

SEED ECOLOGY AS A DETERMINANT OF POPULATION
STRUCTURE IN SOME SOUTHERN AFRICAN SAVANNA *ACACIA*
SPECIES

By

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Declaration

I, the undersigned, hereby declare that the work contained in this thesis is my own original work and that I have not previously in its entirety or in part submitted it at any university for a degree.

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M. Walters

SUMMARY

African *Acacia* species are often major contributors to the progressive increase in the woody component of savannas, a phenomenon commonly referred to as bush encroachment. In Hluhluwe-Umfolozi Park, the numbers of adult *Acacia nilotica* (L.) Willd. Ex Del. trees per hectare far exceed (by 111) that of *A. karroo* Hayne adults. The relative dominance is reversed in the juvenile stage with *A. karroo* (725 ha⁻¹) outnumbering *A. nilotica* (225 ha⁻¹) threefold outside closed woodlands. African acacias produce large quantities of seed and may have large soil-stored seed banks. They suffer pre-dispersal predation by bruchid beetles and may be either wind or animal dispersed. Once dispersed they are vulnerable to post-dispersal attack.

This study tested several hypotheses regarding various aspects of seed ecology of *A. karroo* and *A. nilotica*. The null hypothesis that seed ecology does not contribute to the success of *A. karroo* over *A. nilotica*, was tested.

Acacia karroo trees were smaller (mean basal diameter: 7.8 cm) than *A. nilotica* trees (mean basal diameter: 18.5 cm) on average, but produced more seeds (*A. karroo* mean: 1628; *A. nilotica* mean: 992) for a given basal diameter size class. It was found that *A. karroo* showed less bruchid infestation (mean: 1.36-3.81%) than *A. nilotica* (mean: 14.67-86.70%) at all stages of pod development with a proportion of *A. karroo* seeds (7.1%) being able to germinate after bruchid attack. Bruchid attack rendered *A. nilotica* seeds unviable. There was no difference between the two species with regards to the soil-stored seed bank and the viability of seeds found in the soil. *Acacia karroo* showed higher germination levels (5.1%) and better establishment (4.9%) than *A. nilotica* (1.5% and 0.4% respectively). On average, there was no difference in germination levels between burnt and unburnt seeds, but there was a significant difference in germination of burnt seeds in both burnt (4.5%) and unburnt (2.5%) sites and unburnt seeds in both burnt (2.8%) and unburnt (4.9%) sites when considered separately.

Post-dispersal predation of *A. karroo* seeds (21.8%) was higher than that of *A. nilotica* (12.7%). There was more rodent predation in tall grass areas (26.0%) than short grass (10.7%) or canopy areas (15.2%), and most seeds were lost from unprotected control groups. Rodent presence was a significant factor in unexplained seed disappearance.

The ability of *A. karroo* to germinate easily and the low levels of beetle predation experienced by this species seemed to be its main advantage over *A. nilotica* as an encroaching species in Hluhluwe-Umfolozi Park.

OPSOMMING

Die *Acacia* spesies van Afrika is dikwels belangrike bydraers tot die progressiewe toename in die houtkomponent van savannas. Hierdie verskynsel word algemeen na verwys as bosindringing. In die Hluhluwe-Umfolozi Park is die aantal volwasse *Acacia nilotica* (L.) Willd. Ex Del. bome per hektaar aansienlik meer (111 meer) as die aantal volwasse *A. karroo* Hayne bome. In die jong stadium is die oorheersing omgekeerd, met driekeer soveel *A. karroo* (725 ha⁻¹) as *A. nilotica* (225 ha⁻¹) bome buite beboste gedeeltes.

Afrika se *Acacia* spesies produseer groot hoeveelhede saad en kan oor aansienlike grond-gebergde saadbanke beskik. Voor verspreiding word die saad aan predasie deur bruchid-kewers blootgestel. Die saad kan óf deur wind óf diere versprei word en na verspreiding word dit ook aan predasie blootgestel.

Hierdie studie het verskillende hipoteses rakende verskeie aspekte van die saadekologie van *A. karroo* en *A. nilotica* getoets. Die nulhipotese dat saadekologie nie tot die groter sukses van *A. karroo* teenoor *A. nilotica* bydrae nie, is getoets.

Acacia karroo bome was oor die algemeen kleiner (gemid. basale omtrek: 7.8 cm) as *A. nilotica* (gemid. basale omtrek: 18.5 cm) bome maar het meer saad (*A. karroo* gemid.: 1628; *A. nilotica* gemid.: 992) per gegewe basale diameter grootte klas gelewer. Daar is geen verskil tussen die twee spesies rakende grondgebergde saadbanke en die lewensvatbaarheid van hierdie saad gevind nie.

Acacia karroo het hoër vlakke van ontkieming (5.1%) en beter vestiging (4.9%) as *A. nilotica* (1.5% en .4% respektiewelik) getoon. Daar was oor die algemeen geen verskil in die ontkiemingsvlakke van gebrande en ongebrande sade nie, maar wel 'n beduidende verskil in die ontkieming van gebrande sade in beide gebrande (4.5%) en ongebrande (2.5%) areas en ongebrande sade in gebrande (2.8%) en ongebrande (4.9%) areas as dit afsonderlik geëvalueer is.

Die predasie van *A. karroo* saad na verspreiding (21.8%) was hoër as dié van *A. nilotica* (12.7%). Daar was meer knaagdier-predasie in gebiede met lang gras (26.0%) as dié met kort gras (10.7%) of boomryke gedeeltes (15.2%). Die meeste saad is in onbeskermdede kontrolegroepe verloor. Die teenwoordigheid van knaagdiere het 'n belangrike rol in die onverklaarde verdwyning van saad gespeel.

Dit is gevind dat *A. karroo* se vermoë om maklik te ontkiem, asook die lae vlakke van insek skade aan die saad, die belangrikste voorsprong is wat dié spesie oor *A. nilotica* as 'n indringer in Hluhluwe-Umfolozi Park het.

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"Over the long haul of life on this planet, it is the ecologists, and not the bookkeepers of business, who are the ultimate accountants."

Stewart Udall

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Chapter 1

Introduction

The increasing density in the woody component at the expense of the grass layer, in grasslands and savannas, has been widely reported in South Africa (West, 1947; Scott, 1967; Grossman & Gandar, 1989; O'Connor & Crow, 1999), other African savannas (Prins & van der Jeugd, 1993; Roques, O'Connor & Watkinson, 2001) and on other continents (Archer, 1989; Glatzle, Lajarthe & Hirsch, 1996; Costello, Lunt & Williams, 2000). Both *Acacia karroo* Hayne (O'Connor, 1995; Chirara, Frost & Gwarazimba, 1998) and *A. nilotica* (L.) Willd. Ex Del. subsp. *kraussiana* (Benth.) Brenan (Mackey, 1997; Kriticos *et al.*, 1999) have been reported as being major contributors to this phenomenon, which is commonly referred to as bush encroachment. Bush encroachment is of concern to wildlife managers as it results in habitat loss for certain browsing and grazing species.

In Hluhluwe-Umfolozi Park (HUP), acacias are seen as major contributors to the problem of bush encroachment. The form of *A. karroo* that occurs in the park is morphologically significantly different to the typical form in that it is tall and spindly (Smit, 1999). It is also possible that there may be significant ecological differences between the two forms.

HUP is situated between 28°00' – 28°26' S, 31°43' – 32°09'E, in KwaZulu-Natal, South Africa and comprises a 960 km² fenced protected area comprising the former Hluhluwe and Umfolozi Game Reserves, and the corridor of land that links the areas. The park has a moderate coastal climate with a mean annual rainfall of 990 mm

for the Hluhluwe section and 720 mm for the Umfolozi section of the park (Whateley & Porter, 1983). The mean monthly temperature ranges from 13 °C to 33 °C (Grobler, 1984).

As little as 19 years ago, Whateley & Porter (1983) reported *A. karroo* to be largely confined to the north-eastern part of the park. This was confirmed by Bond, Smythe & Balfour (2001) who reported that in the park, *A. karroo* Woodlands were rare and found no adult trees in any of their transects selected to cover a wide altitudinal range. They did, however, find 111 (62.5 ha⁻¹) adult *A. nilotica* trees despite avoiding closed *A. nilotica* Woodlands. This relative dominance was reversed in juvenile stages with *A. karroo* (725 ha⁻¹) outnumbering *A. nilotica* (225 ha⁻¹) threefold and setting woodland structure to change in the future (Bond *et al.*, 2001).

This study looked at some aspects of the seed ecology of these two species and tried to explain how seed ecology may contribute to the change in dominance between *A. karroo* and *A. nilotica*.

This thesis is presented as a series of chapters in publication format. Each chapter has its own introduction, methods, results, discussion and bibliography, presented in the format of African Journal of Ecology, as required.

In Chapter 2, a review of the literature specific to the questions asked in this study is presented. The objectives are presented in the relevant chapters. Briefly, however, the objectives for each chapter are given below.

In Chapter 3, the aim was to determine whether the differences in current success of *A. karroo* and *A. nilotica* were due to a difference in the available numbers of viable seeds by determining the numbers of seeds produced by *A. nilotica* and *A. karroo*, quantifying the seed-banks of the two species and determining the extent of

bruchid infestation of seeds for both species. This is In Press in *African Journal of Ecology*.

In Chapter 4, the aim was to test whether the null hypotheses that burning, fire intensity and burning of sites do not affect germination, that burning, fire intensity, burning of sites and grass length (shade) do not influence seedling establishment and that all species respond in the same way to these treatments (i.e. that there are no treatment species interactions), were true.

In Chapter 5, the aim was to determine whether structural habitat type had an effect on the level of post-dispersal predation of *A. karroo* and *A. nilotica* seeds, who the possible post-dispersal predators may be and whether the post-dispersal fate of these two species could contribute to the current differences in their success in HUP.

In the concluding chapter (Chapter 6), the possible contribution of seed ecology to bush encroachment in HUP is given, which may provide a better understanding of *Acacia* population ecology. This will contribute towards more meaningful ecological conservation management decisions.

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Chapter 2

Production, storage and pre- and post-dispersal survival of *Acacia* seeds and the effect of fire on seeds and seedlings

2.1 Introduction

To better understand the concepts regarding the problem of bush encroachment and its relevance to HUP, seed production, pre-dispersal seed predation, soil-stored seed-banks and post-dispersal seed predation, as well as the effects of fire on seeds and seedlings with reference to African *Acacia* species are reviewed.

2.2 Seed production

Seed production varies in space and time and total pod and seed production is said to reflect the environmental conditions (Tybirk, 1989). Miller (1994a) reported pod production of 36.33-37.09 m⁻² for *Acacia tortilis* and 2.84-7.02 m⁻² for *A. nilotica* depending on ungulate absence or presence respectively. In a study done by Story (1952) one of the larger *A. karroo* trees in his sample had 2 800 pods with an average of 6.7 seeds per pod translating to about 19 000 seeds. Tybirk (1989) found a mean of 832 pods per *A. nilotica* tree with an average of 10.8 seeds per pod and total seed production varying from 153-34 000 seeds. Sabiiti & Wein (1987) measured seed rain under mature *Acacia sieberiana* trees and found an average of 980 m⁻². In Australia, *A. victoriae* produces between 50 and 3 900 seeds m⁻² (Grice & Westoby, 1987). Australian *Acacia* species may thus produce more seed than African *Acacia* species in South Africa, possibly due to a lack of seed predators and higher densities of seeds stored in the soil (see below). Thus, seed production differs between species and depends on location and

year.

2.3 Soil-stored seed-banks

Acacia nilotica forms at least short-term persistent seed-banks of between 1 and 5 years (Garner & Witkowski, 1997). Tybirk, Schmidt & Hauser (1994) studied several *Acacia* species in Kenya and Senegal and found that seed-banks ranged from 0 to 2 439 seeds m⁻² depending on species and site. Sabiiti & Wein (1987) found about 800 seeds m⁻² under mature *Acacia* trees with two thirds occurring in the upper 2 cm of soil. Witkowski & Garner (2000) found differences in seed-banks on cattle grazed areas compared to areas with indigenous ungulates. They showed that *A. tortilis* had 6 357 vs. 31 910 seeds per parent tree and *A. nilotica* had 1 789 vs. 1 906 seeds per parent tree on farmland and reserve respectively. Seed densities were highest beneath parent trees and decreased with distance beyond the canopy (Witkowski & Garner, 2000). At the landscape scale 1.5 million and 140 000 *A. tortilis* seeds per hectare were found on the reserve and farmland respectively with 23 000 and 86 000 for *A. nilotica* (Witkowski & Garner, 2000).

Acacia longifolia has persistent seed banks (Holmes & Cowling, 1997) ranging between 2078 m⁻² for burnt plots and 2 901 m⁻² for unburnt plots (Pieterse & Cairns, 1986). Milton & Hall (1981) found similar high densities of seeds of Australian *Acacia* species in South Africa.

Rodents (Miller, 1994a) and ants (Auld, 1986a) may add to the seed-banks of plants through burial and soil-stored seed-banks may be affected by annual seed production, dispersal, seed predation, germination (Tybirk, Schmidt & Hauser, 1994) and fire (Pieterse & Cairns, 1986; Whelan, 1986; Auld & Tozer, 1995). It is clear from

the literature that there is some debate as to whether acacias have persistent seed-banks or not.

2.4 Pre-dispersal predation

Pre-dispersal seed predation varies over both space and time (Auld, 1986b) and in *Acacia* species is a much reported on phenomenon. Species of the family Bruchidae are common parasites of *Acacia* seeds (Barnes, Filer & Milton, 1996). These beetles lay their eggs on or inside the fruit, leaving their larvae to feed on and grow inside the seed before they pupate and emerge as adults (Lamprey, Halevy & Makacha, 1974). Only seeds without damage to the embryo and with little of the cotyledons eaten, will survive (Lamprey *et al.*, 1974).

It has been suggested that bruchid exit holes make seeds more permeable to water, and providing the seed is not too damaged, enhances germination (Lamprey *et al.*, 1974). Miller (1994b), however, found no significant difference in germination between infested and intact seeds of three species with 1.5% germination for intact and 2.5% for infested seeds. In a study by Mucunguzi (1995) bruchid beetles significantly reduced the germination and seedling establishment of *A. gerrardii* but promoted early germination and establishment of *A. sieberiana*.

Story (1952) found weevil and wasp infestation of *A. karroo* of between 4 and 49%, with the amount of damage dependent on collection site. He also reported 8% germination of infested *A. karroo* seeds.

Bruchid predation levels vary between individual trees with Travaset (1991) reporting on predation levels of between 0.33-36.59% in one year and 0.01-37.82% in the following year. Pellew and Southgate (1984) found more variation between years

with predation ranging from 5.1-8.4% for *A. tortilis* in successive years. These levels of predation are quite low compared with Lamprey *et al.* (1974) who reported 99.6% bruchid damage for *A. tortilis* in Tanzania. They reported that germination rates were between 1-3% following beetle damage but did not compare it with intact seeds.

Miller (1996) found variation between years for *A. tortilis* and *Acacia hebeclada*, but not for *A. nilotica*. She also found higher predation levels for indehiscent than dehiscent species and for pods on the ground than in the canopy. Bruchid infestation was between 3-68% in one year depending on species and 26.4-79.2% depending on individual tree. It has been reported that larger bruchid beetles are more likely to attack indehiscent seeds than dehiscent seeds (Coe & Coe, 1987).

Variation of infestation rates within and between species was also reported by Ernst *et al.* (1990a) who studied nine African *Acacia* species (*A. burkei*, *A. erioloba*, *A. erubescens*, *A. fleckii*, *A. hebeclada*, *A. karroo*, *A. mellifera*, *A. nilotica* and *A. tortilis*), as well as *Dichrostachys cinerea* and *Peltophorum africanum*. Hoffman *et al.* (1989), studying *A. erioloba*, found higher infestation rates in pods on the ground compared to those held in the canopy. Ernst *et al.* (1989) also found variation in bruchid infestation rates between years and trees that varied from 10 to 82%. They report that due to the high degree of damage to the cotyledon and radicle, damaged seeds had no advantage in germination compared with intact seeds as was suggested by Lamprey *et al.* (1974). Bruchid infestation of 72% for *A. raddiana*, 99% for *A. tortilis* and 64% for *A. gerrardii* was found in Israel with germination of infested seeds ranging between 1 and 6% as compared with intact seeds with germination levels of 25-68% (Halevy, 1974). In some *Acacia* species in Central America bruchid infestation rates ranged from 0-90% again depending on species and individual tree (Janzen, 1969).

Stored seeds have higher levels of infestation than fresh seeds (Miller, 1996). Ernst *et al.* (1990b) noted that during dry storage, the total amount of seeds can be destroyed in a few years and that host specificity in a stored seed pool is low. Bruchid predation rates are also higher early in the fruiting season than late in the fruiting season (Hauser, 1994).

With seeds found in dung, *Stator vachelliae* (Bruchidae) attacked only seeds on the surface and never mined into the dung ball (Traveset, 1990). Traveset (1990) noted that fresh dung did not attract beetles more than dry dung and that beetle attack was limited to areas with fruiting adult trees. Bruchid attack was related to distance from the canopy with higher levels of predation occurring closer to the canopy.

It has been suggested that seed ingestion by herbivores will kill seed beetles, resulting in increased germination of seeds with intact embryos (Halevy, 1974; Lamprey *et al.*, 1974; Hoffman *et al.*, 1989; Miller, 1994b) resulting in a three-way interaction between tree, beetle and ungulate.

Fire has no effect on the level of beetle attack, with pre-fire seed crops showing similar infestation rates to post-fire seed crops of *A. elongata* in Australia (Auld & O'Connell, 1989). Bruchid larvae present in seeds, however are killed by fire, depending on fire intensity, as damaged seeds are more susceptible to heat penetration (Sabiiti & Wein, 1987).

The use of bruchid beetles as a method of biological control of *Acacia* spp, has been suggested (Mucunguzi, 1995). In an attempt to control the invasive *A. nilotica* in Australia, a bruchid species was introduced and impacts of this beetle and a naturalised species were assessed (Radford, Nicholas & Brown, 2001). It was found that seed predation prior to pod drop and ingestion by cattle, was insufficient in having an impact

on *A. nilotica* populations. A subsequent study indicated that the species would be better controlled if targeting seedlings and juveniles (Kriticos *et al.*, 1999).

Bruchid damage varies greatly within and between species as well as between years and sites. It is clear that pre-dispersal predation may affect fecundity and it has been suggested as a means of population control.

2.5 Influence of fire on seeds and seedlings

Fire may determine vegetation pattern and has long been used as a tool for manipulating rangeland composition in South Africa (Bond, 1997). Ben-Shahar (1998) tested the effect of fire and elephants on woodland structure and found that *Acacia erioloba* Woodlands maintained a typical structure and appeared to be influenced by factors other than fire and elephants. Another study showed that while fire and herbivory reduced canopy cover and height of woody species, it did not affect density (Scogings, Trollope & O'Connor, 1996). Another study predicts that fire will slow but not stop the spread of trees and enhance tree aggregation (Hochberg, Menaut & Gignoux, 1994).

Seedling appearance after fires depends on the degree of heat treatment seeds are subjected to during the fire (Whelan, 1986). Seedling establishment of certain species is most likely in the year following a fire (Sabiiti & Wein, 1987; Lamont & Runciman, 1993; Auld & Tozer, 1995; Harrington & Driver, 1995).

Dormancy of seeds may be broken at certain temperatures while other temperatures may be fatal (Auld & Tozer, 1995). Pieterse & Cairns (1986) reported that a fairly intense fire reduces the number of viable *A. longifolia* seeds in the seed bank to 8% of the original through germination or destruction of seeds. A study on *Acacia mangium* set the lethal temperature at about 150 °C with germination taking place at

between 100° and 140 °C (Saharjo & Watanabe, 1997). In a study on 35 Australian legumes, Auld & O'Connell (1991) found highest germination in the temperature range 80-100 °C although long durations at 100 °C caused seed death. They noted that at 120 °C all seeds were killed. Seed viability of *A. tortilis* declined at 50 °C whilst viability of *A. karroo* declined only slightly and seeds were stimulated to germinate (Mbalo & Witkowski, 1997). Seeds of these two species were reported to survive temperatures of 100° and 150 °C, with a few *A. karroo* seeds surviving at 200 °C (Mbalo & Witkowski, 1997). Kanz (2001) found that fire increased germination of *Acacia* seeds relative to controls even at temperatures over 700 °C while germination was less than 15% after fire temperatures exceeding 200 °C. He showed that the threshold temperature for seed mortality was 450 °C while the threshold intensity was 10 °Ch He also found that seedling emergence from planted seeds was higher for unburnt areas than for burnt areas. Story (1952) suggested that burning would cause a flush of seedlings, but that the final number would be less than if the seeds remained unburned, as fire is likely to kill some seeds. In Australia, fire greatly increased seed and seedling mortality of *A. nilotica* in open areas with only 3.2% of first year seedlings surviving (Radford *et al.*, 1999). Seedlings were reduced from 560 seedlings per hectare to 18 seedlings per hectare, making fire an important tool in the management of this invasive shrub.

Seedlings germinating from burnt seeds of *A. karroo* and *A. tortilis* did not show any abnormalities in growth after seed exposure to temperatures of 100°, 150° and 200 °C (Mbalo & Witkowski, 1997). For *A. karroo*, the effect of fire depends on the age of the seedlings and the type of fire (Story, 1952). Seedlings up to 8 weeks were killed by slow and fierce burns while at 12 months no seedlings died in either slow or fierce burns (Story, 1952). Thus, fire is not thought to control older trees of this species, but merely

causes thickening by encouraging coppice growth (Story, 1952). Story (1952) suggested that in order to control the species seeds should be burnt so that they are stimulated to germinate and then the area should be burnt again to kill the young seedlings. Another study suggests frequent fires facilitated by low grazing pressure as a mean of preventing shrub encroachment (Roques, O'Connor & Watkinson, 2001).

Important factors that may affect seed and seedling responses to fire are fire season (Kruger, 1984), frequency (Kruger, 1979; Kruger, 1984), intensity (Kruger, 1984; Ansley, Jones & Kramp, 1996; Mbalo & Witkowski, 1997) and fire type (back/head or crown/surface fires) (Trollope, 1984; Kanz, 2001).

The effect of fire on seeds and seedlings varies greatly and seems to depend on species and fire temperature. Fire is commonly thought to break dormancy in *Acacia* seeds, but its effect on subsequent seedling establishment is less clear.

2.6 Post-dispersal seed predation

Most plants are thought to suffer heavy pre- and/or post-dispersal seed predation by animals (Janzen, 1971) and it is important to consider post-dispersal factors affecting the fate of seeds when considering the effectiveness of dispersers (Andresen, 1999). Seeds may be predated on by insects, mammals and birds (Janzen, 1971). Seed predators may not necessarily destroy seeds and may be dispersal agents. A proportion of ingested seeds may pass unharmed through an animal (Andresen, 1999), may be moved a short distance and discarded (Auld & Denham, 1999), may be cached or buried (Price & Jenkins, 1986; Hulme, 1998) or may be incorporated into nests (Bennet & Krebs, 1987; Auld, 1986a). Rodent chewing may also be advantageous with chewed and discarded *Acacia* seeds germinating better than unchewed seeds (Miller, 1995).

Valone & Thornhill (2001) suggest, however, that herbivory of seeds by rodents outweigh the benefits of seed burial on seedling establishment.

Some granivorous ants take seeds back to their nests for consumption while carnivorous ants move seeds over small distances or not at all, merely removing and consuming the elaiosomes and discarding the seed (Auld & Denham, 1999). Thus, seeds without elaiosomes, such as those of South African acacias, are unattractive to certain (carnivorous) ants. Exclusion of fire over long periods increases seed losses to predators. Auld & Denham (1999) studied *Grevillea* spp. with and without elaiosomes in Australia and found between 82 and 95% seed loss in vegetation unburnt for longer than eight years mainly due to rodents and macropods. Apart from ant removals, rodents and macropods consumed up to 86% of seeds with elaiosomes. They suggest that ants may reduce overall levels of seed predation as seeds removed by ants escape predation and are deposited in safe sites. Seed predation must, however, be viewed in the context of the habitat (Janzen, 1971). Ants for instance have been found to remove greater numbers of seeds from grassy than woody habitat in woodland savanna in Zimbabwe (Linzey & Washok, 2000). Ant harvesting is also highly seasonal with intense harvesting taking place at the onset of the dry season and declines in harvesting thereafter (Gillon, Adam & Hubert, 1984). Ants mainly collect seeds that are the most abundant in the vicinity of their nests (Gillon *et al.*, 1984; Milton & Dean, 1993).

In a study done in a Peruvian rain forest, dung beetles buried 41% of the seeds found in dung (Andresen, 1999). Less than 35% of seeds buried in dung balls at 1 cm, however, remained undiscovered by rodents while 96% escaped rodent detection at a depth of 5 cm.

In Zimbabwe, birds removed significantly more seeds than rodents and ants in

both grassy and woody habitat (Linzey & Washok, 2000). Seed-eating birds can strongly depress the number and biomass of plants with Howe & Brown (1999) reporting a 23% drop in number and 32% drop in biomass of grass in a synthetic tall grass community.

Miller (1994c) investigated granivory of *Acacia* seeds by rodents and found that 0.7-25% of the annual seed crop depending on species may be consumed by rodents. Rodents may have differential impact on *Acacia* seeds. Granivory of *A. nilotica*, for instance, is thought to have a negligible effect on recruitment whereas predation of *A. tortilis* and *A. karroo* seeds are thought to have important implications for seed survival and seedling recruitment (Miller, 1994c). She suggests that the high rate of bruchid infestation of these two species could result in seed limitation and that subsequent rodent predation may be important in reducing seedling recruitment. Rodent predation of seeds was also found to depend on site and species and Miller (1994c) reported a preference for *A. tortilis* seeds over *A. nilotica* seeds. Kerley & Erasmus (1991) found no correlation between rodent predation and gross energy content of seeds, but found that preference hierarchies were highly correlated with energy intake. Hulme (1998) tested the hypothesis that species with persistent seed banks sustain proportionally less predation of buried seeds than species that have transient seed banks irrespective of seed size. A negative relationship between seed bank persistence and predation risk was found with rodents removing more large seeds than small seeds and more seeds from transient seed-banks than persistent seed-banks. Holmes (1990) suggested that ants and rodents may compete for seeds in low density *Acacia* stands and suggested that, as rodents may consume a large proportion of the annual seed production at low *Acacia* densities, ants play a critical role in accumulating *Acacia* seed banks.

While post-dispersal predation is a well-studied phenomenon, few studies have concentrated on African acacias. The level of predation experienced by these species and the post-dispersal predators involved require further study.

As suggested by the literature reviewed, the main causes of mortality of *Acacia* seeds appear to be predation by bruchid beetles, high fire temperatures and granivory by small rodents.

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Chapter 3

Production, storage and viability of seeds of *Acacia karroo* and *Acacia nilotica* in a grassy savanna in KwaZulu-Natal, South Africa*

3.1 Abstract

African *Acacia* species are often major contributors to the progressive increase in the woody component of savannas, a phenomenon commonly referred to as bush encroachment. They produce large quantities of seed and may have large soil-stored seed banks. In Hluhluwe-Umfolozi Park, the numbers of adult *Acacia nilotica* trees per hectare far exceed that of *A. karroo* adults. The relative dominance is reversed in the juvenile stage with *A. karroo* outnumbering *A. nilotica* threefold outside closed woodlands.

Acacia karroo trees were smaller than *A. nilotica* trees on average, but produced more seeds for a given basal diameter size class. *A. karroo* showed less bruchid infestation than *A. nilotica* at all stages of pod development. Unlike *A. nilotica*, a proportion of *A. karroo* seeds was able to germinate after bruchid attack. We detected no difference between the two species in the soil-stored seed bank or in the viability of seeds found in the seed bank.

3.2 Introduction

The increasing density in the woody component at the expense of the grass layer, in grasslands and savannas, has been widely reported (West, 1947; Scott, 1967; Archer,

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1989; Grossman & Gandar, 1989; Roques, O'Connor & Watkinson, 2001), with special mention being made of *Acacia karroo* Hayne (O'Connor, 1995; Chirara, Frost & Gwarazimba, 1998) and *A. nilotica* (L.) Willd. Ex Del. subsp. *kraussiana* (Benth.) Brenan (Mackey, 1997; Kriticos *et al.*, 1999) as major contributors to the phenomenon commonly referred to as bush encroachment.

African *Acacia* species are able to produce large quantities of hard coated seeds and often accumulate high densities of viable seed in the soil (Coe & Coe, 1987; Sabiiti & Wein, 1987). Individual trees may produce as many as 45 000 viable seeds per year (Ross, 1965). African *Acacia* species have been found to have seed banks ranging from 0 - 9400 m⁻² depending on species and location (Tybirk, Schmidt & Hauser, 1994). The size of the seed banks of African *Acacia* species are mainly influenced by addition through annual seed production, dispersal, predation, germination (Tybirk *et al.*, 1994) and seed death. Fire stimulates germination of certain *Acacia* seeds (Mbalo & Witkowski, 1997), and may therefore also affect seed banks by reducing the number of seeds in the soil.

