Post-dispersal fate of *Acacia* seeds in an African savanna

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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-iMfolozi Park, the numbers of adult *Acacia nilotica* (L.) Willd. Ex Del. subsp. *kraussiana* (Benth.) Brenan trees per hectare far exceed those of *A. karroo* Hayne adults. The relative dominance is reversed in the juvenile stage with *A. karroo* outnumbering *A. nilotica* threefold outside closed woodlands. We experimentally investigated the effects of location, structural habitat type, species, predator type and rodent presence on the level of post-dispersal seed predation in an attempt to explain species dominance in Hluhluwe-iMfolozi 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 grazing lawn (10.7%) or canopy areas (15.2%), and most seeds (19.7%) were lost from unprotected control groups. Rodent presence was a significant factor in a model aiming to determine reasons for unexplained seed disappearance. Post-dispersal predation of seeds could not account for the differences in success between *A. karroo* and *A. nilotica* in Hluhluwe-iMfolozi Park.

Key words: *Acacia,* bush encroachment, grassland invasion, Hluhluwe-iMfolozi Park, rodents, seed predation.

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 *et al.* 2001), with special mention being made of *Acacia karroo* Hayne (Du Toit 1967; O'Connor 1995; Chirara *et al.* 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. A study in Hluhluwe-iMfolozi Park (HiP) showed *A. nilotica* trees to produce a mean of 992 and *A. karroo* a mean of 1628 across various size classes (Walters & Milton 2003). Seeds may be either wind dispersed (dehiscent species) or animal dispersed (indehiscent species) (Coe & Coe 1987) with seed dispersal by these agents being an attempt at reaching suitable sites for establishment. Post-dispersal predators may, however, exact a varying toll on dispersed seeds, resulting in varying levels of seedling establishment. Small mammals and insects are important post-dispersal predators, with predation being variable in space and time (Crawley 1992; Andresen 1999).

A net increase in shrub cover in the Hluhluwe section of HiP has been reported for the period 1937 to 1975 (Watson & Macdonald 1983). In HiP acacias are seen as major contributors to bush encroachment. As recently as 22 years ago, Whateley & Porter (1983) reported *A. karroo* to be largely confined to the northeastern part of HiP. This was confirmed by Bond *et al.* (2001) who reported that in HiP, *A. karroo* woodlands were rare, and that they found no adult trees in any of their transects selected to cover a wide altitudinal range. However, they did find 111 (62.5/ha) adult *A. nilotica* trees when specifically avoiding closed *A. nilotica* woodlands. This relative dominance was reversed in juvenile stages with *A. karroo* (725/ha) outnumbering *A. nilotica* (225/ha) threefold and therefore setting woodland structure to

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change in the future (Bond *et al.* 2001).

Bush encroachment and the factors causing it, are poorly understood and various explanations have been given for the phenomenon. Views range from bush encroachment being a general, natural process (Jordaan *et al.* 2004) to it being associated with human activities such as high cattle densities (Skarpe 1990; Ringrose *et al.* 1996). The socio-economic importance of savannas cannot be disputed. South Africa's savanna biome is home to approximately 9.2 million rural inhabitants (Ballance *et al.* 2001) and is mainly used for livestock and game ranching (Grossman & Gandar 1983). Bush encroachment has been shown to decrease herbaceous yield (Angassa 2005) with declining primary productivity translating to declining secondary productivity (de Ridder & Breman 1993). With roughly 18% of the biome under communal tenure (Ballance *et al.* 2001), local communities stand to loose much through the impact of bush encroachment on rural livelihoods. Bush encroachment also decreases the diversity of habitat for some species (Meik *et al.* 2002) and therefore biodiversity as a whole.

This study investigated the effect of structural habitat type on post-dispersal survival of *A. nilotica* and *A. karroo* seeds in HiP. 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 HiP.

METHODS

Study site

The study was done in HiP, KwaZulu-Natal, South Africa (28°00′–28°26′S; 31°43′–32°09′E). HiP is a 960 km^2 fenced 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 to 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 iMfolozi 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). The park comprises two major vegetation types, namely the Zululand Thornveld and the Tropical Bush and Savanna types (Acocks 1988).

