in, and carried over from the previous rainy season. Donaldson (1967) noted that *Acacia mellifera* fruited profusely following a season of “copious” rain in the bush-encroached Molopo area of South Africa, but

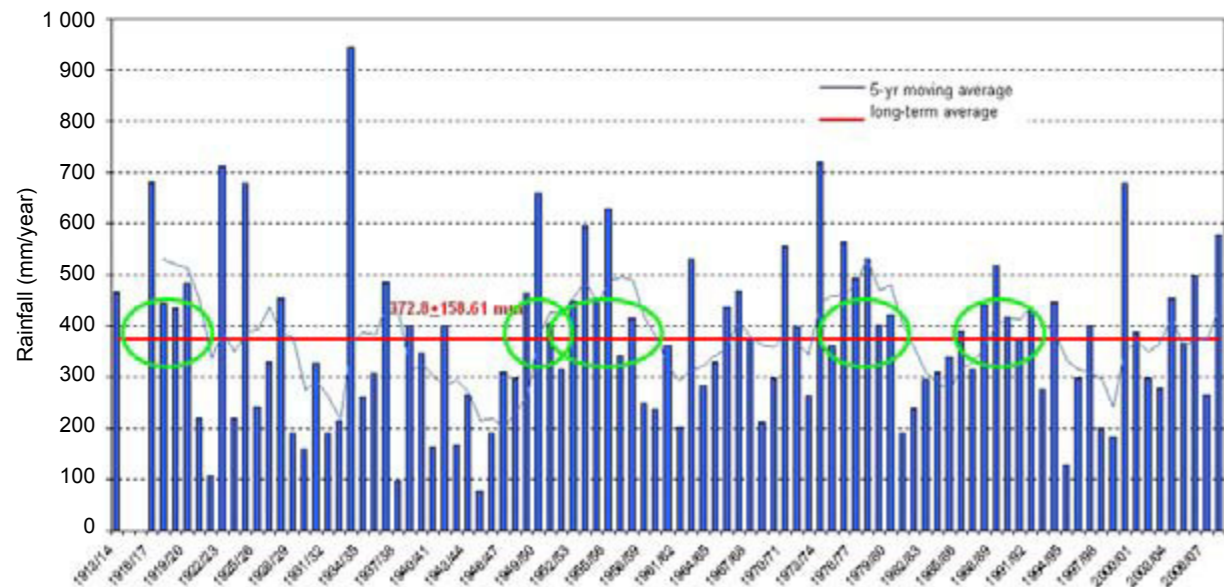


Figure 2. Annual rainfall (mm) received at Neudamm since the 1913/14 season (Rothauge, 2008). Green ellipses indicate favourable rainfall periods with three or more consecutive years of rainfall above the long-term average.

that only 2 % of trees fruited in drier years. At Krumhuk, during the period 1998-2004, copious fruiting was only observed in the two seasons following the exceptional 1999/2000 rainy season, whereas no fruiting occurred in the preceding seasons of below-average rainfall (Joubert, 2007), because flower and especially seed production requires greater energy reserves than can be accumulated in years of below-average rainfall. Flowering “privileged” trees growing along road verges, in gardens, near rivers and dams or in other microhabitats where moisture accumulates sometimes create the impression that a far larger proportion of trees are reproducing than is actually the case, but they are not representative of conditions in the wider landscape.

The second good rainy season is required for the successful germination of recently-formed seeds. Ripe seeds drop from the tree by late November to early December, before the advent of the main rains. Only if the dropped seeds receive good early rains and good follow-up rains will they germinate and establish themselves, before they are depleted by predation or unsuccessful establishment. The chance that rains will be both early and regular is better when the rainy season is above, rather than below average (Figure 3) (Rothauge, 2008). With a good moisture regime, seeds germinate easily and achieve more than 90 % germination (Joubert, 2007). Ease of germination rapidly depletes the seed bank and if establishment is unsuccessful, few seeds remain in reserve. Seeds that have not germinated do not survive long because their testa is soft, offering little protection against seed predators or digestion in the rumen of herbivores (Donaldson, 1967; Smit, 2003). The seeds are relatively small and contain less endosperm than those of large-seeded *Acacia* species, such as *Acacia erioloba*, reducing the long-term survival of seeds. Thus, *Acacia mellifera* seed banks are ephemeral and seedlings can only emerge after seed production in the

same year (Donaldson, 1967; Joubert, 2007). At Neudamm, seedling establishment on 143 plots of 3,14 m<sup>2</sup> each was only observed in 2001 following the exceptional 1999/2000 rainy season and not in the seven rainy seasons thereafter (Figure 4) (Rothauge, 2007b).

A third consecutive good rainy season is required to enable the transition to bush-encroached rangeland to succeed by ensuring the best possible survival of seedlings that emerged in the previous season. After poor rainy seasons, sapling mortality is high (Figure 4). Sapling survival is greatly improved if fires are prevented, by heavy stocking of grazers that diminishes the competitive ability of perennial grasses (Teague & Smit, 1992) and by reducing browsing pressure. In the total absence of fires, seedlings of *Acacia mellifera* establish themselves even in prime grass swards (Rothauge, 2007b), suggesting that bush thickening is inevitable in the absence of fire. Concerning grazing pressure, this transition in the adjacent camelthorn savanna followed upon prolonged periods of stocking more than 45 kg cow mass per hectare (equivalent to 10 ha/LSU) (Rothauge, 2006a). With regard to browsing pressure, sapling density at Neudamm was reduced drastically when they were exposed to small ruminants compared to cattle (Rothauge, 2007b). Suppression of *Acacia mellifera* establishment was even better when they were exposed to indigenous Damara sheep and Boer goats because they browse much more than other breeds like the Dorper or Karakul (Kamupingene, Mukuahima, Rothauge & Abate, 2005). In elevated areas, severe winter frosts may also curtail the establishment of *Acacia mellifera* seedlings.

The successful recruitment of *Acacia mellifera* leads to an unstable transitional state that can either proceed to bush thickening (Transition 6) or revert to the grassy state (Transitions 4 and 5) (Figure 1), representing a crucial juncture for vegetation dynamics and rangeland

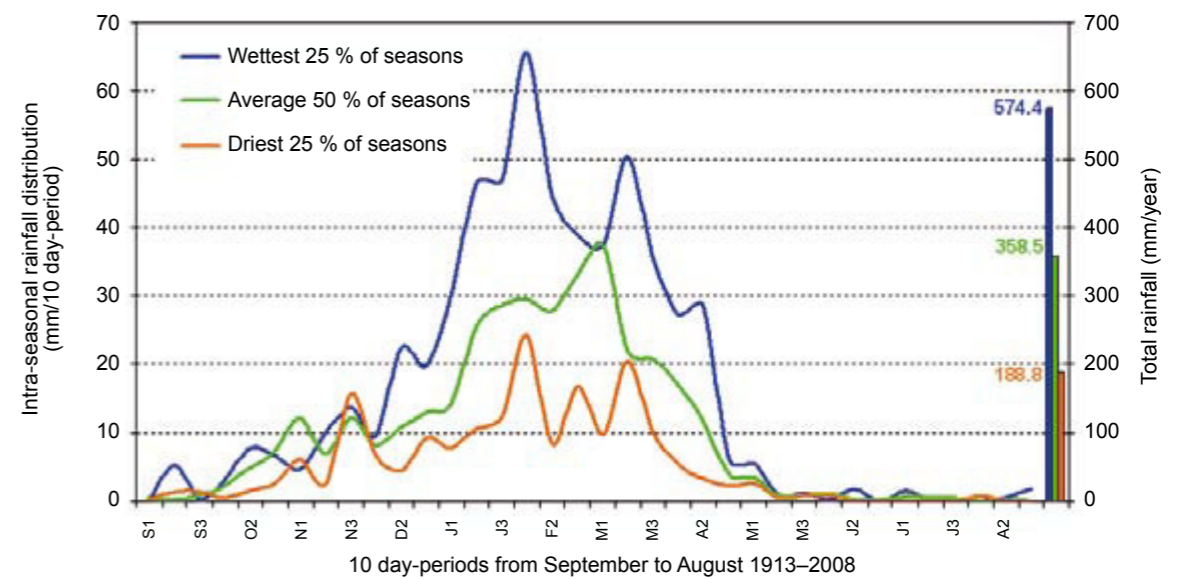


Figure 3. Intra-seasonal rainfall distribution (lines) and total rainfall (bars) at Neudamm from 1913 to 2008, distinguishing between top (wettest) and bottom (driest) quartile (Rothauge, 2008).