Predation by bruchid beetles which lay their eggs on ripening *Acacia* pods has been shown to reduce *Acacia* seed viability (Coe & Coe, 1987; Mucunguzi, 1995; Miller, 1996) by 0 – 82% per tree (Ernst, Tolsma & Decelle, 1989). Infestation by these beetles has been thought to be one of the reasons that *Acacia* species produce such vast amounts of seeds (Sabiiti & Wein, 1987).

In Hluhluwe-Umfolozi Park (HUP), a progressive increase in tree canopy cover has been reported for the period 1937 – 1975 with canopy cover increase in certain areas estimated at between 14% and 20% (Watson & Macdonald, 1983). *Acacia* species are seen as major contributors to bush encroachment in HUP. As little as 19 years ago,

Whateley & Porter (1983) reported *A. karroo* to be largely confined to the north-eastern part of the park. This was confirmed by Bond, Smythe & Balfour (2001) who reported that in the park, *A. karroo* Woodlands were rare and found no adult trees in any of their transects selected to cover a wide altitudinal range. They did, however, find 111 (62.5 ha⁻¹) adult *A. nilotica* trees despite specifically avoiding closed *A. nilotica* Woodlands. This relative dominance was reversed in juvenile stages with *A. karroo* (725 ha⁻¹) outnumbering *A. nilotica* (225 ha⁻¹) threefold and setting woodland composition to change in the future (Bond *et al.*, 2001).

The objective of this study was to determine whether the differences in current success of the above mentioned species was due to a difference in the numbers of viable seeds by: (i) determining the numbers of seeds produced; (ii) quantifying the soil-stored seed-banks of; and (iii) determining the extent of bruchid infestation of seeds for *A. nilotica* and *A. karroo*.

3.3 Materials and Methods

3.3.1 Study site

The study was done in HUP, KwaZulu-Natal, South Africa (28°00' – 28°26' S, 31°43' – 32°09'E). HUP is a 960 km² fenced protected area comprising the former Hluhluwe and Umfolozi Game Reserves, and the corridor of land that links the areas. The park has a moderate coastal climate, ranges in altitude from 60 – 750 m above sea level (Whateley & Porter, 1983) and has a summer rainfall ranging between 760 and 1250 mm per annum. Hluhluwe Game Reserve has a mean annual rainfall of 990 mm, while Umfolozi Game Reserve has a mean annual rainfall of 720 mm (Whateley & Porter, 1983). Periodic fluctuations in above or below average annual rainfall occur, resulting

in wet and dry spells of approximately nine years (Preston-Whyte & Tyson, 1988). The range in average monthly temperature is between 13 and 33 °C (Grobler, 1984).

Most of Hluhluwe Game Reserve is found on rocks of the Ecca and Beaufort series with some basalt in the east (King, 1970). King (1970) identified seven geological formations: (1) the Granite-Gneiss base, (2) the Table Mountain sandstone, (3) the Dwyka tillite, (4) The Ecca and Beaufort series, (5) the Stormberg series, (6) fault breccias and (7) recent deposits.

The main soils types associated with the Ecca and Beaufort series are Swartland and Sterkspruit, while areas of Shortlands, Milkwood and Bonheim series are found in association with the dolerite regions (Whateley & Porter, 1983). They also report that shallow Mispah soils occur extensively in the reserve.

The vegetation in the park has been described as bushveld - savannah comprising five broad vegetation types (Grant & Thomas, 1998). The thickets are wooded groups of similar-sized, small (usually less than three metres) trees of mainly one species that grows densely to the exclusion of other species. The thornveld consists of scattered thorn trees on grassland with deciduous, broad-leaved trees standing out above the thorn trees while the woodlands are densely wooded areas of tall trees that may contain many different, mainly broadleaved species. The well drained, shallow soils of the rocky outcrops support scattered trees of various sizes, while the termite mounds are nutrient rich patches sustaining dense clumps of trees that form small, wooded islands (Grant & Thomas, 1998). Locally the reserve is described as Natal Lowveld Bushveld and falls within the savanna biome (Low & Rebelo, 1996). Dominant broad-leaved species include *Combretum apiculatum* Sonder, *Schotia brachypetala* Sonder, *Sclerocarya birea* (A. Rich.) Hochst. and *Spirostachys africana*

Sonder. Dominant grass species include *Heteropogon contortus* (L.) Roem & Schult., *Hyparrhenia filipendula* (Hochst.) Stapf., *Panicum maximum* Jacq. and *Themeda triandra* Forsk.

3.3.2 Seed production

The pods of *A. nilotica* (indehiscent pods) ($n = 49$) and *A. karroo* (dehiscent pods) ($n = 39$) trees, selected without known bias, were counted between May and July 2000 and the basal diameters measured with vernier callipers. The basal diameters of large trees were calculated from their circumferences, which were measured with measuring tapes. Trees throughout the Hluhluwe and Corridor sections of the park were sampled and were chosen to represent various age classes. The total number of pods per tree was estimated from the mean of two counts. Mean number of seeds per pod for both species was determined from 200 randomly selected pods.

3.3.3 Soil-stored seed bank sampling

Ten mature trees of each species were selected as sampling sites. Soil was extracted and seeds isolated, identified and tested for viability. Only *A. nilotica* and *A. karroo* seeds were extracted from the soil samples. Trees were selected on the basis of not being within 50 m of another tree of the same species to reduce the possibility of seeds in the sample plot being from a tree other than the one being sampled. Twenty-five plots of 1 m² were laid out at each site starting from the base of the tree and extending for 25 m from the tree. An auger with a depth and width of 5 cm was used to take samples from the plots. The area of soil sampled was 19.64 cm². Five random samples were taken in each plot and the samples were pooled, giving a sample area of 0.01 m² per square

metre plot. This was done for all 20 sites. Soil samples were taken between August and December 2000 (after seed rain of both species). Large soil aggregations were broken up by hand and each pooled sample was passed through a 1 x 1 mm sieve.

3.3.4 Viability testing

All seeds found in the soil samples were scarified with sandpaper and placed on moist filter paper in Petrie dishes for germination. Seeds were kept moist and dusted with metalaxyl (Apron C) to prevent pathogen attack. All germinations were recorded for two months. Seeds were considered non-viable if they did not germinate within the two months.

3.3.5 Bruchid damage

Bruchid damage was quantified at various stages of pod ripeness for both species. Pods of *A. karroo* were categorized as green (where pods were green and soft), brown (where pods were ripe, but not yet dehisced) and ripe (dehisced pods), while *A. nilotica* pods were grouped as soft (where pods were brown yet soft), brown (where pods were brown and dry) and ripe (where pods had fallen from the tree). Pods were collected between May and July from twenty trees for each category of *A. karroo* and fifteen trees for each category of *A. nilotica*, and an average of 59 seeds from each sample were examined for evidence of bruchid damage. Soft seeds were dissected to determine larval presence or absence. Pods were not stored before examination. Bruchid exit holes, hollowed out seeds or larval presence, were considered evidence of bruchid attack. The Plant Protection Research Institute, Biosystematics Division (Pretoria, South Africa), identified collected beetles.

3.3.6 Data analysis

SPSS for Windows, standard version (SPSS Inc, 1999) was used for all statistical tests. The data were tested for normality using the Kolmogorov-Smirnov test and for homogeneity of variance with the Levene's test. As the data were found to be skewed and heteroscedastic and conventional transformations could not correct for non-normality, non-parametric tests were used. The Wilcoxon matched pairs test was used to compare the seed banks of the two species and the Chi-square test was used to compare the seed viability of the two species. The 'curve-fitting' feature was used to fit regression lines to data in order to find relationships between the seed bank and distance from a seed bearing tree, and seed production in relation to tree size. Spearman rank correlation coefficient was used to determine the relationship between basal diameter and number of seeds produced. Homogeneity of slopes between the two species was tested by calculating the t -value and comparing it to the values for the t -distribution (Fowler, Cohen & Jarvis, 1998). A Kruskal-Wallis One Way Analyses of Variance on ranks and Dunn's Method for comparing groups of unequal sample size were used to compare the bruchid damage between the different stages of pod ripeness within species. All variation is expressed as the standard deviation from the mean.

3.4 Results

3.4.1 Seed Production

Acacia nilotica trees sampled in all HUP study sites in 2000 produced a mean of $992 \pm 1\,172$ seeds with a range of 5–232 and *A. karroo* a mean of $1\,628 \pm 1\,773$ seeds with a range of 8–216. The mean basal diameter of *A. nilotica* (18.5 ± 7.71 cm) was greater than that of *A. karroo* (7.8 ± 2.58 cm). There was a significant positive correlation between basal diameter and number of seeds produced by *A. nilotica* (Spearman's Rank Correlation Coefficient: $r_s = 0.36$, $n_{trees} = 49$, $P < 0.05$) and *A. karroo* ($r_s = 0.40$, $n_{trees} = 39$, $P < 0.05$). Number of seeds produced increased logarithmically with basal diameter for both *A. nilotica* ($P < 0.01$) and *A. karroo* ($P < 0.05$) (Figure 3.1). There was a significant difference in slopes between the two species ($t = 2.243$, $df = 84$, $P < 0.05$). The mean number of seeds per pod for *A. nilotica* (10.7 ± 2.7 seeds, range: 4–14 seeds) was significantly greater than for *A. karroo* (7.8 ± 1.8 seeds, range: 3–11 seeds) ($U = 2856.5$, $n_{nilotica\ pods} = 200$, $n_{karroo\ pods} = 200$, $P < 0.001$).

3.4.2 Soil seed bank and seed viability

From the 1 250 samples (5 m^{-2}) taken for each species, six *A. karroo* and five *A. nilotica* seeds were found. The estimated soil seed bank was therefore in the order of 110 seeds m^{-2} for under canopy sites (up to 2 m from the base of the tree) for both species. Away from the canopy (2–25 m from the base of the tree) the seed bank was 1.74 seeds m^{-2} . The number of seeds found decreased log-linearly with distance from the tree for both *A. karroo* ($P < 0.001$) and *A. nilotica* ($P < 0.001$) (Figure 3.2). None of the seeds were damaged by bruchids. The density and distribution ($T = 3$, $z = 0$, $P > 0.05$) of the seed bank did not differ significantly between the two species. There was no significant difference (corrected $\chi^2 = 0.43$, $df = 1$, $P = 0.51$) between the viability of soil-stored

seeds of the two species.

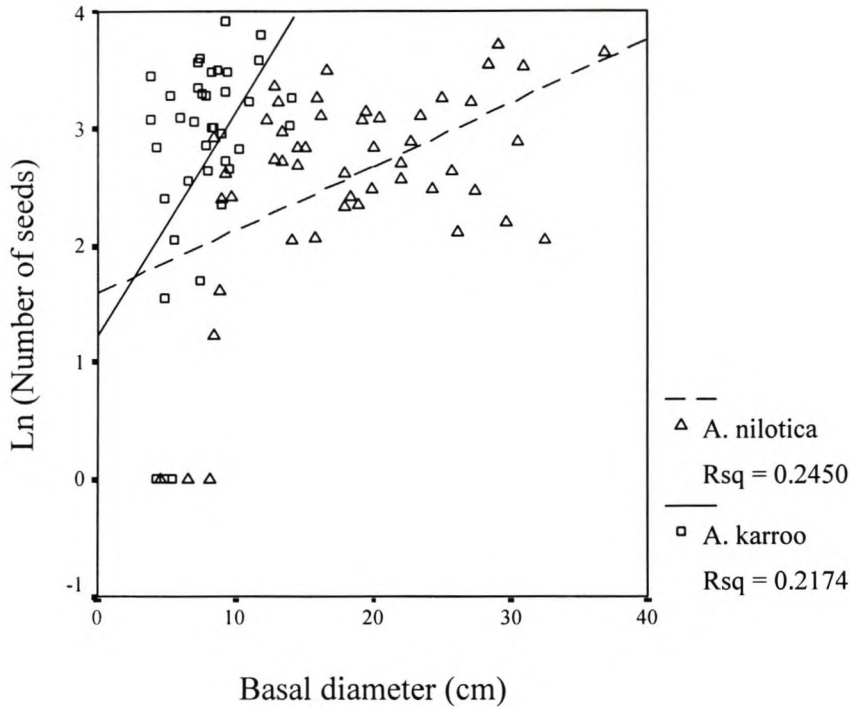
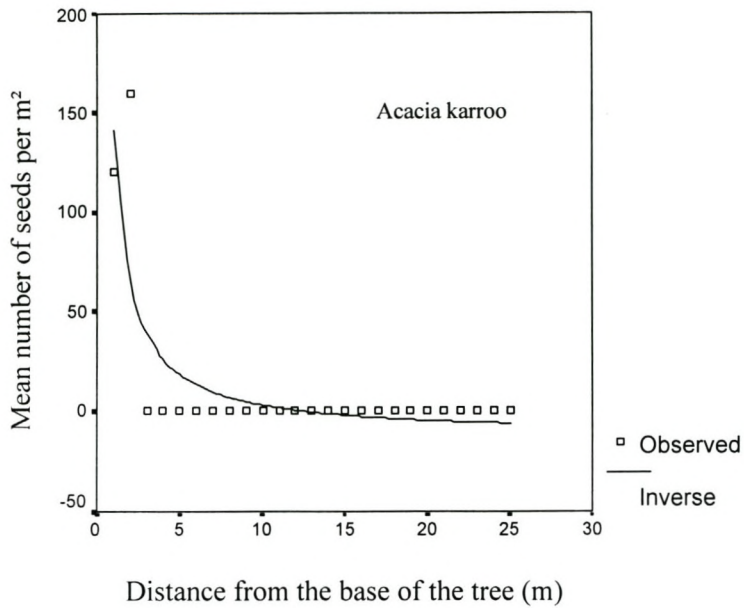


Figure 3.1 Relationships between seed production and basal diameter for *A. nilotica* and *A. karroo* at HUP in 2000. *A. karroo*: $\ln(y) = 1.224 + 0.192x$; *A. nilotica*: $\ln(y) = 1.595 + 0.054x$, where y = number of seeds and x = basal diameter in cm.

3.4.3 Bruchid damage

There was a significant difference in the bruchid damage of pods at different stages of development for *A. karroo* (Kruskal Wallis: $H = 11.62$, $df = 2$, $P < 0.01$) and *A. nilotica* ($H = 29.96$, $df = 2$, $P < 0.001$) (Table 3.1). Damage in *A. karroo* ranged from a mean of $1.36 \pm 2.40\%$ for unripe seeds to $3.81 \pm 3.46\%$ for ripe seeds exerted from their pods. For *A. nilotica* damage ranged from $14.67 \pm 10.47\%$ in green seeds to $86.70 \pm 12.97\%$ for seeds in ripe, fallen pods on the soil surface (Table 3.1).

(a)



(b)

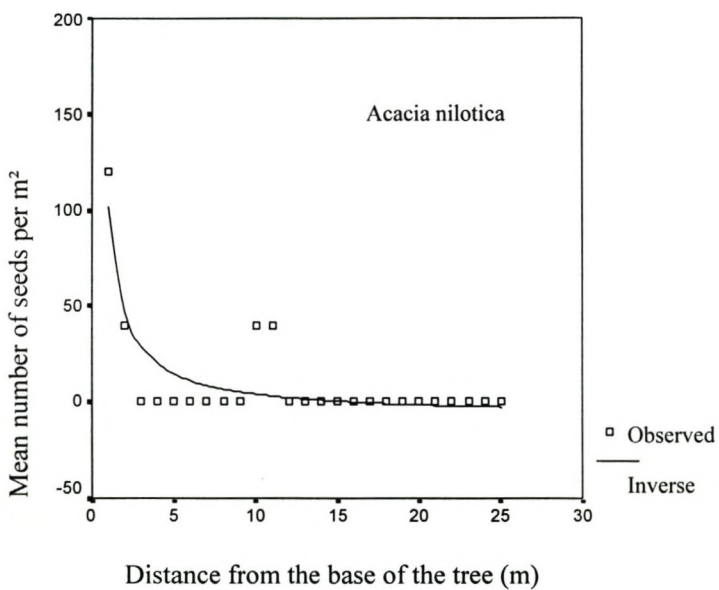


Figure 3.2 Exponential curve fitted to the mean number of seeds found per m⁻² in the soil-stored seed bank of (a) *A. karroo* where $y = -12.258 + (153.686/x)$ and (b) *A. nilotica* where $y = -6.958 + (108.480/x)$, at increasing distance from the base of the tree.

Table 3.1 The mean, range, standard deviation, minimum and maximum percentage damage of *A. nilotica* and *A. karroo* seeds by bruchids as observed for fresh pods at different stages of development

Species	Pod stage	$n_{\text{trees}} \times n_{\text{seeds}}$	Mean	SD	Range	Min	Max
			%	%	%	%	%
<i>A. karroo</i>	green	21 X 50	1.36	2.40	7.81	0.00	7.81
<i>A. karroo</i>	brown	20 X 50	4.26	3.32	10.53	0.00	10.53
<i>A. karroo</i>	ripe	20 X 50	3.81	3.46	11.24	0.00	11.24
<i>A. nilotica</i>	soft	15 X 50	14.67	10.47	38.51	1.49	40.00
<i>A. nilotica</i>	brown	15 X 50	18.77	10.65	34.29	6.06	40.35
<i>A. nilotica</i>	ripe	15 X 50	86.70	12.97	50.00	50.00	100.00

Dunn's Pairwise Multiple Comparison test showed a significant difference in the bruchid damage between green and brown, as well as between green and ripe pods of *A. karroo* ($P < 0.05$). There was no significant difference between brown and ripe pods ($P > 0.05$). *Acacia nilotica* displayed a significant difference between soft and ripe, and brown and ripe pods ($P < 0.05$). There was no significant difference in bruchid damage between brown and soft pods ($P > 0.05$). Ripe pods of *A. nilotica* had significantly more bruchid damage than those of ripe *A. karroo* ($U = 0$, $n_{\text{nilotica trees}} = 15$, $n_{\text{karroo trees}} = 20$, $P < 0.001$). Three bruchid species were found in *A. karroo* seeds, and four species in *A. nilotica* seeds, and in this study none of the seven species were common to both *Acacia* species (Table 3.2). All insect species found in association with the seeds are given in Appendix A.

Table 3.2 Beetle species found in ripe fresh seeds of *A. nilotica* and *A. karroo*

Host species	Family Name	Species Name
<i>A. karroo</i>	BRUCHIDAE: Bruchinae	<i>Bruchidius spadiceus</i> (Fåhraeus)
<i>A. karroo</i>	BRUCHIDAE: Bruchinae	<i>Pygobruchidius</i> species indet.
<i>A. karroo</i>	BRUCHIDAE: Pachymerinae	<i>Caryedon</i> probably <i>acaciae</i> (Gyllenhal)
<i>A. nilotica</i>	BRUCHIDAE: Bruchinae	<i>Bruchidius</i> species indet.
<i>A. nilotica</i>	BRUCHIDAE: Bruchinae	<i>Bruchidius uberatus</i> (Fåhraeus)
<i>A. nilotica</i>	BRUCHIDAE: Bruchinae	<i>Pygobruchidius latiorithorax</i> (Pic)
<i>A. nilotica</i>	CERAMBYCIDAE: Lamiinae	<i>Enaretta varia</i> (Pascoe)

3.5 Discussion

3.5.1 Seed production

Although *A. karroo* produced 1.6 times more seeds per tree than *A. nilotica*, the difference in seed production was found to be insignificant at the 95% confidence level because of high variability among trees of a given species. The difference in slopes, however, indicated that *A. karroo* would produce more seeds at any given basal diameter than *A. nilotica*.

Story (1952) reported as much as 19 000 seeds being produced by *A. karroo*. This far exceeds the maximum number of seeds (8 216) recorded in this study. These data, however, may not be comparable due to differences in tree growth form, with *A. karroo* in HUP being slender and sparingly branched while *A. karroo* in the above study

would have been the 'typical' form with rounded, somewhat spreading crowns (Smit, 1999).

Miller (1994) reported pod densities of 37.09 m⁻² for *A. tortilis* and 7.02 m⁻² for *A. nilotica* in the absence of, and 36.33 m⁻² for *A. tortilis* and 2.84 m⁻² for *A. nilotica* in the presence of ungulates. Although these measurements were taken in different units (m⁻²) to that of the present study (actual number), it is clear that *A. nilotica* in this instance also produced very few pods. Tybirk (1989), however, found a mean pod production and range of 832 and 14 – 3 150 respectively for *A. nilotica* in Kenya. This is much higher than the mean of 93 pods per tree (range: 0 – 476) found in the current study.

These studies report a broad range for the number of pods *A. nilotica* may produce. Pod production in the present study fits somewhere in the lower end of this range with *A. nilotica* in HUP producing very few pods. As pod production was only quantified for one podding season, it is possible that the relatively low reproductive output of these species is a result of unfavourable environmental conditions. Measures of pod production over several years are necessary to determine whether the trees in HUP are producing relatively more or less seed than those found elsewhere.

3.5.2 Soil-stored seed bank

Soil-stored seed banks of both species were small. Tybirk *et al.* (1994) found 14 seeds per m⁻² for *A. nilotica*. They found seed banks to range from 0 (*A. albida*, *A. senegal*, *A. tortilis* and *A. seyal*) for some species to 2439 m⁻² (*A. hockii*) for others. Findings that under-canopy sites showed a higher density of seeds is consistent with the results of Witkowski & Garner (2000), who found seed densities for *A. nilotica* and *A. tortilis* to

be highest below the parent tree. Some *Acacia* species are shade intolerant resulting in decreased seedling establishment in shady areas (Smith & Shackleton, 1988; Belsky, 1994; Kanz, 2001), while others have been found to be tolerant of low light conditions (O'Connor, 1995). *Acacia karroo* is one of these shade tolerant species (O'Connor, 1995). Smith & Goodman (1986) reported that, in contrast, *A. nilotica* was unable to establish in shade. This is consistent with the findings of Bond *et al.* (2001) that *A. karroo* saplings are ten times more abundant in bunch grasslands (> 10cm in height) than in grazing lawns (< 10 cm in height). Bunch grasslands occur across the entire altitudinal range in Hluhluwe. If more *A. karroo* than *A. nilotica* seedlings are able to survive to reproductive maturity in tall grass areas, then they will have a greater seed input to the grassland and any seeds (however few) subsequently added to the soil-stored seed bank below these trees again have a greater chance of germination and survival than *A. nilotica*. This may contribute to the success of *A. karroo* as an invader of grasslands.

3.5.3 Bruchid damage

The level of bruchid infestation of *A. karroo* was very low. This was in contrast to the findings by Miller (1996) who reported predation rates of 40%. Ernst, Decelle & Tolsma (1990) found 15.9% damage in *A. karroo* but between 0 and 61% for *A. nilotica* in various years. The level of bruchid infestation found in *A. nilotica* and *A. karroo* are not matched by other studies on the same species, for which examples are summarised in Appendix B. Predation levels of *A. nilotica* seeds in HUP were much higher than those found in any of the other studies on the same species (Ernst *et al.*, 1990; Miller, 1994; Miller, 1996). *Acacia karroo* seeds, however, experienced far less predation in the

current study than in any of the other studies on the same species (Ernst *et al.*, 1990; Miller, 1996).

According to Mucunguzi (1995), dehiscent *Acacia* species (*A. karroo* in this case) are less able to resist attack by seed predators than indehiscent *Acacia* species (*A. nilotica*) as they afford less protection to their seeds. Our findings suggest, that for the present study, this was not the case.

The suggestion by Coe & Coe (1987) that larger bruchid beetles are more likely to attack indehiscent seeds could explain the difference in predation levels between the two species. They also suggest that larger indehiscent seeds have more seed predators than the dehiscent kind as the smaller resource of the latter type probably restricts the number of bruchids that may attack them. Not only was one of the beetles found feeding on *A. nilotica* seeds much larger than those in *A. karroo*, there were also more beetle species found in *A. nilotica* than *A. karroo* seeds.

It is unlikely that all the beetles feeding on these species in HUP were collected during this study because ripe pods of both species were collected at the same time of year. It is possible that some bruchids emerge from pods earlier or later in the season. Bruchid damage varies between years (Pellew & Southgate, 1984; Ernst *et al.*, 1990; Miller, 1996), and it is possible that bruchid populations also vary between years. More data need to be collected to determine whether there is a difference in bruchid damage between years.

In a study done in the same year (unpublished data) the viability of ripe seeds with bruchid holes was tested. Whilst *A. nilotica* had 0% germination ($n = 190$), *A. karroo* had 7.14% germination ($n = 85$), bruchid infestation apparently rendered *A. nilotica* seeds non-viable, while *A. karroo* seeds still had a chance of germinating.

3.5.4 Conclusion

While soil-stored seed banks were small with no difference between the two species, I suggest that these seed banks might play an important role in success of *A. karroo* as an encroaching species. Due to its shade tolerance, *A. karroo* may be able to take advantage of possible germination sites not suitable for germination by other *Acacia* species. *Acacia karroo* produced more seeds for any given basal diameter than *A. nilotica* but there are also more adult *A. nilotica* than *A. karroo* trees in the park (Bond *et al.*, 2001) suggesting that *A. nilotica* would produce more seeds overall. I suggest, however, that while this species may not be seed limited it is, due to high levels of bruchid attack, predation limited. Seed predators influence plant population dynamics by limiting fecundity (Auld & Denham, 1999) and lowering the frequency with which a safe site may be found by seeds (Janzen, 1971). Thus the high numbers of seeds produced by *A. karroo* in combination with lower bruchid damage translates to large amounts of viable seeds being produced by *A. karroo* as opposed to *A. nilotica*. The aspects of *A. karroo* seed ecology investigated in this chapter could contribute to its success as an invasive species and offer a possible explanation for a change in dominance between these two species in HUP. Any management that results in fewer seeds being added to the grasslands should have an effect on limiting its success. Manipulation of seed predators is unlikely to be a viable option as this may affect other *Acacia* species. It has been found that seed predation by bruchids is insufficient to cause impacts on *A. nilotica* populations in Australia (Radford, Nicholas & Brown, 2001). I suggest that targeting remaining grasslands and preventing *A. karroo* from reaching pod-bearing age in these areas could be a way of slowing down invasion rates. Management such as removal of immature trees (preventing maturation) and regular

burning (killing of seedlings) may also prevent the formation of seed banks in grasslands.

3.6 Acknowledgements

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3.8 Appendices

Appendix A Group, family name and species name of some insects found in *A. karroo* and *A. nilotica* seeds in HUP, 2000.

Group	Family Name	Species Name
COLEOPTERA	BRUCHIDAE: Bruchinae	<i>Bruchidius spadiceus</i> (Fåhraeus)*
	BRUCHIDAE: Bruchinae	<i>Bruchidius</i> species indet.* **
	BRUCHIDAE: Bruchinae	<i>Bruchidius uberatus</i> (Fåhraeus)*
	BRUCHIDAE: Bruchinae	<i>Pygobruchidius latiorithorax</i> (Pic)*
	BRUCHIDAE: Bruchinae	<i>Pygobruchidius</i> species indet.* **
	BRUCHIDAE: Pachymerinae	<i>Caryedon</i> probably <i>acaciae</i> (Gyllenhal)*
	CERAMBYCIDAE : Lamiinae	<i>Enaretta varia</i> (Pascoe) *
	CERYLONIDAE	Genus indet.
	CURCULIONIDAE : Rhythirrinin	Genus indet.
	CURCULIONIDAE : Scolytinae	<i>Hypothenemus</i> sp.
	LAEMOPHLOEIDAE	<i>Planolestes</i> sp.
	TENEBRIONIDAE: Lagriinae	<i>Lagria ? aeneipennis</i> (Fåhraeus)
HYMENOPTERA	EUELMIDAE	<i>Eupelmus ? urozonus</i> (Dalman)
	ICHNEUMONIDAE	Genus indet.
	PTEROMALIDAE	<i>Dinarmus altifrons</i> (Walker)
	PTEROMALIDAE	<i>Dinarmus magnus</i> (Rohwer)

*beetles most likely to predate on seeds

**appears to be an as yet undescribed species

Appendix B The authority, year of study, study area, ground or canopy pod collections, fresh or stored seeds, sample size and mean percentage bruchid infestation given for various *Acacia* species acting as hosts for bruchid predators.

