The influence of size and density of the Camelthorn (*Acacia erioloba* Meyer) on its keystone role in the Xeric Kalahari

Colleen Seymour

Thesis presented for the degree of Doctor of Philosophy in the
Percy FitzPatrick Institute, Department of Zoology, University of
Cape Town, South Africa

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DECLARATION

I hereby declare that this submission describes original research undertaken towards a Ph.D. degree at the Percy FitzPatrick Institute, University of Cape Town. It is my own work and to the best of my knowledge and belief, it contains no material previously published or written by another person nor material which has been accepted for the award of any other degree or diploma of the university or other institute of higher learning, except where acknowledged in the text.

Signed by candidate

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Colleen Lynda Seymour
February 2006

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Abstract

Within the savannas of the southern Kalahari, land use practices can change habitat structure profoundly, so that rangelands either become densely wooded through bush thickening or are cleared completely using arboricides or manual tree felling and bush clearance, or are at some stage in between. Demands for the wood of camelthorn trees (*Acacia erioloba*), (the largest tree species growing on semi-arid and arid Kalahari sands) for firewood has also impacted habitat structure. Large trees are important in the Kalahari ecosystem because they provide shade, nesting and foraging sites for birds and mammals, as well as microhabitats that facilitate the existence of a suite of subcanopy plants. Indeed, large *A. erioloba* trees have been mooted as a context-dependant keystone species, important to other biota and ecological processes. The primary aim of this study was to investigate the importance of *A. erioloba* to biodiversity, focusing on plants and birds.

A study of subcanopy plant assemblages found that those beneath large trees were more species rich than those beneath small trees, and were dominated by animal-dispersed plants. Subcanopy assemblages of large trees across an aridity gradient were relatively consistent compared to those beneath small trees and in the surrounding grassy matrix. Costs and benefits of inhabiting the subcanopy microhabitat of large *A. erioloba* for a subcanopy shrub (*Ziziphus mucronata*) were also investigated. Demography of *Z. mucronata* showed the subcanopy to be important for establishment, but a transplant experiment found that *Z. mucronata* seedlings planted under large trees had a lower survival rate than those planted in the matrix. In the matrix, seedlings died from desiccation, whereas they were trampled by game or livestock or destroyed by invertebrates under trees. For adult *Z. mucronata,* mistletoe infestation was higher in plants growing in the open but flower and fruit production of *Z. mucronata* did not differ between microhabitats. Seed quality differed, however, with seeds from maternal plants growing in the subcanopy environment germinating faster than those from maternal plants growing in the open.

The relationship between habitat structure and bird assemblages showed that bird species differed considerably between bush thickened and non-thickened sites, and bird species diversity was equivalent or higher at bush thickened compared to non-thickened sites. Presence of large trees reduced the influence of shrub diversity on bird assemblage composition. The association between bird life history traits and habitat variables showed that nearly 40% of common bird species in the study sites have life history traits tied to the presence of large trees, indicating that widespread removal of large trees will be significant for birds in the region. The diversity of tree species and the presence of large living trees, and large and small dead trees were also important to birds. All bird species studied exhibited non-random use of these habitat components for perching and foraging, but larger trees were used preferentially for nesting.

A brief study of the demography of *Acacia* species in the Kimberley area showed that both *A. tortilis* and *A. erioloba* have sapling banks, suggesting that escape to greater heights is limiting. An exclusion plot experiment, provision of supplemental water, and removal of grass suggested that slow above ground growth rates and competition with grass are primary factors preventing escape to larger size classes. The effects of fire on *A. erioloba* demography showed that tree abundance and relative representation of large trees was reduced by fire, with concomitant effects on habitat structure. Such changes will have associated effects on plant and bird diversity and abundance.

Acacia erioloba is important both as a large structure and by virtue of its species identity in the Kalahari ecosystem. It functions as a keystone in certain contexts, and simply as part of the woodland tree assemblage in others, and its life-supporting role in this arid region must not be under-estimated. The contextual keystone concept, well supported by this study, is useful for understanding patterns and processes in arid ecosystems, particularly those in southern African arid savannas.

Acknowledgements

Of writing books, Winston Churchill said "To begin with it is a toy, then an amusement, then it becomes a mistress and then it becomes a master and then it becomes a tyrant and, in the last stage, just as you are about to be reconciled to your servitude, you kill the monster and fling him to the public"[1]. On completing my thesis, this quotation rings true. Many have eased the journey from plaything to eventual battle and assassination of the monster, and I owe them my deepest thanks.

I am indebted to my supervisors, Richard Dean and Jeremy Midgley. Richard first suggested the project some years ago, and has continued to believe in and support me despite various setbacks. I have valued his guidance, encouragement, availability for discussion and eagle-eyed editing skills throughout. Jeremy, a mine of ideas and enthusiasm, has also encouraged me along the way, and both supervisors have given me space to follow my own interests.

In the field, a number of friends, and a number of people who became friends, have helped during long, hot, sweaty days. A more resourceful, hardy and enthusiastic group of people I could not have hoped for: Melissa Stander, Richard Allcorn, Rachel Wiseman, Eric Herrmann, Ronelle Visagie, Stuart Priestly, Michelle Taylor, Eddie Riddell, Wayne Dawson and Sue Harris all made life in the field so much more rewarding.

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[1] Reynolds, D. 2004. In command of history (p. 217). Penguin Books Ltd., London

Piet van Wyk, Hugo Bezuidenhout, Deon Joubert, Bernard van Lente, Angus and Sue Anthony, Peter Gibbs, Andrew Soul, Graham Main, Morgan Hauptfleisch, Le Roux Coetzee and Le Roux Button are also thanked. Deon Joubert went beyond the call of duty to help us when we were stuck out in the field one evening after an interesting encounter with "Wildeman". De Beers Diamond Mines Farms and Ecology division, South African National Parks Board and Gamagara generously allowed us access and facilities.

Without Daniel Polakow and Anthony Seymour, I would still be drowning in a daze of data files. Daniel's statistical guidance and Anthony's skills with VBA enabled me to convert reams of data into results. I am particularly grateful to Daniel for his constant encouragement to just finish, and who gave very generously of his own limited time to read over and discuss much of this work.

I am also grateful to Sue Milton, Rob Simmons, Wendy Lloyd and Helen de Klerk for willingly giving advice, encouragement and input along the way. Sue Milton deserves special mention for taking on the additional administrative burden of "stray" students like me. Speaking of administrative burdens - Chris Tobler, Lionel Mansfield, Neville Eden, and Dawood Hattas all provided excellent support, and Danelle du Toit and Margaret Sandwith often performed miracles, accessing many of the less easily available references. When I could no longer bear to look at this work, Glynne Case waded through it with great attention to detail and care. Timm Hoffman kindly gave me matched pictures showing growth of *A. erioloba* over 80 years.

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Dad, Mum, Bev and Ant, friends and colleagues at the FitzPatrick Institute have stood by me through many difficult times and I am very grateful to them. My parents gave me a bushveld upbringing, which no doubt engendered my love of African savannas and bushveld. I dedicate this thesis to the memory of my father, who passed away suddenly on the 21st July 2006 – we were so fortunate to have him.

Finally, Onno Huyser, whose consistent support has been beyond all estimation, cannot be thanked enough. In addition to always being willing to discuss new ideas, I am deeply indebted to you for the huge sacrifices you have made to enable me to complete this - hopefully somehow, I too will be able to offer you unwavering support when you need it. Thank you.

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Introduction

Within the Xeric Kalahari (Figures 1.1 and 1.2), heavy grazing (Donaldson and Kelk 1970, Lloyd 2003) coincident with consecutive years of good rainfall can lead to bush thickening (Ward 2002, Joubert et al. 2003) (Figure 1.3). Bush thickening occurs when woody plant density (usually *Acacia mellifera* (Fabaceae: Benth.), velvet raisin *Grewia flava* (Tiliaceae: DC), sickle bush *Dichrostachys cinerea* (Fabaceae: Wright & Arn.) or three thorn *Rhigozum trichotomum* (Bignoniaceae: Burch.)) increases beyond a certain threshold, leading to suppression of herbaceous plants (Donaldson and Kelk 1970, Richter et al. 2001). The problem is considerable: in the 1980s, bush-thickened areas covered approximately 2.5 million ha in the South African section of the Kalahari alone (Moore et al. 1985). The phenomenon is also widespread in the Botswanan and Namibian sections of the Xeric Kalahari (van Vegten 1983, Skarpe 1990, Herremans 1998, Moleele 1998, Meik et al. 2002). The problem is exacerbated by rainfall stochasticity in the region - a simulation study (Jeltsch et al. 1997) suggested that although stocking these areas at government-recommended stocking rates would not tip the ecosystem towards a state of bush thickening in 20 years, there was a high probability of this occurring over longer time-spans (i.e. within a century).

One of the most cost-effective ways of dealing with bush thickening is by application of arboricides, and in the early 1980s, Tebuthiuron[1] and other arboricides were applied widely to thickened areas (Moore et al. 1985). Initially, only target species succumbed (Moore et al. 1985), but within a few years non-target species, including the slow-growing camelthorn *Acacia erioloba* and shepherds' tree *Boscia albitrunca,* also began to die off (Figure 1.4).

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[1] N-[5-(1,1-dimethylethyl)-1,3,4-thiadiazol-2-yl]-N,N'-dimethylurea

1

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Figure 1.1. Position of the Xeric Kalahari Savanna as delineated by Burgess et al. (2004).

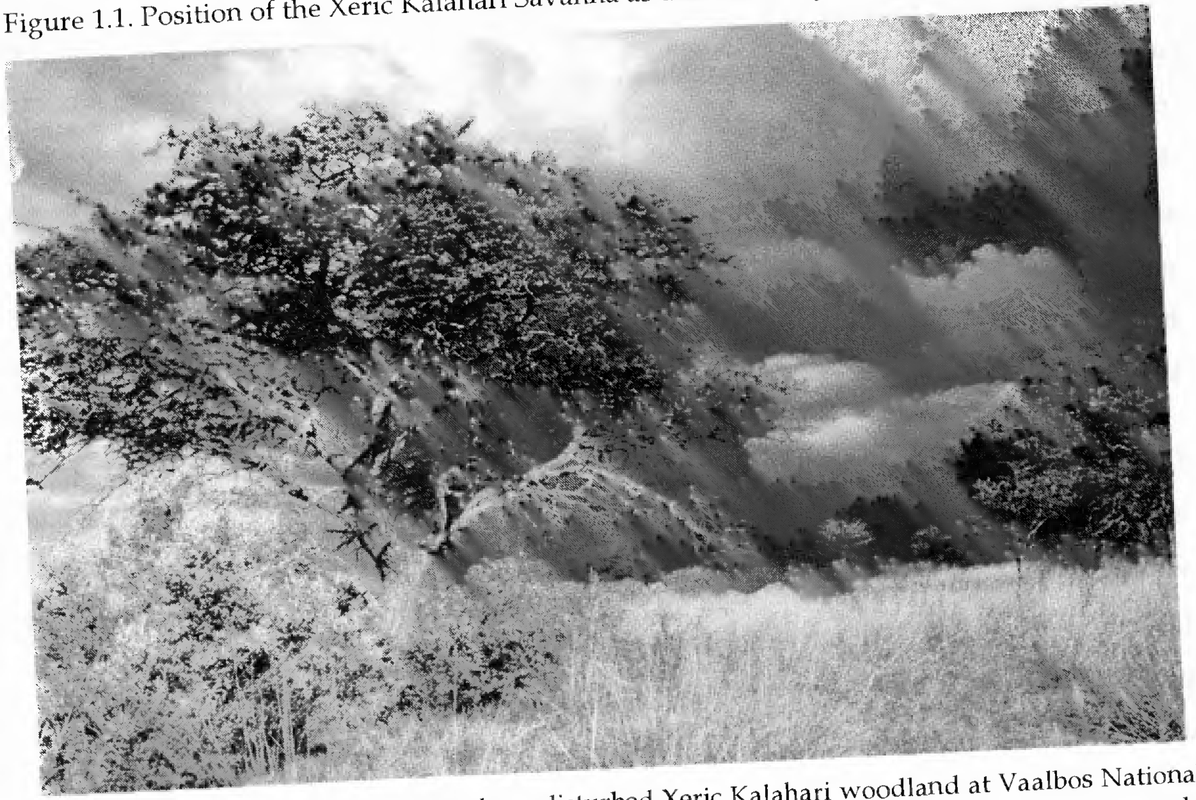

Figure 1.2. An example of a relatively undisturbed Xeric Kalahari woodland at Vaalbos National Park, near Barkley West, South Africa. This picture shows an *Acacia erioloba* tree, approximately 6m high. Beneath it, are the large bird-dispersed *Grewia flava* and *Rhus tenuinervis*, as well as bird nest-dispersed *Tarchonanthus camphoratus* shrubs. *Photograph: Onno Huyser*

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Figure 1.3. Example of a bush thickened area in the southern Kalahari, near Dibeng, in the Northern Cape. The encroaching species in this instance is a mix of *Acacia mellifera* and *Rhigozum trichotomum*. Two white rhinoceros (*Ceratotherium simum*), in the background, are obscured by the bushes.

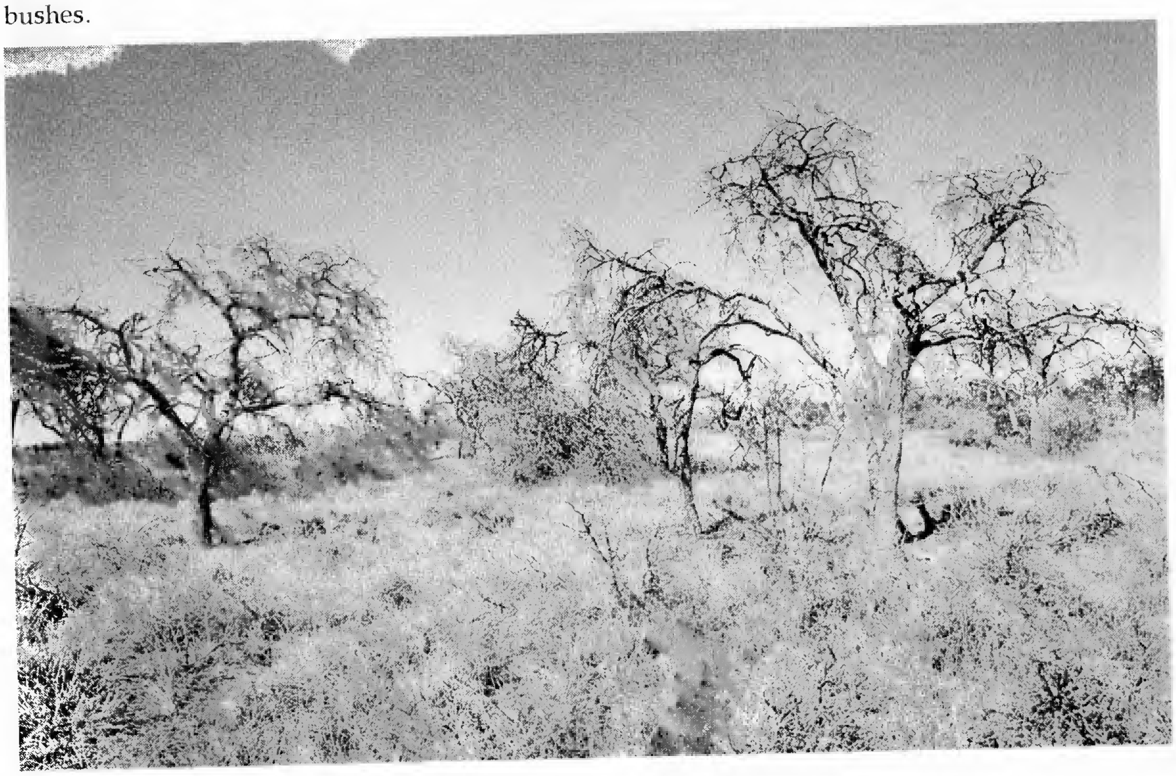

Figure 1.4. After excessive application of arboricide, not only target species are killed, but also mature *Acacia erioloba* trees. The trees in the photograph, taken at Kathu, near Kuruman in the Northern Cape of South Africa are all approximately 6 or 7m high, and probably at least 70 years old. This particular arboricided patch covers only a few ha, but there are areas which have been extensively arboricided extending over thousands of ha.

This habitat degradation has subsequently been augmented by a demand for *A. erioloba* firewood from urban centres for *braais* (barbeques): on some properties, as much as 60 tonnes of wood are removed monthly (Anderson and Anderson 2001). Compounded with local effects (that started in the late 19th century and continue today) such as wholesale clearing of trees for timber for mining operations, or at mine sites themselves, the resultant effect is that in many areas no vertical habitat structure remains (see e.g. Figure 1.5).

Removal of farming subsidies, unpredictable rainfall, the legacy of the division of farms into progressively smaller, economically unsustainable units, and the view that trees compete with pasture (Powell 2001, Seymour and Milton 2003) have all contributed to the widespread harvesting of *A. erioloba* , which is, in fact, a protected species (Department of Water Affairs and Forestry 1998).

Figure 1.5. Demand for firewood and the possible threat from veld fires causes many land owners to remove trees that have been killed during arboriciding, as shown in this photograph, taken near Debeng, Northen Cape. Demand for firewood, however, means that live trees are also often harvested.

ACACIA ERIOLOBA[2] AS A KEYSTONE

The issue of widespread removal of *A. erioloba* is critical to conservation within the Xeric Kalahari, because *A. erioloba* has been proposed as a context-dependent keystone species *sensu* Power et al. (1996) (Dean et al. 1999). In other words, the keystone role is hypothesised to hold only when the tree is large, and when the woody component of the habitat is below certain densities (Milton and Dean 1995, Dean et al. 1999).

On Kalahari sands, in areas of rainfall below 400mm.year^{-1}, *A. erioloba* is the only tree to reach any great size (Acocks 1953). Therefore, the motivation for the status of *A. erioloba* as a keystone species in the Xeric Kalahari is based not so much on its species identity, but because as a large tree, it provides a number of resources important to sustaining and driving biodiversity patterns and processes (Milton and Dean 1995, Dean et al. 1999).

Is there value in identifying and conserving a single species? For decades, ecologists have divided species into categories, based on their contribution to conservation or our understanding of how ecosystems function. A number of single-species approaches exist. They are appealing, because the success or failure of conservation interventions can be measured through changes in abundance or density of the focal species. Flagship species, the "poster animals" of the conservation world, capture imaginations and donations. Umbrella species, owing to the large tracts of land needed for their conservation, ensure protection of habitat, and by implication, species (Simberloff 1998). Indicator species serve as surrogate measures of "attributes too difficult, inconvenient, or expensive to measure for other species or environmental conditions of interest" (Landres et al. 1988, p 317). Endangered species, those at risk of extinction over all or a significant portion of their ranges, also present possible targets for conservation efforts.

These approaches are not always ideal, however. Flagships may not be good indicators, and some threatened ecosystems could be devoid of species charismatic enough to act as flagships (Simberloff 1998). Umbrella species, while intuitively appealing, carry no

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[2] Recent morphological and genetic studies indicate that the genus *Acacia* is polyphyletic. Although the type specimen, *A. nilotica,* is African, an argument has been made for Australian acacias, of a different group to African acacias, to keep the name, an argument that centres primarily on economics. It is proposed that the majority of African acacias will fall into either *Senegalia* or *Vachellia* (Orchard and Maslin 2003), so that *Acacia erioloba* would be renamed *Vachellia erioloba.*

guarantee that their conservation ensures safeguarding of a myriad other species, because some species are limited by ecological factors not necessarily crucial to the umbrella species (Roberge and Angelstam 2004). Use of indicator species is problematic if the needs of indicators do not coincide with those of other species (Landres et al. 1988), and occasionally management of different species can require conflicting actions (Simberloff 1998).

Ecosystem management, an approach that focuses on ecological processes rather than individual species (Meffe and Carroll 1994), has been proposed as a solution to the difficulties associated with single-species management. But some ecosystem processes can be maintained even as species usually responsible for them are lost (Tracy and Brussard 1994). Even in species-poor ecosystems, energy continues to flow and nutrients continue to cycle, rendering this method unreliable for ensuring maintenance of biodiversity patterns and processes (Simberloff 1998).

Keystone species (Paine 1969a) may combine the advantages of both ecosystem management and single species approaches (Simberloff 1998). This approach maintains a single species strategy, while emphasizing processes that govern biodiversity. The definition of keystone species is contentious, however. Although I do not go into a full exposition of the evolution and subsequent refinement of the concept here, I highlight points of importance to its application in this study.

Paine (1969b) originally defined a keystone species as a species of high trophic status that disproportionately affects patterns of species occurrence, distribution and density within the assemblage in which it occurs. Thus, the definition identified a specific ecosystem process of top-down influence (i.e. predation) on species diversity, competitive interaction and community persistence. The concept of keystone species was then extended to a variety of species, being referred to as keystone prey, competitors, mutualists, dispersers, pollinators, engineers, etc. (Davic 2003). This led Mills et al. (1993) to argue that the definition of keystone species was too vague, and the concept too generally used, to be instructive as a base on which to formulate conservation strategy.

But many ecologists believe that the keystone species concept still has the potential to be very useful to both understanding and conserving ecosystems, and so are unwilling to relinquish it merely because of the lack of clarity of definition. Power et al. (1996) attempted to elucidate the definition , defining keystone species as:

(a) Those that have marked effects on community structure and function, and

(b) The size of these effects is disproportionately large relative to the abundance or size of the keystone species.

As pointed out by Hurlbert (1997) (who, incidentally, argued for doing away with the term and concept of "keystone species" altogether) and Kotliar (2000), the second part of this definition creates a fictitious dichotomy between ecologically important species that are ecologically abundant and those that are not. Kotliar (2000) also adds another criterion to the definition as set out by Power et al. (1996) - keystone species must provide functions not carried out by other species or processes. Lastly, of relevance to the role of *A. erioloba* as a keystone in the Kalahari, is the concept of a "keystone structure", forwarded by Tews et al. (2004): 'a distinct spatial structure providing resources, shelter or "goods and services" crucial for other species'.

I investigated the role of *A. erioloba* as a keystone species and/or key structure within the southern Kalahari, and examined, through studies on birds and plants, whether this key role is context-dependent and how various definitions, with their attendant caveats as proposed by Power et al. (1996), Kotliar (2000) and Tews et al. (2004) apply. Therefore, in this thesis, the overarching questions are:

Is *A. erioloba* only functionally important when large?

If so, when large, does it have appreciable effects on community structure and function?

Are these effects disproportionately large, relative to the abundance of *A. erioloba*?

Does *A. erioloba* provide functions not performed by other species or processes?

Is *A. erioloba* best described as a discrete spatial structure providing resources, shelter or "goods and services" critical to other species (i.e. is the appellation "keystone structure" more appropriate?)

This study is opportune because the ecology of the *Acacia* savannas of the Kalahari is relatively poorly known. Although a number of autecological studies have been carried out in the region (e.g., Clutton-Brock et al. 1999, Covas et al. 2004, Eccard et al. 2004, Begg et al. 2005), relatively few have examined how habitat structure interacts with the biodiversity of the ecosystem (but see Herremans 1998, Dean et al. 1999, Cooper and Whiting 2000, Dean et al. 2002). As a leguminous, deep-rooted species, *A. erioloba* is probably important in nitrogen-fixing and nutrient cycling, and may even contribute to water cycles through hydraulic lift, as well as provision of shade, that reduces evaporation rates beneath the canopy, making more water available to plants. The findings of this research are important to conservation within the region because the Kalahari sustains significant fractions of southern African agricultural economic activity. If *A. erioloba is* a keystone species in the Kalahari, then its indiscriminate removal might be expected to initiate widespread losses in biodiversity, as ecosystem processes falter.

THESIS OUTLINE

Each chapter is written primarily as an independent paper to aid publication of results, but to avoid repetition, certain introductory and methodological sections relevant throughout are omitted after the first section.

From the outset it is important to state that to address the importance of *A. erioloba* to biodiversity (in its fullest sense, i.e. patterns and processes, at all levels from genes to landscapes) is beyond the scope of this thesis. The patterns and processes investigated reflect instead my interests, but can still elucidate the relative importance of size and density of this species to biodiversity patterns and processes.

Chapter 2 provides a description of the study area and a literature review of our knowledge of *A. erioloba* to date.

Chapter 3 investigates the relationship between plant species assemblages beneath large and small *A. erioloba* and the encircling, grass-dominated "matrix". I use the tree subcanopy to investigate the species-energy diversity theory, which predicts that all else being equal, plant assemblages away from tree canopies and on the equator-ward side of trees should be more diverse than those found on the opposite side, owing to higher solar radiation (Wright et al. 1993). I also investigate the role of the subcanopy environment of *A. erioloba* as a predictable microhabitat for certain plant species within the southern Kalahari.

In Chapter 4, I investigate whether, over the lifecycle of a subcanopy plant, the presence of the canopy (nurse) plant (i.e. *A. erioloba*) can change from being positive to zero (i.e.

ecologically redundant, *sensu* Walker (1992)), or even negative. A number of species within the subcanopy plant assemblages of the Xeric Kalahari have evolved directed dispersal, presumably to ensure that they reach the subcanopy environment. The subcanopy environment has distinctly different light, water and nutrient regimes to the surrounding grassy matrix (Belsky et al. 1989). Because of shading, evaporation rates are far lower than those of the matrix (Belsky et al. 1989, Akpo and Grouzis 1993), which is particularly important to beneficiaries of nurse-plant interactions in arid systems (Valiente-Banuet and Ezcurra 1991, Fulbright et al. 1995, Callaway et al. 1996). In addition, soils tend to be higher in nutrients because animals focus activity around large trees and perhaps because of nitrogen-fixing by the trees themselves (Georgiadis 1989, Isichei and Muoghalu 1992, Vetaas 1992, Belsky 1994, Roos and Allsopp 1997, Dean et al. 1999, Weltzin and McPherson 1999, Barnes 2001). Although the subcanopy environment has reduced evaporation and elevated nutrients, it is light-limited and also suffers higher levels of animal disturbance (Dean et al. 1999). Therefore, while favourable for germination, the subcanopy may not be ideal for later stages in the life cycle (Grubb 1977, Lamont et al. 1993). Schupp (1995) referred to these disparities as "within-individual conflicts", but little is known about the extent or consequences of these conflicts. I examine the potential for within-individual conflicts for the subcanopy shrub *Ziziphus mucronata* (Willd.) (Rhamnaceae), common in the less arid extent of the Xeric Kalahari and which is also often found in the matrix.

Land use practices often alter vegetation structure (Brown and Archer 1989, Skarpe 1990, Jeltsch et al. 1996), and bird assemblages are in turn influenced by habitat structure (MacArthur et al. 1962, MacArthur and MacArthur 1962, MacArthur et al. 1966, Cody 1981, 1985, Herremans 1995, 1998). In Chapter 5, I investigate how changes to habitat structure resulting from various land use practices influence bird assemblages, both in terms of species richness and assemblage composition.

Chapter 6 examines how changes in bird assemblages may offer insights into the influence of structural changes on ecosystem function (i.e. intra and interspecific interactions of biota, as well as their interactions with the physical environment, e.g. seed dispersal, germination, water and nutrient cycling, etc.). Birds occupy a variety of levels in the food chain, their ecology is well studied, and because some species have large home ranges, changes at coarser scales may also be detected (Hausner et al. 2003). Therefore, changes in dominant bird guilds, and bird carrying capacity, because correlated with changes in ecosystem function, may indicate changes to ecosystem function.

Chapter 7 investigates use of large *A. erioloba vs.* use of other large trees (e.g. *B. albitrunca* and *A. tortilis)* to evaluate whether the application of keystone species vs. keystone structure best applies to *A. erioloba* with respect to birds. In this chapter, I examine whether birds show preferences in terms of tree size and species for foraging, perching and nesting, and whether entire bird species assemblages associated with different tree sizes and species are similar or different.

In Chapters 8 and 9, I study factors influencing population structure of *A. erioloba* at sites near Kimberley, with the aim of offering management recommendations for maintaining maximum plant and bird diversity. In these chapters, I investigate the influence of supplementary water, protection from herbivory (both browsing and grazing) and removal of grass, on sapling growth. I also investigate the influence of fire on *A. erioloba* population structure.

In the concluding section (Synthesis: Chapter 10), I summarise the findings for each of the main groups studied, and relate them to management recommendations. I evaluate how well the proposed definitions of keystone species and keystone structures apply to *A. erioloba* and its role in the ecology of the southern Kalahari, and propose areas for future research. I also relate these to findings from other systems, where facilitation is widely considered a more important biotic interaction than competition in abiotically stressful environments (Bertness and Callaway 1994, Tewksbury and Lloyd 2001, Armas and Pugnaire 2005, Lortie and Callaway 2006), where nurse-plant interactions in particular are critical (Turner et al. 1966, Barnes and Archer 1996, Humberto et al. 1996).

A NOTE ON STUDY SITES, STATISTICS AND METHODS

I include here a brief description of the primary study sites used for this study. In addition, because this research makes use of a wide variety of statistical techniques and methods, many of which are repeated throughout the thesis, I describe those common to multiple sections, for the sake of brevity and convenience of a single source. When techniques or methods are specific to any section, these are described *in situ.*

Study sites

The Kalahari is a semi-arid, summer-rainfall savanna characterised by oligotrophic reddish-brown sands. The vegetation tends to open savanna with grasses (*Schmidtia* spp., *Stipagrostis* spp., *Aristida* spp. and *Eragrostis* spp.) and scattered trees (*Acacia erioloba, A. haematoxylon, Boscia albitrunca, A. mellifera,* with *A. tortilis* in areas of slightly higher rainfall) and shrubs (e.g. *Grewia flava, Ziziphus mucronata, Tarchonanthus camphoratus, Acacia hebeclada, Lycium* spp.).

The primary study sites at which this work was conducted were near Kimberley (425 ± 132 mm.year^{-1}) and Kuruman (377 ± 194mm.year^{-1}). Kimberley sites used were: Benfontein Game and Cattle Farm (28° 52′ S; 24° 51′E), which is moderately grazed, all year round; Susanna Cattle and Game Farm (28° 46′ S; 24° 56′ E), on which paddocks are intensively grazed for short periods of time and otherwise rested; and Rooipoort Game Farm (28° 33′S; 24° 14′E) and Vaalbos National Park (28° 29′S; 24 20′E), which both carry relatively low densities of browsers and grazers. Kuruman sites included Kathu Nature Reserve (27° 40′S, 23° 03′E), and Gamagara Game Farm (27° 30′S, 22° 30′E), which now carry low densities of browsers and grazers but in the past have occasionally been heavily grazed, and a cattle farm near Olifantshoek (27° 43′S, 22° 42′E). Where other study sites are used, details are given in the relevant chapters.

Statistics and methods

Where appropriate, data were first tested for normality and equality of variances (variance ratio test) before subjecting them to parametric analyses. Deviations from normality were assessed using the Shapiro-Wilk's W test (Shapiro et al. 1968). Unless otherwise indicated, the results of these preparatory tests are not presented when inductive parametric statistics are used. In cases where data were transformed, these are noted. All parametric results were checked for homoscedacity in the residual scatter.

Student's t-test was used to test for differences between two samples, and Mann-Whitney U tests were used for analogous non-parametric situations. U statistics were adjusted for tied ranks if they were present (Kendall 1962). Non-parametric tests were also used when the data could not be adequately transformed to normality, or when they continued to exhibit heteroscedascity (unequal variances). Where the two sample data were paired, Wilcoxon's matched-pairs test was used. The Kruskal-Wallis test, analogous to the ANOVA for normally distributed data, was used to test for among sample differences in multisample data. Chi-square analyses are used for testing of significant differences between categorical frequency data. When *a priori* evidence or logic predicts directionality of the test response, one-tailed tests are used; otherwise, all other tests are two-tailed. The alpha level of significance was set at 0.05 for all tests.

Although ANOVA is often thought of as only appropriate for normally-distributed data, it is only sensitive to heterogeneity of variances and non-normality for small, unbalanced samples (Underwood 1997). In situations where samples sizes were large and equal among treatments, therefore, ANOVA was used, even if data were not normally distributed, as non-parametric tests (e.g. Kruskal-Wallis) are sensitive to heterogeneity of variances and ANOVA remains robust to these violations if sample sizes are large and equal among treatments.

Pearson product-moment correlation and Spearman rank-order correlations were used to evaluate relationships between two global variables for normal and non-parametric data, respectively. In cases where one variable could be considered a continuous response variable and the other a continuous predictor variable, least-squares regression was used (Zar 1996). The R^2 statistic generated describes the percentage of variation of the response variable that can be reliably accounted for by its covariation with the independent variable.

In the case of several independent variables, multiple regression was used (Belsley et al. 1980). In all instances in which multiple linear regressions were used, data were tested to confirm a linear relationship with the dependent variable, and residuals were tested for normality. All regression output was analysed for significance using analysis of variance (ANOVA) procedures.

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2

Acacia erioloba - what is known about a Kalahari icon

NOMENCLATURE

The common name of *Acacia erioloba*, "camelthorn", is derived from an English corruption of the Afrikaans name for the giraffe (*"kameelperd"*). The name, giraffe, appears to have arisen from that used for the original type specimen, collected by Lichtenstein on his 1803-06 travels, *Acacia giraffae* (Willd.) (Ross 1975). In the 1970s, however, it emerged that that the type specimen was a hybrid of *A. erioloba* and *A. haematoxylon* (Ross 1975). Ross (1975) thus selected an alternative neotype, a specimen collected and described by E. Meyer, and proposed resurrecting Meyer's name, *A. erioloba*, for the Kalahari's camelthorns.

DESCRIPTION AND DISTRIBUTION

Acacia erioloba occurs on the red sands of the Kalahari of southern Africa, from southern Angola and Namibia, parts of Botswana, south-western Zimbabwe, the north-west of South Africa and just into south-west Mozambique (Barnes et al. 1997) (Figure 2.1). Over its range, rainfall varies from less than 40mm.year^{-1} to 900mm.year^{-1}, and daily temperature ranges vary from less than 15°C to 45°C (Barnes et al. 1997). Kalahari sands extend as far as Congo and Gabon, so during arid periods in the past because of successive glaciations, this species may have been far more widespread (Coe 1998).

Acacia erioloba can reach maximum heights of 16m (Coates Palgrave 1983), but its growth form is dictated by rainfall and availability of water at depth (Barnes et al. 1997). It has straight, stout, white thorns, that are usually between 2 - 5cm long (van Wyk and van Wyk 1997, Timberlake et al. 1999). It is deep-rooted, with root lengths of 60m being reported (Canadell et al. 1996).

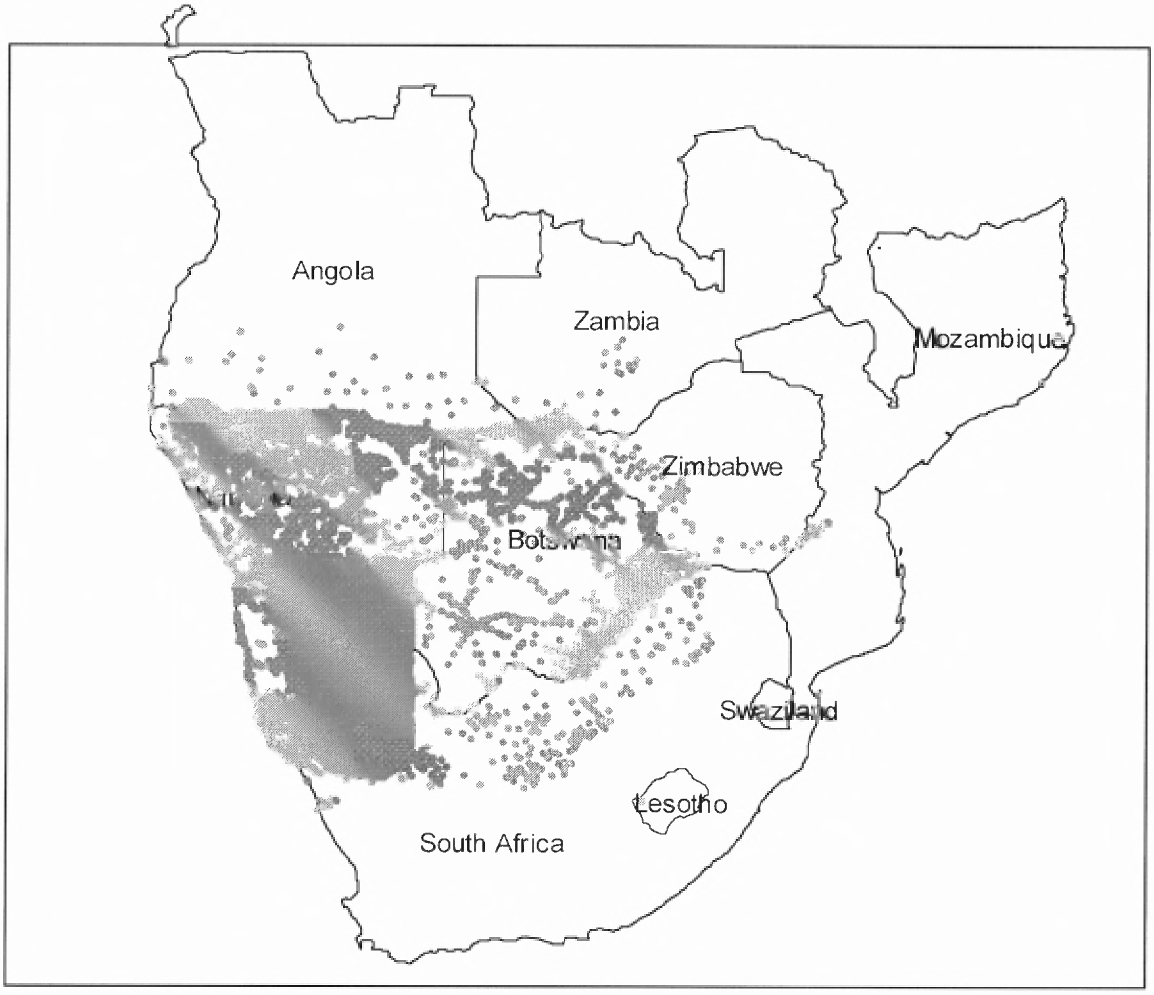

Figure 2.1. Map showing point distribution of *Acacia erioloba*. Note that the density of points reflect availability of data, rather than the actual densities of trees. (Data source: Barnes et al. (1997)). Barred area represents the Xeric Kalahari ecoregion (Burgess et al. 2004).

CONSERVATION STATUS

Acacia erioloba is protected in South Africa so that even the removal of dead specimens is illegal without a permit. The hardwood of this tree has made it popular as a quality *braaiwood* (wood for barbeques) (Raliselo 2002), however, and commercial felling and/or collection for firewood is widespread throughout its range within South Africa (Anderson and Anderson 2001, Liversidge 2001). Because *A. erioloba* is not protected in some of South Africa's neighbouring countries, it is difficult to police sale of this wood, as sellers simply claim that the wood originates beyond the country's borders. The driving forces behind harvesting are only partially understood - economic need engendered as a result of environmental and economic conditions and demand for wood in the major cities. Powell (2001) interviewed a number of farmers in the southern Kalahari, and most cited improved grazing as the reason for clearing this species. Another commonly cited

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justification for clearing camelthorn is that it is a form of job-creation, but closer analysis reveals that farmers and employees *together* earn only a third of the selling price (Milton et al. 2002) (the selling price in 2005 was about R15, i.e. roughly US$ 2, per bundle).

SPECIES ECOLOGY

Seeds of *A. erioloba* trees are dispersed by mammals, not only by wild herbivores (Leistner 1961) but also by livestock (Timberlake et al. 1999), because the pods are quite nutritious (Henkel 1931). Seeds often germinate in dung (Henkel 1931, Dudley 1999, Milton and Dean 2001), and although the importance of ingestion for germination success rate is unresolved, undamaged seeds that pass through the gut of a herbivore germinate far faster than seeds that have not been ingested (Barnes 1999, 2001b).

As with many *Acacia* species, various species of bruchid beetle (Coleoptera: Chrysomeloidea: Bruchidae) parasitise seeds of *A. erioloba,* and the large size of the seed makes them susceptible to infestations by a diversity of bruchid beetle species (Coe and Coe 1987). *A. erioloba* trees produce large amounts of seed, however, and I do not believe this species is seed limited, owing to the almost ubiquitous seedlings seen in the rainy season (C. Seymour, *unpubl. data*). Few appear to survive the dry season, however (Theron et al. 1985, Barnes 1999, C. Seymour *unpubl. data*). Thus, in arid areas, amount and pattern of rainfall are the primary determinants of establishment (Ernst et al. 1990, Barnes 1999, 2001b), so that in the drier parts of its range *A. erioloba* recruits during episodic good rainfall.

Owing to this episodic recruitment, stands of equal-sized individuals often represent cohorts (Theron et al. 1985, Ernst et al. 1990, Barnes et al. 1997, Barnes 2001b). But even if rains are good, recruitment and subsequent size class distributions within *A. erioloba* populations are still dictated by disturbances such as herbivory and/or fire. This may be the case at one of the study sites used for this research (Benfontein, Figure 2.2), where there are a number of large trees, and many small individuals at grass height, but few trees in intermediate size classes (discussed further in Chapter 8). Other examples of this include cohorts of even-sized individuals recorded within a cattle pen at Riemvasmaak (Richtersveld, South Africa) that had been abandoned for 20 years (Hoffman et al. 1994), and on disused agricultural land along the Molopo River, North West Province, South Africa (Milton and Dean 1995). Thus, while ingestion by herbivores may increase germination, subsequent seedling defoliation or trampling can eliminate new recruits

(Hoffman et al. 1989, Ben-Shahar 1998, Barnes 1999), or at least suppress growth, keeping seedlings vulnerable to fire and further herbivory and trampling, delaying growth to reproductive maturity (Barnes 2001a).

