THE DYNAMICS OF BUSH THICKENING BY *ACACIA MELLIFERA* IN THE HIGHLAND SAVANNA OF NAMIBIA

By

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This thesis is dedicated to the memory of my late parents, Bob and Joan Joubert, and my late brother, André, as well as the late Nelson Rohlilahla Mandela. Their memory has always served as an inspiration to be outspoken in my beliefs, scientific and otherwise, popular or unpopular.

TABLE OF CONTENTS

ABSTRACT

Key words: bush thickening; arid savanna; Namibia; state-and-transition; rainfall; fire; competition; browsing; historical evidence.

The dynamics of bush thickening by *Acacia mellifera* in the arid Namibian Highland Savanna was investigated. First, a conceptual state-and-transition model was developed, based on preliminary findings, personal observations and resultant insights. In this model it was proposed that two main states exist, an open, grassy state and a bush-thickened state. Each of these is subdivided into other states. An unstable transitional state with *A. mellifera* seedlings within the grass sward is a crucial juncture between the grassy and bush thickened state. In the model, the transition to this unstable state occurs after at least two, but more likely three, consecutive years of well above-average annual rainfall through seed production followed by germination and establishment. Only an interruption by fire, which has a high probability of coinciding with this establishment if the grass sward is lightly utilised, prevents a further transition to a bush thickened state. Fire returns the vegetation to a grassy state by causing an almost 100 % mortality of seedlings. If fire is absent through a lack of fuel (overgrazing) or fire is deliberately excluded, the transition to a bush-thickened state is a fait accompli, but may take decades to reach. Transitions from the bush-thickened state to a grassy state require drought and the associated fungal dieback, which accelerates the senescence of mature shrubs. The model proposes that a transition towards the unstable transitional state occurs rarely, due to the rarity of suitable climatic conditions (protracted period of consecutive years of above-average annual rainfall). The mechanisms of two key transitions were tested. Firstly, the transition to an unstable state through the en masse production of seeds followed by the successful establishment of seedlings after a protracted period of well above average rainfall was tested during a nine-year period (late 1998 to early 2007). Secondly, the transition back to an open grassy state during a potential establishment event, through the mortality of seedlings after a fire, was tested experimentally (2008 and 2009). Both of these studies confirmed the predictions of the model and the mechanisms proposed for these transitions. Preliminary evidence suggests that browsing by small herbivores, in particular lagomorphs, thins resultant thickets out through herbivory. Preliminary evidence also suggests that competition between grasses and seedlings does not directly stop the transition to a bush thickened state but may prolong the window of opportunity for a fire to be effective, through reducing the growth rate of seedlings and saplings. The findings are of relevance to management, and thus an expert system for rangeland management, with emphasis on bush thickening, was developed, based largely on the findings of this research.

Preliminary historical evidence casts doubt upon the prevailing perception that bush thickening is mostly a phenomenon of the last half century, and, consequently, that bush thickening is the primary cause of the loss of rangeland productivity in the arid rangelands of Namibia during this period. The study suggests that fire in arid savannas is as important as it is in mesic savannas. A general principle could be stated as follows: The importance of the timing of fire in savannas increases with increasing aridity, whilst the importance of the frequency of fire in savannas decreases with increasing aridity.

DECLARATION

I declare that the dissertation hereby submitted by me for the partial fulfilment of the requirement for the degree of Doctor of Philosophy (Grassland Science) at the University of the Free State is my own independent work, and has not been submitted by me to any other university/ faculty. I further cede copyright of the dissertation in favour of the University of the Free State.

David Francois Joubert

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LIST OF TABLES

LIST OF FIGURES

CHAPTER 1: INTRODUCTION

1.1 Savanna ecosystems

Savannas have been variously defined, but most generally can be described as “communities or landscapes with a continuous grass layer and scattered trees” (Scholes and Archer, 1997). According to Scholes and Archer (1997), tropical savannas cover about 16 million km^2, the vast majority of this falling within Africa, Australia and South America (about half of each of these continents is covered by tropical savannas). Savannas and grasslands together occupy about a quarter of the world’s vegetated surface area (30 million km^2; Ramankutty and Foley, 1999). Despite tropical savannas dominating particularly southern hemisphere land masses, there is still much recent literature debating the origins, constraints and patterns of savannas and their associated strata (Mills, et al., 2006; Bond, 2008) which suggests that little consensus exists. A coherent understanding of patterns and processes is not just of academic interest, since a large and growing number of people are dependent upon these savannas for livelihoods, largely through pastoral practices (Scholes and Archer, 1997).

Savannas are constrained by rainfall (amount and temporal distribution), temperature and soil properties, thus boundaries can be relatively stable in the medium and long term, but are also constrained by disturbances such as fire and herbivory (Bond, 2008). The precipitation range for savannas is enormous, ranging from approximately 200 mm to 3 000 mm per annum (Bond, 2008). Some general principles related to the rainfall gradient have been proposed. Generally the woody cover has been noted to increase up to an asymptote and then plateau (but with huge variability) with increasing rainfall (Sankaran et al., 2005). At the lower end, boundaries are mostly constrained by precipitation (e.g. Sankaran et al., 2005) and savanna gives way to desert.

At higher rainfalls, disturbances such as fire and herbivory are considered to play an increasingly important and dynamic role in distinguishing boundaries between savannas, forests, and grasslands (Sankaran et al., 2005; Meyer et al., 2007; Bond, 2008). At the upper end of precipitation, the occurrence of fire sometimes prevents savanna from becoming forest (or converts forest edge to savanna), despite rainfall regimes that are favourable for forest development or maintenance (Backéus, 1992). Conversely, savannas have transformed into forests in the absence of fire in similar rainfall regimes (Bowman et al., 2001), although evidence now suggests that global increases in atmospheric carbon dioxide may play a greater role in this than previously thought (Bond and Midgley, 2000). The reasons for the coexistence of pure grasslands and savannas within similar precipitation regimes have not been adequately resolved. Tinley (1982) suggests that the most important factor determining the distribution of savanna and grassland vegetation types, in areas with similar rainfall, is soil water potential. In soils with alluvial B horizons, with water logging in the wet season and droughty conditions in the dry season, trees tend to be excluded from grasslands (Mills et al., 2006). Frost is another mechanism that tends to exclude trees from grasslands (Acocks, 1953) but this effect is species-, density- and size- dependent (Smit, 1990). The question of grass-tree coexistence is still a contentious topic, despite decades of debate. Mills et al. (2006) even refer to this as the "savanna-grassland problem".

1.2 Bush thickening as a global phenomenon

Within savannas, the density and cover of the woody component varies tremendously. The global trend for the last century or so is for both woody cover and density to increase (Bond and Midgley, 2000). This process, referred to as bush thickening, is highly significant, both economically and ecologically. Bush thickening can be defined as the process whereby the woody layer of a savanna increases in density and cover to such an extent that grass production is negatively affected through the resultant increase in competition. This phenomenon occurs throughout the savanna biome on all continents where savannas occur, as well as in grasslands (Tinley, 1982). The encroachment by woody species into the grasslands is better termed bush encroachment. The mechanisms of encroachment and thickening are varied and not well understood (Ward, 2005). It is likely that there are no clear cut simple generalities regarding causal mechanisms, but that more complex generalities will have to take into account a diversity of implicated species, climates and soil types.

1.3 The Highland Savanna vegetation type in Namibia as an arid savanna

There are five aridity categories (hyper-arid, arid, semi-arid, dry sub-humid and humid) according to the United Nations Convention to Combat Desertification (UNCCD) which can be classified according to their mean annual precipitation and potential evapotranspiration (MAP:PET ratio) (UNESCO, 1977). The Highland Savanna vegetation type (Giess, 1998) has a mean annual rainfall of approximately 360 mm (CV = 40 %) in Windhoek. Due to its high evaporation rate the annual water deficit is approximately 1 800 mm (Mendelsohn et al., 2002). The Highland Savanna therefore has an aridity ratio of approximately 0.17, placing it close to the extremely arid end of the savanna range, and within the range of an arid ecosystem (Aridity ratio of 0.05 – 0.2) (UNESCO, 1977).

1.4 Perceptions of bush thickening in Namibian arid savannas

Bush thickening by *Acacia mellifera* (Vahl) Benth. subsp. *detinens* (Burch.) Brenan and *Dichrostachys cinerea* (L.) Wight & Arn. has long been considered an ecological and economic problem in the rangelands of Namibia (e.g. Walter, 1971) as well as in other southern African countries (e.g. Donaldson, 1967; Skarpe, 1991; Roques et al., 2001; Ward, 2005). The area affected by bush thickening in Namibia is estimated to be about 260 000 km^2 (De Klerk, 2004). This bush-thickened area affects parts of at least seven vegetation types in Namibia, namely Mopane Savanna, Mountain Savanna and Thornveld, Thornbush Savanna, Highland Savanna, Camelthorn Savanna, Forest Savanna and Woodland (Giess, 1998). The bush-thickened areas fall within the arid and semi-arid savannas with rainfall varying from about 300 mm in the west to about 500 mm in the north-eastern parts.

The prevailing perception in Namibia is that bush thickening in arid savannas is largely a fairly recent phenomenon. Bester (1996) notes that, although it had already begun earlier, it was really since the late 1950s and early 1960s that the process dramatically accelerated. This was considered to be the consequence of a prolonged and severe drought in conjunction with an outbreak of foot-and-mouth disease which prevented farmers from destocking their already depleted rangelands. The resultant overgrazing thus released the woody layer from much of the grass competition, allowing the shrubs to grow much quicker and thicken up. Yet, this perception has never really been tested, and most of the evidence for bush thickening during the 20th century in Namibia is anecdotal. There is little or no scientific evidence available to prove or disprove the perception that the major problem has indeed occurred in the last 60 or so years. Interestingly, anecdotal evidence from early explorers suggests that some landscape scale bush thickets occurred as early as the 1850s (Anderson, 1856). Surprisingly little research, besides the occasional documentation of bush densities and cover (e.g. Bester, 1999), has been conducted in Namibia, and few studies aside from for e.g. Wiegand et al. (2006) and Kambatuku et al. (2011) have attempted, prior to this thesis, to understand the dynamics and processes in Namibian arid savannas. Instead, our received wisdom is drawn from other studies, mostly from South Africa and mostly from more mesic savannas. Despite this paucity of local research on bush thickening, much of the blame for the declines in rangeland and beef production has been placed with bush thickening, and enormous amounts of money and effort have been put into treating the existing symptoms (De Klerk, 2004).

1.5 Objectives

This thesis is a contribution to the improved understanding of bush thickening, particularly at the arid end of the rainfall gradient. In this thesis an attempt is made to investigate the development of bush thickening in the Highland Savanna since the 1950s, and explain the major mechanisms involved in the process.

The specific objectives of the study are:

1. To develop a conceptual State and Transition model that provides the conceptual framework for the investigations that follows.
2. To investigate the impacts of rainfall on the production of seed and the establishment of seedlings of *A. mellifera*. Specific questions that are being asked include:

How does the production of viable seed vary with rainfall and tree size?

When does seed germination occur?

How long-lived is the seed bank of *A. mellifera*?

How do competitive interactions with established trees influence recruitment of *A. mellifera* seedlings?

3. To investigate the impacts of fire as a potential inhibitor of bush thickening. The following hypothesis is being tested: “Fire in an arid Namibian savanna, is essential in keeping

savannas in an open grassy state, but only during a relatively small window period at the time of potential *A. mellifera* seedling establishment." The effects of fire intensity and temperature on the mortality and regrowth of saplings and mature shrubs are also investigated.

4. To develop a Decision Support System for the management of bush thickening. Its development, and challenges to its implementation are outlined, and suggestions on how to deal with these challenges are made.
5. To assess whether the suggested conceptual model is supported by the experimental and monitoring evidence of the study and to identify the need for additions to the model to encompass any discrepancies.

CHAPTER 2: CONCEPTUAL MODEL OF VEGETATION DYNAMICS IN THE ARID HIGHLAND SAVANNA OF NAMIBIA, WITH PARTICULAR REFERENCE TO BUSH THICKENING BY A*CACIA MELLIFERA*

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Minor editing changes have been made.

Abstract

Namibian rangelands are encroached with *Acacia mellifera*, partially resulting from a poor understanding of vegetation dynamics. A conceptual state-and-transition model of vegetation dynamics in the arid Highland savanna in central Namibia, emphasising bush thickening by *A. mellifera*, is described. Two main states, a grassy and a bushy state, are identified. These are further subdivided, and 11 transitions are identified. The key transition initiating a change from grassy to bushy state can be termed a ‘‘leap’’(an occasional, infrequent mass recruitment event) following a long ‘‘sleep’’ (no or little change in *A. mellifera* density). It is rare because it requires three consecutive years of above-average rainfall for seedling establishment. Fire, coinciding with seedling establishment, can interrupt it, while a low biomass grass sward facilitates it. The phenology and physiology of the encroaching species, seed predation and sapling herbivory influence this transition. The model proposes opportunistic management interventions, particularly the use of fire, to minimise the risk of further landscape-scale transitions to a bushy state. It highlights areas where understanding of vegetation dynamics is lacking and

recommends crucial research foci. Conceptual models of bush thickening processes need to account for differences in climate and phenological details of encroaching species.

2.1 Introduction

An appropriate conceptual model of vegetation dynamics is an important prerequisite for effective and predictive management of rangelands. Rangeland managers use conceptual models, but these may be flawed, or consist of uncoordinated viewpoints regarding separate phenomena of rangeland change. Namibian arid and semiarid rangeland managers largely rely on the classical rangeland succession model based on Clements (1928) to explain changes in the composition of the grass sward, yet draw from the two-layer competition model of Walter (1971) to explain the dynamics between the woody and herbaceous components of savanna vegetation.

Flawed or incoherent conceptual models may result in poor rangeland management that results in declining productivity and biodiversity (Milton et al., 1994). Bush thickening or the densification and increase in the cover of indigenous woody species, is a major economic and ecological problem in many arid and semiarid parts of the world (Hodgkinson and Harrington, 1985; Archer et al., 1988) including southern Africa (Donaldson, 1967; Skarpe, 1990). Nearly 50 % of the commercial ranching areas of Namibia are affected by bush thickening, mainly by *Acacia mellifera* subsp. *detinens* (hereafter referred to as *A. mellifera*). As a result, an estimated N$700 million was lost to meat production annually by 2004 (De Klerk, 2004)) and this figure is considered to have at least doubled since then (De Klerk pers. comm.) although there is little consensus as to how much of this amount can be ascribed to bush thickening. Reactive interventions are the norm. Despite interventions, bush thickening still remains a problem.

Non-equilibrium theories have permeated mainstream rangeland management, and state-and-transition models have been used to describe vegetation changes and management strategies in arid and semiarid rangelands (Westoby et al., 1989; Milton and Hoffman, 1994) including savanna (Distel and Bóo, 1995; Dougill et al., 1999). However, no complete cohesive conceptual model of arid and semiarid savanna dynamics has usurped the traditional rangeland succession model in southern Africa (Ward, 2005), especially in Namibia. Existing models neglect phenological cycles, the timing of different environmental and anthropomorphic events and animal/plant interactions (e.g. van Langevelde et al., 2003; Sankaran et al. 2005; Wiegand et al., 2006; Meyer et al., 2007). Bush-thickening species differ widely with respect to phenological and physiological aspects of their life history, resulting in different pathways of bush thickening. Mechanistic explanations proposed by Brown and Archer (1999) for *Prosopis glandulosa* in Texas, USA, by Skowno et al. (1999) for *Euclea* species in South Africa and by Roques et al. (2001) for *Dichrostachys cinerea* in Swaziland are thus not necessarily generally applicable.

This chapter introduces the conceptual model which chapters 3 and 4 attempt to validate, and contributes to the debate on bush thickening by proposing a state-and-transition model for vegetation dynamics of the arid Highland savanna of central Namibia that focuses on bush thickening by *A. mellifera*. Information to formulate the model is based on ongoing long-term research at several sites, particularly Krumhuk Farm (20km south of Windhoek) (see Chapter 3 for a description of the study site) and Neudamm Agricultural College (30km east of Windhoek) (see Chapter 4 for a description of the study site).

2.2 Characteristics of the Highland savanna vegetation type

The Highland savanna lies between 22^{o} and 23.30^{o}S and 15.30^{o} and 18.30^{o}E and occupies approximately 45 000 km^2 or 5.5 % of Namibia's land area (Figure 2.1) (Coetzee, 1998). Precipitation is highly variable and seasonal, 80 % of the annual rainfall occurring from January to March. Windhoek's long-term mean annual rainfall (1892–2003) is 361 mm (CV = 40 %). The annual water deficit is approximately 1 800 mm (Mendelsohn et al., 2002). As explained in Chapters 3 and 4, the Highland Savanna can be regarded as an arid ecosystem (UNEP, 1992). In summer, average maximum temperatures are lower (about 29 ^{o}C) than in lower-lying savannas while winters are fairly cold (average minimum temperature: 3 ^{o}C). Frost occurs between 10 and 20 nights/year (Mendelsohn et al., 2002). The terrain is broken and undulating, at altitudes of 1350–2400 m above sea level. Soils (lithic leptosols) are generally shallow, often with a cover of quartzitic pebbles that improves soil moisture retention (Joubert, 1997). Animal and plant biodiversity and endemism are high compared to other regions of Namibia (Barnard, 1998; Mendelsohn et al., 2002), but only 0.2 % is managed as government-protected conservation areas (Barnard, 1998).

Giess (1998) described the Highland savanna as characterised by woody species including *Acacia hereroensis*, *A. hebeclada*, *A. reficiens*, *Euclea undulata*, *Dombeya rotundifolia*, *Tarchonanthus camphoratus*, *Searsia marlothii*, *Albizia anthelmintica* and *Ozoroa crassinervia*. *A. mellifera* is the dominant woody species in large parts of this vegetation type today. Climax grasses include *Brachiaria nigropedata*, *Anthephora pubescens*, *Heteropogon contortus*, *Cymbopogon* spp. and *Digitaria eriantha*, but *Eragrostis nindensis* (considered a subclimax grass) is usually the most abundant (Joubert, 1997). Commercial ranching was initiated in the late nineteenth century.

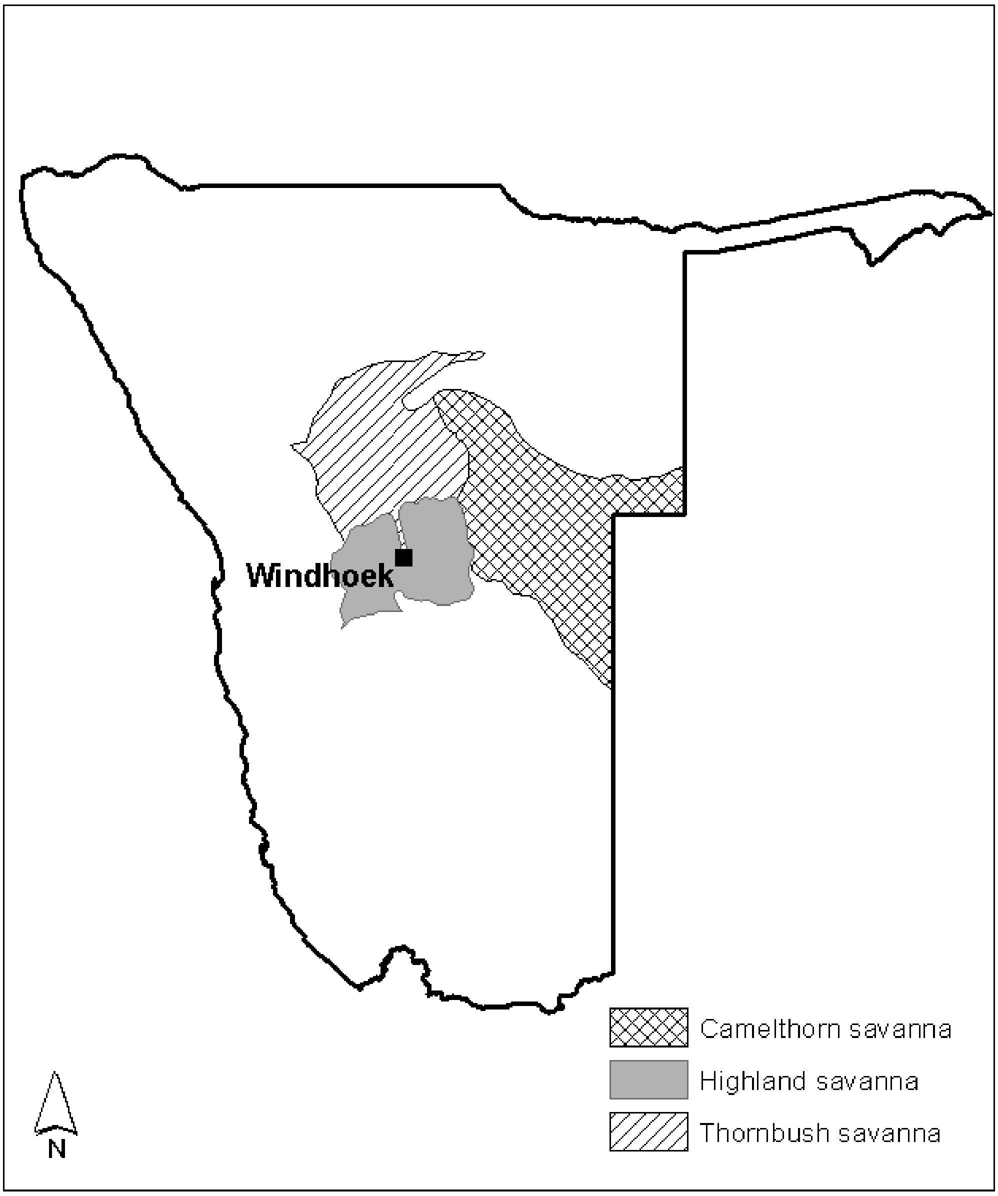

Figure 2.1. The position of the Highland savanna in Namibia with the adjacent Camelthorn and Thornbush savannas indicated.

Commercial cattle ranchers maintain a fairly static stocking rate of about 15 ha/large stock unit (LSU) on farms that are typically 5000 ha in extent. Very little of the area supports a climax grass layer today.

2.3 State-and-transition model for the Highland savanna

A summary of the proposed conceptual model (Figure 2.2) of vegetation dynamics in the semiarid Highland savanna of Namibia is presented as a catalogue of states (Table 2.1) and transitions (Table 2.2). The proposed states and transitions are discussed below with reference to supporting sources of information.

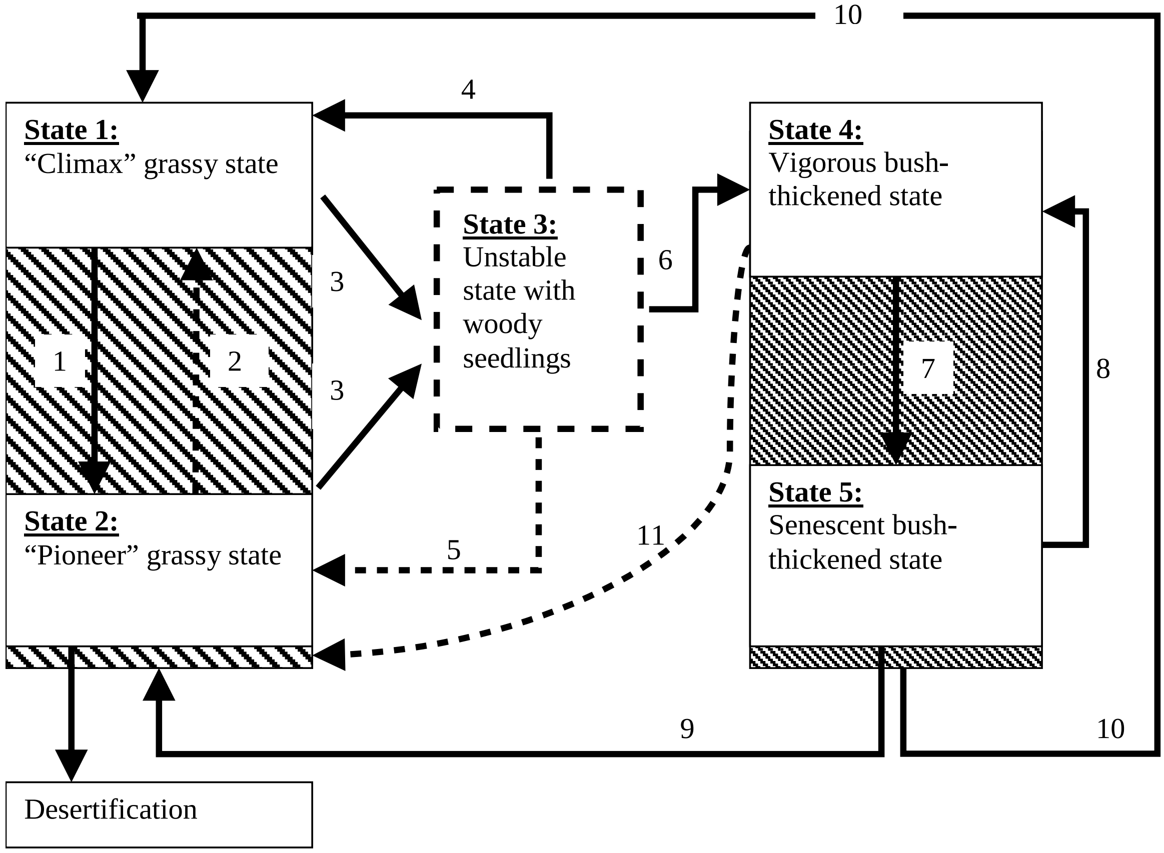

Figure 2.2. Schematic representation of states and transitions in the Highland savanna. Solid lines represent likely transitions and dashed lines represent less likely transitions.

Table 2.1. Catalogue of states in the Highland Savanna.

Grassy States 1 and 2, These two states can be viewed as a continuum.
State 1, Dense grass sward of climax grasses, scattered cover of a variety of trees and shrubs.
State 2, Sparse grass cover of mainly “pioneer” annuals, scattered cover of a variety of trees and shrubs. Erosion and soil capping is evident.
State 3, Unstable state between grassy States 1 and 2 and woody States 4 and 5, with many *A. mellifera* seedlings in the grass sward. Not easily distinguishable from State 1 and State 2 since the seedlings are largely unnoticeable at this stage. A crucial juncture for opportunistic management.
Bushy states 4 and 5, These two states can be viewed as a continuum.
State 4, High density monostands of vigorously growing *A. mellifera* bushes with little grass cover.
State 5, Senescent stand of mature *A. mellifera* trees with a good herbaceous cover and mixed shrub understory.

Table 2.2. Catalogue of transitions between states in the Highland Savanna.

Transition 1, From State 1 to State 2. Typical retrogressive succession in a grass dominated sward, promoted by excessive and continuous grazing, and drought periods.
Transition 2, From State 2 to State 1. Typical succession towards a climax state from a pioneer state in a grass dominated sward, promoted by high rainfall years and lenient grazing. The most important management practice would be to provide adequate rest to the grass sward. It occurs over many years and is not assured. Active management, including overseeding, may be necessary to speed up the transition to a time frame acceptable for resource managers. Few documented data are available regarding successional processes in the grass layer of the Highland Savanna.
Transition 3, From State 1 or 2 to State 3. Occurs with three *consecutive* years of high rainfall, for seed production, seedling survival and establishment of *A. mellifera*.
Transition 4, From State 3 to State 1. Caused by a fire hot enough to kill seedlings and young saplings of *A. mellifera*. There is a high probability of such a fire owing to the likely high grass biomass.
Transition 5, From State 3 to State 2. Has a low probability of occurring since the annual grass biomass may not be sufficient to sustain an effective fire.
Transition 6, From State 3 to State 4. Occurs in the absence of fire. Browsing by small herbivores may reduce the final density of the thicket.
Transition 7, From State 4 to State 5. A gradual almost deterministic successional process as trees grow, self-thin and eventually senesce. Can self-perpetuate through seed with three seasons of good rainfall (Transition 8) and, in exceptional rainfall years, may burn and revert to State 1 or 2 (Transition 10 or 11).
Transition 8, From State 5 to State 4. Occurs with two to three *consecutive* years of high rainfall, for seed production, seedling survival and establishment of *A. mellifera* within an existing thicket. It can be viewed as a cyclic self perpetuation of the bushy state.
Transition 9, From State 5 to State 2. Triggered by the senescence of mature trees in the presence of poor grass cover and may occur in drought years. Dead branches act as a mulch and nursery for grass seedlings.
Transition 10, From State 5 to State 1. Triggered by the senescence of mature trees in the presence of high biomass of climax grass cover and may occur in good rainfall years. Dead branches act as a mulch and nursery for grass seedlings. There are a range of transitional variations depending upon the grass biomass existing under the senescing trees. Reseeding with climax grasses, as well as other interventions, may be necessary to ensure a transition to State 1. Transitions 9 and 10 are transitions back to the grassy state.
Transition 11, From State 4 to State 2. Has a low probability of occurring without intervention (stem burning, chopping and the application of arboricides). Sufficient grass biomass to allow a fierce fire to occur that kills some of the *A. mellifera* shrub might only occur under exceptional rainfall conditions.

2.3.1 The grassy states

2.3.1.1 State 1: ''Climax'' grassy state (Figure 2.3)

This state is dominated by mesophytic, climax perennial grasses (*Schmidtia pappophoroides*, *E*. *nindensis*, *A*. *pubescens* and *B*. *nigropedata*), with a basal cover of up to 12 % (Joubert, 1997). Grass-based carrying capacity ranges from 5 to 20 ha/LSU (Rothauge, 2004). Woody vegetation cover, dominated by 2–3m single-stemmed *A*. *hereroensis*, seldom exceeds 10 % (Joubert, 1997). *A*. *mellifera* is typically rare. Forbs contribute up to 5 % of the herbaceous canopy cover (Rothauge, 2004). State 1 can change to State 2 as a result of continuous grazing in combination with drought (T1 in Table 2.2).

Figure 2.3. Highland Savanna on the Neudamm Farm study site in state 1 (foreground) after recently being burnt (transition 3).

