Three–way interactions between *Acacia*, large mammalian herbivores and bruchid beetles - a review

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Abstract

Large mammalian herbivores are both predators and dispersers of *Acacia* seeds. While some of the seeds are destroyed during passage through the herbivore's digestive tract, others are defecated unharmed. Ingestion by large herbivores facilitates germination by scarification of the seed coat. The extent of the influence of herbivores on seed dispersal and germination depends on seed retention time and tooth size, which are both positively correlated with body size. Infestation by bruchid beetles (Bruchidae) reduces *Acacia* germination. Herbivores may reduce bruchid infestation in several ways. Larvae in recently infested seeds are killed by stomach acids penetrating the seed through the larval entry hole. Seeds that are partly excavated by burrowing larvae in more advanced stages may be crushed by the herbivore's teeth. Lastly, but probably most crucially, herbivores simply remove seeds from the natal tree prior to infestation or at least prior to reinfestation. The timing and magnitude of herbivory is crucial for both the reduction of bruchid infestation and *Acacia* seedling establishment. Although it is widely agreed that a three–way interaction exists between bruchid beetles, *Acacia* trees and large mammalian herbivores, it is also apparent that the relationship is highly complex and is not yet completely understood.

Key words: Bruchidae, germination, herbivory, review, seed beetle

Résumé

Les grands mammifères herbivores sont en même temps des prédateurs et des facteurs dispersants des graines d'*Acacia*. Si certaines graines sont détruites au cours de leur passage dans le tractus digestif des herbivores, d'autres sont expulsées sans dommages. Au contraire, l'ingestion par les grands herbivores facilite la germination grâce à la scarification de l'enveloppe de la graine. L'importance de l'influence des herbivores sur la dispersion des semences dépend du temps que la semence passe à l'intérieur de l'animal et de la taille de ses dents, qui sont tous deux positivement liés à la taille corporelle. L'infestation par les coléoptères bruchidés (Bruchidae) réduit la germination des *Acacia*. Les herbivores peuvent réduire cette infestation de plusieurs manières. Les larves des semences infestées depuis peu de temps sont tuées par les sucs gastriques qui pénètrent dans la semence par le trou d'entrée de la larve. Les semences qui sont partiellement excavées par les larves à des stades plus avancés peuvent être écrasées par les dents des herbivores. Et enfin, ce qui est probablement plus crucial, les herbivores prélèvent les graines sur l'arbre d'origine avant l'infestation ou au moins, avant la réinfestation. Le timing et l'importance du prélèvement par les herbivores sont cruciaux pour la réduction de l'infestation par les bruchidés et pour l'implantation des jeunes plants. Bien qu'il soit généralement admis qu'une triple interaction existe entre les coléoptères bruchidés, les *Acacia* et les grands mammifères herbivores, il est aussi évident que cette relation est extrêmement complexe et qu'on ne la comprend pas encore parfaitement.

Introduction

Acacia trees in Africa and in the Middle East are keystone species in their ecosystems, and a considerable level of coevolution between large mammalian herbivores and the genus *Acacia* has occurred over time (Coe & Coe, 1987; Coe & Beentje, 1991; Rohner & Ward, 1999). The genus *Acacia* (Leguminosae) is a heterogeneous assembly of more than thousand species, most of which

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are trees (Brain, 1987). The greatest number of them is found in Australia; others occur in South-east Asia and in Africa. Another group of *Acacia* species occurs in South and Central America (Ross, 1979). Although there are only about 130 species in Africa, they are the dominant trees in the vegetation of much of the continent south of the Sahara (Ross, 1979; Brain, 1987). In the 19th century, the genus *Acacia* was divided into six series based on vegetative characters by Bentham (1875 *in* Coe & Beentje, 1991). The African *Acacia* species, including the species occurring in the Middle East, belong to the series Gummiferae (Bentham, 1875 *in* Coe & Beentje, 1991; Tame, 1992).