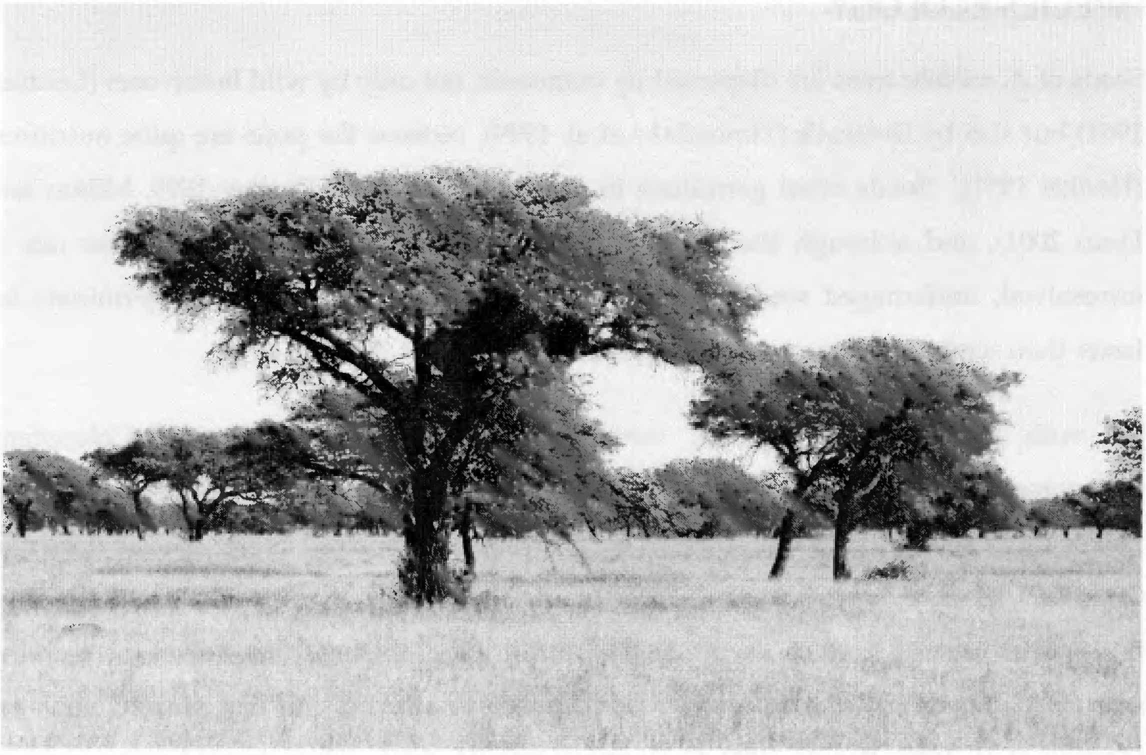

Figure 2.2. Benfontein study site showing a dearth of smaller tree size class. *Photograph: Thomas Mattsson*

Once established, how fast can an individual *A. erioloba* grow? Work in Chobe (500-550 mm.year^{-1}), northern Botswana, suggests not very – and that growth is independent of rainfall, with saplings increasing in height only 50 mm per year in both dry and average rainfall years (Barnes 1999). However a dataset from a longer timespan (93 years) at Chobe suggests a rate approximately three times greater than this, with an average annual vertical growth rate of 170 mm (Sommerlatte 1976, in Wackernagel 1993), which may indicate a subsequent increase in aboveground growth rate once beyond the seedling establishment phase. Van Rooyen et al. (1994) measured an average of 65 mm a year between 1978 and 1994 in the Kalahari Gemsbok National Park (now Kgalagadi Transfrontier Park) (Rainfall: 203mm.year^{-1} ± 91mm.year^{-1}). It is likely that rainfall, herbivory, competition from grass and fire (Belsky 1984, Scholes and Archer 1997, Midgley and Bond 2001) and depth to groundwater influence these growth rates. Since this species is deep rooted, aboveground investment in growth may be slow initially, as the tree constructs a root system, after which growth rates may increase. Recent work in the Kuiseb River, Namibia, suggests that during establishment, the roots of *A. erioloba* seedlings grow at about 1cm.day^{-1} (K. Schachtschneider, *pers. comm.*), implying considerable investment in belowground growth in the earlier stages of this species' life cycle. We do not know about subsequent investment in growth and maintenance of the root system, however, but these could be expected to be considerable.

Acacia erioloba is remarkably long-lived for an *Acacia* (Barnes 2001c). It is estimated to live to 300 years of age (Barnes 2001c), and among specimens within Kgalagadi Transfrontier Park the oldest individual tested was found to be in the region of 250 years of age (Steenkamp 2000). This may signify that certain factors within this species' life cycle have selected for a storage effect (*sensu* Warner and Chesson 1985), whereby populations need to be long-lived to allow for rare and episodic recruitment to reproductive size classes.

I suggest that, if within arid sites recruitment into the seedling bank is episodic, and within more mesic sites recruitment into larger size classes is likely to be restricted by herbivory or fire, then these factors in combination with slow aboveground growth may have contributed towards evolution of longevity in this species. In this thesis, work has been conducted at more "intermediate" (semi-arid) sites (i.e. near Kimberley, rainfall 425mm ± 132 mm.year^{-1}), where it is likely that rainfall, herbivory and fire all influence eventual rate of recruitment into adult size classes. These are examined in Chapters 8 and 9. More specifically, in Chapter 8, I investigate the importance of rainfall to growth of saplings (defined as "established" seedlings - those that have survived at least a few years). Are saplings relatively independent of rainfall as a water source, rather accessing water from groundwater sources? If grasses do better than *A. erioloba* seedlings from rainfall, then is it possible that supplementary water will favour grasses to the extent that rainfall has negative effects on seedlings, owing to shading by the herbaceous layer? In Chapter 9, I investigate how fire can influence the size distribution of *A. erioloba* populations. The few studies that have recorded a response to fire in this species suggest that although able to resprout after fire, survival rates of *A. erioloba* are low for an *Acacia*. Therefore, the influence of fire on demography of this species is likely to have consequences for biodiversity if tree size influences its keystone role.

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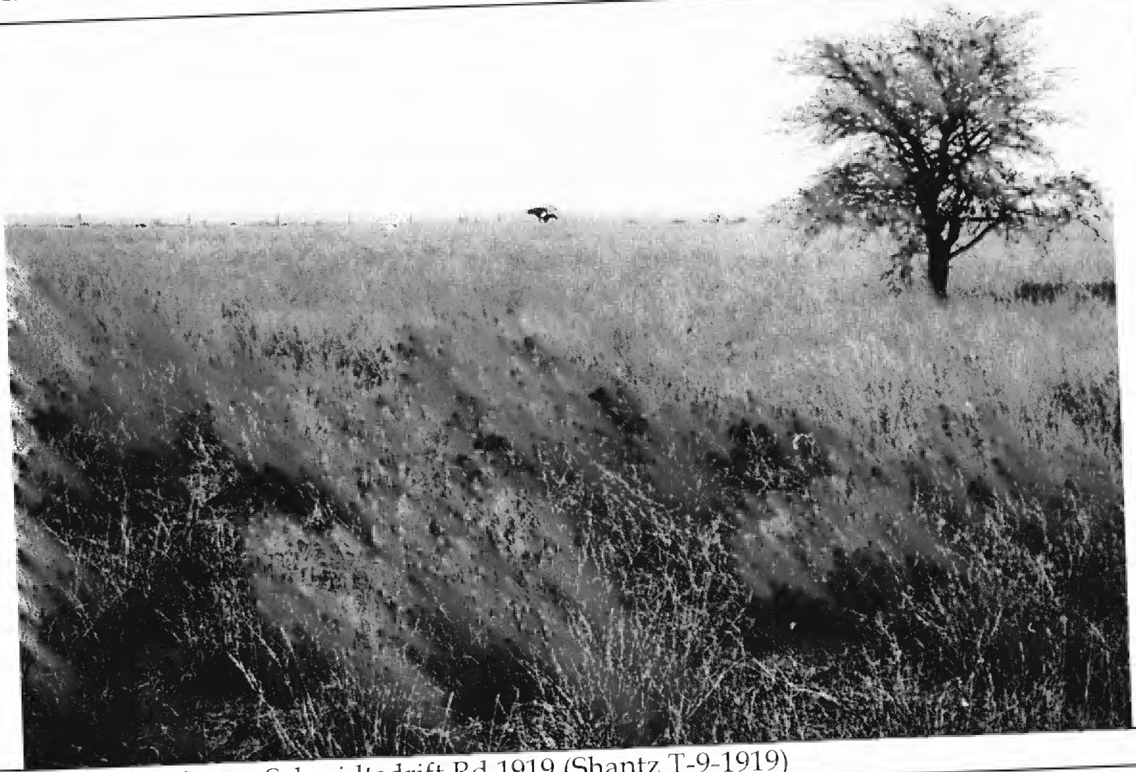
APPENDIX

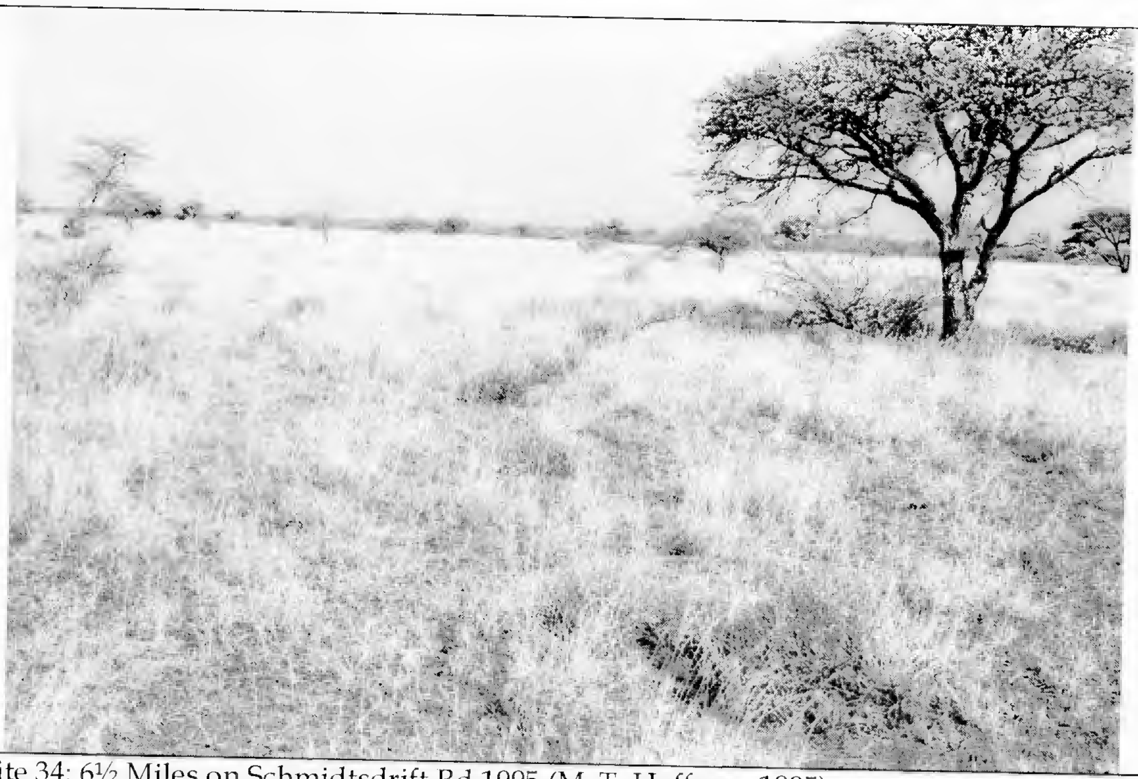
Appendix 2.1. Progression of *A. erioloba* growth over 80 years. Although the age of the tree in 1919 is unknown, these photographs give some impression of the slow growth of this species.



Site 34: 6½ Miles on Schmidtsdrift Rd 1919 (Shantz T-9-1919)

Site 34: 6½ Miles on Schmidtsdrift Rd 1956 (Shantz E-8-1956)

Site 34: 6½ Miles on Schmidtsdrift Rd 1989 (M. T. Hoffman 1989)



Site 34: 6½ Miles on Schmidtsdrift Rd 1995 (M. T. Hoffman 1995)

3

The importance of large trees to plant diversity in the southern Kalahari

ABSTRACT

While it is widely recognised that large trees often contribute to overall biodiversity in savannas by creating distinct microhabitats for the establishment of certain plant species, such contribution has seldom been quantified. In some areas of the southern Kalahari, removal of large trees has been almost complete. Therefore, the importance, if any, of small trees to these subcanopy plants also warrants investigation. This study investigates species richness and assemblage composition beneath large and small trees in the southern Kalahari, South Africa, comparing them to the surrounding matrix. Species richness per 1m^2 was significantly higher under large trees than under small trees and in the grassy matrix, with species richness per 1m^2 declining substantially at the canopy edge of large trees. Cluster analysis and ordination showed that plant species assemblages beneath smaller trees were more similar to those of the matrix than to those of large trees. A BIOENV analysis showed that in the Kimberley area, between sites about 80km apart, tree size was more important than location in determining species assemblage composition, with canopy extent being the best predictor of plant species assemblages. Cluster analysis and ordination by multidimensional scaling found plant assemblages beneath large tree canopies were comparable across sites of differing aridities, although subcanopy assemblages of small trees and the matrix vegetation were variable. Fleshy-fruited plants contributed most to similarities between subcanopy plant assemblages of large trees. The observed patterns are likely a consequence of dispersal mechanisms and facilitation, considered by many ecologists to be more important than competition in abiotically stressful environments. Thus, it appears as if large trees not only contribute significantly to

INTRODUCTION

Earlier models of savanna systems emphasised competitive interactions occurring between the grassland matrix and woody perennials (Walker et al. 1981, Walker and Noy-Meir 1982, McMutrie and Wolf 1983). More recently, a number of studies (Franco-Pizaña et al. 1995, Barnes and Archer 1996, Franco-Pizaña et al. 1996, Barnes and Archer 1999, Dean et al. 1999, Anderson et al. 2001) have shown that larger plants often facilitate the existence of a suite of plant species and thus increase overall biodiversity within these systems - a phenomenon referred to as the "nurse plant effect" (Turner et al. 1966). This facilitation seems to occur through increased nutrient availability in soil beneath trees (Belsky et al. 1993, Belsky 1994), improved water regimes (Joffre and Rambal 1988), and/or dispersal methods (Tréca and Tamba 1997, Dean et al. 1999). The nurse plant effect appears to be critical within drier environments (Armas and Pugnaire 2005).

Although both competition and facilitation are key drivers of semi-arid and arid system assemblage composition, productivity, structure and dynamics (Whitford 2002), ecological theory has held that the balance between competition and facilitation changes with severity of environmental conditions. As a rule, competition is considered of greater importance in more favourable environments, while facilitation is more important where abiotic stress is high (Bertness and Callaway 1994, Callaway and Walker 1997), and the importance of facilitation in harsh environments is becoming increasingly recognized in contemporary ecological theory (Bruno et al. 2003, Tirado and Pugnaire 2005), although there has been some controversy about this, see, e.g. Maestre et al. (2005) and rebuttal by Lortie and Callaway (2006). To investigate the importance of large trees as facilitators of other plant species in the southern Kalahari, I surveyed subcanopy plant assemblages of large and small trees, comparing them with the matrix.

In the semi-arid savanna of the southern Kalahari, southern Africa, Dean et al. (1999) found that subcanopy sites of large camelthorn trees (*Acacia erioloba*) were colonised primarily by zoochorous plants. These subcanopy plants are seldom found in the matrix, so it appears that large trees also increase overall plant diversity in the southern Kalahari. However the relative contribution of large trees to plant diversity has seldom been quantified. Furthermore, whereas the grassy "matrix" vegetation of the Kalahari differs between areas because of different rainfall and management regimes, the stability of the subcanopy environment across these gradients warrants further investigation. This is particularly important in light of often unchecked removal of large *A. erioloba* in the southern Kalahari, particularly since the keystone role of *A. erioloba* appears to hinge on its size (Milton and Dean 1995). This study investigated the following:

How does plant species richness compare between plant assemblages below large and small tree canopies and in the open?

1) Are subcanopy plant assemblages distinct from the matrix, and if so, are the subcanopy plant assemblages of small trees more similar to those of the matrix or to those of large trees?

2) Which tree dimensions have the greatest influence on the observed plant species assemblages?

3) Are subcanopy plant assemblages constant across different rainfall and management regimes?

METHODS

Sampling methods

To investigate the relative importance of the shaded environment and tree size on plant species richness, I surveyed subcanopy plant assemblages of *A. erioloba* at each of three sites in the Kimberley area (Figure 3.1) to ascertain species assemblage composition and diversity, in February-March 2003.

On Benfontein and Susanna, I sampled 20 each of large and small trees in this way, and at Vaalbos National Park, I sampled 15 large and 15 small trees. I surveyed transects along a North-South axis through the tree trunk, using 1m^2 quadrats for each meter. Transects extended to 3m beyond the canopy edge in both directions. Each tree subcanopy transect was paired with a randomly-sited quadrat in the matrix, more than 10m away from the edge of any tree canopies, and each large (>4m high) tree was paired with the nearest neighbouring small (1.5m <height <4m) tree. Geographic co-ordinates, height, largest trunk diameter at 10cm above the ground (d_{10}), lowest canopy height on the North, South, West and East side of the tree, and canopy length along the north-south and east-west axes (hereafter referred to as NS- and EW-canopy, respectively) were recorded. I did not measure diameter at breast height, as for the majority of large trees, the presence of large and thorny species like *Ziziphus mucronata* and *Lycium* spp. made the trunk at breast height inaccessible. I estimated percentage cover and height of vegetation for each 1m^2 quadrat.

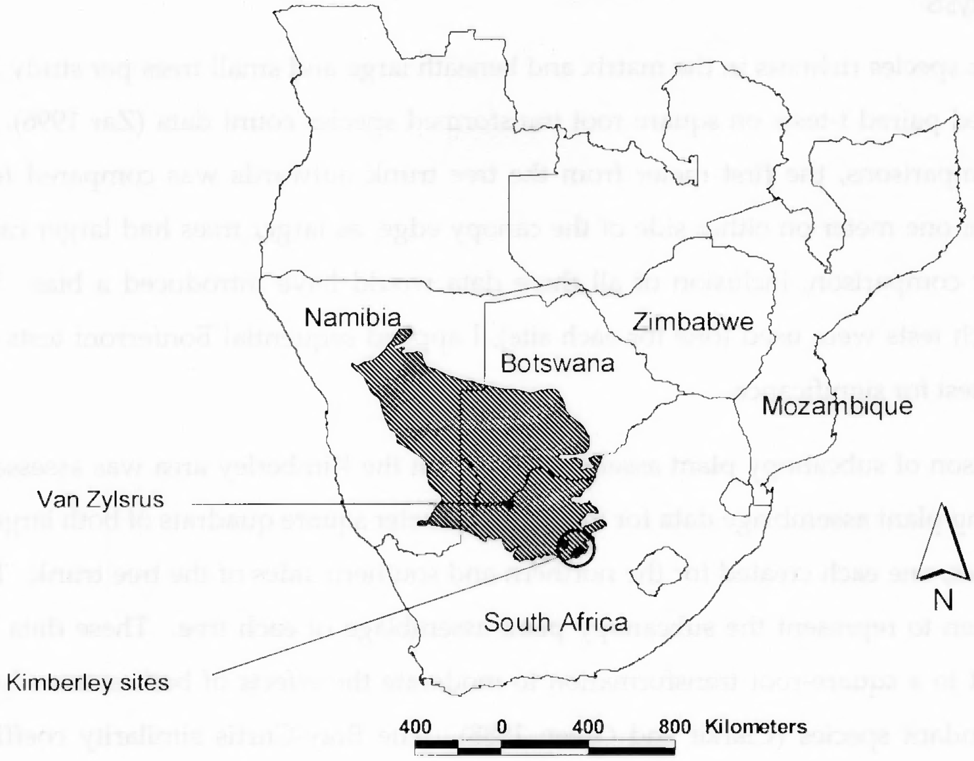


Figure 3.1. Map showing location of study sites. Shaded area indicates the Xeric Kalahari ecoregion (Burgess et al. 2004).

To investigate differences in the composition of plant species assemblages at sites of differing aridities, I surveyed plant assemblages using a line-intercept method (Mueller-Dombois and Ellenberg 1974) in March 2000. Two areas at each of the three sites (Benfontein and Vaalbos, with similar rainfall (425mm ± 132 mm.year^{-1}) and Van Zylsrus (26 49'S, 22 10'E) (203mm.year^{-1} ± 91mm.year^{-1})) were selected, with four large (>4.5 m high) and four small (1.5m<height< 4.5m) trees randomly selected and sampled in each area. Thus, a total of 24 large and 24 small trees and their associated matrices was sampled. I stretched a measuring tape out from the trunk, southwards into the matrix, usually ending 10m from the canopy edge. In some cases, it was not possible to survey the vegetation as far as 10m out, owing to the proximity of other tree canopies. The height and distance over which a plant intercepted the measuring tape for subcanopy and matrix plants (identified to species) were recorded (Nomenclature followed: Germishuizen and Meyer 2003, Appendix 3.1). For each tree, height, average minimum canopy height and two measures of canopy diameter (at 90° to each other) were recorded.

Data analysis

To assess species richness in the matrix and beneath large and small trees per study site, I performed paired t-tests on square root transformed species count data (Zar 1996). For these comparisons, the first meter from the tree trunk outwards was compared for all trees, and one meter on either side of the canopy edge, as larger trees had larger canopy areas for comparison, inclusion of all these data would have introduced a bias. Since three such tests were used (one for each site), I applied sequential Bonferroni tests (Rice 1989) to test for significance.

Comparison of subcanopy plant assemblages within the Kimberley area was assessed by combining plant assemblage data for the first two meter square quadrats of both large and small trees, one each created for the northern and southern sides of the tree trunk. These were taken to represent the subcanopy plant assemblage of each tree. These data were subjected to a square-root transformation to moderate the effects of both extremely rare and abundant species (Clarke and Green 1988). The Bray-Curtis similarity coefficient (Bray and Curtis 1957) and group average sorting method were used to generate a triangular similarity matrix and dendrogram. Since dendrograms suffer certain limitations (outlined in Field et al. 1982), similarities were also displayed in an ordination plot using multidimensional scaling (MDS). A stress function was calculated to indicate how well the two-dimensional plot represents the actual relationships between samples. The lower the value, the more faithful the representation of samples in the ordination (Clarke and Warwick 1994).

Using data from the Kimberley area, I first used a Mantel test (Mantel 1967), using a randomisation (Monte Carlo) test on 105 x 105 similarity matrices of species composition beneath each tree and tree characteristics (e.g. height, canopy width, minimum canopy height, latitutudes and longitudes), to ascertain if there were any correlations between tree characteristics ("microhabitat variables") and species composition. I then used BIOENV (Clarke and Ainsworth 1993), a routine within PRIMER, to discern which environmental variables best explain observed species assemblages (i.e. which tree characteristics, e.g. tree height, canopy diameter, geographic location, minimum canopy height etc.) might influence the actual subcanopy species composition. BIOENV assumes that pairs of trees similar in structure will have similar subcanopy plant species composition, and allows the relative importance of geographical location (with attendant implications for site management) to be ascertained relative to actual tree characteristics as determinants of plant species composition. Thus, the aspects of tree structure that influence subcanopy plant assemblage should be identifiable. If management regimes are vastly different, however, geographic location should be identified as a more important determinant of similarities between plant species assemblages. Essentially, the BIOENV procedure selects the combination of environmental variables that maximizes the correlation between the rank similarity matrices of the sample and environmental data, thus identifying the best possible match. Omission of important factors or inclusion of factors irrelevant to plant species assemblage composition dilute the match (Clarke and Ainsworth 1993). A Spearman rank correlation was used to ascertain which tree characteristics best explained observed similarities in subcanopy species composition. I first tested for the best single factor explaining similarity of subcanopy assemblages, followed by an analysis for the best combination of all factors. To best capture variation and similarities between assemblages, data were untransformed for this analysis, so that the effect of dominant species was not dampened. Plant species most responsible for the observed groupings were identified using similarity percentages.

To assess whether subcanopy assemblages of small trees were more similar to those of large trees or the matrix, I used subcanopy data for the southern side of the tree trunk only, to reduce variability in explanatory variables. I subjected a dataset composed of subcanopy assemblages for large, small and matrix assemblages to the same similarity and ordination analyses as described above for large vs. small trees. The above analyses were carried out using the CLUSTER, MDS, SIMPER and BIO-ENV programs in the computer package PRIMER (Plymouth Routines In Multivariate Ecological Research) (Clarke and Gorley 2001).

RESULTS

Within the subset of data used for MDS analyses comparing large and small trees, 200 plant species were recorded at the Kimberley sites (Appendix 3). Of these, 87 occurred beneath large trees, 84 beneath small trees and 62 species were found within matrix quadrats. Some species were found only within one microhabitat: 27 (31%) were only found under large trees, 13 (16%) only under small trees and 11 (18%) only in the matrix.

Species richness declined precipitously at the canopy edge of large trees (Figure 3.2). There were significantly more species beneath large trees than below small trees

((Bonferroni corrected p values given): Benfontein: t = 2.24, n = 80, $p = 0.0167$; Vaalbos: t = 4.832; n = 73; $p = 0.025$; Susanna: t = 2.32, n = 55; $p = 0.05$).

Although the MDS ordination yielded a relatively high stress value (0.22), the results of the cluster analysis and MDS coincided. The MDS suggested that tree size and geographic site were important in determining species composition (Figure 3.3), and a Mantel randomisation of the two similarity matrices indicated that there was a significant correlation between species composition and tree characteristics (r = 0.378, n = 105, $p < 0.001$). BIOENV analysis identified tree size (represented by NS canopy extent (R = 0.466), followed by EW canopy extent (R = 0.460), d_{10} (0.459), height (R = 0.398)), to be more important than geographic location (latitude (R= 0.268) and longitude (R = 0.256)), although there were not enough sites to draw any firm conclusions about geographic location. The best combination of variables selected NS canopy, d_{10} and longitude (R = 0.593). The ordination did not differentiate between subcanopy assemblages on the north and south sides of the tree trunk.

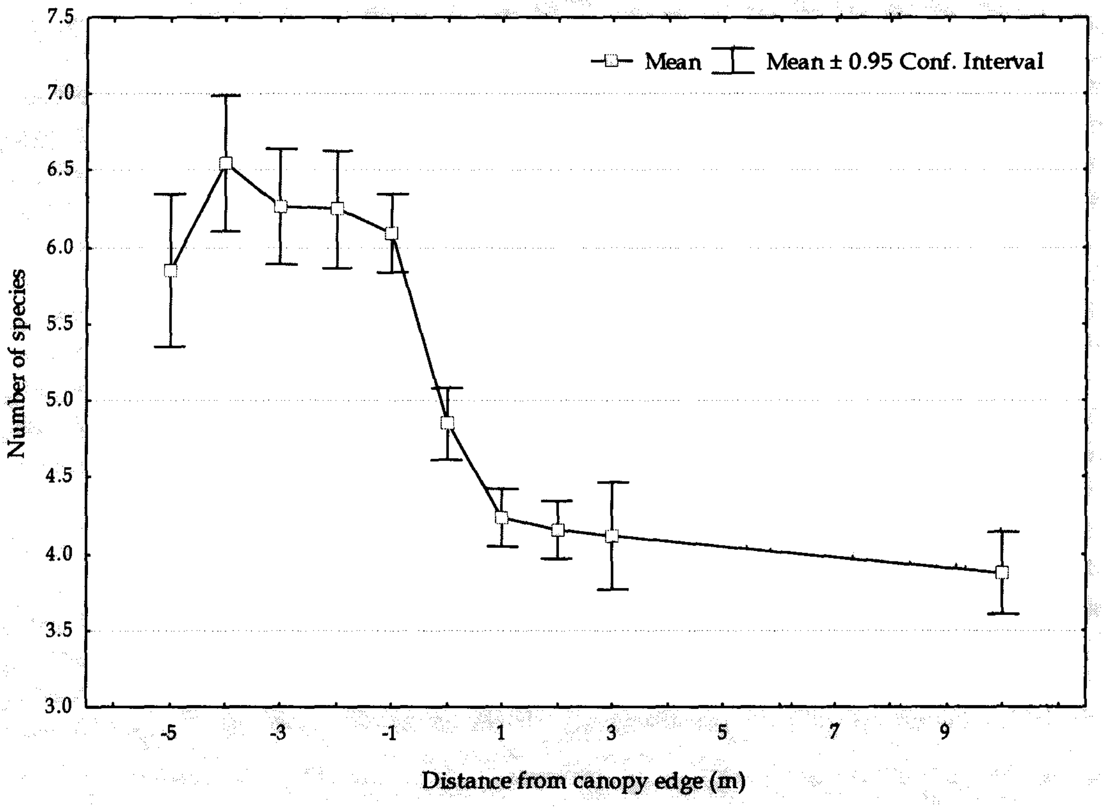


Figure 3.2. Species richness relative to the canopy edge for both large and small *Acacia erioloba* trees at all sites. Zero denotes the canopy edge, negative numbers the distance away from the canopy edge towards the tree trunk, positive numbers the distance away from the canopy edge towards the matrix.

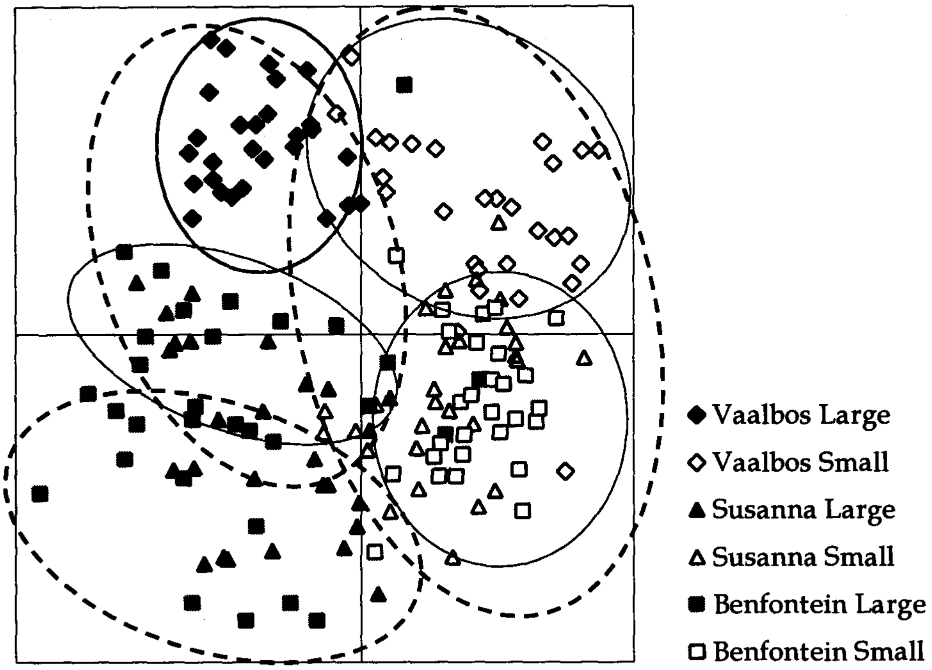


Figure 3.3. A comparison of subcanopy plant assemblages of small and large trees only, using an MDS ordination based on Bray-Curtis similarity matrix for square-root transformed data (Stress = 0.22). Groupings identified by cluster analysis are approximated with ovals around data points: ----- indicates 20% similarity; —— indicates >25% similarity.

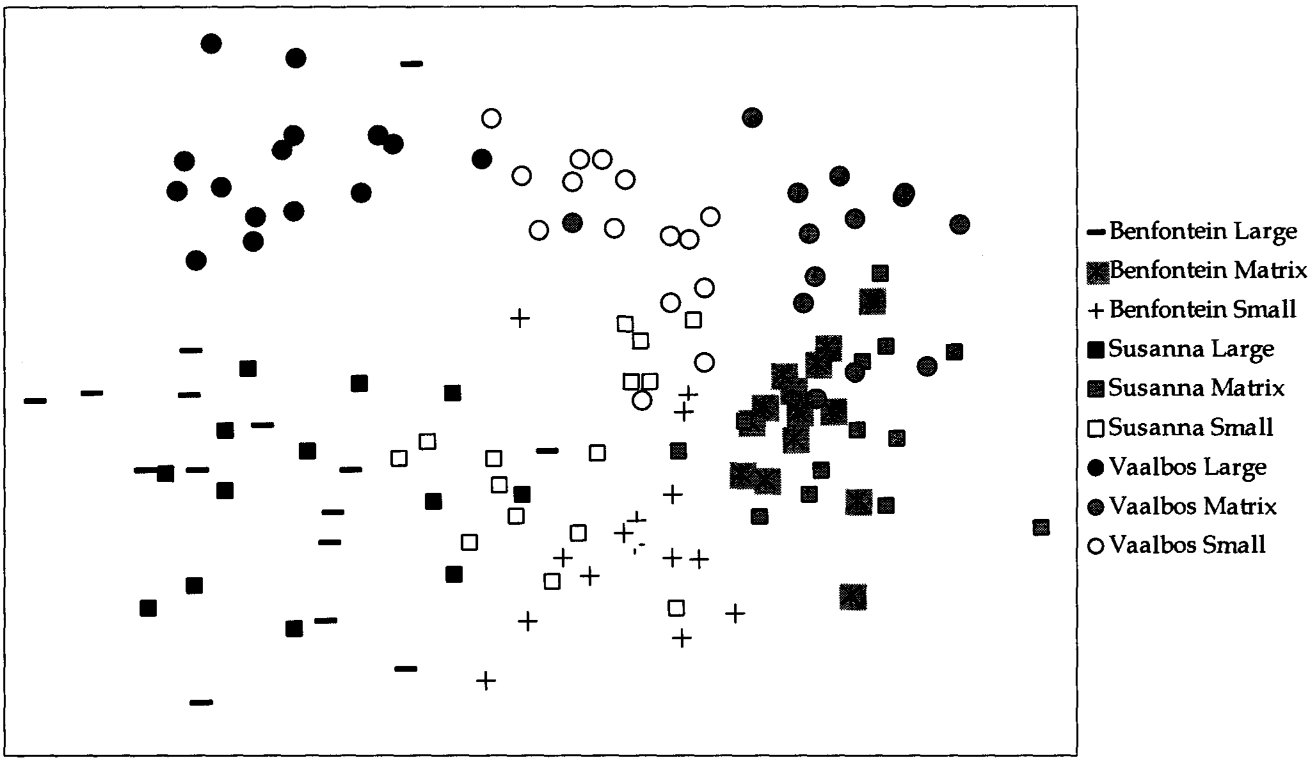


Figure 3.4. MDS ordination of subcanopy assemblages of large and small trees, as well as matrix plant assemblages

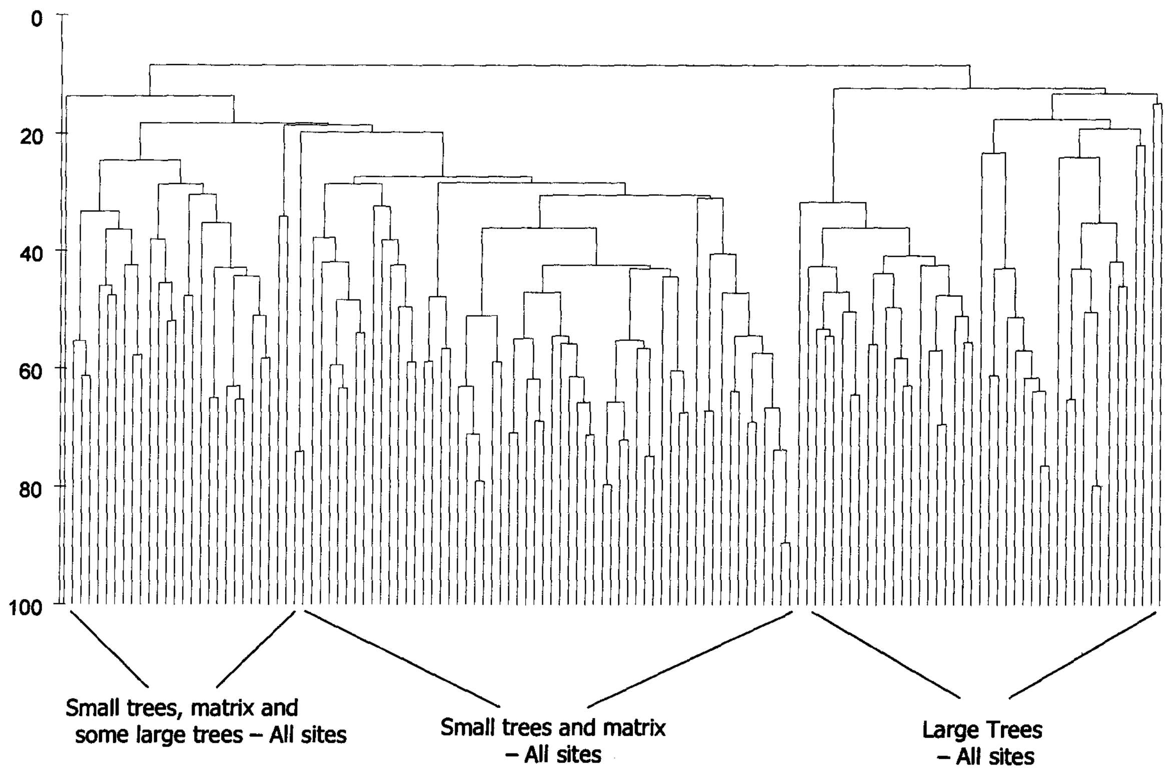


Figure 3.5. Simplified dendrogram based on Bray-Curtis similarity matrix for square-root transformed data.

Subcanopy assemblages of small trees lay on a continuum between those of the matrix and large trees (Figure 3.4), although the dendrogram (Figure 3.5) indicated they were more similar to those of the matrix than large trees.

The MDS ordination (Figure 3.6) produced by the cluster analysis of sites of differing aridities yielded a stress value of 0.13, indicating that the ordination is a reliable representation of the relationships between samples. Plant assemblages beneath large trees tended to cluster together irrespective of site. Plant assemblages beneath small trees clustered together with the matrices of their respective sites. There was also a clear separation of matrix sites, with the two Kimberley sites (Benfontein and Vaalbos) clustering separately from the drier Van Zylsrus site.

Three fleshy-fruited, vertebrate dispersed shrubs (*G. flava, L. hirsutum,* and *Z. mucronata*) explained just over 75% of the similarity between plant assemblages beneath large trees. These same three species also accounted for dissimilarities between large trees and the matrix (44.6%), followed by three grass species, *Schmidtia pappophoroides, Pogonarthria squarrosa* and *Eragrostis lehmanniana* accounting for a further 18%. The fleshy-fruited species were far more abundant under large trees, whilst the grasses dominated matrix quadrats. Differences between small and large trees were also explained by these three fleshy-fruited species (48.75%), again with large trees having far higher abundances. The grasses *Eragrostis lehmanniana* and *Stipagrostis uniplumis,* and the herbaceous perennial, *Chrysocoma ciliata,* all more common beneath small trees, explained a further 10%. Small trees differed from the matrix primarily by abundances of different grass species: *S. pappophoroides,* which was more common in the matrix than beneath trees, explained 18.5% of the dissimilarity, followed by *E. lehmanniana, G. flava* and *S. uniplumis,* all more abundant beneath small trees, and which together explained 25% of dissimilarity. *P. squarrosa, E. trichophora* and *E. pallens* were more common in the matrix, and *C. ciliata* and *A. congesta* were more common under trees, bringing the total percentage of dissimilarity explained to 71%.

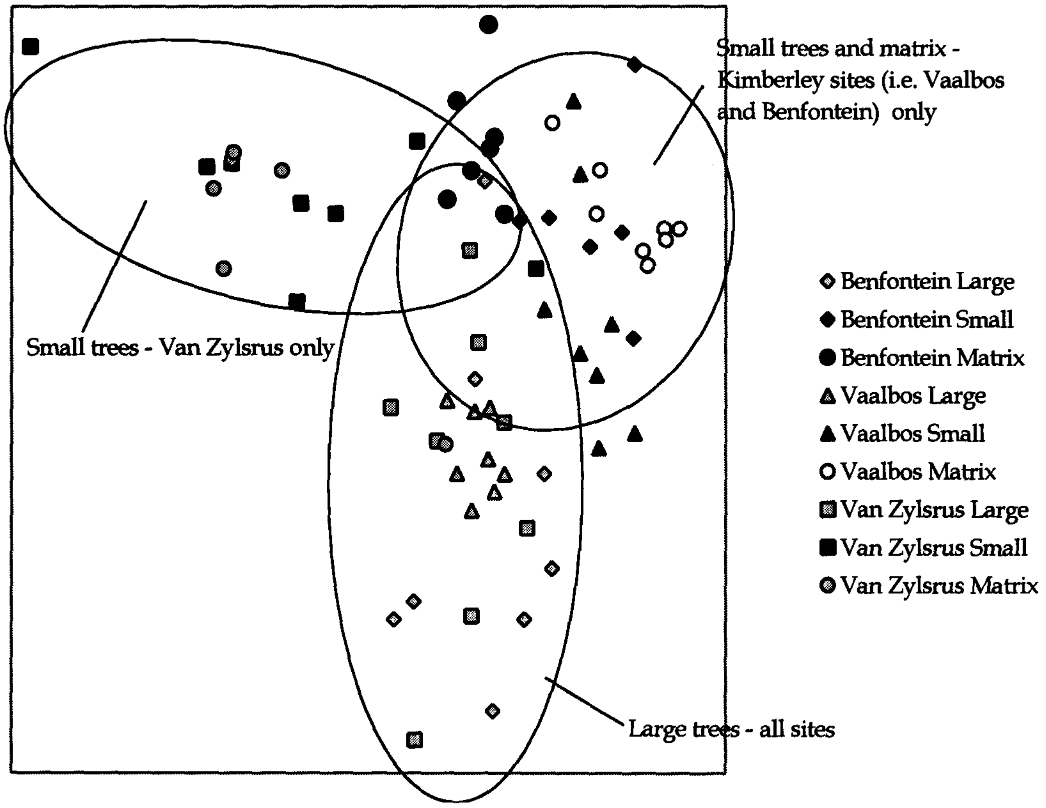


Figure 3.6. Comparison of subcanopy assemblages under different aridities. Plant assemblages beneath large trees seem to be fairly consistent, compared with those in the matrix and beneath small trees, with plant assemblages beneath small trees and in the matrix at Van Zylsrus being very different to those at Benfontein and Vaalbos.

CHAPTER 3

DISCUSSION

Plant species richness beneath tree canopies may be higher than that of the matrix for a number of reasons. Subcanopy plants are shade tolerant, to different degrees, enabling co-existence of a number of plant layers in each metre sampled, whereas plants occurring in the matrix do not exhibit this layering effect.

In addition, species richness is thought to increase with increasing productivity (until a threshold is reached, usually in anthropogenic situations where productivity is too high) (Rosenzweig 1995), and the subcanopy microhabitat is likely more productive owing to greater water and nutrient availability, even though there is less sunlight beneath the canopy. Animal activity, decreased leaching and nutrient pumping (Belsky et al. 1989, Weltzin and Coughenour 1990, Vetaas 1992, Dean et al. 1999) all lead to higher nutrient levels in subcanopy soils relative to the matrix, so that germination rates (Hilhorst and Karssen 2000) and plant cover may be higher in these sites. Reduced evaporation and the flow of rainwater along stems (stemflow) and roots results in elevated moisture levels in subcanopy soils relative to the matrix, making it a favourable site for seedling establishment (Akpo and Grouzis 1993). It is also possible that large trees transport water from deeper roots to drier surface soils via lateral roots, a phenomenon referred to as hydraulic lift (Richards and Caldwell 1987, Caldwell and Richards 1989, Caldwell et al. 1998). Although Thurow et al. (1987) found that soil close to trunks of *Quercus virginiana* may receive over 200% of annual precipitation by stemflow, subcanopy soil further than 10cm away from a trunk received only 50.6% of annual rainfall. Stemflow and throughfall are influenced by tree architecture and foliage density, however, so these figures are not universally applicable. High evaporation rates and regularity of very heavy rainfall events in the study area mean that protection from evaporation is likely more important than prevention of through-flow by the canopy.