Authority	Year	Site	Host species	Ground/ Canopy	Fresh/ Stored	n_{trees}	n_{seeds}	mean % infestation
Lamprey <i>et al.</i> (1974)	?	Serengeti, Tanzania	<i>A. t. spirocarpa</i>	Ground	Stored	-	500	95.60 – 99.6
Halevy (1974)	?	Negev & Sinai, Israel	<i>A. t. raddiana</i>	Ground	Stored	-	200	72.00
	?	Negev & Sinai, Israel	<i>A. t. tortilis</i>	Ground	Stored	-	200	99.00
	?	Negev & Sinai, Israel	<i>A. gerrardii</i>	Ground	Stored	-	200	64.00
Pellew & Southgate (1984)	1979	Serengeti, Kenya & Tanzania	<i>A. tortilis</i>	Ground	Fresh	-	719	8.40
	1980	Seronera, Serengeti	<i>A. tortilis</i>	Ground	Fresh	-	1047	5.10
	1980	Ndutu, Serengeti	<i>A. tortilis</i>	Ground	Fresh	-	597	78.60
Coe & Coe (1987)	?	Zimbabwe	<i>A. albida</i>	Canopy	Fresh	-	393	4.10
	?	South Africa	<i>A. t. heteracantha</i>	Canopy	Fresh	-	754	7.60
	?	Kenya	<i>A. t. spirocarpa</i>	Canopy	Fresh	-	300	6.60
	?	Kenya	<i>A. erioloba</i>	Ground	Fresh	-	80	28.90
	?	Kenya	<i>A. sieberana</i>	Ground	Fresh	-	237	35.00
	1983	Kenya	<i>A. elatior</i>	Canopy	Fresh	-	176	29.00
	1984	Kenya	<i>A. elatior</i>	Canopy	Fresh	-	876	21.60
	1983/ 84	Kenya Kuisieb River Valley,	<i>A. elatior</i>	Canopy	Stored	-	1002	71.00
Hoffman <i>et al.</i> (1989)	1987	Namibia Kuisieb River Valley,	<i>A. erioloba</i>	Canopy	Fresh	5	c. 320	27.48
	1987	Namibia	<i>A. erioloba</i>	Ground	Fresh	5	c. 320	48.24
Ernst <i>et al.</i> (1990)	1983	Modipane, Botswana	<i>A. burkeii</i>	-	Fresh	-	872	13.60
	1983	Khakhea, Botswana	<i>A. erioloba</i>	-	Fresh	-	909	53.50
	1987	Gabane, Botswana	<i>A. erioloba</i>	-	Fresh	-	200	93.90
	1988	Dikeletsane, Botswana	<i>A. erioloba</i>	-	Fresh	-	500	96.00
	1983	Maru-a-pula, Botswana	<i>A. erubescens</i>	-	Fresh	-	1191	32.00
	1987	Gabarone, Botswana	<i>A. erubescens</i>	-	Fresh	-	200	5.00
	1987	Gabarone, Botswana	<i>A. fleckii</i>	-	Fresh	-	100	2.00
	1983	Kokong, Botswana	<i>A. hebeclada</i>	-	Fresh	-	1852	43.10
	1987	Kanye, Botswana	<i>A. hebeclada</i>	-	Fresh	-	120	87.90
1988	Kang, Botswana	<i>A. hebeclada</i>	-	Fresh	-	1000	49.60	

Appendix B Continued:

Authority	Year Site	Host species	Ground/ Canopy	Fresh/ Stored	n_{trees}	n_{seedS}	mean % infestation
	1983 Otse, Botswana	<i>A. karroo</i>	-	Fresh	-	2459	15.90
	1983 Tsolofelo, Botswana	<i>A. mellifera</i>	-	Fresh	-	717	26.20
	1988 Gabarone, Botswana	<i>A. mellifera</i>	-	Fresh	-	500	5.00
	1988 Monwane, Botswana	<i>A. mellifera</i>	-	Fresh	-	509	3.90
	1988 Morwa, Botswana	<i>A. mellifera</i>	-	Fresh	-	400	0.80
	1983 Gabarone, Botswana	<i>A. n. kraussiana</i>	-	Fresh	-	907	61.00
	1987 Gabarone, Botswana	<i>A. n. kraussiana</i>	-	Fresh	-	1450	27.50
	1988 Gabarone, Botswana	<i>A. n. kraussiana</i>	-	Fresh	-	258	7.60
	1987 Gabarone, Botswana	<i>A. n. kraussiana</i>	-	Fresh	-	280	0.00
	1988 Gabarone, Botswana	<i>A. n. kraussiana</i>	-	Fresh	-	101	3.90
	1988 Gabane, Botswana	<i>A. n. arabica</i>	-	Fresh	-	400	2.00
	1983 Gabarone, Botswana	<i>A. tortilis</i>	-	Fresh	-	1050	35.20
	1983 Gabarone, Botswana	<i>A. tortilis</i>	-	Fresh	-	448	78.80
	1987 Gabarone, Botswana	<i>A. tortilis</i>	-	Fresh	-	1217	48.60
	1988 Gabarone, Botswana	<i>A. tortilis</i>	-	Fresh	-	1151	11.90
	1988 Morwa, Botswana	<i>A. tortilis</i>	-	Fresh	-	467	35.10
Miller (1994)	Nylsvlei Nature Reserve, 1992 South Africa	<i>A. tortilis</i>	Canopy	Fresh	10	-	34.16
	Nylsvlei Nature Reserve, 1992 South Africa	<i>A. tortilis</i>	Ground	Fresh	10	-	29.52
	Nylsvlei Nature Reserve, 1992 South Africa	<i>A. nilotica</i>	Ground	Fresh	5	-	45.80
Miller (1996)	1991 South Africa Nylsvlei Nature Reserve,	<i>A. tortilis</i>	-	Fresh	-	2010	31.40
	1991 South Africa Nylsvlei Nature Reserve,	<i>A. nilotica</i>	-	Fresh	-	1652	46.80
	1991 South Africa Nylsvlei Nature Reserve,	<i>A. hebeclada</i>	-	Fresh	-	210	77.30
	1992 South Africa Nylsvlei Nature Reserve,	<i>A. tortilis</i>	-	Fresh	-	200	68.00
	1992 South Africa Nylsvlei Nature Reserve,	<i>A. nilotica</i>	-	Fresh	-	200	36.50
	1992 South Africa Nylsvlei Nature Reserve,	<i>A. hebeclada</i>	-	Fresh	-	200	3.00
	1992 South Africa Nylsvlei Nature Reserve,	<i>A. h. tristis</i>	-	Fresh	-	200	32.00
	1992 South Africa Nylsvlei Nature Reserve,	<i>A. robusta</i>	-	Fresh	-	200	41.50
	1992 South Africa Nylsvlei Nature Reserve,	<i>A. leuderitzii</i>	-	Fresh	-	200	22.00
	1992 South Africa	<i>A. karroo</i>	-	Fresh	-	200	40.00
	1992 Nylsvlei Nature Reserve	<i>A. caffra</i>	-	Fresh	-	200	21.00

Chapter 4

Effects of fire and fire intensity on the germination and establishment of *Acacia karroo*, *Acacia nilotica*, *Acacia luederitzii* and *Dichrostachys cinerea* in the field

4.1 Abstract

While fire has been used to control the increase of woody plants, it has been reported that fire may cause an increase in certain fire-tolerant acacia tree species. This study investigated germination of two woody tree and one shrub species increasing in density as well as a historically successful encroaching woody species in savanna grassland, Hluhluwe-Umfolozi Park, South Africa. I tested the hypothesis that observed increases in certain woody plants in a savanna were related to seed germination and seedling establishment. *Acacia karroo* is thought to be replacing *A. nilotica* as the dominant microphyllous species. Germination is compared among species for burnt and unburnt seeds on burnt and unburnt plots at three different locations for hot and cool fires. *Acacia karroo* showed higher germination (*A. karroo* 5.1%, *A. nilotica* 1.5% and *A. luederitzii* 5.0%) levels and better establishment (*A. karroo* 4.9%, *A. nilotica* 0.4% and *A. luederitzii* 0.4%). Seeds of the shrub *Dichrostachys cinerea* did not germinate in the field after fire and it is thought that some other germination cue is needed. On average, *A. karroo*, *A. nilotica* and *A. luederitzii* did not show a difference in germination levels between burnt and unburnt seeds. There was a significant difference in germination of burnt seeds in both burnt (4.5%) and unburnt (2.5%) sites and unburnt seeds in both burnt (2.8%) and unburnt (4.9%) sites when considered separately.

4.2 Introduction

The increasing density in the woody component of savannas has been widely reported (West, 1947; Scott, 1967; Archer, 1989; Grossman & Gandar, 1989; Roques, O'Connor & Watkinson, 2001) with special mention being made of *Acacia karroo* (O'Connor, 1995; Chirara, Frost & Gwarazimba, 1998) and *A. nilotica* (Mackey, 1997; Kriticos *et al.*, 1999) as major contributors to the phenomenon. In Hluhluwe-Umfolozi Park *Dichrostachys cinerea* and *A. luederitzii* are also thought to contribute to this phenomenon.

In hard seeded legumes dormancy is broken by rupturing part of the seed coat. The rupturing of the seed coat may be induced by heat from fire (Sabiiti & Wein, 1987) enabling water to enter the seed and start the process of germination. Many studies have confirmed a release of legume seeds from dormancy after fire (Pieterse & Cairns, 1986; Sabiiti & Wein, 1987; Auld & O'Connell, 1989; Auld & Tozer, 1995; Bradstock & Auld, 1995; Mucunguzi & Oryem-Origa, 1996; Teketay, 1996; Mbalo & Witkowski, 1997). Fire temperature or intensity also has an effect on the germination of seeds (Auld & O'Connell, 1991; Mbalo & Witkowski, 1997) and low intensity fires may not be enough to break dormancy of hard-seeded legumes (Saharjo & Watanabe, 1997). Kanz (2001), however, found an increase in germination above 700 °C. In other cases lower fire temperatures are preferable for germination with an increase in fire temperature causing seed mortality (Auld & O'Connell, 1991).

While some studies report that a decrease in grass cover favours the establishment of woody seedlings due to reduced competition (Schultz, Lauenbach & Biswell, 1955; Kanz, 2001), others (O'Connor, 1995; Brown & Archer, 1999) challenge these findings. These differences may however, be a result of species reacting

differently to fire or competition.

Some *Acacia* species are shade intolerant resulting in decreased seedling establishment in shady areas (Smith & Shackleton, 1988; Belsky, 1994; Kanz, 2001). Other *Acacia* species have been found to be tolerant of low light conditions and may even experience increased seedling survival (O'Connor, 1995).

The frequency of fires may affect the direction of change in woody plant density (Roques *et al.*, 2001). While it has been suggested that fire may increase acacia densities (Sabiiti & Wein, 1987), it is also used to clear acacias from grassland (Thomas & Pratt, 1967). This contradictory situation in the literature concerning the effect of fire necessitates further research, as it is clear that continuous use of incorrect burning practices may have disastrous consequences.

This study investigated the direct (heat) and indirect (grass removal) effects of fire on seed germination and seedling establishment of *A. nilotica* (L.) Willd. Ex Del. subsp. *kraussiana* (Benth.) Brenan, *A. karroo* Hayne, *A. luederitzii* Engl. var. *retinens* (Sim) Ross & Brenan and *Dichrostachys cinerea* (L.) Wight & Arn. in Hluhluwe-Umfolozi Park (HUP), where an increase in woody plant density over the past 40 years has been reported (Watson & Macdonald, 1983; Skowno *et al.*, 1999; Bond, Smythe & Balfour, 2001). It has also been reported that *A. karroo* is apparently replacing *A. nilotica* as the dominant microphyllous element (Skowno *et al.*, 1999; Bond *et al.*, 2001).

This study aimed to test the null hypotheses that:

1. burning, fire intensity and burning of sites have no effect on germination,
2. burning, fire intensity, burning of sites and grass length (shade) have no influence on seedling establishment,

3. all species respond in the same way to these treatments (i.e. that there are no treatment species interactions).

4.3 Materials and Methods

4.3.1 Study site

The field experiment took place in the Hluhluwe and Corridor sections of the HUP. Climate, vegetation and soil descriptions are given in Section 3.3.1.

Acacia luederitzii occurs in large numbers in certain areas of the Umfolozi part of the reserve but is mostly absent from the Hluhluwe and Corridor sections. *Acacia nilotica*, *A. karroo* and *D. cinerea* are found throughout the park. As opposed to the scattered trees found in Umfolozi, *A. nilotica* covers extensive areas of Hluhluwe and the Corridor and is usually found below the 300 m contour (Whateley & Porter, 1983). Whateley & Porter (1983) described an *A. karroo* – *D. cinerea* induced thicket throughout the area, but particularly in the Corridor and Hluhluwe Reserves. *Acacia luederitzii* seeds used in this study were therefore collected in Umfolozi Game Reserve while those of the other species were collected in Hluhluwe.

4.3.2 Germination

The effect of fire, fire intensity and burning of sites on the germination of seeds of *A. nilotica*, *A. karroo*, *A. leuderitzii* and *D. cinerea* was tested in a field experiment. Seeds of all species were collected between May and August 2000. Parasitized seeds were extracted. Prior to planned management burns, six groups of seeds were placed in tall grass (taller than 0.10 m) and six in short grass (shorter than 0.10 m) at three locations (Nombali, Seme and Le Dube). Sites were cleared of existing pods/ seeds prior to the

experiment and as podding season was over, no uncontrolled additions are expected to have occurred. Tall grass produces hotter fires than short grass due to increased fuel load, which increases available heat energy (Trollope, 1984). *Dichrostachys cinerea* seeds were only put out at Seme and Nombali. Each group contained 22 *A. nilotica*, 25 *A. karroo*, 10 *A. leuderitzii* and 10 *D. cinerea* seeds. Seeds were placed in the field a day before each of the burns (Nombali two days before). Seme and Le Dube were burnt on 2 October and Nombali on 30 September 2000 shortly before the start of spring rains and natural seed release. After the burns, three of the groups of burnt seeds were removed from the tall and short grass and placed on unburnt tall and short grass sites at the same location respectively. Three groups of unburnt seeds were then added to each of the tall and short grass sites. A 13 mm mesh cage with 18 cm x 18 cm x 18 cm sides was used to protect each group of seeds and any germinated seedlings from rodent and herbivore predation. Cages were placed at half metre intervals and seeds placed on the soil surface in a group in the middle of each cage. Seeds were considered to be germinating when a root started showing. A diagrammatical representation of the experiment is given in Figure 4.1. Germination was recorded at 1, 3, 5, 7, 9, 11, 14, 17, 20, 23, 27 and 31 weeks. The experiment ended in May 2001.

I thus applied 96 possible seed treatment combinations for investigating factors affecting germination in the field (4 species x 2 burn treatments x 3 locations x 2 location burn treatments x 2 fire intensities).

4.3.3 Seedling establishment

To test the effect of fire, fire intensity, burning of sites and grass length (shade) on seedling establishment of *A. nilotica*, *A. karroo*, *A. leuderitzii* and *D. cinerea*, data as on

week 31 of the field experiment (described in Section 4.3.2) were used. Seedlings were considered to be established when they were rooted in the ground and the cotyledons replaced with leaves. Establishment was based on the total number of seeds.

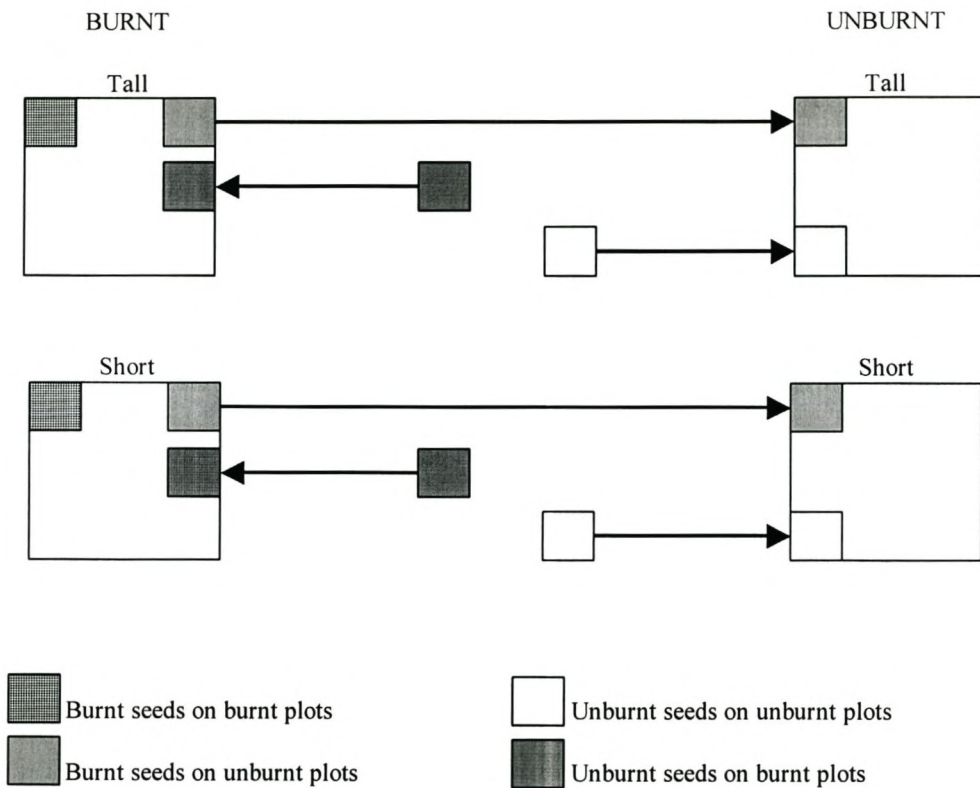


Figure 4.1 Diagrammatical representation of the experimental design used to test the effect of fire on seed germination and establishment.

4.3.4 Data analysis

The “STATISTICA[®]” (v 5.5, StatSoft, Inc., 2000) Generalized Linear Model (GLM) module was used to construct linear logistic models for germination and establishment proportions as response variables for the field experiment. As data were recorded as presence (1) or absence (0) of seedlings, a binomial distribution was assumed (Bustamante, 1997). In both cases, main effects and second order interactions were included in the model. The logit model may therefore be written as follows:

$$\ln \left(\frac{y_{1jklmn}}{y_{2jklmn}} \right) = \lambda' + \lambda_j^{iB} + \lambda_k^{iC} + \lambda_l^{iD} + \lambda_m^{iE} + \lambda_n^{iF} + \lambda_{jk}^{iBC} + \dots + \lambda_{mn}^{iEF}$$

where

λ' = the overall mean effect of the categories

λ_j^{iB} = the effect of the j th species ($j = A. karroo, A. luederitzii, A. nilotica, D. cinerea$)

λ_k^{iC} = the effect of the k th location ($k = \text{Le Dube, Nombali, Seme}$)

λ_l^{iD} = the effect of the l th seed burn status ($l = \text{burnt, unburnt}$)

λ_m^{iE} = the effect of the m th grass length ($m = \text{short, tall}$)

λ_n^{iF} = the effect of the n th site burn status ($n = \text{burnt, unburnt}$)

λ_{jk}^{iBC} = the interaction effect between the j th species and the k th location

λ_{mn}^{iEF} = the interaction effect between the m th grass length and the n th site burn status.

The logit model may be written as a GLM as follows:

$$\ln\left(\frac{v_{1jklmn}}{v_{2jklmn}}\right) = \beta_0 + \beta_1^B \chi_1^B + \beta_2^B \chi_2^B + \beta_3^B \chi_3^B + \beta_1^C \chi_1^C + \beta_2^C \chi_2^C + \beta_1^D \chi_1^D + \beta_1^E \chi_1^E + \beta_1^F \chi_1^F + \beta_{11}^{BC} \chi_{11}^{BC} + \dots + \beta_{11}^{EF} \chi_{11}^{EF}$$

where β_0 , β_1^B , β_2^B , β_3^B , β_1^C , β_2^C , β_1^D , β_1^E , β_1^F , β_{11}^{BC} and β_{11}^{EF} are parameters to be estimated from the data and B, C, D, E and F refer to the explanatory variables species, location, burn status, grass length and site burnt status respectively. The estimated parameters for the GLM were used to obtain the estimated parameters for the logit model. The estimated parameters of the odds were calculated for each factor or combination of factors (including the intercept) as the exponent of the estimated parameters of the logit model. The estimated odds of germination under any condition were then calculated as the product of the estimated parameter of the odds of the intercept (estimated geometric mean odds) and the factor or combination of factors in question. The estimated odds are associated with estimated probabilities and were calculated as follows:

$$P = \frac{odds}{1 + odds}$$

The odds of germination for significant treatment combinations were compared.

The predicted number of seeds germinating and seedlings establishing were seen as being appropriate for interpretation as summaries of the data. Thus, differences in the predicted mean number of seeds germinating and seedlings establishing (given as a fraction of the total number of seeds) were illustrated graphically for each significant

treatment combination.

4.4 Results

4.4.1 Germination

None of the seeds of *D. cinerea* germinated in the field and it was therefore excluded from the model for the field experiment. Testing for differences among treatments was based on the maximum number of seedlings for each species at each location over the 31-week period (Figure 4.2). A description of the factors used in both the germination and establishment models is given in Table 4.1.

The ratio of the model deviance to the degrees of freedom was small (0.29) indicating that the model was a good fit. Location and species were the only main effects significantly affecting germination (Table 4.2) (Figure 4.3). *Acacia karroo* had the highest germination of all species and outnumbered *A. nilotica* 3.96 times (Table 4.1).

Interaction terms that had a significant effect on germination were, location x grass length, burn status x site burn status and grass length x site burn status (Table 4.2) (Figures 4.4 & 4.5). Germination of burnt seeds in burnt sites (4.5%) was significantly higher than that of burnt seeds in unburnt sites (2.5%). Similarly, unburnt seeds in unburnt sites had a higher germination percentage (4.9%) than unburnt seeds in burnt sites (2.8%).

Table 4.1 Descriptions of the factors used in the model to test germination and establishment in the field and the number of seeds used for each factor

Factor	Description	Germination				Establishment			
		Total number of seeds	Number not germinated	Number germinated	Percent germinated	Total number of seeds	Number not established	Number established	Percent established
Total		4073	3923	150	3.68	4062	3966	96	2.36
Location	Seme	1348	1287	61	4.53	1337	1302	35	2.62
Location	Nombali	1364	1300	64	4.69	1364	1316	48	3.52
Location	Le Dube	1361	1336	25	1.84	1361	1348	13	0.96
Species	<i>A. karroo</i>	1786	1695	91	5.10	1788	1701	87	4.87
Species	<i>A. luederitzii</i>	720	684	36	5.00	707	704	3	0.42
Species	<i>A. nilotica</i>	1567	1544	23	1.47	1567	1561	6	0.38
Burnt or unburnt	burnt	2021	1950	71	3.51	2030	1985	45	2.22
Burnt or unburnt	unburnt	2052	1973	79	3.85	2032	1981	51	2.51
Tall or short grass	tall (> 0.1m)	2039	1961	78	3.83	2041	1993	48	2.35
Tall or short grass	short (<0.1m)	2034	1962	72	3.54	2021	1973	48	2.38
Site burnt or unburnt	burnt	2052	1977	75	3.65	2052	2003	49	2.39
Site burnt or unburnt	unburnt	2021	1946	75	3.71	2010	1963	47	2.34

Table 4.2 Log-likelihood III, Chi-square and Wald statistics indicating the significance of the factors and interactions on germination in the field. Significant factors and interactions are indicated in bold

Factor	df	Log-likelihood	Chi-Square	Wald Stat.	p
Location	2	-587.555	13.915	11.547	0.003
Species	2	-597.790	34.386	25.394	0.000
Burnt status	1	-582.073	2.951	2.822	0.093
Grass length	1	-580.622	0.050	0.050	0.822
Site burn status	1	-580.608	0.021	0.021	0.885
Location*species	4	-582.584	3.974	3.827	0.430
Location*burn status	2	-582.929	4.664	4.373	0.112
Location*grass length	2	-586.296	11.397	10.812	0.004
Location*site burn status	2	-580.703	0.212	0.211	0.900
Species*burn status	2	-581.173	1.151	1.145	0.564
Species*grass length	2	-581.019	0.843	0.837	0.658
Species*site burn status	2	-583.309	5.424	5.166	0.076
Burn status*grass length	1	-580.767	0.340	0.341	0.559
Burn status*site burn status	1	-585.060	8.926	8.656	0.003
Grass length*site burn status	1	-587.530	13.866	13.082	0.000

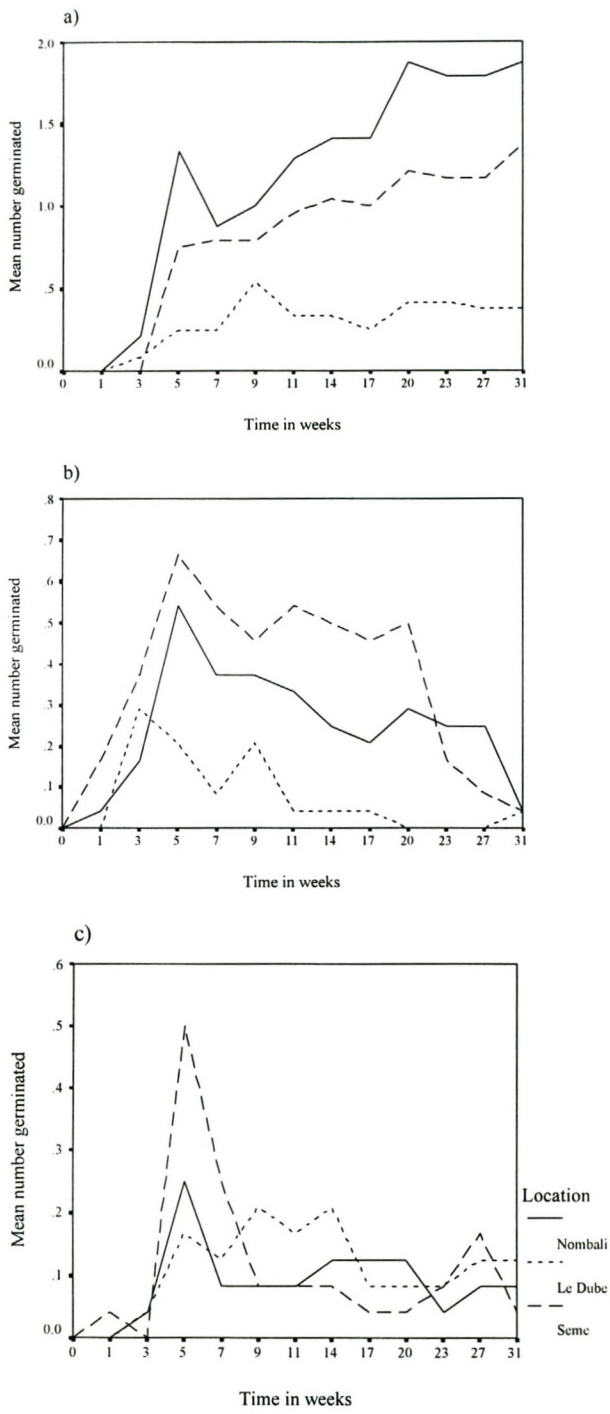
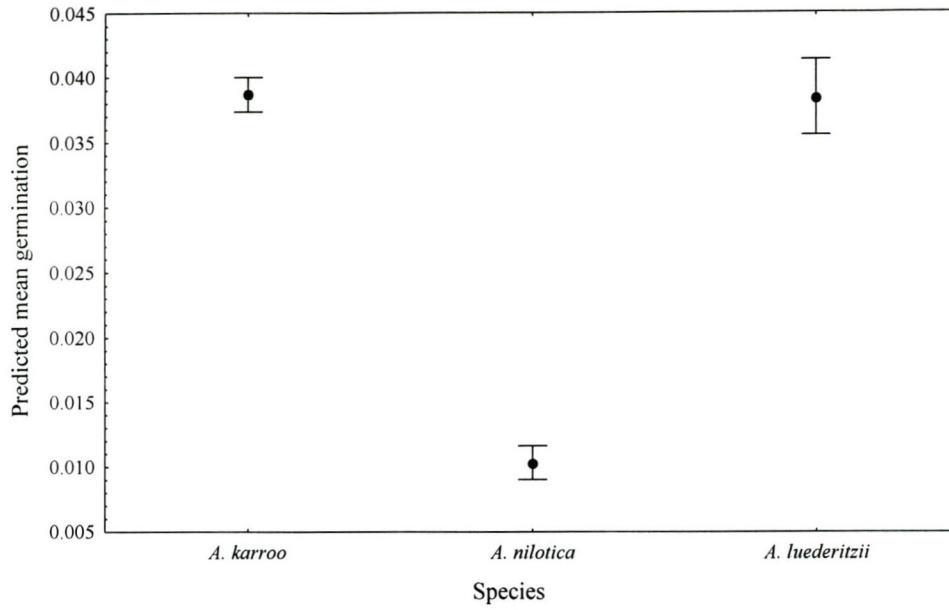


Figure 4.2 Mean number of germinated seeds recorded over a 31-week period at three different locations in HUP for a) *Acacia karroo*, b) *Acacia luederitzii* and c) *Acacia nilotica*.

a)



b)