Field experiment

A field experiment was conducted to determine the post-dispersal fate of *A. karroo* and *A. nilotica* seeds. The experiment took place between 27 July 2000 and 25 January 2001 and was conducted at four sites (Le Dube, Maqanda, Nombali, Seme) in the Hluhluwe section of the park. Each site was represented by three habitat 'types' of interest namely, tall grass, grazing lawn and sub-canopy areas (areas under *Acacia* tree 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 of each cage type were used in each habitat type at each site. 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, as indicated by chewed seed 'shells' and/or rodent droppings within a cage, number of destroyed seeds (shells remaining), number of remaining seeds, number of germinated seeds and number of seedlings were recorded for each *Acacia* species. The number of seeds 'disappeared' was calculated as: 5–(the number destroyed + the number germinated + the number lost through ungulate trampling).

Data analysis

The STATISTICA® (v. 5.5, StatSoft, Inc. 2000) Generalized Linear Model (GLZ) module was used to build models for number of destroyed seeds and number of disappeared seeds as response variables. Data were of a binomial distribution with an inverse normal distribution. The probit model was thus used as the link function. All effects except the fourth order interactions, which were not significant, were included in the models. The probit model for the number of seeds destroyed may be written as follows:

$$NP\ (\text{number destroyed}) = NP(\lambda' + \lambda'^{B}_{j} + \lambda'^{C}_{k} + \lambda'^{D}_{l} + \lambda'^{E}_{m} + \lambda'^{BC}_{jk} + \ldots + \lambda'^{CDE}_{klm})$$

where NP = the normal probability, λ' = the overall mean effect of the categories, λ'^{B}_{j} = the effect of the jth species (j = *A. karroo, A. nilotica*) λ'^{C}_{k} = the effect of the kth site (k = Le Dube, Maqanda, Nombali, Seme), λ'^{D}_{l} = the effect of the *l*th cage type (*l* = small, big, open), λ'^{E}_{m} = the effect of the *m*th structural habitat type (*m* = grazing lawn, tall grass, canopy), λ'^{BC}_{jk} = the interaction effect between the *j*th species and the *k*th site, λ'^{CDE}_{klm} = 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:

$$\text{Number destroyed} = \beta_0 + \beta^B_1\chi^B_1 + \beta^C_1\chi^C_1 + \beta^c_2\chi^C_2 + \beta^C_3\chi^C_3 + \beta^D_1\chi^D_1 + \beta^D_2\chi^D_2 + \beta^E_1\chi^E_1 + \beta^E_2\chi^E_2 + \beta^{BC}_{11}\chi^{BC}_{11} + \ldots + \beta^{CDE}_{111}\chi^{CDE}_{111},$$

where $\beta_0, \beta^B_1, \beta^C_1, \beta^C_2, \beta^C_3, \beta^D_1, \beta^D_2, \beta^E_1, \beta^E_2, \beta^{BC}_{11}$ and β^{CDE}_{111} 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 GLZ were used to obtain the estimated parameters for the probit model.

The model was run twice. Once using data of chewed/destroyed seeds (known seed fate) found in cages and once for data on seed disappearance (unknown seed fate) from cages. The same explanatory variables were used in the model for seed disappearance as for seed destruction with the addition of rodent presence as a main factor.

The predicted frequencies of seeds destroyed 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. Thus, differences in the predicted frequencies of seeds destroyed and disappeared are illustrated graphically for each significant treatment combination.

RESULTS

Number of destroyed seeds

The maximum number of destroyed seeds at each site (as on day 191) was used to test for differences among treatments. The factors used in the model are described in Table 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 and certain interaction effects significantly affected the number of seeds destroyed in the field (Table 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 factor is given in Table 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 4; Fig. 1). Significant interaction effects are also reported (Table 4; Fig. 2).

DISCUSSION

Number of destroyed seeds

The most striking result was that *A. karroo* was more likely to be destroyed than *A. nilotica* with 21.8% of *A. karroo* and 12.7% of *A. nilotica* destroyed. Rodent preference for *A. karroo* could be due to the thinner seed coat of this dehiscent

Table 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.

	Description	Total number of seeds	Number chewed	Number not chewed	Percentage chewed
Total		2135	368	1767	17.24
Cage type	Small	710	83	627	11.69
	Big	710	144	566	20.28
	Open	715	141	574	19.72
Site	Le Dube	520	136	384	26.15
	Maqanda	535	124	411	23.18
	Nombali	540	75	465	13.89
	Seme	540	33	507	6.11
Species	*A. karroo*	1065	232	833	21.78
	A. nilotica	1070	136	934	12.71
Habitat type	Tall grass	700	182	518	26.00
	Grazing lawn	720	77	643	10.69
	Canopy	715	109	606	15.24

Table 2. Log-likelihood III, Chi-square and Wald statistics indicating the significance of the factors and interactions on the number of seeds destroyed in the field. Significant factors and interactions are indicated in bold.

	d.f.	Log–likelihood	Chi–square	Wald statistic	*P*
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

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 of 11 species, including *A. karroo.*

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.