2.3.1.2 State 2: ''Pioneer'' or degraded grassy state

In State 2, the savanna remains open, but is dominated by annual increaser grasses such as *Aristida stipoides*, *Enneapogon cenchroides*, *Eragrostis cylindriflora* and *E. porosa*, *M. repens* subsp. *grandiflora*, *Pogonarthria fleckii* and *Tragus racemosus*. Xeric perennial grasses such as *Aristida congesta* are present (Joubert, 1997). Basal cover is as low as 0.5 % (Joubert, 1997) but after excellent rains, dry matter yield may be substantial (Rothauge, 2006).

Woody cover remains the same but dwarf xerophytic karroid shrubs like *Eriocephalus luederitzianum*, *Leucosphaera bainesii*, *Salsola* spp. and *Monechma* spp. increase noticeably (Rothauge, 2004). Erosion and soil capping reduce water infiltration and may inhibit the reverse transition towards a climax grassy state (Transition 2). If large areas are degraded, seeds of large-seeded climax grass species such as *B. nigropedata*, *A. pubescens* and *S. pappophoroides* may be absent, further reducing the likelihood of a transition back to State 1.

The transition (T2 in Table 2.2) from the degraded grassy State 2 to the climax grassy State 1 appears to result from above average rainfall and lenient grazing, but is not well documented. In Texas, gradual succession towards a climax grass state occurs if the rangeland is left ungrazed, but recovery is intermittent, full recovery occurring only after about 25 years (Fuhlendorf et al., 2001). Exclusion of livestock from Namibian farmland is not economically feasible, and hence the transition is likely to be slow. There is much debate regarding the best rangeland approach to achieve this transition, but adequate rest for the grass sward to recover from grazing (Zimmermann et al., 2008) is probably the most important factor which a rangeland manager should ensure a healthy perennial grass sward.

Three consecutive years of above-average rainfall are necessary for successful recruitment of *A*. *mellifera* (T3 in Table 2.2).This transition is rare in the Highland savanna, probably only occurring on five occasions in the past 90 years (Figure 2.4). This accords well with findings in a semiarid wooded grassland in eastern Australia, where six widespread *Dodonaea attenuata* establishment events were estimated to have occurred in 97 years (Harrington, 1991), but in semiarid grasslands in Texas recruitment of *P*. *glandulosa* seedlings is continuous (Brown and Archer, 1999). Rainfall in the Texas system is more than twice that of the Highland savanna, allowing much more frequent seedling establishment. Also, the harder testa of *Prosopis* seeds allows them to be dispersed by ungulates and to form long-term seed banks, which can react to single above-average rainfall seasons.

The transition is initiated by an exceptional previous rainy season needed for *A*. *mellifera* to produce viable seed. *A*. *mellifera* fruits profusely following an exceptionally wet rain season, but in dry years fruits are absent or insignificant (Donaldson, 1967; Joubert, 2007). ‘‘Privileged’’ trees receiving runoff from road surfaces create the impression that a large proportion of trees reproduce annually, but this is not the case. Seeds are released during December, before the major rains (January–April). Although some seeds are produced after a season of moderate rainfall, these are generally sterile, or consumed by seed eating Bruchidae (Hoffman et al., 1989; Miller, 1994; Okello and Young, 2000) and other pre- and postdispersal seed predators (Walters et al., 2005; Joubert, 2007). After exceptional rain, seed banks are too large for seed predators to reduce the seed bank significantly.

A second consecutive good rainy season is required for the establishment of seedlings. Seeds germinate easily, achieving more than 90 % germination in trials (Rothauge, 2002), but seedlings require a follow-up above-average season with well-spaced effective rain showers of more than 5 mm per week for establishment. For example, at Neudamm and Krumhuk, seedling establishment was only recorded in 2001 following the exceptional 1999/2000 rainy season (Figure 2.5) (Joubert et al., 2013; Chapter 3). In contrast, no seedlings were recorded during 1999/2000. Seeds thus germinate in the same season in which they are formed and seedlings are only present immediately after seed production in the same season (Donaldson, 1967). *A. mellifera* seed banks are therefore ephemeral. A third consecutive good rainy season ensures that a high proportion of the seedlings survive, unlike after poor rainy seasons, when sapling mortality is high (Figure 2.6) (Rothauge, 2005). In Chapter 3 (Joubert et al., 2013) these preliminary conclusions are investigated.

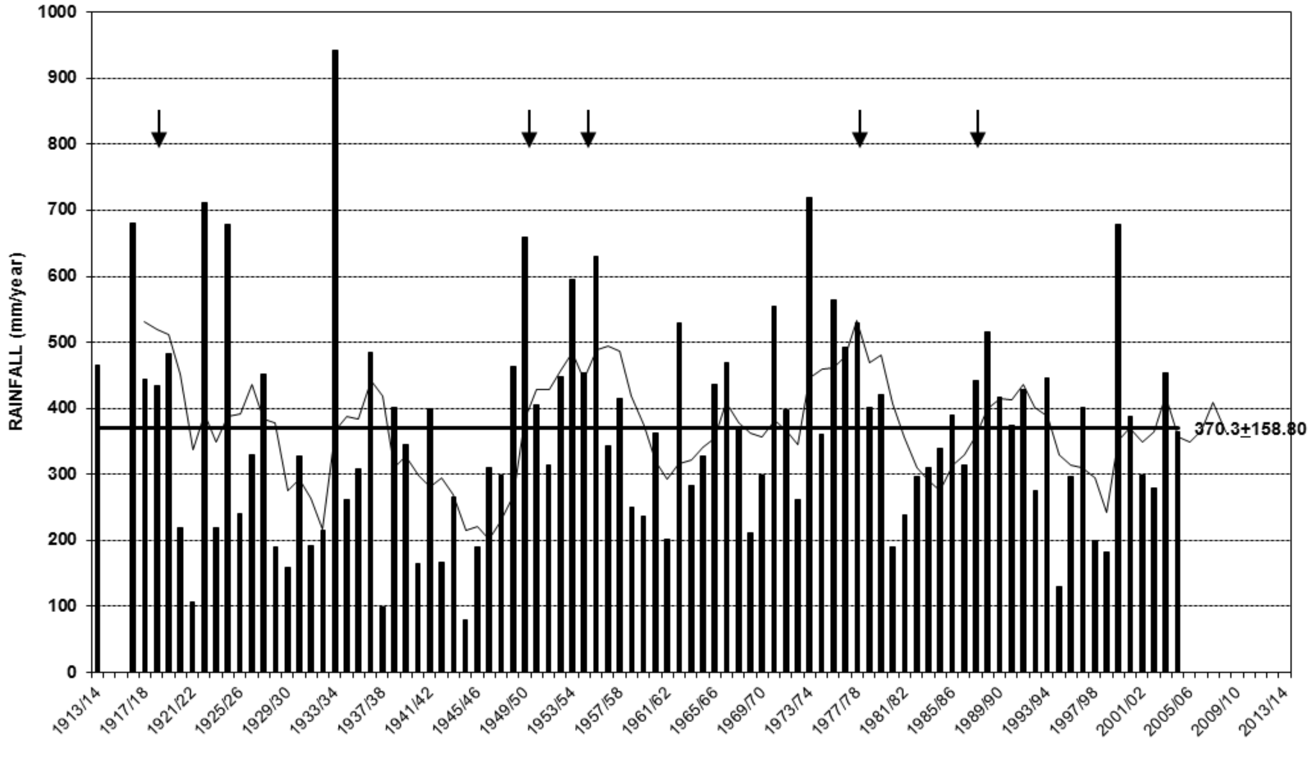

Figure 2.4. Ninety-year rainfall record of Neudamm Agricultural College, with 5-year moving average superimposed upon individual years' data. Arrows denote periods of 3 consecutive rainy seasons above average in which transition 3 is likely to have occurred.

2.3.1.3 State 3: Unstable grassy state with woody seedlings

In this transient state, the grass sward conceals a high density of *A. mellifera* saplings, masking the progression towards a bushy state. *A. mellifera* saplings grow very slowly, typically only reaching a diameter of 0.5 cm after 6 years (Joubert, 2007). State 3 can either proceed to bush thickening (T6 in Table 2.2) or revert to the grassy state (T4 and T5 in Table 2.2). If not interrupted, Transitions 3 and 6 (including State 3) represent a continuum from grass- to bush-dominated savanna. State 3 represents a critical time period for management intervention because seedlings and saplings are likely to be sensitive to fire. Six-year-old saplings that have been dug up reveal long tap roots (at least 50 cm) but no lateral roots. Therefore, it is unlikely that they have the reserves to recover once top killed. The grass species composition in state 3 can be anything between that of State 1 and State 2, and will essentially be the same as it was prior to the transition.

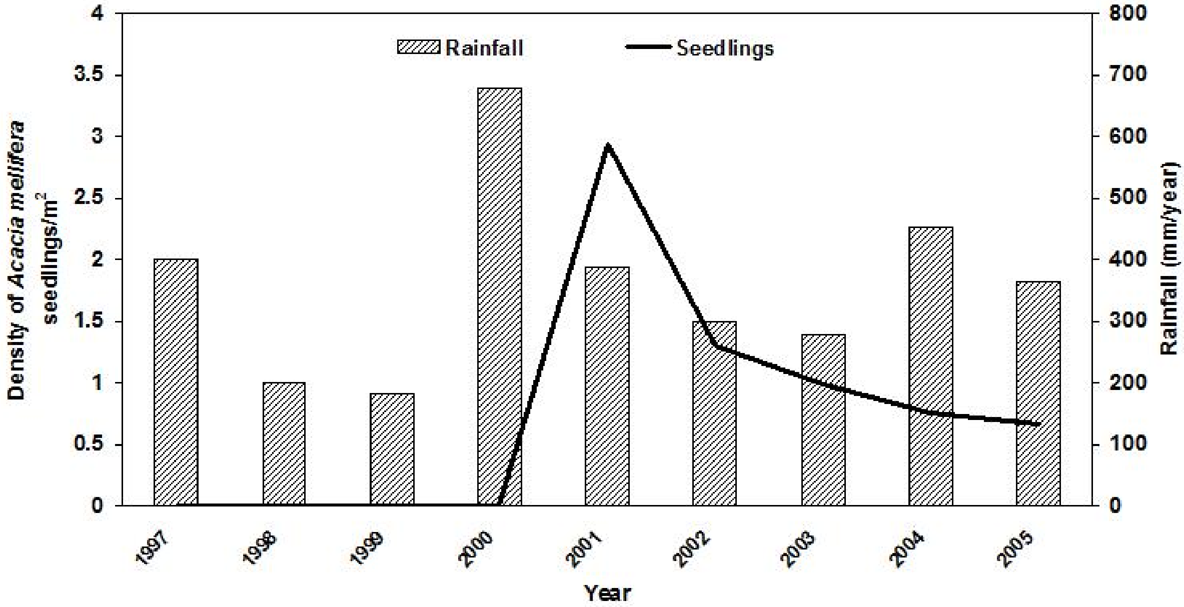

Figure 2.5. Density of *A. mellifera* seedlings from 1997 to 2005 in 143 field plots of, in total, 450 m^2 at Neudamm, showing establishment in 2000/2001 only (after exceptional rains) and subsequent survival of saplings.

The most important driver of transitions back to a grassy state (T4 and T5 in Table 2.2) is fire. Although fire is well known as an important driver of vegetation dynamics and the control of bush thickening in savannas (Trollope, 1984; Teague and Smit, 1992; Smit, 2003), research has been directed on its effects on mature tree and shrub mortality (Sweet, 1982; Trollope,1984; Hodgkinson and Harrington, 1985; Harrington and Driver, 1995; Skowno et al., 1999; Higgins et al., 2000; Roques et al., 2001). Fire is more likely to be effective in killing seedlings and saplings. Kraaij and Ward (2006) only investigated the effects of pre-emergence fires on recruitment. Chapter 4 (Joubert et al., 2012) reports on experiments that tests this component of the conceptual model. It is reasonable to expect that a lower fuel load than Trollope’s (1984) general recommendation of 2 t of fuel per hectare to control mature *Acacia karroo* trees would suffice to control more fire-sensitive seedlings and saplings. The denser the perennial grass sward, the more likely a fire can be sustained that will kill seedlings. Climatic conditions for an effective fire coincide with the conditions for *A. mellifera* establishment.

Direct competition between woody seedlings and the grass sward only plays a secondary role. Many farmers, reluctant to apply a fire for economic reasons, place their faith in this competition. Although a dense and vigorous grass sward is said to outcompete woody seedlings (Walter, 1971; Walker, 1981; Smit and Rethman, 1992), recent studies suggest that the grass sward in low rainfall savannas appears unable to outcompete seedlings (e.g. Kraaij and Ward, 2006) though Ward and Esler (2011) do show some competitive effects. Six-year-old, and older, saplings regularly grow adjacent to and even within tufts of climax grasses at Neudamm. The competitive effects of the grass sward in arid and semiarid savannas may have been overemphasised in the past. The effect of grass competition on seedling, sapling and shrub mortality is currently being tested.

Transition 6 from unstable State 3 to a vigorous bushy State 4 is a continuation of Transition 3 if not interrupted. In contrast to more mesic savannas with an annual rainfall exceeding 600mm (Skowno et al., 1999; Higgins et al., 2000; Roques et al., 2001), the arid Highland savanna rarely has sufficient fuel for a fire that might control *A. mellifera* gullivers and they might escape the fire-sensitive stage more easily. A gulliver is a small, suppressed woody individual (Bond and Van Wilgen, 1996). The absence of grass may allow *A. mellifera* saplings to grow rapidly beyond the fire-sensitive stage (Skarpe, 1990). The major reason that bush thickening is observed in areas of heavy grazing is that the fuel for an effective fire is removed regularly, including during the rare events of *A. mellifera* establishment. Farmers, concerned about temporary productivity losses, suppress fires even when fuel loads are sufficient. Fire in the Highland Savanna is required infrequently because the climatic conditions that initiate bush thickening only occur about five to six times at any one place in a century (Figure 2.4). The crucial stage of onset of bush-thickening events are the rare events of seed production and seedling survival (Transition 3), rather than the release of already existing gullivers from competition by grasses through lack of fire at a later stage. This is one important way in which the dynamics of arid and mesic savannas may differ.

Ungulate browsers are probably ineffective in preventing a transition (Transition 6) towards bush thickening; rather, they regulate the structure of existing thickets (Teague and Smit, 1992). Domestic goats utilise *A. mellifera* but it is not their preferred forage species (Rothauge et al., 2003). Small browsers such as lagomorphs may in fact be far more important regulators of thicket densities (Ostfeld et al., 1997; Weltzin et al., 1997; Chapter 6). Up to 58 % of the damage to A. *mellifera* saplings at Neudamm was caused by lagomorphs (Rothauge, 2005), suggesting that they could significantly reduce the density of developing thickets through browsing damage. At Neudamm, dense stands of *A. mellifera* saplings are sometimes destroyed by helmeted guinea fowl and warthogs searching for food (Rothauge, 2005) similar to the effect of prairie dogs on *Prosopis* saplings in north-central Texas (Weltzin et al., 1997). A more comprehensive study of lagomorph impacts is currently underway (Chapter 6 reports on some of the preliminary findings).

2.3.2 Bushy states

2.3.2.1 State 4: Vigorous bush-thickened state

After *A. mellifera* individuals develop an extensive lateral root system, they suppress grass production (Smit, 2003) to the extent that fire (transitions 4 and 5) is unlikely. In cases where shrubs are topkilled by fire, regrowth is high (Skarpe, 1991; Meyer et al., 2005) and rapid.

Bushes in thickets at this stage are typically similar sized, indicating episodic recruitment. Larger parent trees of around 3–4 m, evidence of a previous transition, may be scattered through the thicket. On a small scale, shrub densities around parent trees can reach 3 shrubs/m^2 and 100 % canopy cover (Joubert, 2007). On a landscape level, shrub densities of 12000 shrubs/ha occur (De Klerk, 2004). Shrubs limit their own growth rate by intense density-dependent inter-shrub competition (Smit, 2003). Increaser grasses of the genera *Aristida*, *Eragrostis*, *Enneapogon* and *Tragus* occur. Animal biodiversity in the thickets is lower than in the grassy state (Barnard, 1998), but thickets act as refugia for animals from fires. Livestock production on vigorously bush thickened range is severely limited.

Transitions occur mainly close to large parent trees and already existing thickets because seed dispersal is inefficient (Donaldson, 1967). Seedlings mainly occur within a few metres of thickets (Rothauge, 2005). The transition (T7 in Table 2.2) towards a senescent bush-thickened state (State 5) is a progressive succession that takes decades. Individual mature shrubs grow typically at rates of about 3.2 cm/year (Joubert, 2007). Broad-leaved shrubs, typically observed in the grassy state, germinate and grow in the protection of the tall thicket. Birds attracted to the thicket transport the seeds of these fleshy-fruited species here.

Figure 2.6. **A** dense stand of *A. mellifera* representing State 4 south of Windhoek. The inefficient dispersal from the parent tree is easily visible in this figure.

2.3.2.2 State 5: Senescent bush-thickened state (Figure 2.7)

This state is characterised by mature and senescing trees of around 4m high, often with an understory of maturing broad-leaved shrubs. The density of trees has typically been reduced to about 2500 trees per hectare, but canopy cover tends to remain high (Joubert, 2007). This declines as trees senesce due to a combination of drought stress, old age and fungal pathogens (Holz and Bester, 2007) (Figure 2.8). In Namibia, tens of thousands of hectares of bush-thickened savanna have opened up as a result of this. Lower-density thickets also occur, as a likely result of prior browsing by lagomorphs.

Figure 2.7. A mature thicket (State 5) on Krumhuk Farm. The > 4 m tall trees are in flower.

Figure 2.8. Senescing trees on the edge of a thicket (State 5). Drought, fungal dieback and intraspecific competition interact to increase mortality.

Broad-leaved forbs grow in the nutrient-rich sub-canopy habitat, followed by shade-tolerant grass species commonly associated with savanna trees (Rothauge, 2004). Elevated nitrogen levels, typically found under *Acacia* trees in savannas (Smit and Swart, 1994; Hagos and Smit, 2005), give grasses a competitive edge over woody seedlings and forbs (Kraaij and Ward, 2006). Sub-canopy areas with decaying tree skeletons are often dominated by subclimax grasses such as *Cenchrus ciliaris* (Rothauge, 2004). Grass accumulates under the open thicket canopy, providing sufficient fuel for fires that may kill senescing trees. Mature or senescing *A*. *mellifera* are less able to resprout than young shrubs (Meyer et al., 2005).

After two to three successive high rainfall years, recruitment occurs in gaps in the canopy of existing thickets of *A. mellifera* trees (Joubert, 2007). At a microsite level, this transition (T8 in Table 2.2) is thus equivalent to the combined transitions 3 and 6. It may occur at any stage between States 4 and 5. It changes thicket structure from a homogenous thicket of even-aged and even-sized shrubs to one that has more than one cohort of shrubs of different ages and sizes establishing in spaces adjacent to and within the thicket.

A transition from State 5 to the degraded grassy state (Transition 9 to State 2) is likely if below-average rainfall conditions and excessive grazing pressure prevail. Ranchers that experience dense stands of *A. mellifera* dying, but do not change the grazing management that facilitated 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 periods. Bush clearing may also initiate this unfavourable transition if the underlying cause is not addressed, if no woody litter is left on the ground as mulch. The woody mulch protects grasses against grazing and the competitive release from woody plants allows a dense and very productive grass sward to develop rapidly (e.g. Smit and Rethman, 1999). This release effect may last for several years. A transition to the climax grassy state (Transition 10 to State 1) may not be feasible without reseeding if there has been local extinction of climax grass species, as has occurred in much of the rangeland (Joubert, 1997).

The precondition for Transition 10 is lenient grazing pressure that allows the desired perennial grass species to recover from grazing, set seed and establish successfully (Smit, 2003). Attempts to force transitions back to a grassy state through tree thinning for wood harvesting and charcoal production effectively result in Transition 8, back to a vigorous bush thickened state, by removing the suppressing effect of mature individuals (Smit, 2004).

The transition (T11 in Table 2.2) from a vigorous bush-thickened state (State 4) to a degraded grassy state (State 2) has a low probability of occurrence because an adequate fuel load is unlikely to build up. It may occur on the boundaries of thickets where fuel loads are higher, reducing thicket sizes over time with successive fires.

2.4 Discussion

Because of life history and climate differences, there are some fundamental differences between the model proposed in this chapter and other explanations for bush thickening. For example, Brown and Archer (1999) propose continuous recruitment for *P. glandulosa* invasions in more mesic savannas in Texas. A similar recruitment pattern is likely for *D. cinerea*, in north-central Namibia because it has hard seeds with an impermeable testa (Bell and Van Staden, 1993), and thus survives ingestion by ungulates, while the seed bank is persistent (Witkowski and Garner, 2000). Increasing fire frequency may maintain an open sward in more mesic savannas (e.g. Skowno et al., 1999; Roques et al., 2001), but in an arid savanna it is more crucial to coincide the fire with seedling establishment and the early stages of sapling development. *A. mellifera* recruitment is episodic. Aerial photography and other remote-sensing techniques detect gradual increases in cover, rather than sudden increases in density, reinforcing the impression that bush thickening in the Highland Savanna is a continuous or ‘‘creeping’’ process, yet at a microsite level, it follows a ‘‘sleep’’ then ‘‘leap’’ mode of progression. Parent trees ‘‘sleep’’ (do not recruit successfully) until three consecutive years of above average rainfall occur, the resultant establishment or ‘‘leap’’ typically only being metres from the parent trees.

Bush thickening is a natural process and the Highland Savanna should ideally consist of a patch mosaic of all states, the thickets forming patches while the open, grassy states form the matrix. There will usually be a spatial mosaic of successes and failures of transitions, depending upon variations in local transition conditions. For example, a mature tree or thicket of mature trees may constantly attract grazers, reducing grass cover and hence the chances of fire, thus allowing seedlings to survive. Away from the tree, grass cover may be sufficient to initiate an adequately hot fire. Fire may destroy some of these ‘‘leap’’ events (seedling establishment), but may miss others, reinforcing this shifting mosaic effect. It is only when conditions are uniformly suitable for a certain transition on a landscape level, for example when grazing at high intensities is maintained throughout the year, for some years, and fire is completely excluded, that thicket patches become the matrix as the mosaic gradually deteriorates. This is often the case on commercial farms where several thousand hectares of rangeland are subjected to a rigid grazing plan and fire is deliberately excluded, or where overgrazing has reduced the fuel load. Bush thickening may be self-perpetuating, since it forces farmers to overgraze existing open patches, thus increasing the likelihood of a transition to bush in these areas.

The virtual exclusion of planned, hot fires on an opportunistic basis is probably the most important controllable variable, which has been neglected in semiarid rangeland management (see Joubert et al., 2012 and Chapter 4). The model emphasises unstable State 3 as a state and not as a continuum because it is a crucial juncture for management decisions. When encroaching gullivers have matured, fire offers a much smaller window of opportunity because of the suppression of grass growth by thickets, the increased fire-tolerance of mature shrubs and the self-protection of thickets against fires. Both the transition towards a bushy state (through seed production and seedling establishment) and the reverse transition (through fire) depend on exceptional rainfall events. The variable thus is the management action during this time. Managers can turn hazards into opportunities, and minimise transitions to bush thickets by recognising this. High grazing pressure does not directly result in a transition to a bushy state if there is insufficient rain for seed production and seedling establishment, although the probability of the transition during future high rainfall seasons is enhanced. The model proposes that the use of fire is an infrequently needed, yet crucial, management tool in the Highland Savanna, and in similar arid and semiarid savannas (see Joubert et al., 2012 and Chapter 4). Owing to the inefficient dispersal of *A. mellifera* seeds, fires need not be extensive, and could be limited to around existing thickets or parent trees where seedlings establish. Monitoring for established seedlings is important.

To date, savanna dynamic theories have attempted to capture a general explanation for bush thickening without explicit recognition that species with different life histories are likely to follow different pathways (for example van Langevelde et al., 2003; Meyer et al., 2007). A more successful approach would be to develop specific state-and-transition models for specific conditions (species, climates and soils), and then develop a general theory, which explicitly recognises and accommodates these differences. An attempt to develop general theories on the demography of African acacias based on life history differences (Midgley and Bond, 2001) is a useful departure point.

Many of the transitional processes discussed here are tested further and reported on in Chapters 3 (Joubert et al., 2013) and 4 (Joubert et al., 2012). Other ideas related to patch formation, the role of interspecific competition and browsing in bush thickening are still under investigation and only have preliminary conclusions at this stage (Chapter 6).

The conceptual model is relevant to management because it explicitly recognises the importance of climatic events and potential management actions, and the timing thereof in driving transitional changes between stable states, whereas prior management models were focussed primarily on the adjustment of stocking rates and drew too much from general theories developed for different species in different climates.

CHAPTER 3: THE INFLUENCE OF RAINFALL, COMPETITION AND PREDATION ON SEED PRODUCTION, GERMINATION AND ESTABLISHMENT OF *ACACIA MELLIFERA*

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Minor editing changes have been made.

Abstract

Seed production and seedling survival are under-researched in savannas. In this chapter these factors are investigated in a population of *Acacia mellifera*, in an arid Namibian savanna over a nine year period (late 1998 - early 2007). The following questions were asked: (i) How does viable seed production vary with rainfall and tree size, (ii) when does seed germination occur, (iii) is the seed bank of *A. mellifera* persistent, and (iv) how do competitive interactions with established trees influence recruitment of *A. mellifera* seedlings? Seed production was highly correlated with annual rainfall. In dry years, there was no viable seed production. En masse seed production only occurred in exceptionally high rainfall years, and was strongly correlated with size among trees >2 m tall. Seed predation was low. Seedlings only emerged directly after en masse seed production, suggesting ephemeral seed banks. Three times more seedlings emerged per m^2, but seedling survival was five times less, under trees than away from trees, indicating strong competition for water with established trees. Seed production is a recruitment bottleneck in this species. Recruitment requires at least two, but more realistically, three consecutive seasons of favourable rainfall, and is highly episodic in arid savannas.

3.1 Introduction

The phenomenon of bush thickening (also referred to as shrub or bush encroachment), that results in the shift from open grass dominated rangelands to thicket dominated rangelands, particularly in savannas, has received a considerable amount of scientific attention, yet consensus has not been achieved regarding a generally accepted theory to explain the dynamics. For details on some of these theories see Bond and Midgley (2000), Higgins et al. (2000), Joubert et al. (2008a) (see Chapter 2), Knoop and Walker (1985), Polley (1997), Scholes and Archer (1997), Roques et al. (2001), Smit (2004), Meyer et al. (2007) and van der Waal et al. (2009). The diversity of explanations for bush thickening is partly due to the fact that different species having varying phenologies in varying climates and soils (Joubert et al., 2008a (see Chapter 2)). Whilst these theoretical arguments are not necessarily contradictory there is need for more cohesion and consensus, since bush thickening has serious economic (De Klerk, 2004) and ecological implications (Blaum et al., 2009; Sirami et al., 2009).

To achieve more applicable generality to the theory of thickening, it is essential to better understand the demography of different thickening species by investigating aspects of their phenology, and how climate, competition, fire and browsing affect these (i.e. determine key recruitment bottlenecks). Actual nonmanipulated occurrences of recruitment events can often only be detected through longer term field monitoring that includes phenological measurements. Yet such studies are considered less valuable than other approaches and are cited infrequently in the literature. Relatively little attention has been applied to recruitment bottlenecks in situ, especially on how life histories or phenologies of the different implicated species might influence these bottlenecks. This is particularly true in savannas. Recruitment studies tend to centre on recruitment as a whole, rather than looking at the different processes within, that is seed production, germination and emergence and seedling establishment. The processes from seed predation to establishment of a nonthickening species, *Acacia erioloba* in Botswana were investigated by Barnes (2001), while Seymour (2008) included rainfall as an explored driver of recruitment of *A. erioloba*, but only on sapling banks. Seed production studies in savannas have focussed overwhelmingly on the role of seed predation in diminishing *Acacia* seed banks, both pre-dispersal (Hoffman et al., 1989; Ernst et al., 1990; Miller, 1994; Barnes, 2001) and post-dispersal (Miller, 1995; Walters et al., 2005).

In their extensive review of the demography of the African Acacias, Midgley and Bond (2001) do not mention the possibility that rainfall might limit seed production, but focus attention on the effects of pollination on seed set and seed predation. Very few studies have investigated seed production in savanna species (for example Donaldson, 1967; Tolsma et al., 1987; Ernst et al., 1989; Smit and Rethman, 1998; Walters and Milton, 2003; Mduma et al., 2007). Tolsma et al. (1987) and Chidumayo (1997) attributed much of the observed variation in seed production to nutrient limitations. Other studies have focussed on germination and establishment alone (Brown and Archer, 1999; Kraaij and Ward, 2006; Chidumayo, 2008; Ward and Esler, 2011). Although mention is made of seed production varying with rainfall in some of the above studies, only Donaldson (1967), in a preliminary study of *A. mellifera* demography in South Africa, and Chidumayo (1997), studying two species in miombo woodland in Zambia, placed some emphasis on how temporal rainfall variation might affect seed production. An implicit assumption from all these studies is thus that seed production, prior to seed predation, is not limiting.

Seedling survival has been studied in more detail in savanna woody species (Barnes, 2001; Seymour, 2008) but these studies have also tended to be short term. In situ studies of recruitment in arid rangelands show varying responses. Harrington (1991) and Joubert et al. (2008a) (see Chapter 2) demonstrated episodic recruitment of *Dodonaea attenuata* in a semi-arid woodland in eastern Australia and *A. mellifera* in an arid savanna in central Namibia, respectively. Watson et al. (1997) demonstrated both episodic peaks in, and continuous recruitment, of two shrub species in arid rangelands in western Australia, whilst Brown and Archer (1999) demonstrated continuous recruitment of *Prosopis glandulosa* seedlings in semiarid grasslands in Texas, USA. Seymour (2008) suggested episodic recruitment from seed but a continuously recruiting sapling bank for *A. erioloba* in an arid South African savanna. This range of observed and reported responses in arid rangelands clearly shows that the process of thickening does not follow a uniform pattern, and lends support to the suggestion that the understanding of which parts of recruitment are the actual bottlenecks could be valuable.