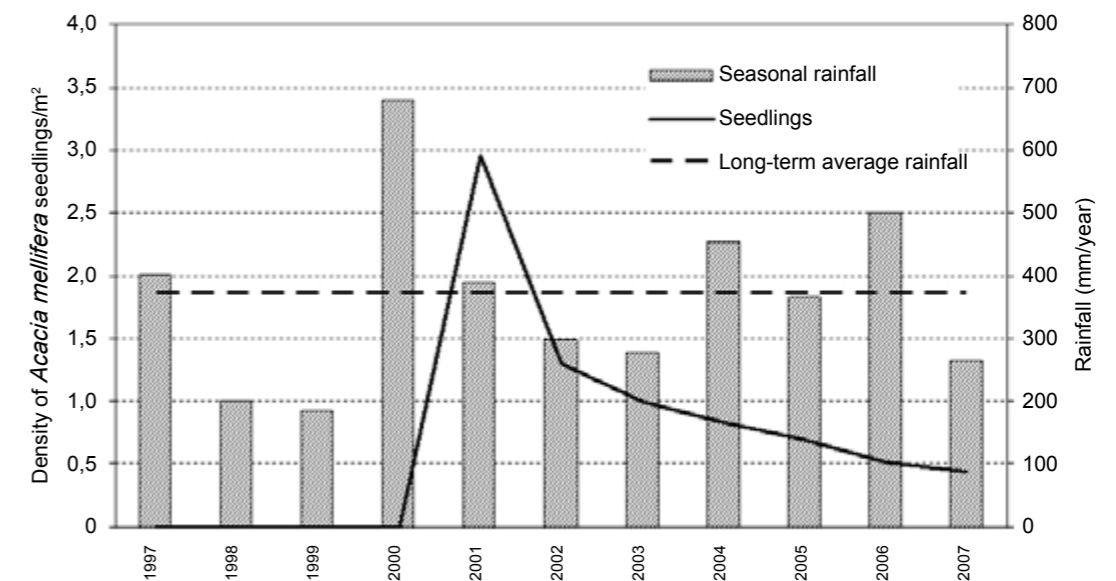


Figure 4. Emergence, establishment and survival of *Acacia mellifera* seedlings (line) at Neudamm in response to rainfall (bars) (Rothauge, 2007b).

management. If not interrupted, Transitions 3 and 6 form a continuous progression from grass- to bush-dominated savanna.

### 1. The role of fire in preventing bush encroachment

The drivers of the restorative transitions 4 and 5, from the transient state of bush seedling establishment towards a grassy state, are fire, frost, seed and seedling predation, and direct competition with the grass sward, in decreasing order of importance.

Fire has long been known to be an important driver of vegetation dynamics in savannas (Trollope, 1984; Teague

& Smit, 1992; Smit, 2003). It may control bush thickening through its effect on mature trees, fruits, seeds (Trollope, 1974; Trollope, 1980; Sweet, 1982; Trollope, 1982; Trollope, 1984; Hodgkinson & Harrington, 1985; Harrington & Driver, 1995; Skowno, Midgely, Bond & Balfour, 1999; Higgins, Bond & Trollope, 2000; Roques, O'Connor & Watkinson, 2001), and seedlings and saplings (Frost & Robertson, 1987; Trollope, Hobson, Danckwerts & Van Niekerk, 1989). Fire restricts the recruitment of woody seedlings into adult size classes (Higgins *et al.*, 2000). In the Highland savanna, a fire is far more effective at the seedling and sapling stage of *Acacia mellifera* because they are more fire-prone than more mature growth stages. An effective fire will take the savanna from the transient state



of bush seedling establishment back to the grassy states through Transitions 4 and 5. Trollope's (1982; 1984) general recommendation of two tons of fuel per hectare to control mature trees is a prudent measure of what would constitute an effective fire, but it is reasonable to expect that a lower fuel load might suffice to control seedlings and saplings.

Fires occur much less frequently today than previously, since farmers are reluctant to accept the risks of burning. Fire is a known danger to ranching because it destroys fodder reserves accumulated as standing hay on the veld and because of its short-term destructive effects on organic life forms in the top layer of soil (Trollope, 1982; 1984). The economic returns after burning may only be realised many years later (Hodgkinson & Harrington, 1985; Harrington & Driver, 1995). However, the lack of fierce fires is one of the main reasons for Transition 6 towards a bushy state. In the absence of fierce fires, bush encroachment is inevitable in Namibia's savanna rangelands. Like in other semi-arid savannas of the world, bush recruitment is a continuous process, independent of herbaceous biomass and density but regulated mainly by fire (Brown & Archer, 1999). The best stage to apply such a fire would be while the savanna is still in the transient state of bush seedling establishment, stifling the initiation of bush thickening.

Fire as a management tool to prevent the transition of a savanna towards the bushy state should emulate nature. Fire should only be used sporadically every 15 to 20 years (Bond, 1997) once environmental conditions (wet spells of at least three consecutive years of above-average rainfall) favour *Acacia mellifera* seedling establishment. Successful establishment of *Acacia mellifera* seedlings can easily be confirmed by monitoring sites close to adult bushes. Quantitative confirmation of impending recruitment should trigger an appropriate response, namely a hot fire that kills most of the bush seed and saplings. Conditions for a hot fire, primarily the accumulation of more than two ton of herbaceous dry matter per hectare to act as fuel, are very likely to occur during the same wet spell that favours bush seedling establishment. Wet spells usually result in more fodder being produced than can be utilised by domestic livestock and thus afford the land user the luxury to burn some off in the interest of manipulating the grass – bush balance of the savanna. If used with this intent, a controlled fire can maintain a savanna in the grassy state and prevent sporadic bush encroachment. It may also initiate the successful establishment of woody climax species such as *Acacia erioloba*, whose seeds need scarring by amongst others, fire to germinate.

Whenever fire is used to prevent *Acacia mellifera* colonisation, it must be managed correctly to maximise its advantages and minimise its danger (Trollope, 1999):

- Infested rangeland should only be burned if there is enough combustible herbaceous material to support a really hot fire that is sure to kill most bush saplings (more than two ton of herbaceous dry matter per hectare).