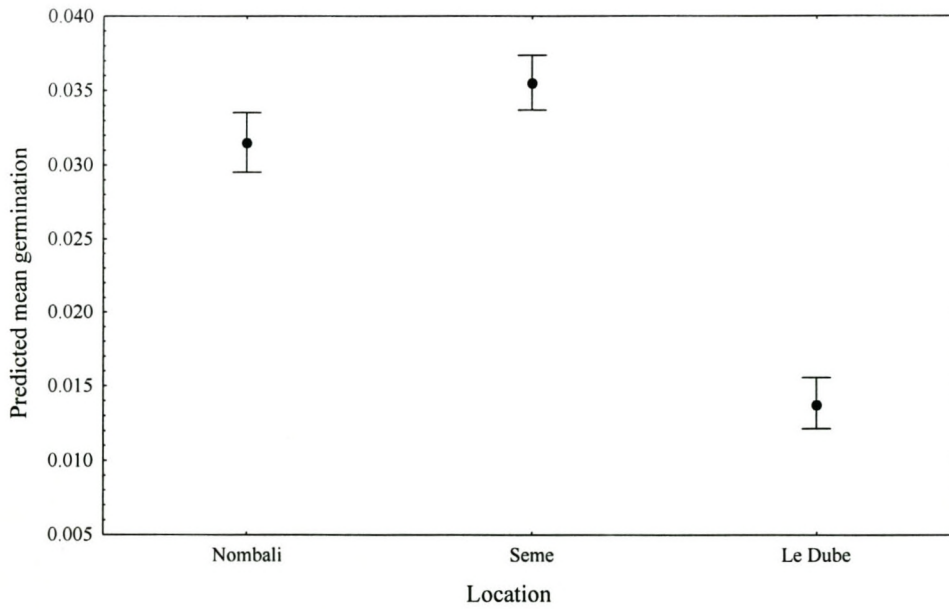
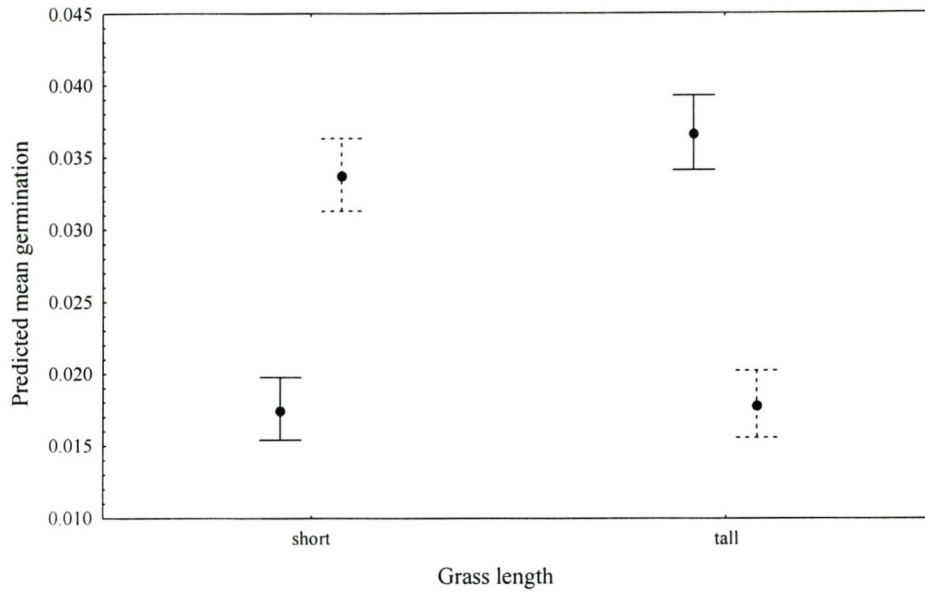


Figure 4.3 Predicted mean germination as a fraction for the significant main effects of a) species and b) location. Vertical error bars show 95% confidence limits.

a)



b)

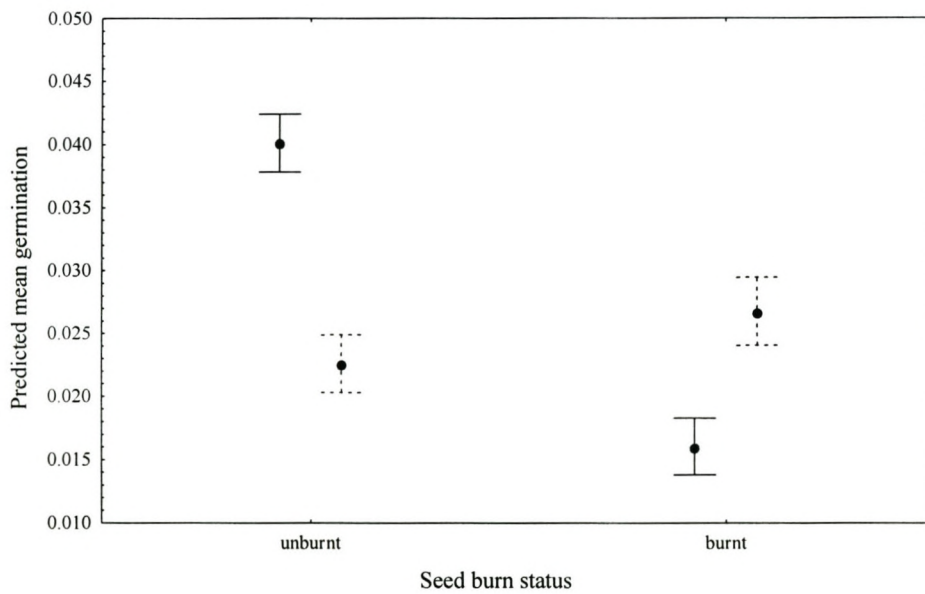


Figure 4.4 Predicted mean germination of seeds as a fraction for the significant interaction of site burn status with a) grass length and b) seed burn status. The solid lines represent unburnt sites and the broken lines burnt sites. Vertical error bars show 95% confidence limits.

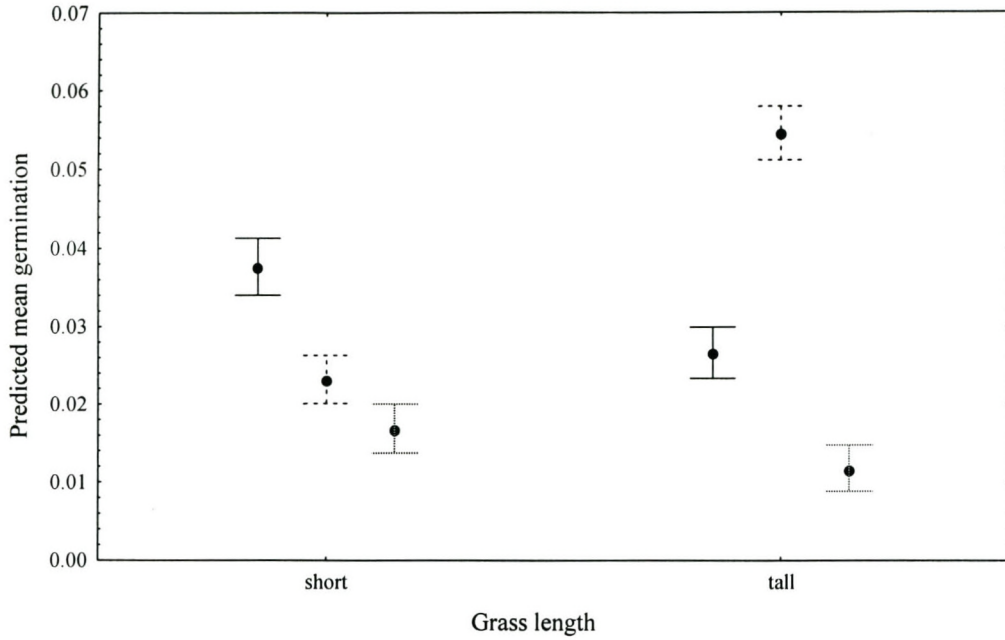


Figure 4.5 Predicted effect of the location x grass length interaction on mean germination. The solid line represents Nombali, the broken line Seme and the dotted line Le Dube. Vertical error bars show 95% confidence limits.

The estimated odds of germination and their associated probabilities for the factors and their interactions are given in Appendix A. The odds ratios for significant effects were calculated. Thus a comparison between *A. karroo* and *A. nilotica* with regards to seeds germinating was made, where

$$\text{Odds ratio} = \frac{\text{estimated odds of germination of } A. \textit{karroo}}{\text{estimated odds of germination of } A. \textit{nilotica}} = 4$$

Thus the odds of germinating are four times more for *A. karroo* than for *A. nilotica*. Similarly *A. nilotica* was four times less likely to germinate than *A. luederitzii* while *A. karroo* and *A. luederitzii* had the same odds of germinating. Differences in germination among species for the various treatments are given in Table 4.3.

There was 2.3 times less germination at Le Dube than at Nombali and 2.6 times less at Le Dube than at Seme. Germinations were 1.2 times more likely at Seme than at Nombali. The odds ratios for the significant interaction effects are given in Table 4.4.

4.4.2 Seedling establishment

The ratio of the model deviance to the degrees of freedom was small (0.17) indicating that the model fitted the data well. Location and species were the only main effects significantly affecting establishment in the field (Table 4.5 & Figure 4.6). *Acacia karroo* showed significantly higher percentage establishment than any of the other species (Appendix B, Table 4.6 & Figure 4.6).

Interaction terms, location x burn status, location x grass length, location x site burn status, burn status x site burn status and grass length x site burn status had a significant effect on establishment (Table 4.5) (Figures 4.7 & 4.8).

Table 4.3 A comparison of germination among species for the different levels of the main factors

	Level of Factor	N	<i>A. karroo</i>			<i>A. luederitzii</i>			<i>A. nilotica</i>					
			Total	Not	%	Total	Not	%	Total	Not	%			
			count	germ	germ	count	germ	germ	count	germ	germ			
Location*Species	Seme	48	591	558	33	5.91	240	224	16	7.14	517	505	12	2.38
Location*Species	Nombali	48	596	551	45	8.17	240	227	13	5.73	528	522	6	1.15
Location*Species	Le Dube	48	599	586	13	2.22	240	233	7	3.00	522	517	5	0.97
Burnt or unburnt*Species	burnt	72	886	839	47	5.60	360	344	16	4.65	775	767	8	1.04
Burnt or unburnt*Species	unburnt	72	900	856	44	5.14	360	340	20	5.88	792	777	15	1.93
Tall or short grass*Species	tall	72	895	851	44	5.17	360	340	20	5.88	784	770	14	1.82
Tall or short grass*Species	short	72	891	844	47	5.57	360	344	16	4.65	783	774	9	1.16
Site burnt or unburnt*Species	yes	72	900	854	46	5.39	360	338	22	6.51	792	785	7	0.89
Site burnt or unburnt*Species	no	72	886	841	45	5.35	360	346	14	4.05	775	759	16	2.11

Table 4.4 Odds ratios for all significant interactions of the germination model

Factor	Level of the factor	Compared with:	Odds ratio
Location*grass length	Le Dube*tall	Le Dube*short	0.656
Location*grass length	Le Dube*tall	Nombali*tall	1.000
Location*grass length	Le Dube*tall	Nombali*short	0.677
Location*grass length	Le Dube*tall	Seme*tall	0.538
Location*grass length	Le Dube*tall	Seme*short	1.235
Location*grass length	Le Dube*short	Nombali*tall	1.524
Location*grass length	Le Dube*short	Nombali*short	1.032
Location*grass length	Le Dube*short	Seme*tall	0.821
Location*grass length	Le Dube*short	Seme*short	1.882
Location*grass length	Nombali*tall	Nombali*short	0.677
Location*grass length	Nombali*tall	Seme*tall	0.538
Location*grass length	Nombali*tall	Seme*short	1.235
Location*grass length	Nombali*short	Seme*tall	0.795
Location*grass length	Nombali*short	Seme*short	1.824
Location*grass length	Seme*tall	Seme*short	2.294
Burn status*site burn status	burnt*burnt	burnt*unburnt	0.571
Burn status*site burn status	burnt*burnt	unburnt*burnt	0.571
Burn status*site burn status	burnt*burnt	unburnt*unburnt	1.000
Burn status*site burn status	burnt*unburnt	unburnt*burnt	1.000
Burn status*site burn status	burnt*unburnt	unburnt*unburnt	1.751
Burn status*site burn status	unburnt*burnt	unburnt*unburnt	1.751
Grass length*site burn status	tall*burnt	tall*unburnt	2.031
Grass length*site burn status	tall*burnt	short*burnt	2.031
Grass length*site burn status	tall*burnt	short*unburnt	1.000
Grass length*site burn status	tall*unburnt	short*burnt	1.000
Grass length*site burn status	tall*unburnt	short*unburnt	0.492
Grass length*site burn status	short*burnt	short*unburnt	0.492

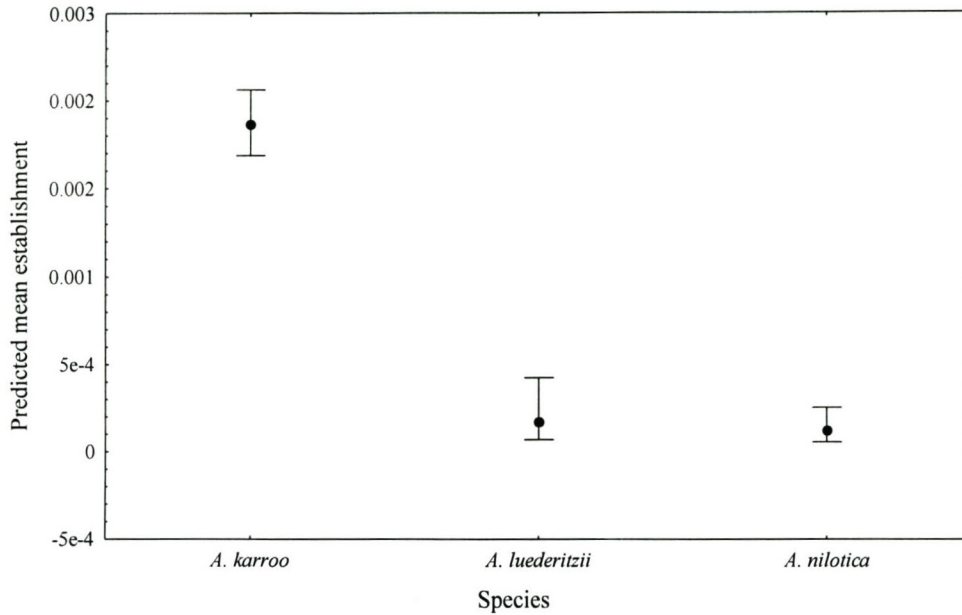
Table 4.5 Log-likelihood I and Chi-square statistics indicating the significance of the factors and interactions on establishment in the field. Significant factors and interactions are indicated in bold

Factor	df	Log-likelihood	Chi-Square	p
Location	2	-443.238	22.292	<0.001
Species	2	-395.199	96.079	<0.001
Burnt status	1	-395.050	0.297	0.586
Grass length	1	-395.049	0.002	0.962
Site burn status	1	-395.040	0.018	0.894
Location*species	4	-391.756	6.568	0.161
Location*burn status	1	-380.850	21.812	<0.001
Location*grass length	2	-373.542	14.617	<0.001
Location*site burn status	2	-367.865	11.353	0.003
Species*burn status	2	-367.468	0.795	0.672
Species*grass length	2	-367.344	0.248	0.884
Species*site burn status	2	-367.180	0.329	0.848
Burn status*grass length	1	-366.723	0.913	0.339
Burn status*site burn status	1	-360.267	12.913	<0.001
Grass length*site burn status	1	-351.784	16.965	<0.001

Table 4.6 A comparison of establishment among species for the different levels of the main factors

Factor	Level of Factor	N	<i>A. karroo</i>				<i>A. luederitzii</i>				<i>A. nilotica</i>			
			Total count	Not estab	% estab	%	Total count	Not estab	% estab	%	Total count	Not estab	% estab	%
Location*Species	Le Dube	48	599	590	9	1.53	240	239	1	0.42	522	519	3	0.58
Location*Species	Nombali	48	598	553	45	8.14	238	237	1	0.42	528	526	2	0.38
Location*Species	Seme	48	591	558	33	5.91	229	228	1	0.44	517	516	1	0.19
Burnt or unburnt*Species	burnt	72	886	843	43	5.10	347	346	1	0.29	797	796	1	0.13
Burnt or unburnt*Species	unburnt	72	902	858	44	5.13	360	358	2	0.56	770	765	5	0.65
Tall or short grass*Species	tall	72	897	854	43	5.04	360	358	2	0.56	784	781	3	0.38
Tall or short grass*Species	short	72	891	847	44	5.19	347	346	1	0.29	783	780	3	0.38
Site burnt or unburnt*Species	yes	72	900	855	45	5.26	360	359	1	0.28	792	789	3	0.38
Site burnt or unburnt*Species	no	72	888	846	42	4.96	347	345	2	0.58	775	772	3	0.39

a)



b)

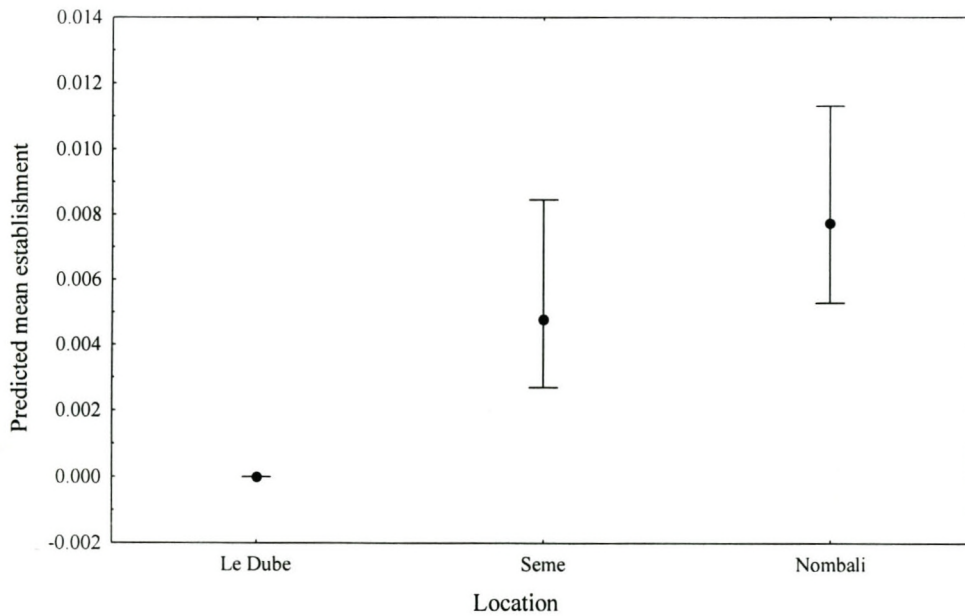
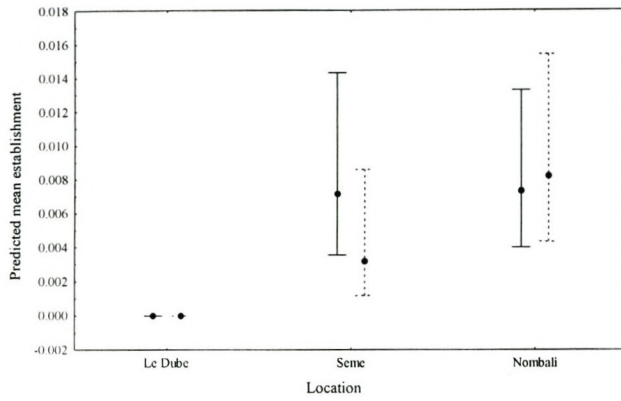
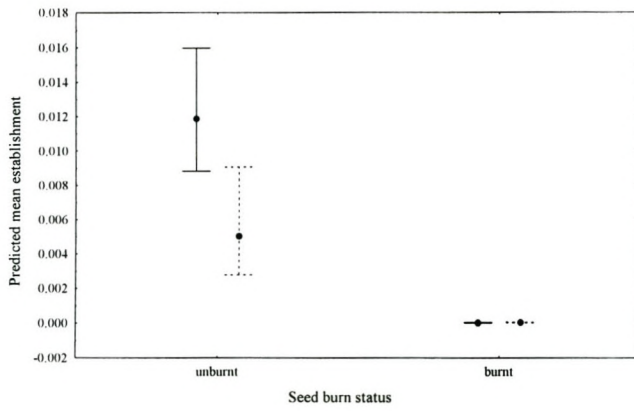


Figure 4.6 Predicted mean establishment for the significant main effects of a) species and b) location. Vertical error bars show 95% confidence limits.

a)



b)



c)

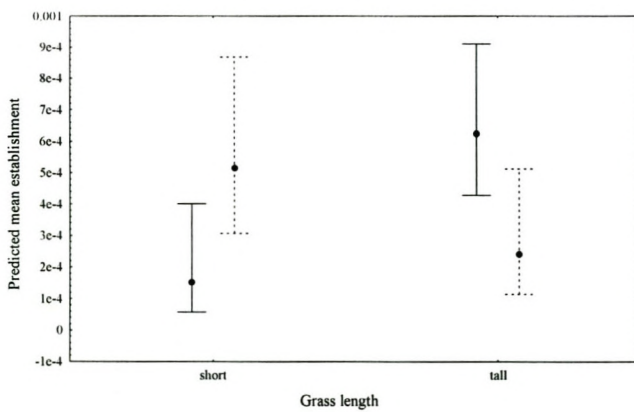


Figure 4.7 Predicted mean establishment for significant interactions of site burn status and a) location, b) seed burn status and c) grass length. The solid line represents unburnt sites and the dotted line burnt sites. Vertical error bars show 95% confidence limits.

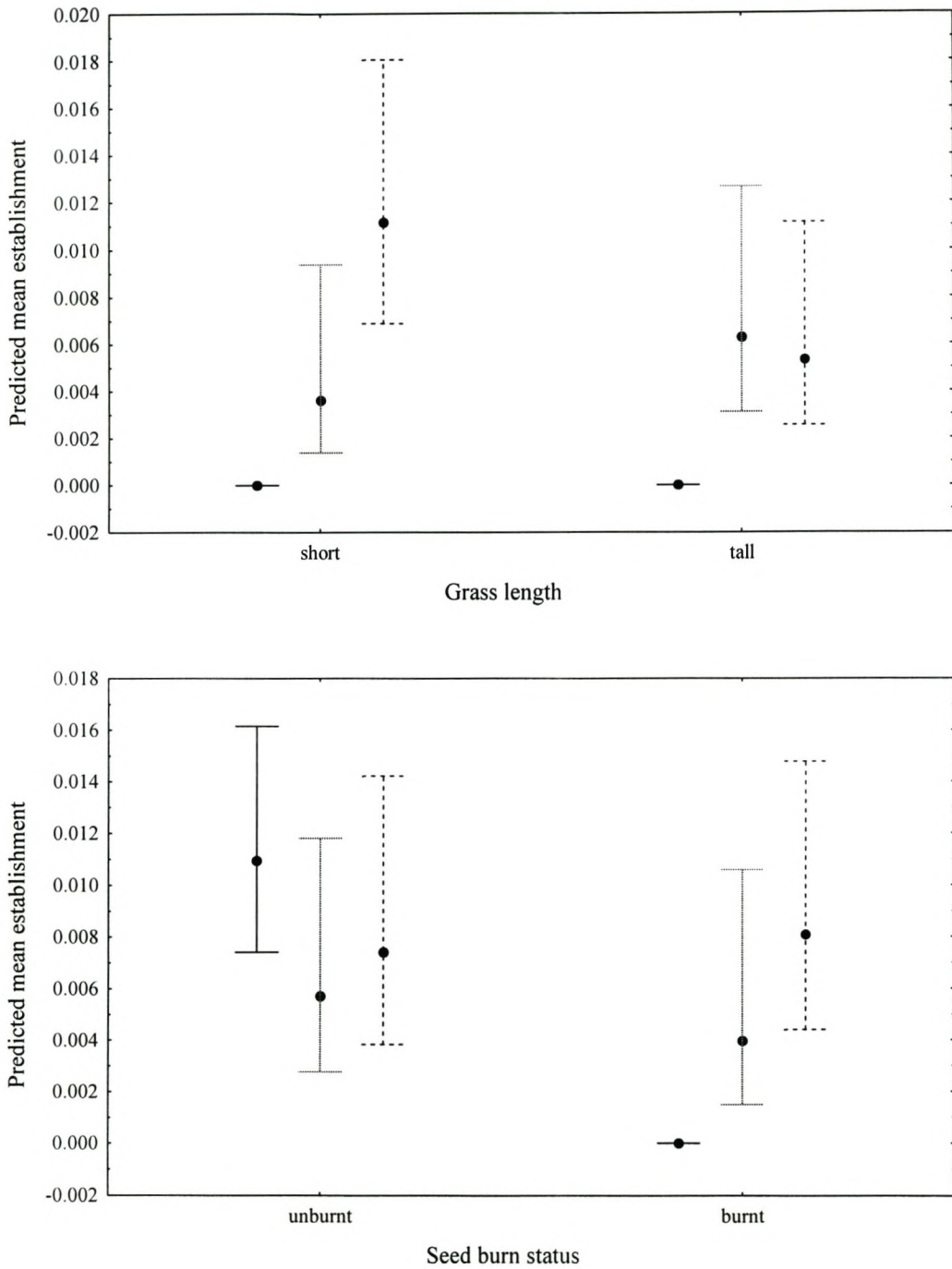


Figure 4.8 Predicted mean establishment for the a) location x grass length and b) location x seed burn status interaction. The solid line represents Le Dube, the dotted line Seme and the broken line Nombali. Vertical error bars show 95% confidence limits.

Appendix B gives the estimated odds of non-establishment and their associated probabilities for the factors and their interactions. The odds ratios for significant effects were calculated in the same way as in Section 4.4.1 and are given in Appendix C.

Acacia karroo was 16.2 times more likely to establish than *A. nilotica*. Similarly *A. luederitzii* was 1.4 times more likely to establish than *A. nilotica* while *A. karroo* had 11.2 times more chance of establishing than *A. luederitzii*. Species differences in establishment for the various treatments are given in Table 4.6.

The odds of establishment were 8046.2 times less at Le Dube than at Nombali and 5850.5 times less at Le Dube than at Seme. 1.4 times more seedlings were likely to establish at Nombali than at Seme. The odds ratios for the significant interaction effects are given in Appendix C.

4.5 Discussion

4.5.1 Germination

The lack of germination of *D. cinerea* in the field suggests that some disturbance other than fire is needed to cause a release from dormancy and commence germination.

Germination of all species in the field was low. Five point one percent of *A. karroo* seeds germinated, which was higher than the other two species. Story (1952) found similar levels of germination for *A. karroo*, with 6.6% of seeds germinating under natural conditions in the field. He also found that *A. karroo* germination was erratic, with germinations still being recorded after 423 days. This was similar to what was found in this study, with the number of *A. karroo* seedlings still increasing until the end of the experiment. *Acacia nilotica* also showed dormancy with sporadic germination events over the 31-week period. *Acacia luederitzii* did not show dormancy with most

germinations taking place in the first 3 weeks of the experiment. *Acacia nilotica* has a thick seed coat, which could account for its poor level of germination. One would predict increased germination of burnt seeds due to a breaking of dormancy (Auld & O'Connell, 1991), but this was not the case. A possible explanation is that the temperature of the fires in this study, though not measured, might not have been sufficient to break dormancy in this species. Some *Acacia* species are temperature specific, suggesting a temperature threshold for germination (Auld & O'Connell, 1991; Kanz, 2001). This is unlikely in this case as Radford *et al.* (1999) found *A. nilotica* seeds to be highly vulnerable to fire with a 80% mortality of seeds on the soil surface. The current study, however, found no difference in germination between burnt and unburnt seed or seeds burnt at different temperatures. This finding is inconsistent with the recent study by Kanz (2001) who found increased seed germination in low fires compared to the control as well as that of Okello and Young (2000) who found increased germination of unburnt seeds. Auld & O'Connell (1991) had similar results to that of Kanz (2001) with strong germination responses to heat.

Location had a significant effect on germination with Le Dube having very low germination overall and Seme having the most germinations. Germination at Nombali and Seme were similar. Site-specific effects may be attributed to various factors such as microclimate or soil type. Sites may also have different water infiltration rates and runoff, which may result in differences in germination levels. Okello and Young (2000), however, found that soil type did not affect germination or establishment of *Acacia drepanolobium* in Kenya.

The current study did not find a difference in the number of seedlings in burnt and unburnt patches. While neither burning of seeds nor burning of sites had any effect

on germination, the interaction factor proved significant with unburnt seeds showing increased germination in unburnt sites as did burnt seeds in burnt sites. Kanz (2001) also found greater seedling emergence of unburnt seeds in unburnt areas. This might be a result of burnt seeds imbibing faster than unburnt seeds, possibly making them more susceptible to rot. Burnt seeds would therefore show poorer germination in unburnt areas due to increased moisture retention. Similarly, unburnt seeds would require more moisture to imbibe, resulting in decreased germination in burnt areas due to decreased moisture in these open areas.