Seed production, predation, seedling recruitment and establishment of a major encroaching species, *Acacia mellifera* (Vahl) Benth. subsp. detinens (Burch.) Brenan, in an arid savanna of Namibia was investigated over a nine year period (late 1998 - early 2007) to better understand bottlenecks within the recruitment process. The following questions were asked:

(i) How does the production of viable seed vary with rainfall and tree size? (ii) When does seed germination occur? (iii) How long-lived is the seed bank of *A. mellifera*? (iv) How do competitive interactions with established trees influence recruitment of *A. mellifera* seedlings?

3.2 Study area

The survey was conducted on the 8450 ha Farm "Krumhuk" (S22.73426^0; E 17.08775^0), 20 km south of Windhoek, Namibia, in the Highland Savanna Vegetation Biome (Giess, 1998), more recently described as Highland Shrubland (Mendelsohn et al., 2002). The Highland savanna has been exposed to commercial ranching since the late nineteenth century. The terrain is highly broken and undulating, at altitudes of 1350-2400 m above sea level and with slopes that are covered by lithic leptosols. These soils are typically > 30 cm in depth, with a very high schist and quartz gravel content. Deeper eutric leptosol pediments are found below these slopes (Mendelsohn et al., 2002).

Precipitation is variable and seasonal, with 80 % or more of the total annual rainfall occurring from January to March. Mean annual rainfall is approximately 360 mm (CV = 40 %) in Windhoek. The mean annual rainfall for the Farm Krumhuk from 1994 to 2006 was 374 mm (CV = 46 %). The annual water deficit is approximately 1800 mm (Mendelsohn et al., 2002). The Highland Savanna has an aridity ratio of approximately 0.17 (precipitation / potential evapotranspiration [UNEP, 1992]), placing it within the range of an arid ecosystem (Aridity ratio of 0.05-0.2). Maximum average temperature is 31 ^{0}C. Minimum temperatures of -7^{0}C are regularly experienced, and frost occurs frequently in winters. A notable physical feature of the Highland Savanna is the surface layer of quartzitic pebbles that reach a cover of almost 100 % on steep slopes. This influences soil moisture through reducing rainsplash and evaporation (Joubert, 2010).

The Highland Savanna is characterized by woody species including *Acacia hereroensis*, *A. hebeclada*, *A. reficiens*, *Euclea undulata*, *Dombeya rotundifolia*, *Tarchonanthus camphoratus*, *Searsia marlothi*, *Albizia anthelminthica* and *Ozoroa crassinervia*. *A. mellifera* subsp. *detinens* and *A. reficiens* typically form small to extensive thickets, reducing grass productivity (Giess, 1998). Climax grasses include *Brachiaria nigropedata*, *Anthephora pubescens*, *Heteropogon contortus*, *Cymbopogon* spp. and *Digitaria eriantha*, but *Eragrostis nindensis* is usually the most abundant grass species (Joubert et al., 2008a) (see Chapter 2). In recent times, the abundance of these valuable climax grasses has been greatly reduced, mainly due to grazing.

At the time of the investigation Krumhuk Farm was a combined livestock (cattle) and game farm, and included a hunting operation. Two herds of cattle on the farm were rotated with short duration, high intensity grazing followed by long rest periods in each paddock. The average stocking rate was approximately 15 ha/LSU (large stock unit) (Meissner, 1982), although this varied from year to year, depending upon rainfall and the grazing available. Historically the livestock stocking rate was higher (10 ha/LSU), however, in recent decades wildlife stocking rates have increased from 20 ha/LSU to 8 ha/LSU. Wildlife species include kudu (*Tragelaphus strepsiceros*, predominantly a browser), oryx (*Oryx gazella*) and springbok (*Antidorcas marsupialis*, grazers that sometimes browse) and mountain zebra (*Equus zebra* subsp. *hartmannae*, grazers). The farm is part of the larger Auas-Oanob Conservancy, a consortium of 13 commercial farms of 120 000 ha, which jointly manages the game populations in the conservancy.

3.3 Methods

Plots (20 m x 20 m; n = 9) were selected on north facing footslopes to represent bush thickets of varying degrees of density, cover, and tree height class distribution. Woody species composition and the density and canopy cover (%) of different height classes of *A. mellifera* subsp. *detinens* were recorded in each plot. Farm rainfall records were used to determine annual rainfall, which is typically recorded from 1 August to 31 July. So the rainfall measured from 1 August 1997 to 31 July 1998 was recorded as 1998 rainfall, for example.

3.3.1 Seed production

The percentage of *A. mellifera* trees producing pods was recorded annually from 1998 to 2006 (excluding 2005) in each plot. The number of pods per tree was also counted from 1998 to 2006 (excluding 2000 and 2005). For both these measures, only those trees >2m were used for further analysis, as shorter trees produced few or no fruits, even in years of high rainfall (Table 3.1). Pods were counted in groups of 10 in the same way in which birds in large flocks are counted. The counts were rounded off to the nearest 10. This method was tested and found to be accurate to within 5 % of the actual number and was thus considered suitable for this study. From 2001, randomly selected trees (n = 10 per plot) were labelled. In addition to the total count on these trees, the number of seeds per pod, as well as the number of viable and predated seeds, was estimated for 10 randomly selected pods. Viable seeds were considered to be those that were well developed, with no abnormal shape or size. In a companion study, >90 % seeds that were classified as viable germinated (Joubert, 2010), confirming this. In southern Africa, flowering and fruit production of *A. mellifera* are highly seasonal and predictable. There is little intra seasonal variation, and only a single flush of flowering and fruit production. Flower production begins around late July-early August. By November, all pods that will be produced are already developing. By early December, pods are ripe and begin falling off the trees. All counts were conducted in late November and thus included all produced pods that have developed or not been browsed. Signs of browsing by ungulates were in all cases much less than 1 % and thus considered negligible.

3.3.2 Seedling recruitment, survival and growth

A 26 m line transect was laid out diagonally at each plot from corner to corner and 56 x 1 m^2 quadrats were set along each transect, 28 on either side of the transect. The direction of each transect was determined randomly. In 2001, an *en masse* germination event occurred and the seedlings from this event were monitored for two years. *A. mellifera* seedlings in each quadrat were counted at specific time intervals: (i) during the early rainy season of 2001 (February) to represent the number of seedlings emerging (considering that a very small proportion would have died prior to the first count), (ii) just after the rainy season of 2001 (June) to represent first year rainy season survival, (iii) during the hot dry season of 2001 (October-December) to represent first year dry season survival, (iv) during April 2002 to represent second year rainy season survival, and (v) during November 2002 to represent survival of seedlings after the two year period.

Based on the rainfall records, germination and emergence would likely have occurred over a period of about eight days from 24 to 31 January, 2001, when 64 mm of rain fell in six precipitation events. Prior to the 21 February survey, an additional 56 mm fell in seven precipitation events. Based on Joubert (2010) this would be sufficient to have ensured an almost 100 % seedling survival in this first period. The first seedling count can thus be considered to be close to the actual emergence rate at the start of the survey. Tree canopy cover over each quadrat was visually estimated to the nearest 10 % in February 2001 and again in April 2003. Canopy cover was later categorised into complete canopy cover (100 %), canopy edge (10 %-90 %) and no canopy cover (0 %). “Canopy edge” is considered important because it is likely to have different hydrological properties to both “complete canopy cover” (where rainfall is intercepted by the canopy) (Donaldson, 1967) and “no canopy” (where rainfall is not intercepted). “Canopy edge” may have mixed hydrological properties since in some instances there may be increased precipitation, through the concentration of raindrops, and in some instances there may be decreased precipitation due to the interception of raindrops by the canopy. One would expect survival to be intermediate between “complete canopy cover” and “no canopy”. Seedlings present and survival of seedlings m^{-2} was plotted through time. In April 2002 100 surviving seedlings that germinated in 2001 were randomly selected and labelled, and their survival measured for an extended period until March 2007. Stem diameters of these seedlings were measured with callipers at the end of 2007.

3.3.3 Data analysis

Spearman rank order correlation coefficient was used to determine the relationship between rainfall of the preceding rainfall season and percentage of >2 m trees bearing fruit and number of pods per tree for trees >2 m. This test was repeated using the rainfall of the rainfall season just prior to the preceding one, to determine whether there was any lag effect. A chi-square test was used to determine differences in the proportion of viable, nonviable and predated seeds each year. A multiple *post hoc* comparison (Kruskal-Wallis test) was used to determine effects of canopy cover on seedling survival. Analyses were performed using Statistica (Statsoft Inc., 2004).

3.4 Results

3.4.1 Seed production

Among trees >2 m height, the percentage bearing fruit (Figure 3.1) and the average number of pods per tree (Figure 3.2) was correlated with rainfall of the preceding rainy season.

No, and virtually no, pods were produced in the low rainfall seasons of 1998 and 1999 respectively. Also, pod production did not show any lag effect. In other words, pod production was not correlated with the rainfall of the season just prior to the preceding one. With the exceptional rains of 1999/2000 there was a flourish of pod production, and this tapered to virtually zero as rainfall decreased in 2001/2002 and 2002/2003. Once again an increase was observed after the 2003/2004 and 2005/2006 rainy seasons. Although the percentage of fruit bearing trees was lower in 2006 than in 2004 (despite higher rainfall in 2005/2006) the actual average number of pods per tree was much higher (Figure 3.2).

Increased rainfall also allowed smaller trees to produce fruit (Table 3.1). After the highest recorded rainfall season of the study (1999/2000) even a few shrubs <1.0 m produced fruit. Predation rates (Figure 3.3) (as a proportion of viable seeds) were low in all years (0 %-6.9 %) except for 2001 (28.7 %), and differences were not significant ($p > 0.05$). Predated seeds were mainly infected with bruchid weevils. Although there was a significant difference ($p < 0.01$) in the proportion of non-viable seeds between years, this was not associated with rainfall differences or seed production (Figure 3.3). The highest recorded number of seeds per tree was from a 4 m tree in 2006 with 4983-6977 seeds (95 % confidence interval), based on a count of 2300 pods with an average of 2.6 seeds per pod and a standard error of 0.2 seeds per pod. Of these, 3067-4293 seeds were viable (95 % confidence interval).

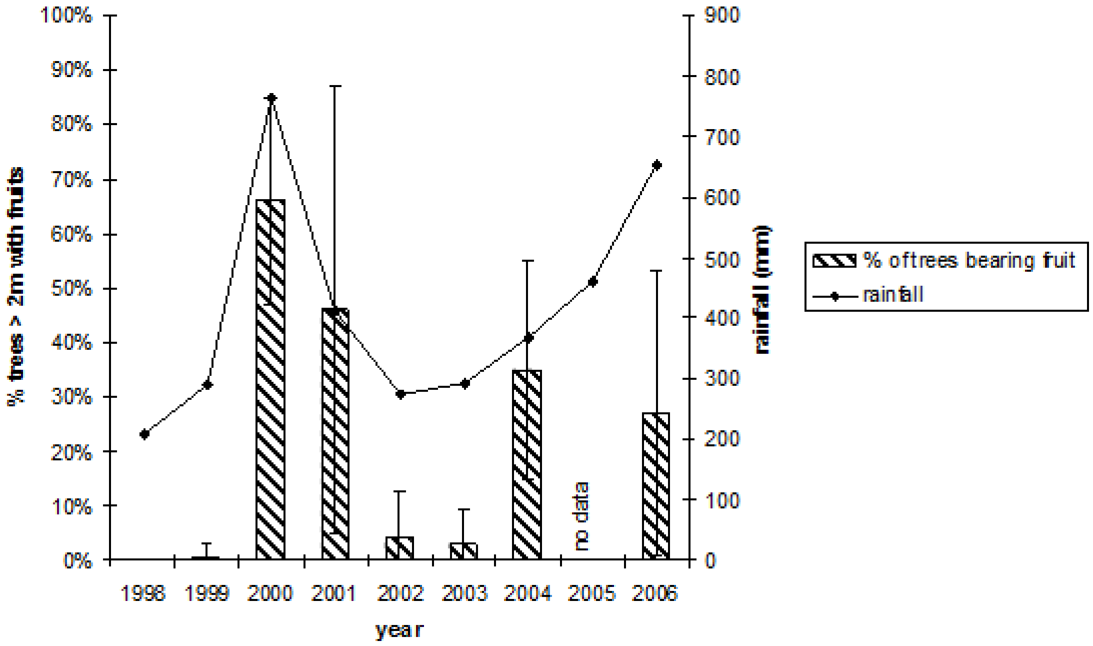

Figure 3.1. Percentage of trees >2 m in height bearing fruit in each of nine plots, and annual rainfall between 1998 and 2006. r = 0.687, p < 0.001, N = 72 (Spearman Rank Order Correlation). Error bars denote standard error. No fruit data are available for 2005.

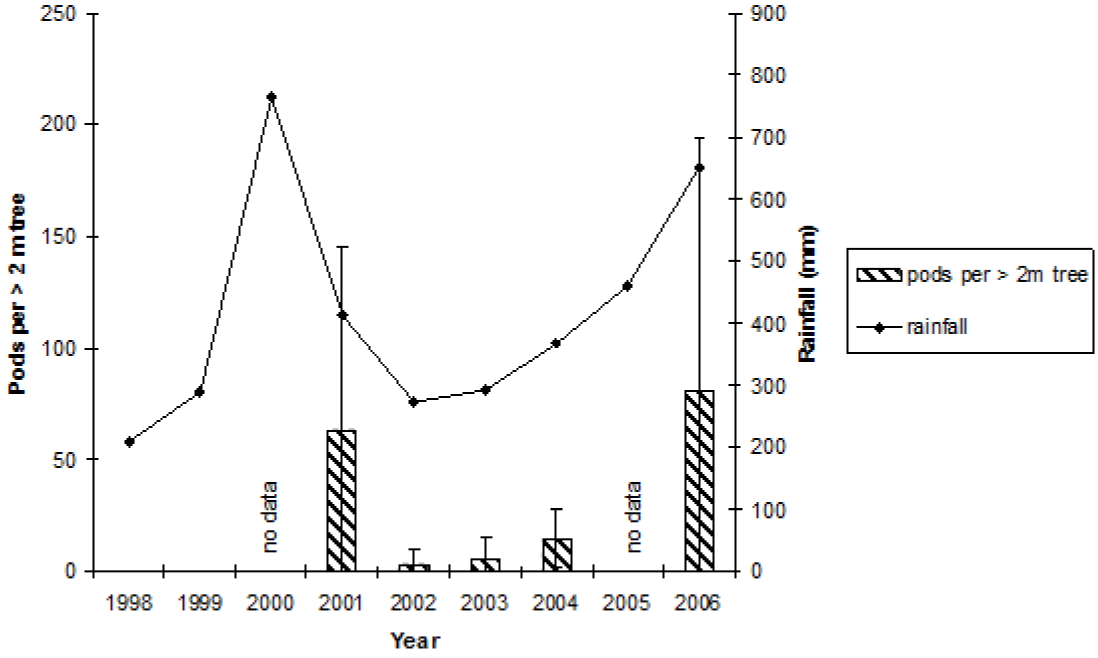

Figure 3.2. Pod production per tree > 2m in each of nine plots and rainfall per year. r = 0.565, p < 0.001, N = 63 (Spearman Rank Order Correlation). Error bars denote standard deviation. No data on pods are available for 2000 or 2005.

Table 3.1. Percentage of trees bearing fruit in different height classes in different years. No data are available for 2005. Heights are categorized into 0.5 m groups from 0-0.5 m to > 5.0 m. All trees are grouped together.

Annual rainfall (mm)	208.1	289	763.5	413	273.5	291.9	368	652
ht. class (n)	1998	1999	2000	2001	2002	2003	2004	2006
0 m – 0.5 m (592)	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%
0.5 m – 1.0 m (267)	0.0%	0.0%	0.4%	0.0%	0.0%	0.0%	0.0%	0.0%
1.0 m – 1.5 m (207)	0.0%	0.0%	1.9%	0.0%	0.0%	0.0%	0.0%	0.0%
1.5 m – 2.0 m (76)	0.0%	0.0%	46.1%	1.3%	0.0%	0.0%	2.6%	0.0%
2.0 m – 2.5 m (57)	0.0%	0.0%	63.2%	47.4%	1.8%	0.0%	15.8%	14.0%
2.5 m – 3.0 m (52)	0.0%	1.9%	55.8%	65.4%	1.9%	1.9%	21.2%	32.7%
3.0 m – 3.5 m (94)	0.0%	1.1%	63.8%	51.1%	12.8%	3.2%	31.9%	28.7%
3.5 m – 4.0 m (79)	0.0%	1.3%	77.2%	50.6%	12.7%	8.9%	40.5%	39.2%
4.0 m – 4.5 m (50)	0.0%	0.0%	70.0%	54.0%	12.0%	6.0%	50.0%	74.0%
4.5 m – 5.0 m (3)	0.0%	0.0%	66.7%	33.3%	0.0%	0.0%	100.0%	0.0%
> 5.0 m (1)	0.0%	0.0%	100.0%	100.0%	0.0%	0.0%	0.0%	0.0%
Total (1478)	0.0%	0.2%	17.9%	12.1%	2.0%	0.9%	7.6%	8.2%

3.4.2 Seedling recruitment and survival

Seedling recruitment was only observed in two years (Figure 3.4). Despite very high rainfall in 1999/2000 no seedlings emerged. Seed germination only occurred in 2001 after the *en masse* seed production in 2000 and in 2002 after reasonable seed production in 2001.

Seeds germinated very easily. They germinated mostly on the surface of the soil, and thus seedlings required a large amount of initial moisture to survive to the stage where the radicle penetrated the soil and the seedling was anchored.

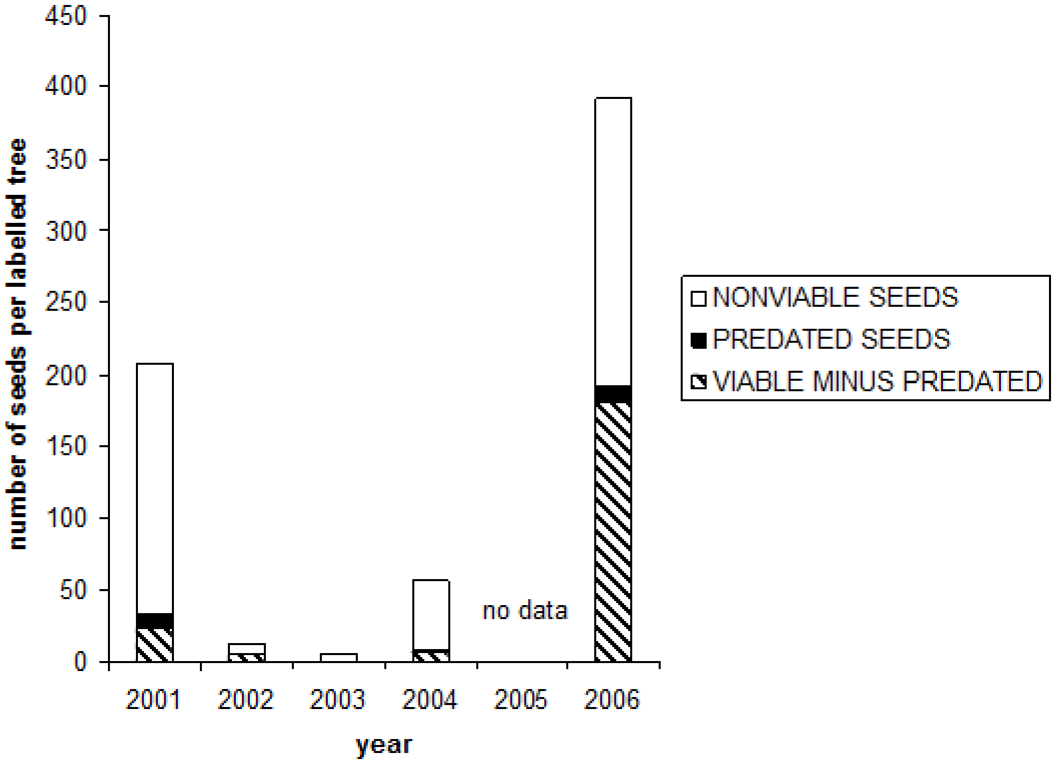

Figure 3.3. Average number of viable, predated and non-viable seeds per year for labelled trees. No significant difference (p > 0.05) in predation between years was found. No data are available for 2005. Seed predation rates: Chi-Square = 13.52025, df = 9, p < 0.140449. Significant differences were found for the frequency of nonviable seeds found between years: Chi-Square = 81.67969, df = 9, p < 0.001.

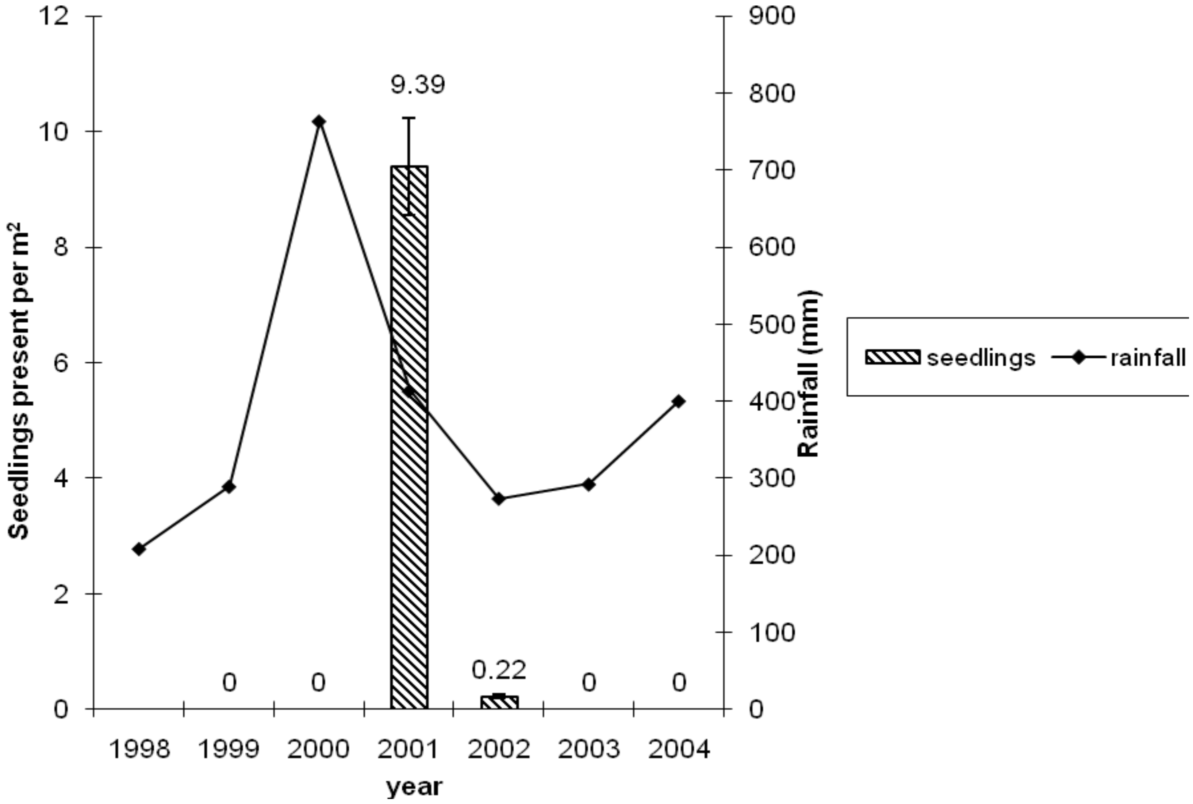

Figure 3.4. Number of seedlings present in relation to rainfall (emergence is related more to rainfall of the previous year and hence related to seed availability). Error bars denote standard error.

Three times more seedlings were present per m^2 under tree canopies than away from the canopy, but three times more seedlings survived per m^2 away from the tree canopy than under canopy, showing a five times greater survival rate (Table 3.2, Figure 3.5). At the canopy edge the number of seedlings present was similar to that away from the canopy, but with only twice the survival rate than under tree canopies. In the latter case this was not significantly different ($p > 0.05$). 19 of the 100 seedlings (19 %) labelled in April 2002 survived to March 2007. Of the 4011 seedlings observed in February, 2001, 168 survived until April 2002. Using the 19 % survival rate of the labelled seedlings from 2002 to 2007, 40 seedlings would have survived. Over a span of six years then, roughly 1 % of seedlings survived. The surviving seedlings had a mean stem diameter of 4.9 mm (SE ± 0.92 mm).

Table 3.2. Percentage survival of seedlings that emerged in 2001 a. under canopy b. at canopy edge and c. away from canopy after 2 years. Superscripts denote significant differences ($p < 0.001$) using multiple *post hoc* comparisons with Kruskal-Wallis test. N denotes sample size).

Category	Seedlings per m^2 (Feb 2001) H (2, N= 312) =37.44	Seedlings surviving per m^2 (Nov 2002) H (2, N= 312) =27.81	No. of plots with emerged seedlings	% survival per plot (calculated only from plots with seedlings) H (2, N= 264) =29.94
Under canopy	22.1^b	0.3^b	103	3.5^b
At canopy edge	7.8^a	0.2^b	60	7.0^b
Away from canopy	7.0^a	1.0^a	101	17.7^a
Overall	12.9	0.5	264	9.8

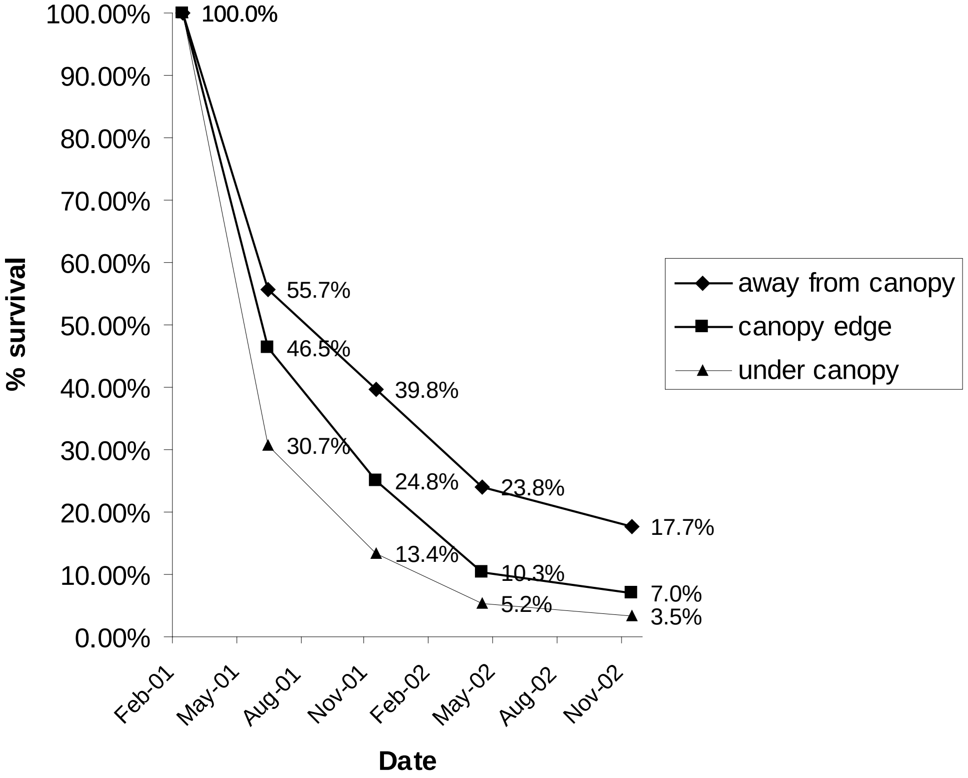

Figure 3.5. Percentage survival of seedlings present at the time of the first count in early 2001 over 2 years under tree canopies, at the canopy edge and away from canopies.

3.5 Discussion

The study identifies viable seed production as a likely demographic bottleneck in *A. mellifera*, and shows seed production to be positively correlated with rainfall. Donaldson (1967) also noted that *A. mellifera* fruited profusely following a season of above average rain in the Molopo area, South Africa but that only 2 % of trees fruited in drier years. This appears to be the most extreme case of masting reported for a woody species in arid savannas, although the concept of masting is well known in tropical forests and northern hemisphere ecosystems (for example Kelly, 1994; Chidumayo, 1997; Monks and Kelly, 2006). Based on Kelly's (1994) definition of different types of masting, *A. mellifera* appears to fall towards the "putative" masting end of the scale, where interannual seed production varies greatly, but it appears to be merely tracking resources (or resource matching), in this case water supplied by rainfall. This is opposed to "normal" masting in which individuals switch resources from vegetative growth to reproductive output (which could be detected by a drop in seed production in the year following mass production), as shown by Monks and Kelly (2006) for *Nothofagus* in New Zealand, and Chidumayo (1997) for *Isoberlinia angolensis* in the miombo woodland of Zambia, or "strict" masting in which a bimodal "all (mass seed production) or nothing" response is observed.

The longest consecutive monitoring period for seed production in this study was only four years (2001-2004). A longer data set would be required to conclusively determine whether there is a component of "normal" masting in *A. mellifera* (perhaps as a predator satiation adaptation [Monks and Kelly, 2006]), particularly considering the high interannual variability in rainfall over the study period. The strong link between rainfall and seed production contrasts observations of other woody species in arid savannas such as *A. erioloba* (Ernst et al., 1990; Barnes, 2001), that might be sourcing water from deeper more predictable sources, and for *I. angolensis* and

Julbernadia globiflora in miombo woodland in Zambia, where seed production was apparently independent of rainfall (Chidumayo, 1997).