The seeds and pods of various *Acacia*s are eaten by many species of wild animals and livestock. The pods, which are available in the dry season, form the most important item in the diet of most savanna browsers (Coe & Coe, 1987; Coe & Beentje, 1991). African *Acacia*s are eaten by various large mammalian herbivores such as elephant (*Loxodonta africana* Blumenbach), white rhino (*Ceratotherium simum* Burchell), giraffe (*Giraffa camelopardalis* Lesson), great eland (*Taurotragus oryx* Pallas), kudu (*Tragelaphus strepsiceros* Pallas), impala (*Aepyceros melampus* Lichtenstein), steenbok (*Raphicerus campestris* Thunberg) and duiker (*Sylvicapra grimmia* Linnaeus) (Miller, 1995). Other consumers of pods and seeds are birds, for example ostrich (*Struthio camelus* Linnaeus) (Miller, 1996), and rodents such as the multimammate mouse (*Praomys* (*Mastomys*) *natalensis* A. Smith) (Miller, 1995). In Costa Rica, *A. farnesiana* (L.) Willd. is eaten by horses (*Equus caballus* L.), white-tailed deer (*Odocoileus virginianus* Zimm) and ctenosaurs (*Ctenosaura similis* Gray: Iguanidae) (Traveset, 1992). In the Middle East, dorcas gazelles (*Gazella dorcas* Linnaeus) and ibex (*Capra ibex nubiana* F. Cuvier) have frequently been observed feeding on pods of *Acacia* (Halevy, 1974).

Acacia seed pods are divided into two types: dehiscent, i.e. where the pod splits and the majority of the seeds are dispersed by wind or gravity; and indehiscent species, the pods of which do not split but remain on the tree until removed by browsers or mechanical action or, as in the case of *A. raddiana* Savi and *A. tortilis* (Forssk.) Hayne, pods drop off the tree but do not split (Ward, personal observation). The seeds of the indehiscent species remain in the pods until they are eaten, trodden on, or degraded by fungal attack (Miller & Coe, 1993). In general, large herbivores prefer to consume pods of indehiscent *Acacia* species, possibly because non-split pods have a high nutritious value even after falling off the tree as a result of the fact that the pods retain their moisture and nutrients while dehiscent pods dry out after opening (Gwynne, 1969).

The herbivores of *Acacia* seeds not only function as seed predators but may also be beneficial to the *Acacia*s by dispersing their seeds (Miller & Coe, 1993). We will not discuss the implications of dispersal by mammalian herbivores, but mention the fact that the distance that seeds are dispersed depends on the herbivore's retention time and therefore on its body size. The larger the mammal, the longer the retention time and therefore the greater the probability that long-distance dispersal will occur (Rohner & Ward, 1999). Rohner & Ward (1999) also found that large mammalian herbivores may also affect the spatial distribution of seeds; large mammals in their study were nearly twice as likely to defecate in open areas away from trees as under *A. raddiana* canopies, which may reduce the degree of intraspecific competition with established trees.

Indehiscent *Acacia* seeds have a very hard seed coat, the testa, which enables some of the ingested seeds to be passed out unharmed in faeces. However, many of the seeds are destroyed by chewing and digestion. The extent of seed destruction is negatively correlated with the size of the herbivore's teeth (Pellew & Southgate, 1984) and positively correlated with its retention time (Rohner & Ward, 1999). Both of the above factors depend on the herbivore's body size (Rohner & Ward, 1999).

