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Seed predation and germination of *Acacia erioloba* in the Kuiseb River Valley, Namib Desert

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We investigated some interactions between mammalian herbivores, bruchid seed predators and seeds of *Acacia erioloba* E. Mey in the Kuiseb River Valley, Namib Desert. Predation by bruchid beetles was significantly lower in canopy-held pods than pods on the ground. Germination success was higher for ingested seed than in an untreated control and almost zero for predated seed. Acid and scarification treatments resulted in almost complete germination success. The study provides some support for a mutualistic relationship between mammalian herbivores and acacias, like *A. erioloba*, with indehiscent pods.

Die interaksies tussen soogdierherbivore, saadparasiterende 'bruchid'-kewers en saad van *Acacia erioloba* E.Mey. in die Kuisebriviervallei, Namibwoestyn is ondersoek. Die parasitering van saad deur 'bruchid'-kewers was aansienlik laer waar die peule nie afgewerp was nie as by peule wat op die grond beland het. Ontkieming was hoër waar die peule deur die herbivore gevreet is en bykans nul by geparasiteerde saad. Suur- en skarifikasiebehandeling het tot 'n hoë persentasie ontkieming gelei. Die ondersoek lewer 'n mate van steun vir die gedagte van 'n mutualistiese verhouding tussen soogdierherbivore en akasias, met nie-oopspringende peule, soos *A. erioloba*.

Keywords: *Acacia*, Bruchidae, germination, herbivory, seed predation

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Introduction

Acacia erioloba E. Mey is widespread in Africa and occurs throughout most of the drier southern African savannas. It is an important tree species in the Kuiseb River Valley of the central Namib Desert (Theron *et al.* 1985) and forms part of a linear oasis, vital to animal migration and plant dispersion patterns (Huntley 1985). *A. erioloba* has indehiscent pods which are an important food source for indigenous and domestic animals (Hamilton *et al.* 1977; Coates Palgrave 1983).

Based on work on *Acacia tortilis* (Forsk.) Hayne, a three-way relationship between herbivores, acacias with indehiscent pods and bruchid beetles has been suggested (Lamprey *et al.* 1974). The seed pods and a proportion of the seeds are consumed by herbivores and form an important part of their diet (Gwynne 1969). By having indehiscent pods and round seeds, most of which pass undamaged through an animal's gut (Leistner 1961; Gwynne 1969; Lamprey 1967; Hamilton *et al.* 1977, but see Jarman 1976), these acacias are thought to be adapted to herbivory. The digestive juices may 'soften' the seed coat (Cavanagh 1980) or fracture the lens, thus facilitating water imbibition during germination (Tran & Cavanagh 1984). Germination success is thereby improved (Lamprey 1967; Halevy 1974; Lamprey *et al.* 1974). Enhanced dispersal and favourable germination microclimates are also possible advantages of being eaten (Coughenour & Detling 1986).

Bruchid beetles are common *Acacia* seed predators (New 1983). Mature adults lay eggs on or in developing pods and the young larvae live off the maturing seeds (Halevy 1974). The pods eventually fall to the ground, remaining there until eaten by herbivores. The longer the pods lie on the ground the greater the insect predation levels (Lamprey *et al.* 1974). If the predators are still in the egg or early larval stages then ingestion of the pods by herbivores will kill them before they are able to mature and eat the seed embryos (Leistner 1961; Lamprey *et al.* 1974). If the seed predators have penetrated the seed but not destroyed the embryo, however, then the beetle exit holes may increase the permeability of the seed coat resulting in rapid germination (Lamprey *et al.* 1974). This may have adaptive significance in environments characterized by unpredictable rainfall events (Halevy 1974).

We studied predation of *A. erioloba* pods collected in the Kuiseb River Valley near Gobabeb, Namib Desert, and investigated the effects of a range of seed treatments on germination. We tested the following hypotheses:

(a) Canopy-held pods would have lower levels of seed predation compared to pods which have lain on the ground (Lamprey *et al.* 1974);
(b) Predated seed and seed which have passed through the gut of mammalian herbivores would have higher germination successes than untreated controls (Halevy 1974; Lamprey *et al.* 1974).

Materials and Methods

Seed predation

Twenty *Acacia erioloba* pods were collected from the canopy and 20 from the ground beneath the canopy from five trees in the Kuiseb River Valley about 10 km east of the research station at Gobabeb in July 1987.

The pods were opened and sorted into predated, non-predated and 'aborted' categories. The exit holes of insect predators easily distinguished predated from non-predated seeds. Although we classified all extensively deformed and shrivelled seed as 'aborted' we did not test that their appearance was as a direct result of abortion, nor did we test their viability.

Germination

We used four replicates of 25 seeds each for the germination trials. Only plump (i.e. no 'aborted' seeds) were used in the experiment. The control consisted of untreated, non-predated, seeds. We compared germination in predated seeds and treated seeds with that of the control. Seed treatments included 30, 60 and 90 min in concentrated sulphuric acid and abrading the seed coat with sand paper. We fed *Acacia erioloba* pods to cattle, collected the seeds from the dung 36 h later and recorded their germination success. We did not have access to other mammalian herbivores known to consume *A. erioloba* seeds [e.g. gemsbok (*Oryx gazella*), chacma baboons (*Papio ursinus*) (Hamilton *et al.* 1977, see also Leistner 1961)] and this precluded their use in the germination trials.