The highest seed production measured for an individual plant was close to 6000 seeds (a 4 m tree) in 2006, whereas Donaldson (1967) estimated that an average sized (around 3 m) *A. mellifera* tree produced around 12 000 seeds in similar rainfall conditions. This is surprisingly few seeds for a species which relies on such infrequent *en masse* viable seed production events for propagation. This might be because the rapid transition from mature seeds to germination allows less opportunity for predation to occur. Predator satiation might be an indirect effect of infrequent seed production, not allowing seed predators to track the resource. Seeds of *A. mellifera* are larger than those for other *Acacia* species that produce similar seed numbers, such as *A. karroo* and *A. nilotica* (Walters and Milton, 2003), and thus require greater resource investments. Wigley et al. (2009) demonstrated an increase in total non-structural carbohydrate (TNC) concentrations in the lignotubers of *A. karroo* saplings after coppicing from fire. Since the flowering and early fruiting of *A. mellifera* occurs prior to leaf set in spring, flowering and fruiting require the mobilisation and utilisation of these TNC reserves from the lignotubers. Therefore, the increased lignotuber TNC reserves produced in good rainfall years appears to be the mechanism promoting reproduction, in dry years there being sufficient TNC reserves to focus only on maintenance and vegetative growth.

Midgley and Bond (2001) did not consider seed production *per se* to be a demographic hurdle in the population dynamics of the *Acacia* genus, perhaps because of the ability of many *Acacia* species to form large persistent soil seed banks, thus ensuring a constant source of viable seeds to germinate. This study shows that *en masse* viable seed production in *A. mellifera* only occurs in years of exceptionally high rainfall, and thus seed production, determined by rainfall, is a recruitment bottleneck in this species. Increasing rainfall not only increases the number of seeds produced per large tree, it also reduces the minimum size of seed bearing trees. Donaldson (1967) noted a high proportion of nonviable *A. mellifera* seeds per tree (38 %) in arid savannas in the Molopo area of South Africa, but in this study an even higher proportion was found (between 51 % and 98 %). Thus, in average rainfall years there is virtually no viable seed production, and in lower than average rainfall years there is no viable seed production, excepting in the case of “privileged” trees, which source runoff water from roadsides, for example (Joubert et al., 2008a). The relatively low level of seed predation in *A. mellifera* in this study (0 % - 28.7 %) and in Donaldson’s (1967) study (2.5 %) indicates that this is not a demographic hurdle in this species, in possible contrast to other species with indehiscent pods and seed banks that are persistent, such as *A. erioloba*, *A. hebeclada* and *A. tortilis*, which have much higher levels of seed predation (Miller, 1996; Ernst et al., 1990; Barnes, 2001).

Once mature, *A. mellifera* seeds disperse and rapidly germinate. Seeds within pods consumed by ungulates are typically digested (Donaldson, 1967), since the testa is thin. There is therefore a limited time for insects such as bruchid weevils to infect seeds while on the trees, and soil seed banks do not generally persist for longer than a month, also limiting post-dispersal predation. In this study predation rates were markedly higher in 2001. However, in 2006, seed production was much higher, yet the predation rate was low. This suggests that seed predator populations had built up due to the very high seed production in 2000 (not measured), but that these populations had dwindled in the intervening low seed production years.

A. mellifera seeds display no dormancy, and require nothing more than adequate water to germinate successfully (Joubert, 2010). Seedling emergence only occurred directly after seed production in the same season (Table 3.3). Seeds mature in December and germinate with the first good rains thereafter, typically in January. Post-dispersal seeds therefore typically last only for a month. The absence of seedlings (and hence seeds) in February 2000, when rainfall was exceptionally high (Table 3.3), supports other studies (Donaldson, 1967; Hagos, 2001; Joubert et al., 2008a) that show that there are no persistent soil seed banks. The ease with which viable seeds germinate (Joubert, 2010) means that the seed bank is destroyed within each season when germination occurs. Thus recruitment requires at least two consecutive favourable rainfall years (Table 3.3) as suggested by Joubert et al. (2008a). In the first rainy season (October-April) very high rainfall rather than favourable temporal distribution is important for the seed production in the following season. In that season, a favourable temporal distribution of rainfall appears to be more important for successful establishment. In 2009, seedlings in the field were exposed to a month of almost continuous rain just after germination, which allowed the roots of seedlings to reach 30 cm and deeper into the moister subsoils, and survive some extended dry periods in the growing season (Joubert, unpublished data). This suggests that even a slightly above average rainfall is sufficient for successful establishment, provided that the distribution of the rainfall is favourable. There is a strong likelihood that successful recruitment might require even more consecutive years of favourable rainfall, since only a tiny proportion of seedlings (using labelled seedlings) survived the study after 7 years. Other field studies suggest sapling survival is affected negatively in dry years (Joubert, unpublished data). Below average rainfall occurred in 2002 and 2003, and this is likely to have reduced survival. Based on rainfall records from 1892, there have probably only been six potential successful recruitment events up to

2006. This study provides support for the episodic recruitment of *A. mellifera* proposed by Joubert et al.(2008a) (see Chapter 2).

Although dispersal is generally very limited, survival was significantly improved away from parent trees. This is a typical pattern followed by other species of *Acacias* in savannas (e.g. Smith and Goodman, 1986; Miller, 1994; Barnes, 2001).Full morning and or afternoon sunlight occurred under many of the tall *A. mellifera* trees in this study in which there was no seedling survival. Also, observations of seedlings growing in the shade of climax grass species show that *A. mellifera* seedlings are shade tolerant (Joubert, unpublished data). Furthermore, differences in the soil nutrient status under and between *A. mellifera* canopies, which occurred in a specific spatial gradient from the stem base of the plants towards the open, uncanopied areas have been demonstrated, with the highest values recorded in the area surrounding the stem base (Hagos and Smit, 2005). In a controlled experiment it was demonstrated that under adequate soil water conditions *A. mellifera* seedlings grow better in soil extracted from under tree canopies due to the higher soil nutrient status (Hagos, 2001). The exact mechanism is not clearly understood, but the most likely inhibitor of seedling survival below parent trees is the reduced water infiltration below the tree. *A. mellifera* is known to very effectively funnel rainwater to the base of the stem, thus reducing water penetration under other parts of the canopy (Donaldson, 1967).

Table 3.3. Summary of the demographic processes of seed production, seed germination and seedling survival, related to seasonal rainfall from 1998 to 2004. Reasons are provided for the occurrence or non-occurrence for each process each season.

Rainfall season	Oct. 1998 - Apr 1999		Oct. 1999 - Apr 2000		Oct. 2000 - Apr 2001		Oct. 2002 - Apr 2003		Oct. 2003 - Apr 2004	
Rainfall	Low (< 300 mm)		Very high (> 700 mm)		High (> 400 mm)		Low (< 300 mm)		High (> 400 mm)	
Month	Nov. 1998	Jan. - Apr 1999	Nov. 1999	Jan. - Apr 2000	Nov. 2000	Jan. - Apr 2001	Nov. 2002	Jan. - Apr 2003	Nov. 2003	Jan.- Apr 2004
Seed production	None	▨	None	▨	En masse	▨	En masse	▨	None	▨
Reason	Previous season's rainfall low	▨	Previous season's rainfall low	▨	Previous season's rainfall high	▨	Previous season's rainfall high	▨	Previous season's rainfall low	▨
Germination	▨	None	▨	None	▨	High	▨	Yes	▨	None
Reason	▨	No seed production	▨	No seed production	▨	*En masse* seed production	▨	*En masse* seed production	▨	No seed production
Seedling survival	▨	▨	▨	▨	▨	Yes	▨	None	▨	▨
Reason	▨	▨	▨	▨	▨	Favourable rainfall this season	▨	Low rainfall this season	▨	▨

Seedling growth rates in the study area are generally very slow, as the results show. Stem diameter increases of less than 1 mm per annum on average were recorded. Resource managers often assume recruitment is continuous because of the large density of small individuals of less than 0.5 m, especially around large parent trees. This study emphasises how misleading such assumptions can be. Based on growth rates here and on concurrent studies (Joubert, unpublished data) this size class could include individuals of 20 years old or older.

Currently, the removal of large, potential seed producing trees, by felling, stem burning or by arboricide application, is favoured as a bush control method. Clearing large trees after *en masse* seed production may dramatically increase available water and hence the survival of germinating seedlings, and thereby promote a recruitment event (Smit, 2004). In addition to the increased soil water, the higher nutrient levels where trees are removed (Hagos and Smit, 2005) may also enhance the survival of seedlings. Whilst the increased nitrogen and water levels will also favour the growth of grasses (Kraaij and Ward, 2006), Joubert and Smit (2009) suggest that competitive effects of grass swards in arid savannas are typically not very strong. Because *A. mellifera* recruitments events are infrequent in arid savannas, fire as a preventative measure to kill seedlings and very young saplings is only needed very infrequently (Joubert et al., 2008a; see Chapter 2). Management of rangelands, including arid savannas, requires an understanding of the phenologies of key plants. Likewise, more phenological studies such as this are required for the development of general theories of bush thickening.

CHAPTER 4: THE ROLE OF FIRE IN PREVENTING TRANSITIONS FROM A GRASS DOMINATED STATE TO A BUSH THICKENED STATE IN AN ARID SAVANNAS

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Minor editing changes have been made.

Abstract

The role of fire in controlling bush thickening in arid savannas was investigated. Three controlled fires were initiated to investigate the responses of planted seedlings, saplings and mature shrubs. The stem diameters of seedlings, saplings and mature shrubs prior to the fire were measured. Other dimensions of the saplings and mature shrubs such as leaf mass were also calculated. The intensity of each fire was estimated. Fire temperatures adjacent to seedlings saplings and mature shrubs were measured using fire paints on steel plates. All three fires were moderately hot. One year after each fire, the mortality of seedlings in the fire treatments was very high (97.1-99.3 %) and significantly greater than in adjacent controls (16.1-51.6 %). Mortality and topkill of saplings and mature shrubs were negatively related to stem diameter. Fire temperature did not significantly affect mortality and topkill in most cases. Surviving saplings showed a much greater resprout response, relative to pre-fire size, than larger shrubs and trees. The results suggest that fire is crucial in interrupting the transition from open grassy savanna to thicket in arid savannas. Managers who prevent fires at this stage are likely to experience bush thickening in the future.

4.1 Introduction

In southern Africa the phenomenon of increasing woody plant density is commonly referred to as bush thickening and involves indigenous woody species occurring in their natural environment. It occurs across the rainfall gradient, from arid savannas (de Klerk, 2004) to mesic savannas (Skowno et al., 1999; Higgins et al., 2000) and has a strongly negative impact on beef production in Namibia (de Klerk, 2004) and elsewhere. The role of fire as a determinant of woody plant density has received considerable attention in the literature. However, this attention has focussed mainly on the mesic savannas rather than the more arid savannas.

Fire is a natural and integral component of the dynamics of savannas and grasslands. It has been considered largely responsible for the expansion of C4-grasslands in the Miocene (Osborne, 2008), and fires of both natural and anthropogenic origin prevent savannas in humid regions of the world from becoming forests (Backéus, 1992; Bond et al., 2005). Fire favours the grass component of savannas over the woody component. It is widely believed that anthropogenic transformations of fire regimes have had a significant effect on the structure of terrestrial ecosystems, including savannas, for millennia, long before modern pastoralist practices occurred (Bond and van Wilgen, 1996; Bird and Cali, 1998; Guyette et al., 2002). However, the evidence for this is considered “circumstantial and controversial” (Bond and van Wilgen, 1996).

In recent years, in most commercial ranching areas of southern Africa, fire has been suppressed, either as policy, or as a consequence of overgrazing and reduction of the fuel load (de Klerk, 2004; Scholes, 2009). In some cases fire is recommended, or tolerated, to maintain a productive grass layer, both through the retardation of woody growth and through the removal of moribund poor quality grassy material (Trollope, 2005). However, the importance of fires in maintaining open savannas is thought to diminish with increasing aridity (Higgins et al., 2000; Roques et al., 2001; Sankaran et al., 2005). Sankaran et al. (2005) analysed a vast number of sites of varying cover from studies in African savannas over a range of mean annual rainfalls ranging from 132 mm (arid) to 1 185 mm (mesic), and concluded that there was a threshold at approximately 650 mm mean annual rainfall, below which fire was increasingly less important in arid savannas. Therefore, the ability of fire alone to prevent bush thickening in savannas at the more arid end of the scale is questioned (Trollope, 1980; Higgins et al., 2000). Trollope (1980) suggests that the role of fire in these areas is to maintain tree height in the browse zone. A general “rule of thumb” is that the fuel load (dry mass of standing grass) required for a fire to effectively topkill shrubs in southern Africa is 2000 kg ha^{-1} (Trollope, 1984). In arid savannas fuel loads are very rarely this high, even if bush thickening has not yet occurred.

It has been suggested that direct competition between grasses and woody seedlings and saplings, for soil water in particular, can suppress the recruitment of woody species (Riginos and Young, 2007; van der Waal et al., 2009; Ward and Esler, 2011), although several studies show no direct competitive effects (O’Connor, 1995; Brown et al., 1998; Brown and Archer, 1999; Kraaij and Ward, 2006). Whilst these contrasting results are probably due to differences in species, climates and soils, preliminary findings in arid Namibia suggest that direct competition for soil water from climax perennial grasses has little effect on the growth of *Acacia mellifera* seedlings and climax grass swards do not prevent recruitment directly (Joubert and Smit, 2009). Yet, woody cover in these savannas ranges from less than 5 % to over 80 % at the hectare scale (100 % at a smaller scale) (Joubert, 2007). Neither competition nor soil water limitations appear to explain this large variability.

One possibility for explaining this variable cover is fire (variability in fire frequency and fire intensity, for example), even though it is considered of lesser importance in this regard in arid savannas (e.g. Sankaran et al., 2005). The majority of research on the effectiveness of burning in reducing bush cover and density is focussed on the visible tree and shrub layer (for example Trollope and Tainton, 1986; Meyer et al., 2005). There has been little emphasis on the effects of fire on tree seedlings and small saplings that do not project above the grass sward. Mesic savannas are prevented from becoming dominated by a woody layer through the topkill of saplings that are unable to escape the fire sensitive stage when fires are sufficiently frequent (Skowno et al., 1999; Higgins et al., 2000). Joubert et al. (2008a) (see Chapter 2) predicted that fire in an arid Namibian savanna, although infrequent and generally cooler than in more mesic savannas, is nevertheless essential in keeping savannas in an open grassy state, but only during a relatively small window period at the time of potential seedling establishment, during a protracted period of well above average rainfall (Joubert et al., 2013; Chapter 3). This hypothesis was tested and the effects of fire intensity and temperature on the mortality and regrowth of saplings and mature shrubs at an arid savanna site was also investigated.

4.2 Study area

The study was conducted in the Highland Savanna (Giess, 1998) in central Namibia on Neudamm Farm, which houses the Neudamm Agricultural Campus of the University of Namibia. The Highland Savanna is described in detail in Joubert et al. (2008a) (see Chapter 2). With a long term (1892-2003) annual rainfall of 361 mm (CV = 40 %), an aridity ratio (UNESCO, 1977) of approximately 0.17, the Highland Savanna represents a savanna at the arid end of the scale. At the time of the study very little of this predominantly commercial ranching area supported a climax grass layer, and this is widely considered a consequence of excessive livestock pressure.

A. mellifera is often dominant, forming thickets of over 80 % canopy cover ranging in size from less than one to several hundred hectares. Such landscape scale encroached areas are also considered to be a symptom of degradation through excessive livestock pressure.

Neudamm Farm covers an area of 10 187 ha. It has been used largely for educational purposes and is thus generally lightly stocked. The south western part of the farm (4 000 ha) is used solely for small stock farming, including different varieties of sheep and goats, at a stocking rate of around 20 ha/LSU. A LSU is the equivalent of a cow with a mass of 450 kg and a mass gain of 500 g per day (Meissner, 1982). Thus, 20 ha of land are used to feed one cow or steer in a year. A loose rotational grazing system is applied.

The camps where the experimental work was conducted included a large component of what is considered savanna close to a climax state, and at the time dominated by large tufted perennials such as *Anthephora pubescens*, *Brachiaria nigropedata*, *Cenchrus ciliaris*, *Heteropogon contortus* and *Schmidtia pappophoroides*, and the much smaller tufted perennial, *Eragrostis nindensis* which is considered a subclimax grass. There was also a low density of *A. mellifera* trees and shrubs and, in places, a high density of small (<0.05 m) *A. mellifera* saplings as well as other woody species typical of the Highland Savanna, including *Tarconanthus camphoratus* (co-dominant), *Acacia hereroensis*, *A. hebeclada*, *Catophractes alexandri*, *Grewia flava*, *Lycium oxycarpum* and *Searsia marlothi*.

4.3 Materials and methods

Three areas of approximately 1 ha each were selected on Neudamm Farm to represent savanna in a climax or near climax savanna state. Two of the areas (A and C) were dominated by

A. *pubescens* and one area (Area B) was dominated by *S*. *pappophoroides*. These two species are considered valuable palatable climax and sub-climax grass species, respectively (Müller, 2007). Grass swards dominated by these grass species might be expected to provide competition for *A*. *mellifera* seedlings, as well as to produce sufficient biomass for an effective fire. In all three study areas *E*. *nindensis* was the most abundant grass although, due to its low production, formed a very small proportion of the biomass. In each area approximately five *A*. *mellifera* seeds were planted next to and away from tufts of climax grass species in 72 x 0.81 m^2 plots in late January 2008. The seeds were collected in December 2007 from mature trees in the vicinity. Only large, well-formed seeds were planted. After extra water was initially provided to ensure successful germination, seedlings were left untreated. Half (36) of the paired plots were in the portion of the area to be burnt (FIRE) and the other half in the area that was not burnt, hereafter referred to as the control (CONTROL).

Seedling stem diameters and heights were measured with a calliper, and survival was determined in the week prior to burning, in both FIRE and CONTROL plots. A representative sample of 71 (FIRE) and 66 (CONTROL) (Area A), 61 (FIRE) and 50 (CONTROL) (Area B) and 63 (FIRE) and 43 (CONTROL) (Area C) *A*. *mellifera* saplings and mature shrubs was randomly selected and labelled. Stem diameters were measured and basal stem surface areas calculated. Estimates of canopy volume (CV), leaf volume (LV), leaf mass (LM) and Browse Tree Equivalents (BTE) (the leaf mass equivalent of a 1.5 m single stemmed tree) were derived for each plant using the BECVOL-model developed by Smit (1989a, 1989b, 1996).

Fuel loads were determined with a harvest method (Grunow et al., 1980). All rooted herbaceous plants were harvested in 30 randomly placed quadrats (1 m^2) per plot. Plants within each quadrat were clipped to stubble height (0.1 cm) using hand clippers. The clipped material was dried to a constant mass (70 ^{o}C) and weighed. Fuel moisture content was also determined prior to each fire. Fire breaks with a width of approximately 4 m were graded around the FIRE treatment to prevent the spread of the fire.

Steel plates of 20 cm x 5 cm were painted with dashes of Tempilac® fire temperature paints of different melting points (79 ^{o}C; 149 ^{o}C; 232 ^{o}C; 288 ^{o}C; 316 ^{o}C; 427 ^{o}C; 510 ^{o}C; 621 ^{o}C; 704 ^{o}C; 816 ^{o}C) to provide information on the fire temperature. Melted paints reflect minimum melting temperatures (MMTs). For instance, on a plate with a melted 79 ^{o}C paint, the actual temperature could be as high as 148 ^{o}C. Despite this, there is a high correlation between these temperatures and temperatures recorded by more sophisticated logger-probes (Iverson et al., 2004). The plates were numbered and tied to metal pegs so that they were suspended 5 cm above the ground. Two fire plates were placed in each of 36 x 0.81 m^{2} plots in FIRE, where there were surviving seedlings. One of these was placed close to seedlings planted adjacent to climax grass tufts (GRASS) and the other placed close to seedlings planted away from the tuft (OPEN). This provided temperatures within flames and just adjacent to flames. A fire plate was also placed next to most labelled and measured saplings and mature plants. In this way the MMTs could be recorded for each seedling and most labelled saplings and mature plants. In addition, MMTs were measured by placing fire plates at 5 cm and 100 cm above the ground on droppers evenly spread throughout FIRE in B and C. These provided a non-biased estimate of the distribution of fire temperatures within FIRE, both horizontally and vertically. Although the recorded temperatures in this method are the temperature of the metal itself, and are a function of a number of sources of heat, they can be considered indicators of differences in true fire intensity (Iverson et al., 2004).

Area A was burnt on 22 October 2008, whereas Areas B and C were burnt on 21 October 2009 and 12 November 2009, respectively. Therefore, seedlings in A had grown for one season, whereas seedlings in B and C had grown for two seasons, at the time of the fires. All fires were ignited between 08h00 and 09h00. Firstly, a back burn was burnt in order to minimise the risk of the fire spreading. Wind speed, relative humidity and air temperature were measured on site. This, along with the rate of spread of the fire was used to determine fire intensity, using the formula: $I = H\ w\ r$ where I is fire intensity (kJ s^{-1} m^{-1}), H is heat yield (kJ kg^{-1}), w is mass of available fuel (kg m^{-2}), r is rate of spread of fire (m s^{-1}). In addition, a regression model (Trollope et al., 2002) was used to estimate fire intensity, based on fuel load, fuel moisture, relative humidity and wind speed. Trollope (pers. comm.) recommended using the regression model due to the difficulties in estimating the rate of spread of fire. The model is as follows: Fire intensity = $2729 + 0.8684FL - (530\sqrt{FM}) - (0.1907RH^2) - e(596/WS)$ where FL is fuel load (kg ha^{-1}), FM is fuel moisture (%), RH is relative humidity (%) WS is wind speed (m s^{-1}). Based on the criteria of Trollope (2005) fires were then categorised as either very cool, cool, moderately hot, hot, or extremely hot.

4.4 Statistical analysis

Wilcoxon's signed rank test was used to compare MMTs at 5 cm and 100 cm above ground. This provided an idea of the vertical temperature distribution of the fire. Wilcoxon's signed rank test was also used to compare MMTs close to grass (GRASS) and away from grass (OPEN) to determine whether seedlings in GRASS were subjected to higher fire temperatures than seedlings in OPEN. A multiple *post hoc* comparison with Kruskal-Wallis test determined whether the fire temperatures (MMTs) experienced by seedlings at A, B and C and in GRASS and OPEN differed significantly from each other. A Chi-square analysis was used to determine whether seedling mortality rates were higher in FIRE than in CONTROL for A and B. Logit regressions (StatsoftInc. 2004) were used to develop a predictive model for the probabilities of two binary responses (topkill and mortality) as effects of MMTs (as categorical predictor), and largest stem diameters (LSD), stem basal surface area (SBSA), and leaf mass as a proportion of leaf mass of a Browse Tree Equivalent prior to the fire (preBTE) (as continuous predictor variables). A Browse Tree Equivalent is the "leaf mass equivalent of a 1.5 m single stemmed tree" (Smit, 1996).

The effects of MMTs, and the other pre-fire dimensions of the plants (as continuous predictor variables), on regrowth, as a % of the preBTE dimensions, was also determined using multiple regression techniques. In this case, death was considered part of the continuous dependent variable of % regrowth and considered as 0 %. BTE was selected since BECVOL was able to discern close to zero values for this parameter.

4.5 Results

4.5.1 Fire behaviour

Despite fairly low fuel loads, fire intensity was estimated to be moderately hot, according to Trollope (2005), largely due to the low fuel moisture and low relative humidity at the time of the fires (Table 4.1). Fire temperatures in the 2009 fires (B and C) were significantly hotter close to the ground than 1 m above the ground (Table 4.2). In A (2008 fire), mean MMTs for GRASS were much higher than OPEN, but in B and C (2009 fires) only slightly higher (and not significantly so in C) (Table 4.3). In many instances MMTs were the same, particularly in B and C (2009 fires). Multiple comparisons with a Kruskal-Wallis test showed that the fire temperatures (MMTs) experienced by *A. mellifera* seedlings in A (2008 fire) were significantly ($p < 0.05$) lower than seedlings in B and that all MMTs were significantly (*p* < 0.05) higher for all treatments than for A OPEN. A wide range of temperatures was thus experienced by seedlings across the three fires (Table 4.3).

Table 4.1. Fire regime as measured for plots A, B and C, respectively: Fuel loads, fuel moisture, relative humidity, air temperature, wind speeds, fire intensity. Values in parentheses are ± standard errors.

Area	Fuel load ($kg.ha^{-1}$)	Fuel moisture (%)	Relative humidity (%)	Air temperature (^{0}C)	Wind speed ($k.h^{-1}$)	Fire intensity ($kJ. s^{-1}.m^{-1}$)	Fire intensity category
A	1128.21	9.01 (0.57)	25	20	2.00 (0.21)	1699	Moderately hot
B	1809.67	19.60 (1.23)	33	25	5.04 (1.18)	1628	Moderately hot
C	1006.00	9.50 (0.58)	23	25	9.60 (2.00)	1806	Moderately hot

Table 4.2. Mean MMTs recorded at 5 cm and 100 cm above ground for B and C which were burnt in 2009. Values for $T^{o}C$ 5cm and $T^{o}C$ 100 cm in parentheses are ± standard deviations. Significant differences were tested for using Wilcoxon's signed rank test. * denotes significant differences ($p < 0.05$).

Area	$T^{o}C$ 5cm	$T^{o}C$ 100 cm
B (N = 10) *	253 (72)	143 (45)
C (N = 20) *	181 (83)	135 (89)

Table 4.3. Fire temperatures (MMTs) next to (GRASS) and away from grass (OPEN). Values in parentheses are ± standard errors. Significant differences between GRASS and OPEN were tested using Wilcoxon's signed rank test for each of the three fires. Superscript numbers denote significant differences ($p<0.05$) between fire temperatures across all six treatments (in this case, all GRASS and OPEN treatments for the three fires were compared together) (multiple comparisons with a Kruskal-Wallis test).

Area	GRASS	OPEN	Significance (Wilcoxon's signed rank test)
A	99 (13)^{1}	42 (8)^{2}	$p < 0.01$
B	201 (14)^{3}	186 (14)^{3}	$p < 0.05$
C	155 (17)^{1,3}	127 (9)^{1,3}	$p = 0.07$ (ns)

Table 4.4. Preburn stem heights and diameters of seedlings in FIRE and CONTROL in A (first year seedlings) and B and C (second year seedlings). A t-test for independent samples was used. N refers to the number of samples in each case. ***** denotes a significant different in stem measurements between FIRE and CONTROL.

Area	FIRE				CONTROL			
	Stem diameter (mm)	Stem height (cm)	N (stem diameter)	N (stem height)	Stem diameter (mm)	Stem height (cm)	N (stem diameter)	N (stem height)
A	1.97	3.63	109	110	1.88	3.74	58	60
B	4.40*	8.71*	151	151	4.07*	7.82*	140	140
C	3.71	6.76	197	197	3.64	6.24	161	161

4.5.2 Impact of fire on seedlings, saplings and mature shrubs

Pre-burn stem diameters and heights were comparable in FIRE and CONTROL for Fires A (2008) and C, but in Fire B were significantly ($p < 0.05$) larger in FIRE than in CONTROL. This poses no problem for the results since chi square-analysis reveals a significantly higher mortality for FIRE in A and B than for CONTROL ($p < 0.001$) (Figure 4.1), despite the larger sizes of the seedlings.

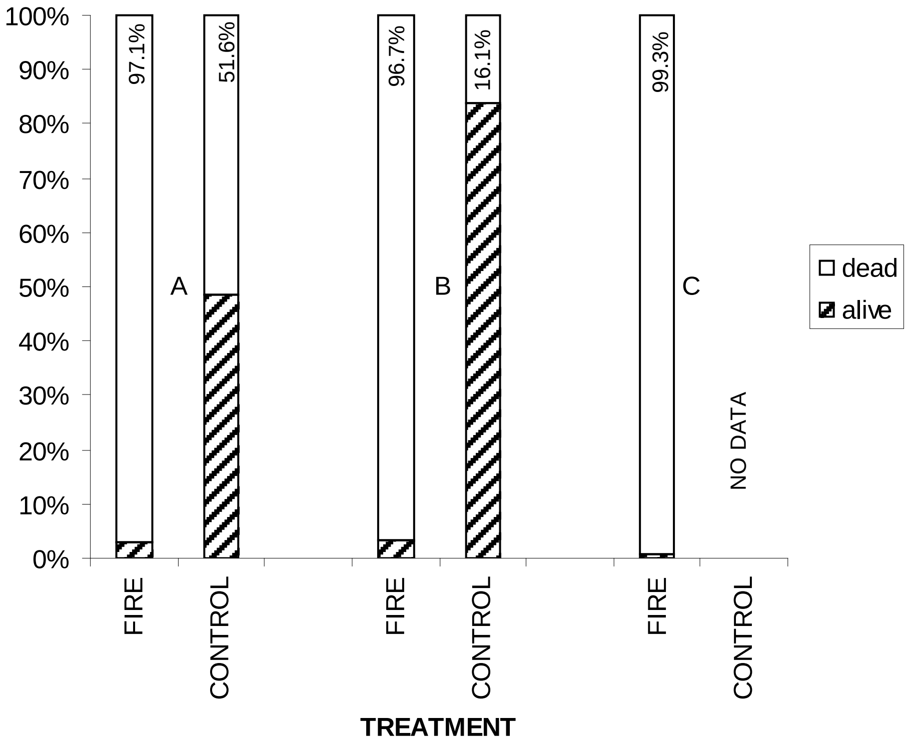

Figure 4.1. Percentage mortality (open) in FIRE and CONTROL (shaded) in A (first year seedlings) and B and C (second year seedlings), (CONTROL data not available for C). Percentage mortality is also indicated in bars.

Almost all the *A. mellifera* seedlings died in each fire (Figure 4.1). The mortality of CONTROL seedlings in B (2009) was much lower than in A (2008). The results show that fire was equally effective in killing seedlings in the second year (2009) as in the first year (2008). This might be due to higher fire temperatures experienced by the larger second year seedlings. In each treatment, the trend is much the same. Almost all seedlings died, about half of saplings < 10 mm died and a small proportion of mature shrubs of higher stem diameter classes (Figure 4.2). All saplings and mature shrubs survived in controls.