- The veld should be burned in late winter when the bushes break their dormancy and are more sensitive to fire than when they are still dormant (too early) or have already completed sprouting (too late), but before the first rains to ensure that the grass fuel is still dry.
- At that stage, perennial grasses may have started the early-season green flush, typical of wet spells, enabling them to survive hot fires better.
- The veld should be burned early in the day when the base of grass tufts is still wet from dew and when wind speed is usually low.
- Back fires burning into the wind, are slower, easier to control and release most of their heat at ground level where they do severe damage to grass tufts. Head fires burning with the wind, are hotter and most of their heat is carried upwards. They ignite wood fuel more effectively, but are more difficult to control because they travel fast. Trollope (1999) recommends the use of head fires to control bush.
- The veld should only be burned if it has been protected by the necessary precautions, such as fire breaks and if burning activities adhere to the fire management guidelines spelt out in the Forest Act of 2001.
- The veld should not be burned when conditions are unsuitable, e.g. insufficient fuel load, high wind speed, insufficient manpower on standby, etc.
- Burned veld should be rested from grazing until the perennial grasses have recovered their vigour by setting seed. With an active green flush due to inter-seasonal soil moisture transfer during a wet spell, this may happen within 60 days of a late dry season fire (Rothauge, 2006b).

Well-timed fierce fires maintain savannas at a high level of productivity and biodiversity whereas most ill-timed "cool" fires do more damage than good to rangeland.

## 2. Other drivers that prevent bush encroachment

The second important driver that can prevent a transition towards bush encroachment is frost. At higher altitudes in the Highland savanna, successive nights with sub-zero temperatures occur regularly. Severe frost after en masse seedling recruitment may kill bush seedlings, even those protected by a dense grass sward and revert the vegetation to a grassy state without seedlings.

The third-most important driver preventing bush encroachment is predation of the seeds, seedlings and saplings of *Acacia mellifera*. Fungi, invertebrates (especially arthropods), birds and small mammals (especially rodents) are major pre-dispersal predators of *Acacia* seeds (Fagg & Stewart, 1994) and may facilitate the transition to the grassy state. Many studies have reported on the effect of bruchid weevils on the dynamics of various *Acacia* species (e.g. Hoffman, Cowling, Douie & Pierce, 1989; Miller, 1994a; Vir, 1996; Okello & Young, 2000). *Acacia* seeds are typically attacked by seed-eating *Bruchidae* while still attached to the adult tree (Abdullah & Abulfatih, 1995) and infested seeds either do not germinate (Vir, 1996) or their

viability is drastically reduced (Hoffman *et al.*, 1989; Miller, 1994a; Okello & Young, 2000). The effect of seed predation is larger in dry than in wet years. At Krumhuk, following good rains in 2001, an average of 200 seeds were counted per *Acacia mellifera* tree. Seventy five percent of these were not viable, having mostly been infected by fungi. A further 12,5 % of seeds were infested with bruchid weevil larvae, leaving 25 viable seeds per tree to germinate. In contrast, following the poor rains in 2002, only four seeds were counted per tree of which three (75 %) were infested with bruchid weevil larvae, leaving only one seed per tree to germinate (Joubert, 2007).

Small mammals, birds and invertebrates are important post-dispersal seed predators (Kerley, 1991; Miller, 1994b; Ostfeld, Manson & Canham, 1997; Weltzin, Archer & Heitschmidt, 1997; Linzey & Washok, 2000) while rodents and ants are noted for their post-dispersal predation of *Acacia* seeds (Walters, Milton, Somers & Midgley, 2005). Mice typically remove only the endosperm and leave an empty testa. Since *Acacia mellifera* seeds germinate with ease, seed banks are depleted on a seasonal basis by predation (Meik, Jeo, Mendelson & Jenks, 2002). In years of exceptional fruit production, seed banks might be too large for seed predators to reduce substantially and the transition towards a bushy state will continue without interruption.

Seed of dehiscent *Acacia* species such as *Acacia mellifera* is typically wind dispersed (Miller, 1994a; Okello & Young, 2000) and is routinely destroyed in the gut of animals. In laboratory conditions, Donaldson (1967) found that only 2 % of *Acacia mellifera* seeds ingested by cattle germinated and it is highly unlikely that seeds of *Acacia mellifera* are dispersed by ungulates. In contrast, the seeds of indehiscent *Acacia* species require some form of gastric or ruminant treatment, even scarring by fire to enhance germination (Miller, 1994a; Okello & Young, 2000). Animals that consume *Acacia* pods include birds, ungulates, rodents, termites and ants (Miller, 1994b; Barnes, 2001).

Small mammals, especially lagomorphs (hares and rabbits) are important seedling and sapling predators in savanna and other ecosystems (Ostfeld *et al.*, 1997; Weltzin *et al.*, 1997), thus regulating vegetation structure. Lagomorphs crop saplings, leaving the branch cut off cleanly at a characteristic diagonal angle. Up to 58 % of the damage to *Acacia mellifera* saplings at Neudamm was caused by lagomorphs and 3 % were infested with aphids (Rothauge, 2007b). Baboons and warthogs dislodge saplings while digging; similar to the effect of prairie dogs on *Prosopis* saplings in north-central Texas (Weltzin *et al.*, 1997). At Neudamm, dense stands of *Acacia mellifera* saplings underneath and close to existing thickets are routinely destroyed by helmeted guinea fowl that scrape under the trees in search of seeds and grubs (Rothauge, 2007b). In the wild, mega-browsers such as elephant contain the establishment of *Acacia* saplings by uprooting them for feeding (Eltringham, 1979; Skinner & Smithers, 1990).

The least-important driver of Transitions 4 and 5 towards the grassy state is competition by the grass sward. A dense and vigorous grass sward may out-compete woody seedlings (Walter, 1971; Walker, 1981; Smit & Rethman, 1992) in accordance with Walter's (1971) two-layer hypothesis and might be expected to reduce fruiting success as well. The survival of woody seedlings and saplings is determined by the amount of excess moisture available after the fibrous roots of perennial grasses have removed their share (Davis, Wrage & Reich, 1998). Therefore, Transition 5 to the pioneer grassy state is less likely to occur than Transition 4 to the climax grassy state as annual grasses have much smaller root systems than the climax perennials (Wolfson & Tainton, 1999). However, Kraaij & Ward (2006) show that the competitive effects of the grass sward of a semi-arid savanna may be negligible; rather, grass has the more important role of providing fuel for a fire.

## TRANSITION 6 FROM BUSH SEEDLING ESTABLISHMENT TO A VIGOROUS BUSHY STATE

This transition is a continuation of Transition 3, if not interrupted. It has a better chance of succeeding in semi-arid than in mesic savannas, as semi-arid savannas rarely have sufficient fuel to produce a fire that might control *Acacia mellifera* saplings and they might escape the fire-prone stage more easily. If the transition occurred from the pioneer grassy state, there would be even less grass cover and hence, insufficient fuel for a fire. Observations in semi-arid Botswana (Skarpe, 1990) suggest that the absence of grass allows *Acacia mellifera* gullivers to grow rapidly beyond the fire-prone stage. A poor grass cover thus facilitates this transition. Thus, the crucial stage of onset of bush encroachment is seed production and seedling survival, rather than the release of already existing gullivers from competition by grasses through lack of fire at a later stage, when the transition towards a bush-thickened state is a *fait accompli*.