Consistent with the vagaries of this abiotically stressful environment, matrix and subcanopy assemblages varied considerably with climate, but plant assemblages below large trees remained fairly constant, implying that subcanopy environments provide a stable refuge for a suite of plants in an environment otherwise marked by strong abiotic gradients. Domination of the subcanopy environment by zoochorous plants (Leistner 1996, Dean et al. 1999, this study) implies that dispersal is a major determinant of observed assemblage composition, and lends support to the hypothesis that fleshy fruited plants require higher nutrient soils (Hughes et al. 1993). Directed dispersal is vital for guaranteeing delivery to a suitable recruitment site (Howe and Smallwood 1982) in an environment in which trees are often far apart and scarce - particularly in the drier parts of the Kalahari. Since in this arid environment much bird and mammal activity is associated with trees, propagule availability is likely to be far higher in the subcanopy environment than the matrix (Guevara et al. 1992). Higher propagule availability in turn raises probability of recruitment, so that zoochorous species are more common in the subcanopy environment. The importance of the subcanopy environment of large trees as an establishment site is examined further in Chapter 4.

Microhabitat and dispersal probably also drive the similarities between small tree understories and the matrix. Shading influences relative success of open-habitat and shade-tolerant species so that vegetation composition varies (Smith and Goodman 1987), but shade provided by small trees seems to be insufficient to drive significant shifts in vegetation composition from matrix to subcanopy assemblages. Variation amongst composition in grass species assemblages between the matrix and small tree subcanopy microhabitats likely indicates varying tolerance of shade, water loss and disturbance amongst these species. The likelihood of a rainfall event adequate for recruitment in combination with propagule presence both increase with time, so tree age (and by implication, size) is an important determinant of understory plant assemblages.

This study has shown that not only do large trees enhance overall biodiversity in the semi-arid Kalahari, but species richness is also greater per unit area, a relationship dictated by proximity to the tree trunk (Figure 3.2). In many systems, competition has received by far the majority of ecologists' attention, and savannas have been no exception, with tree-grass competition tending to be the focus. Bertness and Callaway (1994) argue that the relative roles of competition and facilitation change with environmental stress: competition should be the dominant biotic interaction in the more productive part of the environmental gradient, whereas facilitation is more important under harsh conditions, and this study supports this assertion.

These patterns in species richness are likely to be less marked in wet years, more so in dry years. In wetter years, water availability will likely permit a number of species to exist in the matrix that may not ordinarily have survived. These "extra" species in the matrix would only be annuals, however. The comparison of sites across the aridity gradient suggests that changes in species composition are unlikely to be considerable as rainfall varies, because many subcanopy plants have evolved dispersal methods that ensure their arrival at subcanopy sites.

Whereas plant assemblages of the matrix and subcanopies of small trees vary considerably with rainfall, the environment beneath large trees appears to be sufficiently constant to maintain, compared with the matrix and subcanopy of small trees, a relatively stable plant assemblage. In this way, shade tolerance is a plant characteristic that permits wider geographical distributions than plant species' physiological tolerances would predict: large trees provide suitable microhabitats for recruitment and survival of subcanopy plant species so that overall plant diversity is significantly increased within semi-arid areas.

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APPENDIX

Appendix 3.1. Plants found under large and small trees and in the matrix at Kimberley sites in comparisons between large and small tree subcanopy assemblages. Presence is indicated with a "1", absence with a "0". This list does not include 18 unidentified species.

		Large trees	**Small trees**	**Matrix**
Family	Species			
Acanthaceae	*Barleria rigida*	1	0	0
	Monechma genistifolium	0	0	0
	Monechma incanum	1	0	0
	Monechma sp.	0	0	1
Aizoaceae	*Gisekia africana*	0	0	0
	Limeum arenicolum	0	0	1
	Limeum argute-carinatum	0	0	1
	Limeum fenestratum	0	1	0
	Limeum sulcatum	1	0	1
	Trianthema parvifolia	0	0	0
	Trianthema parvifolia	0	0	0
	Unidentified	0	0	0
Amaranthaceae	*Alternanthera pungens*	0	0	0
	Amaranthus sp.	1	1	1
	Hermbstaedtia sp. (fleckii?)	0	1	0
	Pupalia lappacea	1	1	0
	Unidentified	1	0	0
Amaryllidaceae	*Ammocharis coranica*	0	1	0
	Boophane disticha	0	0	0
Anacardiaceae	*Rhus lancea*	1	1	0
	Rhus tenuinervis	1	0	0
Asclepiadaceae	*Orthanthera jasminiflora(?)*	1	1	1
	Pergularia daemia	0	0	0
	Pergularia daemia	1	0	0
Asparagaceae	*Asparagus cooperi*	1	1	1
	Asparagus nelsii	1	0	0
	Asparagus sp. 2	1	0	0
	Asparagus sp. 3	1	0	0

	Asparagus sp. 4	1	0	0
	Asparagus sp. 5	1	1	0
	Asparagus suaveolens	1	0	1
	Protasparagus sp.?	0	0	0
Asteraceae	*Arctotis leiocarpa*	0	0	0
	Bidens pilosa	1	1	0
	Chrysocoma sp.	1	1	1
	Eriocephalus sp. (cf. merxmuelleri?)	1	0	1
	Felicia sp.	1	1	1
	Gazania krebsiana	0	1	0
	Geigeria ornativa	0	0	0
	Helichrysum arenicola	0	1	0
	Helichrysum argyrosphaerum	1	1	1
	Helichrysum sp. A	1	1	0
	Helichrysum sp. B	1	0	1
	Helichrysum zeyheri	0	0	1
	Hertia pallens	1	1	1
	Nidorella resedifolia	1	1	1
	Nolletia ciliaris	1	1	1
	Othonna pavonia	1	1	0
	Pentzia calcarea	1	1	1
	Pentzia sp. (lanata?)	1	0	0
	Pentzia sp. 1	0	0	1
	Pentzia sp. 2	1	1	0
	Pteronia glauca	0	1	0
	Pterothrix spinescens	1	1	1
	Rosenia humilus	1	0	1
	Tarchonanthus camphoratus	1	1	1
	Unidentfied sp. 1	0	1	0
	Unidentified	1	0	1
	Unidentified	1	0	0
	Unidentified	0	0	0
	Verbesina encelioides	1	0	0
Boraginaceae	*Ehretia rigida*	1	1	0
	Helichrysum sp.	0	0	0
	Heliotropium ciliatum	1	1	1
	Heliotropium lineare	0	0	1
Capparaceae	*Boscia albitrunca*	1	1	0
	Cleome angustifolia	1	0	1
	Cleome gynandra	1	0	0

Chenopodiaceae	*Chenopodium album*	1	1	1
	Salsola sp.	1	1	1
Commelinaceae	*Commelina africana*	1	1	0
	Commelina erecta	1	1	1
Convolvulaceae	*Convolvulus ocellatus*	0	1	1
	Ipomoea hackeliana?	1	0	1
	Xenostegia tridentata?	0	0	0
Cucurbitaceae	*Acanthosicyos naudinianus*	1	0	0
	Citrullus lanatus	1	0	0
	Cucumis africanus	0	0	0
	Kedrostis africana	1	0	0
	Momordica balsamina	1	0	0
	Trochomeria debilis	0	0	0
Cyperaceae	*Kyllinga alba*	0	0	0
Ebenaceae	*Diospyros lyciodes*	1	1	0
Euphorbiaceae	*Chamaesyce inaequilatera*	0	0	0
	Euphorbia braunsii?	1	1	1
	Phyllanthus sp.?	0	0	0
Fabaceae	*Acacia erioloba*	1	1	1
	Acacia hebeclada	1	0	0
	Acacia mellifera	1	0	0
	Acacia tortilis	1	0	1
	Crotalaria sp.	1	0	0
	Cullen obtusifolia	1	1	1
	Elephantorrhiza elephantina	1	1	1
	Indigofera alternans	1	1	1
	Indigofera daleoides	0	0	0
	Indigofera flavicans	0	0	0
	Indigofera sp.	1	0	0
	Indigofera sp.	1	0	0
	Lotonis platycarpa	0	0	0
	Melolobium microphyllum	0	0	0
	Requienia sphaerosperma	1	1	1
	Senna italica	1	1	1
	Unidentified	0	0	1

Hyacinthaceae	*Ledebouria undulata*	0	0	0
	Ornithogalum seineri	0	1	1
Illecebraceae	*Pollichia campestris*	1	1	1
Lamiaceae	*Acrotome inflata*	1	1	0
Lamiaceae	*Ocimum canum*	1	0	0
Leguminosae	*Lebeckia spinescens*	0	0	1
Malvaceae	*Hibiscus marlothii*	1	1	1
	Pavonia burchelli/senegalensis?	1	1	0
Molluginaceae	*Mollugo cerviana*	1	0	0
Nyctaginaceae	*Phaeoptilum spinosum*	0	0	0
Pedaliaceae	*Harpagophytum procumbens*	0	1	1
Poaceae	*Anthephora pubescens*	0	0	0
	Aristida congesta	1	1	1
	Aristida meridionalis	0	1	1
	Aristida stipitata	1	1	1
	Cenchrus ciliaris	1	1	0
	Cynodon dactylon	1	0	1
	Enneapogon cenchroides	1	0	0
	Eragrostis biflora	1	0	0
	Eragrostis lehmanniana	1	1	1
	Eragrostis pallens	0	1	1
	Eragrostis superba	0	0	0
	Eragrostis trichophora	1	1	1
	Eragrostis x pseud-obtusa	1	1	0
	Fingerhuthia africana	0	1	0
	Heteropogon contortus	0	0	0
	Panicum coloratum	0	0	0
	Panicum maximum	1	0	0
	Pogonarthria squarrosa	1	1	1
	Schmidtia pappophoroides	1	1	1
	Setaria verticillata	1	0	0
	Sporobolus fimbriatus	1	1	0
	Stipagrostis uniplumus	1	1	1
	Themeda triandra	1	1	1
	Tragus racemosus	1	1	1
	Urochloa brachyura	1	0	0

Portulacaceae	*Portulaca kermesina*	1	1	0
	Unidentified	0	0	0
Rhamnaceae	*Ziziphus mucronata*	1	1	0
Rubiaceae	*Anthospermum?*	0	0	1
Scrophulariaceae	*Aptosimum albomarginatum*	0	1	0
	Aptosimum marlothii	0	1	1
	Jamesbrittenia atropurpurea	0	0	1
	Nemesia fruticans	0	1	0
	Peliostomum leucorrhizum	1	1	1
	Sutera sp.	0	0	0
Selaginaceae	*Hebenstretia integrifolia*	0	0	1
	Selago dinteri	1	1	1
Solanaceae	*Datura stramomium*	1	1	0
	Lycium cinereum	1	1	1
	Lycium hirsutum	1	1	1
	Lycium sp. 1	0	0	0
	Lycium sp. 2	1	0	1
	Lycium sp. 3	1	0	0
	Lycium sp. 4	1	1	0
	Lycium sp. 5	1	0	0
	Lycium sp. 6	0	1	0
	Solanum sp. 2	1	1	1
	Solanum sp. 3	1	1	0
	Solanum supinum	1	0	0
Sterculiaceae	*Hermannia sp. 1*	1	0	0
	Hermannia sp. 2	1	0	0
	Hermannia tomentosa	1	1	1
	Hermannia vestita	0	0	0
Thymelaeaceae	*Gnidia polycephalas*	0	1	1
Tiliaceae	*Grewia flava*	1	1	1
	Grewia retinervis	1	0	0
Verbenaceae	*Chascanum pinnatifidum*	0	0	0
	Chascanum pumilum	0	0	0
	Lantana rugosa	1	1	0

4

Costs and benefits of the nurse plant effect for *Ziziphus mucronata* (Rhamnaceae) in the southern Kalahari

ABSTRACT

Certain plant species allocate resources to fruit, suggesting that the benefits of directed dispersal outweigh the costs of fruit production, and that directed dispersal confers greater fitness on these species than other dispersal methods. It has been proposed, however, that conditions favourable to germination are not necessarily favourable to all stages of the plant life cycle. Disparities between the requirements for different stages of the lifecycle have been termed "within-individual conflicts". In the Xeric Kalahari, most plant species growing beneath the canopies of large *Acacia erioloba* trees have evolved fleshy fruits for endozoochorous dispersal. The large shrub *Ziziphus mucronata* (Rhamnaceae: Willd.) is one such species, and is common in the southern extent of the Xeric Kalahari, although more so beneath trees than in the surrounding grassy matrix. This species thus provides a good model for detecting within-individual conflicts arising from differences in microhabitat. To investigate effects of these different microhabitat conditions on various stages of the lifecycle, I conducted germination experiments and ascertained *Z. mucronata* seedling survival beneath *A. erioloba* canopies and in the matrix. I also evaluated flower and fruit production as well as the degree of parasitic mistletoe infestation of *Z. mucronata* growing in the open and beneath *A. erioloba*. Seeds from maternal *Z. mucronata* plants growing beneath *A. erioloba* had a higher germination rate than those of seeds from maternal plants growing in the open. Seeds germinating in full sun and in matrix soil had significantly higher germination rates than those in shade and in soil from beneath the *A. erioloba* subcanopy, but this result could have been an artefact of experimental conditions. Demography of *Z. mucronata* suggested that the *A. erioloba* subcanopy is important for establishment, but seedling survival was higher for seedlings transplanted into the matrix than for seedlings planted under trees. Moreover, causes of mortality differed between the two microhabitats, with desiccation a significant factor in the matrix, but invertebrate herbivory and trampling significant beneath trees. The relative severity of these factors is likely to change spatially and temporally, and with

management regimes. Mistletoe infestation was higher for adult plants growing in the open. There was no difference in flower and fruit production between plants growing in the open and beneath trees, contrary to the hypothesis that subcanopy plants require elevated nutrients associated with subcanopy soils. This could be because elevated nutrient levels created by nurse plant *A. erioloba* persist long after the tree's demise.

INTRODUCTION

It has long been known that the highest mortality rates in plants' life cycles occur during dispersal and establishment (e.g. Darwin 1859). Directed dispersal, the process whereby non-random arrival and survival in suitable sites raises fitness (Howe and Smallwood 1982, Wenny and Levey 1998, Wenny 2001), can reduce this mortality, however. That some plants have evolved to allocate resources to fleshy fruits for endozoochorous dispersal to ensure arrival at particular sites has been interpreted by many as ensuring some selective advantage (e.g., Thompson and Willson 1978, Howe and Smallwood 1982, Stiles 1992, Jordano 2000). Sites favourable for germination may however not be equally favourable to later life cycle stages (Grubb 1977, Lamont et al. 1993). Schupp (1995) referred to these disparities as "within-individual conflicts" (page 399), but little is known about the extent or consequences of these conflicts.

Within the southern Kalahari semi-arid savanna (Figure 1.1, p.2), vertebrate-dispersed plants usually grow beneath the canopies of large trees (Milton and Dean 1995, Leistner 1996, Dean et al. 1999), a pattern witnessed elsewhere in savannas (Smith and Goodman 1987, Tréca and Tamba 1997). Since the primary dispersers of these plants are birds (Leistner 1996), the probability of seeds being dispersed to these subcanopy sites is high.

"Nurse" plants are those that facilitate recruitment of other species beneath their canopies owing to the modified subcanopy environment (McAuliffe 1988). The subcanopy environment has distinctly different light, water and nutrient regimes to the surrounding grassy matrix (Belsky et al. 1989). Lower temperatures beneath the canopy ensure reduced evaporation rates compared to the matrix (Belsky et al. 1989, Akpo and Grouzis 1993), particularly important to the beneficiaries of nurse-plant interactions in arid systems (Valiente-Banuet and Ezcurra 1991, Fulbright et al. 1995, Callaway et al. 1996). Soils of the subcanopy environment are also usually higher in nutrients than those of the surrounding matrix (Georgiadis 1989, Isichei and Muoghalu 1992, Vetaas 1992, Belsky 1994, Roos and Allsopp 1997, Dean et al. 1999, Weltzin and McPherson 1999, Schurr 2001). This effect is particularly marked in the Kalahari with its oligotrophic soils (Leistner 1967, Milton and Dean 1995, Dean et al. 1999, Schurr 2001). This elevated nutrient status of subcanopy soils might be expected to influence seed quality and subsequent seedling growth of seeds from maternal plants grown in the subcanopy (see Gutterman 2000 for review), and could positively influence germination, as elevated nutrient levels have been found to increase germination rates in some species (Hilhorst and Karssen 2000).

Although more salubrious in terms of evaporation rates and nutrient levels, the subcanopy environment is light-limited and subject to animal disturbance, as livestock and game seek shade and forage, with attendant chances of trampling or herbivory (Dean et al. 1999). In addition, competition for water and light from the nurse tree itself can also present challenges, particularly to larger plants, which might access deeper water.

The question therefore arises - is the subcanopy microhabitat always better than the surrounding matrix for all stages of fleshy-fruited plants' life cycles? Although it is difficult to evaluate all costs and benefits of microhabitats at all stages of the life cycle, an examination of germination, establishment and certain indicators of adult fitness allows identification of the most ideal and most costly environments to each stage of the life cycle, as summarised in Figure 4.1.

Ziziphus mucronata (Willd.) (Rhamnaceae) is a common species that produces abundant fruit. Although rarer in the matrix than beneath large *Acacia erioloba* (Meyer), it is found in both microhabitats in the southern Kalahari. The subcanopy environment of *A. erioloba* and the surrounding matrix provide ideal microhabitat contrasts in which to test the influence of microhabitat on relative fitness of different stages of the *Z. mucronata* lifecycle. I tested the following null hypotheses:

1) Environmental factors that differ between the subcanopy and matrix environments (e.g. maternal microhabitat, soil nutrient levels and shade) have no influence on *Z. mucronata* seed germination rate;
2) There are no differences in *Z. mucronata* seedling survival rate between the subcanopy and matrix environment;
3) Indicators of adult *Z. mucronata* fitness (i.e. flower production, seed set and mistletoe infestation) do not differ between the subcanopy and matrix environments.

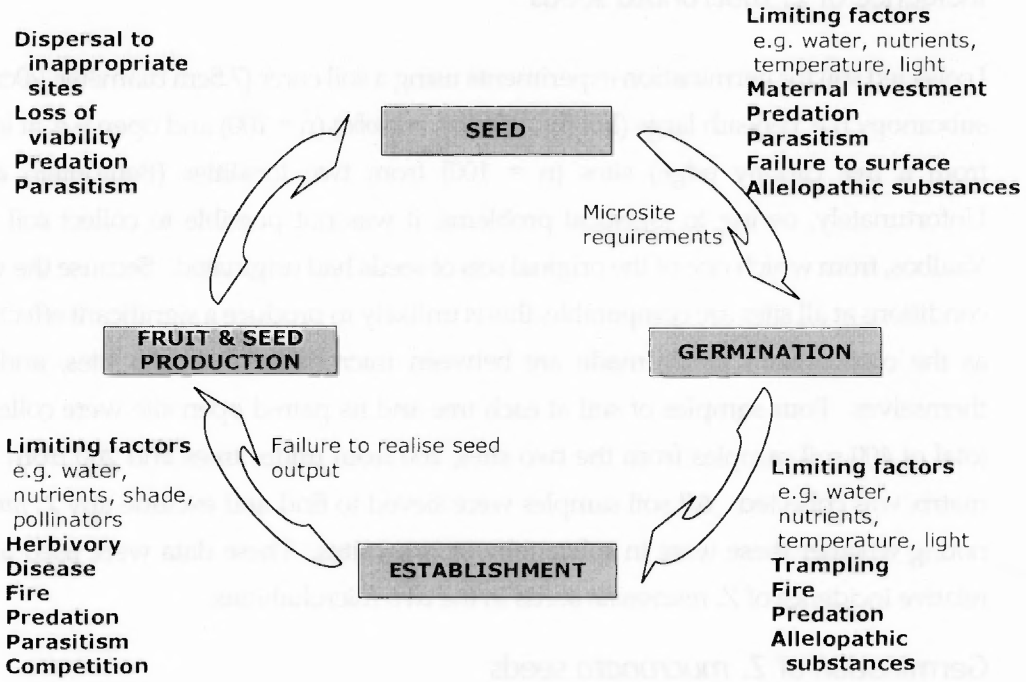

Figure 4.1. Main life stages and possible limiting factors in the lifecycle of *Ziziphus mucronata*. Adapted from Crawley (1986).

METHODS

I collected fruit from 20 *Z. mucronata* individuals growing under *A. erioloba* trees and 20 growing in the open at each of two sites: Benfontein Game and Cattle Farm and Vaalbos National Park in the Northern Cape, South Africa, in May 2003. Each *Z. mucronata* growing beneath a tree was paired with the closest individual of comparable size growing in the open. I collected 30 fruits from each individual, randomly choosing a branch and then harvesting all fruits from that branch and its closest neighbours until 30 fruits were harvested, to minimize bias towards choosing only fruits that appeared to have viable seeds.

Maternal investment in *Z. mucronata* seeds and fruit

I grouped all whole fruits from maternal *Z. mucronata* plants growing beneath *A. erioloba* trees and those growing in the open before removing the fleshy tissue (the "fruit") around the seed. I weighed these in groups of twenty, to reduce the chance of small inaccuracies of the scale affecting the results, but also to keep the sample size above 30 samples per group. I subsequently weighed these groups again, with the fruit removed, i.e. the seeds alone. I used a Mann-Whitney U test to test for differences in mass of seeds with fruit and those without between the two microhabitats.

Incidence of *Z. mucronata* seeds

I collected soil for germination experiments using a soil corer (7.5cm diameter, 20cm depth) from subcanopy (i.e. beneath large (height > 5m) *A. erioloba*) (n = 100) and open (i.e. at least 10m away from a tree canopy edge) sites (n = 100) from two localities (Benfontein and Susanna). Unfortunately, owing to logistical problems, it was not possible to collect soil samples from Vaalbos, from which one of the original sets of seeds had originated. Because the vegetation and conditions at all sites are comparable, this is unlikely to produce a significant effect on the results, as the comparisons being made are between microhabitats within sites, and not the sites themselves. Four samples of soil at each tree and its paired open site were collected, so that a total of 400 soil samples from the two sites, 200 from under trees and 200 from the associated matrix was collected. All soil samples were sieved to find and exclude any *Z. mucronata* seeds, noting whether these were in subcanopy or open sites. These data were used to ascertain the relative incidence of *Z. mucronata* seeds in the two microhabitats.

Germination of *Z. mucronata* seeds

Zietsman and Botha (1987) found far greater germination rates for seeds in which a hole had been made in the endocarp. Since *Z. mucronata* are endozoochorous (primarily dispersed by birds), this might be expected. Therefore, all seeds were scarified by rubbing them along a piece of sandpaper 20 times to produce a small hole in the endocarp. I planted three seeds per seedling bag (80mm x 50mm x 180mm) on 10 February 2004. I placed seedling bags (black plastic, approximately 150mm high, with openings of about 80mm x 60mm) in 20 groups of 20 bags each, half under shade and half in the open. These contained equal numbers of seeds from maternal plants growing in the open and from those growing in the subcanopy environment (Figure 4.2). Soil samples from both microhabitats were also equally represented amongst shaded and non-shaded groups and between the two different maternal origins. I kept the soil moist, watering seedling bags with equal amounts of water, and noted the number of plants germinating and their stage of development (emerged, primary leaf or secondary leaf) every two days after the first plants started to appear.

SHADE CLOTH (70%)				FULL SUN			
Subcanopy soil		Matrix soil		**Subcanopy soil**		Matrix soil	
Maternal plant = Subcanopy **50 plants**	Maternal plant = Matrix 50 plants	**Maternal plant = Subcanopy** **50 plants**	Maternal plant = Matrix 50 plants	**Maternal plant = Subcanopy** **50 plants**	Maternal plant = Matrix 50 plants	**Maternal plant = Subcanopy** **50 plants**	Maternal plant = Matrix 50 plants

Figure 4.2 Treatments for the germination experiment to detect differences in maternal investment, and possible advantages of soil types and shade *vs.* sunlight. Treatments marked in bold equate to conditions expected in the subcanopy microhabitat.

Stage of development is a critical consideration arid environments, where plants need to establish as quickly as possible. To capture this variation and facilitate its inclusion in statistical testing for differences between treatments, I used average time to germinate, to produce leaves or to produce secondary leaves as a weighting for each category, so that those that had germinated were scored as 5, those with primary leaves scored 9, and those with secondary leaves as 12.

Above ground growth in relation to maternal and soil origin

After the germination experiment, I removed 100 seedlings for transplanting out into the field to ascertain seedling survival. I left the remainder to grow in full sun and I harvested above ground growth two weeks later. I oven dried these at 80 °C for 24 hours and then weighed them to measure differences in above-ground growth between those from maternal plants growing under trees and those growing in the open, as well as the effect of substrate in which they were growing (matrix or subcanopy soils).

Seedling survival in relation to microhabitat (i.e. subcanopy vs. open)

I evaluated the importance of the subcanopy environment for seedling survival by transplanting 50 seedlings from subcanopy maternal plants and 50 seedlings from open maternal plants from the germination experiment into a 50-50 mix of soil from beneath trees and matrix soil, to hold constant the effects of seed type and soil type, while manipulating the effects of subcanopy vs. open environments. I grew these in large (350mm x 180mm x 150mm) seedling bags, watering them once every three days. I transplanted these after a month, planting five seedlings under each of five large trees and five in the matrix 10m away from the tree canopy, at each of two sites. I alternated between three or two seedlings to the north and two or three to the south of the tree trunk. I re-evaluated seedling survival after a week, noting causes of mortality where possible, and then re-assessed survival six months later, after a typically dry and cold Kalahari winter.

Ziziphus mucronata size distribution

To evaluate the size class distributions of Z. *mucronata* in the two microhabitats, subcanopy and open matrix, I walked randomly situated transects, noting every single Z. *mucronata,* its size and microhabitat. Frequency of size classes were analysed and represented in a histogram.

Z. mucronata size distribution

A comparison of frequencies within the smallest size class of *Z. mucronata* showed that there were significantly more small individuals under trees than in the open (Chi-square with Yates correction = 6.67, df = 1, $p < 0.01$) (Figure 4.3).

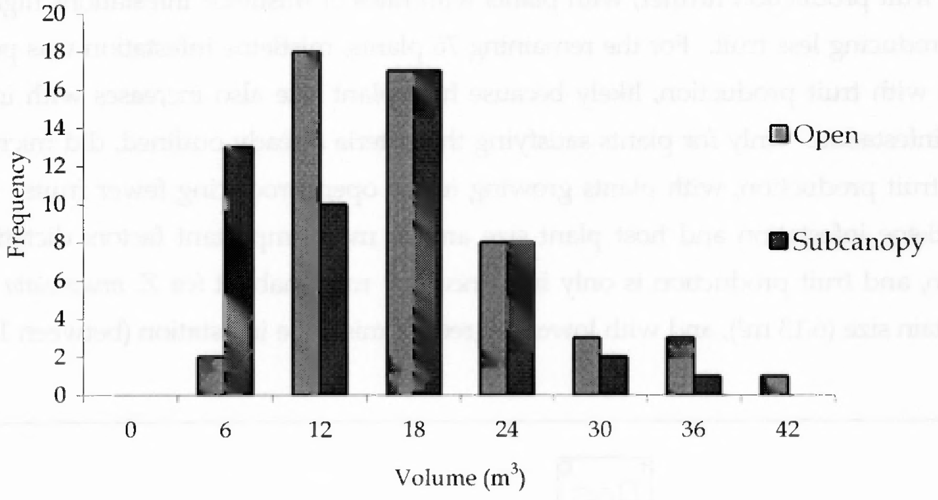

Figure 4.3. Size classes by volume for *Z. mucronata* growing in open environments and growing under the subcanopy of *A. erioloba* trees.

Mistletoe infestation rates in relation to microhabitat

Degree of mistletoe infestation increased with increasing plant size ($p < 0.05$; Robust MM regression). *Z. mucronata* growing in open environments had higher infestation rates than equivalent-sized *Z. mucronata* growing beneath trees ($Z = 4.256$; $n_1 = 52$; $n_2 = 51$; $p < 0.001$; Mann-Whitney U test). In addition, the proportion of dead to healthy mistletoe was significantly higher on *Z. mucronata* growing in the subcanopy environment than for those growing in the matrix environment (Chi-square test: $X^2 = 7.32$; $p < 0.001$).

Flower production and fruit production

Robust MM linear regression indicated that the size of the parent *Z. mucronata* best explained fruit production (coefficient = 0.1343, $p < 0.0001$), although this model only explained 5% of the variation in response. A subsequent regression of residuals produced by this analysis with degree of mistletoe infestation showed that mistletoe volume explained some of the variation. A Mann-Whitney U test comparing residuals obtained from this analysis found no difference in fruit production between open and under, once the effect of size and mistletoe infestation had been removed.

A classification tree was able to divide the plants into smaller groups to analyse factors influencing fruit set. The classification tree first divided the 96 *Z. mucronata* surveyed for fruit set into two main groups (of 15 vs. 81 plants) based on parent plant size: plants with volumes lower than 6.13 m^3 were most likely to have fewer fruits (Figure 4.4).

For plants larger than 6.13m^3, degree of mistletoe infestation (less than or equal to 802.39 cm^3) explained fruit production further, with plants with rates of mistletoe infestations higher than 802 cm^3 producing less fruit. For the remaining 76 plants, mistletoe infestation was positively correlated with fruit production, likely because host plant size also increases with increased mistletoe infestation. Only for plants satisfying the criteria already outlined, did microhabitat influence fruit production, with plants growing in the open producing fewer fruits. Overall, then, mistletoe infestation and host plant size are far more important factors dictating fruit production, and fruit production is only influenced by microhabitat for *Z. mucronata* that are over a certain size (6.13 m^3), and with lower degrees of mistletoe infestation (between 119 – 802 cm^3).

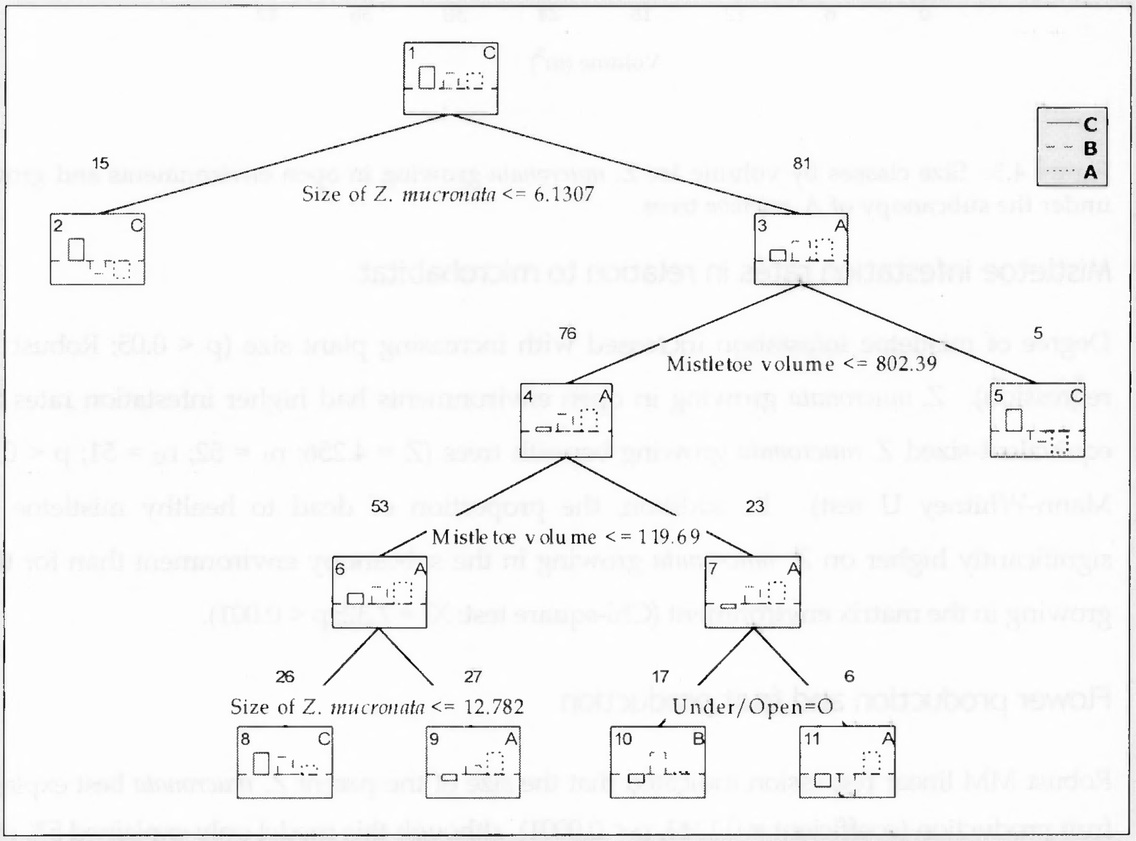

Figure 4.4. Classification tree showing most important factors explaining fruit set in *Z. mucronata*. Plants were divided into three categories, A, B and C. "A" category plants had the highest fruit set; "C" category plants the lowest. Boxes contain a histogram of cases in each category at each node. The condition governing each split is denoted in text beneath each split. The number of cases sent to each node is depicted above each histogram box. ("Under" = Subcanopy).

DISCUSSION

Although Z. *mucronata* has evolved a fleshy fruit, the results of this study imply that directed dispersal to A. *erioloba* subcanopy sites does not favour all aspects of the plant's life cycle. That all Z. *mucronata* seeds found in soil samples were from below trees (although only 3.6% could be said with confidence to have been dispersed), and that there were significantly more small individuals beneath A. *erioloba* trees than in the open indicates, however, that the subcanopy environment is important as an establishment site.

Contrary to these expectations of the subcanopy as a good establishment site, both soil and light conditions associated with the subcanopy microhabitat had lower germination rates than for their matrix equivalents. I kept the soil moist during this experiment in order to investigate phenotypic effects on maternal investment in seeds, but this effectively eliminated the influence of desiccation. Nurse-plant interactions in arid environments are primarily driven by reduced evaporation in the shade provided by nurse plants (Valiente-Banuet and Ezcurra 1991, Fulbright et al. 1995, Callaway et al. 1996), so these germination results are unlikely to hold under normal conditions. Subcanopy soils have poorer drainage (C. Seymour, *unpubl. data*), so germination rates might have been expected to be higher in matrix soils than in subcanopy soils. Although higher nutrient status of subcanopy soils might have been expected to elicit higher germination rates (Hilhorst and Karssen 2000), this effect was not observed here.

Seeds from subcanopy maternal plants did significantly better than those from maternal plants growing in the open. Maternal environment has been shown to influence phenotypic seed quality, manifested in germination or subsequent seedling growth (Gutterman 2000, Valencia-Díaz and Montaña 2005). Chemical composition of fruit is influenced by the soil in which the parent plant grows (Izhaki et al. 2002), so better germination rates could be attributable to higher nutrient status of subcanopy soils in which the maternal plant grows. Many bird-dispersed fruits have been found to contain secondary metabolites which serve primarily as protection against invertebrate and microbial pests (Herrera 1982, Cipollini and Levey 1997, Mack 2000, Tsahar et al. 2002). Thus it is possible that seeds from maternal plants grown in the subcanopy environment may be better protected against attack by microbes or invertebrates.

Although soil and light conditions of the subcanopy environment did not clearly favour germination rate and success, subsequent aboveground growth, in full sun, in soils from the subcanopy was significantly greater. Soil from subcanopies is known to be richer in organic material and therefore nutrients (Parker and Muller 1982, Georgiadis 1989, Isichei and Muoghalu 1992, Vetaas 1992, Belsky 1994, Roos and Allsopp 1997, Dean et al. 1999, Weltzin and McPherson

1999), and this has also been shown to be the case in the Kalahari (Dean et al. 1999, Schurr 2001). The distribution of fleshy-fruited plants is tied to soils with elevated nutrient status (Milewski 1982, Hughes et al. 1993). These elevated nutrients and the high organic content (thus a "mulching effect") are consistent with greater growth rates for *Z. mucronata* seedlings grown in subcanopy soils.

That seeds were more often dispersed to subcanopy sites and that desiccation is likely a determining factor in germination rates implies that more seedlings should germinate in the subcanopy environment, and thus there should be more seedlings becoming established within the subcanopy environment. In this study, however, seedlings planted in the matrix had higher survival rates than those under trees, and causes of mortality were different between the two microhabitats. The very conditions that make the subcanopy environment favourable for germination (reduced evaporation and heat) probably also make it ideal habitat for invertebrate herbivores and a focus for large mammal activity, with associated probability of trampling. This then is a case in which conditions favourable to germination also promote seedling predation and herbivory, and is hence an example of within-individual conflict (Schupp 1995).

The relative influence of factors causing seedling mortality is temporally and spatially variable. For example, in wetter months, desiccation is less likely, so that the matrix might be more favourable for seedlings. In winter and early spring, however, invertebrate herbivory and animal activity beneath trees are lower than in summer, so the subcanopy is less hazardous to seedling recruitment. The savanna structure in which seedling establishment takes place is also important: if there are many large trees, intensity of trampling is likely to be lower as animal activity is not concentrated around a few individual trees. Therefore, removal of large trees focuses animal activity around the few surviving trees, making successful establishment of fleshy-fruited species less likely. On a larger scale, the relative importance of desiccation changes with degree of aridity. In more arid areas of the biome, subsequent survival rates in the matrix are likely to be far lower than those found here.

Fruit pulp is commonly characterised by high water and carbohydrate content (Herrera 1987, 2002). Ready availability of sunlight in the matrix may enable carbohydrate production for fruit flesh, explaining higher fruit mass on plants grown in this microhabitat. Although Howe and Vande Kerckhove (1980) found that fruit dispersers did not discern intraspecifically between size of fruit reward, birds may forage preferentially on individuals beneath canopies to reduce predation risk, and may require incentive in the form of greater fruit reward to forage on individuals in exposed sites. Mack (2000) hypothesised that fruit evolved primarily as a protection for seeds from invertebrate herbivory, so perhaps there has been selection for investment in thicker fruit coatings when resources are abundantly available.

Production of fruit in fleshy fruited plants has been linked to elevated soil nutrients (Hughes et al. 1993), particularly potassium (Milewski 1982). Herrera (1987) found, however, that fruit pulp was not particularly rich in potassium relative to foliage and questioned its importance in fruit pulp production. Effects of soil quality may be obscured because most, if not all, Z. *mucronata* evaluated in this study were growing in soils that were once subcanopy soils, where nutrients persist for some time (Barnes and Archer 1996, Barnes and Archer 1999, Dean et al. 1999). In addition, large Z. *mucronata* provide shade and refuge to a number of smaller animals and their activities may also contribute to elevated nutrient levels in the surrounding soils. Alternatively, mature Z. *mucronata* have extensive root systems, and so are not limited to their immediate surrounds for nutrients. Certainly, if nutrient availability to Z. *mucronata* growing in the matrix is low, it is not low enough to influence fruit production.

The mistletoe *Viscum rotundifolium* in this study requires additional photosynthates from its host plant (de la Harpe et al. 1980). This might explain the higher incidence of mistletoe on Z. *mucronata* grown in the sun and the greater incidence of dead mistletoes on Z. *mucronata* grown in the subcanopy environment: photosynthates are likely less readily available from Z. mucronata growing in the shade, and the mistletoe themselves are less able to produce photosynthates in shaded environments. Host plants with larger xylem vessels may be more prone to parasitism by mistletoes (Dean et al. 1994), but we do not know how the relative size of xylem vessels differs between plants growing in the subcanopy environment and those growing in the open.

CONCLUSIONS

The model of the subcanopy of *A. erioloba* - Z. *mucronata* nurse-plant relationships provides a good example of how within-individual conflicts can arise, and illustrates how such conflicts are likely to be temporally and spatially variable (Figure 4.5).

The watering system used in these experiments obviated the most important feature provided by large trees for germination: that of a less desiccating environment. However, although perhaps better for germination and maternal provisioning of seeds, the subcanopy environment does not guarantee seedling survival. Indeed, in this case, seedling survival within the subcanopy microhabitat was nine times lower than in the matrix, although the chances of seeds being deposited in open habitats is apparently small. In this arid environment, lower evaporation rates beneath the tree canopy likely make germination possible, and likely impossible in the matrix, so although seedling survival was lower under trees, germinating in the first place is unlikely in the open. Large trees are therefore important as establishment sites, although the activities of herbivores and insects makes it hazardous, reducing seedling survival rate. Therefore, large *A. erioloba* are likely important at least for the germination of *Z. mucronata* and perhaps other fruited plants, and is important as a keystone species in that plants can at least germinate in these sites, but subsequent survival rates might be quite low, as the subcanopy microhabitat is not necessary, and may even be detrimental for later stages of plants' lifecycles.

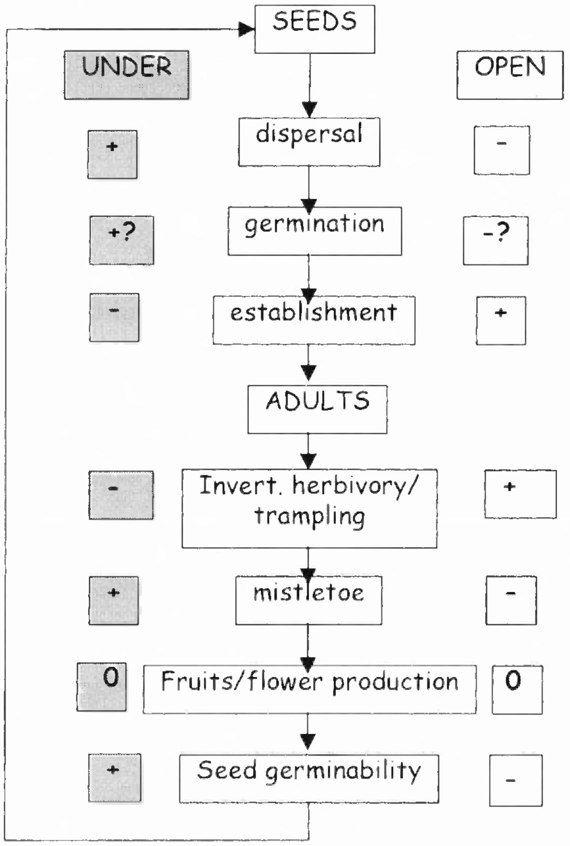

Figure 4.5. The costs (-) and benefits (+) of the subcanopy ("Under") and matrix ("Open") environments on different stages of the lifecycle of *Z. mucronata*.

For adults, apart from higher levels of mistletoe infestation on plants grown in the matrix, flower and fruit production provided no evidence of a difference in fitness according to microhabitat. This study did not, however, investigate behaviour of *Z. mucronata* seed dispersers within the two microhabitats, which could differ substantially, tipping the balance of fitness in favour of one or the other microhabitat.

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5

Land use-induced changes in habitat in the southern Kalahari: Influences on bird diversity and assemblage composition

ABSTRACT

The influence of land use and resultant changes to vegetation structure on bird assemblage species richness, diversity and evenness in the Kimberley and Kuruman areas of South Africa are investigated. Elements of habitat structure best explaining species richness composition of assemblages are also investigated. At Kimberley sites, bush thickened areas had significantly higher species richness and Shannon diversity than sites that were neither bush thickened nor cleared (hereafter referred to as untransformed sites), although they did not differ significantly in terms of bird abundance. At Kuruman sites, however, untransformed and bush thickened areas showed no significant differences, except that birds were significantly more abundant in untransformed areas. Sites at which trees had been arboricided (and in some cases, also cleared) had significantly lower bird abundance and bird species richness. Investigation of the relationship between vertical habitat diversity and bird species richness found a strongly positive correlation for both Kimberley and Kuruman. Results for multiple linear regression identified different aspects of habitat between the two sites as measures of diversity: at Kimberley, bird species richness was best explained by woody cover between heights of 0-2m, maximum tree height and herbaceous cover, whereas at Kuruman, bird species diversity was best explained by woody species coverage between the heights of 2-4m. Similarities between bird assemblages were best explained by the density of woody plants up to a height of 4m at Kimberley sites and by maximum tree height and density of woody plants less than 2m high at Kuruman sites. The tallest trees at Kuruman sites were generally 25-50% taller than those at Kimberley sites, and this may explain the relative importance of tree height at Kuruman. The presence of large trees appears to reduce the effect of bush thickening on bird species assemblage composition.