Whilst more seeds germinated in short grass at both Le Dube and Nombali, those at the short-grass site (Seme) had higher levels of germination in tall grass sites. The short grass site at Seme is a white rhinoceros (*Ceratotherium simum*) grazing lawn with very short grass, which may lead to seeds losing moisture through more direct sunlight. This suggests a similar pattern to the seed burn x site burn interaction. The tall grass site at Seme had higher germination than any of the other tall or short grass sites. This may be due to possible site-specific effects mentioned earlier.

There was also an interaction between grass length and site burn with seeds in burnt, short grass showing higher germination than those in burnt, tall grass and unburnt sites showing higher germination in tall grass. As half of the seeds on a burnt or unburnt site were burnt themselves, it is possible that this interaction is due to temperature sensitivity in seeds. Burning in tall grass (hotter fires) may be detrimental to the germination of seeds (Auld & O'Connell, 1991) while cooler fires may be sufficient to break dormancy and cause germination. Higher germinations in unburnt tall grass areas suggest a shade effect. This is not certain, as the effects of shade and grass competition were not separated in this study. *Acacia karroo* has however been reported as having an

increased ability to survive in shade with recruitment of seedlings being dependent on moisture availability (O'Connor, 1995). Tall grass species may be poorer competitors and retain more moisture than short grass species, affording seeds a better opportunity for germination.

No species factor interactions were observed suggesting that though species had different germination levels, they did not respond differently to the treatments.

4.5.2 Seedling establishment

The same factors and interactions found to be significant influences on germination were found to influence establishment. This was expected as increased germination for these treatments would result in better establishment. The interaction patterns for most of the treatments, however, were different to those of the germination model.

Le Dube again had the least seedlings at 31 weeks while Nombali had the best establishment. Seme, which had the highest level of germination, had establishment levels somewhere between that of the other two sites. It is again suggested that this may be due to soil or rainfall factors. Forty-five out of forty-eight seedlings established at Nombali and thirty-three out of thirty-five at Seme were *A. karroo* seedlings. This species is known to be dependent on moisture availability for survival (O'Connor, 1995) and these two sites might have better water retaining ability than Le Dube.

At week 31, 87 *A. karroo* seedlings had established as opposed to six of *A. nilotica* and three of *A. luederitzii*. The high germination, but poor survival of *A. luederitzii* suggests that the absence of this species in the Hluhluwe section of HUP is not due to seed limitation or germinability, but possibly due to environmental factors decreasing its ability to establish. The differences in seedling survival between species

are consistent with those reported by Kanz (2001) who found higher seedling survival for *A. karroo* than *A. nilotica*.

The location x grass length interaction revealed the same patterns as for germination with regards to Nombali and Seme with Seme showing better establishment in tall grass and Nombali showing better establishment in short grass. There was no difference between establishment on tall and short grass at Le Dube. The short grass site at Nombali had the highest number of seedlings surviving at week 31.

The grass length x site burn interaction displayed the same patterns as for the germination model, but this was not the case for the seed burn status x site burn status interaction. While unburnt seeds still did well on unburnt sites, burnt and unburnt seeds showed decreased establishment on burnt sites suggesting that, as a result of increased irradiance, burnt (open) sites may not hold sufficient moisture for seedlings to survive.

The interaction effects found to be significant for establishment only, both suggest the importance of fire temperature. Location x seed burn status and location x site burn status could both relate to the different grass lengths, and thus specific fire temperatures, at the three sites. Temperature sensitivity in *Acacia* species have been reported elsewhere (Pieterse & Cairns, 1986; Bradstock & Auld, 1995; Mbalo & Witkowski, 1997; Kanz, 2001). Kanz (2001) found increased survival and growth in burnt areas. In this study, Nombali was the only location to have higher establishment on burnt sites, while Seme had increased establishment on unburnt site and Le Dube very little establishment overall. In general, however, this study found no difference in establishment in burnt and unburnt areas.

Chirara, Frost & Gwarazimba (1998) found that intensity of grass defoliation does not affect seedling establishment of *A. karroo* during the first year. Similarly, there

was no difference in establishment of *A. karroo* in burnt or unburnt and tall or short grass sites. Smith & Goodman (1986) reported that *A. nilotica* seedlings, however, almost exclusively occurred away from canopy cover, suggesting an inability to establish in shaded environments. *Acacia tortilis* also showed a greater proportion of established seedlings in open than shaded areas (Smith & Shackleton, 1988). I did not find a difference in establishment of *A. nilotica* in tall and short grass, but its establishment was so low that no real prediction can be made.

Seedling establishment of *A. karroo* is strongly moisture dependent (O'Connor, 1995) and one would expect that *A. karroo* is more likely to invade moist rather than semi-arid grassland. This suggests that Hluhluwe Game Reserve, being an area with moist grassland, would be more prone to invasion by *A. karroo*. It has also been reported that *A. karroo* has the ability to withstand fire (Mbalo & Witkowski, 1997). A combination of these factors may contribute to the success of *A. karroo* in the field and may be the reason for *A. karroo*'s success over *A. nilotica* as the most important encroaching *Acacia* species in HUP at present. The literature does, however, suggest that high intensity fires may result in seed mortality (Auld & O'Connell, 1991; Kanz, 2001). It has, however, been reported that *A. karroo* seedlings survive fires from as little as 12 months of age (Story, 1952). Therefore, if fires are not hot enough to kill the seeds allowing them to germinate and seedlings to establish, management burns in the following year may not be useful in its attempt to control the establishment of this species. Back fires have higher fire intensities than head fires (Kanz, 2001). I therefore suggest that backfires be used during management burns and that fire frequency be increased in an attempt to slow down the rate of encroachment by *A. karroo*. It has been reported that spring burns are the most effective ((Scott, 1949) in Story 1952) and this

should be taken into account.

4.6 Acknowledgements

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4.8 Appendices

Appendix A The parameters of the logit model and odds, estimated odds of germination, the ratio of germination to non-germination and the associated probability of the odds for the factors included in the model for germination of certain *Acacia* seeds in HUP.

Factor	Level of Factor	Parameters of logit model	Parameters of the odds	Estimated odds	<i>p</i> of the odds
Intercept		-3.668	0.026		
Location	Le Dube	-0.607	0.545	0.014	0.014
Location	Nombali	0.241	1.273	0.032	0.031
Location	Seme	0.366	1.441	0.037	0.035
Species	<i>A.k</i>	0.455	1.576	0.040	0.039
Species	<i>A.l</i>	0.446	1.562	0.040	0.038
Species	<i>A.n</i>	-0.901	0.406	0.010	0.010
Burn status	burnt	-0.194	0.824	0.021	0.021
Burn status	unburnt	0.194	1.214	0.031	0.030
Grass length	tall	0.026	1.026	0.026	0.026
Grass length	short	-0.026	0.974	0.025	0.024
Site burn status	burnt	-0.017	0.983	0.025	0.024
Site burn status	unburnt	0.017	1.017	0.026	0.025
Location*species	Le Dube* <i>A.k</i>	-0.196	0.822	0.021	0.021
Location*species	Le Dube* <i>A.l</i>	0.066	1.068	0.027	0.027
Location*species	Le Dube* <i>A.n</i>	0.130	1.139	0.029	0.028
Location*species	Nombali* <i>A.k</i>	0.333	1.396	0.036	0.034
Location*species	Nombali* <i>A.l</i>	-0.038	0.963	0.025	0.024
Location*species	Nombali* <i>A.n</i>	-0.296	0.744	0.019	0.019
Location*species	Seme* <i>A.k</i>	-0.138	0.871	0.022	0.022
Location*species	Seme* <i>A.l</i>	-0.028	0.972	0.025	0.024
Location*species	Seme* <i>A.n</i>	0.166	1.181	0.030	0.029
Species*burn status	<i>A.k</i> *burnt	0.134	1.143	0.029	0.028
Species*burn status	<i>A.k</i> *unburnt	-0.134	0.875	0.022	0.022
Species*burn status	<i>A.l</i> *burnt	-0.062	0.940	0.024	0.023
Species*burn status	<i>A.l</i> *unburnt	0.062	1.064	0.027	0.026
Species*burn status	<i>A.n</i> *burnt	-0.072	0.930	0.024	0.023
Species*burn status	<i>A.n</i> *unburnt	0.072	1.075	0.027	0.027
Species*grass length	<i>A.k</i> *tall	-0.084	0.920	0.023	0.023
Species*grass length	<i>A.k</i> *short	0.008	1.008	0.026	0.025
Species*grass length	<i>A.l</i> *tall	0.123	1.131	0.029	0.028
Species*grass length	<i>A.l</i> *short	-0.123	0.884	0.023	0.022
Species*grass length	<i>A.n</i> *tall	-0.040	0.961	0.025	0.024
Species*grass length	<i>A.n</i> *short	0.040	1.041	0.027	0.026
Species*site burn status	<i>A.k</i> *burnt	-0.017	0.983	0.025	0.024

Appendix A Continued:

Factor	Level of Factor	Parameters of logit model	Parameters of the odds	Estimated odds	<i>p</i> of the odds
Species*site burn status	<i>A.k*</i> unburnt	0.017	1.017	0.026	0.025
Species*site burn status	<i>A.l*</i> burnt	0.355	1.426	0.036	0.035
Species*site burn status	<i>A.l*</i> unburnt	-0.355	0.701	0.018	0.018
Species*site burn status	<i>A.n*</i> burnt	-0.338	0.713	0.018	0.018
Species*site burn status	<i>A.n*</i> unburnt	0.338	1.402	0.036	0.035
Location*burn status	Le Dube*burnt	-0.339	0.713	0.018	0.018
Location*burn status	Le Dube*unburnt	0.339	1.404	0.036	0.035
Location*burn status	Nombali*burnt	0.229	1.258	0.032	0.031
Location*burn status	Nombali*unburnt	-0.229	0.795	0.020	0.020
Location*burn status	Seme*burnt	0.109	1.116	0.028	0.028
Location*burn status	Seme*unburnt	-0.109	0.897	0.023	0.022
Location*grass length	Le Dube*tall	-0.216	0.806	0.021	0.020
Location*grass length	Le Dube*short	0.216	1.241	0.032	0.031
Location*grass length	Nombali*tall	-0.206	0.813	0.021	0.020
Location*grass length	Nombali*short	0.206	1.229	0.031	0.030
Location*grass length	Seme*tall	0.423	1.526	0.039	0.037
Location*grass length	Seme*short	-0.423	0.655	0.017	0.016
Location*site burn status	Le Dube*burnt	-0.078	0.925	0.024	0.023
Location*site burn status	Le Dube*unburnt	0.078	1.081	0.028	0.027
Location*site burn status	Nombali*burnt	0.033	1.034	0.026	0.026
Location*site burn status	Nombali*unburnt	-0.033	0.968	0.025	0.024
Location*site burn status	Seme*burnt	0.045	1.046	0.027	0.026
Location*site burn status	Seme*unburnt	-0.045	0.956	0.024	0.024
Burn status*grass length	burnt*tall	-0.057	0.945	0.024	0.024
Burn status*grass length	burnt*short	0.057	1.059	0.027	0.026
Burn status*grass length	unburnt*tall	0.057	1.059	0.027	0.026
Burn status*grass length	unburnt*short	-0.057	0.945	0.024	0.024
Burn status*site burn status	burnt*burnt	0.280	1.324	0.034	0.033
Burn status*site burn status	burnt*unburnt	-0.280	0.756	0.019	0.019
Burn status*site burn status	unburnt*burnt	-0.280	0.756	0.019	0.019
Burn status*site burn status	unburnt*unburnt	0.280	1.324	0.034	0.033
Grass length*site burn status	tall*burnt	-0.354	0.702	0.018	0.018
Grass length*site burn status	tall*unburnt	0.354	1.425	0.036	0.035
Grass length*site burn status	short*burnt	0.354	1.425	0.036	0.035
Grass length*site burn status	short*unburnt	-0.354	0.702	0.018	0.018

Appendix B The parameters of the logit model and odds, estimated odds of establishment, the ratio of establishment to non-establishment and the associated probability of the odds for the factors included in the model for establishment of seeds of certain *Acacia* species in HUP.

Factor	Level of Factor	Parameters of logit model	Parameters of the odds	Estimated odds	<i>p</i> of odds
Intercept		-8.015	0.000		
Location	Le Dube	-5.834	0.003	0.0000	0.000
Location	Nombali	3.159	23.557	0.0078	0.008
Location	Seme	2.841	17.129	0.0057	0.006
Species	<i>A.k</i>	1.732	5.651	0.0019	0.002
Species	<i>A.l</i>	-0.680	0.506	0.0002	0.000
Species	<i>A.n</i>	-1.051	0.349	0.0001	0.000
Burn status	burnt	-3.161	0.042	0.0000	0.000
Burn status	unburnt	3.327	27.868	0.0092	0.009
Grass length	tall	0.016	1.016	0.0003	0.000
Grass length	short	-0.164	0.849	0.0003	0.000
Site burn status	burnt	-0.067	0.935	0.0003	0.000
Site burn status	unburnt	-0.067	0.935	0.0003	0.000
Location*species	Le Dube* <i>A.k</i>	-0.748	0.474	0.0002	0.000
Location*species	Le Dube* <i>A.l</i>	0.260	1.296	0.0004	0.000
Location*species	Le Dube* <i>A.n</i>	-0.488	0.614	0.0002	0.000
Location*species	Nombali* <i>A.k</i>	0.029	1.030	0.0003	0.000
Location*species	Nombali* <i>A.l</i>	-0.231	0.794	0.0003	0.000
Location*species	Nombali* <i>A.n</i>	-0.062	0.940	0.0003	0.000
Location*species	Seme* <i>A.k</i>	-0.455	0.634	0.0002	0.000
Location*species	Seme* <i>A.l</i>	-0.029	0.971	0.0003	0.000
Location*species	Seme* <i>A.n</i>	-0.426	0.653	0.0002	0.000
Species*burn status	<i>A.k</i> *burnt	0.188	1.207	0.0004	0.000
Species*burn status	<i>A.k</i> *unburnt	-0.188	0.829	0.0003	0.000
Species*burn status	<i>A.l</i> *burnt	0.231	1.259	0.0004	0.000
Species*burn status	<i>A.l</i> *unburnt	-0.231	0.794	0.0003	0.000
Species*burn status	<i>A.n</i> *burnt	-0.418	0.658	0.0002	0.000
Species*burn status	<i>A.n</i> *unburnt	0.418	1.520	0.0005	0.001
Species*grass length	<i>A.k</i> *tall	0.019	1.019	0.0003	0.000
Species*grass length	<i>A.k</i> *short	-0.019	0.981	0.0003	0.000
Species*grass length	<i>A.l</i> *tall	0.128	1.136	0.0004	0.000
Species*grass length	<i>A.l</i> *short	-0.128	0.880	0.0003	0.000
Species*grass length	<i>A.n</i> *tall	-0.147	0.863	0.0003	0.000
Species*grass length	<i>A.n</i> *short	0.147	1.158	0.0004	0.000
Species*site burn status	<i>A.k</i> *burnt	0.115	1.122	0.0004	0.000
Species*site burn status	<i>A.k</i> *unburnt	-0.115	0.891	0.0003	0.000
Species*site burn status	<i>A.l</i> *burnt	-0.221	0.802	0.0003	0.000

Appendix B Continued:

Factor	Level of Factor	Parameters of logit model	Parameters of the odds	Estimated odds	<i>p</i> of odds
Species*site burn status	<i>A.l</i> *unburnt	0.221	1.247	0.0004	0.000
Species*site burn status	<i>A.n</i> *burnt	0.106	1.111	0.0004	0.000
Species*site burn status	<i>A.n</i> *unburnt	-0.106	0.900	0.0003	0.000
Location*burn status	Le Dube*burnt	-6.184	0.002	0.0000	0.000
Location*burn status	Le Dube*unburnt	6.184	484.705	0.1602	0.138
Location*burn status	Nombali*burnt	3.372	29.133	0.0096	0.010
Location*burn status	Nombali*unburnt	-3.372	0.034	0.0000	0.000
Location*burn status	Seme*burnt	3.145	23.220	0.0077	0.008
Location*burn status	Seme*unburnt	-3.145	0.043	0.0000	0.000
Location*grass length	Le Dube*tall	-0.423	0.655	0.0002	0.000
Location*grass length	Le Dube*short	0.423	1.527	0.0005	0.001
Location*grass length	Nombali*tall	-0.535	0.586	0.0002	0.000
Location*grass length	Nombali*short	0.535	1.707	0.0006	0.001
Location*grass length	Seme*tall	0.112	1.118	0.0004	0.000
Location*grass length	Seme*short	-0.112	0.894	0.0003	0.000
Location*site burn status	Le Dube*burnt	0.483	1.622	0.0005	0.001
Location*site burn status	Le Dube*unburnt	-0.483	0.617	0.0002	0.000
Location*site burn status	Nombali*burnt	-0.009	0.991	0.0003	0.000
Location*site burn status	Nombali*unburnt	0.009	1.009	0.0003	0.000
Location*site burn status	Seme*burnt	-0.475	0.622	0.0002	0.000
Location*site burn status	Seme*unburnt	0.475	1.608	0.0005	0.001
Burn status*grass length	burnt*tall	0.089	1.093	0.0004	0.000
Burn status*grass length	burnt*short	-0.089	0.915	0.0003	0.000
Burn status*grass length	unburnt*tall	-0.089	0.915	0.0003	0.000
Burn status*grass length	unburnt*short	0.089	1.093	0.0004	0.000
Burn status*site burn status	burnt*burnt	0.500	1.649	0.0005	0.001
Burn status*site burn status	burnt*unburnt	-0.500	0.606	0.0002	0.000
Burn status*site burn status	unburnt*burnt	-0.500	0.606	0.0002	0.000
Burn status*site burn status	unburnt*unburnt	0.500	1.649	0.0005	0.001
Grass length*site burn status	tall*burnt	-0.542	0.582	0.0002	0.000
Grass length*site burn status	tall*unburnt	0.542	1.719	0.0006	0.001
Grass length*site burn status	short*burnt	0.542	1.719	0.0006	0.001
Grass length*site burn status	short*unburnt	-0.542	0.582	0.0002	0.000

Appendix C Odds ratios for all significant interactions of the establishment model.

Factor	Level of the factor	Compared with:	Odds ratio
Location*burn status	Le Dube*burnt	Le Dube*unburnt	0.000
Location*burn status	Le Dube*burnt	Nombali*burnt	0.000
Location*burn status	Le Dube*burnt	Nombali*unburnt	0.060
Location*burn status	Le Dube*burnt	Seme*burnt	0.000
Location*burn status	Le Dube*burnt	Seme*unburnt	0.048
Location*burn status	Le Dube*unburnt	Nombali*burnt	16.638
Location*burn status	Le Dube*unburnt	Nombali*unburnt	14120.741
Location*burn status	Le Dube*unburnt	Seme*burnt	20.875
Location*burn status	Le Dube*unburnt	Seme*unburnt	11254.800
Location*burn status	Nombali*burnt	Nombali*unburnt	848.712
Location*burn status	Nombali*burnt	Seme*burnt	1.255
Location*burn status	Nombali*burnt	Seme*unburnt	676.458
Location*burn status	Nombali*unburnt	Seme*burnt	0.001
Location*burn status	Nombali*unburnt	Seme*unburnt	0.797
Location*burn status	Seme*burnt	Seme*unburnt	539.164
Location*grass length	Le Dube*tall	Le Dube*short	0.429
Location*grass length	Le Dube*tall	Nombali*tall	1.118
Location*grass length	Le Dube*tall	Nombali*short	0.384
Location*grass length	Le Dube*tall	Seme*tall	0.586
Location*grass length	Le Dube*tall	Seme*short	0.733
Location*grass length	Le Dube*short	Nombali*tall	2.606
Location*grass length	Le Dube*short	Nombali*short	0.894
Location*grass length	Le Dube*short	Seme*tall	1.365
Location*grass length	Le Dube*short	Seme*short	1.707
Location*grass length	Nombali*tall	Nombali*short	0.343
Location*grass length	Nombali*tall	Seme*tall	0.524
Location*grass length	Nombali*tall	Seme*short	0.655
Location*grass length	Nombali*short	Seme*tall	1.527
Location*grass length	Nombali*short	Seme*short	1.909
Location*grass length	Seme*tall	Seme*short	1.251
Location*site burn status	Le Dube*burnt	Le Dube*unburnt	2.630

Appendix C Continued:

Factor	Level of the factor	Compared with:	Odds ratio
Location*site burn status	Le Dube*burnt	Nombali*burnt	1.636
Location*site burn status	Le Dube*burnt	Nombali*unburnt	1.608
Location*site burn status	Le Dube*burnt	Seme*burnt	2.607
Location*site burn status	Le Dube*burnt	Seme*unburnt	1.009
Location*site burn status	Le Dube*unburnt	Nombali*burnt	0.622
Location*site burn status	Le Dube*unburnt	Nombali*unburnt	0.611
Location*site burn status	Le Dube*unburnt	Seme*burnt	0.991
Location*site burn status	Le Dube*unburnt	Seme*unburnt	0.384
Location*site burn status	Nombali*burnt	Nombali*unburnt	0.983
Location*site burn status	Nombali*burnt	Seme*burnt	1.594
Location*site burn status	Nombali*burnt	Seme*unburnt	0.617
Location*site burn status	Nombali*unburnt	Seme*burnt	1.622
Location*site burn status	Nombali*unburnt	Seme*unburnt	0.627
Location*site burn status	Seme*burnt	Seme*unburnt	0.387
Burn status*site burn status	burnt*burnt	burnt*unburnt	2.721
Burn status*site burn status	burnt*burnt	unburnt*burnt	2.721
Burn status*site burn status	burnt*burnt	unburnt*unburnt	1.000
Burn status*site burn status	burnt*unburnt	unburnt*burnt	1.000
Burn status*site burn status	burnt*unburnt	unburnt*unburnt	0.368
Burn status*site burn status	unburnt*burnt	unburnt*unburnt	0.368
Grass length*site burn status	tall*burnt	tall*unburnt	0.339
Grass length*site burn status	tall*burnt	short*burnt	0.339
Grass length*site burn status	tall*burnt	short*unburnt	1.000
Grass length*site burn status	tall*unburnt	short*burnt	1.000
Grass length*site burn status	tall*unburnt	short*unburnt	2.954
Grass length*site burn status	Short*burnt	short*unburnt	2.954

Chapter 5

Post-dispersal fate of *Acacia karroo* and *Acacia nilotica* seeds as affected by site, grass length, canopy cover and rodent presence

5.1 Abstract

African *Acacia* species are often major contributors to the progressive increase in the woody component of savannas, a phenomenon commonly referred to as bush encroachment. They produce large quantities of seed dispersed by wind and animals. In Hluhluwe-Umfolozi Park, the numbers of adult *Acacia nilotica* trees per hectare far exceed that of *A. karroo* adults. The relative dominance is reversed in the juvenile stage with *A. karroo* outnumbering *A. nilotica* threefold outside closed woodlands. This chapter investigated the effects of location, structural habitat type, species, predator type and rodent presence on the level of post-dispersal predation in Hluhluwe-Umfolozi Park. Post-dispersal predation of *A. karroo* seeds (21.8%) was higher than that of *A. nilotica* (12.7%). Predation levels depended on site, structural habitat type, level of protection from different predator types and rodent presence/absence. There was more rodent predation in tall grass areas (26.0%) than short grass (10.7%) or canopy areas (15.2%), and most seeds were lost from unprotected control groups. Rodent presence was a significant factor in a model aiming to determine reasons for unexplained seed disappearance.

5.2 Introduction

The increasing density in the woody component at the expense of the grass layer, in grasslands and savannas, has been widely reported (West, 1947; Scott, 1967; Archer, 1989; Grossman & Gandar, 1989; Roques, O'Connor & Watkinson, 2001) with special mention being made of *Acacia karroo* Hayne (O'Connor, 1995; Chirara, Frost & Gwarazimba, 1998) and *A. nilotica* (L.) Willd. Ex Del. subsp. *kraussiana* (Benth.) Brenan (Mackey, 1997; Kriticos *et al.*, 1999) as major contributors to the phenomenon commonly referred to as bush encroachment.

African *Acacia* species are able to produce large quantities of hard coated seeds that are either wind dispersed (dehiscent species) or animal dispersed (indehiscent species) (Coe & Coe, 1987). Seeds are dispersed by these agents in an attempt at reaching suitable sites for establishment. Post-dispersal predators may, however, exact a varying loss of dispersed seeds, resulting in varying levels of seedling establishment.

In Hluhluwe-Umfolozi Park (HUP), acacias are seen as major contributors to bush encroachment. As little as 19 years ago, Whateley & Porter (1983) reported *A. karroo* to be largely confined to the north-eastern part of HUP. This was confirmed by Bond, Smythe & Balfour (2001) who reported that in HUP, *A. karroo* Woodlands were rare and found no adult trees in any of their transects selected to cover a wide altitudinal range. They did, however, find 111 (62.5 ha⁻¹) adult *A. nilotica* trees while specifically avoiding closed *A. nilotica* Woodlands. This relative dominance was reversed in juvenile stages with *A. karroo* (725 ha⁻¹) outnumbering *A. nilotica* (225 ha⁻¹) threefold and setting woodland structure to change in the future (Bond *et al.*, 2001).

Small mammals and larger insects are important post-dispersal predators, with predation being variable in space and time (Crawley, 1992; Andresen, 1999).

This study investigated the effect of structural habitat type on post-dispersal survival of *A. nilotica* and *A. karroo* seeds in HUP. The current study also aimed to identify possible post-dispersal predators and attempted to relate the post-dispersal fate of these two species to the current differences in their success in HUP.

5.3 Materials and Methods

5.3.1 Study site

The field experiment took place in the Hluhluwe and Corridor sections of HUP. Climate and vegetation descriptions are given in Section 3.3.1.

5.3.2 Field experiment

A field experiment was conducted to determine the post-dispersal fate of *A. karroo* and *A. nilotica* seeds. The experiment was conducted at four sites. Each site was represented by three habitat 'types' of interest namely, tall grass (>0.1 m), short grass (<0.1 m) and canopy areas (areas under *Acacia* canopies). Three types of cages, each containing five *A. karroo* and five *A. nilotica* seeds, were placed in each of the structural habitat types at all four sites. Cages were classified as small (made from 13 mm chicken wire netting), big (made from 58 mm wire netting) and open (unprotected controls). Six replications of cage type were used (Figure 5.1). The cages aimed to exclude different types of predators from the seeds. The removal of seeds was monitored on a weekly basis up to 35 days and every 12 – 14 days thereafter up to 191 days. Rodent presence indicated by chewed seed 'shells' and/or rodent droppings, number of chewed seeds (shells remaining), number of remaining seeds, number of germinated seeds and number of seedlings were recorded for each of the species. The number of seeds that

‘disappeared’ were calculated as: $5 - (\text{the number chewed} + \text{the number germinated} + \text{the number lost through ungulate trampling})$.

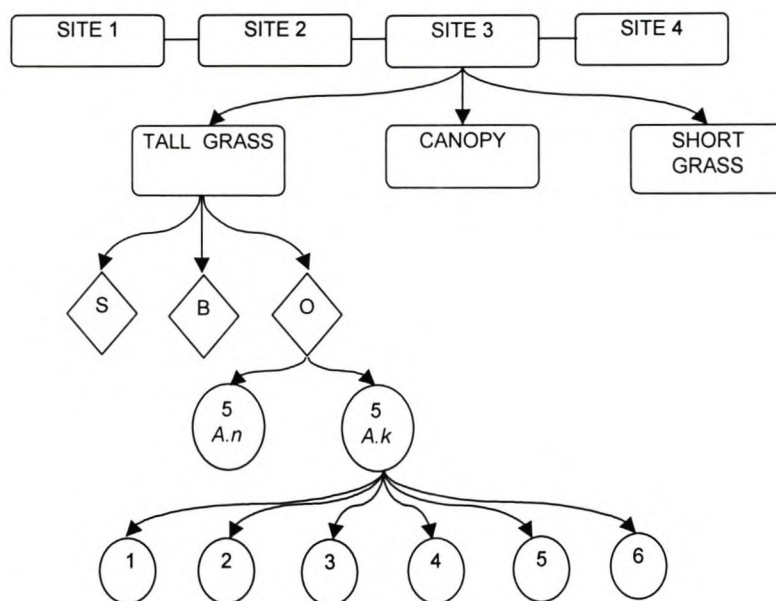


Figure 5.1 Experimental design to determine the post-dispersal fate of *A. nilotica* and *A. karroo* seeds. The letters S, B and O refer to small, big and ‘open’ cages respectively while *A.n* and *A.k* refer to *Acacia nilotica* and *Acacia karroo* respectively. Numbers 1 to 6 refer to the number of replications.