Ungulate browsers effectively maintain woody species at a much lower height than if they had not been browsed (Belsky, 1984) and thus control seedlings, saplings and gullivers (O'Connor, 1996), but cannot eradicate mature bush. Boer goats utilise *Acacia mellifera* at all growth stages, including fruits, seedlings and adults, but it is not their preferred forage species (Rothauge & Engelbrecht, 2000; Rothauge, Abate, Kavendji & Nghikembua, 2003). Thus, there is concern that the browsing pressure which would be required to control *Acacia mellifera* infestations will have adverse effects on other more desirable fodder bushes and the herbaceous layer (Zimmermann & Mwazi, 2002). Goat pressure in conjunction with controlled burning was able to control bush thickening by *Acacia karoo* in South Africa (Trollope, 1980), but had little effect on *Dichrostachys cinerea* (Zimmermann & Mwazi, 2002), another encroaching species. Ungulate browsers by themselves are probably ineffective in preventing a transition towards bush thickening. Rather, they regulate vegetation structure (Teague & Smit, 1992) and should be used in aftercare following other bush control measures (De Klerk, 2004).

## THE VIGOROUS BUSHY STATE

After the gullivers of *Acacia mellifera* have emerged above grass height, the shrubs exert such an influence on the environment that a transition back to a grassy state becomes virtually impossible without some form of active management intervention. This is largely due to the species' competitive ability to successfully extract water from the soil (Smit, 2003; De Klerk, 2004). In this state, *Acacia mellifera* remains dominant irrespective of grazing pressure or rainfall and is highly unlikely to be removed by fire. Unfortunately for Namibian ranchers that engage in extensive animal production with mainly grazing livestock, the vigorous bushy state is a very stable state that requires active intervention to change.

The increase in bush density and cover causes a substantial decline in grass production, mainly through competition for soil moisture (Van Vegten, 1983; Skarpe, 1990; Smit, 2003; De Klerk, 2004). A dense stand of *Acacia mellifera* dries out the soil, lowers the groundwater table and severely restricts the amount of water for use by other rangeland plants. *Acacias* are C<sub>3</sub>-plants that use comparatively more water during photosynthesis and transpire more water in hot climates than C<sub>4</sub>-plants, like tropical grasses. De Klerk (2004) reports that a 2,5 m high *Acacia mellifera* plant with a canopy spread of 6 m<sup>2</sup> uses up to 64,8 litres of water during an eight hour day in the growing season, equivalent to 38,9 litres of water per day used by an ETTE. A thicket of 5 000 ETTE/ha would thus transpire the equivalent of 19,5 mm of rainfall per day for its own purposes. This would deplete the season's total rainfall in less than three weeks and allow virtually no rainwater to remain for use by other plants. The amount of water transpired by *Acacia mellifera* is four times higher than that transpired by macrophyllous savanna trees such as *Terminalia sericea* or *Boscia albitrunca*. One *Acacia mellifera* plant transpires

as much water as 188 tufts of *Antheophora pubescens*, 559 tufts of *Schmidtia pappophoroides* or 864 tufts of *Eragrostis lehmanniana* (calculated from De Klerk, 2004). Similarly, a *Prosopis*-infested mesic rangeland in the south-western USA transpired three-and-a-half times more water than adjoining, dense grassland (Qi *et al.*, 1998). After successful establishment, *Acacia mellifera* has its water-absorbing infrastructure firmly in place. Its shallow lateral roots can extend at least seven times further horizontally than the height of the bush (Figure 5). Its superior water absorption capacity enables its roots to keep on extracting water from soil so dry that grasses are already wilting (Hipondoka, Aranibar, Chirara, Lihavha & Macko, 2003; Smit, 2003). Little wonder that natural springs and fountains all over Namibia's bush-encroached rangelands dry up spontaneously, irrespective of trends in precipitation (Bockmühl, 2009; Christian, De Klerk, Bockmühl, Van der Merwe & Mostert, 2010).

Initially, the bushy state consists of a fairly homogenous stand of similar-sized shrubs, mostly below one metre in height, with little grass cover (Joubert, 2007). The homogeneity of the stands attests to the episodic nature of the recruitment event, rather than it being a continuous, gradual process. It reflects the long periods of "sleep" with few vegetation dynamic events, followed sporadically by a "leap" mode of sudden and considerable change. A few larger parent trees of around 3 m to 4 m high, from which the shrubs originated, may be scattered through the thicket. These parent trees probably reflect the original "natural density" of *Acacia mellifera* in the savanna. Shrub densities around parent trees can reach three shrubs per square metre and almost 100% canopy cover, but are usually lower than this (Joubert, 2007). On a landscape level, shrub densities of 4 000 to 8 000 shrubs per hectare are common in bush-encroached parts of the Highland savanna and



Figure 5. The extensive lateral root system of *Acacia mellifera* (picture courtesy of Prof. G.N. Smit).

12 000 shrubs per hectare are not unusual (Bester, 1998; De Klerk, 2004).

Shrubs limit their own growth rate by intense density-dependent inter-shrub competition (Smit, 2003) and may remain immature (not reproductive) for decades until some event initiates self-thinning; enabling the survivors to grow out to maturity. Grasses are out-competed for light, soil nutrients and water under the canopy. The soil underneath bush thickets is often bare, but erosion is limited due to the dense, shallow network of *Acacia mellifera* roots and the high (woody) canopy cover. Increaser grasses, predominantly annuals of the genera *Aristida*, *Eragrostis*, *Enneapogon* and *Tragus*, dominate the grass layer. Their yield is low and erratic, depending on the rainfall. Animal biodiversity in these thickets is considerably lower than in the grassy state (Barnard, 1998), even though some animal species utilise thickets as refugia. Livestock production on vigorously bush-encroached range is severely limited by the lack and inaccessibility of palatable grasses. Wood harvesting for electricity generation (Von Oertzen, 2007), firewood and especially charcoal production is increasingly a strategy used by rangeland managers to generate income and return the vegetation to a grassy state. Charcoal production becomes an option as trees mature and stem diameter increases beyond 20 mm (Bester & Reed, 1997).

Transitions to the vigorous bushy state occur close to parent trees and already existing thickets, because seed dispersal is inefficient and seeds do not travel far from the parent plant (Donaldson, 1967; Joubert, 2007). Of 143 plots of 3,14 m<sup>2</sup> each monitored at Neudamm, the 10% of plots most heavily infested with *Acacia mellifera* seedlings were located only 3,2 ± 3,4 m from the closest presumed parent tree, whereas the 10% least infested plots were 18,7 ± 18,04 m removed from the closest presumed parent tree (Rothauge, 2007b). Shrub growth is encouraged by good rainfall. Frost and fires only affect the edges of a thicket. Unmanaged "cold" fires may even hasten shrub growth by weakening competing grasses.

## TRANSITION 7 TOWARDS A SENESCENT BUSHY STATE

Transition 7, towards a senescent thicket of *Acacia mellifera*, is a progressive succession that takes decades. It is a gradual and inevitable transition, since fierce fires that control the bush are highly unlikely due to the sparse grass sward and the density of the thicket. Self-thinning continues within the thicket due to intra-specific competition for, primarily, soil moisture (Skarpe, 1990; 1991; Teague & Smit, 1992), but canopy cover remains much the same (Joubert, 2007). As the tree canopy gets taller, allowing light to filter into the sub-canopy habitat, broad-leaved shrubs such as *Boscia albitrunca*, *Rhus marlothii*, *Tarchonanthus camphoratus* and *Ziziphus mucronata* that normally form a component of the grassy state, germinate and grow in the protection of the tall thicket (Joubert, 2007), which acts as a "nursery" to them. Birds that are attracted to the thicket transport the seeds of these fleshy-fruited species to this location.