INTRODUCTION

Land use practices can substantially alter habitat structure (Brown and Archer 1989, Skarpe 1990, Jeltsch et al. 1996), thereby influencing bird community composition (MacArthur et al. 1962, Hildén 1965, MacArthur et al. 1966, James 1971, Cody 1981, Herremans 1995, 1998, Aleixo 1999, Boren et al. 1999). In the Xeric Kalahari, as defined by Burgess et al. (2004) (Figure 1.1, p.2), heavy grazing in combination with good rains has led to bush thickening (Chapter 1). Although the influence of bush thickening on plant diversity and production has received attention, there have been few investigations into the effects of bush thickening on biodiversity patterns or processes for other taxa (but see Herremans 1998 for a large-scale study on birds, Meik et al. 2002 for reptiles).

Some landowners have responded to the problem by application of arboricides and/or subsequent clearing (Anderson and Anderson 2001). To date, no studies have examined the influence of tree-clearing on avian biodiversity in the Kalahari, although Joubert and Zimmerman (2003) offered some speculation based on literature review. Indiscriminate removal of *A. erioloba* is believed to be particularly damaging, as this species is often the only tree to reach any great size in the more arid regions of the Kalahari (Acocks 1953), thus constituting an important component of vertical habitat structure.

Bird species richness and abundance have been found to increase with increasing foliage height diversity (MacArthur and MacArthur 1961, MacArthur et al. 1962, Cody 1981), but the relationship with horizontal heterogeneity is less clear (Rotenberry and Wiens 1980, Keller et al. 2003). In addition to structure, birds can respond to the floristic composition of their habitats (Wiens and Rotenberry 1981, Robinson and Holmes 1982, Rotenberry 1985, Bersier and Meyer 1994, Gabbe et al. 2002). Fleishman et al. (2003) found that although bird diversity was unaffected by floristics, composition of bird assemblages was affected. In a study in this study area, however, Dean et al. (2002)found that bird diversity was affected by floristics, although it appears as if this was linked to changes in habitat structure. Changes to habitat structure brought about by land use also see changes in floristic composition, with a relative decline in representation of *A. erioloba* and an increase in *Acacia mellifera* and other species like *Grewia flava*. Issues of the importance of floristics to bird diversity and assemblage composition are investigated in Chapter 7. This chapter focuses primarily on changes to habitat structure brought about by land use practices.

This study, carried out near Kuruman and Kimberley in the southern Kalahari, South Africa, investigated avian community assemblages in bush thickened, untransformed and arboricided and/or cleared areas. Although these categories are useful for discerning effects of anthropogenic habitat change on avian assemblages, the classification is overly simplistic: in reality, a gradient of habitats exists between heavily bush thickened to open and cleared habitats. Therefore, I also investigated the elements of habitat structure governing bird species richness. Specifically, this study addresses the following questions:

1) How do bird species richness and diversity differ between bush thickened, untransformed and cleared habitats?
2) Which aspects of habitat structure best explain species richness?
3) Which aspects of change to habitat structure explain species composition of bird assemblages?

Both bush thickening and tree removal are not exclusively southern African phenomena (see e.g., Janzen 1986, Brown and Archer 1989, Greenberg et al. 1997, Aleixo 1999), and investigations of biodiversity change are therefore also globally relevant.

METHODS

Study Area

To determine species richness and abundance, three observers conducted bird point counts at four sites (Benfontein, Susanna, Vaalbos National Park and Rooipoort) near Kimberley, and two observers carried out point counts at three sites (Olifantshoek, Kuruman, Debeng) near Kuruman between November 2003 and April 2004. (Figure 5.1).

We censused each point three times, rotating observers and timing in order to minimize bias arising from variation in observers and bird behaviour (Bibby et al. 2002). Data were analysed to detect bias arising from observer variation; point counts for which biases were detected were omitted. Ultimately, data were used from 119 untransformed and 28 bush thickened sites at Kimberley; and 18 cleared, 22 untransformed and 20 bush thickened sites at Kuruman. Habitats were categorized as "bush thickened" if they had over 40 % woody plant cover up to a height of 2m.

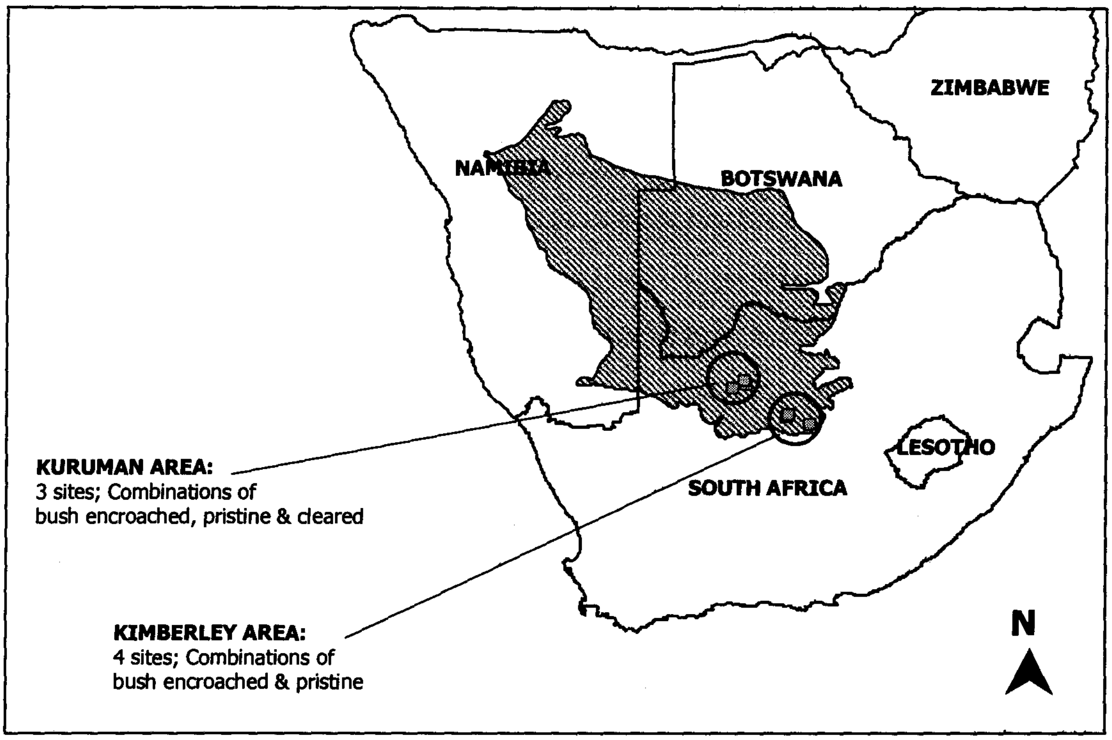


Figure 5.1 Position of the study sites within the Xeric Kalahari. The shaded area represents the Xeric Kalahari, as defined by Burgess et al. (2004).

Census methods

Point counts were used because they enable detection of less mobile and less visible birds and minimize detection differences between habitats of varying densities (Buckland et al. 1993), and are thus appropriate for comparisons of bird assemblages among habitat types. Raptors and aerial foragers were counted but not included in data analyses, because point counts are unsuitable for accurately censusing these birds (Bibby et al. 2002).

Points were randomly chosen, and sited at least 400m apart, to avoid double-counting birds. All counts lasted 15 minutes, and were carried out within 4 hours of sunrise. We did not census on days that were rainy, very windy or cloudy. We tried, as far as possible, to census stations at the beginning and end of the summer season, but this was not possible for the Kuruman sites, or for Vaalbos/Rooipoort in the Kimberley area. All birds within a radius of 120m from the central point were censused, using visual and audio identification. If we were uncertain whether an individual bird had already been counted within the census period, we ignored it. Any birds flushed from near the plot on approach of an observer were recorded.

Habitat measurements

We measured every tree and shrub within a 30m radius for "untransformed" and "cleared" sites, and for bush thickened sites, we sub-sampled a quarter circle (i.e. 90° of 360°). We measured tree height using a telescopic tree pole. We also measured longest axis of the tree canopy (d1) and the axis of the canopy at right angles to that (d2), average minimum canopy height, and number of stems. We measured ground cover using the line intercept method (Mueller-Dombois and Ellenberg 1974), by running a measuring tape over 30m from the central point in a random direction, and recording height and extent of interception with the tape.

Data analysis

To model species' detection curves with any degree of accuracy, sufficient records must be obtained (Lloyd et al. 1998, Marsden 1999), typically between 60 to 100 records per species (Buckland et al. 1993, Rosenstock et al. 2002). Of the species censused, only 25 (18%) and 7 (8%) of species yielded more than 60 observations in the Kimberley and Kuruman areas, respectively. Therefore, calculating densities for all species was not feasible, and relative abundance (number of birds/point) was used instead.

I compared habitat structure between bush thickened and untransformed sites in Kimberley by comparing percentage cover of herbaceous layer, 0-2m, >2-4m, >4-6m and >6m woody species cover. This was done using Mann-Whitney U tests (Zar 1996) followed by sequential Bonferroni corrections (Rice 1989) for Kimberly sites. I also compared differences in these coverage categories (i.e., herbaceous cover, woody cover at 0-2m, etc.) at bush thickened, untransformed and cleared sites at Kuruman, using Kruskal-Wallis ANOVA median tests (Zar 1996) and sequential Bonferroni corrections (Rice 1989). Multiple comparisons of mean ranks for all groups were used as *post hoc* tests to identify sources of variation. All tests were conducted using STATISTICA (StatSoft 2001).

Vertical habitat heterogeneity was assessed by applying the Shannon-Weiner diversity index to the different vegetation layers (grass and herbaceous, 0-2m, >2-4m, >4-6m and >6m) to the habitat measurements for each point count. I then performed a linear regression between vertical habitat heterogeneity and species richness to ascertain if there was a relationship between the two.

I used ANOSIM, a statistical test analogous to ANOVA to compare assemblage composition at Kimberley and Kuruman sites, to ascertain whether they should be analysed separately or together. ANOSIM was run in PRIMER (Plymouth Routines In Multivariate Ecological Research) v.5 (Clarke and Gorley 2001).

To compare species diversity between sites, I evaluated average species richness (n) and Shannon (H') diversity indices. Shannon diversity indices are most sensitive to changes in rare species, so may be more revealing than merely species richness counts (Magurran 1988). I tested for statistical differences in diversity measures between habitat types at Kuruman and Kimberley, using a Mann-Whitney U test, followed by a Nemenyi test with Dunn correction (Dunn 1964) to identify which habitat types were responsible for significant differences found within the Kuruman samples (three habitat types).

I used multiple linear regression to explore the relationship between species richness and habitat variables at Kimberley and Kuruman sites.

To examine composition of bird assemblages across different habitats, I constructed a triangular similarity matrix for the Kimberley and Kuruman fourth-root transformed datasets, using the Bray-Curtis similarity coefficient (Bray and Curtis 1957), sorting the data using group-averaging. Data were fourth-root transformed to reduce the influence of common species. I used non-metric multidimentional scaling (MDS) to display the similarity matrix in an ordination plot. This method usually performs well (Kenkel and Orlóci 1986), and is the preferred ordination technique for assemblage data, owing to its universal applicability and reliance on few assumptions (Clarke and Warwick 1994). These analyses were performed in PRIMER (Clarke and Gorley 2001).

I then used a Mantel test (Mantel 1967), using randomisation on similarity matrices of species composition habitat characteristics, to ascertain if any environmental variables correlated with species composition. If effects were significant, I used a BIOENV (Clarke and Ainsworth 1993), on a species composition similarity matrix and a habitat variables distance matrix, to discern which environmental variables (e.g. tree height, grass height, woody plant density) best explain species composition of bird assemblages (see Chapter 3 for a more detailed explanation).

RESULTS

1. How do different habitat structures affect bird species richness, diversity and evenness in the southern Kalahari?

Variation in habitat structure is represented in broad categories, represented in Figures 5.2 and 5.3.

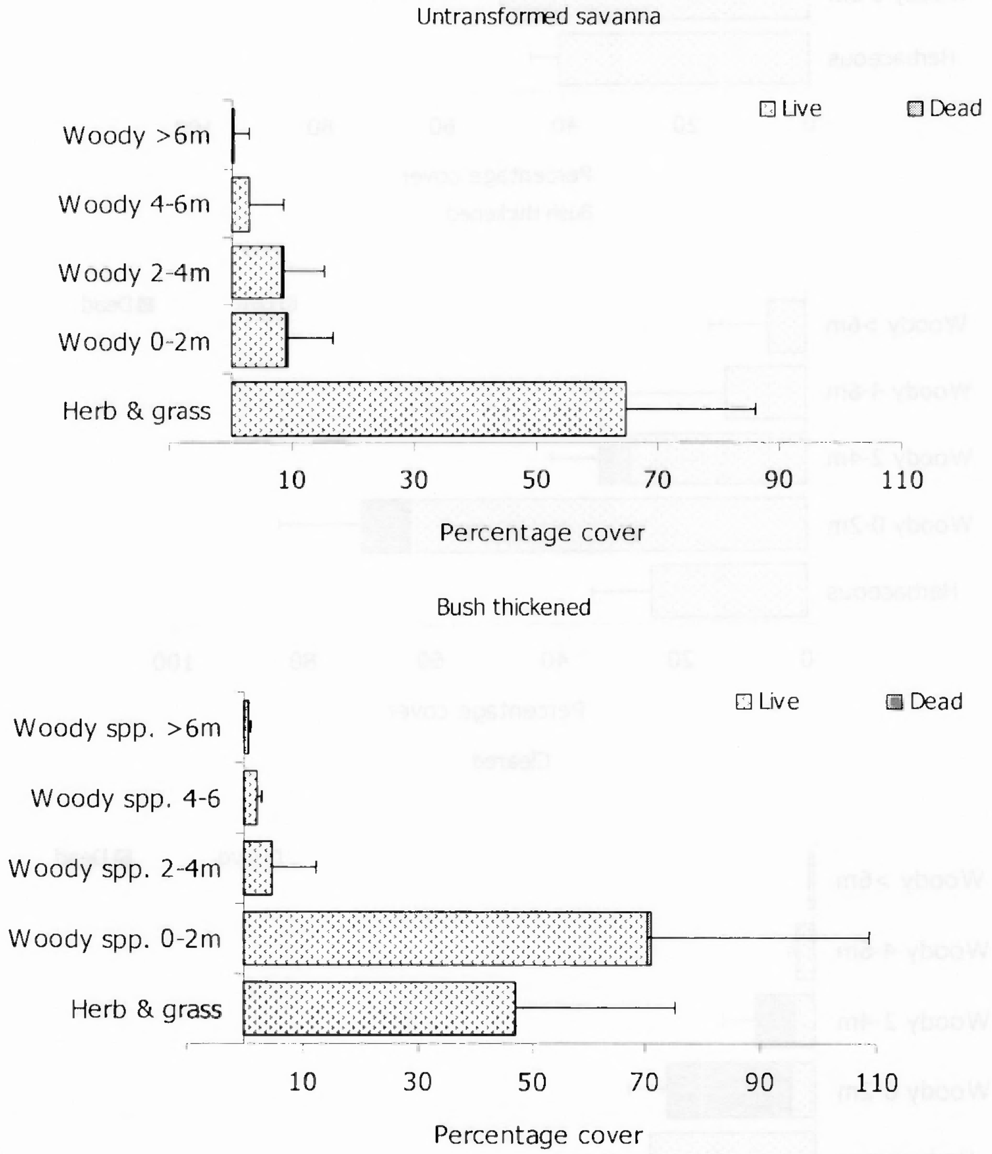
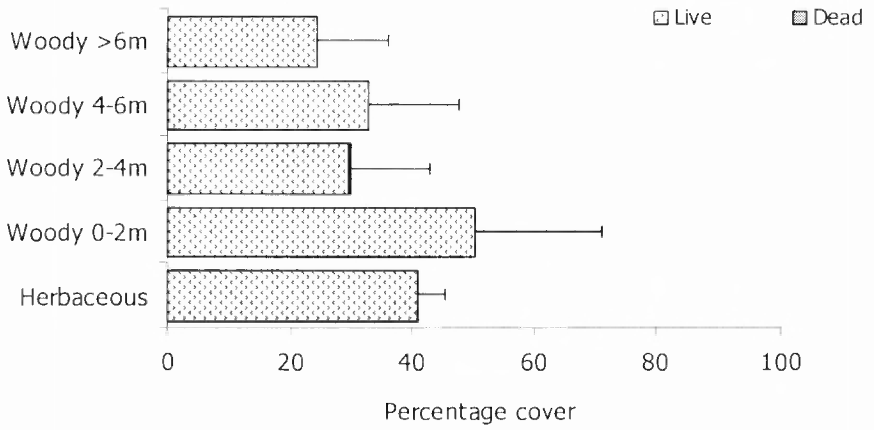
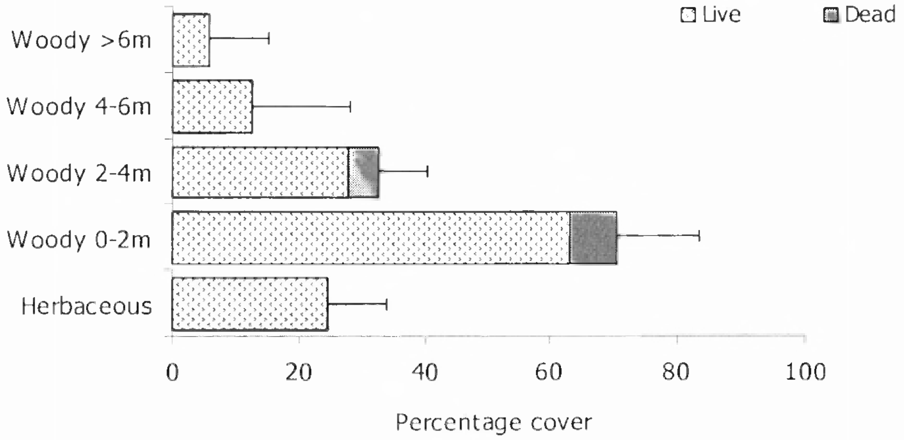


Figure 5.2. Habitat structure at Kimberly sites.

Untransformed savanna



Bush thickened



Cleared

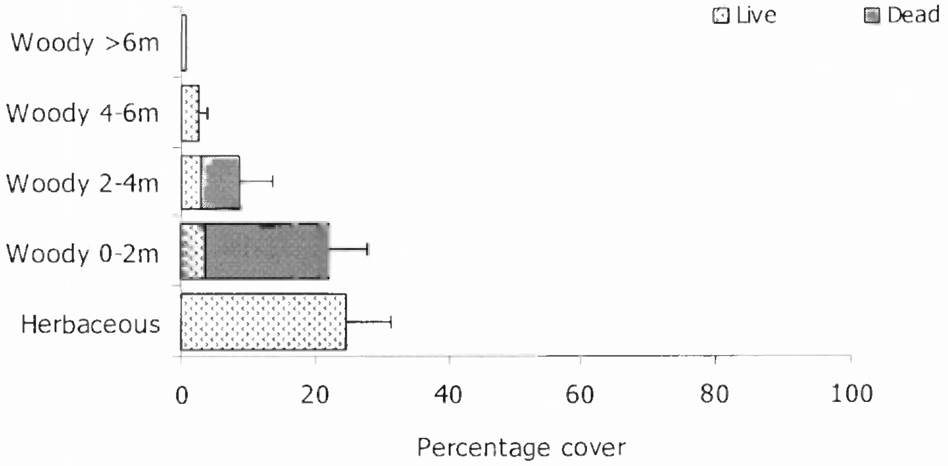


Figure 5.3. Variation in habitat structure at Kuruman sites

Untransformed savanna sites at Kimberley had significantly higher herbaceous and grass cover, and woody cover at heights of 2-4m, and 4-6m ($p < 0.05$ for all tests, after Bonferroni corrections). Bush thickened sites had significantly higher woody species cover than untransformed savanna sites between the heights of 0-2m ($p<0.05$). Median percentage woody species cover over 6m was close to zero for both untransformed and bush encroached sites (0.05%), and was not significantly different ($p>0.05$).

Percentage cover was significantly different between groups for all categories within Kuruman sites. *Post hoc* tests for differences indicated that bush thickened sites had significantly lower herbaceous and grass cover than cleared and untransformed savanna. Cleared areas had significantly lower woody cover than bush thickened and untransformed savanna for 0-2m, >2-4m, and >4-6m. Kuruman bush thickened sites had higher percentage cover of woody plants between 0-2m than untransformed sites, but did not differ significantly in woody cover for heights of >2-4m and >4-6m. Untransformed savanna had significantly higher percentage woody cover >6m. There was no significant difference in cover of woody species between 0-2m at bush-thickened sites at Kimberley, when compared with sites at Kuruman. There was, however, significantly higher cover of woody species of heights greater than 6m, between Kimberley and Kuruman bush thickened sites.

Bird species richness was positively correlated with vertical habitat heterogeneity at both Kimberley ($r^2 = 0.1503$, $n = 147$, $p < 0.05$), and Kuruman ($r^2=0.2316$, $n = 60$, $p <0.05$).

ANOSIM found bird assemblages were significantly different between Kimberley and Kuruman sites, so these data were analysed separately. Comparison of species richness, abundance and Shannon Weiner diversity showed bush-thickened areas to be more diverse than untransformed areas in the Kimberley area (Table 5.1). This was not the case for Kuruman sites, where, apart from having lower bird abundance in bush thickened sites than untransformed, there were no differences in terms of species richness or diversity between bush-thickened and untransformed areas. Cleared areas scored significantly lower on all measures, however (Table 5.2).

Table 5.1. Average diversity indices and standard deviations (in brackets) for Kimberley areas, classified as bush thickened and untransformed. Where results are significantly different, Bush thickened are identified as "BT" and untransformed as "UN".

	Bush thickened (n=28)	Untransformed (n=119)	Statistical significance
No of species	16.53 +/- 2.77	14.77 +/- 3.75	t-test ($p < 0.05$) BT > UN
Abundance (N)	30.67 +/- 6.32	30.97 +/- 13.39	Not significant
H'(loge) (Shannon Wiener)	2.64 +/- 0.17	2.43 +/- 0.30	Mann-Whitney U test ($p < 0.001$); BT > UN

Table 5.2. Average diversity indices and standard deviations (in brackets) for Kuruman areas, classified as bush thickened, cleared and untransformed. Where results are significantly different, groups responsible for the relationship are identified as CL = Cleared, BT = Bush Thickened, UN= Untransformed. (K-W indicates Kruskal-Wallis test)

	Bush Thickened	**Cleared**	**Untransformed**	**Statistical significance**
No of species	12.83 +/-3.79	8.25 +/-2.99	15.18 +/-4.10	K-W ($p < 0.001$), Nemenyi test with Dunn correction; CL < BT, UN
Abundance (N)	22.39 +/-6.63	12.75 +/-5.46	30.14 +/-10.26	K-W ($p < 0.001$), Nemenyi test with Dunn correction CL < BT < UN
H' (loge) (Shannon-Wiener)	2.37 +/-0.32	1.94 +/-0.33	2.52 +/-0.27	K-W ($p < 0.001$), Nemenyi test with Dunn correction CL < BT, UN

2. Which aspects of habitat structure best explain species richness?

Multiple linear regression identified woody species density between 0-2m ($p < 0.001$, $\beta = 0.36$), maximum tree height ($p < 0.01$, , $\beta = 0.27$) and percentage herbaceous cover ($p < 0.05$, $\beta = 0.21$) as the main contributors explaining bird species richness in the Kimberley area. For the Kuruman area, however, bird species richness was best explained by woody species cover between the heights of 2-4m ($p < 0.05$, $\beta = 0.36$) and significantly negatively with average grass height ($p < 0.05$, $\beta = -0.28$).

3. Do bird assemblages differ between untransformed, bush thickened and cleared environments, and if so, which aspects of change to habitat structure best explain the observed species assemblages?

Although not clearly separated from untransformed sites, bush thickened sites did cluster to one corner of the MDS (multidimensional scaling) ordination, regardless of geographic location (Figure 5.4). Although the stress value was high (0.19) (and low stress values indicate a good representation of the relationship between sites), the results of a cluster analysis superimposed on the groups supported the grouping indicated by the ordination by identifying two clusters dominated by bush-thickened sites.

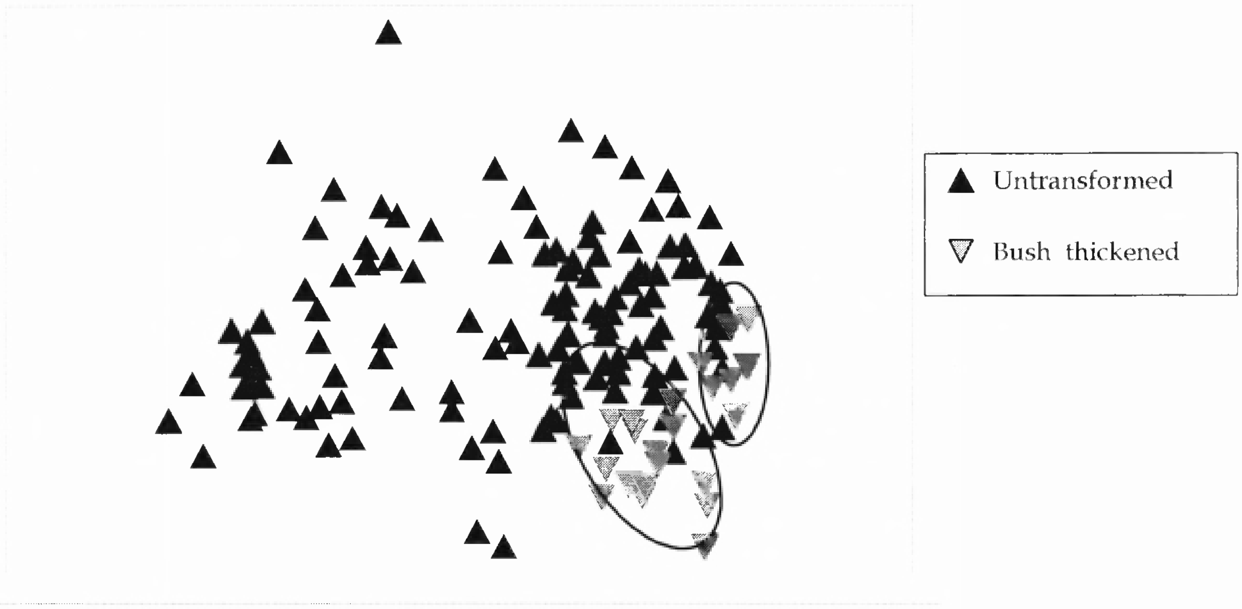


Figure 5.4. MDS for Kimberley using 4th Root transformed data in a Bray-Curtis similarity matrix (Stress value = 0.19). Groupings of bush thickened sites signify similarity at the 60% level.

For Kuruman, stress values for the 2-dimensional representation were high (0.22), and super-imposing a cluster analysis did not support the 2-dimensional arrangement. In three dimensions stress values remained high (0.17). The MDS was therefore uninformative.

Mantel tests found significant correlations between similarities of species assemblages and habitat characteristics at both Kimberley ($p < 0.01$) and Kathu ($p < 0.05$). At Kimberley sites, BIOENV analysis identified density of woody plants of heights 0-2m, and density of woody plants between 2-4m as the best habitat components best correlated with similarities between bird assemblages ($r = 0.479$). Including tree height reduced the strength of the correlation ($r = 0.420$). At Kuruman sites, however, tree height and percentage herbaceous cover were the best correlates of similarity between bird assemblages (r = 0.204), with tree height alone yielding a relatively high value for r (r = 0.203).

DISCUSSION

Studies of the relationships between bird assemblages and habitat structure have a long history (see Hildén 1965 for review), but knowledge of how landscape changes effected by human activities influence biodiversity is both apposite and important. Habitat structure alone is not the only determinant of bird habitat selection, however, and other factors, primarily competition, predation, food availability and nest sites are also influential (Cody 1981, 1985). That said, habitat structure itself often governs levels of predation (Chamberlain et al. 1995, Hatchwell et al. 1996), availability of nest sites (Pulido and Díaz 1997) and food (Peach et al. 2004), as well as the ability to capture it (Brownsmith 1977, Robinson and Holmes 1982, Holmes and Recher 1986). In addition, this study and many others have found influence of habitat structure to be a principal force in determining bird assemblage diversity and structure (MacArthur and MacArthur 1961, MacArthur et al. 1962, MacArthur et al. 1966, Karr and Roth 1971, Willson 1974, and more recently Herremans 1995, Skowno and Bond 2003, Watson et al. 2004).

Species richness and diversity indices in bush-thickened sites were higher than (Kimberley) or equal to (Kuruman) untransformed sites. Initially, this is counter-intuitive: surely bush thickened habitats are more homogeneous than untransformed habitats? It is doubtful that the observed increases in species richness are an artefact of sampling methods: if anything, birds are less likely to be detected in bush-thickened areas. Availability of cover may afford protection from both aerial and terrestrial predators, as these may be excluded by high density vegetation (Blaum et al. 2005). Furthermore, food availability may be higher in bush thickened areas for birds that forage on resources associated with woody plants (e.g. invertebrates). Shade provided in bush thickened areas may also decrease water demands for birds within these habitats.

On more rigorous measures of habitat structure than classification of habitats into "bush thickened" or "untransformed", species richness increased with increasing vertical habitat heterogeneity, consistent with long-held paradigms (Hildén 1965, MacArthur et al. 1966, James 1971, Karr and Roth 1971, Willson 1974, Cody 1981, 1985). This relationship was strongly significant for both Kimberley and Kuruman, but in terms of habitat components measured, the variables explaining species richness differed: at Kimberley, woody species density between 0-2m, maximum height and percentage herbaceous cover were the best predictors, but at Kuruman, woody species density between heights of 2-4m was the best predictor. At first, the negative relationship between bird species richness and grass cover seems counterintuitive, but grass cover was higher at cleared, as well as untransformed sites, so it is likely that this result has emerged because of higher grass cover in cleared sites, which have low vertical habitat heterogeneity. The actual composition of assemblages (i.e. identity of bird species present) was dictated primarily by tree height and habitat density, with tree height being the main determinant of assemblage composition at Kuruman sites, but decreasing the strength of the explanatory ability of environmental correlates at Kimberley sites. Bush thickened sites separated out within Kimberley sites using MDS, but were not distinct from untransformed sites in the ordination for Kuruman sites. Thus, bird assemblages do not necessarily reflect human perceptions of "bush thickened" and "untransformed" (based on density of woody plants of 2m high or less), but rather respond to a variety of habitat cues, and not merely woody plant density. Diversity for some taxa is lower in bush thickened than in untransformed habitats, e.g. reptiles (Meik et al. 2002), dung beetles (Steenkamp and Chown 1996). Yet others have exhibited an increase in diversity, e.g. ants in *Prosopis* thickened areas (Bestemeyer 2005). Bird diversity here was strongly correlated with vertical habitat structure, so it seems likely that the presence of large trees might moderate any effects on bird diversity brought about by shrub encroachment.

Vertical structure differs substantially between Kimberley and Kuruman sites. At Kimberley sites, 85% of bush thickened sites had maximum tree heights below 5m, and none had maximum tree heights greater than 6m. In contrast, only 35% of bush thickened sites near Kuruman had maximum tree heights below 5m, and 40% had maximum tree heights above 6m. Tests of differences in habitat structure between the two sites found them to be comparable in cover between 0-2m, but that Kuruman had significantly greater woody cover over 6m. These findings suggest that as long as vertical structure is maintained, the influence of bush thickening on bird assemblages is not as marked. Thus, although certain species (e.g. ground foraging or species that perch and pounce) might be adversely affected by bush thickening, the presence of trees with canopies that extend above the thicker lower layers may enable use by bird species for which type and structure of ground cover is unimportant (e.g. birds that hawk (sally) from tall branches).

Analysis of habitat characteristics found that cleared sites had comparable levels of herbaceous and grass cover to untransformed sites, and that both had significantly higher cover than bush thickened sites, suggesting that clearing is succeeding at least in meeting farmers' needs to improve percentage herbaceous cover. But cleared sites were generally far more structurally impoverished than bush thickened or untransformed sites, and bird species richness and diversity reflected this paucity. Other studies have found that areas that have been cleared with herbicides are not adversely affected in terms of bird assemblages (Beaver 1976, Schulz et al. 1992), or only influence bird species richness, but not abundance (Easton and Martin 1998). In this study, however, cleared sites were both lower in abundance and species numbers. Part of the observed responses could be attributable to injudicious application of herbicides: lower levels of arboricide application may manage to maintain more habitat structure, and just as comparing bush thickened areas with more untransformed environments is a human-constructed comparison, "cleared" areas exist along a gradient of severity in terms of habitat modification.

What have other studies investigating changes the effects of bush thickening on birds found? Herremans (1998), working on a far larger scale than this study (one degree squares), found marked changes to bird species assemblages in Botswana. In more mesic *Acacia* savannas, Skowno and Bond (2003) found that vegetation structure was the primary determinant of bird community composition, and suggested that changes in vegetation structure brought about by bush thickening would influence bird community composition.

Looking to the future, what are the implications for birds in terms of global climatic change? There is a growing body of work suggesting that anthropogenic increases in atmospheric CO_2 will favour the woody over the grassy component of savannas, so bush thickening will become more likely (Reynolds 1996, Polley 1997, Bond and Midgley 2000, Hoffmann et al. 2000, Bond et al. 2002). Yet it is difficult to predict just how the vegetation of the Kalahari will respond, given that future climate scenarios for the region predict that amount of rainfall is expected to decrease, yet flooding and droughts are expected to become more common (Tyson and Crimp 1998), and that fire frequency may increase, too. A recent study predicts that loss in vegetation cover on dunes, combined with increased wind activity may lead to enhanced dune activity in the northern South African extent of the Kalahari (Thomas et al. 2005) with catastrophic consequences for habitat structure. Since *Acacia* recruitment appears to be reliant on successive years of good rainfall (Ward 2002, Joubert et al. 2003), and fire and drought have been shown to decrease the rate and intensity of bush thickening (Roques et al. 2001), it is difficult to ascertain if bush thickening will become more or less likely in future. Fire can also be expected to have marked effects on habitat structure. The question then becomes one of whether bird assemblages will be able to move to track the habitat components to which they are tied.

CONCLUSIONS

Within bush thickened areas, bird species richness and abundance are high, but the identities of the species present changes, compared to untransformed areas. The presence of large trees within bush thickened areas appears to dampen the effects of these habitat changes on bird assemblages, however, probably by allowing certain species to persist. Removal of larger trees (usually *A. erioloba*) in these areas therefore amplifies the changes to bird assemblages brought about by bush thickening. Clearing habitats in the Kalahari has been detrimental to bird species both in terms of richness and abundance, yet there is pressure for clearing to continue, in light of the demand for *A. erioloba* wood and the belief that trees compete with grazing pasture.

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6

How do bird life history traits within bird assemblages covary with habitat structure in the southern Kalahari?

ABSTRACT

Anthropogenic habitat alteration in the southern Kalahari often involves an increase in woody plant density through bush thickening, and/or removal of large trees. This is an increasing trend on private rangelands, which may further accelerate with global climate change and the impacts of land reform in South Africa. The association between life history traits of bird species inhabiting the southern Kalahari and habitat variables was investigated in this study using RLQ analysis, with particular reference to increasing woody plant density and removal of large trees, to ascertain how these habitat changes might influence bird assembly species composition and diversity. Smaller bodied birds, insectivorous gleaners and ball and cup nesters, as well as birds with low wavelength plumage colours dominated habitat with high tree density (hereafter "bush thickened areas"). Birds found within bush thickened areas also tended to have ranges extending into more arid areas, suggesting that these species are more arid-adapted. Seed-eaters, burrow and ground nesters, bark foragers, birds that hawk (or sally), and birds that perch and swoop to the ground were all negatively associated with increasing bush thickening. Cavity nesters, bark foragers, hawkers, frugivores and birds that perch and swoop were all associated with large trees. Frugivores are secondarily dependent upon large trees since fleshy-fruited shrubs and trees are closely linked to the sub-canopy environment. Birds with iridescent plumage were also associated with large trees. Whilst this analysis excluded rare species, nearly 40% of the species analysed have life history traits tied to the presence of large trees, suggesting that widespread removal of large trees will be detrimental to bird diversity in the region. Where both thickening and

large tree removal occurs (a common occurrence throughout the Southern Kalahari), the long-term presence of birds with life history traits associated with large trees or negatively associated with bush thickening are at risk. The results of this study support the notion that certain life history traits are filtered by habitat characteristics, and the relationships between habitat characteristics and life history traits likely arise from a complex combination of ecological factors interacting with evolutionary history of the species concerned.

INTRODUCTION

Changes in the composition of bird species assemblages in response to land use-induced habitat changes have already been investigated (Chapter 5). These changes in habitat structure entailed repositioning habitats along gradients of increasing woody shrub density (bush thickening) or decreasing vertical structure (which arises through injudicious application of arboricides and/or removal of large trees for firewood).

Although it is instructive to consider how overall bird species richness, diversity and assemblage composition (measures of biodiversity "pattern") respond to habitat alteration, these investigations do not reveal how functional aspects of biological diversity (i.e., interactions between organisms, like predation and competition, and the ways that they modify the environment) are influenced. Moreover, one of the primary goals of predictive ecology is to determine whether species with certain traits will persist under a certain set of environmental conditions (Rice et al. 1983).

Bird behaviour is mutable to some extent, but morphology can restrict a species' ability to find, catch and handle food (Cody 1981, 1985). In addition, other factors, such as nest site availability, predation and competition will also influence a species' ability to occupy certain habitats (Cody 1981, 1985). Given that species have evolved within the limitations of their environments, life history traits and habitat variables should correlate to some degree (Ricklefs 1991). Land use-induced change has provided a natural experiment with which to test these ideas in the southern Kalahari. We can expect land use-induced habitat change to filter out some life history traits in birds, while favouring others. The number of species lost (or perhaps gained) is governed by the dispersion of species traits within bird assemblages, and how they correspond to the altered habitat attributes. Therefore, an understanding of the linkages between habitat attributes and life history traits confers some predictive power in terms of changes to bird assemblages that might be expected as habitats are altered. Furthermore, an investigation of life history traits of birds as they relate to habitat structure (e.g. woody species density or tree height) may also offer insights into how changes in ecosystems overall are altered. Birds are particularly good candidates for examining how structural changes to an ecosystem might alter its functioning (e.g., through fruit dispersal, pollination, insectivory and predation), because they occur at various levels of the food chain, their ecology is well studied, and, since several species have large home ranges, changes at coarser scales can also be discerned (Hausner et al. 2003).

Traditionally, life history traits have been linked to environmental attributes by assigning species to functional groups or guilds based on their traits, and then relating these groups to environmental factors. It is often difficult to determine exactly *which* types of guilds (e.g., foraging, nesting, movements) to use, however, as some changes in habitat may elicit responses detectable in one type of guild classification, but not another (e.g. foraging vs. nesting guilds) (e.g., Canterbury et al. 2000). Usually, data are collected as a set of species observations and habitat characteristics per site, with no statistical method to directly analyse the relationship between the biological or behavioural characteristics of species and the attributes of the habitat in which they are found. Two statistical methods, the 4th corner statistic (Legendre et al. 1997) and RLQ analysis (Dolédec et al. 1996) that consider all species traits simultaneously have been developed. These approaches circumvent problems associated with assigning species to categories based on only one life history trait, and also enables quantitative aspects (e.g. habitat density, maximum tree height) to be linked to life history traits, instead of merely investigating broad, human-defined habitat types (e.g. "bush thickened" or "cleared"). This approach therefore reduces observer bias, and enables hypothesis testing, as significance levels can be calculated. In their entirety, these methods also offer superior resolution to other methods.

Although 4th corner analysis produces easily interpretable results, at present it only considers bird species presence-absence data. RLQ includes considerations of relative abundances, however, and so was selected for this analysis. RLQ aims to obtain an ordination of sites and species using the species-sites table, and to project the variables in the habitat and species trait tables onto the ordination axes for interpretation.

Bush thickening is already widespread in the southern Kalahari (Chapter 5), and removal of farming subsidies may have increased the incentive for farmers to remove large *A. erioloba* for sale as fire-wood to supplement income (Anderson and Anderson 2001, Powell 2001). The future trajectory for habitat structure is unclear, considering the effects of climate change, but changes effected by land reform policies may favour further bush thickening and wood removal. Bush thickening and removal of large trees for firewood, or accidental and intentional tree death through imprudent application of arboricides are the greatest changes in habitat structure occurring in the Kalahari. I therefore addressed the following questions:

1) Which bird life history characteristics predominate in natural and bush thickened areas?
2) Which bird life history characteristics are most adversely affected by removal of large trees (i.e. *A. erioloba,* over much of the Kalahari)?
3) What is the impact upon bird life history characteristics of the interaction between large tree removal and bush thickening?

METHODS

Birds were censused in Kimberley as described in Chapter 5. Life history traits and morphometrics were taken primarily from Hockey et al. (2005), a standard reference on southern African birds, and geographic information (e.g. range size, minimum annual precipitation) was taken from de Klerk (1999).

RLQ analysis

RLQ analysis (Dolédec et al. 1996) was performed to ascertain how life history traits relate to habitat correlates. This analysis involves concurrent ordination of three sets of data: (1) species composition at each point count (L); (2) environmental variables associated with each point count (R), and (3) life history traits for each of the species in L (Q) (Figure 6.1). Life history traits were divided into quantitative (Q-Quant) and qualitative (Q-Qual) tables.

Before the RLQ analysis can be performed, ordinations must first be carried out on the separate R, L and Q tables. A correspondence analysis (CA) was performed on L, the species composition table. The quantitative species traits table (Q-Quant) and the environmental data (R) were subjected to principal component analysis (PCA), using stand scores in L as weights, allowing R and Q-Quant to be linked to the L table. Multiple correspondence analysis (MCA), the statistical equivalent of PCA with qualitative variables (Tenenhaus and Young 1985) was performed on Q-qual.

RLQ analysis then combines these three separate ordinations in such a way as to maximize covariation between environmental variables and species traits. Stand (i.e. individual point count) scores in R constrain stand scores contained in L; and species scores in the Q table constrain species scores in the L table. Working within these constraints, co-inertia analysis then selects the axes that maximize covariance between species and stand scores in L (Dolédec et al. 1996). A permutation test establishes the significance of the relationship between the environmental variables (R) and species traits (Q): the number of permutations that generate higher values than the observed total inertia sets the statistical significance of the relationship (Dolédec et al. 1996). The percentage of variation in each separate analysis taken into account by the RLQ analysis was calculated for the major axes in the R, L and Q tables, enabling evaluation of the strength of these relationships. All analyses associated with the RLQ analysis were carried out using ADE-4 software, version W1.0 (Thioulouse et al. 1997).