In experiments done by Midgley *et al.* (2002) on *Leucadendron sessile* dispersal, less than 2% of seeds remained as husks 'on site'. Our experiment showed a higher proportion of seeds being eaten 'on site'. One of the reasons for this could be that different rodent communities may be involved. *Acacia* rodent predators and their seed preferences

Table 3. Description of the factors and number of seeds used in the model to determine which factors affect seed disappearance in the field.

	Description	Total number of seeds	Number disappeared	Number not disappeared	Percentage disappeared
Total		2162	536	1626	24.79
Cage type	Small	722	170	552	23.55
	Big	725	198	527	27.31
	Open	715	168	547	23.50
Rodents	Yes	1152	413	739	35.85
	No	1010	123	887	12.18
Site	Le Dube	547	174	373	31.81
	Maqanda	535	162	373	30.28
	Nombali	540	121	419	22.41
	Seme	540	79	461	14.63
Species	*A. karroo*	1080	326	754	30.19
	A. nilotica	1082	210	872	19.41
Habitat type	Tall grass	720	205	515	28.47
	Grazing lawn	722	163	559	22.58
	Canopy	720	168	552	23.33

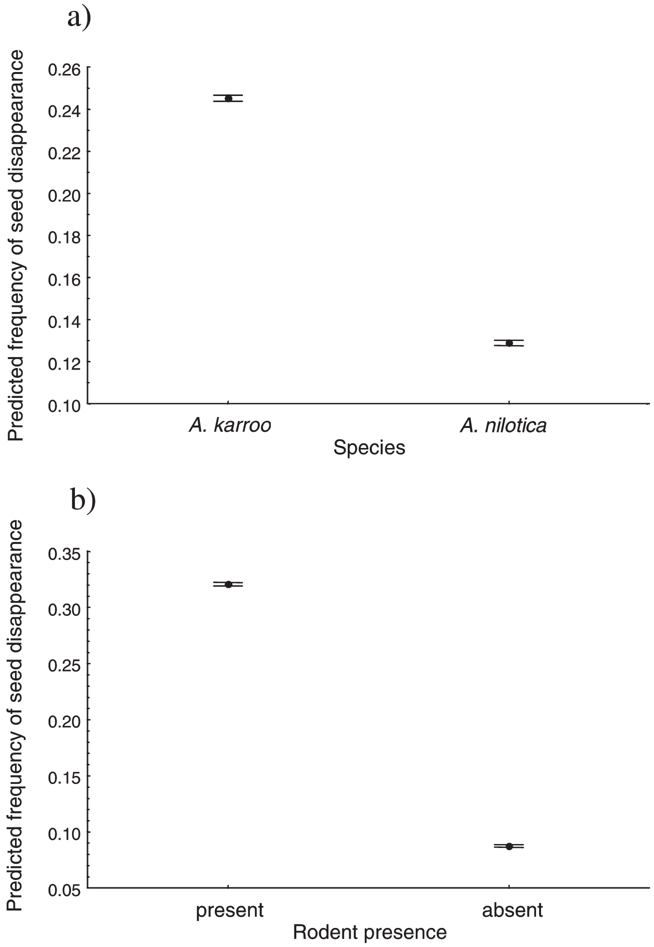

Fig. 1. Predicted frequencies of disappeared seeds for the main effects of (**a**) species and (**b**) rodent presence. Vertical error bars show 95% confidence limits.

may hold some clues for bush encroachment and requires further research.

Although the actual proportion of seeds destroyed in small, big and open cages was 11.7%, 20.3% and 19.7%, respectively, open cages had the highest predicted frequency of destroyed seeds. There was very little difference between small and big cages, but big cages showed high variation in the number of destroyed seeds. Open cages allow easiest access to seeds by rodents explaining the higher levels of predation from these cages.

Seeds were more likely to be destroyed in tall grass areas than grazing lawn or canopy sites, with the latter two habitats having a similar likelihood of having destroyed 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 destroyed 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 *et al.* 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; however, they did not distinguish between grazing lawn and tall grass habitats.