5.33 Data analysis

The “STATISTICA[®]” (v 5.5, StatSoft, Inc., 2000) Generalized Linear Model (GLM) module was used to build models for number of chewed seeds and number of disappeared seeds as response variables. Data was of a binomial nature with an inverse normal distribution. The probit model was thus used as the link function. All effects except the fourth order interactions were included in the models. The probit model for

the number of seeds chewed may be written as follows:

$$NP(\text{number chewed}) = NP(\lambda' + \lambda_j^{iB} + \lambda_k^{iC} + \lambda_l^{iD} + \lambda_m^{iE} + \lambda_n^{iF} + \lambda_{jk}^{iBC} + \dots + \lambda_{mm}^{iEF})$$

where

NP = the normal probability

λ' = the overall mean effect of the categories

λ_j^{iB} = the effect of the j th species ($j = A. \textit{karroo}, A. \textit{nilotica}$)

λ_k^{iC} = the effect of the k th site ($k = \text{Le Dube, Maqanda, Nombali, Seme}$)

λ_l^{iD} = the effect of the l th cage type ($l = \text{small, big, open}$)

λ_m^{iE} = the effect of the m th structural habitat type ($m = \text{short grass, tall grass, canopy}$)

λ_{jk}^{iBC} = the interaction effect between the j th species and the k th site

λ_{klm}^{iCDE} = the interaction effect between the k th site, the l th cage type and the m th structural habitat type.

The probit model is written as a GLM as follows:

$$\text{Number chewed} = \beta_0 + \beta_1^B \chi_1^B + \beta_1^C \chi_1^C + \beta_2^C \chi_2^C + \beta_3^C \chi_3^C + \beta_1^D \chi_1^D + \beta_2^D \chi_2^D + \beta_1^E \chi_1^E + \beta_2^E \chi_2^E + \beta_{11}^{BC} \chi_{11}^{BC} + \dots + \beta_{111}^{CDE} \chi_{111}^{CDE}$$

where $\beta_0, \beta_1^B, \beta_1^C, \beta_2^C, \beta_3^C, \beta_1^D, \beta_2^D, \beta_1^E, \beta_2^E, \beta_{11}^{BC}$ and β_{111}^{CDE} are the parameters estimated from the data and B, C, D and E refer to the explanatory variables species, site, cage type and structural habitat type respectively. The estimated parameters for the GLM were used to obtain the estimated parameters for the probit

model. The exponents of the estimated parameters give the estimated parameters of the odds and were calculated for each factor or combination of factors (including the intercept). The product of the estimated parameters of the odds of the intercept (estimated geometric mean odds) and the factor or combination of factors in question, equals the estimated odds of being chewed for the given factors or combination of factors. The estimated odds are associated with estimated probabilities and were calculated as follows:

$$P = \frac{odds}{1 + odds}$$

The odds of being chewed or disappearing were compared for significant treatment combinations. The same explanatory variables were used in the model for seed disappearance with the addition of rodent presence as a main factor.

Following Kanz (2001), the predicted frequencies of seeds chewed and disappeared were seen as being appropriate for interpretation as summaries of the data. As the data were aggregated, the predicted values are reported as predicted frequencies and not predicted means as in Chapter 4. Thus, differences in the predicted frequencies of seeds chewed and disappeared were illustrated graphically for each significant treatment combination.

5.4 Results

5.4.1 *Number of chewed seeds*

The maximum number of chewed seeds at each site (as on day 191) (Figure 5.2) was used to test for differences among treatments. The factors used in the model are

described in Table 5.1.

The ratio of the model deviance and the degrees of freedom was small (0.99) indicating that the model fits the data very well. All the explanatory variables significantly affected the number of seeds chewed in the field (Table 5.2). Significant interaction effects were habitat x site, habitat x cage type, site x cage type, habitat x site x species and habitat x site x cage type.

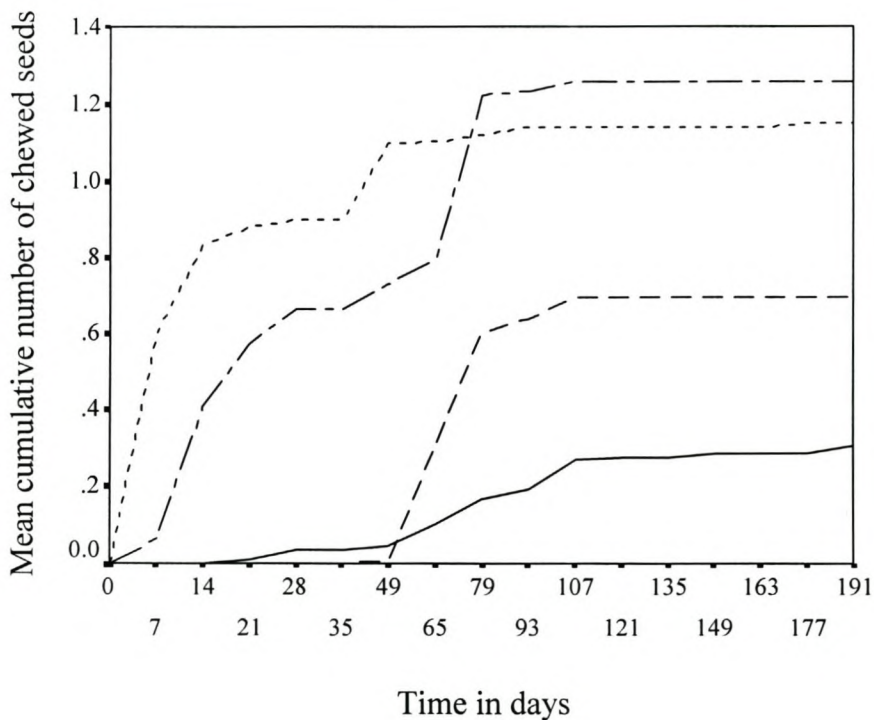


Figure 5.2 Cumulative number of seeds (out of a total of five) chewed over time at Le Dube (intermittent line), Maqanda (dotted line), Nombali (broken line) and Seme (solid line).

Table 5.1 Description of the factors and number of seeds used in the model to determine which factors affect seed predation by rodents in the field

Factor	Description	Total number of seeds	Number chewed	Number not chewed	Percent chewed
Total		2135	368	1767	17.24
Cage type	small	710	83	627	11.69
Cage type	big	710	144	566	20.28
Cage type	open	715	141	574	19.72
Site	Le Dube	520	136	384	26.15
Site	Maqanda	535	124	411	23.18
Site	Nombali	540	75	465	13.89
Site	Seme	540	33	507	6.11
Species	<i>A. karroo</i>	1065	232	833	21.78
Species	<i>A. nilotica</i>	1070	136	934	12.71
Habitat type	tall grass (>0.1m)	700	182	518	26.00
Habitat type	short grass (<0.1m)	720	77	643	10.69
Habitat type	canopy	715	109	606	15.24

Table 5.2 Log-likelihood III, Chi-square and Wald statistics indicating the significance of the factors and interactions on the number of seeds chewed in the field. Significant factors and interactions are indicated in bold

	df	Log-likelihood	Chi-Square	Wald Stat.	<i>p</i>
Habitat type	2	-785.584	41.621	35.296	<0.001
Site	3	-788.425	47.302	43.215	<0.001
Species	1	-775.806	22.064	21.763	<0.001
Cage type	2	-769.992	10.436	10.397	0.006
Habitat*site	6	-787.090	44.632	34.299	<0.001
Habitat*species	2	-764.877	0.206	0.205	0.903
Site*species	3	-768.872	8.197	7.635	0.054
Habitat*cage type	4	-773.788	18.029	12.286	0.015
Site*cage type	6	-784.174	38.801	22.231	0.001
Species*cage type	2	-766.272	2.997	3.012	0.222
Habitat*site*species	6	-782.908	36.269	28.524	<0.001
Habitat*site*cage type	12	-782.312	35.076	24.356	0.018
Habitat*species*cage type	4	-767.846	6.144	6.157	0.188
Site*species*cage type	6	-768.373	7.199	7.065	0.315

The parameters of the probit model and the estimated odds for all factors and interaction factors are given in Appendix A. The estimated odds were used to calculate the odds ratios for all significant factors and second order interaction factors (Appendix B). Thus the odds of *A. karroo* being chewed were 1.5 times that of *A. nilotica* being chewed, where

$$\text{Odds ratio} = \frac{\text{estimated odds of being chewed for } A. \textit{karroo}}{\text{estimated odds of being chewed for } A. \textit{nilotica}} = 1.5$$

The odds of a seed being chewed were highest in tall grass areas while open cages had better odds of containing chewed seeds than small or big cages. Le Dube had the highest odds of having a chewed seed followed by Maqanda, Seme and Nombali, with the latter two showing similarities in odds.

5.4.2 Number of seeds disappeared

The total number of seeds unaccounted for as on day 191 was used in the model. The number of seeds disappearing for each explanatory variable is given in Table 5.3.

The ratio of the model deviance to the degrees of freedom was relatively small (1.80), once again indicating that the model was a reasonably good fit. Species and rodent presence were the only main effects of any significance (Table 5.4) (Figure 5.3). Significant interaction effects were habitat x site, habitat x cage type, site x cage type, species x cage type, habitat x site x species and habitat x site x cage type (Table 5.4) (Figure 5.4).

Table 5.3 Description of the factors and number of seeds used in the model to determine which factors affect seed disappearance in the field

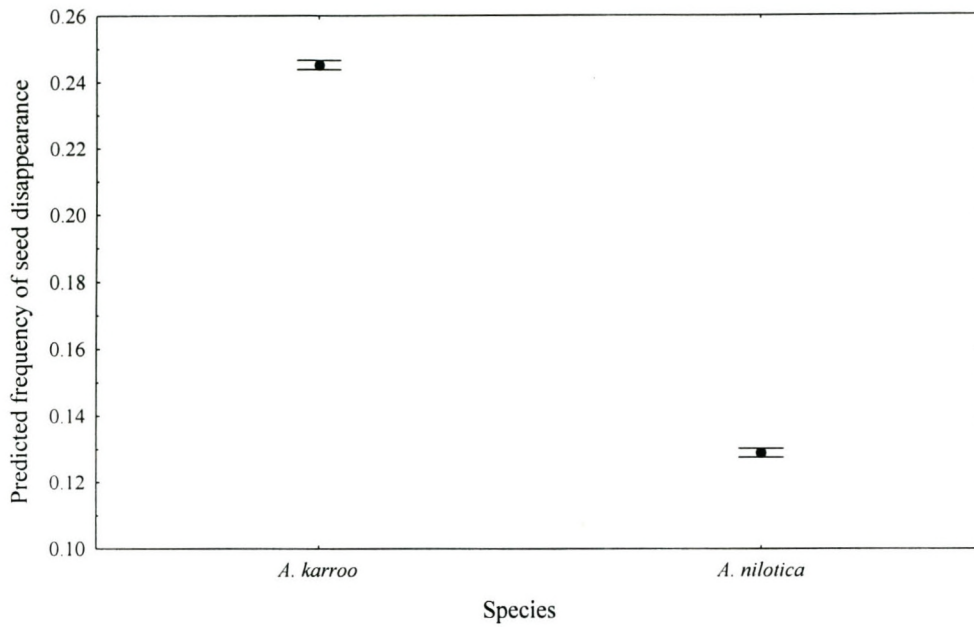
Factor	Description	Total number of seeds	Number disappeared	Number not disappeared	Percent disappeared
Total		2162	536	1626	24.79
Cage type	small	722	170	552	23.55
Cage type	big	725	198	527	27.31
Cage type	open	715	168	547	23.50
Rodents	yes	1152	413	739	35.85
Rodents	no	1010	123	887	12.18
Site	Le Dube	547	174	373	31.81
Site	Maqanda	535	162	373	30.28
Site	Nombali	540	121	419	22.41
Site	Seme	540	79	461	14.63
Species	<i>A. karroo</i>	1080	326	754	30.19
Species	<i>A. nilotica</i>	1082	210	872	19.41
Habitat type	tall grass (>0.1m)	720	205	515	28.47
Habitat type	short grass (<0.1m)	722	163	559	22.58
Habitat type	canopy	720	168	552	23.33

Table 5.4 Log-likelihood III, Chi-square and Wald statistics indicating the significance of the factors and interactions on the number of seeds disappearing in the field..

Significant factors and interactions are indicated in bold

	df	Log-Likelihood	Chi-Square	Wald Stat.	<i>p</i>
Habitat type	2	-943.690	0.748	0.7336	0.693
Site	3	-946.340	6.057	6.0714	0.108
Species	1	-963.410	40.189	38.765	<0.001
Cage type	2	-943.840	1.045	1.0398	0.595
Rodents	1	-1008.080	129.531	120.7465	<0.001
Habitat*site	6	-959.900	33.173	31.1848	<0.001
Habitat*species	2	-943.380	0.134	0.133	0.936
Site*species	3	-947.030	7.440	7.3132	0.063
Habitat*cage type	4	-970.200	53.771	51.3879	<0.001
Site*cage type	6	-949.730	12.839	12.9892	0.043
Species*cage type	2	-949.550	12.479	12.1565	0.002
Habitat*site*species	6	-971.530	56.427	50.4577	<0.001
Habitat*site*cage type	12	-998.840	111.055	97.2158	<0.001
Habitat*species*cage type	4	-945.170	3.712	3.7302	0.444
Site*species*cage type	6	-946.410	6.196	6.0915	0.413

a)



b)

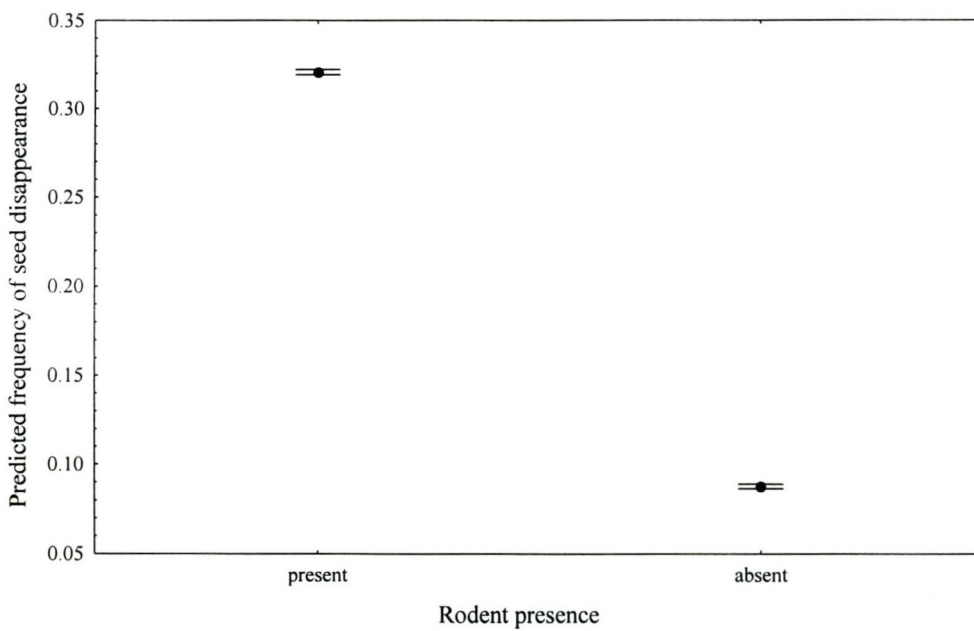


Figure 5.3 Predicted frequencies of disappeared seeds for the main effects of a) species and b) rodent presence. Vertical error bars show 95% confidence limits.

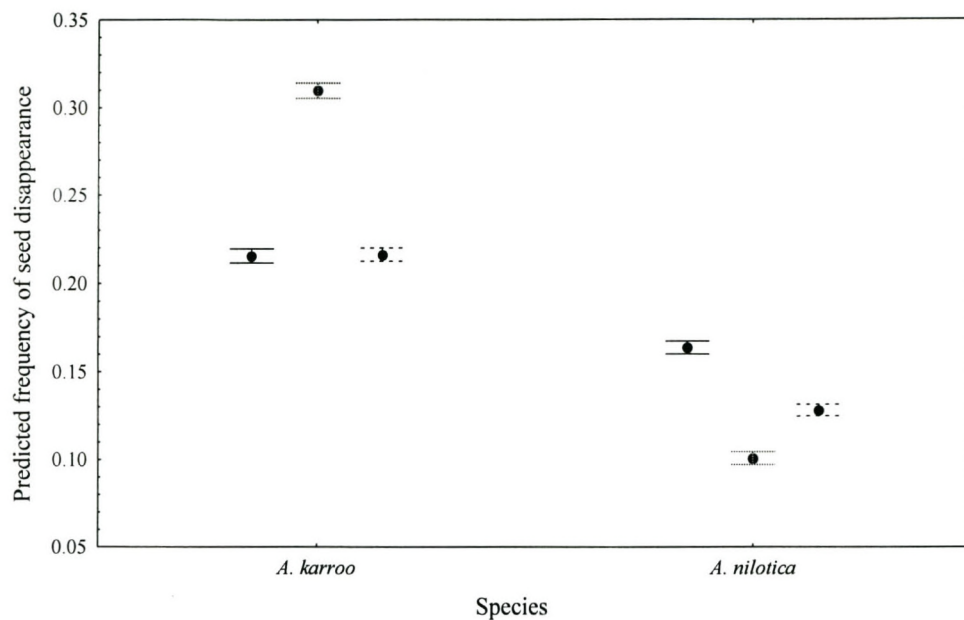


Figure 5.4 Predicted frequencies of disappeared seeds for the significant interaction effect of cage type with species. The solid lines represent small, the dotted lines big and the broken lines open cages. Vertical error bars show 95% confidence limits.

The parameters of the probit model for seed disappearance and the estimated odds for all factors and interaction factors are given in Appendix C. The odds of *A. karroo* disappearing were 1.6 times that of *A. nilotica* disappearing. Predictably, the odds of a seed disappearing were 2.4 times higher in the presence of rodents than in their absence.

The odds ratios for all significant factors and second order interaction factors are given in Appendix D.

5.5 Discussion

5.5.1 Number of chewed seeds

The most striking result was that *A. karroo* was 1.5 times more likely to be chewed than *A. nilotica* with 21.8% of *A. karroo* and 12.7% of *A. nilotica* chewed. Rodent preference for *A. karroo* could be due to the thinner seed coat of this dehiscent species (Coe & Coe, 1987). Miller (1994) found that rodents preferred *A. tortilis* seeds above those of *A. karroo* and *A. nilotica* when looking at numbers of seeds removed, while *A. karroo* was preferred to *A. nilotica*. It is also possible that preferences are based on energy content of seeds. Kerley & Erasmus (1991), however, found no correlation between rodent preference and gross energy content of seeds. Preferences may also be due to differences in seed size. Hulme (1998) found that in temperate grassland, rodents removed proportionally more large seeds than small seeds, while the opposite was true for the current study with the smaller seeded *A. karroo* having higher levels of rodent predation.

Though the number of seeds chewed in small, big and open cages was 11.7%, 20.3% and 19.7% respectively, open cages had the highest predicted frequency of

chewed seeds. There was very little difference between small and big cages, but big cages showed high variation in the number of chewed seeds. Open cages allow access to seeds by rodents explaining the higher levels of predation from these cages.

Seeds were more likely to be chewed in tall grass areas than short grass or canopy sites, which had a similar likelihood of having chewed seeds. Tall grass sites may provide cover for rodents, while canopy sites, though providing cover, may also provide perches for raptors. There was much variation in the number of chewed seeds in canopy sites and it is possible that certain woodland areas are better habitats for rodents than others, which may be related to raptor habitat requirements and distribution. The total number of seeds attacked by rodents and beetles varies with canopy openness (Hammond, Brown & Zagt, 1999). Structural habitat type is considered an important factor in post-dispersal predation (Janzen, 1971) with Linzey & Washok (2000) reporting higher levels of rodent predation in grassy habitat than woody habitat. They, however, did not distinguish between short grass and tall grass habitats.

The significance of site, habitat x cage type, site x cage type, habitat x site and cage type x site x habitat factors are also thought to be related to rodent habitat preference. The short grass area at Nombali, however, showed high rodent predation. This may be explained by it being a smaller short grass patch than at the other sites while being surrounded by tall grass, providing rodent cover in close proximity. Patch sizes and types may affect the movement, distribution and abundance of animals (Zollner & Lima, 1999; Doak, 2000) and I suggest that, though not investigated here, patch sizes may be important with regards to rodent predation of seeds.

The species x site x habitat interaction effect may be related to the combination of rodent preference in structural habitat type and *Acacia* species as reported earlier.

5.5.2 Number of seeds disappeared

Unlike the 'number chewed' model, only *Acacia* species and rodent presence were main factors affecting the disappearance of seeds. Thirty per cent of *A. karroo* seeds disappeared as compared with 19.4% of *A. nilotica*. All rodent predated seeds may not be eaten on site, but stored or eaten elsewhere. Caching of seeds (Price & Jenkins, 1986) could account for seeds disappearing and for the increased disappearance of *A. karroo* as a result of rodent preferences mentioned earlier.

Almost 36% of seeds disappeared in the presence of rodents, while 12.2% disappeared without obvious signs of rodent predation. It is thus thought that rodents may also have removed a proportion of seeds disappearing in the 'absence' of rodents as a result of caching for later consumption (Price & Jenkins, 1986).

The habitat x site and cage type x habitat interactions are again related to rodent habitat with patch size playing an important role in seed disappearance. Seed disappearance from small cages was mostly due to losses from short grass areas and it is suggested that ants may be responsible. Seed harvesting by ants is not uncommon (Gillon, Adam & Hubert, 1984; Bennet & Krebs, 1987) and ants have been reported to move more seeds than rodents in grassy (Linzey & Washok, 2000) and semi-arid (Kerley, 1991) habitats. Linzey & Washok however, made no distinction between short and tall grass areas. In HUP, ant presence was noted more frequently in short grass than tall grass or canopy sites (unpublished data). While South African acacias do not have elaiosome bearing seeds, *Acacia nilotica* pods secrete an aromatic, sticky substance (Coe & Coe, 1987), which may stick to seeds, making them attractive to ants. The possible effect of bird and beetle predation was, however, not controlled for and cannot be separated from the possible effect of ants.

Most *A. karroo* seeds disappeared from big cages followed by open cages, while most *A. nilotica* seeds disappeared from small followed by open cages. This might again suggest a rodent preference for *A. karroo*. Davidson, Inouye & Brown (1984), however, reported that in a desert habitat, rodents removed seeds of large-seeded species, while ants removed seeds of smaller-seeded species. The present data suggests that for the two *Acacia* species studied, the opposite is true.

The site x habitat x species interaction is suggested to be a result of ant and rodent seed preferences with all canopy sites and most tall grass sites showing more *A. karroo* than *A. nilotica* seeds disappearing.

It has been suggested that ants play a critical role in accumulating seed-banks of elaiosome-bearing Australian *Acacia* species (Holmes, 1990). These seed banks could contribute to the invasion of grasslands by *Acacia* species. The present study, however, found few seeds in the soil for either species and no difference in the size of the soil-stored seed-banks of the two species (Chapter 3). The ability of seeds to germinate depends on depth of burial (Auld, 1986) and if seeds are buried too deeply they may not be able to emerge successfully.

Kangaroo rats (*Dipodomys*), while thought to promote the establishment of woody shrubs in grassland by caching seeds, were found to have a negative effect on seedling establishment of *Prosopis* in arid grasslands (Valone & Thornhill, 2001). It has been suggested that *Acacia* seeds chewed and discarded by rodents germinate better than unchewed seeds (Miller, 1995). Rodent preferences for *A. karroo* seeds may thus result in higher numbers of germinating seeds for this species. The facilitation of seedling establishment of encroaching woody plant species by rodents in HUP, deserves further investigation.

5.6 Acknowledgements

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5.8 Appendices

Appendix A The parameters of the probit model and odds, estimated odds of being chewed and the associated probability of the odds for the factors included in the model for chewed seeds of *A. karroo* and *A. nilotica* seeds in HUP.

Factor	Level of Factor	Parameters of probit model	Parameters of the odds	Estimated odds	<i>P</i> of odds
Intercept		-1.284	0.277		
Habitat type	tall grass	0.469	1.599	0.443	0.307
Habitat type	short grass	-0.163	0.849	0.235	0.190
Habitat type	canopy	-0.306	0.736	0.204	0.169
Site	Le Dube	0.457	1.579	0.437	0.304
Site	Maqanda	0.324	1.382	0.383	0.277
Site	Nombali	-0.396	0.673	0.186	0.157
Site	Seme	-0.385	0.680	0.188	0.159
Species	<i>A. karroo</i>	0.200	1.222	0.338	0.253
Species	<i>A. nilotica</i>	-0.200	0.819	0.227	0.185
Cage type	small	-0.085	0.919	0.254	0.203
Cage type	big	-0.160	0.853	0.236	0.191
Cage type	open	0.244	1.276	0.353	0.261
Habitat*site	tall grass*Le Dube	0.156	1.169	0.323	0.244
Habitat*site	tall grass*Maqanda	-0.023	0.978	0.271	0.213
Habitat*site	tall grass*Nombali	0.326	1.385	0.383	0.277
Habitat*site	tall grass*Seme	-0.459	0.632	0.175	0.149
Habitat*site	short grass*Le Dube	-0.377	0.686	0.190	0.160
Habitat*site	short grass*Maqanda	-0.559	0.572	0.158	0.137
Habitat*site	short grass*Nombali	0.673	1.961	0.543	0.352
Habitat*site	short grass*Seme	0.263	1.301	0.360	0.265
Habitat*site	canopy*Le Dube	0.221	1.247	0.345	0.257
Habitat*site	canopy*Maqanda	0.582	1.790	0.495	0.331
Habitat*site	canopy*Nombali	-0.999	0.368	0.102	0.093
Habitat*site	canopy*Seme	0.196	1.217	0.337	0.252
Habitat*species	tall grass* <i>A. k</i>	-0.017	0.983	0.272	0.214
Habitat*species	short grass* <i>A. k</i>	0.028	1.029	0.285	0.222
Habitat*species	canopy* <i>A. k</i>	-0.011	0.989	0.274	0.215
Habitat*species	tall grass* <i>A. n</i>	0.017	1.017	0.282	0.220
Habitat*species	short grass* <i>A. n</i>	-0.028	0.972	0.269	0.212
Habitat*species	canopy* <i>A. n</i>	0.011	1.011	0.280	0.219
Site*species	Le Dube* <i>A. k</i>	0.182	1.200	0.332	0.249
Site*species	Le Dube* <i>A. n</i>	-0.182	0.834	0.231	0.188
Site*species	Maqanda* <i>A. k</i>	-0.016	0.984	0.272	0.214
Site*species	Maqanda* <i>A. n</i>	0.016	1.016	0.281	0.220
Site*species	Nombali* <i>A. k</i>	-0.003	0.997	0.276	0.216
Site*species	Nombali* <i>A. n</i>	0.003	1.003	0.278	0.217

Appendix A Continued:

Factor	Level of Factor	Parameters of probit model	Parameters of the odds	Estimated odds	P of odds
Site*species	Seme*A.k	-0.163	0.850	0.235	0.190
Site*species	Seme*A.n	0.163	1.177	0.326	0.246
Habitat*cage type	tall grass*small	-0.382	0.683	0.189	0.159
Habitat*cage type	tall grass*big	0.311	1.365	0.378	0.274
Habitat*cage type	tall grass*open	0.071	1.074	0.297	0.229
Habitat*cage type	short grass*small	-0.087	0.916	0.254	0.202
Habitat*cage type	short grass*big	0.295	1.343	0.372	0.271
Habitat*cage type	short grass*open	-0.208	0.812	0.225	0.184
Habitat*cage type	canopy*small	0.469	1.598	0.443	0.307
Habitat*cage type	canopy*big	-0.606	0.546	0.151	0.131
Habitat*cage type	canopy*open	0.137	1.147	0.317	0.241
Site*cage type	Le Dube*small	-0.047	0.954	0.264	0.209
Site*cage type	Le Dube*big	0.321	1.379	0.382	0.276
Site*cage type	Le Dube*open	-0.274	0.760	0.210	0.174
Site*cage type	Maqanda*small	-0.624	0.536	0.148	0.129
Site*cage type	Maqanda*big	0.553	1.739	0.481	0.325
Site*cage type	Maqanda*open	0.071	1.074	0.297	0.229
Site*cage type	Nombali*small	0.710	2.035	0.563	0.360
Site*cage type	Nombali*big	-1.030	0.357	0.099	0.090
Site*cage type	Nombali*open	0.319	1.376	0.381	0.276
Site*cage type	Seme*small	-0.039	0.962	0.266	0.210
Site*cage type	Seme*big	0.155	1.168	0.323	0.244
Site*cage type	Seme*open	-0.116	0.890	0.247	0.198
Species*cage type	A.k*small	-0.025	0.975	0.270	0.213
Species*cage type	A.k*big	0.095	1.099	0.304	0.233
Species*cage type	A.k*open	-0.070	0.932	0.258	0.205
Species*cage type	A.n*small	0.025	1.025	0.284	0.221
Species*cage type	A.n*big	-0.095	0.909	0.252	0.201
Species*cage type	A.n*open	0.070	1.073	0.297	0.229
Habitat*site*species	tall grass*Le Dube*A.k	-0.404	0.668	0.185	0.156
Habitat*site*species	tall grass*Maqanda*A.k	0.221	1.247	0.345	0.257
Habitat*site*species	tall grass*Nombali*A.k	0.141	1.152	0.319	0.242
Habitat*site*species	tall grass*Seme*A.k	0.042	1.043	0.289	0.224
Habitat*site*species	short grass*Le Dube*A.k	0.520	1.682	0.466	0.318
Habitat*site*species	short grass*Maqanda*A.k	-0.261	0.770	0.213	0.176
Habitat*site*species	short grass*Nombali*A.k	-0.277	0.758	0.210	0.174
Habitat*site*species	short grass*Seme*A.k	0.017	1.017	0.282	0.220
Habitat*site*species	canopy*Le Dube*A.k	-0.116	0.890	0.247	0.198
Habitat*site*species	canopy*Maqanda*A.k	0.040	1.041	0.288	0.224
Habitat*site*species	canopy*Nombali*A.k	0.135	1.145	0.317	0.241
Habitat*site*species	canopy*Seme*A.k	-0.060	0.942	0.261	0.207
Habitat*site*species	tall grass*Le Dube*A.n	0.404	1.498	0.415	0.293
Habitat*site*species	tall grass*Maqanda*A.n	-0.221	0.802	0.222	0.182
Habitat*site*species	tall grass*Nombali*A.n	-0.141	0.868	0.240	0.194