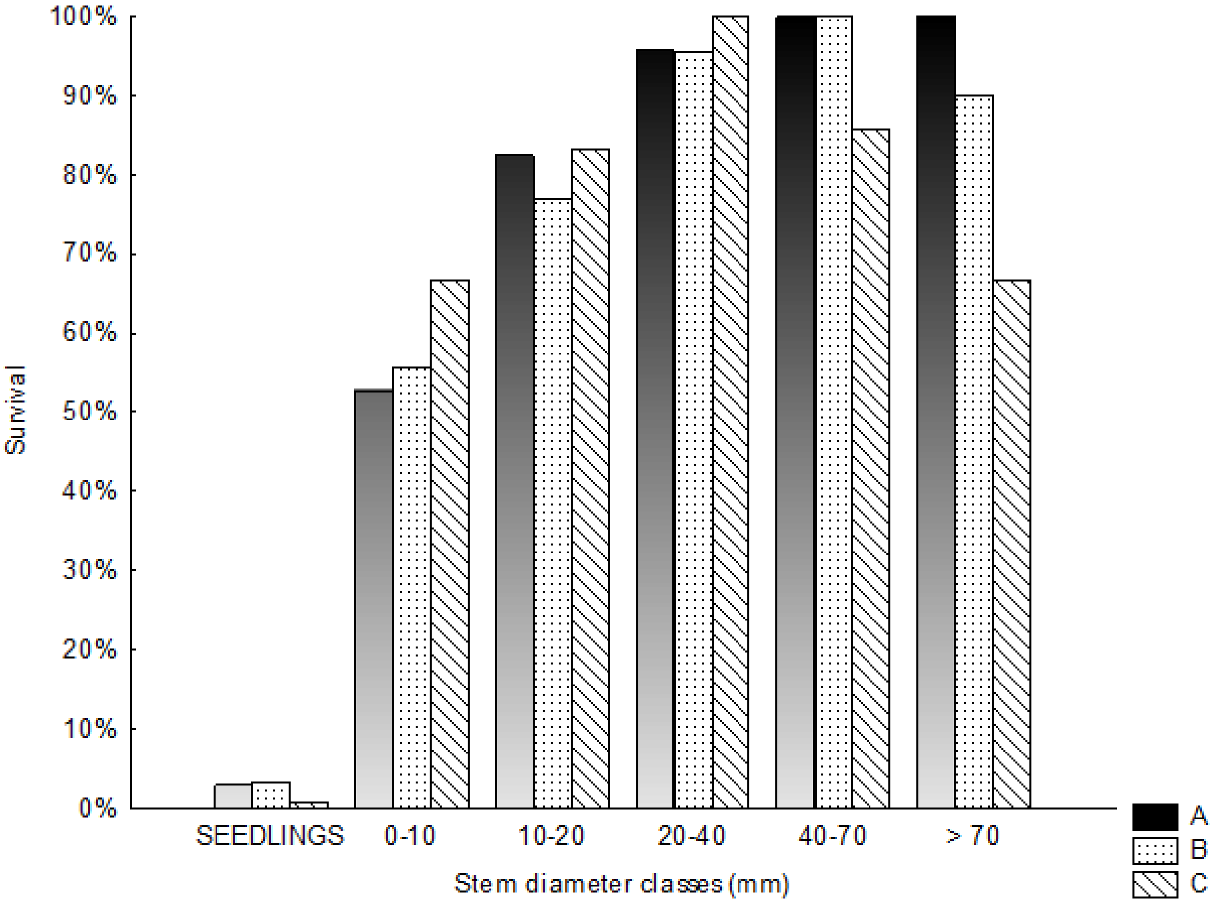

Figure 4.2. Percentage survival in FIRE in relation to stem diameter classes for all *A. mellifera* seedlings, saplings and mature shrubs. Seedlings are grouped together.

Logit regression analysis showed that pre-fire stem diameter strongly affected both topkill, and mortality ($p < 0.001$) (Figure 4.3). However, logit regression analysis showed no effect of MMTs on either of these binary responses and MMTs are thus not included in the model. The effect of preBTE (leaf mass equivalent as a proportion of the leaf mass of a Browse Tree Equivalent prior to the fire) on mortality was not significant ($p = 0.153$), but was highly significant on topkill. Since preBTE and stem diameter were highly correlated ($r = 0.822$) stem diameter was used as the continuous predictor variable. Topkill shows a slower, more gradual decline with increasing stem diameter, whereas survival shows a dramatic increase from virtually zero to almost 100 % within a stem diameter of 30 mm. This coincides well with the actual data shown in Figure 4.2. When regrowth was considered as a continuous dependent variable in a multiple regression (with MMT and stem diameter as independent variables) however (with death = 0 % regrowth) MMTs were shown to negatively affect regrowth (*r* = -0.32), whilst stem diameter positively affected regrowth (*r* = 0.40) (regrowth as a proportion of preBTE).

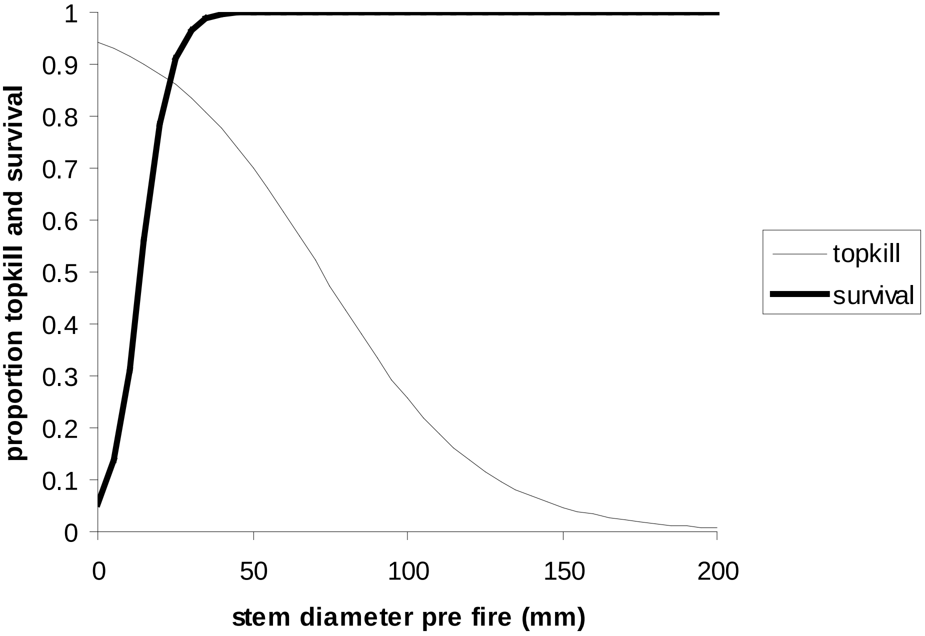

Figure 4.3. Logit regression model of the probabilities of topkill and survival in relation to pre fire stem diameter. The survival model includes seedlings. In both cases $p < 0.001$.

From Figure 4.4 it is evident that in terms of effect of fire on relative regrowth of surviving individuals, larger trees are far more adversely affected than small saplings, if topkill occurs. Small saplings show a rapid resprouting growth response whereas large mature shrubs show a much slower response, as a proportion of their original leaf mass. Fire A (2008) and B both had a relatively high number of mature shrubs which were not topkilled, whereas in C there were only two.

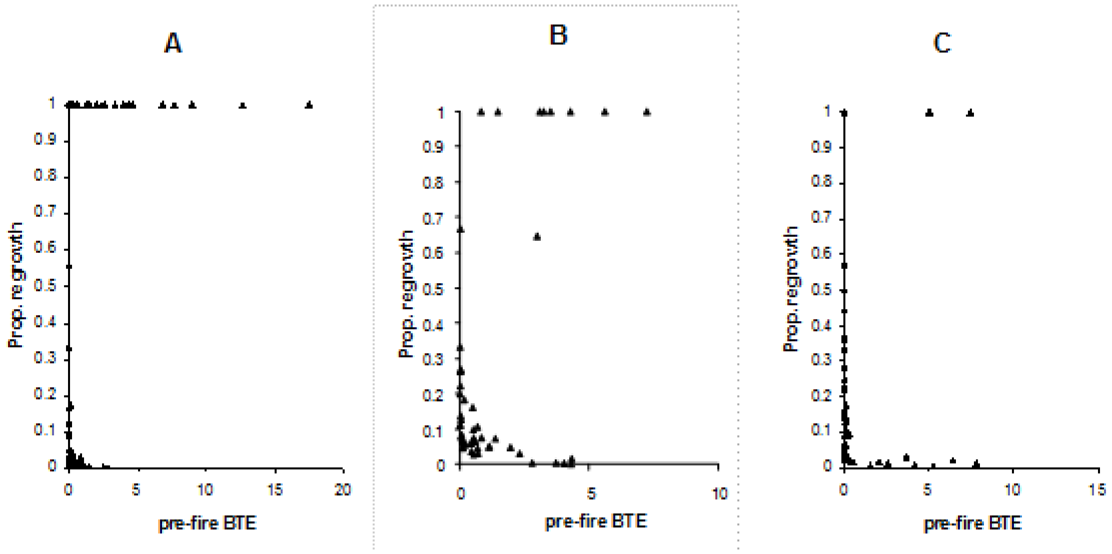

Figure 4.4. Scatterplot showing the responses of survived *A. mellifera* saplings and mature shrubs to fires A, B and C, in terms of proportion regrowth (Y-axis) in relation to pre-fire BTE (X-axis). Data points with a proportion regrowth of 1 were not topkilled, excepting for two saplings of < 1 BTE which regrew to pre-fire dimensions.

4.6 Discussion

Despite relatively low fuel loads, fire intensities of all fires were estimated to be “moderately hot”. This was mostly due to the low fuel moisture and relative humidity levels present at the time of the fires. Fire temperatures of the first fire in 2008 (field A) were generally much lower than those of the 2009 fires (fields B and C), despite the estimated fire intensities being similar. However, seedlings experienced similar mortality rates, since the seedlings in 2008 were younger and smaller. Fire temperature generally had little effect on seedling, sapling and mature shrub survival, as well as topkill. Fire temperatures next to and away from the grass tufts were sufficient to kill almost all seedlings in each trial. It would appear that a threshold temperature was exceeded and that survival was thus more dependent upon the existing condition of the individual plants, in particular the basal stem diameters. The survival response increased rapidly with increasing stem diameter, while the topkill response was much more gradual. Larger stem diameters are greater heat sinks and also would suffer relatively less xylem damage (Balfour and Midgley, 2006). It is likely also that smaller saplings, as well as seedlings, did not have sufficient carbohydrate reserves in the roots to enable coppice growth. Although Bond and van Wilgen (1996) state that fire intensity, season and burn area can have vastly different “event dependent” effects on both the grass layer and the woody layer, the topkill of woody species in semi-arid savannas of the Eastern Cape and Kruger National Park, South Africa, was not much affected by fire intensity (Trollope et al., 2002). Bush mortality in the same areas (Trollope and Tainton, 1986; Trollope et al., 1990) increased with fire intensity, but remained very low (9.3 % and 1.3 %, respectively). In the case of the three applied fires in this study, overall fire intensity played a relatively minor role in both topkill and mortality, although the rate of regrowth was negatively affected by fire temperature.

Many of the studies of the effects of fire have focussed on the measured outcomes (particularly the changes in cover) rather than the processes that result in the outcome (survival and resprouting of a cohort of seedlings and young saplings for example). Havstad and James (2010) report that a single fire did not make a difference to the percentage woody cover, either of a grass dominated, or a shrub dominated, arid grassland in New Mexico, USA. However, the effects of fire, as is shown here, might be dependent upon whether seedlings and young saplings were present at the time of the fire. Given the size of seedlings, and the very slow growth rates of both seedlings and mature *A. mellifera* plants in general (Joubert, 2007), cover changes over 13 years might not even be detectable. Thus, a study of the effects of fire in the study area on cover change if no small seedlings and saplings were present at the time of fire, or if the study was carried out over a ten year period (with slow growing seedlings and saplings present), might have shown no changes relative to controls. This study focused on the direct impacts of the fire as a recruitment filter on individuals, emphasising the importance of the fire occurring during a small window of a few years. It affirms that fires are infrequent, yet crucial, events in controlling arid savanna dynamics by interrupting the otherwise foregone transition towards a bushy state. Competition (primarily for moisture) appears too weak to interrupt this transition (Joubert and Smit, 2009) though it may slow it down. Other studies show no direct competitive effects between grass tufts and woody seedlings (O'Connor, 1995; Brown et al., 1998; Brown and Archer, 1999; Kraaij and Ward, 2006). In the arid southern African savannas, recruitment events involving *A. mellifera* coincide with protracted periods of above average and favourably distributed rainfall, which is also coincident with high fuel loads (Joubert et al., 2008a) (see Chapter 2), but only when rangelands are not overgrazed. In arid savannas, fires coincident with establishment events kill seedlings, whereas small saplings that are in the region of ten years old (around 10 mm stem diameters depending upon growing conditions) already display a reasonably high survival rate (Figure 4.2and Figure 4.3), and those that survive show a very rapid resprouting response, recovering in some cases almost to their pre-fire leaf mass after one year. A similar trend was reported for the same species by Meyer et al. (2005). Thus, a small window of opportunity exists for rangeland managers to exploit fire. In mesic savannas, the timing of fires is less important, and fairly frequent fires hold saplings at a stage where combinations of fire and browse maintain an open savanna (Skowno et al., 1999; Bond and Midgley, 2000; Higgins et al., 2000; Bond et al., 2003). The topkill of survivors was remarkably high relative to other studies (Trollope et al., 2002), particularly considering the relatively low fire intensities in this study.

The slow growth response of larger shrubs after the burn (Figure 4.4) suggests that fire in an arid savanna may also reduce the canopy cover of woody shrubs and with frequent fires maintain an open savanna. Trollope (1980) emphasizes the importance of browsers in combination with fire in maintaining an open sward in arid savannas, but the experience of rangeland managers in Namibia is that browsers such as goats tend to avoid *A. mellifera* resprout owing to the presence of already hard thorns and a woody stem. However, other encroaching species, such as *Dichrostachys cinerea*, are far more acceptable to browsers. In view of this, and given the very low frequency of natural and anthropogenic fires in arid savannas as suggested by van Wilgen et al. (1997) and Joubert et al. (2008a), regrowth is likely to return shrubs to a size close to their pre-fire size in the fire interval period, depending upon the rainfall, grazing intensity and associated build-up of grass fuel.

Increased fire frequencies in arid savannas may also have negative ecosystem impacts. The production of important perennial grass species one year after fire in the study area was significantly reduced (Joubert, unpublished data). Furthermore, during burning, significant nutrient losses from the soil are produced by volatilization and ash convection in the smoke column (Raison et al., 1985; Gillon and Rapp, 1989). These losses are especially relevant in high intensity fires (Little and Ohmann, 1988). When fire frequency is above a certain threshold, insufficient time is available for succession-related nutrient inputs to replace fire-related losses. This can result in a long term decline in soil fertility and eventual desertification, as shown by Cobo and Carreira (2003) in Mediterranean semi-arid shrublands of southeastern Spain. A similar situation is likely to be the case in arid savannas, where carbon accumulation is much slower than in mesic savannas. Thus, although more frequent fires might maintain mature shrubs at a much smaller size, essentially keeping the savanna open, the consequences of this on other ecosystem components such as grass production and ecosystem nutrient capital are negative.

In a natural system where fire intervals are determined by lightning strikes, the intervals are likely to be long enough for the various nutrient inputs and outputs to balance, and at the same time are coincident with establishment events. Prior to the advent of more intensive commercial ranching, fire coincident with seedling establishment was most likely the main reason why the Highland Savanna (as well as other arid savannas) was a more open savanna. Rangeland managers who deliberately exclude fires, and rely on competition from grasses to interrupt the transition from an open grassy savanna to bush thicket will fail to stop the transition. Rangeland managers have to include fire management, but they must ensure that fires are coincident with establishment events. A general principle that can be drawn from this study, in combination with studies from other more mesic savannas is that fire frequency is an increasingly important variable in mesic savannas in maintaining an open savanna, whereas the coincident timing of fire is increasingly important in maintaining open arid savannas.

CHAPTER 5: THE DEVELOPMENT OF AN EXPERT SYSTEM FOR ARID RANGELAND MANAGEMENT IN CENTRAL NAMIBIA WITH EMPHASIS ON BUSH THICKENING

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Minor editing changes have been made.

Abstract

An online expert system derived from research and expert knowledge was developed for arid rangeland management in Central Namibia. The expert system emphasises the control of bush thickening and is divided into three forms of decisions: adaptive, reactive and ongoing good management. Adaptive decisions are mostly related to periods of protracted high rainfall, as this is a critical window both in terms of a hazard (transition to bushy thickened state if no fire is applied) and opportunity (transition back to an open savanna if fire is applied). Currently, the expert system uses wiki technology, as this allows a high level of interaction between user and administrator. The expert system includes embedded links to photographs and additional information. It allows easy updating of the knowledge base. An additional booklet was also developed, since access to computers and the internet is still limited in many rural areas. Although the evaluation of the expert system will be determined partly by its acceptance by rangeland managers, many of the Critical Success Factors relating to Decision Support Systems were adhered to in its development. The chapter discusses some key strategies for the success of this and similar Decision Support Systems for improved rangeland management in the future.

5.1 Introduction

A coherent and accepted conceptual model of rangeland dynamics is an important prerequisite for successful rangeland management. However, the translation of concepts to improved management is difficult, and requires various forms of facilitation. One such facilitation is the use of expert systems. According to Noble (1987, p115), an expert system is a computer programme that is “capable of holding an apparently intelligent conversation with the user”. “Decision Support System” (DSS) is a generic term referring to a variety of computer systems designed to provide decision support. Besides the recognition of the value of expert and other decision support systems in the business world (Guimaeres et al., 1992), they are also considered to be potentially useful when applied to natural resource management problems (Davis et al., 1989). Some expert systems have been developed specifically for the use and management of fire. These include SHRUBKILL (based on BURNTIME) for management burns in semi-arid Australian savannas to control the establishment of woody plants (Ludwig, 1988), an expert system for burning in Kakadu National Park, Northern Australia (Davis et al., 1986), a support tool integrating bush control and management (Nobel and Walker, 2006), FIRETOOL, for fire management in Brazilian Savannas (Pivello and Norton, 1996) and one for fire management in the fynbos of Western Cape, South Africa (Richardson et al., 1994). Other applications include wetland, biodiversity and forest management (Stock and Rauscher, 1996), as well as the screening of invasive species in Fynbos, South Africa (Tucker and Richardson, 1995). Currently the only rangeland management expert system known to be available in Namibia, is BushExpert (Barac et al., 2004) which relies on a database of best practices of relevance to the restoration of already encroached land. The expert system described in this chapter emphasises adaptive and preventative management, and includes decisions related to restoration as well.

Bush thickening by *Acacia mellifera* and *Dichrostachys cinerea* has long been considered a major ecological and economic problem in the rangelands of Namibia (e.g. Walter and Volk, 1954; De Klerk, 2004) as well as in other southern African countries (e.g. Donaldson, 1967; Scott, 1967; Skarpe, 1990; Smit et al., 1999; Higgins et al., 2000). Bush thickening also affects many other parts of the world (e.g. Hodgkinson and Harrington, 1985; Archer et al., 1988). The area affected by bush thickening in Namibia is estimated to be about 260 000 km^2 (De Klerk, 2004) (almost a third of the surface area of the country). The bush-thickened areas fall mainly within the semi-arid savannas with rainfall varying from about 300 mm in the west to about 500 mm in the north-eastern parts. A decade ago it was estimated that N$ 700 million was lost to the economy annually as a result of declining stocking rates and decreased beef production since 1959 (De Klerk, 2004) and this figure is considered to have at least doubled since then (De Klerk pers. comm.) although there is little consensus as to how much of this amount can be ascribed to bush thickening. However, this figure does not take into account the costs of control measures, such as the application of arboricide.

A conceptual model of rangeland dynamics for the arid Highland Savanna of Namibia with an emphasis on bush thickening by the major thickening species, *A. mellifera* is described in Chapter 2 (Joubert et al., 2008a). The model explicitly accounts for the effects of extreme rainfall events, frost and fire as drivers of transitions between stable states. These event-driven transitions represent important hazard or opportunity windows for rangeland managers in the language of state-and-transition conceptual models (Westoby et al., 1989). The conceptual model (Figure 5.1) recognises two major stable states (grass dominated and bush dominated) that require major disturbances (fire, extreme rainfall seasons and fungal diseases) to trigger transitions between them. This conceptual model, as well as a problem tree for bush thickening

(Zimmermann et al., 2008), forms the conceptual basis upon which most of the expert system has been constructed. Aspects of the conceptual model relevant to the expert system include:

- The requirement of three consecutive years of above average rainfall, for seed production, seed germination and seedling establishment. Seed banks of *A. mellifera* are not persistent for more than a season (Joubert et al., 2013; Chapter 3) due to their ease of germination, ease of digestion after ingestion, and their proneness to predation.
- The requirement of a hot fire to kill seedlings and young saplings and revert back to a grassy state, and thus prevent a further transition to a bushy state (Joubert et al., 2012; Chapter 4).
- The eventual senescence of mature *A. mellifera* thickets due to drought and fungal dieback (Holz and Schreuder, 1989; Holz and Bester, 2007) and the consequent reversion back to a grassy state (Joubert et al., 2008a; Chapter 2). The dynamics of the fungal dieback are uncertain but appear to be density dependent and related to drought conditions.
- Dieback from extreme frost events (Smit, 1990), which, when coupled with fire a year later, might also maintain savannas in a more open grassy state. Larger trees are relatively far more affected than smaller saplings. These observations have not been substantiated through rigorous experimentation as yet.

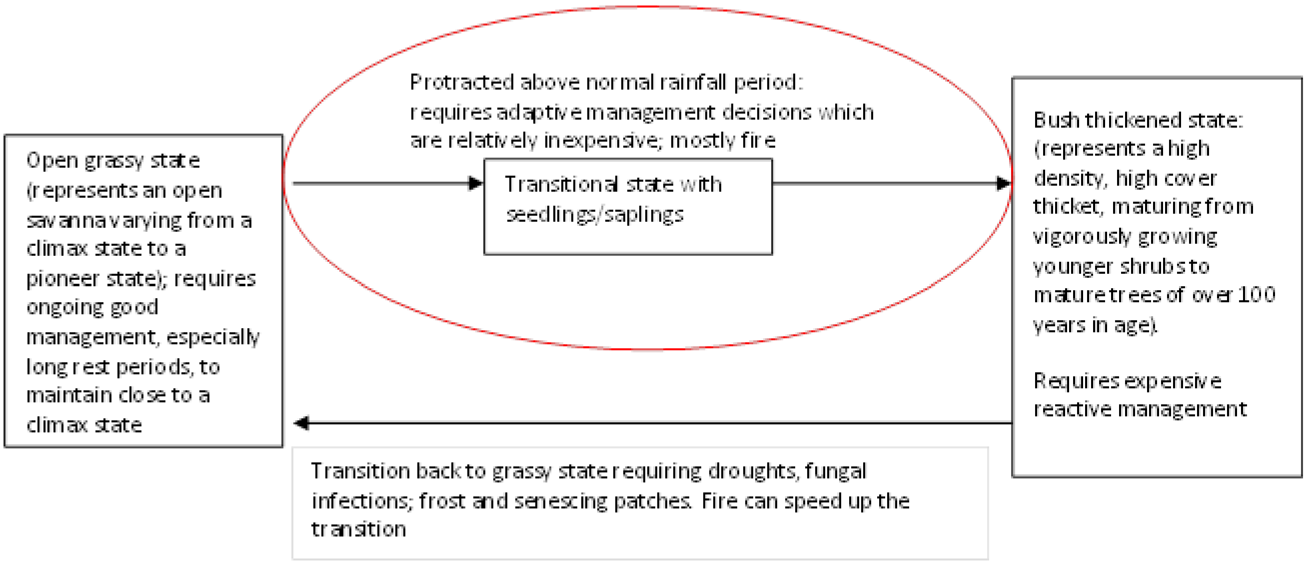

Figure 5.1. A simplified state-and-transition model of vegetation change in semiarid Namibian savanna with reference to *A. mellifera*, highlighting the potential transition in high rainfall years (adapted from Joubert et al., 2008a; see Chapter 2, Figure 2.2).

This chapter describes an expert system (including statements, decisions and rules), and its development, for arid rangeland management in Central Namibia, with an emphasis on bush thickening by *A. mellifera*. It highlights lessons learnt from its development and suggests ways forward for making it, and similar decision support systems, more applicable for natural resource management.

5.2 Methods

The expert system’s knowledge base (decisions, questions and rules) was largely constructed from accumulated expert knowledge, from the state and transition conceptual model of bush thickening (Figure 5.1) described in Chapter 2 (Joubert et al., 2008a), the literature (e.g. Donaldson, 1967; Smit et al., 1999; Kraaij and Ward, 2006) and from the knowledge of rangeland managers, including farmers, and advisers. This accumulated knowledge was used to construct a “problem tree” (Zimmermann et al., 2008) which links all the factors that affect bush thickening with arrows pointing from cause to causation and ultimately ending at the problem. Both the conceptual model and the problem tree were important in synthesizing the information into a coherent whole.

The relevant knowledge base was summarised in the form of a decision tree (Figure 5.2, Figure 5.3 and Figure 5.4) that captures, in abbreviated form, the sequence of questions and answers, ultimately arriving at a suggested decision. Although Starfield and Bleloch (1991) suggest that decision trees can quickly become unwieldy and that decision tables are easier to construct, the decision tree provides a visual representation of the natural sequence of steps taken in making the decisions. Farmers at workshops also found it useful to take a page with the decision tree into the field to facilitate *in situ* decision making.

Five workshops with farmers (between 2004 and 2007), and one workshop with extension officers (in 2010) were conducted. Each of these workshops had between 10 and 15 participants. The first workshop with farmers merely presented the expert system to an interested group of farmers and then demonstrated it to them in the field. The other workshops were more structured, and divided into three parts:

1) Testing the knowledge base and decisions against the decisions taken by farmers, 2) testing the software and usability issues of the interface and 3) presenting the expert system and its rules.
    1) Testing the knowledge base: Farmers were presented with six different rangeland scenarios in the field. Each farmer was independently required to identify the most suitable management practices for each scenario, using a semi-structured questionnaire. Responses were recorded and later analysed, and are reported in

Joubert et al. (2008b). The involvement of the farmers and land managers served various purposes. The workshops provided a forum to compare the farmers’ decisions with those recommended through the expert system. This provided insights into decision making by farmers, and gave a sense of how varied farmers’ decisions were for various scenarios (Joubert et al., 2008b). The involvement of the farmers in the development of the expert system also encouraged farmers to take ownership of the expert system and helped to gauge their expectations.

2) Testing the software and usability issues of the interface: At the workshops, the software and usability issues were tested, by filming the participants while they used the expert system, analysing their responses to the interface, and by asking direct questions through questionnaires. Participants’ responses were used to modify the interface and develop communication tools. In this way, end-user concerns and ideas were accounted for in the development of the expert system.
3) Presenting the expert system and its rules: Finally, a presentation of the conceptual model of bush thickening and of the expert system was given to the farmers, followed by an open-ended discussion.

The workshop with extension officers of the Extension Services of the Ministry of Agriculture, Water and Forestry followed a similar course to that outlined above, but the testing of the knowledge base and usability was done as a group discussion in the field and as a group in a computer laboratory respectively, rather than individually. Each participant was provided with a cd containing a non-editable version of the wiki expert system, and asked to test the expert system and provide feedback, both on the knowledge base and the interface. After the workshop with extension officers, the expert system was introduced to a group of approximately 50 farmers by extension services.

In 2008, the expert system was introduced to about 70 members of the public and invited key people such as rangeland researchers, at a BIOTA Open Day. Participants were able to run through the expert system with different scenarios at their leisure. Besides these hands on demonstrations, the expert system was also presented to three Farmer’s Days to approximately 50 people in each case.

After preparation of the initial knowledge base, an independent expert provided two short inputs into the development of the expert system. First, before being shown the expert system, he was asked to provide appropriate recommendations to deal with 15 different scenarios of rangeland condition used in the expert system, but for each of sandy and loamy soil. After his response, he was provided with the booklet form of the expert system, with the decisions recommended by the system, and asked to comment on it. These comments were subsequently evaluated and, where appropriate, incorporated into the knowledge base.

During the course of the development, a number of expert system shells were explored to determine the most appropriate way to present the expert system. The expert system knowledge base was updated occasionally as new expert knowledge was obtained, and as errors were identified.

5.3 Results and Discussion

5.3.1 The development and functioning of the expert system

Approximately 80 farmers and extension officers were able to experience and test the expert system “hands on”. In addition approximately another 100 were introduced to it through rangeland forums and farmer’s days. The expert system was well received by the vast majority of participants.

During the evaluation of the web-based expert system the need for an on-line feedback and discussion tool was identified to allow farmers and experts to communicate in a semi-formal way to discuss their general bush encroachment experiences as well as particular features or problems of the expert system itself. After considering an e-Mail or mailing-list-based solution, it was realised that many of the features needed were readily available through Wiki technology. A Wiki is an on-line collaboration platform which allows users to interactively create, edit and link web pages. The "DokuWiki" software was first installed and initially populated with a set of pages exactly resembling the booklet version of the expert system. Key terms (such as "bush thickening", "*Acacia mellifera*" and "seedlings"), were used to create additional Wiki pages providing more detailed background information and further references on the topic, along with photographs. The flexible nature of the Wiki allows users who identify missing or incorrect information to easily add or change pages through a web browser while a history of old page versions is automatically kept by the Wiki. In this way any version of a page can be referred to at any time while the risk of users accidentally removing important information is virtually non-existent.