The seeds were germinated in 9-cm petri dishes each containing three No 2 Whatman filter papers. We added 3 ml of a fungicide (Benlate) at a concentration of 0,075%. Seeds were incubated at equal periods of 12 h at 30°C in the light and at 15°C in the dark. Germinated seeds (those with the radicle emerging 1–2 mm beyond the seed coat) were recorded and removed every day for 10 days and thereafter every second day until days 33.

Statistical methods

The number of predated seeds in a pod can be modelled as a binomial distribution with probability of predation depending on factors such as whether the pod was on the ground or the canopy and individual tree differences. The effects of these factors were estimated using a generalized linear model with a binomial error distribution and a logistic link function (McCullogh & Nelder 1983). Similarly, the probability of germination depends on the treatment and a generalized linear model was used to estimate treatment effects.

Results

Predation

The number of seeds per pod for the five *Acacia erioloba* individuals studied was 16,1 ± 3,7 (n = 200 pods). The range of seed predation levels was high for both canopy-held pods and pods on the ground (Table 1). Levels of seed abortion appeared fairly constant between trees and whether pods were collected from the canopy or ground.

Table 2 Results of fitting the generalized linear model to number of predated seeds. A deviance of 194,3 with 192 degrees of freedom indicates a good fit to the model (P>0,5). A scale factor of 9 was used, indicating considerable overdispersion (McCullogh & Nelder 1983)

(a) Regression coefficients

Factor	Regression coefficients	*S.E.*	*T*
Constant	–0,26	0,27	–0,97
Ground	1,07	0,25	4,28
Tree 2	0,13	0,36	0,36
Tree 3	–1,08	0,37	–2,90
Tree 4	–1,15	0,39	–2,90
Tree 5	–0,19	0,38	–0,50

(b) Predicted probability of predation

	Canopy	Ground
Tree 1	0,43	0,69
Tree 2	0,47	0,72
Tree 3	0,21	0,43
Tree 4	0,20	0,42
Tree 5	0,38	0,65

Seeds from pods collected from the ground had a significantly higher probability of being predated than seed from canopy-held pods (Table 2). Trees 3 and 4 were significantly less predated than trees 1, 2 and 5.

The bruchid beetle, *Bruchidius senegalensis* (Pic) was the dominant seed predator. Coleopteran (cf. Bupres-

Table 1 Predation of *Acacia erioloba* seeds in pods taken from the canopy and the ground beneath the canopy of five trees in the Kuiseb River Valley

	Ground (%)			Canopy (%)		
Tree	Predated	Non-predated	Aborted	Predated	Non-predated	Aborted
1	51,1±34,4	33,6±30,2	15,3±11,7	43,1±40,9	45,8±39,9	11,1±12,0
2	70,2±36,4	23,9±33,9	5,9± 8,5	29,5±27,4	57,1±27,4	10,9±22,2
3	45,0±42,5	40,1±35,9	11,7±16,1	10,2±22,8	74,8±22,8	15,0±13,4
4	32,4±17,6	56,4±18,1	10,6±10,3	18,8±25,3	57,5±25,1	23,7±13,3
5	42,5±33,1	36,2±28,7	21,9±20,2	35,8±27,5	41,1±27,9	23,2±20,0

tidae) and Lepidopteran larvae were also rarely found as was a species of parasitic wasp (Pteromalidae: *Habrocytus* sp.).

Germination

Abrading the seed coat and soaking the seeds in acid increased germination success (Figure 1).

Germination success after 3 days was erratic and no significant difference between treatments could be detected at this stage (Table 3). There was no significant difference in the final germination success between seed coat abrasion and acid treatments. Most of the embryo was eaten in the predated seeds and only one seed germinated. Compared to the control, final germination success was lower in predated seeds and higher in seed fed to cattle.

Discussion

Our data are consistent with the hypothesis that higher levels of predation would be recorded for seed on the ground compared to canopy-held seed. This is probably because the former seed are older, and there is more time available for larval development of the predator (Halevy 1974; Lamprey *et al.* 1974). Seed predation also appears to differ significantly between trees.

Seeds of *Acacia erioloba* are similiar to those of many other acacias in that special treatments are necessary to break innate dormancy (Harper 1977) due to hard seededness which prevents the passage of water and oxygen (Cavanagh 1980). In nature, dormancy is presumably overcome when the seed coat breaks down as a result of the action of micro-organisms, soil acids, and temperature fluctuations (Cavanagh 1980). However, seeds of acacias with indehiscent pods remain relatively unexposed to these factors. Halevy (1974) and Lamprey *et al.* (1974) suggest that seed predators and herbivores may be important in breaking seed dormancy for species with indehiscent pods. Our study supports the assertion that ingestion of the seed by mammalian herbivores enhances germination success. However, contrary to Halevy's (1974) findings, no positive effect of seed predation by bruchid beetles on germination was found. As only one predated seed germinated, the data are insufficient to make any comment about the change in seed permeability due to the action of bruchids.