Appendix A Continued:

Factor	Level of Factor	Parameters of probit model	Parameters of the odds	Estimated odds	P of odds
Habitat*site*species	tall grass*Seme*A.n	-0.042	0.959	0.265	0.210
Habitat*site*species	short grass*Le Dube*A.n	-0.520	0.595	0.165	0.141
Habitat*site*species	short grass*Maqanda*A.n	0.261	1.298	0.359	0.264
Habitat*site*species	short grass*Nombali*A.n	0.277	1.319	0.365	0.268
Habitat*site*species	short grass*Seme*A.n	-0.017	0.983	0.272	0.214
Habitat*site*species	canopy*Le Dube*A.n	0.116	1.123	0.311	0.237
Habitat*site*species	canopy*Maqanda*A.n	-0.040	0.961	0.266	0.210
Habitat*site*species	canopy*Nombali*A.n	-0.135	0.874	0.242	0.195
Habitat*site*species	canopy*Seme*A.n	0.060	1.062	0.294	0.227
Habitat*site*cage type	tall grass*Le Dube*small	-0.083	0.920	0.255	0.203
Habitat*site*cage type	tall grass*Le Dube*big	-0.204	0.815	0.226	0.184
Habitat*site*cage type	tall grass*Le Dube*open	0.288	1.334	0.369	0.270
Habitat*site*cage type	tall grass*Maqanda*small	-0.045	0.956	0.265	0.209
Habitat*site*cage type	tall grass*Maqanda*big	-0.084	0.920	0.255	0.203
Habitat*site*cage type	tall grass*Maqanda*open	0.128	1.137	0.315	0.239
Habitat*site*cage type	tall grass*Nombali*small	-0.203	0.816	0.226	0.184
Habitat*site*cage type	tall grass*Nombali*big	0.771	2.162	0.598	0.374
Habitat*site*cage type	tall grass*Nombali*open	-0.568	0.567	0.157	0.136
Habitat*site*cage type	tall grass*Seme*small	0.331	1.392	0.385	0.278
Habitat*site*cage type	tall grass*Seme*big	-0.483	0.617	0.171	0.146
Habitat*site*cage type	tall grass*Seme*open	0.152	1.164	0.322	0.244
Habitat*site*cage type	short grass*Le Dube*small	0.227	1.254	0.347	0.258
Habitat*site*cage type	short grass*Le Dube*big	-0.329	0.720	0.199	0.166
Habitat*site*cage type	short grass*Le Dube*open	0.042	1.043	0.289	0.224
Habitat*site*cage type	short grass*Maqanda*small	0.635	1.887	0.522	0.343
Habitat*site*cage type	short grass*Maqanda*big	-0.677	0.508	0.141	0.123
Habitat*site*cage type	short grass*Maqanda*open	0.042	1.043	0.289	0.224
Habitat*site*cage type	short grass*Nombali*small	-0.409	0.664	0.184	0.155
Habitat*site*cage type	short grass*Nombali*big	1.011	2.750	0.761	0.432
Habitat*site*cage type	short grass*Nombali*open	-0.602	0.548	0.152	0.132
Habitat*site*cage type	short grass*Seme*small	1.170	3.222	0.892	0.471
Habitat*site*cage type	short grass*Seme*big	-0.006	0.994	0.275	0.216
Habitat*site*cage type	short grass*Seme*open	0.458	1.581	0.438	0.304
Habitat*site*cage type	canopy*Le Dube*small	-0.143	0.867	0.240	0.194
Habitat*site*cage type	canopy*Le Dube*big	0.533	1.704	0.472	0.321
Habitat*site*cage type	canopy*Le Dube*open	-0.170	0.844	0.234	0.189
Habitat*site*cage type	canopy*Maqanda*small	0.612	1.844	0.511	0.338
Habitat*site*cage type	canopy*Maqanda*big	0.761	2.140	0.593	0.372
Habitat*site*cage type	canopy*Maqanda*open	-0.170	0.844	0.234	0.189
Habitat*site*cage type	canopy*Nombali*small	-0.610	0.543	0.150	0.131
Habitat*site*cage type	canopy*Nombali*big	-1.782	0.168	0.047	0.045
Habitat*site*cage type	canopy*Nombali*open	1.170	3.222	0.892	0.471
Habitat*site*cage type	canopy*Seme*small	0.121	1.129	0.312	0.238
Habitat*site*cage type	canopy*Seme*big	0.488	1.629	0.451	0.311

Appendix A Continued:

Factor	Level of Factor	Parameters of probit model	Parameters of the odds	Estimated odds	P of odds
Habitat*site*cage type	canopy*Seme*open	-0.610	0.543	0.150	0.131
Habitat*species*cage type	tall grass*A.k*small	-0.179	0.836	0.231	0.188
Habitat*species*cage type	tall grass*A.k*big	0.051	1.053	0.291	0.226
Habitat*species*cage type	tall grass*A.k*open	0.128	1.137	0.315	0.239
Habitat*species*cage type	short grass*A.k*small	0.066	1.069	0.296	0.228
Habitat*species*cage type	short grass*A.k*big	-0.015	0.985	0.273	0.214
Habitat*species*cage type	short grass*A.k*open	-0.051	0.950	0.263	0.208
Habitat*species*cage type	canopy*A.k*small	0.113	1.120	0.310	0.237
Habitat*species*cage type	canopy*A.k*big	-0.036	0.965	0.267	0.211
Habitat*species*cage type	canopy*A.k*open	-0.076	0.927	0.257	0.204
Habitat*species*cage type	tall grass*A.n*small	0.179	1.196	0.331	0.249
Habitat*species*cage type	tall grass*A.n*big	-0.051	0.950	0.263	0.208
Habitat*species*cage type	tall grass*A.n*open	-0.128	0.880	0.244	0.196
Habitat*species*cage type	short grass*A.n*small	-0.066	0.936	0.259	0.206
Habitat*species*cage type	short grass*A.n*big	0.015	1.015	0.281	0.219
Habitat*species*cage type	short grass*A.n*open	0.051	1.052	0.291	0.226
Habitat*species*cage type	canopy*A.n*small	-0.113	0.893	0.247	0.198
Habitat*species*cage type	canopy*A.n*big	0.036	1.037	0.287	0.223
Habitat*species*cage type	canopy*A.n*open	0.076	1.079	0.299	0.230
Site*species*cage type	Le Dube*A.k*small	0.004	1.004	0.278	0.218
Site*species*cage type	Le Dube*A.k*big	-0.026	0.974	0.270	0.212
Site*species*cage type	Le Dube*A.k*open	0.022	1.022	0.283	0.221
Site*species*cage type	Maqanda*A.k*small	-0.126	0.881	0.244	0.196
Site*species*cage type	Maqanda*A.k*big	0.152	1.165	0.322	0.244
Site*species*cage type	Maqanda*A.k*open	-0.026	0.974	0.270	0.212
Site*species*cage type	Nombali*A.k*small	-0.053	0.949	0.263	0.208
Site*species*cage type	Nombali*A.k*big	0.133	1.142	0.316	0.240
Site*species*cage type	Nombali*A.k*open	-0.080	0.923	0.256	0.204
Site*species*cage type	Seme*A.k*small	0.175	1.191	0.330	0.248
Site*species*cage type	Seme*A.k*big	-0.259	0.772	0.214	0.176
Site*species*cage type	Seme*A.k*open	0.084	1.088	0.301	0.231
Site*species*cage type	Le Dube*A.n*small	-0.004	0.996	0.276	0.216
Site*species*cage type	Le Dube*A.n*big	0.026	1.026	0.284	0.221
Site*species*cage type	Le Dube*A.n*open	-0.022	0.978	0.271	0.213
Site*species*cage type	Maqanda*A.n*small	0.126	1.134	0.314	0.239
Site*species*cage type	Maqanda*A.n*big	-0.152	0.859	0.238	0.192
Site*species*cage type	Maqanda*A.n*open	0.026	1.026	0.284	0.221
Site*species*cage type	Nombali*A.n*small	0.053	1.054	0.292	0.226
Site*species*cage type	Nombali*A.n*big	-0.133	0.875	0.242	0.195
Site*species*cage type	Nombali*A.n*open	0.080	1.083	0.300	0.231
Site*species*cage type	Seme*A.n*small	-0.175	0.839	0.232	0.189
Site*species*cage type	Seme*A.n*big	0.259	1.296	0.359	0.264
Site*species*cage type	Seme*A.n*open	-0.084	0.919	0.271	0.213

Appendix B Odds ratios for the significant main effects and second order interactions

for the 'number chewed' model.

Factor	Level of the factor	Compared with:	Odds ratio
Cage type	small	big	1.1
Cage type	small	open	0.7
Cage type	big	open	0.7
Site	Le Dube	Maqanda	1.1
Site	Le Dube	Nombali	2.3
Site	Le Dube	Seme	2.3
Site	Maqanda	Nombali	2.1
Site	Maqanda	Seme	2.0
Site	Nombali	Seme	1.0
Species	<i>A. karroo</i>	<i>A. nilotica</i>	1.5
Habitat type	tall grass	short grass	1.9
Habitat type	tall grass	canopy	2.2
Habitat type	short grass	canopy	1.2
Site*cage type	Le Dube*small	Le Dube*big	0.7
Site*cage type	Le Dube*small	Le Dube*open	1.3
Site*cage type	Le Dube*small	Maqanda*small	1.8
Site*cage type	Le Dube*small	Maqanda*big	0.5
Site*cage type	Le Dube*small	Maqanda*open	0.9
Site*cage type	Le Dube*small	Nombali*small	0.5
Site*cage type	Le Dube*small	Nombali*big	2.7
Site*cage type	Le Dube*small	Nombali*open	0.7
Site*cage type	Le Dube*small	Seme*small	1.0
Site*cage type	Le Dube*small	Seme*big	0.8
Site*cage type	Le Dube*small	Seme*open	1.1
Site*cage type	Le Dube*big	Le Dube*open	1.8
Site*cage type	Le Dube*big	Maqanda*small	2.6
Site*cage type	Le Dube*big	Maqanda*big	0.8
Site*cage type	Le Dube*big	Maqanda*open	1.3
Site*cage type	Le Dube*big	Nombali*small	0.7
Site*cage type	Le Dube*big	Nombali*big	3.9
Site*cage type	Le Dube*big	Nombali*open	1.0
Site*cage type	Le Dube*big	Seme*small	1.4
Site*cage type	Le Dube*big	Seme*big	1.2
Site*cage type	Le Dube*big	Seme*open	1.5
Site*cage type	Le Dube*open	Maqanda*small	1.4
Site*cage type	Le Dube*open	Maqanda*big	0.4
Site*cage type	Le Dube*open	Maqanda*open	0.7
Site*cage type	Le Dube*open	Nombali*small	0.4
Site*cage type	Le Dube*open	Nombali*big	2.1
Site*cage type	Le Dube*open	Nombali*open	0.6
Site*cage type	Le Dube*open	Seme*small	0.8
Site*cage type	Le Dube*open	Seme*big	0.7
Site*cage type	Le Dube*open	Seme*open	0.9
Site*cage type	Maqanda*small	Maqanda*big	0.3

Appendix B Continued:

Factor	Level of the factor	Compared with:	Odds ratio
Site*cage type	Maqanda*small	Maqanda*open	0.5
Site*cage type	Maqanda*small	Nombali*small	0.3
Site*cage type	Maqanda*small	Nombali*big	1.5
Site*cage type	Maqanda*small	Nombali*open	0.4
Site*cage type	Maqanda*small	Seme*small	0.6
Site*cage type	Maqanda*small	Seme*big	0.5
Site*cage type	Maqanda*small	Seme*open	0.6
Site*cage type	Maqanda*big	Maqanda*open	1.6
Site*cage type	Maqanda*big	Nombali*small	0.9
Site*cage type	Maqanda*big	Nombali*big	4.9
Site*cage type	Maqanda*big	Nombali*open	1.3
Site*cage type	Maqanda*big	Seme*small	1.8
Site*cage type	Maqanda*big	Seme*big	1.5
Site*cage type	Maqanda*big	Seme*open	2.0
Site*cage type	Maqanda*open	Nombali*small	0.5
Site*cage type	Maqanda*open	Nombali*big	3.0
Site*cage type	Maqanda*open	Nombali*open	0.8
Site*cage type	Maqanda*open	Seme*small	1.1
Site*cage type	Maqanda*open	Seme*big	0.9
Site*cage type	Maqanda*open	Seme*open	1.2
Site*cage type	Nombali*small	Nombali*big	5.7
Site*cage type	Nombali*small	Nombali*open	1.5
Site*cage type	Nombali*small	Seme*small	2.1
Site*cage type	Nombali*small	Seme*big	1.7
Site*cage type	Nombali*small	Seme*open	2.3
Site*cage type	Nombali*big	Nombali*open	0.3
Site*cage type	Nombali*big	Seme*small	0.4
Site*cage type	Nombali*big	Seme*big	0.3
Site*cage type	Nombali*big	Seme*open	0.4
Site*cage type	Nombali*open	Seme*small	1.4
Site*cage type	Nombali*open	Seme*big	1.2
Site*cage type	Nombali*open	Seme*open	1.5
Site*cage type	Seme*small	Seme*big	0.8
Site*cage type	Seme*small	Seme*open	1.1
Site*cage type	Seme*big	Seme*open	1.3
Habitat*cage type	tall grass*small	tall grass*big	0.5
Habitat*cage type	tall grass*small	tall grass*open	0.6
Habitat*cage type	tall grass*small	short grass*small	0.7
Habitat*cage type	tall grass*small	short grass*big	0.5
Habitat*cage type	tall grass*small	short grass*open	0.8
Habitat*cage type	tall grass*small	canopy*small	0.4
Habitat*cage type	tall grass*small	canopy*big	1.3
Habitat*cage type	tall grass*small	canopy*open	0.6
Habitat*cage type	tall grass*big	tall grass*open	1.3
Habitat*cage type	tall grass*big	short grass*small	1.5
Habitat*cage type	tall grass*big	short grass*big	1.0

Appendix B Continued:

Factor	Level of the factor	Compared with:	Odds ratio
Habitat*cage type	tall grass*big	short grass*open	1.7
Habitat*cage type	tall grass*big	canopy*small	0.9
Habitat*cage type	tall grass*big	canopy*big	2.5
Habitat*cage type	tall grass*big	canopy*open	1.2
Habitat*cage type	tall grass*open	short grass*small	1.2
Habitat*cage type	tall grass*open	short grass*big	0.8
Habitat*cage type	tall grass*open	short grass*open	1.3
Habitat*cage type	tall grass*open	canopy*small	0.7
Habitat*cage type	tall grass*open	canopy*big	2.0
Habitat*cage type	tall grass*open	canopy*open	0.9
Habitat*cage type	short grass*small	short grass*big	0.7
Habitat*cage type	short grass*small	short grass*open	1.1
Habitat*cage type	short grass*small	canopy*small	0.6
Habitat*cage type	short grass*small	canopy*big	1.7
Habitat*cage type	short grass*small	canopy*open	0.8
Habitat*cage type	short grass*big	short grass*open	1.7
Habitat*cage type	short grass*big	canopy*small	0.8
Habitat*cage type	short grass*big	canopy*big	2.5
Habitat*cage type	short grass*big	canopy*open	1.2
Habitat*cage type	short grass*open	canopy*small	0.5
Habitat*cage type	short grass*open	canopy*big	1.5
Habitat*cage type	short grass*open	canopy*open	0.7
Habitat*cage type	canopy*small	canopy*big	2.9
Habitat*cage type	canopy*small	canopy*open	1.4
Habitat*cage type	canopy*big	canopy*open	0.5
Habitat*site	tall grass*Le Dube	short grass*Le Dube	1.7
Habitat*site	tall grass*Maqanda	short grass*Maqanda	1.7
Habitat*site	tall grass*Nombali	short grass*Nombali	0.7
Habitat*site	tall grass*Seme	short grass*Seme	0.5
Habitat*site	tall grass*Le Dube	tall grass*Maqanda	1.2
Habitat*site	tall grass*Le Dube	tall grass*Nombali	0.8
Habitat*site	tall grass*Le Dube	tall grass*Seme	1.8
Habitat*site	tall grass*Le Dube	short grass*Maqanda	2.0
Habitat*site	tall grass*Le Dube	short grass*Nombali	0.6
Habitat*site	tall grass*Le Dube	short grass*Seme	0.9
Habitat*site	short grass*Le Dube	tall grass*Maqanda	0.7
Habitat*site	short grass*Le Dube	tall grass*Nombali	0.5
Habitat*site	short grass*Le Dube	tall grass*Seme	1.1
Habitat*site	short grass*Le Dube	short grass*Maqanda	1.2
Habitat*site	short grass*Le Dube	short grass*Nombali	0.3
Habitat*site	short grass*Le Dube	short grass*Seme	0.5
Habitat*site	tall grass*Maqanda	tall grass*Nombali	0.7
Habitat*site	tall grass*Maqanda	tall grass*Seme	1.5
Habitat*site	tall grass*Maqanda	short grass*Nombali	0.5
Habitat*site	tall grass*Maqanda	short grass*Seme	0.8
Habitat*site	short grass*Maqanda	tall grass*Nombali	0.4

Appendix B Continued:

Factor	Level of the factor	Compared with:	Odds ratio
Habitat*site	short grass*Maqanda	tall grass*Seme	0.9
Habitat*site	short grass*Maqanda	short grass*Nombali	0.3
Habitat*site	short grass*Maqanda	short grass*Seme	0.4
Habitat*site	tall grass*Nombali	tall grass*Seme	2.2
Habitat*site	tall grass*Nombali	short grass*Seme	1.1
Habitat*site	canopy*Le Dube	canopy*Maqanda	0.7
Habitat*site	canopy*Le Dube	canopy*Nombali	3.4
Habitat*site	canopy*Le Dube	canopy*Seme	1.0
Habitat*site	canopy*Le Dube	short grass*Maqanda	2.2
Habitat*site	canopy*Le Dube	short grass*Nombali	0.6
Habitat*site	canopy*Le Dube	short grass*Seme	1.0
Habitat*site	canopy*Le Dube	tall grass*Maqanda	1.3
Habitat*site	canopy*Le Dube	tall grass*Nombali	0.9
Habitat*site	canopy*Le Dube	tall grass*Seme	2.0
Habitat*site	canopy*Le Dube	short grass*Le Dube	1.8
Habitat*site	canopy*Le Dube	tall grass*Le Dube	1.1
Habitat*site	canopy*Maqanda	canopy*Nombali	4.9
Habitat*site	canopy*Maqanda	canopy*Seme	1.5
Habitat*site	canopy*Maqanda	short grass*Nombali	0.9
Habitat*site	canopy*Maqanda	short grass*Seme	1.4
Habitat*site	canopy*Maqanda	tall grass*Nombali	1.3
Habitat*site	canopy*Maqanda	tall grass*Seme	2.8
Habitat*site	canopy*Maqanda	short grass*Le Dube	2.6
Habitat*site	canopy*Maqanda	tall grass*Le Dube	1.5
Habitat*site	canopy*Maqanda	short grass*Maqanda	3.1
Habitat*site	canopy*Maqanda	tall grass*Maqanda	1.8
Habitat*site	canopy*Maqanda	canopy*Seme	1.5
Habitat*site	canopy*Nombali	short grass*Nombali	0.2
Habitat*site	canopy*Nombali	short grass*Seme	0.3
Habitat*site	canopy*Nombali	tall grass*Nombali	0.3
Habitat*site	canopy*Nombali	tall grass*Seme	0.6
Habitat*site	canopy*Nombali	short grass*Le Dube	0.5
Habitat*site	canopy*Nombali	tall grass*Le Dube	0.3
Habitat*site	canopy*Nombali	short grass*Maqanda	0.6
Habitat*site	canopy*Nombali	tall grass*Maqanda	0.4
Habitat*site	canopy*Seme	short grass*Nombali	0.6
Habitat*site	canopy*Seme	short grass*Seme	0.9
Habitat*site	canopy*Seme	tall grass*Nombali	0.9
Habitat*site	canopy*Seme	tall grass*Seme	1.9
Habitat*site	canopy*Seme	short grass*Le Dube	1.8
Habitat*site	canopy*Seme	tall grass*Le Dube	1.0
Habitat*site	canopy*Seme	short grass*Maqanda	2.1
Habitat*site	canopy*Seme	tall grass*Maqanda	1.2

Appendix C The parameters of the probit model and odds, estimated odds of disappearing and the associated probability of the odds for the factors included in the model for disappearance of *A. karroo* and *A. nilotica* seeds in HUP.

Factor	Level of Factor	Parameters of probit model	Parameters of the odds	Estimated odds	<i>p</i> of odds
Interc		-0.911	0.402		
Habitat type	tall grass	0.026	1.027	0.413	0.292
Habitat type	short grass	-0.045	0.956	0.385	0.278
Habitat type	canopy	0.019	1.019	0.410	0.291
Site	Le Dube	0.097	1.102	0.443	0.307
Site	Maqanda	0.072	1.075	0.432	0.302
Site	Nombali	-0.033	0.967	0.389	0.280
Site	Seme	-0.136	0.872	0.351	0.260
Species	<i>A. karroo</i>	0.221	1.247	0.502	0.334
Species	<i>A. nilotica</i>	-0.221	0.802	0.323	0.244
Cage type	small	0.027	1.027	0.413	0.292
Cage type	big	0.023	1.024	0.412	0.292
Cage type	open	-0.050	0.951	0.383	0.277
Rodents	yes	0.445	1.561	0.628	0.386
Rodents	no	-0.445	0.641	0.258	0.205
Habitat*site	tall grass*Le Dube	0.196	1.216	0.489	0.329
Habitat*site	tall grass*Maqanda	0.003	1.003	0.404	0.288
Habitat*site	tall grass*Nombali	0.023	1.023	0.412	0.292
Habitat*site	tall grass*Seme	-0.222	0.801	0.322	0.244
Habitat*site	short grass*Le Dube	-0.235	0.791	0.318	0.241
Habitat*site	short grass*Maqanda	-0.186	0.831	0.334	0.250
Habitat*site	short grass*Nombali	0.353	1.424	0.573	0.364
Habitat*site	short grass*Seme	0.067	1.070	0.430	0.301
Habitat*site	canopy*Le Dube	0.039	1.040	0.418	0.295
Habitat*site	canopy*Maqanda	0.182	1.200	0.483	0.326
Habitat*site	canopy*Nombali	-0.376	0.686	0.276	0.216
Habitat*site	canopy*Seme	0.155	1.167	0.470	0.320
Habitat*species	tall grass* <i>A. k</i>	0.010	1.010	0.406	0.289
Habitat*species	short grass* <i>A. k</i>	-0.019	0.981	0.395	0.283
Habitat*species	canopy* <i>A. k</i>	0.009	1.009	0.406	0.289
Habitat*species	tall grass* <i>A. n</i>	-0.010	0.990	0.398	0.285
Habitat*species	short grass* <i>A. n</i>	0.019	1.019	0.410	0.291
Habitat*species	canopy* <i>A. n</i>	-0.009	0.991	0.399	0.285
Site*species	Le Dube* <i>A. k</i>	0.138	1.148	0.462	0.316
Site*species	Le Dube* <i>A. n</i>	-0.138	0.871	0.350	0.259
Site*species	Maqanda* <i>A. k</i>	0.023	1.024	0.412	0.292
Site*species	Maqanda* <i>A. n</i>	-0.023	0.977	0.393	0.282
Site*species	Nombali* <i>A. k</i>	-0.034	0.967	0.389	0.280
Site*species	Nombali* <i>A. n</i>	0.034	1.035	0.416	0.294

Appendix C Continued:

Factor	Level of Factor	Parameters of probit model	Parameters of the odds	Estimated odds	<i>p</i> of odds
Site*species	Seme* <i>A.k</i>	-0.127	0.880	0.354	0.262
Site*species	Seme* <i>A.n</i>	0.127	1.135	0.457	0.314
Habitat*cage type	tall grass*small	-0.430	0.651	0.262	0.207
Habitat*cage type	tall grass*big	0.116	1.123	0.452	0.311
Habitat*cage type	tall grass*open	0.314	1.368	0.550	0.355
Habitat*cage type	short grass*small	0.441	1.554	0.625	0.385
Habitat*cage type	short grass*big	-0.164	0.848	0.341	0.254
Habitat*cage type	short grass*open	-0.277	0.758	0.305	0.234
Habitat*cage type	canopy*small	-0.011	0.989	0.398	0.285
Habitat*cage type	canopy*big	0.048	1.050	0.422	0.297
Habitat*cage type	canopy*open	-0.037	0.964	0.388	0.279
Site*cage type	Le Dube*small	-0.025	0.975	0.392	0.282
Site*cage type	Le Dube*big	-0.086	0.917	0.369	0.270
Site*cage type	Le Dube*open	0.111	1.118	0.450	0.310
Site*cage type	Maqanda*small	-0.224	0.799	0.322	0.243
Site*cage type	Maqanda*big	0.260	1.297	0.522	0.343
Site*cage type	Maqanda*open	-0.036	0.965	0.388	0.280
Site*cage type	Nombali*small	0.208	1.231	0.495	0.331
Site*cage type	Nombali*big	-0.107	0.899	0.362	0.266
Site*cage type	Nombali*open	-0.101	0.904	0.364	0.267
Site*cage type	Seme*small	0.041	1.042	0.419	0.295
Site*cage type	Seme*big	-0.067	0.936	0.376	0.273
Site*cage type	Seme*open	0.025	1.025	0.413	0.292
Species*cage type	<i>A.k</i> *small	-0.125	0.883	0.355	0.262
Species*cage type	<i>A.k</i> *big	0.170	1.185	0.477	0.323
Species*cage type	<i>A.k</i> *open	-0.045	0.956	0.385	0.278
Species*cage type	<i>A.n</i> *small	0.125	1.133	0.456	0.313
Species*cage type	<i>A.n</i> *big	-0.170	0.844	0.339	0.253
Species*cage type	<i>A.n</i> *open	0.045	1.046	0.421	0.296
Habitat*site*species	tall grass*Le Dube* <i>A.k</i>	-0.469	0.626	0.252	0.201
Habitat*site*species	tall grass*Maqanda* <i>A.k</i>	0.172	1.188	0.478	0.323
Habitat*site*species	tall grass*Nombali* <i>A.k</i>	0.116	1.123	0.452	0.311
Habitat*site*species	tall grass*Seme* <i>A.k</i>	0.180	1.198	0.482	0.325
Habitat*site*species	short grass*Le Dube* <i>A.k</i>	0.558	1.747	0.703	0.413
Habitat*site*species	short grass*Maqanda* <i>A.k</i>	-0.063	0.939	0.378	0.274
Habitat*site*species	short grass*Nombali* <i>A.k</i>	-0.227	0.797	0.321	0.243
Habitat*site*species	short grass*Seme* <i>A.k</i>	-0.269	0.764	0.308	0.235
Habitat*site*species	canopy*Le Dube* <i>A.k</i>	-0.089	0.915	0.368	0.269
Habitat*site*species	canopy*Maqanda* <i>A.k</i>	-0.109	0.896	0.361	0.265
Habitat*site*species	canopy*Nombali* <i>A.k</i>	0.110	1.116	0.449	0.310
Habitat*site*species	canopy*Seme* <i>A.k</i>	0.088	1.092	0.439	0.305
Habitat*site*species	tall grass*Le Dube* <i>A.n</i>	0.469	1.598	0.643	0.391
Habitat*site*species	tall grass*Maqanda* <i>A.n</i>	-0.172	0.842	0.339	0.253
Habitat*site*species	tall grass*Nombali* <i>A.n</i>	-0.116	0.890	0.358	0.264
Habitat*site*species	tall grass*Seme* <i>A.n</i>	-0.180	0.835	0.336	0.252