## THE SENESCENT BUSHY STATE

This state is characterised by mature and senescing trees of around 4 m high, often with an understory of immature broad-leaved shrubs and trees that was established during Transition 7. It is not known at what age senescence sets in. The density of trees has typically been reduced to about 2 500 trees per hectare although canopy cover tends to remain high, even 100% (Joubert, 2007) but slowly declines as trees senesce due to drought stress, old age, fungal pathogens (Holz & Schreuder, 1989a) or combinations of these. Fungi of the *Cytospora* and *Phoma* genera, especially *Phoma glomerata*, attack the red heartwood and sapwood at the base of the trunk and upper taproot of mature *Acacia mellifera* trees, progressively weakening the tree until an external stressor, e.g. competition from other trees in the thicket or a drought, eventually kills the infected tree (Holz & Schreuder, 1989a, b; Holz & Bester, 2007). The fungi appear to be more active in wet spells than during dry periods. Tens of thousands of hectares of bush-encroached savanna have been cleared in this manner in Namibia.

Gradually, as the canopy cover shrinks and dead trees and branches fall and decompose, conditions favourable for herbaceous plants begin to develop. Initially, broad-leaved forbs, especially of the *Amaranthus* family, grow in the filtered, nutrient-rich sub-canopy habitat, eventually followed by shade-tolerant grass species commonly associated with savanna trees and the nutrient-rich soil below their canopy, e.g. *Cenchrus ciliaris*, *Eragrostis scopelophila* and *Eragrostis lehmanniana* (Rothauge, 2007a). Kraaij & Ward (2006) show that the elevated nitrogen levels found under *Acacia* trees in savannas (Smit & Swart, 1994; Rothauge, Smit & Abate, 2003) give grasses a competitive edge over woody seedlings and forbs. *Acacia mellifera* is a deciduous legume, enriching the soil with rhizomatous nitrogen, dropped leaves and imported nutrients derived from bird droppings and animals resting in the shade of the canopy. The sites of fallen, decaying tree skeletons, rotting gradually over a period of 5 to 20 years (Milton & Dean, 1996), are often dominated by *Cenchrus ciliaris* (Rothauge, 2007a), a nitrogen-loving sub-climax grass. Grass cover and the grass-based carrying capacity is variable, but better than in the vigorous bushy state and possibly even in the pioneer grassy state. Bush senescence is thus a rare opportunity to recover the original production potential of Namibia's central savanna ecosystems.

The build-up of grasses, herbs and forbs under the open thicket canopy, especially on the edges, provides fuel for fires that may be fierce enough to kill the senescing trees. Mature or senescing *Acacia mellifera* are less able to resprout than young shrubs (Meyer, Ward, Moustakas & Wiegand, 2005). Thus fires are much more effective at removing trees in this state than in the vigorous bushy state. This presents another window of opportunity to land managers to force a transition back to the grassy state (Transitions 9 and 10 to pioneer and climax grassy states, respectively) failing which, this state may cyclically remain in a bushy state (Transition 8 back to bushy state).



## TRANSITION 8 BACK TO THE VIGOROUS BUSHY STATE FROM THE SENESCENT BUSHY STATE

After two to three successive high rainfall years, new individuals from the ephemeral seed bank replace the senescent trees and recruitment occurs from the existing thicket of *Acacia mellifera* trees, similar to Transition 3. Establishment is close to, but not directly under the senescing parent trees, as seeds are not distributed far (Joubert, 2007). It is facilitated by reduced browsing pressure that could check coppice re-growth and seedlings, overgrazing that removes the accumulating grass fuel load and injudicious burning with “cold” fires that damage the grass sward, but not mature trees. Transition 8 may occur at any time between State 4 and 5, provided that the rainfall favours fruiting and seedling establishment and gaps between canopies are present, and is equivalent to the combined Transitions 3 and 6. Transition 8 changes thicket structure from a homogenous thicket of even-aged and even-sized shrubs to a more diversified, patchwork thicket consisting of different cohorts of shrubs of different age and size.

## TRANSITION 9 AND 10 BACK TO THE GRASSY STATE FROM THE SENESCENT BUSHY STATE

A senescent bush thicket may revert back to the pioneer grassy state by Transition 9 or to the climax grassy state by Transition 10. Transition 9 to the pioneer grassy state is likely if below-average rainfall conditions (drought) and excessive grazing pressure prevail, or if a fire clears the senescent bush, but is not followed by active management interventions that facilitate the establishment of perennial sub-climax and climax grass species (e.g. climax grass re-seeding). Ranchers that experience dense stands of *Acacia mellifera* dying, but do not change the grazing management that assisted bush thickening in the first place, risk this transition, and increase the probability of a return to a bushy state in the following high rainfall period. Bush clearing may also initiate this unfavourable transition if the underlying cause of poor grazing management is not addressed, if no wooden litter is left on the ground as mulch and if there is too little browsing pressure to check re-growth of harvested trees and bushes.

Transition 10 to the climax grassy state may require a hot fire, but certainly requires artificial re-seeding if perennial, climax grass seeds are not naturally available in adjacent areas. The palatable perennial grasses preferred by domestic livestock tend to become locally extinct under intense grazing pressure and subsequent bush encroachment. Grass re-seeding has to be followed by protection from grazing to allow the re-introduced grasses to establish themselves successfully. After re-seeding, a dense and very productive grass sward develops rapidly, benefiting from soil enrichment by leguminous *Acacia mellifera* plants, the competitive release from woody plants and protection from grazing by woody mulch (Smit & Rethman, 1992). This release effect may last for several years (Smit, 2003).

The precondition for Transition 10 is lenient grazing pressure that allows the desired perennial grass species targeted rest periods to recover from grazing, set seed and establish successfully (Smit, 2003; Rothauge, 2007c). Browsing pressure may be necessary to control re-sprouting trees and bushes. If this transition occurs during a two to three year above-average rainfall spell, there is a danger of reverting to the transitional state with bush seedlings. In this case, a fierce fire will be required to kill as many of the senescing trees, coppicing bushes and emerging woody seedlings as possible. In Namibia, Transitions 9 and 10 are currently being forced by wood harvesting for firewood or charcoal production without changing the underlying conditions that caused bush encroachment in the first place.

## TRANSITION 11 BACK TO THE PIONEER GRASSY STATE FROM THE VIGOROUS BUSHY STATE

Modern technology enables Namibian ranchers to de-bush encroached rangeland using mechanical or chemical means or a combination thereof. De Klerk (2004) describes these control measures in great detail. They result in an open savanna as the invasive species, *Acacia mellifera*, is in many instances eradicated completely. This creates a new imbalance as the woody component of the savanna is now under-represented, opening a window of opportunity for other woody opportunists to exploit and fill the void rapidly. Many ranches that were cleared of *Acacia mellifera* are now invaded by a variety of non-thorny, broad-leaved shrubs such as *Laggeta decurrens* in weak grass swards, *Grewia flava* on sandy aeolian soil, *Catophractes alexandrii* on limy sub-soil, *Tarchonanthus camphoratus* on shallow mountain soil and *Phaeoptilum spinosum* on soils that receive extra moisture (e.g. low-lying areas) or become saturated easily (brackish soils). Smit (2003) therefore recommends that not all *Acacia mellifera* bushes should be eradicated but that the largest trees are left standing to control re-colonisation by the same, or a different woody species. Besides competitive control, the large individuals contribute to a more diversified habitat, appreciated by game animals and with increased plant and animal biodiversity. Of course, the large survivors are also a potential source of seeds and renewed infestation. However, chemical and mechanical control mechanisms present the land user with an opportunity to restore degraded savanna and recover its potential production capacity, if those factors that caused bush encroachment in the first place, are also addressed. Otherwise, the encroachment cycle will merely repeat itself after a short delay.