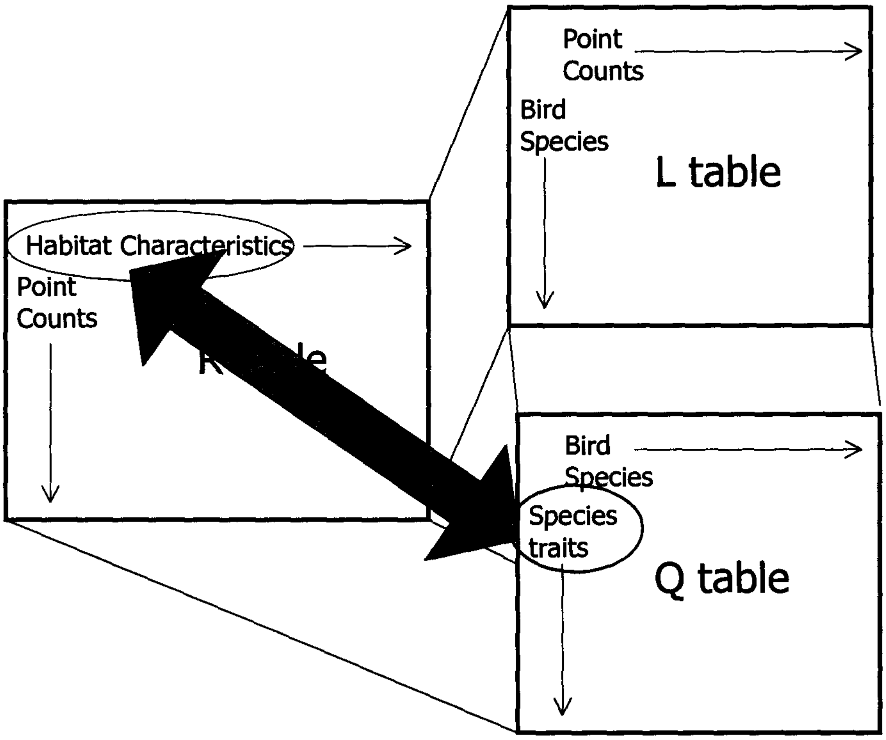


Figure 6.1. Graphical representation of how the tables relate to each other in RLQ analysis, to enable identification of correlations between life history traits and habitat variables.

To minimize the influence of common species, the species-sites table (i.e. L) was square root-transformed. To investigate life history characteristics most likely to be affected by removal of trees, I investigated correlates with tree height; by bush thickening, I used woody plant density between the heights of 0-2m.

Birds used for these analyses are listed in Appendix 6.1, habitat variables used are listed and briefly described in Appendix 6.3. A number of environmental variables were strongly co-linear, and so were removed from the analysis (e.g. fruited plant density between heights 2 - 4m was strongly correlated with maximum tree height, so was omitted). I selected bird species traits I assumed would be relevant in determining how birds are affected by habitat structure. Table 6.1 lists the quantitative and Table

6.2 the qualitative traits used in the analysis. Species that belonged to more than one category were allocated to categories of which they were most commonly members (e.g., a species in which 70% of the diet comprises insects, 30% fruits, would have been included as an insectivore, but not as a frugivore).

Table 6.1. Quantitative life history variables for species included in the RLQ analysis

Variable	Description	Data source
Mean mass (g)	Mean weight for species, after averaging male and female mass	(Hockey et al. 2005)
Usual clutch size	Average clutch size	(Hockey et al. 2005)
Breeding season length	Maximum number of months between beginning and end of breeding season	(Hockey et al. 2005)
Geographic range size	Number of one degree squares in Africa in which the species is found	(de Klerk 1999)
Maximum CV of annual rainfall ("Max CV of annual rainfall")	Across the grid squares in which a species is found, the coefficient of variation (CV) of rainfall of the grid square in which CV rainfall is maximum	(de Klerk 1999)
Minimum annual rainfall (mm)	Rainfall of the driest grid square in which a bird species is found	(de Klerk 1999)

For qualitative life history traits, primary food source gives an indication both of how food resources may have changed, or they may point to a decline in important groups, e.g. frugivores, with attendant implications for ecosystem processes like dispersal. Foraging strategy gives an indication of how habitat may have selected for, or excluded certain groups, as would nesting category.

Movement and co-operative breeding were included as indicative of life history strategies that may be selected for by certain habitat structures. Finally, plumage colouration was included to see if perhaps habitat structure can influence display of certain plumage colours.

Amongst the quantitative life history variables considered, some were included as an indication of whether species were generalists, in terms of their habitat use, for example, the inclusion of geographic range size and length of breeding season. Mean mass was included to ascertain if certain body sizes are favoured by differences in habitat struture, and as in indication of possible "carrying capacities" of areas - smaller birds have higher metabolic rates. Maximum CV of annual rainfall, minimum annual rainfall and clutch size would be expected to identify birds adapted to arid environments.

Table 6.2. Qualitative life-history variables for species included in the RLQ analysis

Variable	Categories	Data source
Nesting category	Hole nesters (includes primary and secondary hole nesters) Cup nesters Burrow nesters Ball nests (includes woven nests, e.g. nests of *Ploceus velatus* and *Plocepasser mahali*) Brood parasites Non-breeding migrants	(Hockey et al. 2005)
Primary food source	Invertebrates Fruits Seeds	(Hockey et al. 2005)
Foraging strategy	Hawkers (hawk aerial invertebrates) "Perch and swoop"ers (swoop to ground to capture invertebrates) Frugivores Gleaners Bark Foragers Ground feeders	(Hockey et al. 2005)
Movements	Resident Seasonal movements Nomadic Migratory	(Hockey et al. 2005) (Harrison et al. 1997)
Cooperative breeding?	Not cooperative Facultative cooperative Obligate cooperative	(du Plessis et al. 1995)
Plumage colouration	Predominantly grey or brown Predominantly black and white Low frequency colour plumage (e.g. yellow, orange or red) present Iridescent colours	(Hockey et al. 2005)

RESULTS

Bird species seen at fewer than 5% of point counts were considered rare and omitted from the analysis. By this criterion, 19 species were omitted, so that the dataset contained 147 sites, with 44 species, based on 5466 bird observations.

Correspondence Analysis (CA)

The first five axes of the CA for the species abundance matrix explained 42.13% of the total variance (Table 6.3). The square root of the eigenvalue for the first axis yields the optimum correlation possible between species and sites, as 0.627.

Table 6.3. Eigenvalues and percentage variance of the first five axes of the separate CA of the species abundance table.

Statistic	**Axis 1**	**Axis 2**	**Axis 3**	**Axis 4**	**Axis 5**
Eigenvalue	0.3921	0.20516	0.1284	0.1187	0.1101
Percentage of variance	17.3%	9.05%	5.67%	5.24%	4.86%
Cumulative percentage of variance	17.3%	26.36%	32.03%	37.27%	42.13%

The first three axes produced by PCA of the habitat variables explained 63.21% of total variance (Table 6.4). The first axis was most strongly correlated with woody plant density (0-2m), an indication of the degree of bush thickening, and percentage shrub cover. Of all variables describing habitat structure, maximum tree height was most strongly negatively correlated with this axis. The second axis was most strongly positively correlated with maximum tree height, and most negatively with percentage and height cover of herbaceous plants. The third axis was most strongly correlated with density of fruited plants between the heights of 0-2m.

The first axis of the PCA performed using quantitative species traits was most strongly correlated with maximum coefficient of variation in rainfall across the species range, negatively correlated with minimum annual rainfall, and weakly negatively correlated with mean bird species mass (Table 6.5). The second axis correlated with mean clutch size and weakly with breeding season length, and negatively with size of geographic range (Table 6.5). The third axis correlated negatively with mean weight and length of breeding season, the fourth axis correlated with geographical range (Table 6.5).

Table 6.4. Correlation between the variable and the first two axes of the separate PCA of the environmental characteristics of the sites.

Statistic	Axis 1	Axis 2	Axis 3
Eigenvalue	0.1893	0.1372	0.11605
Percentage of variance	27.04%	19.6%	16.58%
Cumulative percentage of variance	27.04%	46.64%	63.21%
Maximum height	-0.54827	0.4059	0.16624
Fruited plants 0-2m	-0.19778	0.20346	0.8021
Woody plant density (0-2m)	0.72736	-0.36289	0.15621
Average grass height	0.35347	0.39881	0.45634
Herb cover (%)	-0.47173	-0.66462	0.038553
Average herb height	-0.4266	-0.60333	0.43631
Shrub cover (%)	0.70303	-0.26335	0.25488

The first four axes of the PCA of quantitative species traits explained 83% of variation (Table 6.5).

Table 6.5. Correlation between variables of the quantitative species traits and the first three axes of the PCA.

Statistic	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalue	1.680	1.343	1.071	0.8947
Percentage of variance	28%	22.38%	17.84%	14.91%
Cumulative percentage of variance	28%	50.38%	68.22%	83.14%
Breeding season length	0.31309	0.50427	-0.64442	0.31765
Mean weight	-0.40147	-0.22685	-0.78946	-0.22247
Mean clutch size	0.025143	0.86029	0.13052	0.18459
Minimum annual rainfall	-0.79669	0.10348	0.11384	0.2663
Maximum CV of annual rainfall	0.83202	-0.02994	-0.01876	-0.25572
Geographic range	0.3056	-0.53414	-0.03979	0.75759

Six ordination axes were included for the MCA of qualitative life history variables. These accounted for 63.6% of total variance (Table 6.6). The first axis was most strongly correlated with foraging and nesting strategies, and weakly with food type and plumage (Table 6.6). Foraging strategy was also strongly related to the second to fifth axes. Food type was strongly related to the second axis, and nesting strategy to the second, fourth and sixth axes. Migratory status was only influential in the third axis and cooperative breeding status only weakly linked to the first axis. Plumage colouration had its highest correlation with the fifth axis. Although none of the variables had their highest correlation with the sixth axis, nesting strategy was still important to this axis; hence, it was retained (Table 6.6).

Table 6.6. Correlation ratios between first six axes of the separate MCA of the qualitative species traits for species considered in the RLQ analysis

Statistic	**Axis 1**	**Axis 2**	**Axis 3**	**Axis 4**	**Axis 5**	**Axis 6**
Eigenvalue	0.521	0.473	0.373	0.3438	0.284	0.231
Percentage of variance	14.9%	13.5%	10.65%	9.82%	8.12%	6.6%
Cumulative percentage of variance	14.89%	28.4%	39.05%	48.9%	56.99%	63.59%
Nesting	0.80278	0.61557	0.46119	0.50157	0.30309	0.75058
Food type	0.51418	0.62601	0.23548	0.36587	0.02853	0.01560
Foraging strategy	0.81187	0.8842	0.64264	0.77189	0.60418	0.03746
Migratory status	0.2128	0.2674	0.47352	0.09032	0.15489	0.36959
Cooperative	0.31245	0.19351	0.29288	0.16251	0.07928	0.13215
Plumage colours	0.47205	0.25215	0.13059	0.17056	0.53426	0.08067

RLQ analysis

The significance of the relationship between the habitat variables (R) and species traits (Q) were investigated using a permutation test (Dolédec et al. 1996). The number of permutations yielding higher values than the total inertia when running 1000 random permutations between the R and Q table sets the statistical significance of the relationship. For both quantitative and qualitative species traits, none of the random permutations generated a number greater than the total inertia. The relationship between species traits and environmental variables is therefore highly significant ($p < 0.001$).

The RLQ analysis using quantitative species traits yielded an ordination in which the first two axes explained 91.1% of the variance, the first axis explaining 61.07%, the second 30.7% (Table 6.7a). For qualitative species traits, the first two axes explained 65.4% and 28.6% of the variance, a total of 94% (Table 6.7b).

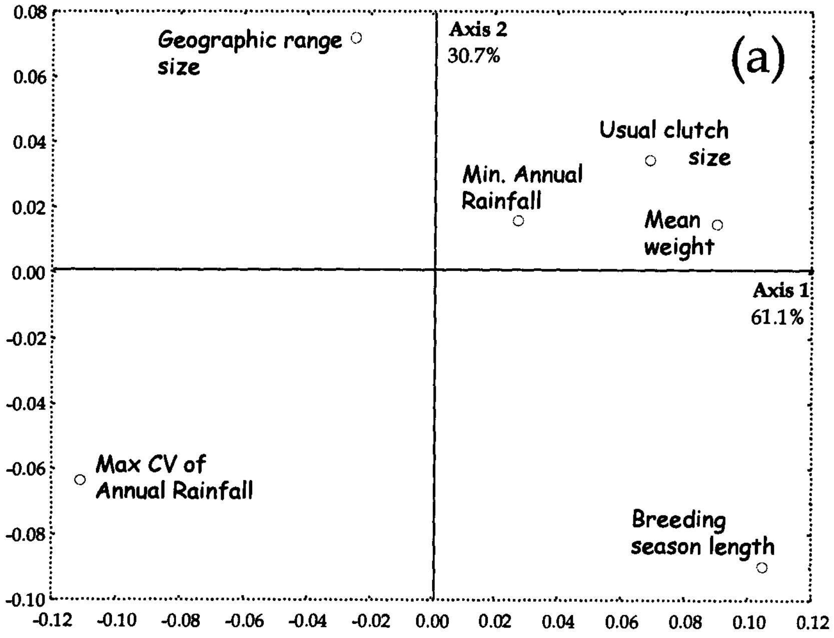
Table 6.7. Results of the RLQ analysis of a) quantitative species traits and b) qualitative species traits. Note that the first axis explains more than double the variation explained by the second axis, and therefore arrangement along the first axis is considerably more important than arrangement along the second axis.

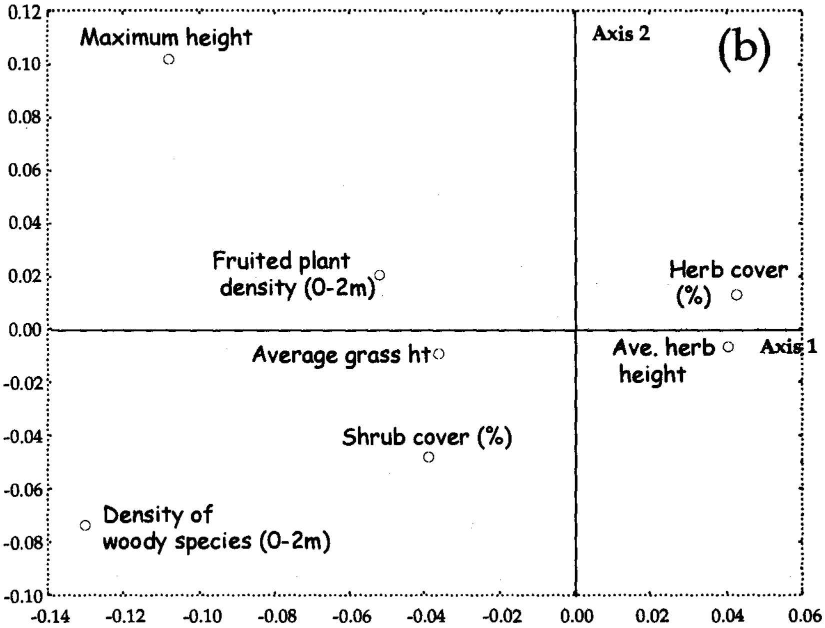
Statistic	**Axis 1**	**Axis 2**
a) Quantitative species traits		
Eigenvalues	0.03758	0.01889
Total variance	61.1%	30.7%
Covariance	0.194	0.137
Correlation	0.176	0.109
Variance		
Habitat	0.989	1.649
Traits	1.229	0.9695
b) Qualitative species traits		
Eigenvalues	0.03860	0.01687
Total variance	65.4%	28.6%
Covariance	0.196	0.13
Correlation	0.255	0.22
Variance		
Habitat	1.753	0.9061
Traits	0.9061	0.385

The correlations produced here are considerably lower than those produced by the CA for the table L. There is a considerable decline in value (from 0.626 to 0.176 and 0.255, for quantitative and qualitative species traits, respectively). This is likely because the species traits records used do not capture the subtleties of the original species table, and perhaps not capture all life history traits important in shaping the observed patterns (Dolédec et al. 1996). The weighted standardized scores for sites and species, computed by RLQ analysis for the R ($R = -0.598$, $n = 147$), and Q ($R = -0.348$, $n = 44$)

tables are, however, well correlated with the row and column scores of the correspondence analysis.

For the quantitative species traits in RLQ, the first two axes explained 91.8% of the variance, the first axis explaining 61.1% and the second 30.7% (Figures 6.2). Positioning of species traits and stand attributes along the first axis is therefore more important than their arrangement along the second axis. With increasing density of woody species, mean clutch size, mean bird weight, minimum annual rainfall and length of breeding season all decrease. Range size and maximum variability of rainfall within a species range increased with increasing woody species density, however. Interestingly, maximum tree height and woody density were on the same side of the first axes, but the second axis differentiated between the two. Therefore, the same factors that increased for woody species density increased with increasing tree height, according to their arrangement along the first axis. Geographic range size, mean clutch size, mean weight and minimum annual rainfall were unequally distributed relative to tree height and woody species density along the second axis, however, all of these factors increased with increasing tree height.





Figures 6.2.a. and b. Diagrams of RLQ analyses for (a) quantitative life history variables and (b) habitat characteristics. Their relative positioning along the axes indicate associations between factors. For example, Maximum tree height is positively associated with geographic range size, but density of woody species is negatively associated with mean bird weight.

Although I conducted the analysis of all qualitative species traits together, within Figure 6.2, I have separated them for the sake of clarity into features broadly associated with breeding and feeding. As with the quantitative analysis, the first axis explained more than double the variability explained by the second. The ecological factors of interest, woody species density and maximum tree height, separated out on opposite sides of the first axis.

With increasing woody plant density, there was an increase in cup nesters, ball nesters and birds with yellow, red or orange within their plumage, gleaners and insectivores, and nomadism. Ground, hole and burrow nesters decreased, as did co-operative breeders, brood parasites and birds with iridescent plumage. Bark and ground foragers, as well as birds that forage by hawking or "perching and swooping" also declined with increasing density of woody plant species. The opposite trend applied to increasing maximum height for all these factors.

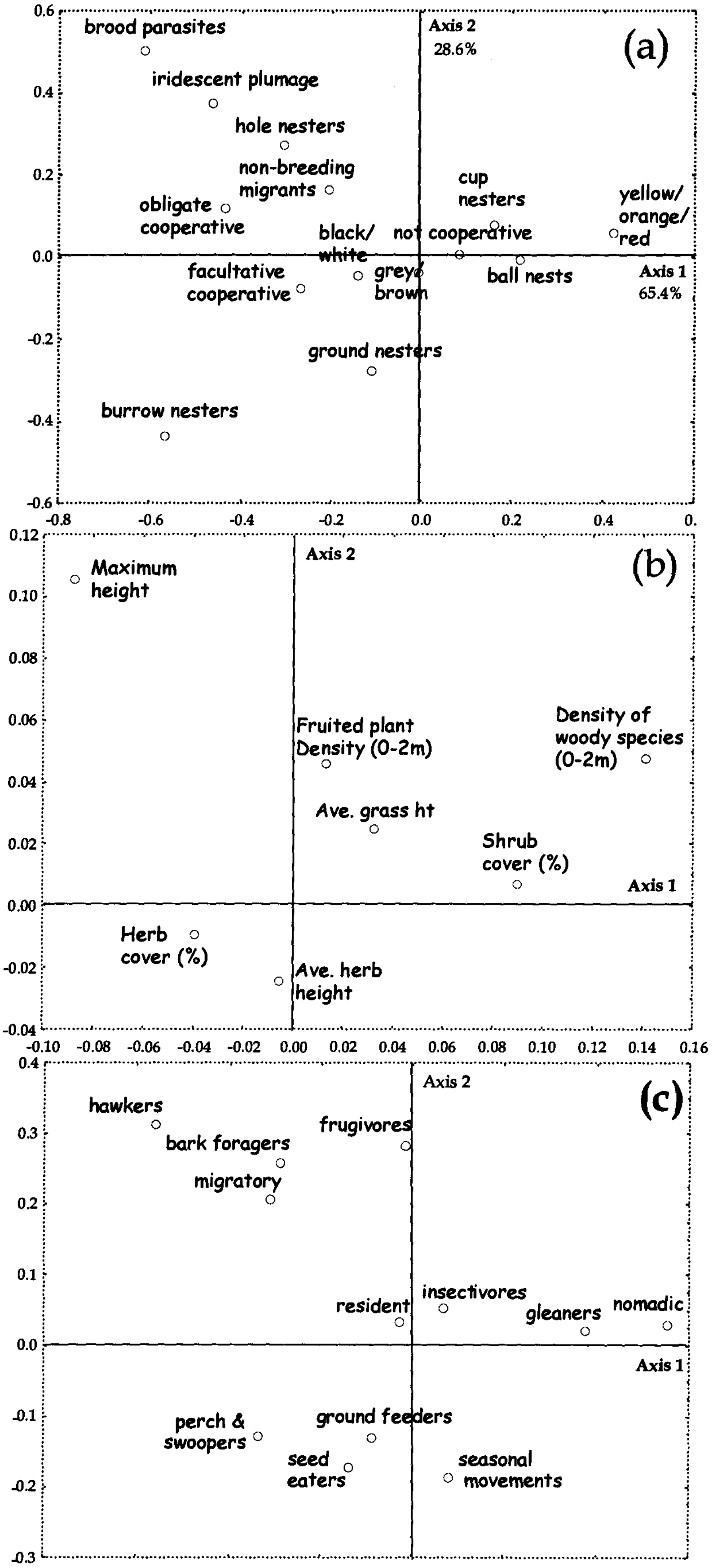


Figure 6.2. a.b and c. Diagrams of RLQ analyses for (a) qualitative life history variables associated with breeding (b) habitat characteristics and (c) qualitative life history traits associated with diet and foraging niche.

Data interrogation

Although *post hoc* statistical tests are generally not valid, investigation of the findings of statistical tests can enable erection of new hypotheses for further testing. Therefore, based on results from the RLQ analysis, further interrogation of the data revealed the following:

1. A trend of increasing frugivores with increasing tree height was observed in the data, but an MM regression showed that this was only weakly linear ($p < 0.1$).

2. Abundance of cavity nesters was influenced by tree height: 82% of hole nesters were observed in plots with maximum tree height over 4.5m, although only 58% of habitats had maximum tree heights over 4.5m. Chi-squared tests showed this difference to be statistically significant ($p < 0.001$). In addition, abundance of hole nesting birds increased linearly ($\beta = 0.955$) with maximum tree height within habitats, regardless of shrub density ($p < 0.001$).

3. Abundance of gleaners increased linearly with increasing habitat density (regression coefficient = 6.87; $p < 0.001$), while abundance of birds that hawk or perch and swoop showed the opposite trend (regression coefficient = -1.23, $p < 0.001$). This guild of birds increased with increasing maximum tree height, however (beta = 0.447; $p < 0.001$); as did bark foragers (beta = 0.60; $p < 0.001$) and ground feeders (beta = 1.48; $p < 0.001$). Even after applications of Bonferroni tests, these results remained significant.

4. The relationship between average bird mass and habitat density was logarithmic and significantly negative, so

$$\text{Habitat density} = -0.1621x \log(\text{bird mass}) + 1.7736, \; p < 0.0001$$

DISCUSSION

This study found that changes in habitat structure correlate with changes in life history traits represented within bird assemblages. These may reflect changes in ecosystem functioning, either because of, or as a consequence of, changes in bird assemblages.

Some shortcomings are inherent in an analysis of this nature. For example, it is impossible to include *all* life history characteristics that might influence bird behaviours and niche choices, and loss of information associated with coercion of species into single categories (e.g. labelling a species that is only 70% insectivorous as an "insectivore") no doubt exacerbated the decline in explanatory power demonstrated by low correlations produced by RLQ analysis when compared with the COA (Dolédec et al. 1996). Nevertheless, that the weighted standardized scores correlated well with the row and column scores of the correspondence analysis indicates that we can still place confidence in the results produced (Dolédec et al. 1996).

Also, while data used in this study were from one breeding season only, the large sample size used in this study (147 sites, nearly 5 500 bird observations) likely addresses this weakness. Van Horne (1983) showed that density of species in a habitat is not always a direct measure of habitat quality, and that under certain conditions a positive correlation between habitat quality and density may not hold. I assumed that since all birds surveyed were included in this analysis, and that conditions leading to a breakdown in the relationship between habitat quality and density were only likely for the minority of species, higher abundances could be assumed to equate to higher habitat suitability. In addition, since sampling was carried out during the breeding season when predation and competition pressure for food and nest sites are most intense, the results found here are probably a good reflection of the resulting pressures on birds and their response to these demands. The results of this study can be used to further investigate whether assumptions of habitat quality with density hold true in this environment: measures of individual survival, and likelihood of reproductive success could be included in the measure of habitat quality (van Horne 1983).

Life history traits of birds in bush thickened areas

At least some of the observed relationships between habitat measurements and life history variables can be attributed to the restrictions imposed by the physical structure of habitats. For example, with increasing woody plant density, there was a decline in bird body size. Small birds are better suited to moving within dense habitats and foraging on thin, unstable and flexible substrates, like foliage and twigs, that require an agility only possible for the small and nimble (Croxall 1977, Norberg 1977, Winkler and Leisler 1985, Tellería and Carrascal 1994).

Foraging strategies are likely also influenced by physical habitat structure, explaining the decline in hawkers, bark foragers and birds that tend to perch and swoop in bush thickened areas. With the exception of Kalahari robin (*Cercotrichas paena*) and bokmakierie (*Telophorus zeylonus*), most of the ground feeders in this study were also seed-eaters, and this may explain the decline in ground feeders: seed-eaters rely largely on grass, which is progressively excluded with increasing bush thickening (Donaldson and Kelk 1970).

Minimum annual rainfall across species' ranges decreased with increasing woody plant density, implying that birds found in these thicker habitats have ranges that extend into areas that are more arid. Mean clutch size also decreased, which may also be an indicator of arid adaptation (Tieleman et al. 2004). Although nomadism is an arid adaptation, its presence here with increasing woody plant density could be an artefact of sample size, as there were only two species listed as "nomadic" in this analysis.

That ground and burrow nesters were not well represented in bush thickened areas is likely a function of the density of burrows available and the suitability of the habitat for ground nests. The aardvark (*Orycteropus afer*), the mammal primarily responsible for creating the burrows used by burrow nesting birds, tends to favour open habitats (Skinner and Smithers 1990). Once again, with the exception of the desert cisticola, the ground nesters in this study were also listed as seed eaters, so their exclusion may reflect a food limitation. That insectivores, and in particular, gleaners are well represented in these habitats suggests greater availability of invertebrates in bush thickened areas. The vertical structure provided by shrubs in bush thickened areas probably provide more substrate for invertebrates, and it is thought that physically defended plants (e.g. *Acacias*) invest less in chemical defences (Coe and Coe 1987, Owen-Smith and Cooper 1987) and are therefore more attractive to invertebrates, leading to a concomitant increase in insectivorous birds (Greig-Smith 1978, Greenberg et al. 1997). The relationship between the proportion of physically defended (i.e. *A. mellifera*) to non-physically defended (i.e.

Grewia flava and *Tarchonanthus camphoratus*) plants in bush thickened areas to insectivore gleaner abundance was however not significant in this study.

That birds with yellow, orange or red colouration within their plumage were more common within bush thickened areas could be because lower-wavelength colours are more visible within shaded (closed) habitats (Endler 1993, Marchetti 1993, McNaught and Owens 2002).

Removal of large trees: influence on birds

Many life history traits associated with large trees are also negatively associated with bush thickening, suggesting that birds with these traits are particularly vulnerable where increasing bush thickening and removal of large trees occurs simultaneously.

The incidence of hole (or cavity) nesters increased with increasing tree height: an analysis of the data showed that 60% of point counts had maximum tree heights over 4.5m, but contained 81.5% of the hole-nesters seen. A decline in dead trees has been linked to a decline in hole nesters (du Plessis 1995), but it appears that here, large live trees are also important, perhaps because of the greater shelter conferred by the foliage of a live tree from the temperature extremes in this environment. Therefore, removal of large trees is likely to precipitate a decline in cavity nesting birds.

Species that hawk, bark forage, and perch and swoop were also associated with taller-treed habitats. Tall trees provide good launching points for hawkers and "perch and swoopers", and bark foragers probably find more invertebrate prey and places to perch while foraging in the layers of bark on older trees. Frugivores were also associated with large trees, which is not surprising as fruited plants in the Kalahari tend to occur in the subcanopy of large trees (Milton and Dean 1995, Leistner 1996, Dean et al. 1999 and Chapter 3), which tend to act as establishment sites (Chapter 4).

Birds with iridescent-coloured plumage were also associated with large trees, and iridescent display has likely evolved in species that display in full light. All species listed as having iridescent coloured plumage are often seen on exposed posts, a behaviour which may have evolved in tandem with iridescent plumage.

Minimum annual rainfall, mean clutch size and mean weight were negatively associated with maximum tree height for the first axis, but not the second, indicating selection for aridity for the first axis, but not the second. These results suggest that aridity is the first driving factor of those analysed here of the relationship between habitat and these life history variables.

Only two species in the final sample were listed as brood parasites (African cuckoo *Cuculus gularis* and greater honey guide *Indicator indicator*), and their presence within a habitat is likely determined by the birds they parasitise. African cuckoo parasitise fork-tailed drongos (*Dicrurus adsimilis*), which tend to be associated with large trees. The primary hosts of the greater honey guide are burrow nesters, which tend to be associated with less dense habitats.

Both obligate and facultative cooperative breeders were associated with large trees, probably because both groups tend to have nests associated with large trees or foraging habits associated with large trees. Du Plessis et al. (1995) also found a trend for obligate cooperative breeders to be associated with large trees, although this trend did not hold for facultative cooperative breeders, which tended to be associated with more open, arid scrublands.

What do the results of this study imply about ecosystem functioning overall? Both primary and secondary hole-nesters increased with increasing tree height. There was a slight linear trend for frugivores to increase with increasing tree height, possibly because they depend upon the subcanopy fruited plants found beneath large trees (see Chapters 3 and 4). The main frugivores in this study are also cavity nesters (*Tricholaema leucomelas* and *Lamprotornis nitens*), so loss of these birds from the system owing to decline of large trees will likely considerably reduce the pool of available dispersers. Also with loss of large trees, we expect to see declines in larger insectivorous species, like shrikes, drongos and flycatchers, which could lead to an increase in their prey species, with concomitant changes to the ecosystem.

Two scenarios currently exist for the long-term patterns of vegetation density in the southern Kalahari. Under the first scenario, the decrease in rainfall, and increase in drought and fire frequency should tend to decrease the extent of bush thickening (Roques et al. 2001, Ward 2002). The second scenario would see an increase in bush thickening, owing to elevated levels of atmospheric CO_2 associated with anthropogenic climate change, facilitating more efficient growth and resprouting in woody plants (Reynolds 1996, Drake et al. 1997, Polley 1997, Hoffmann et al. 2000).

Under scenario one, we can expect reduction of habitat in bush thickened areas, with concomitant reduction in bird assemblage diversity. The *status quo* will be maintained to a large extent, except at local scales where the current arboriciding practice by farmers will continue. Interestingly, there is a perception within the farming community that trees compete with grass, which motivates removal of trees with arboricides (Powell 2001). Furthermore, farmers are also directly felling trees for firewood production. It is possible that whilst regionally the Kalahari will remain bio-climatically stable, increasing local pressures (i.e. decline in rainfall, removal of farming subsidies, which will lead to pressure to derive financial income in secondary ways, e.g. removal of tree wood for sale as firewood) will drive changes across the entire landscape.

Under scenario two, we can expect the opposite: within the arid climes of the southern Kalahari increasing range restriction of hole, burrow and ground nesters, bark foragers, hawkers, and birds that perch and swoop, and birds with iridescent coloured plumage. In turn, this will impact on system functioning in the long-term by reducing the dispersal of fleshy fruits, as well as the loss of avian predators of small mammals and larger invertebrates.

The second scenario appears far more likely, owing to local impacts already alluded to in scenario one above, plus the pressures derived from South Africa's land reform policies are likely to lead to increased stocking density associated with bush thickening, in combination with overall reduction in rainfall. These questions are best treated within a resource economics context, but the biological data here would provide a key input to such a study.

CONCLUSIONS

Widespread removal of large trees in the southern Kalahari can be expected to adversely influence cavity nesters as well as hawkers, bark foragers and birds that "perch and swoop". Without large trees, frugivores may also decline over the long term, as large tree subcanopies appear to be important as establishment sites for fleshy-fruited plant species. As many as 17 of the 44 bird species (i.e. 38.6%) included in this analysis feature one or more of these life history traits, so removal of large trees can be predicted to have a considerable impact on bird species richness in the southern Kalahari, particularly since this analysis excluded rare species. In addition, many life history traits associated with large trees are also negatively associated with bush thickening, implying that the twin threats of bush thickening and large tree removal present a formidable obstacle to these species.

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APPENDICES

Appendix 6.1. Species used in the RLQ analysis - Table L

Common name	Scientific name
Red-crested bustard	*Lophotis ruficrista*
Northern black korhaan	*Afrotis afraoides*
Cape turtle dove	*Streptopelia capicola*
Laughing dove	*Streptopelia senegalensis*
African cuckoo	*Cuculus gularis*
Redfaced mousebird	*Urocolius indicus*
European bee-eater	*Merops apiaster*
Common scimitarbill	*Rhinopomastus cyanomelas*
Acacia pied barbet	*Tricholaema leucomelas*
Greater honeyguide	*Indicator indicator*
Goldentailed woodpecker	*Campethera abingoni*
Rufousnaped lark	*Mirafra africana*
Clapper lark	*Mirafra apiata*
Fawncoloured lark	*Calendulauda africanoides*
Spikeheeled lark	*Chersomanes albofasciata*
Fork-tailed drongo	*Dicrurus adsimilis*
Ashy tit	*Parus cinerascens*
Cape penduline tit	*Anthoscopus minutus*
Red-eyed bulbul	*Pycnonotus nigricans*
Anteating Chat	*Myrmecocichla formicivora*
Kalahari robin	*Cercotrichas paena*
Chestnutvented titbabbler	*Parisoma subcaeruleum*
Longbilled crombec	*Sylvietta rufescens*
Yellowbellied eremomela	*Eremomela icteropygialis*
Desert cisticola	*Cisticola aridula*
Neddiky	*Cisticola fulvicapillus*
Blackchested prinia	*Prinia flavicans*
Rufouseared warbler	*Malcorus pectoralis*
Spotted flycatcher	*Muscicapa striata*
Marico flycatcher	*Bradornis mariquensis*
Fiscal flycatcher	*Sigelus silens*
Pririt batis	*Batis pririt*
Lesser grey shrike	*Lanius minor*
Fiscal shrike	*Lanius collaris*
Redbacked shrike	*Lanius collurio*
Crimson-breasted shrike	*Laniarius atrococcineus*
Brubru	*Nilaus afer*
Threestreaked tchagra	*Tchagra australis*
Bokmakierie	*Telophorus zeylonus*
Glossy starling	*Lamprotornis nitens*
Sparrow weaver	*Plocepasser mahali*
Sociable weaver	*Philetairus socius*
Scalyfeathered finch	*Sporopipes squamifrons*
Yellow canary	*Crithagra flaviventris*

Appendix 6.2. Qualitative variables used for bird species. Note: N-B M = Non-breeding migrant, BP = Brood parasite; Y,R,O = Yellow, red or orange; P & S = Perches and swoops. Nomenclature follows Hockey et al. (2005).

Bird Species	Nesting category	Primary food source	Foraging strategy	Movements	Co-operative breeders?	Plumage colouration
Lophotis ruficrista	Ground	Granivore	Ground	Resident	Not coop.	Grey/brown
Afrotis afraoides	Ground	Granivore	Ground	Resident	Not coop.	Black/white
Streptopelia capicola	Cup	Granivore	Ground	Seasonal	Not coop.	Grey/brown
Streptopelia senegalensis	Cup	Granivore	Ground	Seasonal	Not coop.	Grey/brown
Cuculus gularis	BP	Insectivore	Hawks	Migratory	Not coop.	Grey/brown
Urocolius indicus	Cup	Frugivore	Frugivore	Seasonal	Obligatory	Grey/brown
Merops apiaster	Burrow	Insectivore	Hawks	Migratory	Facultative	Y,R,O present
Rhinopomastus cyanomelas	Cavity	Insectivore	Bark	Resident	Not coop.	Iridescent
Tricholaema leucomelas	Cavity	Frugivore	Frugivore	Resident	Not coop.	Y,R,O present
Indicator indicator	BP	Insectivore	Gleans	Resident	Not coop.	Grey/brown
Campethera abingoni	Cavity	Insectivore	Bark	Resident	Not coop.	Y,R,O present
Mirafra africana	Ground	Granivore	Ground	Resident	Not coop.	Grey/brown
Mirafra apiata	Ground	Granivore	Ground	Resident	Not coop.	Grey/brown
Calendulauda africanoides	Ground	Granivore	Ground	Resident	Not coop.	Grey/brown
Chersomanes albofasciata	Ground	Granivore	Ground	Seasonal	Facultative	Grey/brown
Dicrurus adsimilis	Cup	Insectivore	Hawks	Resident	Not coop.	Iridescent
Parus cinerascens	Cavity	Insectivore	Bark	Resident	Facultative	Black/white
Anthoscopus minutus	Oval/ ball	Insectivore	Gleans	Nomadic	Facultative	Y,R,O present
Pycnonotus nigricans	Cup	Frugivore	Frugivore	Seasonal	Not coop.	Y,R,O present
Myrmecocichla formicivora	Burrow	Insectivore	P & S	Resident	Facultative	Black/white
Cercotrichas paena	Cup	Insectivore	Ground	Resident	Not coop.	Black/white
Parisoma subcaeruleum	Cup	Insectivore	Gleans	Resident	Not coop.	Grey/brown
Sylvietta rufescens	Oval/ ball	Insectivore	Gleans	Resident	Not coop.	Grey/brown
Eremomela icteropygialis	Cup	Insectivore	Gleans	Nomadic	Not coop.	Y,R,O present
Cisticola aridula	Ground	Insectivore	Gleans	Seasonal	Not coop.	Grey/brown
Cisticola fulvicapillus	Oval/ ball	Insectivore	Gleans	Resident	Not coop.	Grey/brown
Prinia flavicans	Oval/ ball	Insectivore	Gleans	Resident	Not coop.	Y,R,O present
Malcorus pectoralis	Oval/ ball	Insectivore	Gleans	Resident	Not coop.	Y,R,O present
Muscicapa striata	N-B M	Insectivore	P & S	Migratory	Not coop.	Grey/brown
Bradornis mariquensis	Cup	Insectivore	P & S	Resident	Facultative	Grey/brown
Sigelus silens	Cup	Insectivore	Hawks	Seasonal	Not coop.	Black/white
Batis pririt	Cup	Insectivore	Gleans	Resident	Not coop.	Black/white
Lanius minor	N-B M	Insectivore	P & S	Migratory	Not coop.	Black/white
Lanius collaris	Cup	Insectivore	P & S	Seasonal	Not coop.	Black/white
Lanius collurio	N-B M	Insectivore	P & S	Migratory	Not coop.	Grey/brown
Laniarius atrococcineus	Cup	Insectivore	Gleans	Seasonal	Not coop.	Y,R,O present
Nilaus afer	Cup	Insectivore	Gleans	Resident	Not coop.	Black/white
Tchagra australis	Cup	Insectivore	Gleans	Resident	Not coop.	Grey/brown
Telophorus zeylonus	Cup	Insectivore	Ground	Resident	Not coop.	Y,R,O present
Lamprotornis nitens	Cavity	Frugivore	Frugivore	Resident	Obligatory	Iridescent
Plocepasser mahali	Oval/ ball	Granivore	Ground	Resident	Obligatory	Grey/brown
Philetairus socius	Oval/ ball	Granivore	Ground	Resident	Obligatory	Grey/brown
Sporopipes squamifrons	Oval/ ball	Granivore	Ground	Nomadic	Facultative	Black/white
Crithagra flaviventris	Cup	Granivore	Ground	Seasonal	Not coop.	Y,R,O present

Appendix 6.3. Environmental variables used in RLQ analysis (R table).

Variable	**Description**
Maximum height	Height of tallest tree measured within point count area
Density of woody species (0-2m)	Density of "woody species", i.e. *Acacia* spp., as well as *Grewia flava, Tarchonanthus camphoratus, Ziziphus mucronata, Rhus lancea,* etc.) between the heights of 0-2m, within the point count area
Fruited plant density (0-2m)	Density of fruiting species, e.g. *Zizphus mucronata, Grewia flava,* etc., within the point count area
Average grass height	Average height of grass measured using Mueller-Dombois line intercept method for each point count
Shrub cover (%)	Percentage ground cover consisting of shrubs lower than 1m, using Mueller-Dombois line intercept method
Average herb height	Average height of herbaceous plants measured using Mueller-Dombois line intercept method for each point count
Herb cover (%)	Percentage ground cover consisting of herbaceous plants, using Mueller-Dombois line intercept method

7

Do tree size and floristics determine bird use of trees and shrubs in the Xeric Kalahari?

ABSTRACT

Both vertical and horizontal habitat structure have been shown to be important to bird assemblages within the Kalahari (Chapters 5 & 6). Although over much of the Kalahari *Acacia erioloba* is the only tree to reach any great size, in some parts it co-occurs with other tree species (e.g. *A. tortilis, A. leuderitzii* and *Boscia albitrunca*) that are also demographically diverse and which can also become large. This chapter therefore aims to investigate whether, at a finer scale, vertical habitat structure in the form of big trees is important (i.e. whether birds use large trees more often), and whether floristics and the presence of dead trees are important to birds, so that they show non-random use of tree species. This study also investigates whether non-random use is made of trees as nesting sites, both in terms of size and species. Using point count data from study sites in the Kimberley and Kuruman areas, this study found that in terms of proportional numerical representation, large trees were used far more than would be expected at both Kimberley and Kuruman. In terms of proportion of available canopy volume within the habitat, the opposite was true for Kimberley, with no preference shown at Kuruman. For bird species for which there were sufficient data (i.e. more than 30 observations), all bird species showed non-random use of tree species, with dead trees having the most species positively associated with them in both the Kimberley and Kuruman areas, followed by *A. erioloba*. An analysis of similarities showed that when controlled for tree size, different tree species had different assemblages of birds associated with them. Average size of trees containing birds' nests was significantly larger than average tree size without nests, for both *A. erioloba* and *A. tortilis*. *Acacia tortilis* contained significantly more nests than *A. erioloba*, and average size of *A. tortilis* used as nesting sites was smaller than that of *A. erioloba* used as nesting sites. Therefore, it appears as if *A. erioloba* is important both as a

large structure and by virtue of its species identity (i.e. species-specific effects), but that other species are also important. Changes to habitat floristics caused by land use practices can modify bird assemblages and perhaps even reduce bird species diversity. Bearing in mind the relevance of changes to habitat structure (demonstrated elsewhere in Chapters 3, 5 and 6), these changes also suggest a detrimental influence on overall biodiversity.

opposite trend was true ($\chi^2 = 7.56$; d.o.f.= 2; $p < 0.05$; n = 2444) (Figure 7.1). At Kuruman sites, large trees were also used far more than their numerical representation within the habitat would have predicted ($\chi^2 = 93$; d.o.f. = 2; $p < 0.01$; n = 767) (Figure 7.2). When canopy cover was considered, however, differences in use of trees of different heights were not statistically significant.