Currently, few farmers monitor vegetation changes in Namibia. Ideally the expert system should be used in conjunction with suggested monitoring procedures (Zimmermann et al., 2003). However, the expert system can be used without a monitoring programme being in place, and can be based on careful observation and at the discretion of the farmer. The current version of the expert system has a series of 22 questions and 21 decisions (Appendix 1). The decision pathway is represented with either “no” or “low” answers moving left from the question, whereas “yes” or “high” answers branch to the right. The Decision Tree (Figure 5.2, Figure 5.3 and Figure 5.4) used to fit onto a single page, for easy reference to in the field. With recent additions to the expert system, the Decision Tree has been expanded onto 3 pages, each page representing decisions related to 3 types of management.

Decisions 1 to 8 (Figure 5.2) are adaptive or opportunistic management decisions, including monitoring prompts that are related to decisions to be taken as a consequence of climatic events and fungal disease. Adaptive or opportunistic decision-making mostly mimics likely events in a natural system where there are minimal anthropogenic influences, and mostly involve the use of fire. The presence of seedlings (rare), dried skeletons (top-killed from fungal infections, drought, and frost) with resprout are ideal opportunities for the use of fire, provided fuel loads are sufficient. Moderately intense fires, with fuel loads of around 1000 kg. ha^{-1}, caused an almost 100 % mortality of one and two year-old seedlings, as well as approximately 60 % of saplings of stem diameter of around 10 mm (Joubert et al., 2013; Chapter 3). The decision to burn (Decisions 4, 6, 9 and 19) is perhaps the most significant, and controversial, decision in the adaptive or opportunistic decision part of the expert system.

A recent addition to the expert system has been the inclusion of the use of the “Tree Popper”. The Tree Popper is a simple levering device designed by Mr. Terry Negis in Somerset West, South Africa in the 1990s. It was originally designed as a tool to pull out alien invasive plant saplings in South Africa and Australia, but trials in 2012 showed that it was very effective in pulling out *A. mellifera* saplings with stem diameters of up to 3 cm, showing a success rate of 94 % during the rainy season. The Tree Popper removes a substantial amount of the root, and thus no regrowth occurs. The Tree Popper can then be used when there appears to be little visible thickening, but where there are many saplings with the potential to increase thickening. This provides the manager with an opportunity to interrupt the transition to State 4 (vigorous bush thickened state) when saplings are already resistant to fire (see Chapter 4). It is much more effective during the wet months when the soil is more friable. An economic evaluation of this method has not yet been conducted.

The remaining decisions relate to “treating the symptoms” or rehabilitating an existing bush thickening problem (Decisions 9 to 11 and 20 to 21, Figure 5.3), and ongoing good preventative management (Decisions 12 to 19, Figure 5.4) that are not particularly related to extreme climatic events but refer to situations in which bush thickening is not yet a problem. Appendix 1 outlines the complete sequence of questions, answers and decisions, but, for purposes of space, background information providing context to questions and decision are excluded.

The online wiki expert system has a series of embedded information that can be accessed through links. This allows for a large amount of background information to be made available to the user. The extra information is in the form of photographs, additional explanations, articles of relevance and links to other institutions and experts. Extra information also includes biodiversity considerations, since bush thickets, despite their lowering of grazing productivity, are preferred habitat for a number of species. Through this, managers are exposed to information that may lead them to consider leaving patches of thickets in a more open savanna matrix, to maximise diversity.

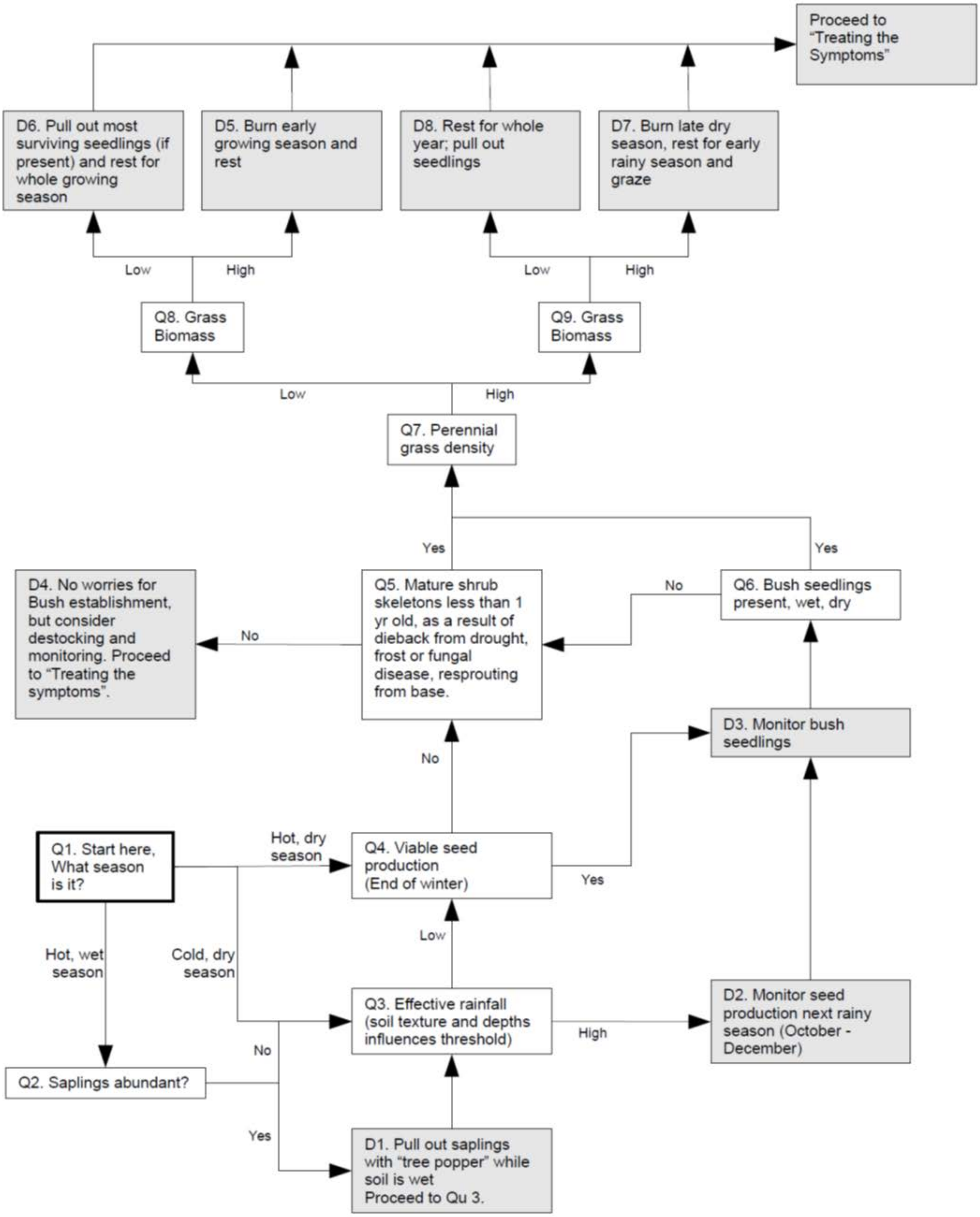

Figure 5.2. Decision tree or flow diagram for Adaptive, or "opportunistic" rangeland management with an emphasis on bush thickening. Decisions are in shaded rectangles.

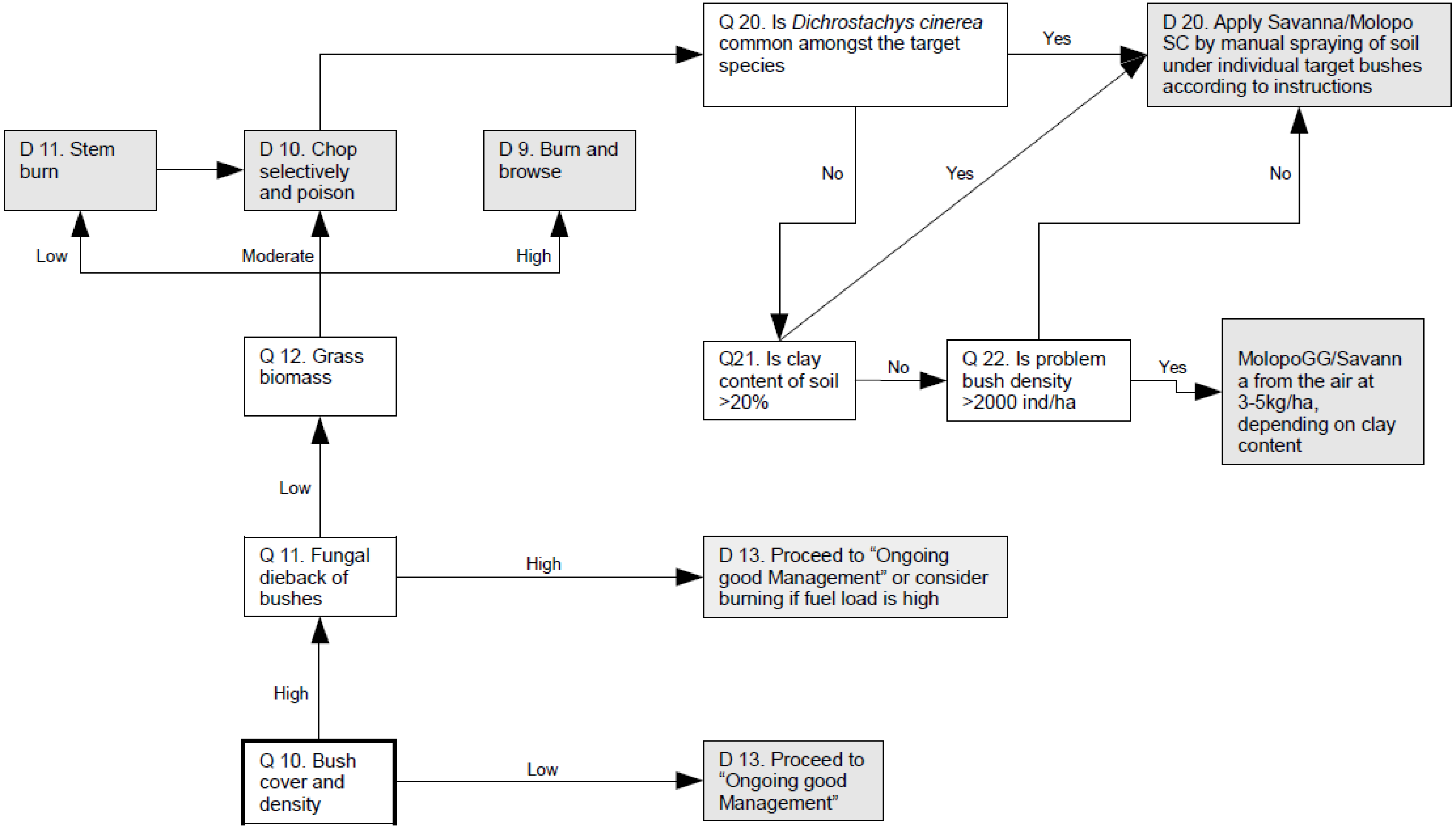

Figure 5.3. Decision tree or flow diagram for reactive, or "treating the symptoms" rangeland management with an emphasis on bush thickening. Decisions are in shaded rectangles.

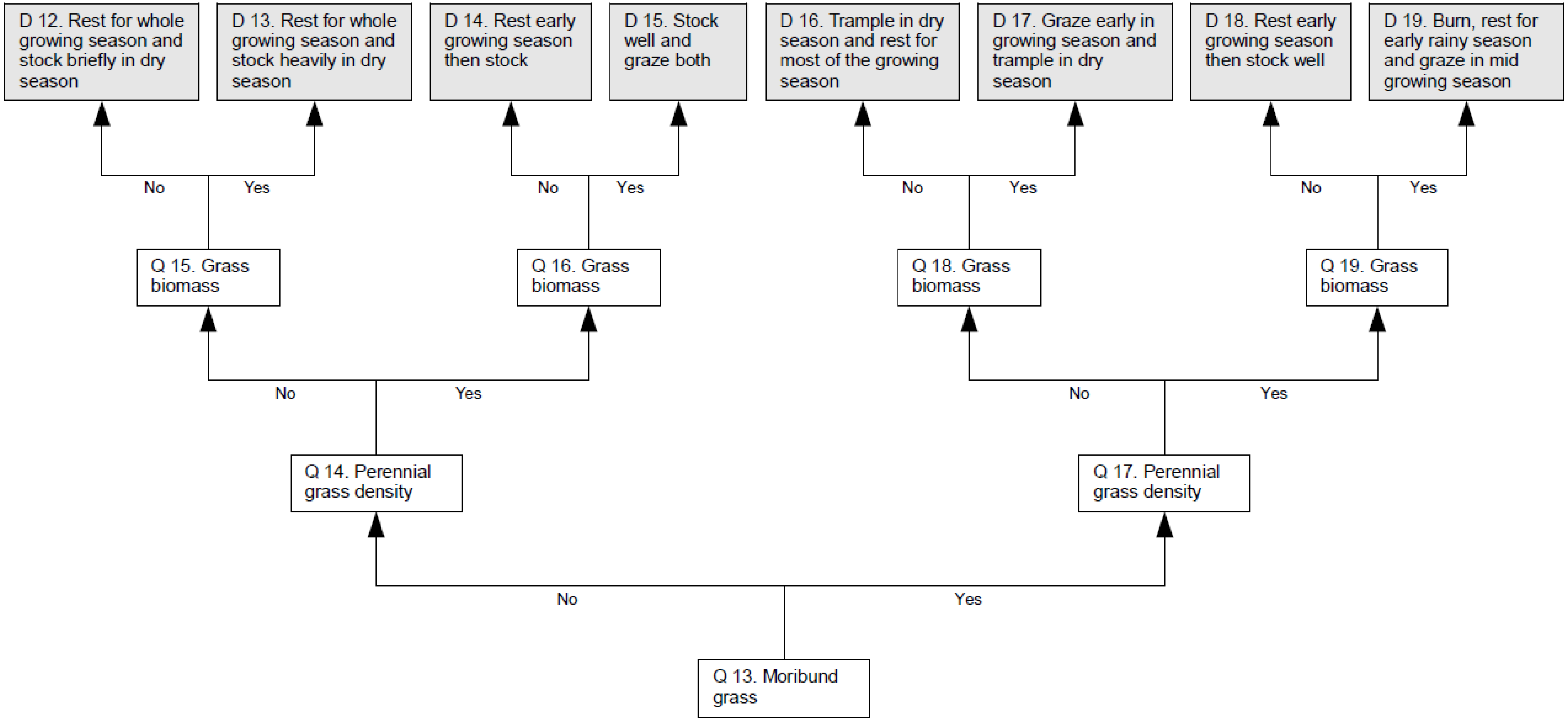

Figure 5.4. Decision tree or flow diagram for ongoing "good" or "preventative", rangeland management with an emphasis on bush thickening. Decisions are in shaded rectangles.

During the first workshop, farmers appreciated the decision tree being available on a single page of paper since it could be taken into the field for *in situ* decision making. This prompted the development an A5 “Expert System” booklet, in which individual questions and decisions are dealt with on separate pages to avoid clutter (Joubert et al., 2009). Answers to individual questions refer the user to the page with the next relevant question, and, ultimately, to the page with the decision. Only one question or decision is presented on each page. This simulates the expert system as seen on a computer screen. As far as is known, this approach is unusual, but, in instances where computers are not available, is likely to prove useful, especially if translated into local languages. Farmers often found this more useful than the computer based expert system, because they could refer to it in the field, and it was in a familiar format.

5.3.2 Farmers’ decision making compared to the expert system

Perhaps the most significant, and controversial, decision in the adaptive or opportunistic decision part of the expert system is the decision to burn (Decisions 5, 7, 9 and 19). Although fires are occasionally applied in savannas as a form of bush control, most of the prescribed burning for this purpose is targeted at healthy mature bushes (Trollope, 1980; Davis et al., 1989; Ludwig, 1990; Pivello and Norton, 1996). The success of such fires in arid savannas, where fuel loads are typically relatively low, is limited, unless mature trees have been topkilled by drought, fungal disease, frost or combinations of the above as outlined earlier. Although farmers appeared to largely concur with the decision to burn when seedlings and young saplings and a high fuel load are present, based on the responses given at the workshops (58 % concurrence), in reality very few farmers actually use fire as a management tool, especially to control seedlings and young saplings (Joubert et al., 2008b; Appendix 2). As a rule, fire is consciously excluded, mostly as a result of perceived economic losses incurred in the form of a temporary loss of grazing after the application of fire, and concern for legal repercussions associated with runaway fires.

Farmers in Namibia are largely focussed on reactive decision making (or “treating the symptoms”) despite the large costs associated with clearing (Honsbein et al., 2009) and are particularly interested in the application of arboricides in treating existing thickets of mature shrubs, and even in treating recently emerged seedlings and saplings (Joubert et al., 2008b; Appendix 2). This use of arboricides is often not appropriate and the expert system suggests other decisions besides arboricides, depending upon the scenario. For example, when fungal dieback is prevalent, the expert system suggests that the shrubs are left alone since they are already dying, and the application of arboricides in these conditions would then be an unnecessary cost. Another option, if fuel load is high, would be to burn. This would kill already weakened shrubs. When shrub thickets are healthy, and grass biomass, cover and density is low, the expert system suggests stem burning, since there is no risk of a runaway fire. It is very difficult to convince managers to apply adaptive management decisions because of the slow growth of *A. mellifera*. This means saplings are often unnoticed for many years after establishment and there is a psychological uncoupling of management actions (and inactions) and outcomes. The perception of rangeland managers and scientists in Namibia is that arboricides are not harmful to biodiversity in general. Smit et al. (1999) outline some of the disadvantages of using the various arboricides. If done incorrectly, serious damage can be done with long-term ecological consequences (e.g. the loss of well established, large trees through non-selective applications). However, there have been no studies to investigate the direct and indirect side effects on biodiversity and ecosystem functioning in Namibia (Honsbein et al., 2009). This is something that needs to be addressed.

Ongoing good management decisions reflected in the flow diagram (Figure 5.4) were based on the opinion of the consultant. It is likely that other decisions could be as suitable or even more suitable for this part of the expert system, particularly when applied to areas with different management challenges. Most importantly these decisions should all strongly emphasise the importance of long rest periods between grazing. Once again, the expert system should be constantly changing and should be adapted towards farmers' experiences in a specific area with specific circumstances.

5.3.3 Successes, challenges, lessons learnt and future plans

The evaluation of decision support systems, including expert systems, is difficult. Ideally, an improvement in rangeland management by farmers after they start using the expert system would be the best indicator of its success, but this is obviously not possible to determine in most cases. Various authors (e.g. Guimaeres et al., 1992; Averweg and Erwin, 1999; Newman et al., 2000) have investigated "Critical Success Factors" (CSFs) in the development of decision support systems in general. Guimaeres et al. (1992) empirically investigated the factors related to successful decision support system implementation and concluded that user participation, management support, availability of information and user training and expertise were directly and positively related to decision support system success. Averweg and Erwin (1999) tested these CSFs in South Africa (as an example of a developing country) and found that even if these CSFs were not present, decision support systems could be successful. They also identified a new CSF which they termed "the ability to utilise appropriate decision support system tools"

(Averweg and Erwin, 1999). In other words, the expert system requires tools appropriate to the level of technology acceptable and available to the community. In addition, Newman et al. (2000) noted the importance of participatory learning approaches, and stressed that decision support system development should be “manageable and small in scope”. They encouraged the development of “super tools” which are easy to use and useful, rather than “power used tools” (useful but difficult to use) or “toys” (easy to use but not very useful). The acceptance and success of the expert system is also dependent upon cultural, social, psychological and historical context and this needs to be considered strongly (Winschiers-Theophilus et al., 2008). Stock and Rauscher (1996) point out which factors inhibit successful decision support system use. These include unfriendly user interfaces, exclusion of users in the design process, lack of general applicability and lack of spatial representation.

It is believed that the development of the expert system has followed, to a large extent, the CSFs mentioned above. The development of the A5 expert system booklet is an example of utilising appropriate and acceptable technologies for specific communities. Users were involved in the development of the expert system to some extent and user participation was important. User training was maximised as much as limited time and funding allowed, by bringing the Extension Services of the Namibian Ministry of Agriculture, Water and Forestry on board. Based on the literature, it appears that the successful use of expert systems thus far has largely been restricted to institutional situations (e.g. Stock and Rauscher, 1996), which makes management support and user training a relatively simple matter. The acceptance and use of expert systems by a relatively unconnected wider community (as is the case with farmers in Namibia) that is not part of a corporate environment where training is routinely possible, is an important challenge. Decision making in this environment is independent of corporate goals and rules, and is consequently very individualistic. This is borne out by the diverse array of responses for each scenario provided by farmers during workshops (Joubert et al., 2008b; Appendix 2). The Namibian Ministry of Agriculture, Water and Forestry extension division has expressed a strong interest in the expert system, and this acceptance is likely to enhance the use of the expert system, since it will facilitate the “management support” and “user training” mentioned above.

Since the function of extension officers is to provide support to farmers, they, and the farmers, in a sense potentially function as a rather loosely connected institution, despite the two parties’ respective autonomies. The expert system can serve as a vehicle for discussion between extension officers and farmers, but can also serve to train new extension officers. Furthermore, farmer study groups might use the expert system as a springboard for their discussions regarding management. It is also envisaged that the expert system concept will be used to develop expert systems for various other management problems, including bush thickening by *D. cinerea*, a species that has different life history strategies (see Table 6.1) and thus requires some different management strategies. For example, in contrast to *A. mellifera*, *D. cinerea* forms persistent seed banks, and seed dispersal is facilitated by ungulates. This is likely to increase both the rate of establishment of seedlings and their dispersal. *D. cinerea* is much more resistant to arboricides containing tebuthiuron and bromacil, and mechanical disturbance to its roots encourages root suckering, making it far more difficult and expensive to treat an existing problem. In these workshops, a facilitator would facilitate the development of expert systems, essentially designed by the rangeland managers themselves, with the support of researchers and agricultural extension officers.

While some expert systems are technologically complex, and expert system shells often have powerful logic capabilities (for example an earlier version of the expert system) (Fendler and Dietrich, 2003), the expert system in its wiki format is essentially “low key” currently, with limited logical flexibility. However, where information required to solve problems is often more heuristic than mathematical (as is currently the case), a complex expert system shell is unnecessary and unwieldy and is probably not optimal for rangeland management in Namibia for a number of reasons. For example, the exact values of parameters at which thresholds occur are not known and vary with changes in many other parameter values. Secondly, rangeland managers have different perceptions of what constitutes bush thickets, and would differ in opinion regarding a threshold for action. The current wiki expert system leaves much of this to the rangeland manager’s discretion. The wiki expert system allows a constantly changing knowledge base, as well as access to research results that are not entirely related to the situation (different species, different climates, and different soils) but that may provide the resource manager with tools for more informed decision making. The wiki expert system can be adapted by different farming communities to suit their differing circumstances. The expert system is expected to be constantly changing and expanding as users communicate criticisms and ideas. In this way, the expert system can serve as a vehicle for adaptive management (Starfield and Bleloch, 1991). The development of expert systems is also a powerful learning tool itself.

Thus far, only limited testing of the acceptability of the expert system by farmers has taken place at workshops. It still needs to be tested over longer periods of time on their farms. Similarly, the validity of the decisions requires more testing in the field. Ongoing research and experience by farmers as well as researchers will be used to update the knowledge base. It has been found that the expert system is not only a vehicle for fast tracking research results and concepts into management practice, it has also allowed the revisiting of hypotheses, and refocusing of research priorities.

Currently, the expert system should be used camp by camp (in multi camp systems) or, at the manager's discretion. It might not always be possible for a farmer to carry out a decision (for example, to rest for a season, in a situation where all camps should be rested, according to the condition) in each camp that it requires. The expert system has no answer to this dilemma, and the farmer will have to prioritise (or perhaps rent grazing elsewhere to rest the farm). However, over time, if the rules of the expert system are followed, the likelihood of this dilemma should decrease. Similarly, a farmer will not be able to carry out a decision to burn over most of the farm, in the case of a large establishment event. However, research suggests that fires can effectively kill seedlings at least three years after germination (Joubert et al., 2013; Chapter 3) allowing farmers more time to make use of the opportunity.

Not all decisions are based on published results of experimental and other scientific studies. As mentioned, some decisions are based on expert knowledge of farmers, agricultural extension officers and researchers, including the authors. This means that some decisions need to be tested. The idea is that these could be tested by willing farmers. Currently, agricultural extension services are doing this with farmers in the Khomas Region. No results are as yet available. Farmers' study groups could also use the expert system as a powerful focussing tool, by debating the rules and decisions and adjusting them as they see fit.

Until recently, reliable economic data on the costs and benefits of bush clearing were lacking. A recent cost-benefit study (Honsbein et al., 2009) shows that none of the symptom treatments are economically beneficial (i.e. treatment costs exceed financial benefits of increased grazing), unless the wood is sold to offset costs. Unfortunately the opportunistic use of fire was omitted from the study. Further studies need to investigate the economic costs of *not* using adaptive decisions such as burning, and on-going good management decisions such as applying rest, and this should be incorporated into the expert system, as additional information.

Since it was officially launched in 2009, the online wiki expert system has not been used by farmers in any significant way (based on the lack of feedback). However, potential users and researchers continue to respond very positively about the system when it is being demonstrated to them, emphasizing its potential value. In order for the expert system to fulfil this potential, a critical analysis of its flaws, both in its functioning and the process of its development, was necessary. A number of important lessons were learnt. A few fundamental flaws have contributed significantly to the limited success and uptake of the expert system by farmers:

Lack of control over the IT platform: In 2012, the online wiki expert system was inadvertently removed from the Polytechnic of Namibia server by server technicians, “cleaning” the server. One of the team suddenly left the Polytechnic of Namibia, resulting in an inability to restore the system. In hindsight, such an outcome should have been anticipated, and provisions made for it. This leads to the next important factor:

“Beyond the project” vision: Although the owners of the system had a “beyond the project” vision, they did not adequately anticipate the ever-changing political, social, economic as well as technological landscape. Although the agricultural extension services staff were (and still are) very keen to use the system, key personnel either resigned or went on study leave. This, combined with the removal of the online system, has significantly hampered the "roll out" and broader acceptance of the system.

Management support: One of the Critical Success Factors mentioned in the literature that was not adequately dealt with was the "buy in" of "management". Because of the diffuse nature of the rangeland management community, it is difficult to define who is represented by 'management'. Expert systems have been mainly adopted by finite corporations, and conservation agencies, with limited staff numbers and largely top down decision making, where user training and adoption of a system is mandatory. In this case, both Polytechnic of Namibia management, and Ministry of Agriculture, Water and Forestry management, for various reasons, did not adequately support the project.

Currently the above three challenges are being addressed. Ownership and control can be strengthened by appointing permanent or semi-permanent staff towards the maintenance of the rules, communication and software and network issues. In the past, these were all done by the authors of the expert system, as components of heavy workloads. Currently, a GIZ (Deutsche Gesellschaft für Internationale Zusammenarbeit) funded "Debushing" project has incorporated the idea of continuing with the development of this, and another (BUSHKILL (Barac et al. 2004)), expert system (which was discontinued, largely for similar reasons to the temporary breakdown of this system), will contribute greatly to increasing the sustainability of the system. Within this period of funding, it will be critical to obtain the "buy in" from "management" from the Ministry of Agriculture, Water and Forestry, as well as the Polytechnic of Namibia. Once this is accomplished, the expert system is expected to become integrated into innovative farmers’ management practices, and, through study groups and workshops and seminars, to slowly be adopted by other farmers.

CHAPTER 6: GENERAL DISCUSSION AND CONCLUSION

6.1 Introduction

The purpose of this thesis was firstly to compile a conceptual model for bush thickening by *Acacia mellifera* in an arid savanna, based on insights gained from existing research and personal observations, and secondly to test some of the important mechanisms whereby transitions from an open grassy state to a bush thickened state occur (rainfall events promoting establishment with a lack of fire) and also whereby the transition is suppressed (rainfall events promoting establishment followed by fire). Finally, based on the model and the empirical support for it, an expert system was developed to assist rangeland managers to deal both with existing problems of bush thickening (reactive management) and prevent bush thickening from occurring (adaptive management). This chapter sets out to investigate the limitations to the model and discuss how important preliminary investigations and observations validate the model and refine it further. Thereafter, the chapter briefly discusses the only true non-anecdotal historical evidence for rates and patterns of encroachment. This includes the accounts of the mid-19th century explorer, Charles Anderson, the study of Rohde and Hoffman (2011) based on historic repeat photography spanning approximate a century, as well as a preliminary time series study of aerial photographs of the Highland Savanna from 1958 to 2007. The implications of this on our understanding of arid savanna dynamics are discussed, as are the implications of this on the pervasive perception in Namibia that bush thickening is the major driver of declines in rangeland productivity. The chapter thereby serves to evaluate the model and the assertions of the preceding chapters and synthesise this with additional preliminary evidence.

Finally, this chapter discusses the possibility of developing generalities for bush thickening in savannas that take into account differences across climatic gradients. This chapter is based both on the preceding chapters and preliminary unpublished findings and thus ends with a new beginning: the suggestion to more rigorously test some interesting hypotheses that challenge the current received wisdom regarding bush thickening in Namibia.

6.2 Limitations of the proposed state-and-transition model

6.2.1 A slow transition to a bush thickened state that is difficult to detect

Although the state-and-transition model approach (Westoby et al., 1989) is considered an appropriate way of explaining vegetation dynamics in arid, unpredictable environments, transitions are not as abrupt as implied. Due to the very slow growth of *A. mellifera*, the transition to a bush thickened state may take decades. This is illustrated by the slow growth of seedlings at both Neudamm and Krumhuk during the study but also by the slow growth of saplings and young shrubs, also measured in the Highland Savanna (Table 6.1). Mr. Argo Rust, the owner of Sonnleiten farm adjacent to Neudamm set out a series of marked quadrats, each with a radius of 5 m in 1972 in order to monitor growth and survival of woody and grassy vegetation. During 2007, there was an opportunity to remeasure the heights of *A. mellifera* individuals, and thus determine the growth rate, as well as survivorship, of saplings over a period of 35 years. Saplings increased in height by an average of 3.19 cm per annum over this 35 year period. In addition, of the 31 trees marked in 1972, only 12 survived to 2007 (survivorship = 38.7 %). This illustrates how slow the growth of individuals can be, and with the relatively high mortality experienced, how slow the increase of cover can be.