Would Transition 11 occur naturally? The main possible drivers of such a transition would be fire and mega-herbivores. In nature, fire is highly unlikely to control an established, vigorous bush thicket. Even a fierce fire will not penetrate a thicket for lack of grass fuel inside the thicket. At best, a fierce fire may kill trees on the boundary, thus reducing the size of the thicket. Edges of thicket and less dense stands will be opened up, creating a mosaic effect and presenting a small window of opportunity for land users.

Mega-herbivores such as elephant and black rhino may have contributed substantially to the fragmentation of bush thickets in the past due to their destructive feeding and resting habits, thereby facilitating Transitions 9, 10 and 11 from the bushy back to the grassy state. These mega-herbivores used to occur in large numbers in the savannas of Namibia in general (Skinner & Smithers, 1990) and in the Highland savanna in particular, according to the writings of early big game-hunters (e.g. Anderson, 1856) and prominent historians (e.g. Vedder, 1934). Elephants are migratory, congregate in big herds and are estimated to have contributed up to 60 % of the animal biomass on pristine African savannas (Du Toit, 2005), thus exerting huge pressure on savanna vegetation. They are mixed feeders and feed very destructively on woody vegetation (Eltringham, 1979; Skinner & Smithers, 1990). A mature elephant requires about 200 kg of feed per day, at least half of which is derived from the woody component of a savanna. It destroys about as much woody vegetation again as it consumes and may affect about two tons of woody vegetation per week. Elephants also uproot *Acacia* saplings to feed on them. Although elephants do not prefer *Acacia mellifera* to the same extent as other invasive woody species such as mopane (*Colophospermum mopane*), they opened up and fragmented thickets, increased their edges and exposed them to the effect of wildfires, thus contributed to limiting the extent of bush encroachment. Similarly, the habit of black rhino to lie up in shady places and to have middens on the edge of thickets would have opened up such thickets and exposed them to the effect of wildfires, although probably on a smaller scale than elephants. However, re-introducing elephant into bush-encroached areas will result in the destruction of valuable, tall fodder trees in the short term, long before the positive effects on bush thickets permeates the landscape in the long term. They probably played a bigger role in preventing bush encroachment in the first place, rather than restoring an encroached landscape.

## IN SUMMARY

Bush encroachment by *Acacia mellifera* probably follows a wet spell of three successive, above-average rainfall years which allows the parent plant to accumulate enough energy reserves to flower and set ripe seeds. Once these are shed, they require regular rainfall to establish successfully. These favourable circumstances occur only sporadically in Namibia. At the same time, seedlings can only establish if fierce fires are prevented, if the grass sward is weakened by incorrect grazing and browsing pressure is low. Once bush gullivers have outgrown the fire-prone stage, they grow and mature inexorably towards a bush-encroached landscape that does not clear itself, unless the bush has become senescent. Prior to old age, active mechanical or chemical intervention to clear or thin the thickets of invasive *Acacia mellifera* is required. Bush control has to be followed by active aftercare that prevents a return to bush thickening at the first opportunity and facilitates the establishment of desirable perennial grasses. A bush-encroached savanna is a very stable state and is highly unlikely to return to a grassy state on its own within the productive lifetime of a Namibian

farmer. Fire and increased browsing pressure are valuable tools in caring for a landscape in which *Acacia mellifera* was controlled. Desirable perennial grasses become locally extinct in bush-encroached landscapes and have to be re-introduced artificially, whereafter they need enough time to establish themselves before grazing commences. Once the grass sward has recovered, it needs to be tended and renewed transition towards woody seedling establishment needs to be checked, if a recurrence of the whole bush encroachment cycle and problem is to be avoided.

Custodians of Namibia's savanna rangelands cannot allow these to swing from one ecological extreme (allowing bush encroachment to happen – to another – wiping out every individual of the invasive species) without being at least aware of the drastic changes this will force in their means of production, the land and its fragile cover of savanna vegetation. The sporadic nature of bush encroachment and the longevity of the invasive species make it difficult to predict its life cycle and reaction to transforming events. Even if *Acacia mellifera* can be managed successfully, the next major invasive species, *Dichrostachys cinerea* (sickle bush, “sekelbos”), promises to be an even more difficult species to manage. *Dichrostachys cinerea* is a major problem in low-frost areas of north-central Namibia. It has hard seeds with an impermeable testa (Bell & Van Staden, 1993) and thus survives ingestion by ungulates. Its persistent seed bank and ability to form root suckers enable it to invade landscapes continuously, rather than sporadically, presenting an even more formidable challenge to Namibian land users. In addition, the effects of global climate change are expected to enhance woody growth; making a thorny situation even more difficult.

## ACKNOWLEDGEMENTS

I gratefully acknowledge my many colleagues in Namibia, South Africa and elsewhere who have stimulated and challenged my thinking on savanna dynamics and encouraged me to publish this series of papers as a waypoint in understanding our savanna environment. I am especially indebted to Dave Joubert of the Polytechnic of Namibia for his invaluable contributions to this article. Dave, also the senior author of the international baseline article on this topic (Joubert *et al.*, 2008) is currently busy with PhD research into the bush-encroachment model. I also thank the numerous students of Neudamm College and the Faculty of Agriculture & Natural Resources who participated in field experiments and monitoring.

## REFERENCES

- ABDULLAH, M.A.R. & ABULFATIH, H.A., 1995. Predation of *Acacia* seeds by bruchid beetles and its relation to altitudinal gradient in south-western Saudi Arabia. *Journal of Arid Environments* 29: 99–105.
- ANDERSON, C.J., 1856. *Lake Ngami; or, Explorations and Discoveries during four years wanderings in the wilds of South Western Africa*. Hurst & Blacket Publishers, London.
- BARNARD, P. (ed.), 1998. *Biological Diversity in Namibia: A Country Study*. Namibian National Biodiversity Task Force, Directorate of Environmental Affairs, Windhoek, Namibia.