Use of all tree species

There were more than 30 observations for 33 bird species (Appendix 7.1) within the Kimberley area dataset. All bird species exhibited non-random habitat use in terms of floristics, and all chi-square tests were strongly significant ($p < 0.01$) after application of sequential Bonferroni corrections.

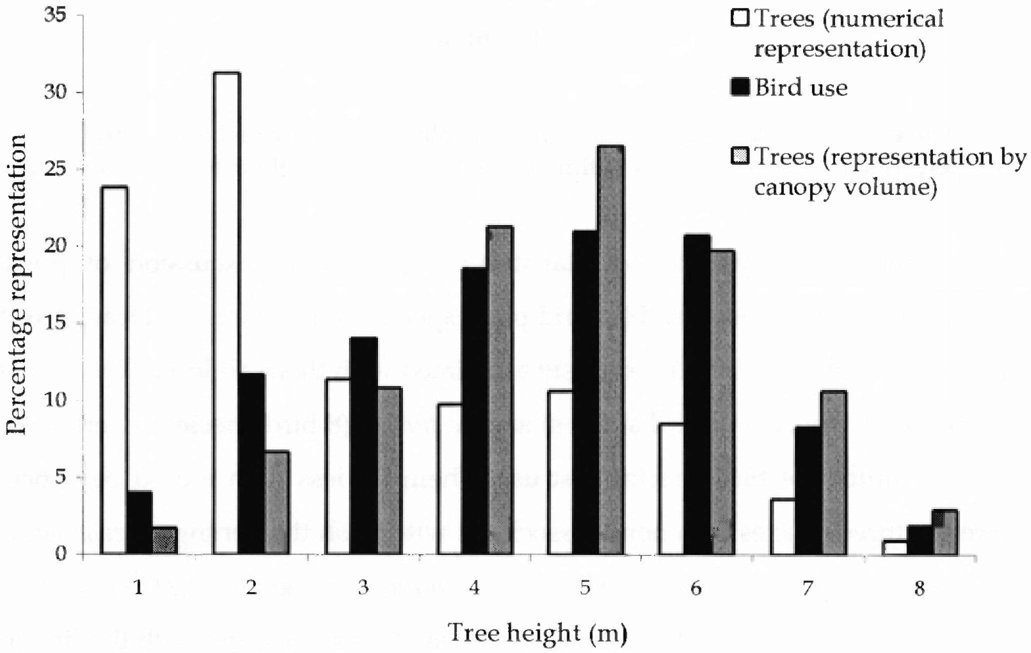

Figure 7.1. Percentage of trees represented (numerically and by canopy available) across all habitats vs. percentage of bird sightings within each of those tree height categories, for Kimberley sites.

Lamprotornis nitens) positively associated with *A. erioloba* at Kimberley sites showed no significant association with this tree species at Kuruman sites. Another two species (*Parus cinerascens* and *Plocepasser mahali*) positively associated with dead trees at Kimberley sites showed lower than expected use at Kuruman sites. The last two instances were for *Parisoma subcaeruleum,* which had no association with *A. mellifera* or *Z. mucronata* at Kimberley sites but was positively associated with these species at Kuruman sites.

All foraging groups (i.e. frugivores, insectivores, granivores) had most species positively associated with *Acacia erioloba.* The vast majority (87.5%) of granivorous species were negatively associated with *A. mellifera.* Most foraging guilds had neither positive nor negative associations with *A. tortilis,* although 50% of granivores were positively associated with this tree species. Only 14% of insectivores were negatively associated with dead trees: the rest of the bird species analysed were either positively associated or showed no association. Frugivores had a marked positive association with fruit producing species, with 75% of species showing positive associations.

Bird assemblages associated with tree sizes and tree species

Within Kimberley sites, ANOSIM found significant differences between bird assemblages using large and small trees, when averaged across species (Global R = 0.239; $p < 0.05$). There were also significant differences between bird assemblages according to tree species, when averaged across tree size (Global R = 0.255; $p < 0.01$).

Nest site preferences

At Benfontein, 548 trees (391 *A. erioloba*, 157 *A. tortilis*) were surveyed and 149 nests were found. At Vaalbos, 400 trees (294 *A. erioloba* , 106 *A. tortilis*) were surveyed and 50 nests found. Average size of trees containing nests was greater for both species at both sites, and average size of trees used for nests was greater for *A. erioloba* than for *A. tortilis* (Figure 7.3).

INTRODUCTION

The justification for the status of *A. erioloba* as a keystone species in the Kalahari has been based on its contribution to habitat structure when it is large, and not owing to its species-specific traits, primarily because over much of the Kalahari it is the only tree to reach any great size (Milton and Dean 1995, Dean et al. 1999). For this reason, Tews et al. (2004) described it as a "keystone structure": an entity which by virtue of its spatial structure provides resources, goods or services essential to other species.

In some parts of the Kalahari, however, other tree species can become large. In the Kimberley area, for example, *A. tortilis* grows to sizes comparable with *A. erioloba,* and around Kuruman, *Boscia albitrunca* is often as large, if not larger than *A. erioloba.* The relative importance to bird assemblages of habitat physiognomy and plant species composition (floristics) varies with spatial scale (Rotenberry 1985, Lee and Rotenberry 2005). As a general rule, the coarser the scale, the greater the importance of physiognomy over floristics, so that physiognomy is more influential in among-habitat comparisons, but floristics more important to within-habitat comparisons (Rotenberry 1985). Within habitats, many birds gravitate towards specific structural features (Tomoff 1974) or species for foraging (Holmes and Robinson 1981) or nesting (Martin and Roper 1990).

To date, studies have found evidence of both greater bird abundance associated with large trees for foraging and nesting (e.g., Dean et al. 1999, Díaz et al. 2005) and no relationship (Pulido and Díaz 1997). There is also evidence to suggest that thorn trees enhance avian diversity because they provide protected nest sites and structure that enables foraging space to be subdivided (Parker 1986), although the most important nest predators in my study sites are snakes (usually boomslang *Dispholidus typus* and cape cobra *Naja nivea*), which seem to be immune to thorns.

For between habitat comparisons, previous chapters (Chapters 5 & 6) have shown that both vertical (i.e. tree height) and horizontal (i.e. habitat density) structure are fundamental to bird assemblages in the Kalahari. Moreover, through filtering out bird life history traits (Chapter 6), changes in habitat structure indicate possible changes in ecosystem functioning. This chapter focuses at the finer scale, on selection of various components within the habitat. The aim here is to test whether species-specific traits also contribute to the keystone status of *A. erioloba,* i.e. whether it is merely a keystone structure or a context-specific keystone species, using birds as a measure of biodiversity. I therefore investigated bird selection of trees by size and species, to address the following questions:

1) Do birds prefer certain tree sizes and species for foraging, perching and nesting?
2) Are bird species assemblages associated with different tree sizes and tree species similar or largely different?

METHODS

Point counts were carried out as described in Chapter 5. For each bird observation, the species of tree used and the tree's height were noted.

Bush-thickened areas were excluded from the analysis, so that only more open savanna sites were used in these analyses, to control for variation in habitat structure to some extent. In addition, inclusion of bush-thickened sites would have introduced bias against small trees. This is because within bush-thickened sites, there were fewer visual records of birds in trees, as birds in this thick habitat type were more often identified by call. Since shorter trees dominate these sites, the proportion of available habitat represented by small trees would have been very high, with few bird observations to match.

I compared the percentage of trees of various heights within the habitat with actual bird use of the different tree height size classes (taken as observations of birds within those trees during point counts), to ascertain if there were any discernible patterns. I constructed histograms to aid visual interpretation of the data, and carried out chi-square tests to ascertain if observed differences were significant. Trees were classified as small (0-3m), medium (3-5m) and large (>5m). I assumed that all species were equally likely to be used by birds, and took their numerical representation as a percentage of the habitat as the "expected" frequency of bird use, and actual bird use as "observed" values.

Since larger trees have large canopies, with attendant greater chances of accommodating birds within them, I also standardised the data, calculating an approximate of canopy volume for each tree. This value was calculated by modelling the tree canopy as an ellipsoid. These percentages of habitat representation were also compared with relative bird use.

To ascertain whether bird species use all floristic components of the habitat randomly, I summed all observations for bird species for which there were 30 or more observations. Proportion of tree and shrub habitat represented by each of the main tree and shrub species were calculated. These were taken as the "expected" habitat use for the null hypothesis, and "observed" habitat use was calculated as percentages of times birds of each species were observed within that tree or shrub species. These were then tested using chi-square tests (Zar 1996). To adjust for simultaneous testing, sequential Bonferroni tests for non-independent samples were applied (Rice 1989). In instances in which the null hypothesis was rejected (i.e. birds showed non-random use of plant species within the habitat), the data were inspected to reveal positive or negative nonconformity to the expected values. Although it is not statistically rigorous to formulate conclusions *a posteriori*, inspection of results enables detection of trends and development of additional hypotheses.

To ascertain if there are statistically significant differences in assemblages of birds associate with certain tree or shrub species, the data for the three main Kimberley sites (Benfontein, Susanna and Vaalbos), according to tree/shrub species use and tree/shrub size, with each site being treated as a replicate, were used. Kuruman sites were not analysed as the available dataset did not contain sufficient replicates. For example, there were three "replicates" for large *A. erioloba*, one from each of the Kimberley sites. Trees or shrubs were classified as "small" if they were less than 3m in height, "medium" if between 3 and 5m tall, and large if greater than 5m in height. A 2-way crossed analysis of similarities (ANOSIM: Clarke and Warwick 1994) was performed to ascertain whether bird species using trees differed among tree species regardless of size, and whether bird species assemblages using trees of different sizes differed regardless of species. The null hypotheses were:

> H_{01}: Bird species assemblages using different tree species do not differ between tree species, averaged across tree sizes
>
> H_{02}: Bird species assemblages using different tree sizes do not differ between trees of different sizes, averaged across tree species

opposite trend was true ($\chi^2 = 7.56$; d.o.f.= 2; $p < 0.05$; n = 2444) (Figure 7.1). At Kuruman sites, large trees were also used far more than their numerical representation within the habitat would have predicted ($\chi^2 = 93$; d.o.f. = 2; $p < 0.01$; n = 767) (Figure 7.2). When canopy cover was considered, however, differences in use of trees of different heights were not statistically significant.

Use of all tree species

There were more than 30 observations for 33 bird species (Appendix 7.1) within the Kimberley area dataset. All bird species exhibited non-random habitat use in terms of floristics, and all chi-square tests were strongly significant ($p < 0.01$) after application of sequential Bonferroni corrections.

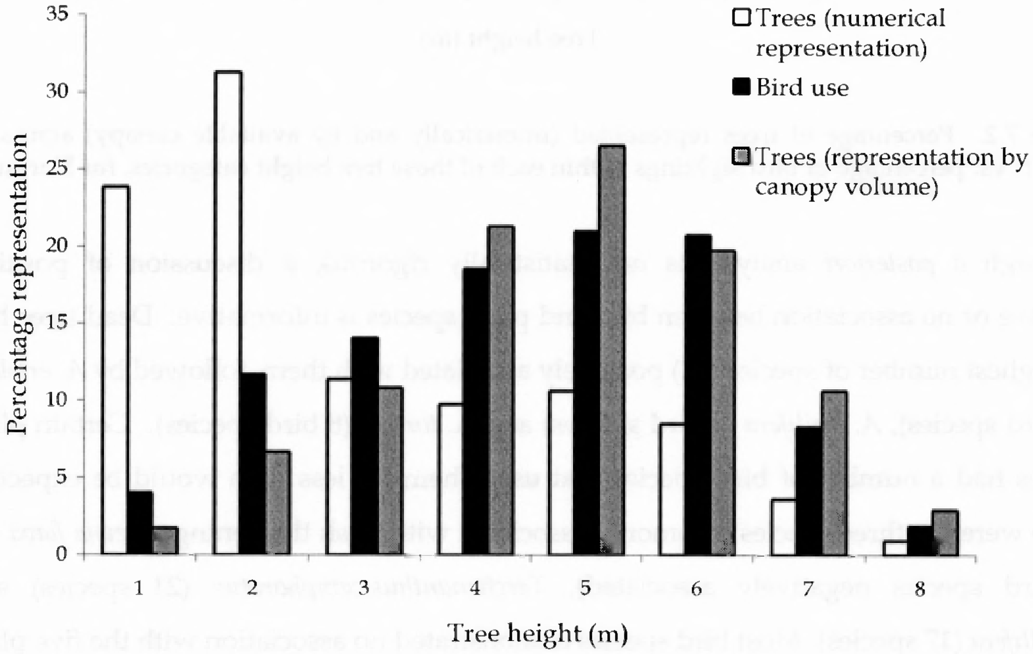

Figure 7.1. Percentage of trees represented (numerically and by canopy available) across all habitats vs. percentage of bird sightings within each of those tree height categories, for Kimberley sites.

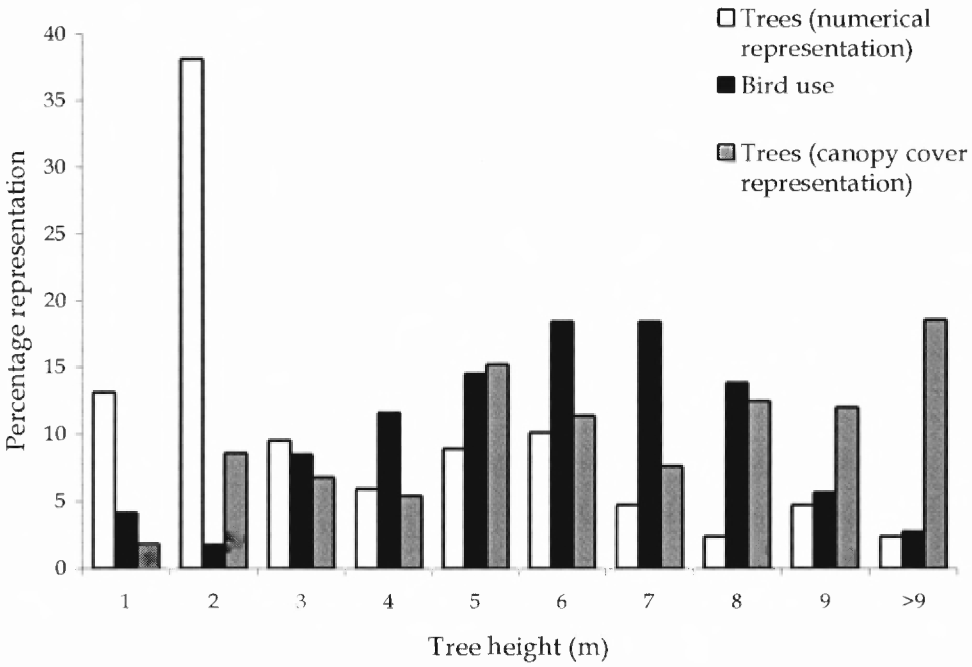

Figure 7.2. Percentage of trees represented (numerically and by available canopy) across all habitats vs. percentage of bird sightings within each of those tree height categories, for Kuruman sites.

Although *a posteriori* analysis is not statistically rigorous, a discussion of positive, negative or no association between bird and plant species is informative. Dead trees had the highest number of species (22) positively associated with them, followed by *A. erioloba* (17 bird species), *A. mellifera* (9 bird species) and *A. tortilis* (8 bird species). Certain plant species had a number of bird species that used them far less than would be expected. These were the three species commonly associated with bush thickening: *Grewia flava* (all 33 bird species negatively associated), *Tarchonanthus camphoratus* (21 species) and *A. mellifera* (17 species). Most bird species demonstrated no association with the five plant species (*Ehretia rigida, Diospyros lycioides, Boscira albitrunca, A. karroo,* and *Lycium* spp.) that represented less than 2% of the habitat.

Within Kuruman sites, there were more than 30 observations for nine bird species (Appendix 7.2). As with the Kimberley sites, all bird species exhibited non-random habitat use in terms of floristics (chi-square tests; $p < 0.01$). Although a complete comparison of the sites was not feasible because certain plant species were not present at both sites, for those for which such comparisons were possible, in 89% of cases there was concurrence in positive or negative associations between birds and certain tree/shrub species. Of those that did not concur, two bird species (*Streptopelia capicola* and

Lamprotornis nitens) positively associated with *A. erioloba* at Kimberley sites showed no significant association with this tree species at Kuruman sites. Another two species (*Parus cinerascens* and *Plocepasser mahali*) positively associated with dead trees at Kimberley sites showed lower than expected use at Kuruman sites. The last two instances were for *Parisoma subcaeruleum,* which had no association with *A. mellifera* or *Z. mucronata* at Kimberley sites but was positively associated with these species at Kuruman sites.

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Within Kimberley sites, ANOSIM found significant differences between bird assemblages using large and small trees, when averaged across species (Global R = 0.239; $p < 0.05$). There were also significant differences between bird assemblages according to tree species, when averaged across tree size (Global R = 0.255; $p < 0.01$).

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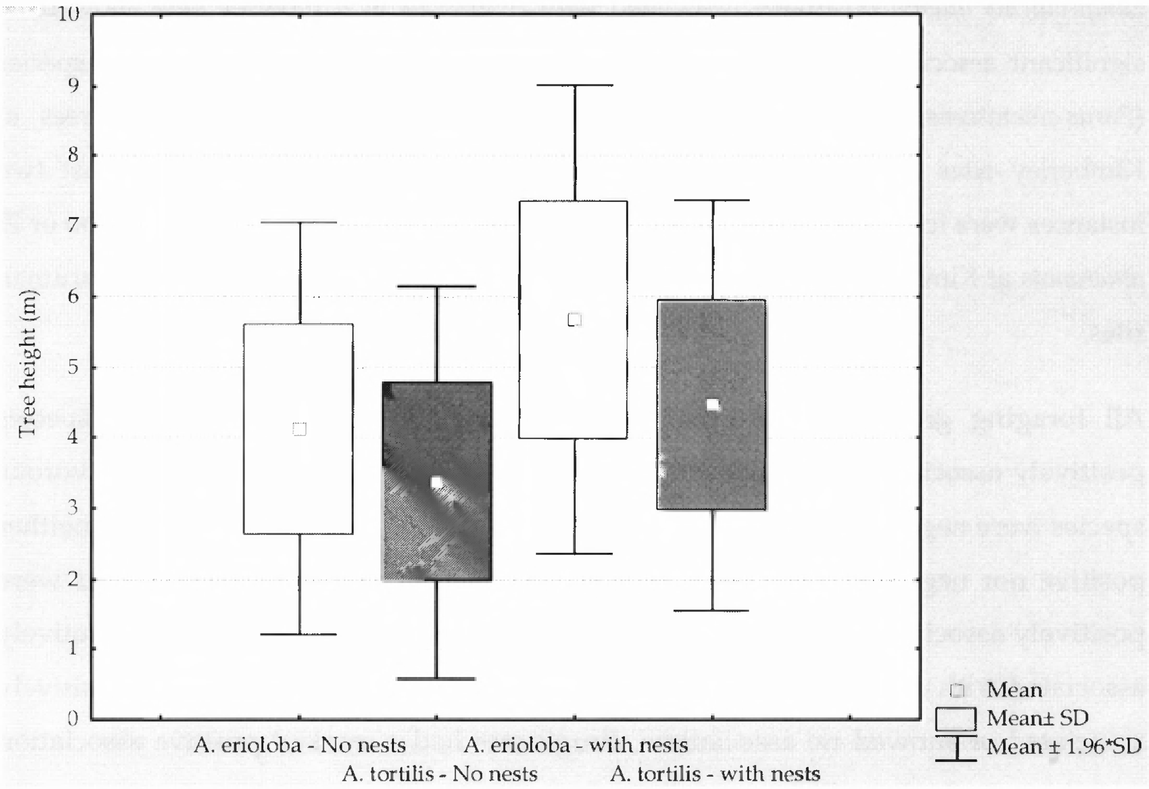

Figure 7.3. Box plot showing average tree size (m) for *A. erioloba* and *A. tortilis* with and without nests at Benfontein and Vaalbos.

Chi-square tests with Haber corrections for continuity showed that choice of nest site was not independent of tree height, when averaged across tree species ($\chi^2 = 13.02$; d.o.f. = 1; $p < 0.01$; $n = 948$). Inspection of the data indicated that there was a preference for larger over smaller trees. Furthermore, bird nest site choice was not independent of tree species, when averaged across sizes ($\chi^2 = 6.21$; d.o.f. = 1; $p < 0.025$; $n = 948$), with *A. tortilis* used for nesting more frequently than *A. erioloba* .

DISCUSSION

Bird species used habitat components in a significantly non-random fashion, with respect to both tree height and species. Foliage height diversity was positively correlated with tree height. So, that height was important is not surprising: foliage height diversity is and and continues to be recognized as an important predictor of bird diversity (e.g., MacArthur and MacArthur 1961, MacArthur et al. 1966, Karr and Roth 1971, and more recently, Skowno and Bond 2003, Watson et al. 2004, amongst others). Overall, birds used large trees preferentially, although when corrected for canopy size, this effect was reversed (Kimberley) or disappeared (Kuruman). From a biological viewpoint, however, of a number of bird species being positively associated with it, however, its popularity as a nesting site is lower than for *A. tortilis,* in the Kimberley region, at least. This leads to the conclusion that floristic diversity is as important as structural diversity, which is particularly important in light of changes in habitat structure and tree composition caused by land use practices.

bird use occurs as a function of individual trees, not canopies alone, thus large trees are important components of bird habitat. Furthermore, by virtue of their size, large trees present greater canopy volume in which birds can forage, shelter and nest.

That floristics also influences bird assemblages has also been shown elsewhere (e.g., Holmes and Robinson 1981, Bersier and Meyer 1994, Gabbe et al. 2002), but until now, the importance of *A. erioloba* to biodiversity in the southern Kalahari has been attributed primarily to its structural contribution to the habitat (Milton and Dean 1995, Dean et al. 1999, Tews et al. 2004). This study shows that floristic identity is also important, even when some of the alternative tree species available are not phylogenetically distant. Within the Kimberley area, half of the birds for which there were sufficient data (and by implication, the more common birds) were positively associated with *A. erioloba.* There were also eight species (24% of those analysed) negatively associated with *A. erioloba.* Of these, however, two (*Pycnonotus nigricans* and *Crithagra flaviventris*) were positively associated with *Ziziphus mucronata,* one of the subcanopy plants reliant on *A. erioloba* as an establishment site (Chapters 3 and 4). These species can therefore be considered secondarily positively associated with *A. erioloba.* For bird and plant species occurring at both Kimberley and Kuruman, agreement in terms of positive or negative associations was good, with nearly 90% concurrence, suggesting that the observed trends are valid. Furthermore, although Bonferroni tests have been judged too conservative (Moran 2003), statistical significance still held after application of these tests, implying that these results are legitimate.

Dead trees had the most bird species positively associated with them, at both sites. This result appears counter-intuitive, however, when viewed in context of the virtual absence of birds within arboricided areas (Chapter 5). Although dead trees provide a resource (e.g. perches from which to sally, or from which to watch for predators) for birds within a "living" habitat, alone they are incapable of supporting bird assemblages, because they are unable to provide all resources (food, nesting sites) necessary for survival.

A number of bird species showed negative associations with shrub species typically associated with bush thickening, and few birds exhibited positive associations with these species. This is likely an artefact of removing bush-thickened sites from the analyses. Birds ordinarily associated with bush-thickened areas (and therefore associated with these shrub and tree species) would be less likely to be found within unaltered habitats (Chapter 5 and 6). Johnson (1980) proposed that selection of habitat was hierarchical, with coarse physiognomic features being chosen first, followed by finer selection based on floristics within habitats. Birds would therefore be expected to associate primarily with dense shrubby habitat and secondarily with the shrubby plants that compose that habitat, and hence be rare to absent from the sites analysed here.

Analyses of associations between foraging guilds were consistent with expectations. *Acacia erioloba* tends to be associated with open habitats, and larger individuals usually have assemblages of fleshy-fruited plants beneath their canopies. Thus, it is unsurprising that all foraging groups had most species positively associated with this tree. Similarly, *A. tortilis* is also often associated with open habitats, explaining the positive association of granivores with this tree species. *Acacia mellifera* tends to be associated with closed habitats, so grassy habitat is minimised and the vast majority of granivorous species could be expected to be excluded, which explains the lower incidence of granivores in association with *A. mellifera.* Dead trees appear to make only positive or no difference to bird species, with only a few insectivores showing a negative association with these species. This could be because these species tend to avoid exposed perches, perhaps to avoid predation from aerial predators. That frugivores had a marked positive association with fruit producing species was expected.

Analysis of similarities of bird species assemblages associated with different tree species across tree sizes confirmed that bird assemblages associate with habitat constituents based on both physiognomy and floristics, adding evidence that *A. erioloba* may be more than just a keystone structure.

Differences in bird use between broad-leaved components of the habitat like *Ziziphus mucronata* and *Grewia flava* and fine leaved *Acacias* were to be expected, but finer discernment by birds among *Acacias* was surprising. *Acacias* may appear superficially similar, but resource availability and suitability for bird use may differ considerably, based on branch structure, thickness and flexibility. Fleishman et al. (2003) found that although exotic *Tamarix ramosissima* conformed to the general physiognomy of the habitat under consideration (thus producing minimal structural changes), bird assemblages still tracked floristics rather than habitat physiognomy alone.

It is well known that birds do not place their nests randomly within the environment, and that a number of factors, primarily predation risk, influence nest site selection (Collias and Collias 1984, Wiens 1989). Site selection in tree nesting species probably represents a trade-off between concealment, visibility for the incubating bird and reducing thermal stress on the incubating bird and chicks. Within this study, larger trees were preferred, and *A. tortilis* was preferred over *A. erioloba.* Larger trees likely provide more hiding places within the canopy so that the precise location of the nest can be better concealed. Birds have even been found to change nest location as concealment availability in deciduous trees (Nolan 1978 in Collias and Collias 1984) and microhabitat requirements (Horvàth 1964) changed with season. Although many predators within this savanna habitat readily climb trees, and in fact, some spend the majority of their lives in trees (e.g., boomslang *Dispholidus typus*), taller trees may reduce the variety of predators that can actually reach high nests, thus reducing the probability of nest predation.

Both *A. tortilis* and *A. erioloba* are armed with thorns, although the thorns differ in size and shape. The thorns of *A. tortilis* are smaller than those of *A. erioloba* and consist of a combination of straight and hooked thorns, whereas *A. erioloba* only bears straight, stout, thorns. Snakes, one of the major predators of tree-nesting birds in the area, seem immune to thorns, however, and are often seen moving about within both tree species with ease. What might drive the choice between *A. tortilis* and *A. erioloba,* then? The two tree species differ in the size and flexibility of their twigs: the twigs of *A. tortilis* are far thinner than those of *A. erioloba,* and it is likely that larger snakes would be unable to access nests built on the distal ends of branches, effectively limiting the pool of predators that can access the nest site. Closer inspection of the data was consistent with this hypothesis; the majority of nests found within *A tortilis* were woven nests with roofs that can be placed on the distal ends of branches, while the roofs provide protection from sunlight.

Although nest predation rates are very high in these savanna environments (e.g. 70% of all broods in the sociable weaver, *Philetairus socius* (Covas Monteiro 2002)), and is thus expected to be the primary driving force behind nest site choice, environmental factors may also be influential, e.g. nests may be placed in ways aimed at prolonging nest life (Ferguson and Siegfried 1989) or reducing solar radiation. The finer foliage of *A. tortilis* may also provide better shade in this arid environment, but this would need to be tested.

CONCLUSIONS

This study has confirmed the importance of large *A. erioloba* to bird diversity and demonstrated the importance of this species floristically, as well as structurally. In spite

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APPENDICES

Appendix 7.1. Bird species at the Kimberley study sites for which there were 30 or more observations detailing both bird species and tree species being used. These data were used to ascertain positive or negative associations between certain bird and plant species. Plant species for which there were fewer than two associations with any bird species have been omitted. *Grewia flava* has also been omitted, as all species were negatively associated with it, but this is likely an artefact of sampling method (see discussion). Positive associations are indicated by "1", negative associations by "-1" and no association are left blank.

Bird species	*A. erioloba*	*A. hebeclada*	*A. mellifera*	*A. tortilis*	Dead	*Rhus lancea*	*T. camphoratus*	*Z. mucronata*
Streptopelia capicola	1	-1	-1	-1	1		-1	-1
Urocolius indicus	1			1		1		1
Merops apiaster	-1	-1	-1	-1	1		-1	-1
Rhinopomastus cyanomelas	1		-1	-1	1		-1	
Tricholaema leucomelas	1	-1			1		-1	1
Mirafra africana	1		-1	-1	1		-1	
Mirafra apiata			-1		1	1	1	
Calendulauda africanoides	1	-1	-1		1		-1	-1
Dicrurus adsimilis	1		-1		1		-1	-1
Parus cinerascens	1	-1	-1		1		-1	
Anthoscopus minutus	-1	-1	1	1	-1		1	-1
Pycnonotus nigricans	-1		1			1		1
Myrmecocichla formicivora	1		-1		1			-1
Cercotrichas paena					1		-1	
Parisoma subcaeruleum		-1		1			-1	
Sylvietta rufescens	-1		1					-1
Eremomela icteropygialis			1		-1		1	-1
Cisticola aridula			-1		1			
Cisticola fulvicapillus					1			1
Prinia flavicans	-1	1	1		1		1	
Muscicapa striata	1		-1		1		-1	
Bradornis mariquensis	1						-1	
Batis pririt			1				-1	1
Lanius minor	1		-1	-1	1		-1	-1
Lanius collaris	1		-1		1		-1	
Lanius collurio	-1		1	1	1		1	
Laniarius atrococcineus		-1	1		-1		-1	
Nilaus afer	1	-1		-1			-1	-1
Lamprotornis nitens	1		-1	-1	1		-1	-1
Plocepasser mahali	1		-1	1			-1	-1
Philetairus socius	1		-1	1	1		-1	-1
Sporopipes squamifrons			-1	1	1	1	-1	
Crithagra flaviventris	-1		1	1	1			1

Appendix 7.2. Bird species at the Kuruman study sites for which there were 30 or more observations detailing both bird species and tree species being used. These data were used to ascertain positive or negative associations between certain bird and plant species. Plant species for which there were fewer than two associations with any bird species have been omitted. Positive associations are indicated by "1", negative associations by "-1" and no association are left blank. Where the floristic elements differ with those found at Kimberley sites, the associations for Kimberley sites are given in brackets, in bold typeface.

Bird species	*A. erioloba*	*Dead*	*Ziziphus*	*A. mellifera*	*Boscia albitrunca*	*Grewia flava*
Streptopelia capicola	**(1)**	1	-1	-1		-1
Calendulauda africanoides		1	-1	-1		
Dicrurus adsimilis	1	1	-1	-1	1	-1
Parus cinerascens	1	-1 **(1)**	1	-1		-1
Cercotrichas paena	1	1		-1		-1
Parisoma subcaeruleum			1 **(0)**	1 **(0)**	1	
Lanius minor	1	1	-1	-1		-1
Lamprotornis nitens	**(1)**	1	-1	-1		
Plocepasser mahali	1	-1 **(1)**	-1	-1		-1

8

Grass, rainfall and herbivores as determinants of *Acacia erioloba* demography

> *"But on looking closely between the stems of the heath, I found a multitude of seedlings and little trees, which had been perpetually browsed down by the cattle. In one square yard, at a point some hundreds yards distant from one of the old clumps, I counted thirty-two little trees; and one of them, judging from the rings of growth, had during twenty-six years tried to raise its head above the stems of the heath, and had failed. No wonder that, as soon as the land was enclosed, it became thickly clothed with vigorously growing young firs. Yet the heath was so extremely barren and so extensive that no one would ever have imagined that cattle would have so closely and effectually searched it for food."*
>
> (Darwin 1859)

ABSTRACT

Acacia species in arid environments might be expected to exhibit cohorted recruitment, as they can only successfully establish in years of above average rainfall. A number of studies support this assertion. I studied demography of *Acacia* species in the Kimberley area to establish whether they undergo episodic recruitment in this area. The two most common species, *A. tortilis* and *A. erioloba* both had seedling banks. This result suggests that even though cohorted recruitment may occur, it is not the primary limiting factor in this area to becoming large: once recruited, these *Acacias* still have to overcome herbivory, competition from grass, and fire to become reproductive adults. An experiment on the influence of extra water and protection from herbivory on *A. erioloba* growth rates, and a second experiment on responses of different sized *A. erioloba* saplings to removal of grass competition showed that a combination of slow growth rates and competition from grass for light and possibly water are influential in suppressing progress by saplings to larger size classes. At both study sites, grazers dominate the herbivore assemblage, and at sites where browsers are better represented, browsing may also be important. The relationship between *Acacia* growth and belowground stem size was positively linear, implying that larger plants have faster growth rates. Furthermore, the coefficient of the relationship between growth and belowground stem size was greater for *Acacia* from which surrounding grass had been removed than for those from which grass had not been removed, although this difference was not statistically significant. These differences may be biologically significant, however, with removal of grass allowing some advantage to trees growing in areas where escape from fire and herbivory is all-important.

CHAPTER 8

INTRODUCTION

Large trees are important for the maintenance of certain biodiversity patterns and processes in the southern Kalahari (Chapters 3 - 7). It is therefore informative to examine some of the processes facilitating or hindering establishment of the large tree component (i.e. *Acacia erioloba*) in the southern Kalahari.

Within the drier parts of *A. erioloba's* range, groups of trees of roughly the same size, assumed to be cohorts, are often seen. This cohorted nature of acacias in arid areas is widely interpreted as evidence of the importance of abiotic factors (particularly quantity and pattern of rainfall) to intermittent bouts of successful recruitment (Ernst et al. 1990, Barnes et al. 1997, Midgley and Bond 2001).

There is some support for these inferences: in a four year (1994-1997) study in Chobe, Barnes (1999, 2001b) found low seedling emergence and zero survival in drought years, and in an average rainfall year, only 15% of seedlings survived the first two months and none survived to the following wet season, suggesting that establishment only occurs in above-average rainfall years. A survey of the literature suggests that on Kalahari sands with mean annual precipitation (MAP) below 550mm, rainfall is indeed a limiting factor in recruitment (e.g. Theron et al. 1985, Skarpe 1991, Barnes 1999, 2001b). At moister sites (MAP 600mm), however, *A. erioloba* size class representation appears to be more heterogeneous (Ben-Shahar 1998). Therefore, all else being equal, the presence of cohorts at the Kimberley study sites, where rainfall is about 430mm.year^{-1}, might be expected.

Alternatively, what appear to be cohorts may not be even-aged individuals at all. For example, previous clearing or cattle grazing (with concomitant release from grass competition) can allow seedlings of different age classes to escape simultaneously, giving the appearance of cohorted recruitment (Hoffman et al. 1994, Milton and Dean 1995, Timberlake et al. 1999).

Although much work has implicated African Elephants *Loxodonta africana* (Laws 1970, Pellew 1983, Wackernagel 1993, Barnes 1999, Western and Maitumo 2004) and fire (Donaldson 1966, Skarpe 1980, Belsky 1992, Bond and van Wilgen 1996, Scholes and Archer 1997, Barnes 2001a, Roques et al. 2001) in the decline of the woody component of savannas, the influence of smaller herbivores (e.g., duiker (*Sylvicapra grimmia*), steenbok (*Raphicerus campestris*)) has received less attention. But these smaller herbivores appear to be at least as important as fire in restricting seedlings to heights of <1m (Belsky 1984, Martin and Moss 1997, Weltzin et al. 1997, Barnes 1999), where seedlings remain susceptible to fire and further herbivory. These effects can be significant: Augustine and McNaughton (2004) found impacts of small browsers to be equivalent to a 6-fold reduction in recruitment of shrubs into the 0.5 - 1.5m class. For *A. erioloba* in Botswana, Barnes (1999) noted frequent browsing by impala (*Aepyceros melampus*) and steenbok on new shoots was important in suppressing seedling height. In summary, browsers may be particularly important in keeping tree saplings in check, restricting them to heights <1m. Midgley and Bond (2001) cite drought followed by herbivory as major obstacles to *Acacia* recruitment in arid areas, thus context, in terms of climate and disturbance regime, governs acacia demography in these areas.

In response to fire, woody plants in savanna systems invest in belowground growth. These plants, which are neither seedlings nor saplings, have been termed "Gullivers" (Bond and van Wilgen 1996), owing to their entrapment by grasses, which maintain periodic fires, thus keeping woody plants within heights at which they are susceptible to fire and herbivory. It is conceivable that woody plants respond to herbivory in a similar way. If for each year of suppression by herbivores, saplings invest in belowground reserves, we might expect individuals with larger stems to exhibit a greater response to release from herbivory, so that the relationship between belowground stem diameter and growth rate is linear and positive. For the purposes of this chapter, I refer to these older individuals, which may have large underground stems but are below 60cm in height, as saplings.

Lastly, if saplings have deep root systems, then they might not compete with grass for water. They may, however, compete with grass for light.

This study therefore set out to address the following:

1) Does the size class distribution of *Acacia* species at two sites near Kimberley, Benfontein and Susanna, suggest cohorted or continuous recruitment, or cohorted release?
2) How does provision of supplemental water influence growth rates in *A. erioloba* saplings?
3) How does exposure to herbivores (both grazers and browsers) influence relative growth rates of *A. erioloba* saplings?

4) Does competition from grass influence *A. erioloba* sapling growth?

METHODS

Acacia demography

I used a random number generator to select grid squares on a map in which to survey *Acacia* demography within the sandveld of Benfontein (35 plots) and Susanna (18 plots) (see Chapter 1 for site descriptions). Plots were 25m x 25m, and randomly located within the study sites. I thoroughly searched each plot for *Acacias* of any species (i.e. *A. tortilis, A. erioloba, A. mellifera, A. hebeclada* and *A. karroo*). For each acacia found, I recorded species, height, maximum canopy width (d_1) and canopy width at 90° to d_1 (d_2), number of stems, diameter of thickest stem above ground (d_a), and for small (<1.5m) individuals, I measured stem diameter 3cm below ground (d_b). Using the above measurements, I used a multiple linear regression to generate an equation for predicting underground stem diameter.

Exclusion plots

I set up five plots of 300m x 300m on Benfontein and Susanna. Within each plot, I first searched for 12 saplings, allocating each to a treatment. Each plot had three replicates of each of the following treatments: herbivores excluded (A); herbivores excluded and supplemental water given (B); herbivores not excluded and supplemental water given (C); and no supplemental water, no exclusion of herbivores (i.e. controls) (D) (Figure 8.1). I endeavoured to ensure equal representation of different size classes within each treatment, because larger (assumed older) individuals may potentially grow faster than smaller individuals. Therefore, there were 30 saplings in each treatment distributed across 10 sites at two different farms. Exclusion plots were built around individual saplings, and were made of wire mesh (2.5cm holes), supported by iron rods (1.2cm diameter, 1.4 m height), which effectively excluded any herbivores larger than a small rodent. The same amount of supplemental water (5*l* over an area of 1m^2) was given to the "water treatments", once every two weeks for the summer growth period (i.e. the five months from November 2003 to March 2004), the time over which the experiment was run.

Figure 8.1. Treatments used for saplings at each plot.

	Exclosure	Water	
A	Herbivores excluded	No water	3 x each treatment (A, B, C & D) at 10 sites on two farms
B	Herbivores excluded	Water	
C	No exclosure	Water	
D	No exclosure	No water	

I measured height of the tallest growing stem, the extent of the canopy (d_1, the longest axis, and d_2, at right angles to it), number of stems, and diameter of the thickest live stem.

Grass-removal experiment

In September 2004, using the same individuals from the Benfontein plots as used for the exclusion experiment, I removed exclusion plots and cleared entire grass plants in a $1m^2$ area around half of the saplings (those that had had herbivores excluded and supplemental water, and the controls (i.e. B and D)), and left the other saplings (those that had had just herbivores excluded or just supplemental water (i.e. A and C)) as controls. After 6½ months, and a summer season of not exceptionally high, but consistent rainfall (257 mm), I measured the length of all new growth on the saplings.

Statistical methods

For the exclusion plot experiment, I used changes in height as a measure of growth. This method is susceptible to mis-measurement (e.g. soil level shifts relative to the top of the plant). I therefore elected to exclude outliers by removing all observations outside the range of ± 1.5 standard deviations around each group mean. Consequently, I removed 2 data points from group A, 3 from group B, 1 from group C and 4 from group D. I applied an ANOVA to the exclusion plot data to ascertain any significant differences between groups.

For the grass removal experiment, I used both linear regression and breakpoint regression (using STATISTICA (StatSoft 2001)), to compare growth (dependent variable) with height (independent variable). A breakpoint regression model is used when the relationship between x and y is hypothesized to be linear, but with a change in the slope at a certain threshold value of the x variable, so that the relationship is described as:

$$y = (b_0 + b_1 * x) * (x \leq X) + (b_3 + b_2 * x) * (x > X),$$

where X is the threshold value at which the slope changes, and $b_{0,1,\ldots,3}$ are constants. I performed a breakpoint regression to detect any threshold heights at which height might increase at a different rate, e.g. as a result of escaping competition with grass.

RESULTS

Size-class distributions

Within the Benfontein plots, I recorded a total of 225 *Acacias*, the species composition of which was 48% *A. erioloba*, 40.9% *A. tortilis*, 9.3% *A. hebeclada*, and 1.8% *A. mellifera*. The number of acacias found within plots on Benfontein was highly variable, from 0 to 31 trees (Mean = 6.4; (Std. Dev. = 7.0). Within Susanna plots, a total of 170 acacias were found, of which 35.8% were *A. erioloba*, 52.4% *A. tortilis*, 9.4% *A. hebeclada*, 1.8% *A. karroo*, 0.6% *A. mellifera*. The number of acacia found within plots on Susanna ranged from 3 to 18 plants (Mean = 9.5, Std. Dev. = 3.2).

The majority of *A. erioloba* were shorter than the grass sward: 93% and 65% were less than or equal to 30cm in height on Benfontein and Susanna, respectively. For both sites together, 80% of individuals were below 50cm and 86% below 1m in height. With regard to belowground diameter, 94% and 63% were less than or equal to 2cm diameter on Benfontein and Susanna, respectively. Thus, belowground diameter suggested that the population on Susanna was older, for both *A. erioloba* (Figure 8.2) and *A. tortilis* (Figure 8.3). These differences were statistically significant (Mann-Whitney U test: $p < 0.001$). Plots of height vs. belowground growth showed no differences between the two sites, suggesting that the relationship between height and belowground growth is the same at both sites.