Appendix C Continued:

Factor	Level of Factor	Parameters of probit model	Parameters of the odds	Estimated odds	<i>p</i> of odds
Habitat*site*species	short grass*Le Dube*A.n	-0.558	0.572	0.230	0.187
Habitat*site*species	short grass*Maqanda*A.n	0.063	1.065	0.428	0.300
Habitat*site*species	short grass*Nombali*A.n	0.227	1.255	0.505	0.335
Habitat*site*species	short grass*Seme*A.n	0.269	1.309	0.526	0.345
Habitat*site*species	canopy*Le Dube*A.n	0.089	1.093	0.440	0.305
Habitat*site*species	canopy*Maqanda*A.n	0.109	1.115	0.449	0.310
Habitat*site*species	canopy*Nombali*A.n	-0.110	0.896	0.360	0.265
Habitat*site*species	canopy*Seme*A.n	-0.088	0.916	0.368	0.269
Habitat*site*cage type	tall grass*Le Dube*small	-0.185	0.831	0.334	0.250
Habitat*site*cage type	tall grass*Le Dube*big	0.145	1.157	0.465	0.318
Habitat*site*cage type	tall grass*Le Dube*open	0.040	1.041	0.419	0.295
Habitat*site*cage type	tall grass*Maqanda*small	-0.422	0.656	0.264	0.209
Habitat*site*cage type	tall grass*Maqanda*big	0.233	1.262	0.508	0.337
Habitat*site*cage type	tall grass*Maqanda*open	0.190	1.209	0.486	0.327
Habitat*site*cage type	tall grass*Nombali*small	0.385	1.469	0.591	0.371
Habitat*site*cage type	tall grass*Nombali*big	-0.388	0.678	0.273	0.214
Habitat*site*cage type	tall grass*Nombali*open	0.004	1.004	0.404	0.288
Habitat*site*cage type	tall grass*Seme*small	0.223	1.250	0.503	0.335
Habitat*site*cage type	tall grass*Seme*big	0.010	1.010	0.406	0.289
Habitat*site*cage type	tall grass*Seme*open	-0.233	0.792	0.319	0.242
Habitat*site*cage type	short grass*Le Dube*small	-0.345	0.708	0.285	0.222
Habitat*site*cage type	short grass*Le Dube*big	0.095	1.099	0.442	0.307
Habitat*site*cage type	short grass*Le Dube*open	0.250	1.285	0.517	0.341
Habitat*site*cage type	short grass*Maqanda*small	0.945	2.573	1.035	0.509
Habitat*site*cage type	short grass*Maqanda*big	-0.826	0.438	0.176	0.150
Habitat*site*cage type	short grass*Maqanda*open	-0.119	0.888	0.357	0.263
Habitat*site*cage type	short grass*Nombali*small	-0.078	0.925	0.372	0.271
Habitat*site*cage type	short grass*Nombali*big	0.302	1.352	0.544	0.352
Habitat*site*cage type	short grass*Nombali*open	-0.224	0.799	0.322	0.243
Habitat*site*cage type	short grass*Seme*small	-0.522	0.593	0.239	0.193
Habitat*site*cage type	short grass*Seme*big	0.430	1.537	0.618	0.382
Habitat*site*cage type	short grass*Seme*open	0.092	1.097	0.441	0.306
Habitat*site*cage type	canopy*Le Dube*small	0.530	1.699	0.683	0.406
Habitat*site*cage type	canopy*Le Dube*big	-0.240	0.787	0.316	0.240
Habitat*site*cage type	canopy*Le Dube*open	-0.290	0.748	0.301	0.231
Habitat*site*cage type	canopy*Maqanda*small	-0.523	0.593	0.238	0.193
Habitat*site*cage type	canopy*Maqanda*big	0.594	1.811	0.729	0.421
Habitat*site*cage type	canopy*Maqanda*open	-0.071	0.932	0.375	0.273
Habitat*site*cage type	canopy*Nombali*small	-0.307	0.736	0.296	0.228
Habitat*site*cage type	canopy*Nombali*big	0.087	1.090	0.439	0.305
Habitat*site*cage type	canopy*Nombali*open	0.220	1.247	0.501	0.334
Habitat*site*cage type	canopy*Seme*small	0.299	1.349	0.543	0.352
Habitat*site*cage type	canopy*Seme*big	-0.440	0.644	0.259	0.206
Habitat*site*cage type	canopy*Seme*open	0.141	1.151	0.463	0.317
Habitat*species*cage type	tall grass*A.k*small	-0.122	0.885	0.356	0.263

Appendix C Continued:

Factor	Level of Factor	Parameters of probit model	Parameters of the odds	Estimated odds	<i>p</i> of odds
Habitat*species*cage type	tall grass* <i>A.k</i> *big	0.060	1.061	0.427	0.299
Habitat*species*cage type	tall grass* <i>A.k</i> *open	0.063	1.065	0.428	0.300
Habitat*species*cage type	short grass* <i>A.k</i> *small	0.084	1.088	0.438	0.304
Habitat*species*cage type	short grass* <i>A.k</i> *big	0.005	1.005	0.404	0.288
Habitat*species*cage type	short grass* <i>A.k</i> *open	-0.089	0.915	0.368	0.269
Habitat*species*cage type	canopy* <i>A.k</i> *small	0.038	1.039	0.418	0.295
Habitat*species*cage type	canopy* <i>A.k</i> *big	-0.064	0.938	0.377	0.274
Habitat*species*cage type	canopy* <i>A.k</i> *open	0.026	1.027	0.413	0.292
Habitat*species*cage type	tall grass* <i>A.n</i> *small	0.122	1.130	0.454	0.312
Habitat*species*cage type	tall grass* <i>A.n</i> *big	-0.060	0.942	0.379	0.275
Habitat*species*cage type	tall grass* <i>A.n</i> *open	-0.063	0.939	0.378	0.274
Habitat*species*cage type	short grass* <i>A.n</i> *small	-0.084	0.919	0.370	0.270
Habitat*species*cage type	short grass* <i>A.n</i> *big	-0.005	0.995	0.400	0.286
Habitat*species*cage type	short grass* <i>A.n</i> *open	0.089	1.093	0.440	0.305
Habitat*species*cage type	canopy* <i>A.n</i> *small	-0.038	0.963	0.387	0.279
Habitat*species*cage type	canopy* <i>A.n</i> *big	0.064	1.066	0.429	0.300
Habitat*species*cage type	canopy* <i>A.n</i> *open	-0.026	0.974	0.392	0.282
Site*species*cage type	Le Dube* <i>A.k</i> *small	-0.016	0.984	0.396	0.284
Site*species*cage type	Le Dube* <i>A.k</i> *big	-0.053	0.948	0.381	0.276
Site*species*cage type	Le Dube* <i>A.k</i> *open	0.069	1.072	0.431	0.301
Site*species*cage type	Maqanda* <i>A.k</i> *small	0.051	1.052	0.423	0.297
Site*species*cage type	Maqanda* <i>A.k</i> *big	0.041	1.042	0.419	0.295
Site*species*cage type	Maqanda* <i>A.k</i> *open	-0.092	0.912	0.367	0.268
Site*species*cage type	Nombali* <i>A.k</i> *small	-0.110	0.896	0.360	0.265
Site*species*cage type	Nombali* <i>A.k</i> *big	0.159	1.173	0.472	0.321
Site*species*cage type	Nombali* <i>A.k</i> *open	-0.049	0.952	0.383	0.277
Site*species*cage type	Seme* <i>A.k</i> *small	0.075	1.078	0.434	0.303
Site*species*cage type	Seme* <i>A.k</i> *big	-0.147	0.863	0.347	0.258
Site*species*cage type	Seme* <i>A.k</i> *open	0.072	1.075	0.432	0.302
Site*species*cage type	Le Dube* <i>A.n</i> *small	0.016	1.016	0.409	0.290
Site*species*cage type	Le Dube* <i>A.n</i> *big	0.053	1.054	0.424	0.298
Site*species*cage type	Le Dube* <i>A.n</i> *open	-0.069	0.933	0.375	0.273
Site*species*cage type	Maqanda* <i>A.n</i> *small	-0.051	0.950	0.382	0.277
Site*species*cage type	Maqanda* <i>A.n</i> *big	-0.041	0.960	0.386	0.279
Site*species*cage type	Maqanda* <i>A.n</i> *open	0.092	1.096	0.441	0.306
Site*species*cage type	Nombali* <i>A.n</i> *small	0.110	1.116	0.449	0.310
Site*species*cage type	Nombali* <i>A.n</i> *big	-0.159	0.853	0.343	0.255
Site*species*cage type	Nombali* <i>A.n</i> *open	0.049	1.050	0.422	0.297
Site*species*cage type	Seme* <i>A.n</i> *small	-0.075	0.928	0.373	0.272
Site*species*cage type	Seme* <i>A.n</i> *big	0.147	1.158	0.466	0.318
Site*species*cage type	Seme* <i>A.n</i> *open	-0.072	0.931	0.374	0.272

Appendix D Odds ratios for the significant main effects and second order interactions for the seed disappearance model.

Factor	Level of factor	Compared with:	Odds ratio
Rodents	yes	no	2.4
Species	<i>A. karroo</i>	<i>A. nilotica</i>	1.6
Habitat*site	tall grass*Le Dube	short grass*Le Dube	1.5
Habitat*site	tall grass*Maqanda	short grass*Maqanda	1.2
Habitat*site	tall grass*Nombali	short grass*Nombali	0.7
Habitat*site	tall grass*Seme	short grass*Seme	0.7
Habitat*site	tall grass*Le Dube	tall grass*Maqanda	1.2
Habitat*site	tall grass*Le Dube	tall grass*Nombali	1.2
Habitat*site	tall grass*Le Dube	tall grass*Seme	1.5
Habitat*site	tall grass*Le Dube	short grass*Maqanda	1.5
Habitat*site	tall grass*Le Dube	short grass*Nombali	0.9
Habitat*site	tall grass*Le Dube	short grass*Seme	1.1
Habitat*site	short grass*Le Dube	tall grass*Maqanda	0.8
Habitat*site	short grass*Le Dube	tall grass*Nombali	0.8
Habitat*site	short grass*Le Dube	tall grass*Seme	1.0
Habitat*site	short grass*Le Dube	short grass*Maqanda	1.0
Habitat*site	short grass*Le Dube	short grass*Nombali	0.6
Habitat*site	short grass*Le Dube	short grass*Seme	0.7
Habitat*site	tall grass*Maqanda	tall grass*Nombali	1.0
Habitat*site	tall grass*Maqanda	tall grass*Seme	1.3
Habitat*site	tall grass*Maqanda	short grass*Nombali	0.7
Habitat*site	tall grass*Maqanda	short grass*Seme	0.9
Habitat*site	short grass*Maqanda	tall grass*Nombali	0.8
Habitat*site	short grass*Maqanda	tall grass*Seme	1.0
Habitat*site	short grass*Maqanda	short grass*Nombali	0.6
Habitat*site	short grass*Maqanda	short grass*Seme	0.8
Habitat*site	tall grass*Nombali	tall grass*Seme	1.3
Habitat*site	tall grass*Nombali	short grass*Seme	1.0
Habitat*site	canopy*Le Dube	canopy*Maqanda	0.9
Habitat*site	canopy*Le Dube	canopy*Nombali	1.5
Habitat*site	canopy*Le Dube	canopy*Seme	0.9
Habitat*site	canopy*Le Dube	short grass*Maqanda	1.3
Habitat*site	canopy*Le Dube	short grass*Nombali	0.7
Habitat*site	canopy*Le Dube	short grass*Seme	1.0
Habitat*site	canopy*Le Dube	tall grass*Maqanda	1.0
Habitat*site	canopy*Le Dube	tall grass*Nombali	1.0
Habitat*site	canopy*Le Dube	tall grass*Seme	1.3
Habitat*site	canopy*Le Dube	short grass*Le Dube	1.3
Habitat*site	canopy*Le Dube	tall grass*Le Dube	0.9
Habitat*site	canopy*Maqanda	canopy*Nombali	1.7
Habitat*site	canopy*Maqanda	canopy*Seme	1.0
Habitat*site	canopy*Maqanda	short grass*Nombali	0.8
Habitat*site	canopy*Maqanda	short grass*Seme	1.1
Habitat*site	canopy*Maqanda	tall grass*Nombali	1.2

Appendix D Continued:

Factor	Level of factor	Compared with:	Odds ratio
Habitat*site	canopy*Maqanda	tall grass*Seme	1.5
Habitat*site	canopy*Maqanda	short grass*Le Dube	1.5
Habitat*site	canopy*Maqanda	tall grass*Le Dube	1.0
Habitat*site	canopy*Maqanda	short grass*Maqanda	1.4
Habitat*site	canopy*Maqanda	tall grass*Maqanda	1.2
Habitat*site	canopy*Maqanda	canopy*Seme	1.0
Habitat*site	canopy*Nombali	short grass*Nombali	0.5
Habitat*site	canopy*Nombali	short grass*Seme	0.6
Habitat*site	canopy*Nombali	tall grass*Nombali	0.7
Habitat*site	canopy*Nombali	tall grass*Seme	0.9
Habitat*site	canopy*Nombali	short grass*Le Dube	0.9
Habitat*site	canopy*Nombali	tall grass*Le Dube	0.6
Habitat*site	canopy*Nombali	short grass*Maqanda	0.8
Habitat*site	canopy*Nombali	tall grass*Maqanda	0.7
Habitat*site	canopy*Seme	short grass*Nombali	0.8
Habitat*site	canopy*Seme	short grass*Seme	1.1
Habitat*site	canopy*Seme	tall grass*Nombali	1.1
Habitat*site	canopy*Seme	tall grass*Seme	1.5
Habitat*site	canopy*Seme	short grass*Le Dube	1.5
Habitat*site	canopy*Seme	tall grass*Le Dube	1.0
Habitat*site	canopy*Seme	short grass*Maqanda	1.4
Habitat*site	canopy*Seme	tall grass*Maqanda	1.2
Habitat*cage type	tall grass*small	tall grass*big	0.6
Habitat*cage type	tall grass*small	tall grass*open	0.5
Habitat*cage type	tall grass*small	short grass*small	0.4
Habitat*cage type	tall grass*small	short grass*big	0.8
Habitat*cage type	tall grass*small	short grass*open	0.9
Habitat*cage type	tall grass*small	canopy*small	0.7
Habitat*cage type	tall grass*small	canopy*big	0.6
Habitat*cage type	tall grass*small	canopy*open	0.7
Habitat*cage type	tall grass*big	tall grass*open	0.8
Habitat*cage type	tall grass*big	short grass*small	0.7
Habitat*cage type	tall grass*big	short grass*big	1.3
Habitat*cage type	tall grass*big	short grass*open	1.5
Habitat*cage type	tall grass*big	canopy*small	1.1
Habitat*cage type	tall grass*big	canopy*big	1.1
Habitat*cage type	tall grass*big	canopy*open	1.2
Habitat*cage type	tall grass*open	short grass*small	0.9
Habitat*cage type	tall grass*open	short grass*big	1.6
Habitat*cage type	tall grass*open	short grass*open	1.8
Habitat*cage type	tall grass*open	canopy*small	1.4
Habitat*cage type	tall grass*open	canopy*big	1.3
Habitat*cage type	tall grass*open	canopy*open	1.4
Habitat*cage type	short grass*small	short grass*big	1.8
Habitat*cage type	short grass*small	short grass*open	2.0
Habitat*cage type	short grass*small	canopy*small	1.6
Habitat*cage type	short grass*small	canopy*big	1.5

Appendix D Continued:

Factor	Level of factor	Compared with:	Odds ratio
Habitat*cage type	short grass*small	canopy*open	1.6
Habitat*cage type	short grass*big	short grass*open	1.1
Habitat*cage type	short grass*big	canopy*small	0.9
Habitat*cage type	short grass*big	canopy*big	0.8
Habitat*cage type	short grass*big	canopy*open	0.9
Habitat*cage type	short grass*open	canopy*small	0.8
Habitat*cage type	short grass*open	canopy*big	0.7
Habitat*cage type	short grass*open	canopy*open	0.8
Habitat*cage type	canopy*small	canopy*big	0.9
Habitat*cage type	canopy*small	canopy*open	1.0
Habitat*cage type	canopy*big	canopy*open	1.1
Site*cage type	Le Dube*small	Le Dube*big	1.1
Site*cage type	Le Dube*small	Le Dube*open	0.9
Site*cage type	Le Dube*small	Maqanda*small	1.2
Site*cage type	Le Dube*small	Maqanda*big	0.8
Site*cage type	Le Dube*small	Maqanda*open	1.0
Site*cage type	Le Dube*small	Nombali*small	0.8
Site*cage type	Le Dube*small	Nombali*big	1.1
Site*cage type	Le Dube*small	Nombali*open	1.1
Site*cage type	Le Dube*small	Seme*small	0.9
Site*cage type	Le Dube*small	Seme*big	1.0
Site*cage type	Le Dube*small	Seme*open	1.0
Site*cage type	Le Dube*big	Le Dube*open	0.8
Site*cage type	Le Dube*big	Maqanda*small	1.1
Site*cage type	Le Dube*big	Maqanda*big	0.7
Site*cage type	Le Dube*big	Maqanda*open	1.0
Site*cage type	Le Dube*big	Nombali*small	0.7
Site*cage type	Le Dube*big	Nombali*big	1.0
Site*cage type	Le Dube*big	Nombali*open	1.0
Site*cage type	Le Dube*big	Seme*small	0.9
Site*cage type	Le Dube*big	Seme*big	1.0
Site*cage type	Le Dube*big	Seme*open	0.9
Site*cage type	Le Dube*open	Maqanda*small	1.4
Site*cage type	Le Dube*open	Maqanda*big	0.9
Site*cage type	Le Dube*open	Maqanda*open	1.2
Site*cage type	Le Dube*open	Nombali*small	0.9
Site*cage type	Le Dube*open	Nombali*big	1.2
Site*cage type	Le Dube*open	Nombali*open	1.2
Site*cage type	Le Dube*open	Seme*small	1.1
Site*cage type	Le Dube*open	Seme*big	1.2
Site*cage type	Le Dube*open	Seme*open	1.1
Site*cage type	Maqanda*small	Maqanda*big	0.6
Site*cage type	Maqanda*small	Maqanda*open	0.8
Site*cage type	Maqanda*small	Nombali*small	0.6
Site*cage type	Maqanda*small	Nombali*big	0.9
Site*cage type	Maqanda*small	Nombali*open	0.9
Site*cage type	Maqanda*small	Seme*small	0.8

Appendix D Continued:

Factor	Level of factor	Compared with:	Odds ratio
Site*cage type	Maqanda*small	Seme*big	0.9
Site*cage type	Maqanda*small	Seme*open	0.8
Site*cage type	Maqanda*big	Maqanda*open	1.3
Site*cage type	Maqanda*big	Nombali*small	1.1
Site*cage type	Maqanda*big	Nombali*big	1.4
Site*cage type	Maqanda*big	Nombali*open	1.4
Site*cage type	Maqanda*big	Seme*small	1.2
Site*cage type	Maqanda*big	Seme*big	1.4
Site*cage type	Maqanda*big	Seme*open	1.3
Site*cage type	Maqanda*open	Nombali*small	0.8
Site*cage type	Maqanda*open	Nombali*big	1.1
Site*cage type	Maqanda*open	Nombali*open	1.1
Site*cage type	Maqanda*open	Seme*small	0.9
Site*cage type	Maqanda*open	Seme*big	1.0
Site*cage type	Maqanda*open	Seme*open	0.9
Site*cage type	Nombali*small	Nombali*big	1.4
Site*cage type	Nombali*small	Nombali*open	1.4
Site*cage type	Nombali*small	Seme*small	1.2
Site*cage type	Nombali*small	Seme*big	1.3
Site*cage type	Nombali*small	Seme*open	1.2
Site*cage type	Nombali*big	Nombali*open	1.0
Site*cage type	Nombali*big	Seme*small	0.9
Site*cage type	Nombali*big	Seme*big	1.0
Site*cage type	Nombali*big	Seme*open	0.9
Site*cage type	Nombali*open	Seme*small	0.9
Site*cage type	Nombali*open	Seme*big	1.0
Site*cage type	Nombali*open	Seme*open	0.9
Site*cage type	Seme*small	Seme*big	1.1
Site*cage type	Seme*small	Seme*open	1.0
Site*cage type	Seme*big	Seme*open	0.9
Species*cage type	<i>A.k</i> *small	<i>A.k</i> *big	0.7
Species*cage type	<i>A.k</i> *small	<i>A.k</i> *open	3.5
Species*cage type	<i>A.k</i> *small	<i>A.n</i> *small	5.2
Species*cage type	<i>A.k</i> *small	<i>A.n</i> *big	9.9
Species*cage type	<i>A.k</i> *small	<i>A.n</i> *open	10.3
Species*cage type	<i>A.k</i> *big	<i>A.k</i> *open	1.2
Species*cage type	<i>A.k</i> *big	<i>A.n</i> *small	3.2
Species*cage type	<i>A.k</i> *big	<i>A.n</i> *big	7.3
Species*cage type	<i>A.k</i> *big	<i>A.n</i> *open	8.3
Species*cage type	<i>A.k</i> *open	<i>A.n</i> *small	0.8
Species*cage type	<i>A.k</i> *open	<i>A.n</i> *big	4.1
Species*cage type	<i>A.k</i> *open	<i>A.n</i> *open	5.7
Species*cage type	<i>A.n</i> *small	<i>A.n</i> *big	1.3
Species*cage type	<i>A.n</i> *small	<i>A.n</i> *open	3.5
Species*cage type	<i>A.n</i> *big	<i>A.n</i> *open	0.8

Chapter 6

Conclusions

The role of certain seed ecological aspects in bush encroachment in HUP

Acacia karroo produced more, although smaller, seeds than *A. nilotica* with less bruchid damage. Though the numbers of seeds found in the soil were similar for both species, the higher seed production and lower bruchid damage translates to higher numbers of intact *A. karroo* seeds being available for reaching safe sites. *Acacia karroo* thus has greater potential for being an encroaching species in HUP than *A. nilotica*. Three times as many *A. karroo* as *A. nilotica* seedlings have been reported in HUP (Bond, Smythe & Balfour, 2001) suggesting that seeds of *A. karroo* are indeed reaching safe sites for germination and establishment. In this study there were higher levels of germination for *A. karroo* than *A. nilotica* and 14.5 times more established seedlings of *A. karroo* than *A. nilotica* in the fire experiment. Biological control using bruchid beetles has not worked for *A. nilotica* in Australia (Radford, Nicholas & Brown, 2001). Control of *A. karroo* populations using host-specific bruchid beetles is unlikely because indigenous predator species are seldom successful at controlling indigenous host species, largely due to the presence of predators and disease that prevent rapid population growth of biological control species. Although *A. nilotica* is not thought to be seed limited, it may be predation limited. In the 1940s DDT was used to kill tsetse flies (*Glossina* spp.) in HUP in an attempt to control the outbreak of nagana (trypanosomosis) (Du Toit, 1954; Kappmeier, Nevill & Bagnall, 1998). The many *A. nilotica* adults found in HUP may be a result of the DDT spraying possibly having lowered bruchid numbers subsequently

allowing more intact seeds to reach safe sites. Seed predators influence plant population dynamics by limiting fecundity (Auld & Denham, 1999) and lowering the frequency with which a safe site may be hit by seeds (Janzen, 1971). It is possible that the DDT spraying may also have affected ant populations in the park. Ants may contribute to the soil-stored seed-banks of some species (Holmes, 1990) and the lack of younger *A. nilotica* stands may be due to low numbers of seeds in the seed-bank preventing mass germination events.

African acacias face many important hurdles from seed to seedling (Figure 6.1) and in this study *Acacia karroo* had higher levels of germination and establishment than *A. nilotica* after being burnt. Burning of seeds at various fire intensities did not affect subsequent germination or establishment. The fire experiment also showed that neither grass length nor site burn status affected germination and establishment as main effects, but featured as second order interaction effects.

The number of post-dispersal seeds chewed depended on structural habitat type, species, site and cage type. More *A. karroo* than *A. nilotica* seeds were chewed and most were chewed in tall grass. More seeds were chewed in open than small or big cages. Unexplained seed disappearance was dependent on species and rodent presence. More *A. karroo* than *A. nilotica* seeds disappeared and most seeds disappeared in the presence of rodents. Only rodents could be identified as post-dispersal predators with any certainty. The level of post-dispersal predation of the two species does not reflect their current level of success in HUP.

Further studies should include the effect of vegetation patches on post-dispersal predation, by rodents in particular, to determine how patches may contribute to safe sites for germination and establishment. The role of ants and termites in moving seeds

underground and thus possibly contributing to soil-stored seed-banks should be investigated as well as whether it could contribute to mass germination events. Soil-stored seed-banks should be sampled before and after fire to see if fire is a sufficient germination cue for buried seeds. Studies on seed production and pre-dispersal predation should be conducted over a number of fruiting seasons and it should be determined whether *A. nilotica* is predation limited or not. Germination in the field should be investigated so that it may be compared with experimental germination levels.

From Figure 6.1. it is clear that the effects of bruchid beetles on seed mortality and/or germination has been well studied. This study has added to the available literature by quantifying bruchid damage for an area where no data on the subject has been published. Other causes of pre-dispersal mortality such as pathogen attack have not been studied. Pathogens may also cause mortality in newly germinated seeds or young seedlings in the wild.

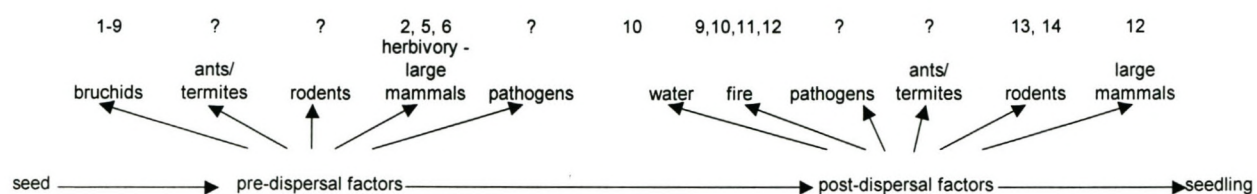
The effects of rodents on pre-dispersal mortality of seeds may be particularly important for indehiscent pods that may drop to the ground when ripe. Neither pre- nor post-dispersal movement of seeds by ants have been recorded and whether ants play any role in the movement of non-elaiosome bearing *Acacia* seeds is not known.

The effects of herbivory and fire on seeds and seedlings has received attention, but there is much contradiction in the literature regarding the effects of fire. This study has added to the debate and undoubtedly raises more questions. The effect of fire in the field is certainly dependent on many factors before even considering the spatio-temporal effects. The aim of the fire experiment in this study was to determine the possible effects of fire on dispersed seeds under management burning practice and how it may or may not relate to bush encroachment. This was done with the idea of making

management recommendations that do not involve prescribed fire temperatures (fuel loads), air temperatures, relative humidity etc. as that would be of little use to managers.

Management considerations

Although burning of seeds at various fire intensities did not affect subsequent germination or establishment, it is suggested that fire may be a management tool for the control of *A. karroo* in HUP. Burning usually takes place in the dry season when most *Acacia* species have ripe seeds. Any seedlings that establish in that year would be about 12 months old at the time of the next burn. *Acacia karroo* seedlings are fire resistant from as young as 12 months and are able to survive even high intensity fires (Story, 1952). Fire cannot control established *A. karroo* and may in fact cause thickening by encouraging coppice growth (Story, 1952). It is suggested that spring burns after first rain and seedling germination, would be more effective as a means of control of *A. karroo*. It is suggested that the effects of fire be more thoroughly investigated in HUP and that fire exclusion plots be set up. Fire is thought to be the main demographic hurdle for *Acacia* species in productive areas where grass can grow tall (Midgley & Bond, 2001) such as in Hluhluwe Game Reserve. As it is also the only demographic hurdle under management control, further investigation is essential.



¹PELLEW, R.A. & SOUTHGATE, B.J. (1984)

²COE, M. & COE, C. (1987)

³HOFFMAN, M.T., COWLING, R.M., DOUIE, C. & PIERCE, S.M. (1989)

⁴ERNST, W.H.O., DECELLE, J.E. & TOLSMA, D.J. (1990)

⁵HAUSER, T.P. (1994)

⁶MILLER, M.F. (1994a)

⁷MUCUNGUZI, P. (1995)

⁸MILLER, M.F. (1996)

⁹This study

¹⁰STORY, R. (1952)

¹¹SABIITI, E.N. & WEIN, R.W. (1987)

¹²KANZ, W.A. (2001)

¹³MILLER, M.F. (1994b)

¹⁴MILLER, M.F. (1995)

Figure 6.1 Important hurdles for African acacias from seed to seedling

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