- BARNES, M.E., 2001. Seed predation, germination and seedling establishment of *Acacia erioloba* in northern Botswana. *Journal of Arid Environments* 49: 541–554.
- BELL, W.E. & VAN STADEN, J., 1993. Seed structure and germination of *Dichrostachys cinerea*. *South African Journal of Botany* 59: 9–13.
- BELSKY, A.J., 1984. Role of small browsing mammals in preventing woodland regeneration in the Serengeti National Park, Tanzania. *African Journal of Ecology* 22: 271–279.
- BESTER, F.V., 1998. Major problem: bush species and densities in Namibia. *Agricola* 10: 1–3.
- BESTER, F.V. & REED, E., 1997. Charcoal production in the Karstveld: facts to ponder upon. *Spotlight on Agriculture* pamphlet series no. 2, Ministry Agriculture, Water & Rural Development, Windhoek, Namibia.
- BOCKMÜHL, F., 2009. The Platveld Aquifer study. Presentation at 13<sup>th</sup> Namibian Rangelands Forum, 27 to 29 October 2009, Neudamm Agricultural College, Windhoek, Namibia.
- BOND, W.J., 1997. Fire. In: R.M. COWLING, D.M. RICHARDSON & S.M. PIERCE (eds.) *Vegetation of Southern Africa* ch. 18, Cambridge University Press, Cambridge, United Kingdom.
- BOND, W.J. & VAN WILGEN, B.W., 1996. *Fire and Plants*. Chapman & Hall, London.
- BROWN, J.R. & ARCHER, S., 1999. Shrub invasion of grassland: recruitment is continuous and not regulated by herbaceous biomass or density. *Ecology* 80: 2 385–2 396.
- CHRISTIAN, C., DE KLERK, J.N., BOCKMÜHL, F., VAN DER MERWE, B. & MOSTERT, A., 2010. *Desktop Study on the Effect of Bush Encroachment on Groundwater Resources in Namibia*. Report for the Namibia Agricultural Union, Windhoek, Namibia.
- DAVIS, M.A., WRAGE, K.J. & REICH, P.B., 1998. Competition between tree seedlings and herbaceous vegetation: support for a theory of resource supply and demand. *Journal of Ecology* 86: 652–661.
- DE KLERK, J.N., 2004. *Bush Encroachment in Namibia*. Report on Phase 1 of the Bush Encroachment Research, Monitoring and Management Project, Ministry of Environment and Tourism, Windhoek, Namibia.
- DONALDSON, C.H., 1967. *Bush encroachment with special reference to the Blackthorn problem of the Molopo area*. Department of Agricultural Technical Services, Armoedsvlakte Research Station, Vryburg, South Africa.
- DU TOIT, J.P., 2005. Working within constraints: managing African savannas for animal production and biodiversity. *Pastoral Systems in Marginal Environments, Proc. Satellite Workshop 20<sup>th</sup> Int. Grassl. Congress* pp. 81–89, 3 to 6 July 2005, Glasgow, Scotland.
- ELTRINGHAM, S.K., 1979. *The Ecology and Conservation of Large African Mammals*. Macmillan Press, London, UK.
- FAGG, C.W. & STEWART, J.L., 1994. The value of *Acacia* and *Prosopis* in arid and semi-arid environments. *Journal of Arid Environments* 27: 3–25.
- FROST, P.G.H. & ROBERTSON, F., 1987. The ecological effects of fire in savannas. In: B.H. WALKER (ed.) *Determinants of Tropical Savannas* pp. 93–140. ICSU Press, Miami, USA.
- GIESS, W., 1971. A preliminary vegetation map of South West Africa. *Dinteria* 4: 31–45.
- HARRINGTON, G.N., 1991. Effects of soil moisture on shrub seedling survival in a semi-arid grassland. *Ecology* 72: 1 138–1 149.
- HARRINGTON, G.N. & DRIVER, M.A., 1995. The effects of fire and ants on the seed-bank of a shrub in a semi-arid grassland. *Australian Journal of Ecology* 20: 538–547.
- HIGGINS, S.I., BOND, W.J. & TROLLOPE, W.S.W., 2000. Fire, resprouting and variability: a recipe for grass-tree coexistence in savanna. *Journal of Ecology* 88: 213–229.
- HIPONDOKA, M.H.T., ARANIBAR, J.N., CHIRARA, C., LIHAVHA, M. & MACKO, RSA, 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, K.C. & HARRINGTON, G.N., 1985. The case for prescribed burning to control shrubs in eastern semi-arid woodlands. *Australian Rangeland Journal* 7: 64–74.
- HOFFMAN, M.T., COWLING, R.M., DOUIE, C. & PIERCE, S.M., 1989. Seed predation and germination of *Acacia erioloba* in the Kuiseb River Valley, Namib Desert. *South African Journal of Botany* 55: 103–106.
- HOLZ, G., BESTER, F.V., 2007. A dieback/decline disease of blackthorn (*Acacia mellifera* subsp. *detinens*): Monitoring the growth of plants in stands from 1986 to 2005. *Agricola* Special Edition, 8–58.
- HOLZ, G. & SCHREUDER, W., 1989a. Dieback of blackthorn (*Acacia mellifera* subsp. *detinens*) in South West Africa. *Agricola* 7: 32–36.
- HOLZ, G. & SCHREUDER, W., 1989b. Soil moisture stress and infection of blackthorn (*Acacia mellifera* subsp. *detinens*) by fungi associated with blackthorn dieback. *Agricola* 7: 48–54.
- JOUBERT, D.F., 2007. The population dynamics of *Acacia mellifera* in relation to climate and microsite factors. Unpublished report, Polytechnic of Namibia, Windhoek, Namibia.
- JOUBERT, D.F., ROTHAUGE, A. & SMIT, G.N., 2008. A conceptual model of vegetation dynamics in the semiarid Highland savanna of Namibia, with particular reference to bush thickening by *Acacia mellifera*. *Journal of Arid Environments* 72(12): 2 201–2 210.
- KAMUPINGENE, G.T., MUKUAHIMA, G., ROTHAUGE, A. & ABATE, A.L., 2005. Comparative diet selection of the Damara, Dorper and Karakul sheep breeds at Neudamm Farm. *Proc. 9<sup>th</sup> Nam. Rangeland Forum* p. L9, 16 to 18 August 2005, Sandveld Research Station, Gobabis district, Namibia.
- KERLEY, G.I.H., 1991. Seed removal by rodents, birds and ants in the semi-arid Karoo, South Africa. *Journal of Arid Environments* 20: 63–69.
- KRAAIJ, T. & WARD, D., 2006. Effects of rain, nitrogen, fire and grazing on tree recruitment and early survival in bush-encroached savanna. *Plant Ecology* 186: 235–246.
- LINZEY, A.V. & WASHOK, K.A., 2000. Seed removal by ants, birds and rodents in a woodland savanna habitat in Zimbabwe. *African Zoology* 35: 295–299.
- MEIK, J.M., JEO, R.M., MENDELSON, J.R. & JENKS, K.E., 2002. Effects of bush encroachment on an assemblage of diurnal lizard species in central Namibia. *Biological Conservation* 106: 29–36.
- MEYER, K.M., 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.
- MILLER, M.F., 1994a. The costs and benefits of *Acacia* seed consumption by ungulates. *Oikos* 71: 181–187.
- MILLER, M.F., 1994b. Seed predation by nocturnal rodents in an African savanna ecosystem. *South African Journal of Ecology* 29: 262–266.
- MILTON, S.J. & DEAN, W.R.J., 1996. Rates of wood and dung disintegration in arid South African rangelands. *African Journal of Range and Forage Science* 13: 89–93.
- O'CONNOR, T.G., 1996. Individual, population and community response of woody plants to browsing in African savannas. *Bulletin of the Grassland Society of South Africa* 7 (Suppl. 1): 14–18.
- OKELLO, B.D. & YOUNG, T.P., 2000. Effects of fire, bruchid beetles and soil type on germination and seedling establishment of *Acacia drepanolobium*. *African Journal of Range and Forage Science* 17: 46–51.
- OSTFELD, R.S., MANSON, R.H. & CANHAM, C.D., 1997. Effects of rodents on survival of tree seeds and seedlings invading old fields. *Ecology* 78: 1 531–1 542.