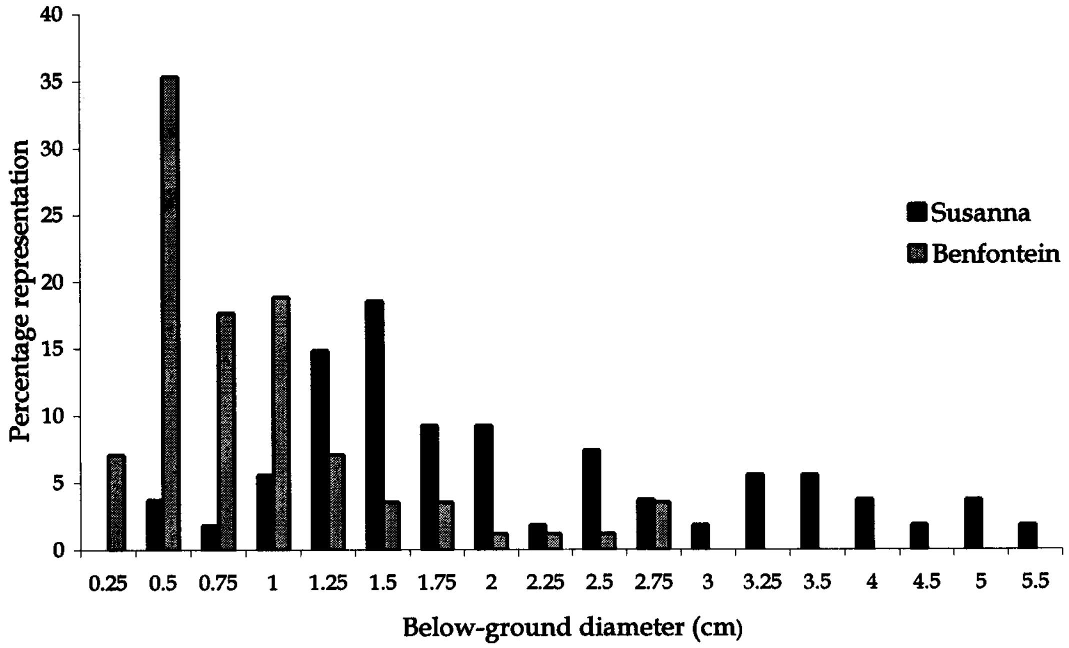

Figure 8.2. Percentage representation of *A. erioloba* within size classes at Susanna and Benfontein farms, based on below-ground stem diameter.

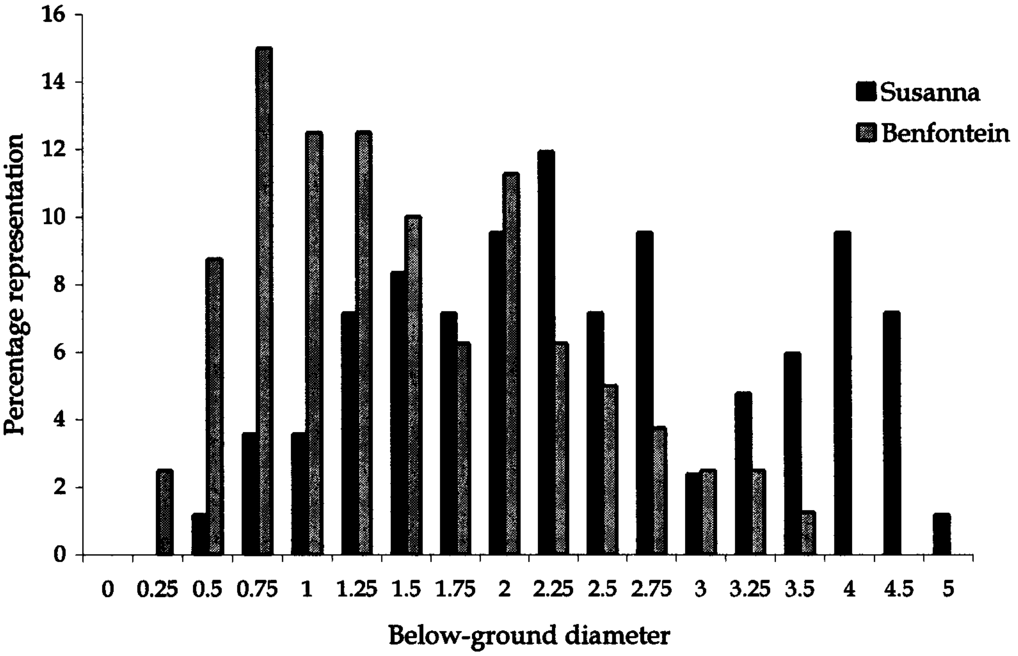

Figure 8.3. Size class distribution of *A. tortilis* saplings at Benfontein and Susanna, based on belowground stem diameter.

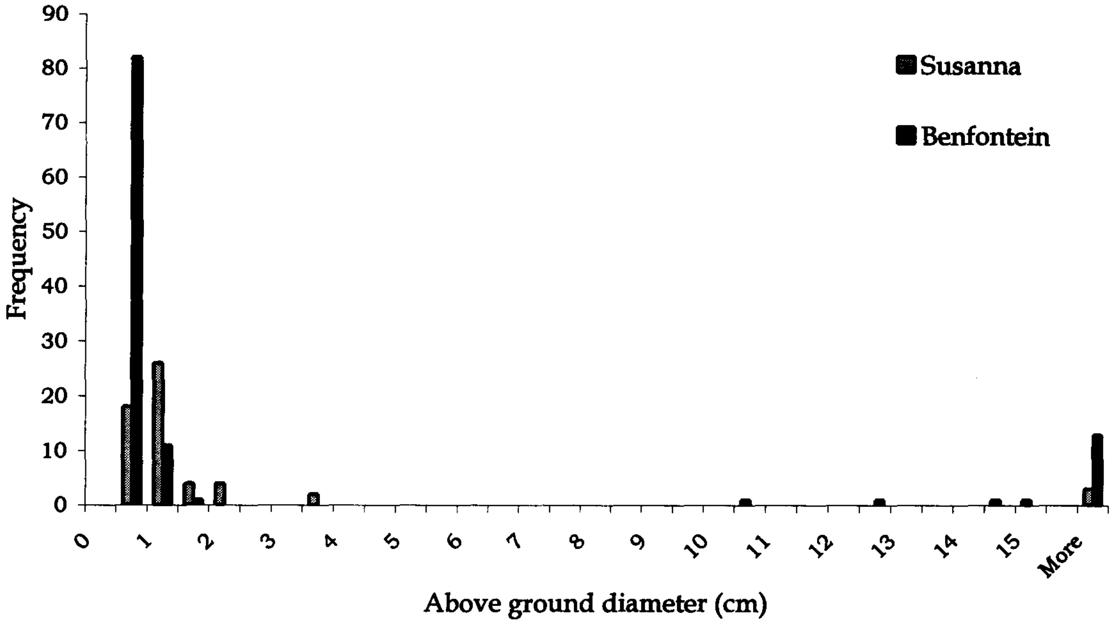

Figure 8.4. Aboveground stem diameters of *A. erioloba* on Susanna and Benfontein.

Aboveground stem diameter showed that most individuals had stems smaller than 2cm, and that the size distribution of *A. erioloba* on both sites followed a J-shape (Figure 8.4).

I used data collected for *A. erioloba* saplings on Benfontein and Susanna to predict belowground stem thickness, which might correlate with ability to respond to release from herbivory or competition with grass. A multiple linear regression showed number of stems, d_2, d_a and height to be significant predictors of d_b, according to the following equation:

$d_b = 1.44 * \text{height} + 0.34 * \text{no. of stems} + 1.21 * d_a$

($R^2 = 0.92$, $p < 0.001$, n =126 (13 points +/- 3SD from the mean removed); std. error of estimate = 0.323).

Exclusion plots

There were no significant differences in height increases between plants that received supplemental watering and those that did not (Figure 8.5). There was also no significant difference between plants protected from herbivory and those not protected (Figure 8.6). There was, however, an interaction between supplemental water and protection from herbivores. Plants that had been watered but not protected did significantly better than those that had been watered and protected (Figure 8.7).

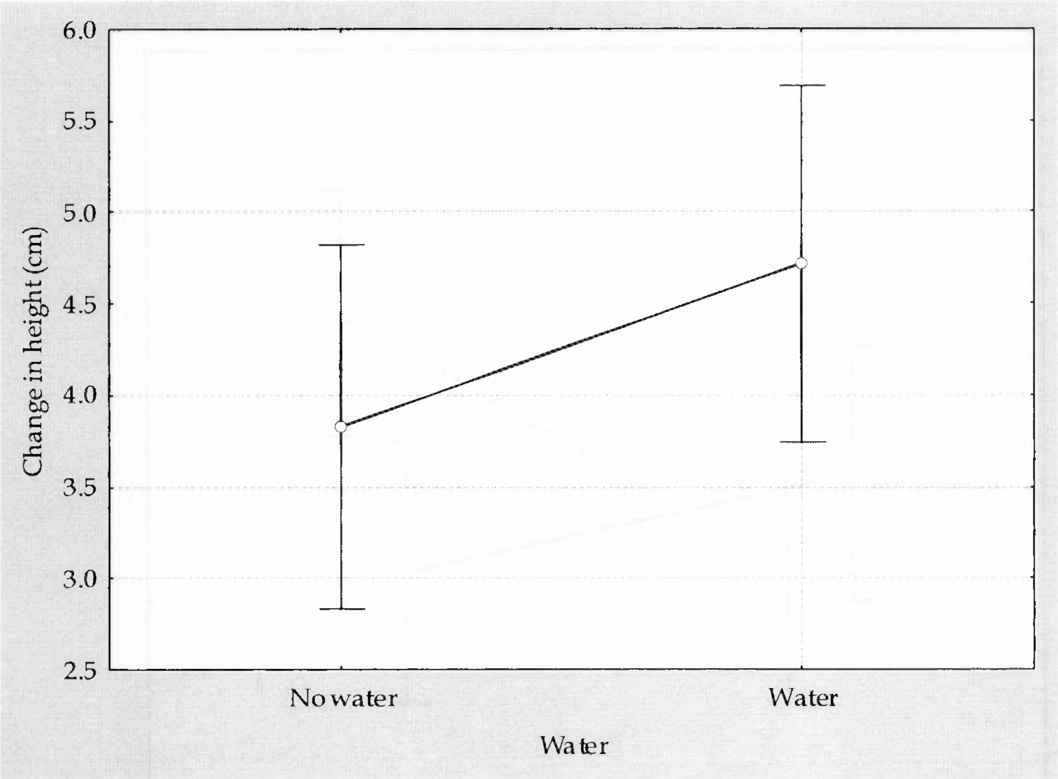

Figure 8.5. Height increase for *A. erioloba* saplings for watered and non-watered treatments. Height increases were statistically insignificant between the two treatments ($p > 0.5$).

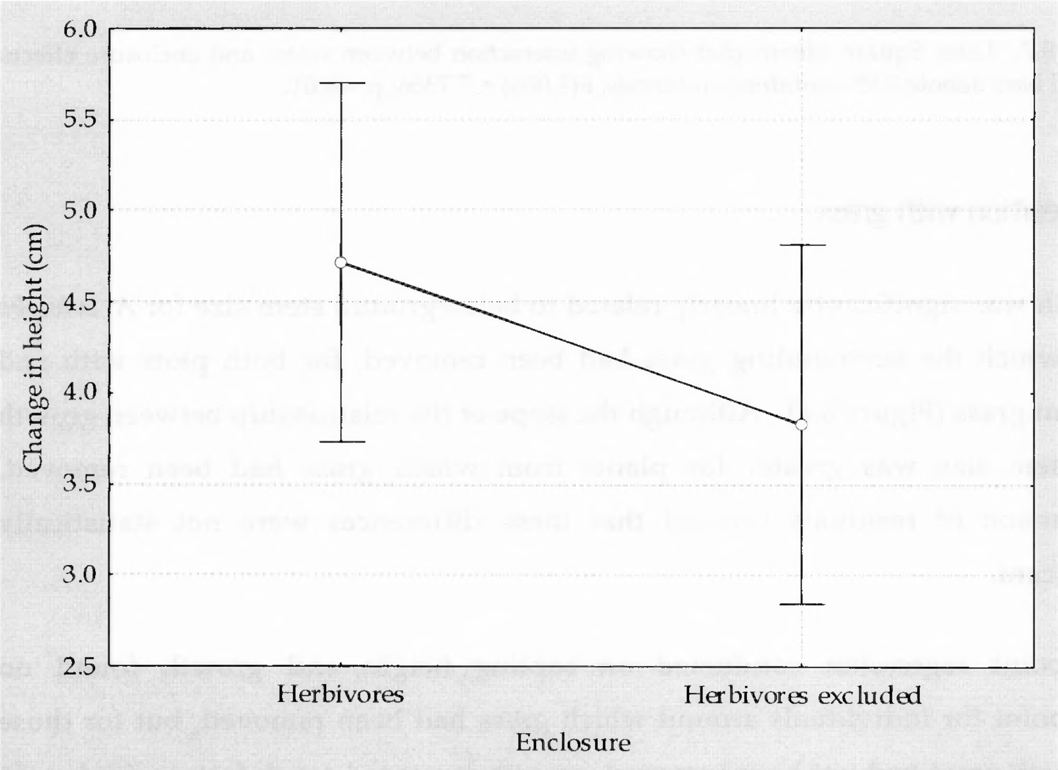

Figure 8.6. Height increases for *A. erioloba* saplings according to protection from herbivory. Differences were not statistically significant ($p < 0.5$).

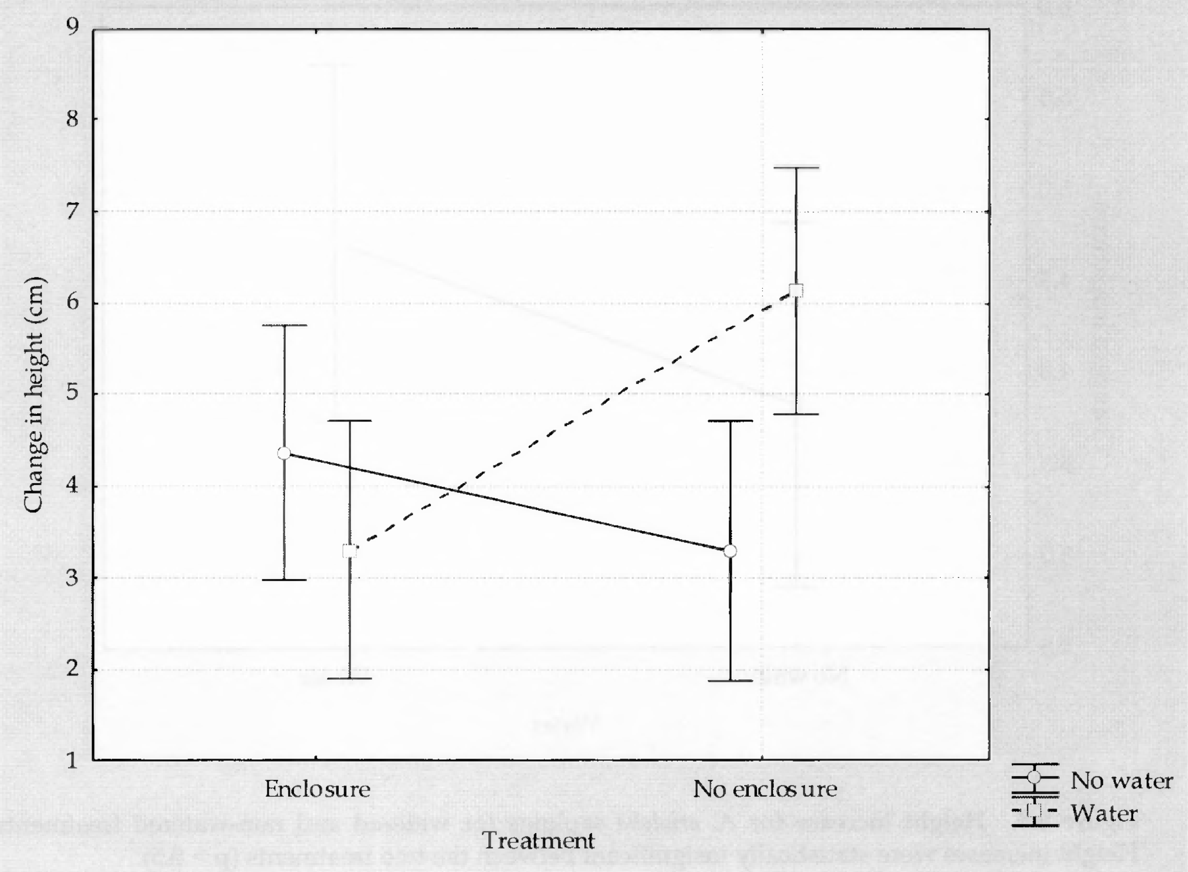

Figure 8.7. Least Square Means plot showing interaction between water and enclosure effects. Vertical bars denote 0.95 confidence intervals; F(1.006) = 7.7356; p < 0.01.

Competition with grass

Growth was significantly linearly related to belowground stem size for *A. erioloba* from which the surrounding grass had been removed, for both plots with and without grass (Figure 8.8). Although the slope of the relationship between growth and stem size was greater for plants from which grass had been removed, comparison of residuals showed that these differences were not statistically significant.

Breakpoint regression conducted on sapling height and growth found no breakpoint for individuals around which grass had been removed, but for those for which grass had not been removed, growth increased much faster with height for saplings below 26cm in height than for those above this height (Figure 8.9).

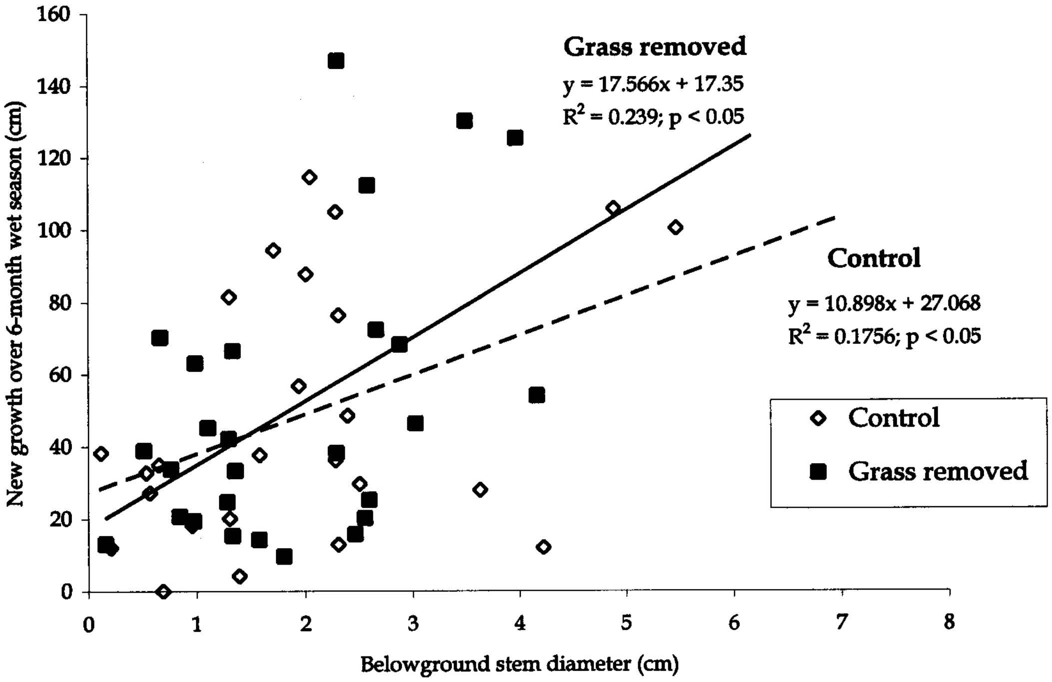

Figure 8.8. New growth measured on saplings in plots with grass (controls) and with grass removed.

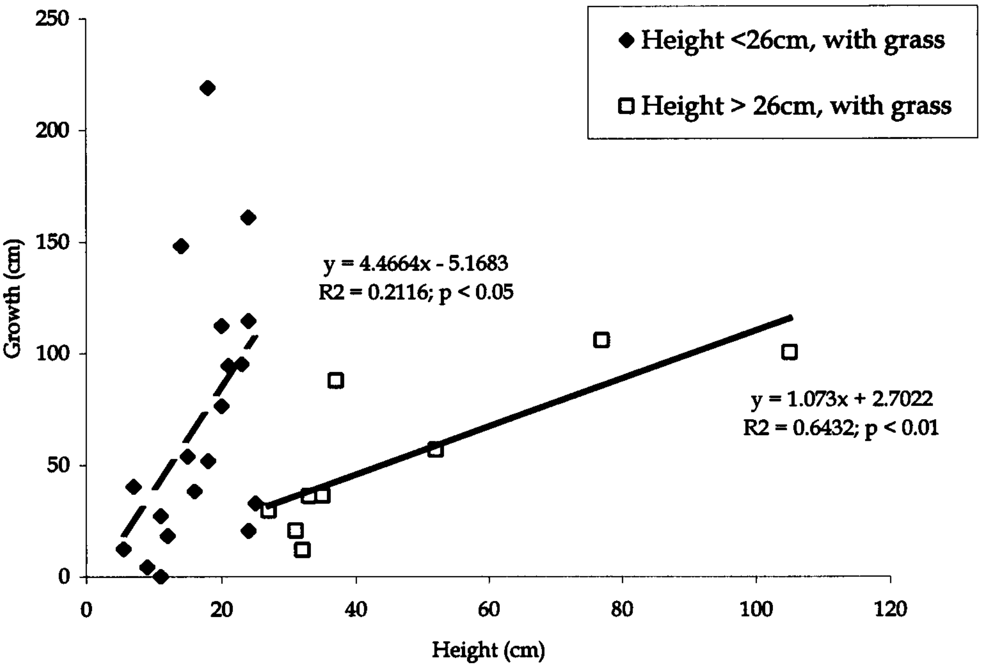

Figure 8.9. Growth according to height for saplings growing within the grass sward. Above 26cm height, growth relative to height slowed down compared to that for individuals below 26cm height.

CHAPTER 8

DISCUSSION

Since the early 1970s, the importance of seed limitation to *Acacias* via e.g. bruchid beetle predation, has been a subject of investigation (e.g., Lamprey et al. 1974, Jarman 1976, Pellew and Southgate 1984, Coe and Coe 1987, Hoffman et al. 1989, Miller 1993, 1994, Miller 1996, Rohner and Ward 1999, Walters and Milton 2003). Despite these studies finding high levels (between 47 and 96%) of bruchid predation of *A. erioloba* seeds (Ernst et al. 1990, Barnes 2001b) and low to zero probability of germination of parasitised seeds (Hoffman et al. 1989, Barnes 2001b), it appears that within the Kimberley area, it is not seed limitation that presents the greatest challenge to this species, but rather escape to larger size classes to heights above the grassy layer.

Previous studies have found establishment of *A. erioloba* seedlings to be restricted to years of regular rainfall (Briers 1988, Barnes 1999, 2001b). Thus, one would expect cohorted recruitment, only in years of good rainfall. Belowground stem sizes in this study revealed few true seedlings. Furthermore, although in terms of height, saplings appeared to be the same size, the array of sizes in belowground diameter suggests that these seedlings are of differing ages, and that seedlings "dribble" into the system. The predominance of short plants here implies that once established, many plants have yet to escape to higher size classes, so in the Kimberley area, escape or reversals can present a major obstacle to reaching maturity.

But what is preventing escape? Results of the exclusion plot experiments and removal of grass suggested that neither water availability nor competition from grasses exclusively govern growth rates, although these factors produced significant differences in concert. Many studies point to detrimental effects of herbivory on woody plant growth and survival rates (Belsky 1984, Weltzin et al. 1997, Barnes 1999, Augustine and McNaughton 2004). Browsing was noted on two thirds of the unprotected plants, but because exclusion of herbivores also excluded grazers, the negative effects of competition with grass obscured any positive effects of protection from browsing. The literature contains conflicting reports on the influence of grasses on tree recruitment, with both positive (Brown and Archer 1989, Davis et al. 1998) and negative (Walker et al. 1981, Harrington 1991) effects being recorded. That *A. erioloba* seedlings are almost without exception never found beneath other trees (C. Seymour, *unpubl. data*) suggests that shade intolerance is a driving factor of this response.

Inability to escape is exacerbated by slow growth rates for *A. erioloba* saplings, keeping them within heights at which negative effects from herbivory, fire and competition with grasses for light (and perhaps water) are influential. The group that fared best in the exclusion plot experiment only achieved mean height increases of 60mm during one growing season (95% confidence intervals: 40 and 80 mm). Barnes (1999) found similar growth rates in her study, where average increase in seedling height was only 48mm per growing season, although browsing seems to have been more intense at her sites. At a drier site, Kgalagadi Transfrontier Park (mean annual rainfall = 233mm.year^{-1}), van Rooyen et al. (1994) found average growth rates of 65 mm a year between 1978 and 1994.

These apparently slow growth rates may be because most early growth is concentrated belowground: a seedling only 25 cm high can have roots longer than 320 cm (Leistner 1967), and even a tiny seedling (5cm high and estimated to be two months old) can have a tap root of nearly 110 cm (C. Seymour & O. Huyser *unpublished data.*). Larger individuals have been recorded to have roots to depths of 60m (Canadell et al. 1996). Brown and Archer (1989) attributed slow growth rates of *Prosopis glandulosa* seedlings to investment in belowground structures: these seedlings were able to maintain net photosynthesis throughout the growing season, even though moisture in the upper 25cm of soil declined from 16% to 4%, and it is possible that *A. erioloba* seedlings do likewise.

Growth rates changed with sapling height, increasing steeply with height for plants up to 26cm (Figure 8.9). At heights over 26cm, growth rates slowed considerably. Mean grass height over the study area is between 30-40cm (C. Seymour, *unpubl. data*). Perhaps shading becomes less problematic with increasing height up until the height of the grass sward, but above that height, saplings become conspicuous to herbivores, and suffer increased browsing.

If well-established saplings are deep-rooted, then provision of supplementary water should not be expected to significantly influence growth. Indeed, the group that received supplementary water and protection from herbivores fared worst of all, likely because the grasses monopolized supplementary water (see e.g. Knoop and Walker 1985, Weltzin and McPherson 1997, Schenk and Jackson 2002, van Langevelde et al. 2003) responding with far greater growth rates than the *Acacias,* and outcompeting them for light. Removal of grass by grazing likely reduces competition for water, but more importantly for shade intolerant, deep-rooted species like *A. erioloba,* it reduces competition for light.

Despite being neighbouring farms, individuals on Susanna were larger than those on Benfontein (mean underground stem diameter: 2.06cm vs. 0.76cm) for all measurements, a pattern that also held for *A. tortilis*, the other common *Acacia* at both sites. These differences are unlikely attributable to soil differences, as plots sampled on the two farms were sometimes closer to each other than plots sampled within the same farm. Comparison of height versus belowground stem size showed no difference between the two sites, suggesting that proportionate investment above ground and in the belowground stem is the same at both sites, so differences in size classes probably cannot be attributed to resprouting responses to browsing and fire. The two sites differ in fire history, however, with fires being actively excluded on Benfontein, the last fire having occurred 11 years prior to this study. Differences in size classes may therefore reflect different times of seedling establishment on the two different sites.

Warner and Chesson (1985) coined the term "storage effect" to describe the phenomenon whereby successful recruitment to adult size classes is episodic and a species' continued existence relies on the continued survival of its adult population. Recruitment events are effectively stored in the adult population until favourable recruitment conditions arise. This could account for the exceptional longevity (up to 300 years (Barnes et al. 1997)) of *A. erioloba* compared to other *Acacias*. More important, however, is that the adult population is critical to continued existence of the species, and unchecked harvesting of adults is of conservation concern, for both the species and the biota and ecosystem processes so reliant upon it. By and large, saplings will not be reproductive, hence the population is dependent upon proportionally few long-lived individuals for the majority of the reproductive effort. The seedling bank does suggest, however, that once escape is achieved, there will be incremental recruitment into larger size classes.

What conditions might favour escape? The slow aboveground growth rate of seedlings suggests that they are still investing in belowground root infrastructure before allocating resources to above ground growth. On these study sites, ground-water is quite deep – at between 50-60m and so it is likely that only some of the larger saplings will have roots that reach the water table. In addition to having grown sufficiently large to reach the water table, grazing no doubt would favour this species growth, although competition from grass may be more for light than water, and larger individuals may be taller. Exclusion of browsers and fire would also promote the growth of these saplings. Importantly, heavy grazing, exclusion of browsers and fire also favours growth of bush encroaching woody species. Evidence suggests, however, that the seed banks of *Acacia mellifera,* one of the primary bush encroaching species in the area, requires at least two successive years of good rainfall, the first to produce viable seeds and the second to enable recruitment of seedlings. *A. erioloba* may not have this rainfall requirement, however, as the seeds are longer-lived, and established seedlings, although favoured by rainfall, are able to grow even in average rainfall years.

Although slow growing, if large trees are not harvested, and the system is managed with moderate levels of browsing and grazing, *A. erioloba* seedlings are likely to eventually escape to higher size classes. Harvesting of large trees, however, removes the large reproductive individuals from the system, adding to the time required before large trees are again part of the landscape, as there is a lag as medium and small sized individuals grow to reproductive size.

Of interest for future work would be how anthropogenic increases in atmospheric CO_2 will affect growth rates of *A. erioloba* seedlings, since increased CO_2 is expected to favour woody plants (Bond and Midgley 2000, Bond et al. 2002), and increase their water use efficiency (Polley 1997). Climate change itself as a consequence of global warming is expected to see more extreme events (both droughts and floods) as well as fires, so modeling exercises may be able to shed light on anticipated change. Fire, although relatively rare, at once every 15 to 20 years, can have significant effects on recruitment and also causes high mortality rates amongst large individuals (Skarpe 1980, Van der Walt and Le Riche 1984, Ben-Shahar 1996, and see Chapter 9). Furthermore, recent work carried out in Amazonia (Laurance et al. 2004) found that representation of faster-growing tree genera had increased within long-term monitored plots, likely as a result of elevated CO_2. It would be interesting to know if such changes would be likely within genera, and if so, how elevated CO_2 might see the dynamic change between *A. erioloba* and bush thickening species like *A. mellifera.*

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9

Fire and the demography of *Acacia erioloba* in the southern Kalahari - evidence for a bonfire effect?

ABSTRACT

The role of fire in semi-arid savannas is not deemed as important as in mesic savannas because fires are more rare in arid environments. I investigated mortality and resprouting response as a function of height of *Acacia erioloba* after two fires, one at Vaalbos National Park, six months prior to the study, and one at Susanna Farm, 18 months previously. I also investigated differences between burnt and unburnt assemblages in subcanopy and open microhabitats. The largest size class of *A. erioloba* suffered greatest mortality rates, with damage for this size class either very severe or minor. A classification and regression tree (CART) showed resprouting response 18 months after a fire to be greatest in trees <6.5m in height. Within this size group, estimated extent of foliage damage by fire and bark thickness were the next best predictors of resprouting vigour. The observed high mortality rates within the largest size class indicate that with fire both tree abundance and relative representation of large trees declines. Since large trees are important to biodiversity in the southern Kalahari, too frequent fires can have considerable impacts on biodiversity. High mortality rates in the largest size class are hypothesized to be attributable at least in part to burning of flammable subcanopy plants (e.g. *Grewia flava* and *Tarchonanthus camphoratus*), which effectively produce a bonfire beneath large trees with well-developed subcanopy assemblages. Fire blurred distinctions between plant assemblages in different microhabitats, probably because certain plants are better adapted to fire and post-fire environmental conditions. Overall mortality rates of adult *A. erioloba* were high at Susanna (29%) and comparable with those found in other studies. Mortality rates at Vaalbos were much lower (9%), but may subsequently have increased with further mortalities in the following dry season. High mortality rates suggest that although able to resprout, *A. erioloba* is fire-sensitive and, in combination with being slow growing, may explain its restriction on Kalahari sands to areas where rainfall is less than 900mm.year^{-1}.

and control fires. It may be that few plants in the Kalahari are fire dependent, as this disturbance appears to occur quite rarely. This must be seen in the context of a long-lived, slow-growing tree like *A. erioloba,* which could experience 20 or more fires in its lifetime.

Bark thickness has been proposed as a predictor of protection from fire, and all else being equal, taller, thicker-stemmed trees with thicker bark should have a greater chance of surviving fire (Gignoux et al. 1997). Bark can protect the cambium beneath it from damage, and thicker bark has better insulating properties (Uhl and Kauffman 1990). External bark characteristics have been found to influence heat absorption: rough bark with numerous fissures of variable depth (i.e. with a relatively large surface area) had lower external bark temperatures than those with smoother textured and lower surface areas (Uhl and Kauffman 1990), so survivorship is higher in the former (Pinard and Huffman 1997). The bark of *A. erioloba* is highly fissured, suggesting that it could contribute to an effective lowering of internal temperatures during fire. The importance of bark thickness in limiting fire damage may only hold for low intensity fires, however. For example, Wright and Bailey (1982) found that bark can provide protection, but exposure to temperatures of 60°C or more for 60s or longer can cause death in vascular plant tissues. Bark thickness has been found to increase with tree size (Pinard and Huffman 1997, Eriksson et al. 2003), so low intensity fires may be less damaging to larger trees.

A number of studies, and previous chapters in this thesis, have pointed to the importance of habitat structure to biodiversity. Although it is difficult to ascertain how habitat structure will change merely using post-fire information on resprouting and mortality gathered from uncontrolled 'natural experiments', it is possible to extrapolate and generalize to some degree as to how habitat structure might be influenced by fire.

In this chapter I investigate the following:

1) How does mortality and resprouting response differ among A. erioloba height size classes?
2) What is the relationship between re-sprouting patterns and individual size, bark thickness and injury sustained?
3) How do plant assemblages differ between burnt and unburnt plots?

METHODS

Data were gathered after fires on two sites in March/April 2003. Both sites had burnt in the summer, near the beginning of the wet growing season. The first site, Vaalbos, had burnt 6 months prior to data collection, in October 2002. The second site, Susanna, had burnt in November 2001.

I do not have details of the circumstances of the fire on Susanna. The fire on Vaalbos was a headfire, having started on the neighbouring property on a hot (36 °C) and windy (70 $km.hr^{-1}$) day (Deon Joubert, *pers. comm.*). Owing to low herbivore densities on Vaalbos National Park, fuel loads were very high (C. Seymour, *unpubl. data*).

In most cases, the skeleton of this hardwood tree remains after fire, allowing height before burning to be estimated. At Vaalbos, five sites were chosen and a tree was randomly selected as a starting point. At least 30 trees were surveyed within the immediate vicinity of each randomly chosen tree. At Susanna, three sites were chosen and about 20 trees were sampled at each of the three sites. No data were collected for trees below 1m in height. At both sites, I measured tree height with a telescopic pole, but in cases where the trees had been felled by the fire, a tape measure was used to obtain a best estimate of height before burning.

I rated damage to bark using the following categories: (1) Slight to no damage; (2) blackened, but not cracked; (3) Cracked, but wood beneath unburnt; (4) bark burnt and wood beneath also burnt; (5) tree burnt to the ground (this category includes those that had been felled by the fire). If less than 5% was black or cracked, damage was rated in the category below, e.g. "2" for only a small amount of cracking, rather than being rated as a "3".

I assumed that all trees had full foliage before the fire, as there had been no invertebrate herbivore (e.g. the caterpillar, *Gonometa postica*) outbreaks before the fire. Damage to foliage was similarly rated into categories, as follows: (1) two-thirds or more of foliage still present; (2) between one and two thirds present; (3) less than one third present; (4) no green foliage left; (5) burnt to the ground (including those that had been felled).

Resprouting effort was also categorized, using: (1) no attempt to resprout; (2) resprouted, but resprout subsequently died; (3) average resprout length less than

20cm in length; (4) average resprout length between 20 and 60cm in length; (5) average resprout length greater than 60cm.

Position of resprout was also recorded. A ground resprout was one growing out of the ground, but within 1m of the tree trunk, but more than 10 cm away from it. Sprouts within 10cm of the tree base were counted as "base sprouts". Other resprouting categories were from the trunk or branches. I explored factors influencing sprouting response using a Classification and Regression Tree (CART) (see Chapter 4 for more details), in STATISTICA (ver. 6) (StatSoft 2001).

Resprouting by subcanopy plants, particularly where the nurse *A. erioloba* has burnt to the ground and died, may indicate possible succession, where plants that established beneath *A. erioloba* resprout after a fire that has killed the over-canopy tree. I evaluated plant assemblages to the south of trees within the burnt area using $1m^2$ quadrats at 0-1m from the tree bole, 2-3m, 4-5m and then either edge and edge + 2 or edge +1 with edge +3. I also recorded plant assemblages within quadrats in the matrix. I classed these as subcanopy assemblages of large or small trees, canopy edges and the matrix. I subjected percentage cover data to a square-root transformation to reduce the influence of large species and increase the relative contribution of rare species (Clarke and Green 1988). These data were then used to construct a similarity matrix using the Bray-Curtis (Bray and Curtis 1957) coefficient. A cluster analysis, using the group-average sorting method was performed, and a dendrogram constructed. Similarities were also displayed in an ordination plot using multidimensional scaling (MDS), and a stress function calculated. I standardized the dataset and then used a similarity percentages analysis (SIMPER) to ascertain which species were most responsible for the observed division. These multivariate analyses were carried out using the computer package PRIMER (Plymouth Routines In Multivariate Ecological Research) (Clarke and Gorley 2001).

Since the two fires were separate events, all analyses for the two sites were carried out separately. Multivariate analyses of plant assemblages were only performed for the Vaalbos data, and the CART analysis was only performed using data from Susanna.

RESULTS

Resprouting response and mortality as a function of size class

Owing to time constraints and extent of area burnt, more trees were surveyed at Vaalbos than at Susanna (

Table 9.1). Almost all trees that survived the fire resprouted to some extent. Survival at Vaalbos was higher than at Susanna.

Table 9.1. Summary data for Vaalbos and Susanna.

Site	n	Dead	Resprout	Survival %
Vaalbos	166	23	139	86%
Susanna	60	16	42	73%

A number of trends were evident from resprouting and mortality data according to size class (Figures 9.1 and 9.2). Firstly, the percentage of individuals sprouting at ground level or from the base of the tree was far higher for smaller than larger individuals; secondly, the percentage of individuals sprouting from the trunk or canopy increased with increasing tree size; lastly, mortality rates were far higher in the largest size classes than in other size classes.

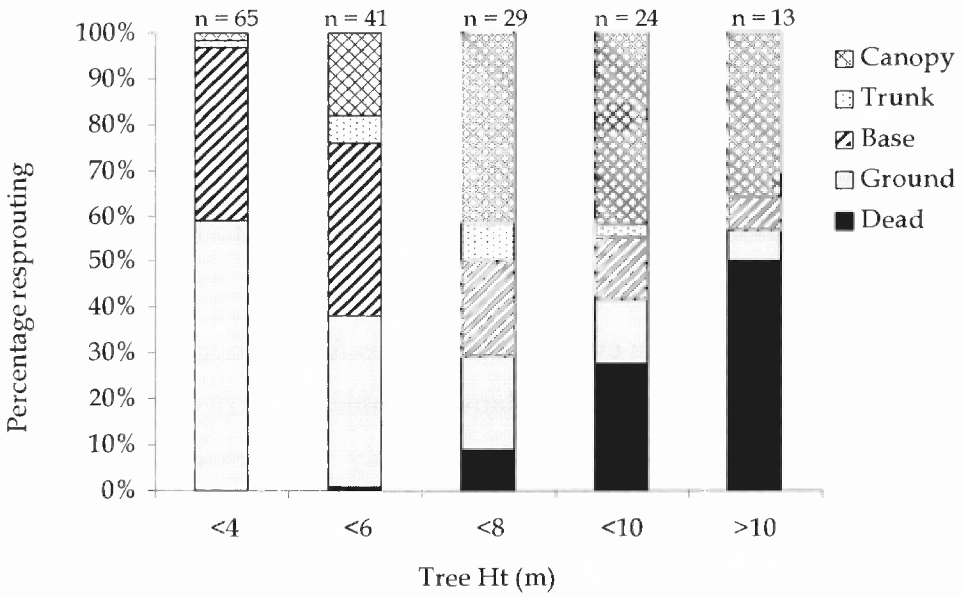

Figure 9.1. Mortality or sprouting according to size class for *A. erioloba* at Vaalbos, six months after fire. Total number of trees sampled = 166.

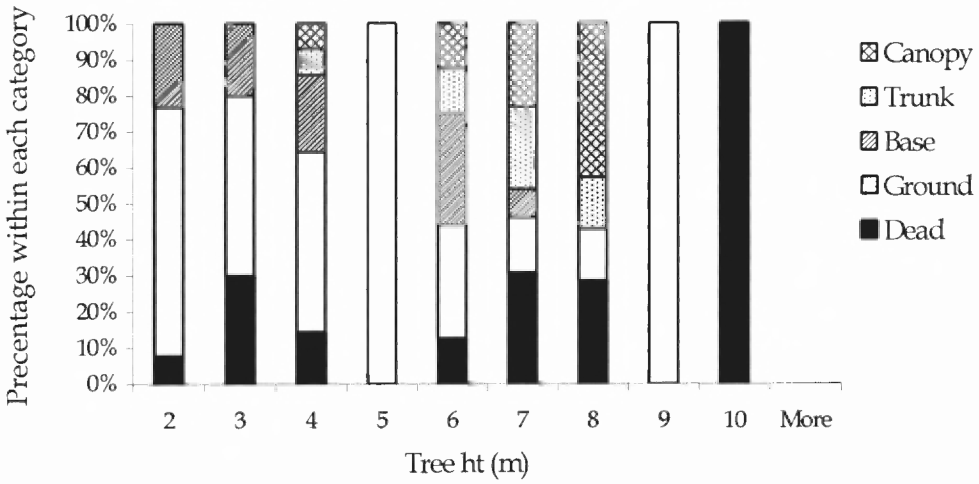

Figure 9.2 Mortality or sprouting response across *A. erioloba* size classes at Susanna, 18 months after a fire. Total number of trees sampled = 60.

In other words, resultant proportional representation of tree size classes after fire sees total number of trees decline (average survival over both sites was 81.7%), and amongst surviving trees, proportion representation of large trees declines for both sites (Figure 9.3).

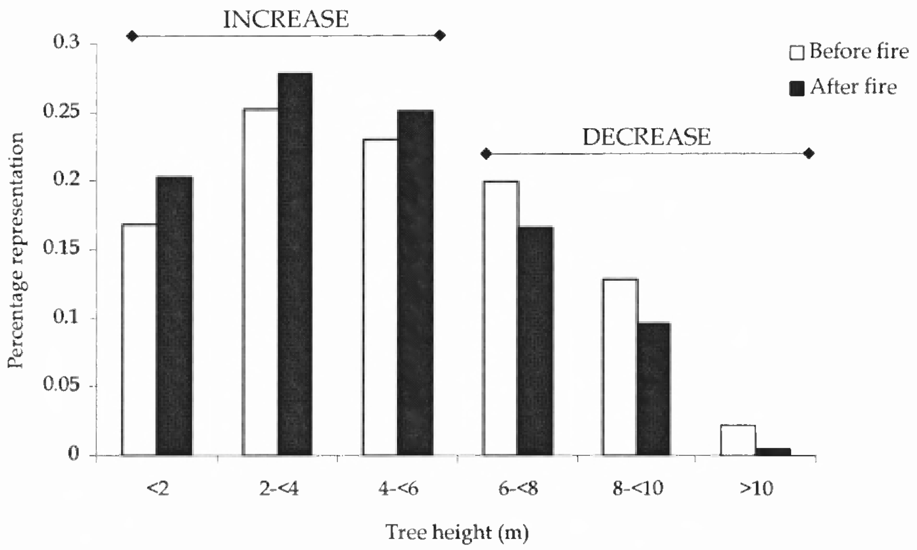

Figure 9.3. Percentage representation within each size class before and after fire, using average data from both Susanna and Vaalbos fires.