Table 6.1. Growth rates of seedlings and saplings under different situations in the Highland Savanna.

Parameter measured	Place	Growth stage	Growth rate/annum	Duration
Stem diameters	Krumhuk	Seedlings from germination	0.82 (S.E. = 0.15 mm)	6 years
Stem diameters	Neudamm, in veld dominated by *Anthephora pubescens*	Seedlings from germination	1.84 mm (SE = 0.03 mm)	2 years
Stem diameters	Neudamm in veld dominated by *Schmidtia pappophoroides*	Seedlings from germination	2.13 mm (SE = 0.04 mm)	2 years
Height	Sonnleiten Farm (adjacent to Neudamm)	Saplings between 30 cm and 70 cm in height in 1972	3.19 cm (SE = 0.38 cm)	35 years

During this transition time, there may still be a productive grass layer dominated by climax grass species such as *A. pubescens*, *Brachiaria nigropedata* and the subclimax grass *S. pappophoroides* as was the case in the Neudamm study area (Figure 6.1). Much of the study area was actually within the transition between 1 and 4, having passed the unstable state 3, without a fire at the time of establishment to arrest the continued transition to state 4. However, it could very easily be considered to be in State 1, because the saplings were hardly visible growing between and in the climax grasses. In Chapter 4 (Joubert et al., 2012) it was shown that topkilled saplings rapidly regrow after fire, and mortality rates are low. In other words, although the transition is not complete, it is a *fait accompli*, as pointed out in the description of the model in Chapter 2 (Joubert et al., 2008a).

Figure 6.1. An *A. mellifera* sapling growing through a climax grass tuft (*A*. *pubescens*) at the Neudamm study site. Vegetation with this combination is already in Transition 4, towards a bush thickened state. Despite its small size, this sapling is probably about seven years old and will vigorously resprout after a fire.

In this way then, although the transition is apparently inevitable, it is gradual and predictable, thus fitting more comfortably within the framework of classical succession. In Chapter 2 (Joubert et al., 2008a) the likelihood that some of the vegetation dynamics is more successional in nature is discussed.

6.2.2 One species, one climate (how generally applicable is the model)

The model is focussed on bush thickening by *A*. *mellifera*, based on the phenology and life history of this species, and not on other major "problem" species, such as *Dichrostachys cinerea* (Table 6.2). Chapter 2 (Joubert et al., 2008a) has stressed that the dynamics of bush thickening is species specific and that generalities are best extracted from specific case studies. The spread of *A. mellifera* encroachment is slow, because dispersal is inefficient, and the growth of the individual shrubs is generally slow (Joubert, unpublished data). Seedlings are killed by fire, but fire usually only topkills mature shrubs which tend to regrow rapidly (Joubert, unpublished data, Johan van Eck pers. comm.) although there are examples of high percentages of whole plant mortality after fire (pers. obs.). *A. mellifera* appears to be susceptible to drought (pers. obs., Johan Du Plessis, pers. comm.; Dr. Ibo Zimmermann pers. comm.) and combinations of drought and dieback caused by fungal infection (Holz and Schreuder, 1989; Holz and Bester, 2007). *D. cinerea*, the other major encroacher in Namibia, grows more rapidly after resprouting, is browsed more heavily, has a hard seed coat, is dispersed by browsers and thus spreads more rapidly, but is more susceptible to frost (Table 6.2). These major differences in life history strategies have implications for bush encroachment mechanisms, and thus preventative management strategies.

Table 6.2. Life history attributes of *A. mellifera* and *D. cinerea* that differ.

A. mellifera	***D. cinerea* (based on Bell and Van Staden (1993), Van Staden et al. (1994) and Roques et al. (2001))**	**Possible implications for *D. cinerea* and its management**
Thin seed coat.	Hard thick seed coat.	Germination does not occur easily and thus a persistent seed bank occurs. Recruitment thus can probably occur with only one excellent rainy season.
Seeds not dispersed by animals (digested).	Seeds dispersed by animals (ingestion promotes germination)	*D. cinerea* dispersal tends to be more widespread. Livestock and wild ungulates are dispersal agents.
Significant seed production occurs only in exceptional rainy seasons.	Seed production figures unknown	*D. cinerea* seed production in relation to rainfall requires study.
Does not usually resprout vigorously from damaged roots.	A vigorous resprouter from damaged roots	Any mechanical form of clearing *D. cinerea* is likely to promote further thickening in the long term.
Resprout after fire. Is not very palatable due to hard thorns.	Resprout is very palatable after fire.	*D. cinerea* thickening can be controlled through the use of fire and browsing.

A. mellifera	***D. cinerea* (based on Bell and Van Staden (1993), Van Staden et al. (1994) and Roques et al. (2001))**	**Possible implications for *D. cinerea* and its management**
Not very frost sensitive, although dieback does occur during extreme cold spells.	Frost sensitive.	*D. cinerea* dies back frequently in the Highland Savanna and is thus generally not a problem. Skeletons of died back individuals may allow fire to burn longer around the resprout, further weaken the resprout or kill it outright.
Sensitive to prolonged drought.	Not as drought sensitive.	Drought is unlikely to be as useful as an adaptive tool in the management of *D. cinerea.*
Relatively slow growing from seed.	Faster growing.	Bush thickening occurs more rapidly.

The question arises if the model described in Joubert et al. (2008a) (Chapter 2) adequately explains bush thickening by *D. cinerea*? If not, what modifications would be needed? Would it need to be substantially altered or would the basic framework remain the same? For example, the transitions between the grassy states (1 and 2) to the bushy state 4 through state 3 would probably occur more frequently and more rapidly than in the described model. The persistent seed bank of *D. cinerea* means that seed is already present and would require only one good rainy season. The effect of fire on *D. cinerea* seedlings is likely to be similar to what has been observed with *A. mellifera* (Joubert et al., 2012; Chapter 4), that is a transition will be arrested. However, there would appear to be an additional opportunity, not available in the described model, to revert back to a grassy state with the use of fire, and browsers (since *D. cinerea* resprout is highly palatable (Table 6.2). Since *D. cinerea* is much more frost prone than *A. mellifera*, the more frequent die back, followed by browsing (to arrest the regrowth) and fire (to kill individuals outright after resprouting), allows for more frequent transitions back to a grassy state. However, *D. cinerea*'s proneness to frost also limits its distribution.

In areas in which both *A. mellifera* and *D. cinerea* are equally dominant, it would seem that the expert system described for *A. mellifera* in Chapter 5 would adequately cover the management of the two species, since the arboricide application for *D. cinerea* is already dealt with. However, a comprehensive focussed literature research, as well as a workshop with experienced farmers, would help to confirm this or alternately help to adopt a new management expert system for *D. cinerea* dominated systems. Interestingly, *D. cinerea* is highly invasive outside its native distribution whereas, as far as the author knows, *A. mellifera* is not considered an invasive alien outside its distribution. Experience with the two species' different invasive histories reflects current thinking of invasive traits. The two species' different invasiveness might also largely be due to the history of its transport by humans.

6.3 Evidence for other factors affecting the transition to a bush thickened state

The study set out to also investigate other aspects of the dynamics of bush thickening by *A. mellifera*, namely the competition between seedlings of *A. mellifera* and climax grass species and the impacts of browsing on seedling survival. Currently, only a limited amount of data is available to make very preliminary conclusions. This section discusses the implications of this preliminary data on the predictions of the model, and on our general understanding of the dynamics of this species, and suggests important areas for further study.

6.3.1.1 Competition between seedlings of A. mellifera *and climax grass species*

Although the received wisdom states that a "healthy" grass sward increases competition for the seedlings and thus reduces growth rates, the evidence for this is ambivalent. In addition, there are not just competitive interactions between seedlings and grasses. Grasses create a microenvironment that partially might benefit a seedling or sapling in some ways. There may be an increase in organic content of the soil and an increase in certain macro and or micro nutrients. Although one would expect soil water to be reduced around a grass tuft, relative to away from a grass tuft, this may be reversed at times as well. Soil and ambient temperatures may also be reduced or variations in these may be reduced. Scholes and Archer (1997) suggest that “no universal predictive model exists” to determine whether the interactions between grasses and woody species is overall positive (facilitative) or negative (competitive) and further suggest that the possibilities vary with regards to time, space and resource availability. Silvertown (2004) states that plant species coexist by sharing resources such as light, soil water and nutrients differentially along gradients or niche axes, in other words, the net interaction is dependent upon this. However, interspecific competition still occurs, and is viewed as an important driver of ecosystem dynamics, shaping community structure and composition (Fowler, 1986). In arid ecosystems, the role of competition has been questioned more strongly but has still been shown to influence community structure (Fowler, 1986).

In savannas, interspecific competition between the grass and tree layers is considered a strong determinant of the relative dominance of these two components (Knoop and Walker, 1985; Riginos, 2009). Increased grass production has been shown to reduce the growth of even mature trees (Riginos, 2009). A reduction in grass production is considered a major reason for bush thickening (De Klerk, 2004), both through an opportunity for mature shrubs to grow more rapidly and thus in turn inhibit grass growth (Riginos, 2009), and through the increased survival of woody seedlings (van der Waal et al., 2009; Ward and Esler, 2011) and saplings (Riginos and Young, 2007; Seymour, 2008). Although grass reduces the growth of mature trees in fertile East African savannas (Riginos, 2009) it would be reasonable to assume that the grass layer more effectively competes with establishing woody seedlings, since they should be more in more directly competition for the major limiting resource, water, in the same topsoil layers, prior to the proliferation of lateral roots and the extension of a tap root of the woody species into deeper soil. Thus, competition between grasses and woody seedlings should, through conventional wisdom, have a more important effect on structuring savannas, in particular the relative dominance of the woody and grass strata. A number of studies have investigated competitive interactions between the grass layer and seedlings and show competitive inhibition by grasses (Kraaij and Ward, 2006; Mopipi et al., 2009; van der Waal et al., 2009; Kambatuku et al., 2011; Ward and Esler, 2011).

Not all studies have confirmed, however, that there is substantial competition afforded by grass to woody seedlings. Other studies have either shown no net competitive interactions (Brown et al., 1998; Brown and Archer, 1999) or a net facilitative effect of grasses on shrub seedlings (Maestre et al., 2001; Maestre et al., 2004). Both facilitation and competition are now known to shape ecosystems, but it is generally considered that facilitative effects increase with increasingly stressful conditions (Callaway et al., 2002; Maestre et al., 2004), for example aridity. A widely held opinion in Namibia is that the major increase in woody cover resulted from a drought in 1960 followed by a foot and mouth outbreak in 1961, which prevented farmers from being able to destock. The consequent overgrazing, in addition to the weakening effect of the drought on the grasses, was thought to lead to reduced competition and thus a dramatic increase in the survival and growth of aggressively growing woody species (Bester, 1999). If this was so, one would expect savannas with a good cover of productive climax grasses to show resistance to bush thickening events.

Joubert and Smit (2009) measured stem diameters and heights of seedlings planted next to and away from grasses. They showed slight competitive effects, but grasses caused no increase in mortality. In many instances, there appeared to be net positive effects of seedlings growing in and next to climax grass tufts. Increased potassium and organic carbon levels next to grasses offset the negative interactions of competition, most probably for water. However, there were no significant differences in measured water potential between the two treatments (as measured with a soil moisture meter with gypsum blocks placed 10 cm beneath the ground). Water relations in Highland Savanna soils are complex, due in part to the very heterogeneous nature of the soil in terms of gravel, soil depth, gravel composition (mica schist vs. quartz) and the quartz pebble mulch mentioned in Chapter 2 (Joubert et al., 2008). It is also notable that seedlings in the Krumhuk study area (Chapter 3; Joubert et al., 2013), in which perennial grass cover was minimal, grew slower than seedlings in the Neudamm study area (Chapter 4; Joubert et al., 2012) where potential competitive effects were much greater (Table 6.1). It should be noted of course that these growth rates were not measured at the same time or the same area and thus the results are strictly speaking not directly comparable.

It would seem that competition with climax grasses has a limited effect on the growth rate of *A. mellifera* seedlings. It is possible that the window of opportunity for Transition 3 (back to a grassy state from the unstable State 3 through fire) is reduced by speeding up the accumulation of resistance to fire through increased growth. In any event, saplings are frequently found in climax grass tufts, and so any competitive effects appear not to increase the mortality rate directly. This needs further investigation though, since the age and growth rate of saplings in grass tufts and away from grass tufts have not been measured, and the age of these saplings has not been determined.

6.3.1.2 The role of browsing in inhibiting or suppressing transitions

The state-and-transition model predicts that browsing by small mammals such as hares does not interrupt a transition to a bushy state but rather modifies the outcome in terms of final density. In other words, it predicts that small browsers that focus on seedlings and saplings results in thickets of lower density. Again, preliminary evidence supports this (Joubert et al., 2012; Appendix 3).

6.4 Climatic situations as opportunities for favourable transitions

Chapters 2 (Joubert et al., 2008a) and 3 (Joubert et al., 2013) emphasise how protracted periods of well above average rainfall represent both a hazard (establishment of *A. mellifera* seedlings) and an opportunity (favourable conditions for a fire) for rangeland managers. Chapters 2 (Joubert et al., 2008a) and 5 (Joubert et al., in press) also mention how drought conditions can actually be viewed as an opportunity to move towards an open savanna. Therefore protracted drought is also an important driver of change. This section elaborates further.

Drought, or “the abnormal situation caused by a protracted period of deficient precipitation” (Du Pisani, 2002) is typically regarded as a negative situation in rangeland management, due to the clear positive relationship between rainfall and grazing and browsing capacity. However, droughts also present opportunities due to their impact on dieback of woody species. The dieback of woody species in relation to drought in semi-arid climates has occasionally been documented (Leistner, 1967; Parry, 1989; Milton et al., 1995; Fensham and Holman, 1999). In Namibia, the combination of fungal dieback and drought stress is implicated in the dieback and death of large numbers of *A. mellifera* (Holz and Schreuder, 1989). Other evidence of *A. mellifera* being relatively drought sensitive includes the fact that it is mostly absent from the arid west of Namibia where other species (*A. reficiens*, *A. erubescens*, *A. erioloba* and *D. cinerea*), which coexist with them in moister areas, occur (Curtis and Mannheimer, 2005), suggesting that it has a lower tolerance for prolonged periods of moisture stress than other species. This might be due to *A. mellifera*'s reliance mostly on a very extensive shallow root system, in contrast to other species such as *A. reficiens* and *A. erioloba* that depend on a deeper tap root system and thus a more persistent source of water. Dieback might only be manifested some years after a prolonged drought. It is likely that, as density and cover of bush thickets has increased in the past 112 years, dieback has increased. This is possibly one reason why mass dieback has only been fairly recently documented (since the early 1970s) (De Klerk, 2004) (Figure 6.2). It is likely that this dieback was at least partially initiated by the extended dry years from 1958/1959 to 1961/1962. Long term data sets for tree dieback in Namibia are not available to validate this. Personal observations, as well as observations by farmers, however, strongly support this. In December 2013, it was estimated that 60 % of *A. mellifera* of all sizes died back as a result of the drought experienced in the Ghanzi District, north western Botswana (I. Zimmermann, pers. comm.).

Figure 6.2. Mass fungal dieback of *A. mellifera* in the Thornbush Savanna. The grass *Cenchrus ciliaris* is flourishing as a result of the flush of nutrients.

Although the role of frost was briefly mentioned as a driver of transitions towards and open grassy state in Chapter 2 (Joubert et al., 2008a) and Chapter 5 (Joubert et al., in press) it was only recently that its combinatorial role with fire was considered. A massive dieback of large trees was noticed on the lower footslopes and pediments in and around Neudamm in 2011 after unusually severe frost occurred. Upon inspection during the growing season, these individuals were observed to be resprouting. However, the presence of the dried skeletons after one year represents another potential transition to an open grassy state provided there is sufficient fuel to support a fire. Dried skeletons would continue to burn after the fire front had passed them, effectively killing the resprout. This combined effect of frost and subsequent fire might be part of the reason why bush thickening in the Highland Savanna is not generally found on pediments.

6.5 The history of bush thickening through photographic and other evidence. Implications for policy

The prevailing perception of rangeland scientists and managers in Namibia is that rangelands have thickened up rapidly, and particularly, since the late 1950s-early 1960s. Yet quantitative data and objective accounts are virtually non-existent. Following from this is the perception that bush thickening is the single most important cause of the perceived decline in productivity in the livestock industry since the late 1950s. The evidence largely quoted for this is the dramatic decline in cattle numbers in the commercial farming sector from 2.6 million in 1958 to 1.2 million by 1995 (De Klerk, 2004). This perceived relationship is untested. No quantitative data on bush thickening trends between then and today exist, besides the very preliminary data reported on in this chapter. This section of the chapter presents evidence from three sources to put forward an alternative proposal that thickening has been rather modest and was in existence for much longer than currently thought. These are (a) historic accounts from the explorer Charles Anderson from the 1850s, (b) matched photography spanning 130 years (Rohde and Hoffman, 2011) and (c) preliminary aerial photography analysis between 1958 and 2007.

a. Historic accounts from Charles Anderson (Anderson, 1856): Charles Anderson explored the interior of Namibia, and also visited Lake Ngami in neighbouring Botswana. In his accounts, he described six situations in which his travels were seriously hampered by the presence of landscape scale bush thickened areas. Although the exact whereabouts of these thickets is difficult to pinpoint, they can be approximately determined. Here are two extracts from his book, Lake Ngami (Anderson, 1856) describing his passage i. towards, and close to, the Waterberg, and ii. departing from, and close to, Lake Otjikoto.

i. “... we began to flatter ourselves that we had at last passed the boundary-line of those thorny woods which had so long and pertinaciously harassed us. In this, however, we were disappointed. The very next day we entered a region far worse than any we had yet seen, which indeed bade fair to stop us altogether. Our poor cattle were cruelly lacerated and it was with the utmost difficulty we succeeded in getting the waggons through.”

ii. “We only stayed a day at Otjikoto. The next day, after a few hours’ travel, we lost sight of all landmarks; and were now making our way through dense thorn-coppices, which harassed and delayed us exceedingly. To say nothing of tearing our clothes to rags, they, now and, then extracted some article from the saddle bags.”

Although these accounts do not give quantitative data of density and cover, they do illustrate the point that thickening was a part of the landscape already in the mid-19th century. It is notable that all six of the encounters with landscape scale thickets were close to areas of permanent water. This suggests that intense and continuous grazing either by cattle owned by Herero pastoralists, present in the area for 300 years BP (Rohde and Hoffman, 2011), or game, or both, close to permanent water resulted in the exclusion of fires, and the transition from an open grassy savanna to a bush thickened state. Since these areas of permanent natural water existed for centuries, these thickets are likely to have also existed for centuries and were largely self-perpetuating, as explained in Chapter 2 (Joubert et al., 2008a).

b. Matched photography spanning 130 years: Rohde and Hoffman (2011) rephotographed photographs taken by Palgrave during an expedition to Namibia in 1876. They found a surprisingly modest overall increase in woody cover of 1.5 % (range -5 % to 15 %) for shrubs

< 1.5 m and 22 % (range -5 % to 48 %) for trees > 1.5 m in what they termed “tree and shrub savannas” which broadly corresponds with the Highland Savanna in this study. This is in stark contrast to the perception that prevails today.

c. Preliminary aerial photography analysis between 1958 and 2007: The author has undertaken a preliminary analysis of aerial photographs taken in 1958 and 2007 (spanning 50 years) from 1. Neudamm Farm, 2. Sonnleiten (where the growth rates of saplings was measured) and 3. Paulinenhof, a farm approximately 10 km south west of Neudamm, which is well known for being in a state equivalent to State 1 of the model (Open savanna dominated by climax grasses). 1 km x 1 km subsets of the 1958 aerial photos were georeferenced with 1 km x 1 km subsets of georectified orthophotos taken in 2007 using Quantum GIS freeware (Quantum GIS Development Team (2010) (Table 6.3; Table 6.4). Percentage woody cover was visually estimated with 400 m^2 randomly located plots within each view for 1958 and 2007 (Figure 6.3; Figure 6.4; Figure 6.5).

Table 6.3. Synopsis of management practices on the three farms where aerial photography analysis was done.

Farm	Stocking rate	Rotation/management	Fire
Neudamm	conservative	“Rotational”	Few
Sonnleiten	High	holistic management since the 1980s	None
Paulinenhof	Moderate	Flexible, visual determination of grass condition	Frequent

Table 6.4. Estimated cover changes for three farms in the Highland Savanna region, from 1958 to 2007 including changes in carrying capacity that might be attributed to bush thickening alone (loosely based on Richter et al., 2001).

Farm	% cover in 1958	% cover in 2007	% change	% change in carrying capacity likely to be attributed to bush thickening alone
Neudamm	17.5	14.5	-17	8
Sonnleiten	14.0	21.0	50	-10
Paulinenhof	5.5	11.0	100	-11
Mean	12.3	15.5	26	-6

The percentage cover changes shown are modest but not as modest as the matched photography estimates of Rohde and Hoffman (2011). It must be noted that aerial photography analysis only detects cover of individual trees and shrubs with a diameter of > 0.5 m (in this study). Cover changes under this resolution are thus excluded from this preliminary analysis. Interestingly, Neudamm study site shows negative changes in cover (-17 %). This reduction in cover is likely due to dieback of senescing trees during times of drought and fungal infection. At the Neudamm site there was a strong negative correlation between initial (1958) percentage cover and percentage cover changes (Figure 6.6), and thickets with a cover of around 20 % (according to the correlation) are likely to open up. At Sonnleiten the correlation between original cover in 1958 and changes in cover is poor (Figure 6.7), suggesting that management in the intervening years, in particular, very high stocking rates and the absence of fires, promoted the survival of mature thickets, perhaps by reducing competition. This supports the assertion of the model (Chapter 2; Joubert et al., 2008a) that senescing thickets are likely to open up. A similar trend was observed at the Paulinenhof site however in this case, because large mature thickets were mostly absent, there were no negative changes in cover (Figure 6.8). Although one cannot be certain at this stage that the thickets of highest cover are necessarily the most senescent, it appears likely that this is the case. This is partially because the resolution of the aerial photos is at best 0.5 m and hence smaller shrubs are overlooked. The suggested trends are speculative at this stage, and further analysis is needed. Most of the thickets in the views (Figure 6.3; Figure 6.4; and Figure 6.5) were already in existence by 1958. This places serious doubt on the prevailing assertion that the major increase in bush thickening was initiated in the late 1950s and early 1960s (Bester, 1996). This novel perception should however be adopted cautiously since the study was conducted in the Highland Savanna, whereas bush thickening is a far greater problem further north in the Thornbush Savanna. Evidence from these three historical investigations has important implications on our ideas regarding the decline of rangeland productivity. Based on the preliminary estimates of cover change from aerial photography in the Highland Savanna, bush thickening alone seems to have played a much smaller role in the decline of productivity in the grass layer and the dependent beef industry (De Klerk, 2004) than previously thought.

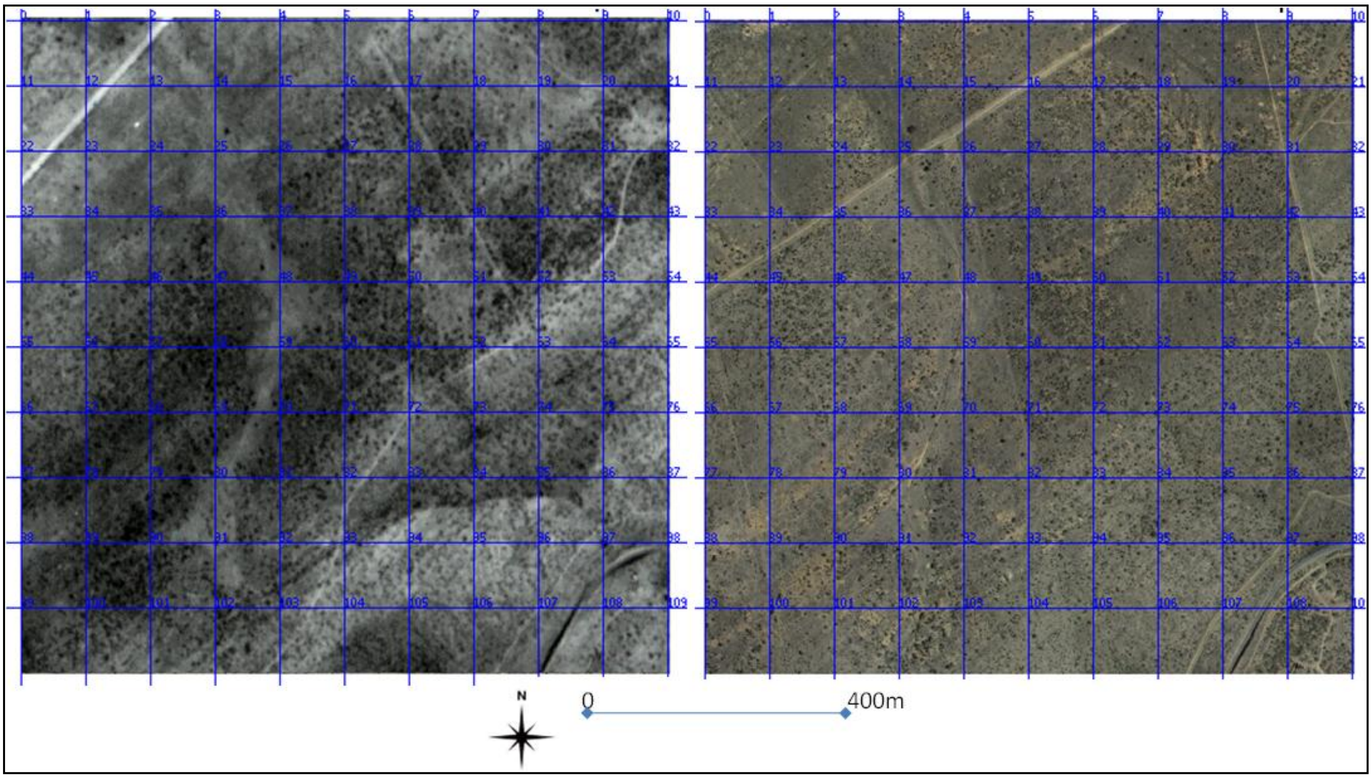

Figure 6.3. Matched aerial photographs from Neudamm (1958 on the left; 2007 on the right). A thinning out of the thicket left of centre is evident in the 2007 view.

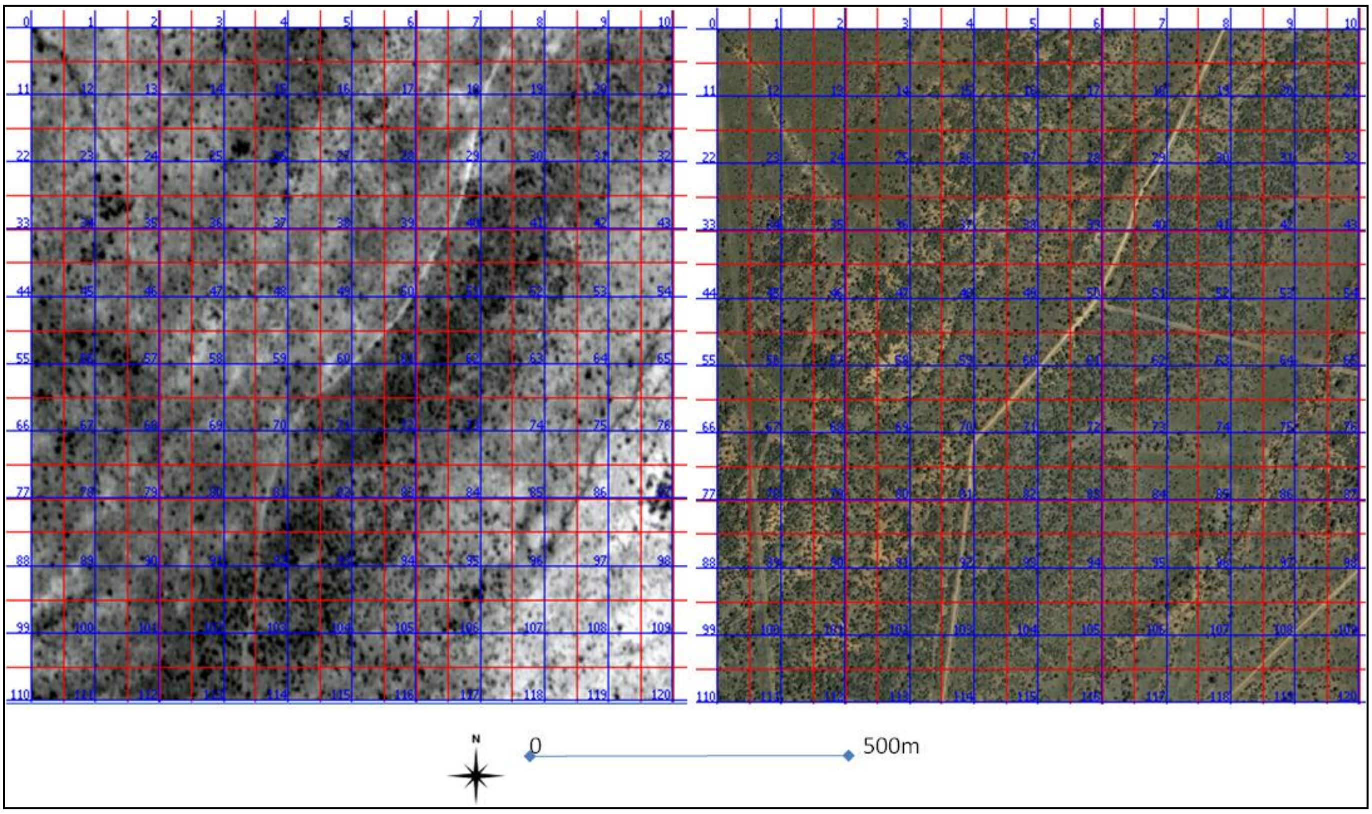

Figure 6.4. Matched aerial photographs from Sonnleiten (1958 on the left; 2007 on the right). “New” thickets (at the resolution of the aerial photographs) are evident in the centre and bottom right of the 2007 view.