- QI, J., MORAN, M.S., GOODRICH, D.C., MARSETT, R., SCOTT, R., CHEHBOUNI, A., SCHAEFFER, S., SCHIELDGE, J., WILLIAMS, D., KEEFER, T., COOPER, D., HIPPS, L., EICHINGER, W. & NI, W., 1998. Estimation of evapotranspiration over the San Pedro riparian area with remote sensing and *in situ* measurements. Special Symposium on Hydrology paper 1.13, 11 to 16 January 1998, American Meteorological Society, Phoenix, Arizona, USA.
- ROQUES, K.G., O'CONNOR, T.G. & WATKINSON, A.R., 2001. Dynamics of shrub encroachment in an African Savanna: relative influences of fire, herbivory, rainfall and density dependence. *Journal of Applied Ecology* 38: 268–280.
- ROTHAUGE, A., 2006a. *The effect of frame size and stocking rate on diet selection of cattle and rangeland condition in the camelthorn savanna of east-central Namibia*. Ph.D. thesis, University of Namibia, Windhoek, Namibia.
- ROTHAUGE, A., 2006b. After-effects of a hot fire in 2001/2002. Unpublished report, Neudamm Agricultural College, Windhoek, Namibia.
- ROTHAUGE, A., 2007a. A decade of monitoring grazed rangeland transects at Neudamm. Unpublished report, Neudamm Agricultural College, Windhoek, Namibia.
- ROTHAUGE, A., 2007b. Emergence, establishment and survival of *Acacia mellifera* under normal farming conditions. Unpublished report, Neudamm Agricultural College, Windhoek, Namibia.
- ROTHAUGE, A., 2007c. Some principles of sustainable rangeland management in Namibia. *Agricola* 17: 7–15.
- ROTHAUGE, A., 2008. A century of rainfall statistics at Neudamm. Unpublished report, Neudamm Agricultural College, Windhoek, Namibia.
- ROTHAUGE, A., ABATE, A.L. KAVENDJI G. & NGHIKEMBUA, M.L., 2003. Forage preference of Boer goats in the Highland savanna of Namibia during the rainy season. I: Diet selection. *Agricola* 13: 35–42.
- ROTHAUGE, A. & ENGELBRECHT, J., 2000. Forage preference of Boer goats in the Highland savanna of Namibia during the dry season. *Agricola* 11: 57–60.
- ROTHAUGE, A., SMIT, G.N. & ABATE, A.L., 2003. The effect of the sub-habitat below savanna trees on soil, grass and its utilization by cattle. *Proc. 7<sup>th</sup> International Rangeland Congress* pp. 106–109, 26 July to 1 August 2003, Durban, South Africa.
- SKARPE, C., 1990. Shrub layer dynamics under different herbivore densities in an arid savanna, Botswana. *Journal of Applied Ecology* 27: 873–885.
- SKARPE, C., 1991. Impact of grazing in savanna ecosystems. *Ambio* 20: 351–356.
- SKINNER, J.D. & SMITHERS, R.H.N., 1990. *The Mammals of the Southern African Subregion*. Univ. Pretoria, Pretoria, South Africa.
- SKOWNO, A.L., MIDGELY, J.J., BOND, W.J. & BALFOUR, D., 1999. Secondary succession in *Acacia nilotica* (L.) savanna in the Hluhluwe Game Reserve, South Africa. *Plant Ecology* 145: 1–9.
- SMIT, G.N., 1989. Quantitative description of woody plant communities: Part I. An approach. *African Journal of Range and Forage Science* 6: 186–191.
- SMIT, G.N., 2003. The importance of ecosystem dynamics in managing the bush encroachment problem in southern Africa. Proceedings of the 7<sup>th</sup> International Rangelands Congress, pp. 14–22, 26 July to 1 August 2003, Durban, South Africa.
- SMIT, G.N. & RETHMAN, N.F.G., 1992. Inter-related floristic changes associated with different long-term grazing treatments in sourish mixed bushveld. *Journal of the Grassland Society of South Africa* 9: 76–82.
- SMIT, G.N. & SWART, J.S., 1994. Influence of leguminous and non-leguminous woody plants on the herbaceous layer and soil under varying competition regimes in Mixed Bushveld. *African Journal of Range and Forage Science* 11: 27–33.
- SWEET, R.J., 1982. Bush control with fire in *Acacia nigrescens/ Combretum apiculatum* savanna in Botswana. *Proceedings of the Grassland Society of Southern Africa* 17: 25–28.
- TEAGUE, W.R. & SMIT, G.N., 1992. Relations between woody and herbaceous components and the effect of bush-clearing in southern African savannas. *Journal of the Grassland Society of South Africa* 9: 60–71.
- TROLLOPE, W.S.W., 1974. Role of fire in preventing bush encroachment in the Eastern Cape. Proceedings of the Grassland Society of Southern Africa 9: 67–72.
- TROLLOPE, W.S.W., 1980. Controlling bush encroachment with fire in the savanna areas of South Africa. *Proceedings of the Grassland Society of Southern Africa* 15: 173–177.
- TROLLOPE, W.S.W., 1982. Ecological effects of fire in South African savannas. In: B.J. HUNTLEY & B.H. WALKER, (eds.) *Ecology of Tropical Savannas* pp. 292–306. Ecological Studies Vol. 42, Springer Verlag, New York, USA.
- TROLLOPE, W.S.W., 1984. Fire in Savanna. In: P. DE V. BOOYSEN & N.M. TAINTON (eds.) *Ecological Effects of Fire in South African Ecosystems Savannas* pp. 199–218. Springer Verlag, New York, USA.
- TROLLOPE, W.S.W., 1999. Veld burning. In: N.M. TAINTON (ed.) *Veld Management in South Africa* ch. 9, University of Natal Press, Pietermaritzburg, South Africa.
- TROLLOPE, W.S.W., HOBSON, F.O., DANCKWERTS, J.E. & VAN NIEKERK, J.P., 1989. Encroachment and control of undesirable plants. In: J.E. DANCKWERTS & W.R. TEAGUE (eds.) *Veld Management in the Eastern Cape* pp. 73–89. Department of Agriculture and Water Supply, Pretoria, South Africa.
- VAN VEGTEN, J.A., 1983. Thornbush invasion in a savanna ecosystem in eastern Botswana. *Vegetatio* 56: 3–7.
- VEDDER, H., 1934. *Das Alte Südwesafrika: Südwesafrikas Geschichte bis zum Tode Mahareros 1890 (The Old South West Africa: South West Africa's History Until the Death of Maharero 1890)*. Martin Warneck Verlag, Berlin, Germany.
- VIR, S., 1996. Bruchid infestation of leguminous trees in the Thar desert. *Tropical Science* 36: 11–13.
- VON OERTZEN, D., 2007. Turning Namibian invader bush into electricity: the CBEND Project. *Proc. 12<sup>th</sup> Agricultural Scientific Society of Namibia (Agrisson) Congress* (CD), Neudamm Agricultural College, Windhoek, Namibia.
- WALKER, B.H., 1981. Is succession a viable concept in African savanna ecosystems? In: H.H. SHUGART, D.C. WEST & D.B. BOTKIN (eds) *Forest Succession: Concepts and Applications* pp 431–447. Springer Verlag, New York, USA.
- WALTER, H., 1971. *Ecology of Tropical and Subtropical Vegetation*. Oliver and Boyd, Edinburgh, UK.
- WALTERS, M., MILTON, S.J., SOMERS, M.J. & MIDGLEY, J.J., 2005. Post-dispersal fate of *Acacia* seeds in an African savannas. *South African Journal of Wildlife Research* 35: 191–199.
- WELTZIN, J.F., ARCHER, S. & HEITSCHMIDT, R.K., 1997. Small mammal regulation of vegetation structure in a temperate savanna. *Ecology* 78: 751–763.
- WOLFSON, M.M. & TAINTON, N.M., 1999. The morphology and physiology of the major forage plants. Grasses. In: N.M. TAINTON (ed.) *Veld Management in South Africa* ch. 3. University of Natal Press, Pietermaritzburg, South Africa.
- ZIMMERMANN, I & MWAZI, F.N., 2002. The effect of a prescribed burn, followed up with browsing pressure, on rangeland condition in the Mountain savanna and Karstveld of Namibia. *Dinteria* 27: 49–57.