Bark and foliage damage as a function of size class

Damage to foliage showed clear trends according to tree size class. Over 90% of smaller trees (<4m) exhibited major damage, i.e. no foliage remaining (Figure 9.4 and Figure 9.5). At the opposite end of the size class spectrum, the largest tree size class (8m - <10m) showed one of two extremes: either very little damage to foliage (12.5%

of trees within the size category at Vaalbos, although zero at Susanna), or very extreme damage (75% at Vaalbos, 83% at Susanna). The medium size class (4-<6m height) exhibited the lowest level of foliage damage at both sites.

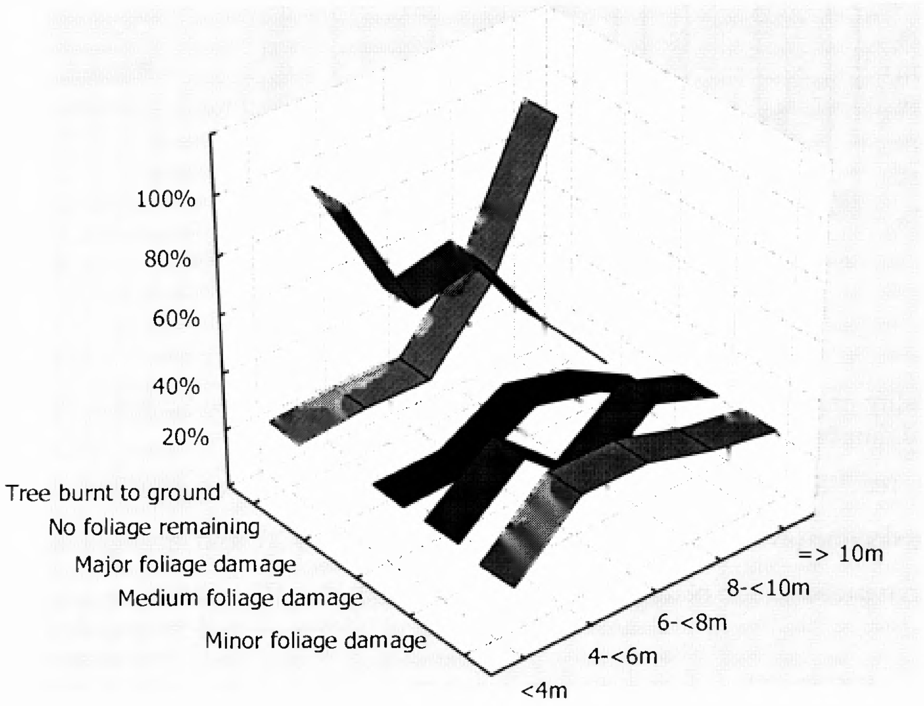

Figure 9.4. Severity of foliage damage and response as a function of size class at Vaalbos.

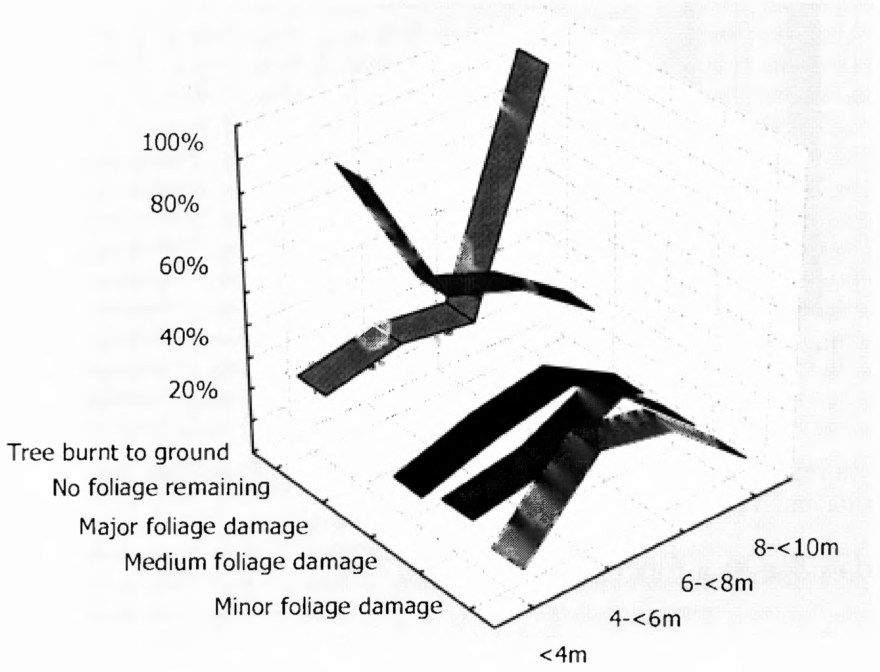

Figure 9.5. Severity of foliage damage response as a function of size class at Susanna.

Damage to bark also showed clear trends according to size class (Figure 9.6 and Figure 9.7). Severity of bark damage increased with increasing size class. Bark damage was positively correlated with tree height (R = 0.698, n = 55, $p < 0.001$), so that the bigger the tree, the more acute the damage. Although the bark of small trees was almost entirely blackened on the majority of individuals, the damage was seldom severe, with bark only very rarely cracked.

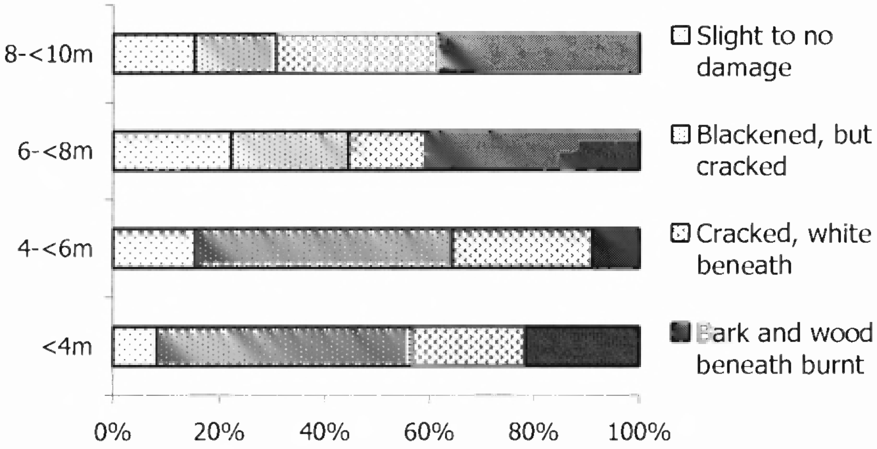

Figure 9.6. Bark damage within size classes at Vaalbos.

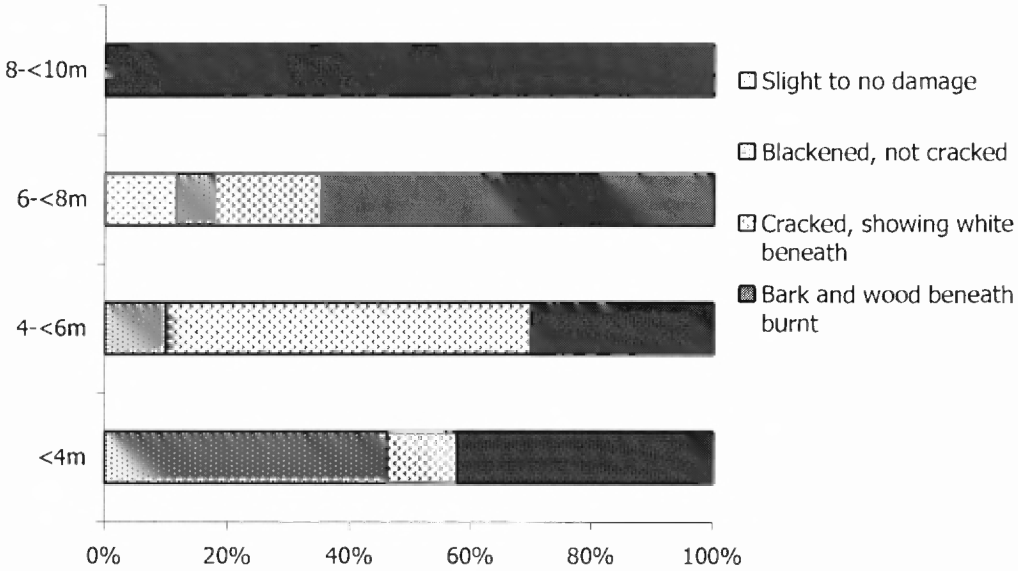

Figure 9.7. Bark damage within size classes at Susanna

Resprouting response as a function of size

Plant height was the first main factor influencing resprouting response: trees shorter than 6.48m showed a far more vigorous sprouting response (Figure 9.8). For the remaining trees, all greater in height than 6.47m, severity of fire damage to foliage dictated resprouting response. A finer partitioning of the remaining plants found bark damage to be the next most important factor explaining resprouting vigour: slight to no damage did not elicit a resprouting response, but trees with cracked bark also exhibited a poor resprouting response.

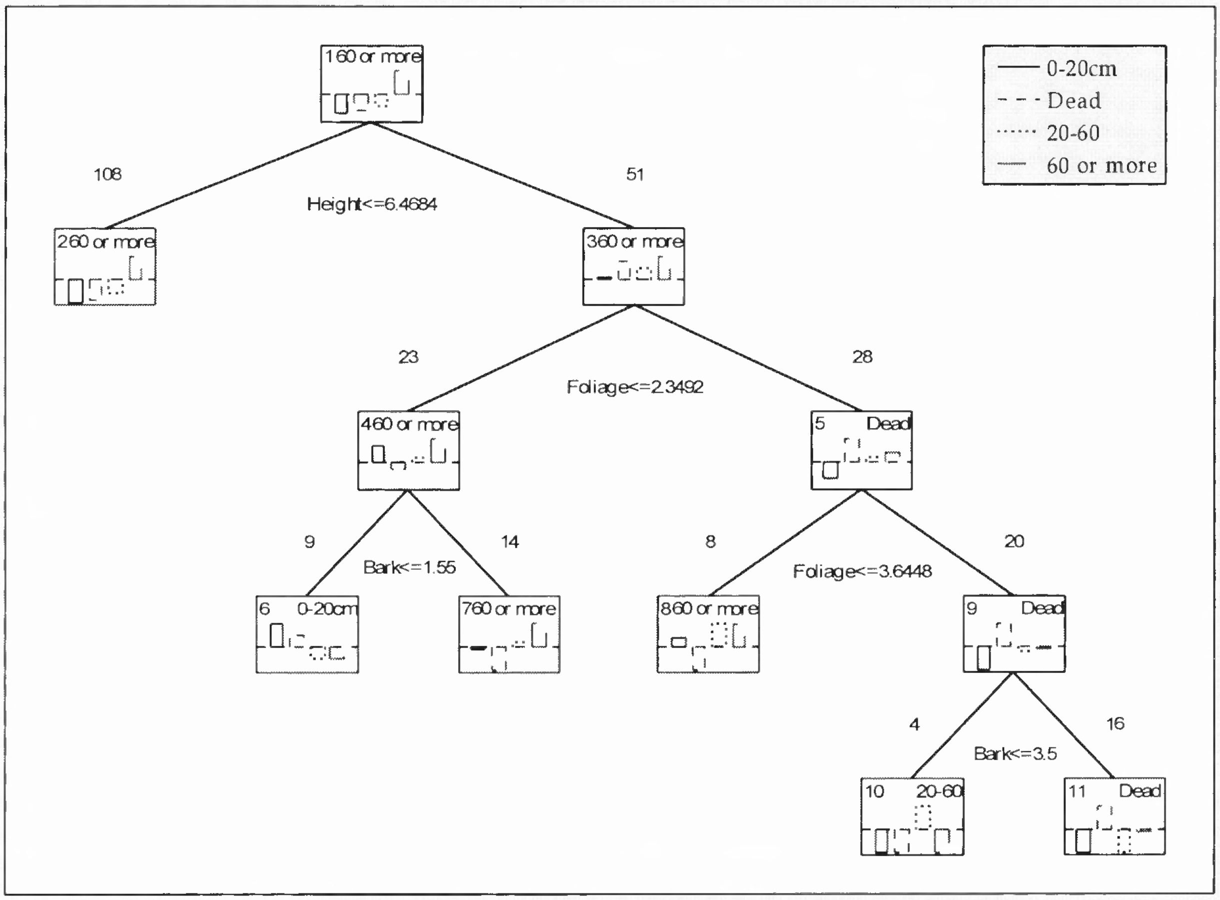

Figure 9.8. Classification tree of resprouting response as a function of damage to bark, foliage and tree size at Vaalbos.

Plant assemblage response to burning

Subcanopy and open microhabitat plant assemblages were much less distinct from each other in burnt than in unburnt sites (Figure 9.9), suggesting that fire leads to some degree of breakdown in usual plant assemblage groupings.

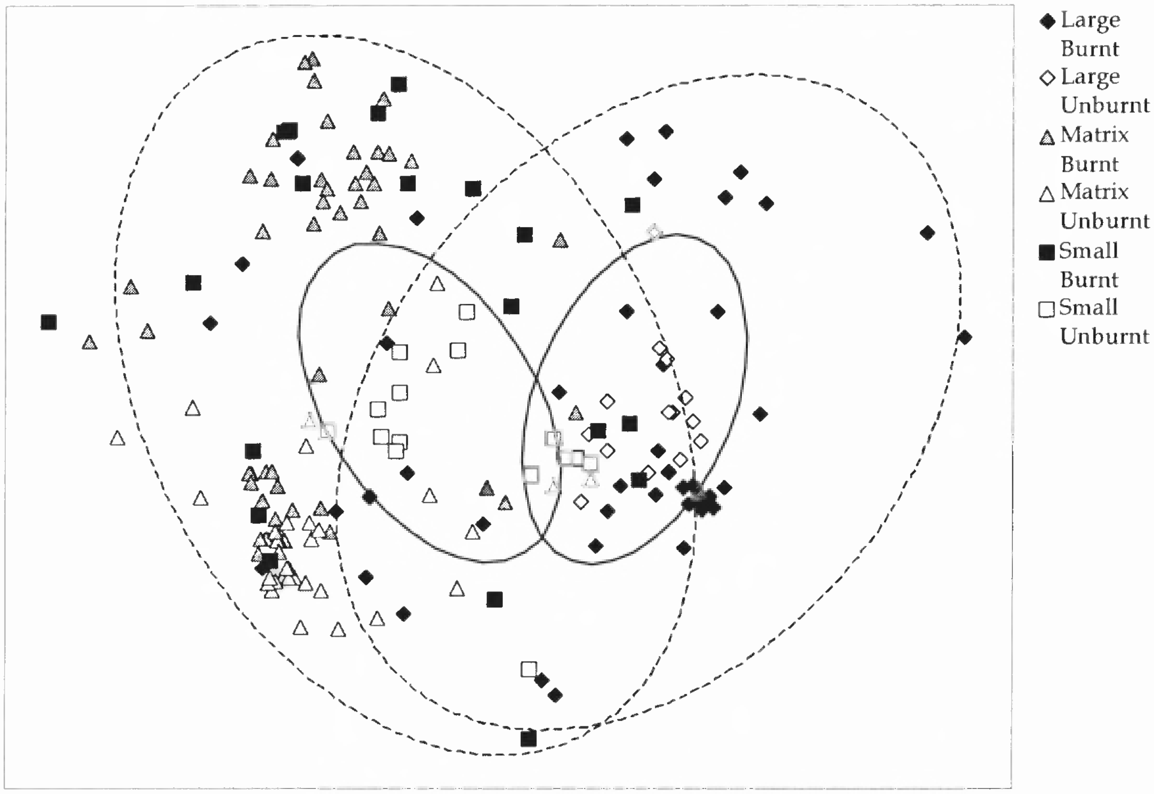

Figure 9.9. Ordination showing burnt and unburnt subcanopy plant assemblages for large trees, small trees and the matrix. Solid lines demarcate the unburnt state, whereas broken lines indicate burnt plant assemblages. Minimum Stress = 0.15.

A SIMPER analysis showed that although many subcanopy perennial shrubs (e.g. *Grewia flava, Ziziphus mucronata, Rhus lancea* and a number of *Lycium* and *Asparagus* spp.) resprouted, their relative importance within the quadrats declined after burning. The relative importance of herbs and grasses (e.g. *Schmidtia pappophoroides, Pollichia campestris,* and *Salsola* spp.) increased in burnt subcanopy plant assemblages. The plant species explaining most of the differences between burnt and unburnt large subcanopy assemblages are listed in Table 9.2.

This process implies a fire-induced simplification of plant assemblages, with lower species richness and domination by species tolerant of fire or adapted to post-fire conditions.

Table 9.2. Species contributing to dissimilarities between burnt and unburnt plant assemblages. Species whose relative abundance increased with burning are underlined.

Comparison	Plant species	Contribution to dis/ similarity	Cumulative dis/ similarity	Increase or decrease in average abundance wit burning?
Subcanopy large burnt vs. unburnt	*Grewia flava*	29.13%	29.13%	Decrease
	Lycium hirsutum	12.16%	41.29%	Decrease
	Schmidtia pappophoroides	7.62%	48.91%	Increase
	Ziziphus mucronata	6.65%	55.56%	Decrease
	Pollichia campestris	6.04%	60.60%	Increase
Subcanopy small burnt vs. unburnt	*Senna italica*	15.66%	15.66%	Increase
	G. flava	15.27%	30.93%	Decrease
	S. pappophoroides	10.58%	41.51%	Slight decrease
				Decrease
	Eragrostis lehmanniana	6.34%	47.85%	Increase
	Salsola spp.	6.32%	54.17%	Increase
	P. campestris	4.84%	59%	
Matrix burnt vs. unburnt	*S. pappophoroides*	29.66%	29.66%	Decrease
	Senna italica	21%	50.66%	Increase
	G. flava	7.29%	57.95%	Decrease
	Elephantorrhiza elephantina	6.82%	64.77%	Increase
	Lineum fenestratum	5.55%	70.32%	Increase

DISCUSSION

Mortality and resprouting among size classes

At first glance, mortality as a function of tree size seems counter to accepted wisdom: as a general rule, large trees escape fire and smaller trees are most adversely affected (Trollope 1984, Dublin et al. 1990, Gignoux et al. 1997). Many leguminous savanna trees in southern Africa exhibit high mortalities in both large and small size classes, however, referred to by Bond and van Wilgen (1996) as type III fire survivorship. In the case of *A. erioloba*, the effect is almost certainly compounded by subcanopy plant assemblages, which tend to have increased biomass (Chapter 3) with increased tree size, if herbivore densities are low. If understory plants are set alight, they may keep the fire burning under the canopy or next to the tree bole, thus increasing the chances and degree of damage suffered by large trees. I would call this a 'bonfire effect'. Van der Walt and Le Riche (1984) also suggested that subcanopy plants, and the nesting activities of certain fauna contribute large amounts of dry fuel to fires. Nesting activities sometimes also damage the tree bark, or branches actually break off on occasion, when the nest becomes too heavy, so that the damaged area also makes the tree prone to fire damage.

Mortality rates at Vaalbos (9%) and Susanna (29%) fall between the two extremes of virtually no mortalities (Barnes 1999) and those found by Skarpe (1980) and van der Walt and Le Riche (1984) of about 30%. That the Susanna mortality rates were comparable to those reported in these previous studies may be a function of time: plants that appeared to be alive after 6 months at Vaalbos might not have survived the next dry season. Intensity of fire no doubt is also important, and Barnes (1999) implies that the fires in her study were of low intensity. Season, and weather conditions at the time of the fire (wind speed, time since rain) would also lead to differences in fire intensity, with concomitant effects for vegetation. Resprouting ability may vary with location, as certain species display varying resprouting vigour across their ranges (Bond and van Wilgen 1996).

Of importance to biodiversity overall and *A. erioloba* 's role as a keystone species, in particular, is that fires tend to substantially reduce the number of large trees, with concomitant effects for plant and bird assemblages. In addition, population size structure before the fire will determine how well the population overall will respond to a fire, and previous management actions (e.g. harvesting large trees for firewood), will compound the effect of fires on demography. Recolonisation by *A. erioloba* is likely to only be possible if there is sufficient rainfall to enable establishment (Barnes 2001b) and if they have an opportunity to escape to higher size classes (Chapter 8, this thesis).

Resprouting response as a function of size

Smaller (by implication, younger) plants exhibited a greater resprouting response. Over a certain age, some plant species lose the capacity to resprout (e.g., Kayll and Gimingham 1965, Hobbs and Mooney 1985), which may be attributable to regeneration buds in juvenile tissue becoming overgrown by secondary stem growth (Hobbs and Mooney 1985). Furthermore, resprouting response is also influenced by degree of injury (Cirne and Scarano 2001), this is likely because allocation of storage reserves in combination with resources gathered by the surviving plant constituents contribute to the growth of new leaves, stems and roots (Hodgkinson 1998). If there is little or no photosynthetic tissue to enable generation of more resources, resprouting attempts will be limited by availability of reserves stored before the fire (Hodgkinson 1998). Larger individuals likely resprouted from higher up in the canopy because higher plant parts are more likely to have escaped injury from the fire, and thus have the ability to resprout.

Changes to plant assemblages after fire

Fire blurs the distinction between plant assemblages of different microhabitats to a degree, probably because after fire, nutrient availability changes (Bond and van Wilgen 1996). Therefore soil characteristics, greater light availability, and life history traits of the plants themselves act to enable certain plants to dominate assemblages, regardless of microhabitat. Furthermore, "subcanopy" assemblages may no longer be so, as the umbrella tree may have been felled, so seeds of plants ordinarily unable to establish in the subcanopy environment now may be able to do so.

Within many areas of the southern Kalahari, patches of "subcanopy" plants can be observed in the matrix. Often, a tree skeleton still present. It is likely that one of the mechanisms by which these patches arise is through fire: subcanopy plants resprout after the nurse plant, which was perhaps important for establishment, but is no longer crucial to survival, has been felled. One of these subcanopy plants, *Z. mucronata,* has been shown to survive and produce viable seeds, with no significant difference in flower and fruit production between subcanopy and matrix plants (Chapter 4), and other species, e.g. *Grewia flava* seem to do as well in producing fruit in the open environment as in the subcanopy environment (Schurr 2001).

Judging by the resprouting responses of many "subcanopy" plants, it appears as if some (e.g. *Grewia flava, Tarchonanthus camphoratus*), if not most, are "Type I" plants: those with a low probability of surviving fire while young, but with increasing age, mortality rates become minor and dwindling (Bond and van Wilgen 1996). In a study on the dynamics between the nurse plant *Acacia nilotica* and the evergreen subcanopy shrub *Euclea divinorum,* Smith and Goodman (1987) found *E. divinorum* seedlings exclusively beneath *A. nilotica* canopies, just as seedling *G. flava* (Schurr 2001) and *Z. mucronata* (Chapter 4) are found in the southern Kalahari. *E. divinorum* displayed a "Type I" survivorship pattern, excluding fire when large, to the extent where *E. divinorum* succeeded *A. nilotica* as the dominant species. Within the southern Kalahari, a similar mechanism may operate, although I have not observed areas where succession has been complete.

A number of predictions now arise. Firstly, high mortality rates for large *A. erioloba* suggest that above a certain threshold of fire frequency, populations are unable to persist. These mortality rates are no doubt influenced by fuel load, amount of plant biomass benath the tree canopy and the existence of nesting and other materials within the tree canopy. The severity of consequences of a fire for a population depends on the season and severity of the fire itself, in turn dependent on fuel load, weather conditions at the time of the fire, growth season, etc.

Secondly, the storage effect (Warner and Chesson 1985), in which there is selection for longevity to compensate for rare recruitment events, should be counterbalanced by high mortality rates of larger (arguably, older) individuals, so there may be differences in longevity between populations as one moves across the aridity gradient. In other words, in areas with higher rainfall, recruitment is likely to be more frequent, and fires are also more frequent. There has likely been more pressure on populations in arid areas to evolve longevity than on populations in more mesic areas, where mortality to fire and recruitment are both more common.

Thirdly, tree architecture is likely to change with fire frequency, so there may be a difference in tree shapes with age across the aridity gradient. Archibald and Bond (2003) found fire to exert considerable selective pressure on tree architecture in South African savannas. I would therefore predict that lower hanging branches on large individuals would only be seen in the more arid extent of *A. erioloba's* range.

Lastly, fire frequency in different parts of the geographic distribution of *A. erioloba* may have selected for genetic variation between populations. This would certainly concur with the finding that height growth in this species was strongly negatively correlated with latitude of the origin of seeds (Barnes et al. 1997). Lower latitude sites in which *A. erioloba* occurs tend to be wetter, and by implication, have more frequent fires, so there would have been evolutionary pressure for seedlings to grow taller faster in areas with higher fire frequency.

CONCLUSIONS

In northern Botswana, Ben-Shahar (1996) failed to find *A. erioloba* in plots with high fire frequency, suggesting that fire can exclude *A. erioloba.* As a general rule, fire frequency in southern African savannas tends to increase with increasing rainfall (Higgins et al. 2000). High mortality rates amongst larger trees suggest that high fire frequencies would eventually exclude this species, and this may explain the absence of *A. erioloba* on Kalahari sands where rainfall exceeds 900mm.year^{-1}. Even within lower rainfall areas, the size-dependent mortality patterns observed here implicate fire interval as a key determinant of population change. Fire acts to both reduce the abundance of trees and reduce the proportional representation amongst the survivors towards smaller individuals. That many subcanopy plants survive fire and resprout suggests that the woody component itself may not necessarily decline, although too frequent fires will change habitat structure towards less vertical complexity, with important consequences for plants and birds.

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10

Synthesis

GENERAL DISCUSSION AND CONCLUSIONS

This study was prompted by personal observations whilst travelling in the southern Kalahari and seeing rampant habitat change induced through heavy grazing leading to bush thickening, and unchecked removal of large *Acacia erioloba* for firewood. In the course of investigating the importance of large trees more specifically and habitat structure in general, a number of contributions to our knowledge of the Kalahari as a system, have been achieved.

1) Kalahari savannas are characterised by large trees, usually *A. erioloba,* interspersed within a grassy matrix. As an *A. erioloba* individual grows, there is a succession of plants present beneath it, from matrix plants to those progressively tolerant of shade, to those totally adapted to the subcanopy environment (e.g. *Eragrostis biflora*) (Chapter 3). Thus trees of different sizes allow a spectrum of plants to exist within a semi-arid to arid environment, from assemblages of predominantly wind-dispersed matrix plants to vertebrate-dispersed, shade-tolerant species (Leistner 1996, Chapter 3 of this thesis, Dean et al. 1999). Subcanopy plant assemblages of large trees are richer in species per m^2 than plant assemblages beneath small trees or in the matrix. The microhabitat beneath large trees also enables a relatively constant assemblage of plant species to exist across a greater aridity gradient than they might otherwise be able to tolerate (Chapter 3). This in turn might be expected to support further diversity at higher trophic levels within e.g. arthropods/insects. That increased plant diversity equates to increased invertebrate diversity is yet to be conclusively shown, but the assumption is that greater structural and species diversity amongst plants will provide greater invertebrate habitat availability. Either way, it appears that through its role as a nurse plant, *Acacia erioloba* is important to subcanopy plants,

able to provide a suitable environment for germination and establishment of fruited species, although the advantages of the subcanopy environment might not hold for all phases of subcanopy plant species' lives.

2) Within this pattern, the level of herbivore disturbance adds another level of complexity, with decreasing representation of more disturbance-sensitive subcanopy species as herbivore densities increase (Belsky et al. 1993, Chapter 4). At more extreme levels of grazing disturbance, good rains can lead to an increase in the shrubby layer (usually e.g. *A. mellifera, Rhigozum trichotomum* or *Grewia flava)* (Ward 2002, Joubert et al. 2003), so that the grassy layer is suppressed, producing significant changes in habitat structure, with concomitant consequences for birds (see point 5) and likely for other taxa (e.g. invertebrates (Steenkamp and Chown 1996) and reptiles (Meik et al. 2002)) and processes (e.g. water and nutrient cycling, dispersal of subcanopy plants (Chapter 4)).

3) Although fire is not typically considered an important process in the southern Kalahari, I hypothesize here that during fires, subcanopy plant assemblages can be perilous to their overstory nurse plants such as large *A. erioloba* (Chapter 9). Although not necessarily highly flammable, these plants do burn (Wendy Lloyd, *personal communication*) and I suggest that they enable fires to spread into the canopies of large trees and can often result in the death of the nurse plant. These subcanopy plants then resprout, so that a form of succession can be seen in areas where subcanopy plants have grown large. Furthermore, fire also changes habitat structure, by decreasing both the density of trees and the proportion of large trees represented within the tree component (Chapter 9).

4) Disturbances (bush thickening, fire and clearing of large trees) have in turn dramatic effects on habitat structure, leading to concomitant changes in bird assemblages. Large trees unquestionably contribute to vertical habitat structure, with which avian diversity was found to increase both in this system (Pianka and Huey 1971, Chapter 5) and as a more generally established rule (e.g., MacArthur and MacArthur 1961, Cody 1981). Sites from which trees had been cleared had significantly lower bird abundance and bird species richness (Chapter 5).

5) The importance of large trees was further illustrated at Kuruman sites (where trees were generally 25-50% taller than those at Kimberley sites). These large

trees ameliorated the influence of bush thickening on bird species assemblages and diversity (Chapter 5). This probably occurs because large trees provide perches above the shrubby milieu, from which species that would ordinarily be excluded by this habitat type can use large trees from which to sally and hawk above the uniform canopy structure created by bush thickening. That is not to say that bush thickening was completely detrimental to birds: bird species richness actually increased with density of woody species at Kimberley sites, demonstrating the importance of horizontal habitat complexity (Chapter 5).

6) Habitat structure (physiognomy) alone was not the only important determinant of the structure of bird species assemblages. Investigation of bird use of habitat at a finer scale found that all birds show clear negative or positive associations with certain tree species, no matter how strongly phylogenetically related are the tree species under investigation (Chapter 7).

7) Analysis of life history traits with different habitat structure pointed to considerable differences in representation of different life history traits within bird assemblages, highlighting the importance of investigating functional differences in plant and animal assemblages, in addition to differences in diversity (Chapter 6). Of great concern was that of the common bird species analysed, 40% had one or more life history traits positively associated with large trees, implying that indiscriminate removal of large trees will be significant for bird diversity within the biome (Chapter 6). In addition, loss of these species is likely to produce knock-on effects for other aspects of ecosystem functioning. For example, the principal avian frugivores are also hole-nesters: and the removal of large trees will see a significant decline in frugivores, with associated implications for dispersal of fruited plants.

8) *Acacia erioloba* is a slow-growing tree (Chapter 8), and the ecosystem is unlikely to recover to its former state within a short time period (certainly not within a human's lifetime). These systems do regain their structure and, likely functioning, however, when one considers that in the late 1800s/early 1900s, much of the area around Kimberley was cleared of large *A. erioloba* for the mining industry (Shillington 1985), but now appear quite healthy, although we have no way of knowing what may have been lost during that exercise. For three

decades, the importance of seed limitation to *Acacias* via e.g. bruchid beetle predation, has been a subject of investigation (e.g., Lamprey et al. 1974, Jarman 1976, Pellew and Southgate 1984, Coe and Coe 1987, Hoffman et al. 1989, Miller 1993, 1994, Miller 1996, Rohner and Ward 1999, Walters and Milton 2003). But despite studies finding high levels (between 47 and 96%) of bruchid predation of *A. erioloba* seeds (Ernst et al. 1990, Barnes 2001a) and low to zero probability of germination of parasitised seeds (Hoffman et al. 1989, Barnes 2001a), it appears that within the Kimberley area, it is not seed limitation that presents the greatest challenge to this species, but rather escape to larger size classes to heights above the grassy layer (Chapter 8). One study site in particular (Benfontein) illustrates this quite clearly: there are a number of large trees, and many small individuals at grass height, but very few trees in intermediate size classes (Chapter 8). Provision of supplementary water and protection from herbivory, and a test of responses of different sized *A. erioloba* saplings to removal of grass competition showed that a combination of slow growth rates and competition from grass for light and possibly water, are influential in preventing growth to larger size classes (Chapter 8).

9) That large *A. erioloba* were found to be vulnerable to fire reinforces the imperativeness of conserving those trees that have managed to become large (Chapter 9). To maintain habitat structure, it is also important to protect individuals from a range of size classes, as well as ensuring that *A. erioloba* seedlings periodically escape into higher size classes. Barnes et al. (1997) found that seeds from *A. erioloba* populations in more mesic (and by implication, more fire-prone) habitats, grew faster than seeds from more arid populations. This may be a phenotypic maternal effect (Gutterman 2000, Valencia-Díaz and Montaña 2005), or could reflect a genuine difference in genotypes. Whatever the explanation, this suggests that this species may have at least some adaptations to deal with fire in the parts of its distribution range in which fire is common. I suggest that its relatively slow growth rate and high mortality rates during fire plays an important role in limiting its distribution in areas on the upper end of the rainfall scale on Kalahari sands.

Keystone concepts revisited?

This project was initiated with the aim of investigating the keystone role of *A. erioloba*. The importance of its size and density (i.e., its context dependency) were discussed in Chapters 3 - 6, while Chapter 7 investigated the possibility that it is more than a keystone structure, but also important as a keystone species.

This thesis has confirmed the view that large *A. erioloba* are ecologically important in the southern Kalahari, as has been pointed out by Milton and Dean (1995), Dean et al. (1999) and Tews et al. (2004). When large, this species' presence provides microhabitats and structural diversity, which in turn enables the existence of a suite of plant and bird species (Chapters 3 - 7) and facilitates a number of processes (e.g. seed dispersal and seedling establishment (Chapter 4), nutrient and water cycling (Barnes et al. 1997). Some of these plant and animal taxa, in turn, are likely important for other groups, for example, certain subcanopy plant species are probably necessary, if not vital, to a number of invertebrates. The subcanopy environment, through its nurse-plant role not only provides microhabitat for a number of species, but also has significantly higher plant diversity than the matrix, likely because of higher productivity (Rosenzweig 1995), as a consequence of lower evaporation rates and elevated nutrient status.

In terms of the ecological lexicon, a large *A. erioloba* tree can be considered an "ecosystem engineer" (e.g. Jones et al. 1994), "habitat modifier" (Power 1997) and "keystone structure" (Tews et al. 2004). In terms of identifying species and processes important to conservation strategy, what matters is that it is indeed ecologically crucial.

Mills et al. (1993) point out that to really test for "keystoneness", removal of the species of interest is required. This was carried out naturally, through tree clearing by land-owners (Chapters 5 and 6), which enabled an investigation of the effects of differences in habitat physiognomy to bird assemblages. Selection of microhabitat for comparisons at finer scales (Chapters 3 and 4) also enabled some investigation into the importance of large structures. These investigations identified large *A. erioloba* as important to other species and processes. The only definition that might exclude *A. erioloba* from being a keystone is one of the most established definitions: that of the keystone species (Paine 1969) - using the reworked definition arrived at by Power et al. (1996: p. 609), a keystone species as one "whose impact on its community or ecosystem is large, and disproportionately large *relative to its abundance*" (my emphasis). As pointed out by

Hurlbert (1997) and Kotliar (2000), this creates a false division between abundant and less abundant species that are nevertheless ecologically important. Indeed, as with Kotliar's (2000) prairie dogs (*Cynomys ludovicianus*), *A. erioloba* becomes increasingly important with increasing abundance. For example, having more large trees available makes successful establishment of subcanopy plants more likely, as the disturbance by mammalian herbivores is less probable per tree with increasing large tree abundance (Chapter 4), because mammal activity is spread among a lot more trees. Increasing the number of large trees also sees an increase in bird diversity (Chapter 5), and with each species added, greater possibilities exist for dispersal of fruit, building of hole nests, etc. (Chapter 6).

FUTURE RESEARCH

As with many studies, this thesis has generated a number of questions.

1) Although this study unearthed changes evident in ecosystem functioning through changes in bird life history traits with habitat, these can only be elucidated further by investigation of the importance of large trees and the effects of bush thickening for invertebrates and vertebrates other than birds. These are very important components of ecosystem functioning, and a study of the importance of large *A. erioloba* to these taxa would be informative and would clarify how ecosystem processes change with anthropogenic changes to habitat, and perhaps how best to ameliorate these changes.

2) Subcanopy plant assemblages seem to be aided by the more favourable water and nutrient regimes of the subcanopy microhabitat (Dean et al. 1999, Schurr 2001) (Chapters 3 and 4). But is this merely an artefact of shading produced by the canopy, or is the mechanism more active - perhaps hydraulic lift is also significant? Hydraulic lift occurs when plants redistribute water from deep in the soil to the shallower layers. During the day, photosynthetic demand for water is high, but plants' shallower roots are unable to meet this demand, as shallower soils are often dry. Hydraulic lift appears to be a solution to this problem: at night, plants lift water through their deep roots, passively exuding it into the upper drier soil layers (Horton and Hart 1998). This process has now been described in a few systems (e.g. Mooney et al. 1980, Richards and Caldwell 1987,

Caldwell and Richards 1989, Emerman and Dawson 1996, Ludwig et al. 2002), but we do not know if it occurs in the Kalahari. Moreover, even if it does occur, we do not know if the amount of water redistributed is sufficient to significantly affect plant-water relations. Once water has been lifted and exuded into the soil, there is theoretically nothing to prevent neighbouring plants from making use of this water, so that areas around large, deep rooted *A. erioloba* may have higher productivity than would be predicted. If hydraulic lift does occur and is important to water cycles, there are important implications for assessing the influences of predicted anthropogenic climate change and wholesale removal of large trees, at least regionally. For example, Lee et al. (2005) have modelled transpiration rates over the Amazon and found hydraulic lift (referred to in their paper as "hydraulic redistribution") affects seasonal cycles of temperature through changes in latent heat, so that there is a direct link between plant root functioning and climate. The effect of the Amazon was found to extend to a global scale (Lee et al. 2005). Whether tree cover in the Kalahari and other arid zones would be sufficient to effect changes on a global scale is probably unlikely, but they may be important for more regional weather patterns, particularly in such a drought-prone environment.

3) While it seems that the subcanopy environment is beneficial to some species, the question remains as to whether these species are positive or negative for the nurse tree itself. Observations after fires at my study sites (average rainfall 431 mm.year^{-1}) suggest that the subcanopy species present a potentially lethal hazard beneath the tree. Over more arid areas of the Kalahari, fires may not be sufficiently frequent, or subcanopy material not abundant enough to create the "bonfire" effect alluded to in Chapter 9. (An exception would be the Kgalagadi Transfrontier Park, where, although dry, relatively low herbivore densities allow the build-up of subcanopy plant assemblages (Van der Walt and Le Riche 1984)). The question in these areas may be more one of whether these plants influence fitness of the nurse plant by competing for resources, more particularly water.

4) Perhaps one of the more pressing questions arising from this study, in the context of the threat of anthropogenic climate change revolves around the potential for "mismatches" likely to arise as a result of elevated atmospheric CO_2. For example, elevated CO_2 arising from anthropogenic climate change could see an

increase in woody plant growth (Polley 1997). Bond and Midgley (2000) and Bond et al. (2002) suggest that in the more mesic areas at least, bush thickening would become increasingly likely with increased CO_2. We do not know how land management practices may change against a backdrop of more frequent extreme events (i.e. droughts and floods) (Tyson and Crimp 1998, Intergovernmental Panel on Climate Change 2001), removal of farming subsidies and land reform, but these changes in climate and policy suggest that bush thickening is more, not less, likely in the southern Kalahari in future. Climate change is likely to directly influence biota in certain ways, e.g. small birds are likely to be adversely affected (Simmons et al. 2004). This study found that small-bodied birds are *favoured* by increasing bush thickening however, so the combined effects of climate change acting directly on species and indirectly on habitat may be calamitous to a large number of bird species.

5) Remaining on the subject of anthropogenic climate change, recent work by Laurance et al. (2004) on long-term changes in representation within Amazonian tree assemblages reveals significant increase in representation towards fast-growing genera, and towards large trees over subcanopy species, perhaps as a result of elevated CO_2 related to anthropogenic climate change. Whether such changes might occur in the context of a semi-arid savanna is unknown, but as a rule, bush thickening species tend to be fast-growing, while *A. erioloba* is a slow growing species, thus the findings of Laurance et al. (2004) may have implications for future savanna dynamics and biodiversity in the southern Kalahari.

MANAGEMENT RECOMMENDATIONS

The importance of large trees to plants and birds, and through these, possibly to biodiversity in general in the Kalahari has now been demonstrated without doubt. Although investigations into the influence of environmental factors on *A. erioloba* demography (and by implication, habitat structure) were based on single season data sets, some useful information emerged.

1) The existence of sapling banks at some sites, while not problematic now, may signal management problems in future, if there were to be a significant fire or all the large trees were to senesce simultaneously, as witnessed in Amboseli National

Park, Kenya, with *Acacia xanthophloea* (Young and Lindsay 1988). *Acacia xanthophloea* is a relatively fast-growing, short-lived tree, in comparison with *A. erioloba* however, so the "storage effect" (Chapter 9) may reduce the likelihood of contemporaneous die-off.

2) That *A. erioloba* seedlings were never found beneath large trees (Chapter 8) (in spite of high probabilities of dispersal to these sites, within dung or from fallen pods), and their poor performance when surrounding grass was long, suggests shade intolerance. Thus, should rehabilitation efforts of bush thickened areas be carried out, sufficient thinning of the shrubby component will be vital to reduce shading so as to enable the establishment of this species.

3) Although legislation exists to protect *A. erioloba* within South Africa, the dearth of protection over national boundaries makes it difficult to enforce protection within the region. Indeed, implementation is difficult even within South Africa, as firewood vendors merely claim that the wood originated outside of South Africa. Since the tree is clearly important to conservation of biodiversity, a case must be made for protection of this species in all the countries in which it is found.

4) The observed high mortality rates within the largest size class indicate that with fire, not only does tree abundance decline, but also the relative representation of large trees. Chapters 3-4 and 5-7 have illustrated the ecological implications of large tree loss to bird and plant assemblages.

5) The issue of harvesting and the demand for *A. erioloba* wood cannot be viewed in isolation to the socio-economic context in which it occurs. Degradation of South African savannas is linked to increasing costs of production, loss of subsidies, misconception about grazing strategies, changes in fire regimes, perverse incentives and subdivision of farms into units that are not economically viable (Seymour and Milton 2003). Environmental policy-making routinely ignores economic considerations, yet environmental conservation cannot take place without inclusion of these considerations (Mogaka et al. 2001). The potential of African *Acacias* to improve agricultural productivity is unequivocal (Barnes 2001b), but must be demonstrated with proof of economic return and development of appropriate practice (Barnes 2001b). If we assume that *A. erioloba* must "pay for itself", then non-consumptive use of this slow-growing species

must be explored. At present, farmers and their employees bare the greatest risk for the smallest returns, in harvesting this species. This may indicate that farmers and their employees are unaware of the potential damage that uncontrolled harvesting is visiting upon the well-being of their farms, or that short-term financial concerns govern decisions. Given the importance of *A. erioloba* to biodiversity in the region, these decisions can in turn have cascading and long-term effects.

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