Our data therefore provide some support for the mutualistic relationship between mammalian herbivores and acacias with indehiscent pods as outlined by Halevy (1974) and Lamprey *et al.* (1974). Clearly, the ingestion of seed by herbivores prior to the maturation of the larvae of predators will affect favourably the fitness of the acacias. This is probably also an important way in which seed is removed from the pods and thus exposed

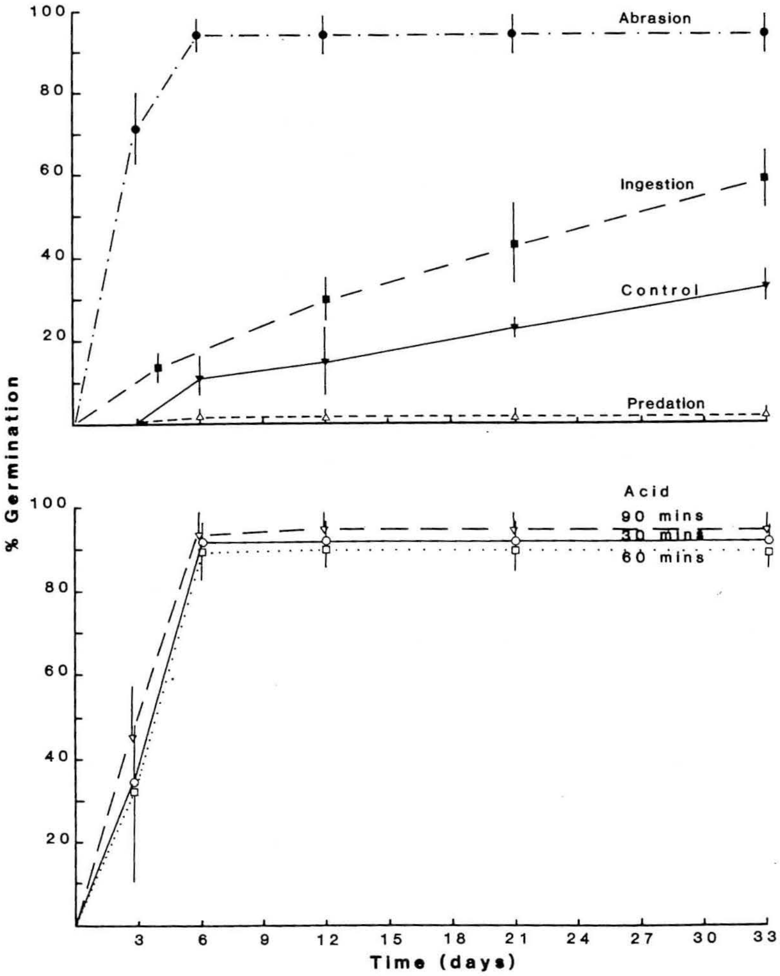

Figure 1 Germination of *Acacia erioloba* seeds collected in the Kuiseb River Valley.

Table 3 Results of fitting the generalized linear model to number of germinating seeds. At 3 days the deviance of 37,6 with 21 degrees of freedom indicates an unsatisfactory fit ($P<0,05$). At 33 days the deviance of 16,58 with 21 degrees of freedom indicates a very good fit ($P>0,5$)

(a) Regression coefficients

	3 days			33 days		
Treatment	Regression Coefficient	*S.E.*	*T*	Regression Coefficient	*S.E.*	*T*
Control	-12,0	24	–0,50	–0,71	0,21	-3,38
Abrasion	0,9	24	0,04	2,75	0,47	5,85
Acid 30 min	–0,7	24	–0,03	2,44	0,43	5,67
60 min	–0,7	24	–0,03	2,31	0,41	5,63
90 min	–0,2	24	–0,01	2,95	0,50	5,90
Predation	-12,0	34	–0,35	–4,60	1,02	–4,51
Ingestion	-1,9	24	0,08	0,35	2,96	0,12

(b) Predicted probability of germination after 33 days

Treatment	Probability
Control	0,33
Abrasion	0,94
Acid 30 min	0,92
60 min	0,91
90 min	0,95
Predation	0,01
Ingestion	0,59

to dormancy-breaking factors (see also Hamilton *et al.* 1977).

The riverine woodlands of the Namib are important both as a forage resource for game during dry periods (Hamilton *et al.* 1977; van Wyk *et al.* 1985) and to stabilize sediment transfer in water courses subjected to occasional but massive water flow (Hattle 1985). Although Topnaar Hottentot communities in the Kuiseb River Valley do possess cattle, these herbivores are obviously not entirely representative of natural processes in these habitats (see Hamilton *et al.* 1977). This needs to be emphasised, as Leistner (1961) has shown that germination success may differ, depending on the herbivore used. Finally, while germination may be enhanced by ingestion, seedling defoliation could likewise eliminate new recruits. Population studies, therefore, would provide greater insights into management problems in the region.

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