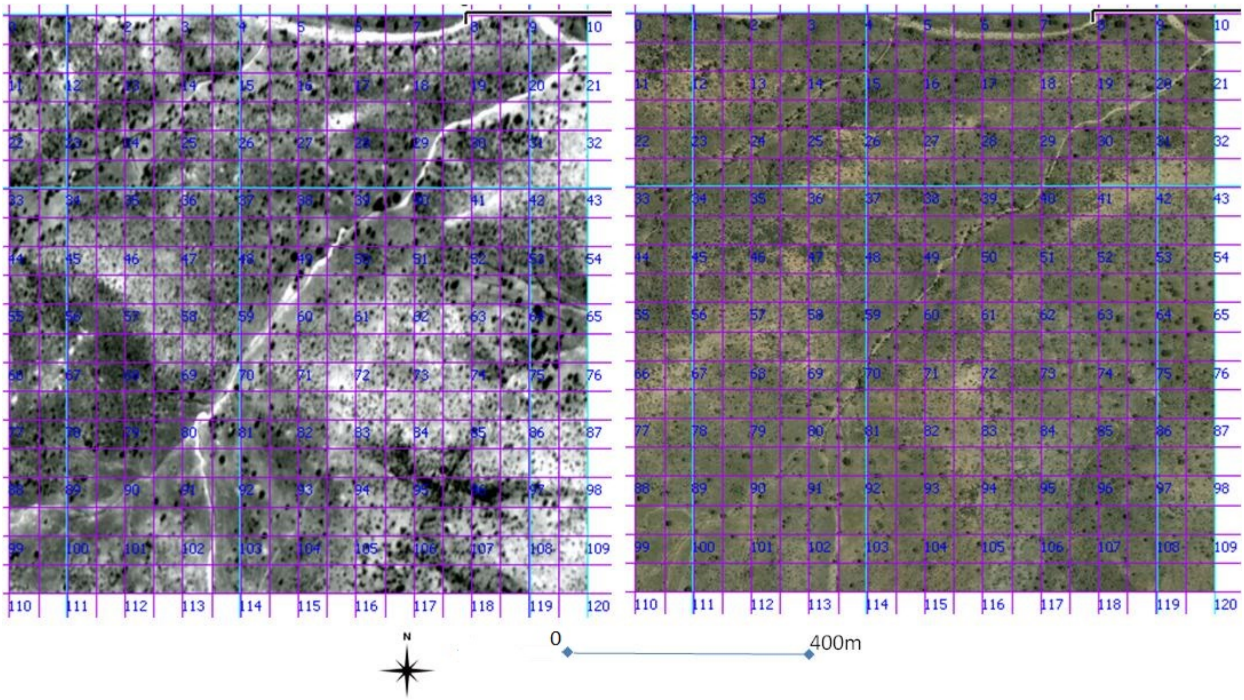

Figure 6.5. Matched aerial photographs from Paulinenhof (1958 on the left; 2007 on the right). A general thickening up is evident but no new thickets are visible.

Bush thickening (states 4 and 5) on such a large scale is one symptom of rangeland degradation amongst others (e.g. state 2) rather than a cause. Notwithstanding the obvious value of bush thickets for various ecosystem processes (Eldridge et al., 2011) rangeland managers and policy makers will need to evaluate the role of bush thickening in productivity decline much more rigorously than is currently the case.

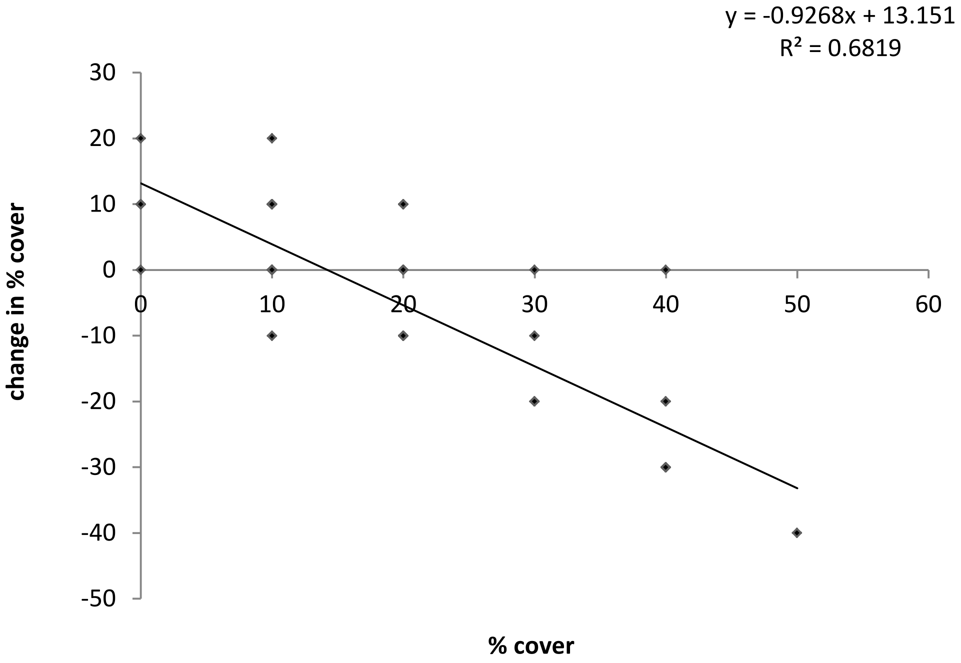

Figure 6.6. Change in % cover in relation to starting % cover at the Neudamm site. R^2 = 0.6819.

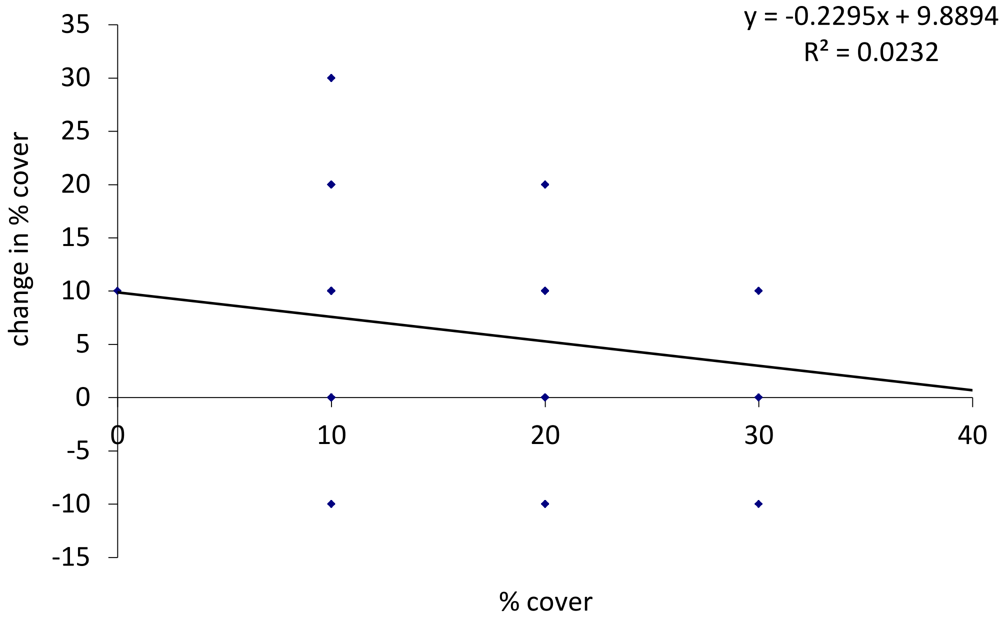

Figure 6.7. Change in % cover in relation to starting % cover at the Sonnleiten site. R^2 = 0.0232.

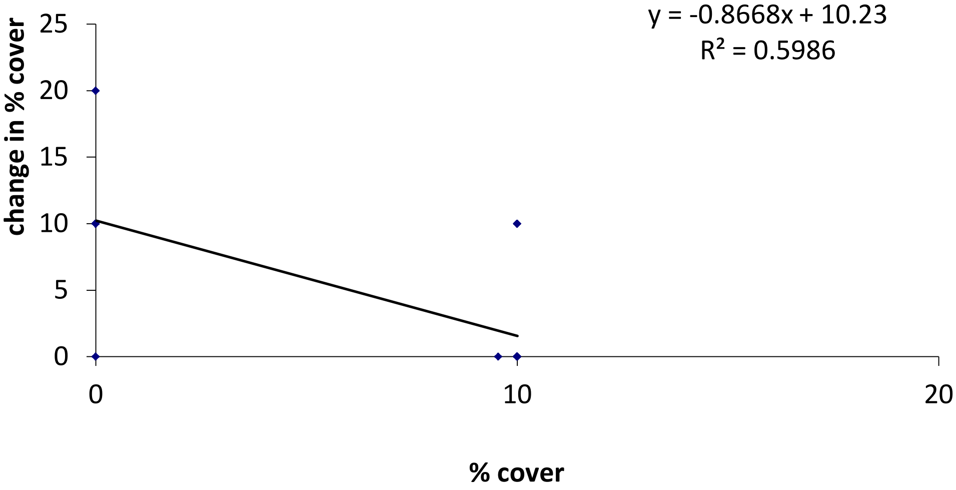

Figure 6.8. Change in % cover in relation to starting % cover at the Paulinenhof site. $R^2 = 0.5986$.

6.6 Arid to mesic savannas: what generalities can be deduced from this and other studies?

Only after studies of the dynamics of specific species in specific climates are conducted and combined can a more universal explanation for bush thickening be put forward. This study investigated some of the dynamics of bush thickening at the arid end of the scale by one species, *A. mellifera*. The role of fire in arid savannas was discussed in Chapter 4 (Joubert et al., 2012). It was emphasized that, although fires in arid savannas are much less frequent, and less intense, than in more mesic savannas, their importance does not diminish with increasing aridity. Rather the emphasis of importance changes, that is, instead of fire frequency driving dynamics, fire *timing* (in terms of coinciding with woody seedling establishment) is pivotal. The importance of fire frequency increases with decreasing aridity, whereas the importance of fire timing decreases with decreasing aridity. Figure 6.9 simply illustrates this suggested relationship. This is perhaps why rangeland managers in arid savannas have always been so reluctant to use fire to inhibit the transition. Text books to date have always placed emphasis on fire frequency, whereas the "desired" fire frequency in arid savannas is a function of woody seedling establishment events and is thus not fixed. In mesic savannas, fires are effective in maintaining the gullivers below the grass sward, provided the *frequency* and *intensity* of the fire is adequate (Roques et al., 2001). In other words, the exact year in which a fire occurs is less important than the frequency.

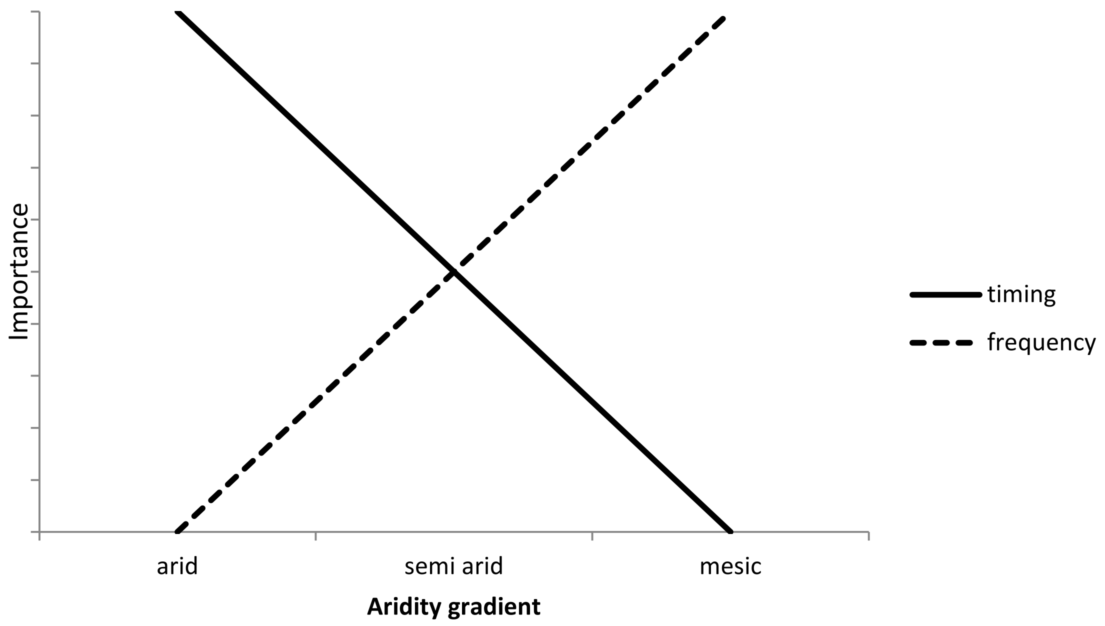

Figure 6.9. Importance of timing (year) and frequency of fire along a savanna aridity gradient.

6.7 Conclusion

This final chapter has attempted to summarise the evidence for the model presented in the preceding chapters, evaluating the combined evidence for the proposed model, and supplementing this with some preliminary data collected. The chapter has then emphasised some aspects that were less emphasised in the original model but that the author feels enhance the value of the model both from a theoretical perspective, as well as a management perspective. Finally, by investigating the history of thickening from objective sources, albeit in a preliminary fashion, the author has challenged the received wisdom regarding bush thickening (both its history and its impacts on productivity). It was shown that bush thickening is a phenomenon that has been present in Namibia, at a landscape scale for perhaps centuries, and that its proliferation in the last century and half century has been far more modest, as has been its effect on rangeland productivity. These assertions need to be investigated more extensively, rigorously and over a greater part of the arid savannas of Namibia. The author hopes that this thesis has significantly contributed to the understanding of bush thickening in arid savannas, and to savannas as a whole.

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APPENDICES

APPENDIX 1. EXPERT SYSTEM QUESTIONS AND DECISIONS

(Background explanations are omitted for space considerations, but these are available in Joubert et al., 2009).

Decisions 1 to 8 relate to adaptive or opportunistic management decisions and are dependent upon rainfall, seed production of bushes and seedling survival of bushes.

Question 1: What season/ time of year is it?

1. End of summer/Cold dry season (winter) (May to July): Go to question 3
2. Hot wet season (January to April): go to Question 2
3. End of winter beginning of hot dry season (August to December): Go to Question 4

Question 2: Are saplings < 0.5 m abundant? (Hot, wet season)
Yes: Decision 1
No: Question 5

Decision 1: Pull out saplings with Tree Popper while soil is moist. This can be done in conjunction with other decisions. Proceed to Question 3 at the end of summer.

Question 3: End of summer/Cold dry season (winter) (May to July): Was the rainfall of the previous season above average?
Yes: Decision 2
No: Question 4

Decision 2: Winter: Monitor seed production in August to December. Proceed to Question 4.

Question 4: End of winter beginning of hot dry season (August to December): Has there been viable seed production? Did bush seedlings (if there were some to begin with) survive the hot wet and cold dry seasons?
Yes: Decision 3

No: Question 5

Decision 3: Monitor for the germination and survival of bush seedlings (August to October). Proceed to Question 6.

Question 5: Are there mature shrub skeletons ≥ a year old present, as a result of dieback from drought, frost or fungal disease, resprouting from base.
Yes: Question 7
No: Decision 4

Decision 4: You need not worry about a bush encroachment event occurring, but consider destocking anyway. You might as well monitor seed production as well, in case current theory overlooks other factors. Now proceed to question 10 and "Treating the Symptoms". Later it will be necessary to go to back to Question 1 to determine new conditions next season.

Question 6: Are there survived seedlings present around parent trees and elsewhere?
Yes: Question 7
No: Question 5

Question 7: Is the perennial grass density very low, such as below one per square metre?
Yes: Question 8
No: Question 9

Question 8: Is grass biomass sufficiently high, in the area where the seedlings are, to produce a fire intense enough to kill the seedlings?
Yes: Decision 5
No: Decision 6

Decision 5: Burn at end of dry season/beginning of rainy season, trample briefly and rest. Proceed to Question 10 (questions related to ongoing management and treating of symptoms). Later it will be necessary to go to back to Question 1 to determine new conditions next season.

Decision 6: Pull out surviving seedlings with pliers, or use a hoe to chop them out, and rest the veld for the remainder of the growing season. Proceed to Question 10 (questions related to ongoing management and treating of symptoms). Later it will be necessary to go to back to Question 1 to determine new conditions next season.

Question 9: Is grass biomass sufficiently high, in the area where the seedlings are, to produce a fire intense enough to kill the seedlings?
Yes: Decision 7
No: Decision 8

Decision 7: Burn at end of dry season/beginning of rainy season, graze and rest. Proceed to Question 10 (questions related to ongoing management and treating of symptoms). Later it will be necessary to go to back to Question 1 to determine new conditions next season.

Decision 8: Rest the veld for the whole year if possible. Pull out surviving seedlings with pliers, or use a hoe to chop them out. Proceed to Question 10 (questions related to ongoing management and treating of symptoms). Later it will be necessary to go to back to Question 1 to determine new conditions next season.

The questions asked from this point on relate to decisions regarding “treating the symptoms” (Decisions 9 to 11 and 20 to 21), and ongoing good preventative management (Decisions 12 to 19). The farmer must use his/her discretion as to when these questions should be asked. Questions related to grass biomass should be asked at the end of the rainy season.

Question 10: Is the cover of bush high enough to suppress grass growth significantly (i.e. in your opinion, is the area bush encroached)?
Yes: Question 11
No: Question 13 (proceed to “ongoing good management” decisions)

Question 11: Is the incidence of fungal and/or other dieback of *Acacia mellifera* high?

Yes: Question 13 (proceed to “ongoing good management” decisions)
No: Question 12

Question 12: In your opinion, is grass biomass high, medium or low?

High: Decision 9

Moderate: Decision 10

Low: Decision 10 or Decision 11

Decision 9: Burn the thickets of high cover and browse after they resprout. Consider changing your grazing management to prevent bush thickening from occurring on a large scale.

Decision 10: Chop trees and shrubs selectively and apply herbicide to chopped trees and shrub. If the application of herbicide is considered, then go to Question 20.

Decision 11: Stem burn selectively.

Question 13: Is more than 50 % of the perennial grass moribund?

No: Question 14

Yes: Question 17

Question 14: Is perennial grass density higher than 1 grass m^{-2}?

No: Question 15

Yes: Question 16

Question 15: Is grass biomass higher than 200gDM m^{-2}?

No: Decision 12

Yes: Decision 13

Decision 12: Rest for whole growing season and stock briefly in the dry season. If bush seedlings are present (question 6 check) refer back to Decision 6.

Decision 13: Rest for the whole growing season and stock heavily in the dry season. However, if seedlings have been detected in the hot dry season, you should have reached decision 5.

Question 16: Is grass biomass higher than 200gDM m^{-2}?

No: Decision 14

Yes: Decision 15

Decision 14: Rest for the early growing season, and stock well when the re-growth is vigorous.

Decision 15: Stock well and graze in both seasons.

Question 17: Is perennial grass density higher than 1 grass m^{-2}?

No: Question 18

Yes: Question 19

Question 18: Is grass biomass higher than 200gDM m^{-2}?

No: Decision 16

Yes: Decision 17

Decision 16: Trample briefly in dry season and rest for most of growing season.

Decision 17: Graze early in the growing season, shortly after annual grasses are big enough to provide food, and trample in the dry season.

Question 19: Is grass biomass higher than 200gDM m^{-2}?

No: Decision 18

Yes: Decision 19

Decision 18: Rest early in the growing season, then stock well.

Decision 19: Burn, rest the veld for the early rainy season, and graze in mid growing season.

The questions asked from here on relate to arboricide application.

Question 20: Is there a lot of *Dichrostachys cinerea* amongst the problem bushes?

Yes: Decision 20

No: Question 21

Decision 20: Apply Savanna / Molopo SC herbicide by manual squirting of soil under individual target bushes according to instructions.

Question 21: Is clay content of the soil greater than 15 %?
Yes: Decision 20
No: Question 22

Question 22: Are there more than 2000 problem bushes per hectare?
No: Decision 20
Yes: Decision 21

Decision 21: Broadcast the herbicide Molopo GG by aeroplane at 3 - 5kg/ha, depending upon clay content and according to instructions.

APPENDIX 2. COMPARING A DSS AND FARMERS' DECISIONS FOR RANGELAND MANAGEMENT IN SEMI ARID NAMIBIA

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Keywords: *bush thickening; preventative management; wiki format*

Introduction

Rangeland management in Namibia is largely reactive, with large sums of money being used in attempts to eradicate indigenous bush species that form thickets. A Decision Support System (DSS) for rangeland management with emphasis on preventing bush thickening has been developed in a wiki format and also in booklet form (Joubert *et al*. 2005) (http://chameleon.polytechnic.edu.na/wiki/). Decisions are of three types: opportunistic or adaptive; reactive (treating of symptoms); and ongoing good management. Workshops were conducted to involve land users in the DSS development. As part of the workshops, the DSS decisions were compared with decisions taken by farmers, in order to develop insights into farmer decision making. This paper reports on this comparison.

Materials and methods

A total of 19 farmers in two workshops (Groups One and Two) separated spatially by about 300 km, but both in semiarid savanna, were individually introduced to six scenarios in the field. Farmers provided the decisions they thought would be appropriate for each scenario. Participants' responses to each scenario were recorded and compared with the decisions recommended in the DSS (expressed as % of respondents with responses corresponding to suggested decision) (Table 1). The participants of the two workshops' responses were also compared using the Renkonen Index (Krebs, 1999) in order to determine whether proximity influenced land user decisions.

Results

Seventeen response categories were identified. The greatest variation in response categories (13) was for Scenario 1, a treatment of a symptom that farmers are most concerned with. This also had the lowest concurrence with our suggested decision (0 %) (Table 1).

Table 1: Decisions suggested by DSS (abbreviated) and the % of farmers with same or similar response

Scenario and decisions suggested by the DSS for their management	Respondents
Scenario 1: Dense stand of healthy mature bushes (bush thickened) with a sparse cover of annual grasses. Decision: Stem burn selectively	0 %
Scenario 2: Dense stand of healthy mature bushes (bush thickened) with a dense cover of perennial grasses. Decision: Burn the thickets of high cover and browse after they resprout.	48 %
Scenario 3: Dense stand of mature bushes (bush thickened) with sparse cover of annual grasses. Many bushes are dying back as a result of fungal infection and drought. Decision: Do nothing to the bushes.	37 %
Scenario 4: Dense stand of mature bushes (bush thickened) with a dense cover of perennial grasses. Many bushes are dying back as a result of fungal infection and drought. Decision: Do nothing to the bushes. Consider a burn to hasten opening up the stand, since bushes are dry and will easily burn.	53 %
Scenario 5: Open savanna with scattered trees. *Acacia mellifera* seedlings are present at the end of the dry season (due to two consecutive good rainy seasons). There is very little cover of predominantly annual grass. Decision: Pull out most surviving seedlings, rest rangeland for remainder of growing season.	11 %
Scenario 6: Open savanna with scattered trees. *Acacia mellifera* seedlings are present at the end of the dry season. There is dense cover of predominantly climax perennial grass (due to two consecutive good rainy seasons). Decision: Burn late dry season, rest for the early rainy season and then graze.	58 %

Respondents showed the highest concurrence with our DSS decision for Scenario 6. There was a low % similarity *between* groups for decisions for scenarios (ranging from 38 % for scenario 1 to 54 % for scenario 4) suggesting an influence on decision making by neighbours.

Group 1 showed a far greater reliance on herbicides than Group 2 (for 5 scenarios and 1 scenario respectively). Group 2 generally agreed with our decision for scenarios 4 and 5.

Conclusions

Contrary to the agreement with our DSS suggestion for scenario 6, an adaptive decision that is required very infrequently (after two to three consecutive high rainfall years), farmers are in reality reluctant to burn, due to perceived economic losses. The results show that decision making in a similar environment for any particular scenario is highly diverse. An easy to use wiki DSS, if marketed vigorously through extension, can greatly improve communication and debate, and improve consensus in decision making. Currently, farmers are more interested in symptom treating than adaptive preventative measures, partially since a fairly large proportion of land is already encroached.

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APPENDIX 3. DO HARES HELP TO KEEP SEMI-ARID SAVANNAS OPEN? PRELIMINARY EVIDENCE SUGGESTS THEY DO

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Key words: *Acacia mellifera*; browse; browsers; saplings; seedlings; survival

Introduction

Bush thickening has lowered beef productivity significantly in Namibia, southern Africa. Although fires can be effective in killing seedlings and young saplings, fire is rarely applied in Namibia. The question arises if other biological agents such as hares can help to keep savannas open. Some reports suggest that hares in high densities can negatively affect the establishment of woody species (Gibbens *et al*., 1993; Rao *et al*., 2003). Hares regularly browse seedlings and saplings of *Acacia mellifera* and other encroaching species in Namibia. A preliminary investigation of the browsing of *A. mellifera* seedlings was conducted as part of a larger study investigating the influences of rainfall, fire, competition and browsing on *A. mellifera* recruitment.

Materials & Methods

The study was conducted in central Namibia. *Acacia mellifera* seeds were planted in 144 exclosures (0.81 m^2) and associated open plots to test the roles of fire, competition and browsing on seedling establishment. Seeds were planted during February 2008 and seedling survival and vigour were determined at the end of the rainy season (June ?) and the end of the dry season (September ?) of 2008 and 2009. Thirty-six of the exclosures and associated open plots were analysed in this study. Seedlings were regularly inspected for signs of hare browsing and mortalities that were clearly due to hare browsing recorded. Seedling survival in exclosure and open plots was compared through a chi square analysis.

Results and Discussion

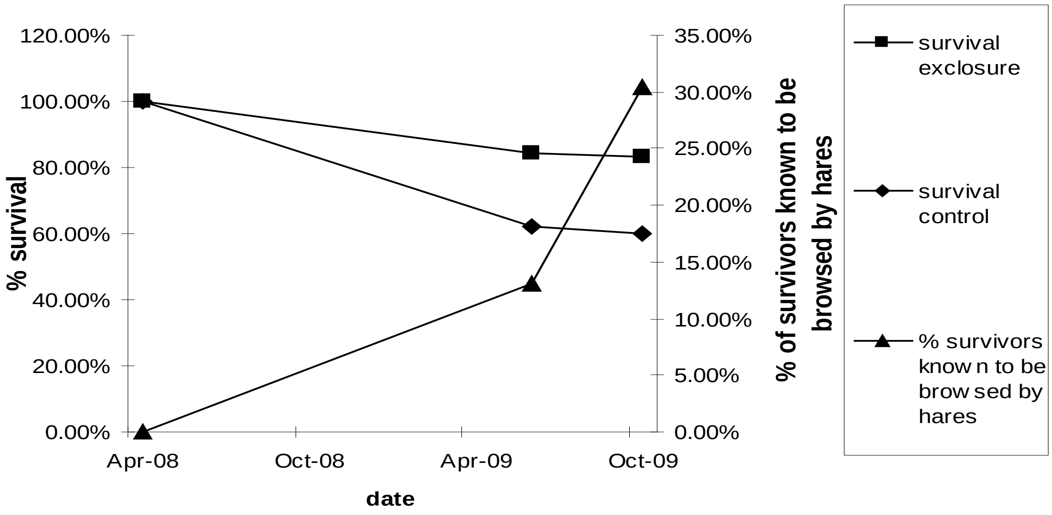

Figure 1. % Survival of seedlings in exclosure and open plots; % of survivors known to be browsed by hares.

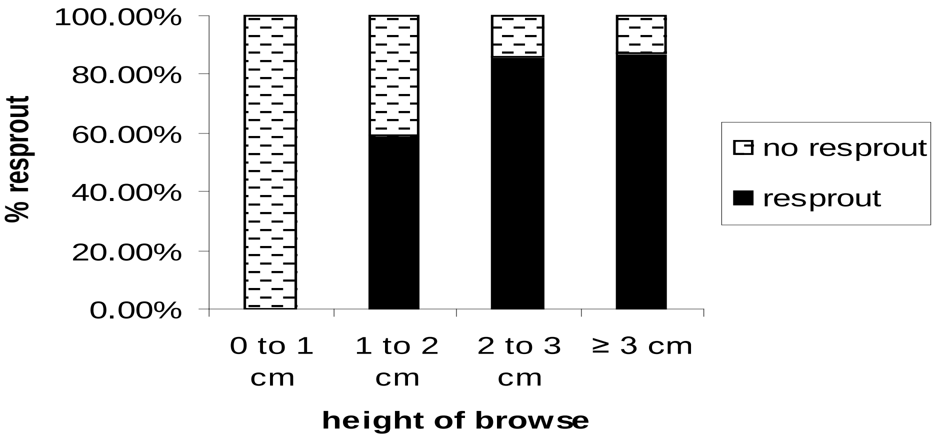

Figure 2. Percentage resprouting of seedlings browsed at different heights by hares (n = 56).

Survival in open plots was significantly lower (60 %) than in exclosures (83 %) ($p < 0.001$; chi square) (Figure 1). During the dry season browsing by hares increased drastically (Figure 1). The lower the height of browse, the smaller the resprouting probability of the seedling (Figure 2). Currently it is assumed that seedlings which did not resprout will not survive. If this assumption is correct, 54 % of browsed seedlings will die. This preliminary analysis suggests that hares do significantly reduce establishment densities of *A. mellifera* by thinning out seedlings, particularly during dry seasons when alternative food sources for the hares becomes scarce. A study of browsed saplings in a parallel study suggests that effects on seedling establishment diminish with time.

Conclusion

Research in Namibia is mainly focussed on large mammals and studies directly related to rangeland productivity. Based on the results of this study it appears that small browsers such as hares can play an important, but cryptic role in savanna dynamics. It is suggested that the effects of vegetation structure, arboricide use and poaching on hare population dynamics be studied in more detail.

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