The significance of site and the interaction effects: habitat × cage type, site × cage type, habitat × site and cage type × site × habitat, are also thought to be related to rodent habitat preference. The grazing lawn area at Nombali,

Table 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.

	d.f.	Log-likelihood	Chi-square	Wald statistic	*P*
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

however, showed high rodent predation. This may be explained by it both being a smaller grazing lawn patch than at the other sites and 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 we suggest that, though not investigated here, patch sizes may be important with regards to rodent predation of seeds. The species × site × habitat interaction effect may be related to the combination of rodent preference in structural habitat type and *Acacia* species as reported earlier.

Midgley *et al.* (2002) tagged seeds to determine seed fate and found that 98% of relocated seeds were moved more than 2 m and buried less than 2 cm deep. In HiP, Walters & Milton (2003) found very few seeds in the soil for either *Acacia* species with no difference in the size of the soil-stored seed-banks of the two species when sampling up to a depth of 5 cm and up to a distance of 20 m from the tree canopy. Therefore, it does not seem that rodent predation would exercise a strong effect on the size of the seed banks and thus seed availability.

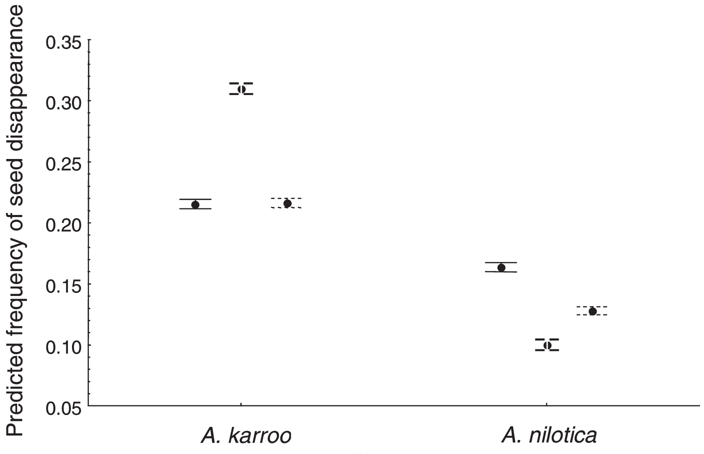

Fig. 2. Predicted frequencies of disappeared seeds for the significant interaction effect of cage type with species. Solid lines = small cages; broken lines = open cages; dotted lines = big cages. Vertical error bars show 95% confidence limits.

Number of seeds disappeared

Unlike the 'number destroyed' model, only *Acacia* species and rodent presence were main factors affecting the disappearance of seeds. Thirty per cent of *A. karroo* seeds disappeared 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. Midgley *et al.* (2003) found that while less than 2% of seed husks were left behind, more than 90% of seeds were removed by rodents, with the majority being buried.

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 areas showing no signs of predation by rodents as a result of caching for later consumption (Price & Jenkins 1986).

The habitat × site and cage type × habitat interactions again are 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 grazing lawn areas and it is suggested that ants may be responsible. Seed harvesting by ants is not uncommon (Gillon et al. 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. In HiP, ant presence was noted more frequently in grazing lawn than tall grass or canopy sites (M. Walters, unpubl. 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 again might suggest a rodent preference for *A. karroo.* Davidson *et al.* (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 suggest that for the two *Acacia* species studied, the opposite is true.

The site × habitat × 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. Seed banks for these two species are, however, very small in HiP (Walters & Milton 2003). The ability of seeds to germinate also 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.

This study found that *Acacia* species, structural habitat type, site and cage type were the main factors influencing seed destruction, while *Acacia* species and rodent presence were the main factors affecting seed disappearance. Structural habitat type, cage type and site, however, did not affect seed disappearance in the field. Although this study could not relate post-dispersal fate of seeds to species abundance, the facilitation of seedling establishment of encroaching woody plant species by rodents in HiP deserves further investigation.

While a significant shortcoming of this study is that a large proportion of seeds was lost to an unknown fate, it is not thought that those seeds were buried, as soil seed bank studies yielded very few seeds (Walters & Milton, 2003). We suggest that future experimental research similar to that done by Midgley *et al.* (2002) would prove valuable in determining seed fate in savannas and might yield results that further our understanding of savanna ecology and possibly bush encroachment.

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