Many *Acacia* species are subjected to infestation by seed beetles of the family Bruchidae (Coleoptera). Bruchid beetles are seed pests, mainly on plants of the family Leguminosae (Mimosoideae) (Fox & Dingle, 1994). Adult females lay their eggs on or in *Acacia* pods (depending on the bruchid species); the larvae drill into the seed and feed on its contents (Southgate, 1979). Larvae of smaller bruchid species (e.g. *Bruchidius arabicus* Decelle, 2.3–3.5 mm (Anton, Halperin & Calderon, 1997)) pupate inside the seed. Adults emerging from pupae exit the seeds by drilling a larger exit hole. In larger species (e.g. *Caryedon palaestinicus* Southgate, 2.8–5.2 mm (Anton *et al.*, 1997)), the larvae exit the seed before pupation and pupate on the ground or attached to the dry pod (Southgate, 1979). The number of bruchid beetles developing in each seed depends on the size of both beetle and seed. In small bruchid species, several beetles can infest one seed (e.g. five beetles of the genus *Bruchidius* may infest one seed of *A. raddiana* (Or, personal observa-

tion)). Larger larvae may exploit more than one seed, moving to adjacent seeds in the same pod (Southgate, 1979). Some *Acacia* pods (e.g. *A. nilotica* (L.) Willd. ex Del) are fragmented so that larvae would not be able to move from one seed to another (Center & Johnson, 1974).

The damage caused to *Acacia* seeds by bruchid beetles depends primarily on the consumption of the embryo by the larvae and secondarily on the proportion of cotyledons eaten (Lamprey *et al.*, 1974). Bruchid beetle larvae can destroy a considerable proportion of the cotyledons, and thus infestation can have an enormous effect on *Acacia* seed viability and on seedling vigour (Coe & Coe, 1987; Rohner & Ward, 1999).

Separating vertebrate seed dispersers from vertebrate seed predators is not always possible as a result of the fact that many vertebrates are both dispersers and predators (Sallabanks & Courtney, 1992). Bruchid infestation level may be the factor determining the ratio of predation to dispersion. That is, seeds that have had large amounts of the cotyledons consumed by bruchids may be consumed by herbivores, while hard, intact seeds may be impossible to digest and hence are dispersed. Very little is known about the dispersal of bruchid beetles or their flight ability. It is possible that seed-dispersing herbivores might also disperse the bruchid beetle larvae inside ingested seeds from the natal tree to another tree or from one patch of trees to another.

Although it is now widely agreed that there is a three–way interaction between the bruchid beetles, *Acacia* trees and mammalian herbivores, it is also obvious that the relationship is highly complicated and is not yet completely understood (Halevy, 1974; Lamprey *et al.*, 1974; Coe & Coe, 1987; Traveset, 1992; Miller & Coe, 1993; Miller, 1994b, 1996; Rohner & Ward, 1999). Several potential interactions between *Acacia* trees, herbivores and bruchid beetles are described in the literature (Halevy, 1974; Lamprey *et al.*, 1974; Miller & Coe, 1993; Hauser, 1994; Rohner & Ward, 1999). Experiments regarding a certain interaction often result in contrasting conclusions. The following is a review of the possible mechanisms of the interactions between *Acacia* trees, bruchid beetles and large mammalian *Acacia* herbivores.

The effects of large mammalian herbivores on *Acacia* seed germination

Germination of most uninfested *Acacia* seeds without an external factor that scarifies the seed coat (testa) is very low or zero (Lamprey, 1967; Halevy, 1974). Passage through an herbivore's gut or artificial chemical or mechanical scarification of the seeds increases the seed germination level (Table 1). Lamprey (1967) found the germination level of eight species of dehiscent *Acacia* (*A. drepanolobium* Harms ex Sjöstedt, *A. brevispica* Harms, *A. xanthophloea* Benth., *A. clavigera* E. May, *A. Senegal* (L.) Willd., *A. lahai* Steud & Hochst. ex Benth, *A. polyacantha* Willd. and *A. kirkii* Olive) to range from 0 to 27%, and that of four indehiscent species (*A. sieberiana* DC., *A. albida* Del. (now called *Faidherbia albida* (Roupsard *et al.*, 1999)), *A. tortilis* and *A. nilotica*) to range from 1 to 2%. Halevy (1974) recorded a mean of 25% germination of intact seeds of *A. raddiana*, 68% in *A. pachyceras* O. Schwartz (previously named *A. gerrardii* ssp. *negevensis* (Danin, 1983, 2000)) and no germination in *A. tortilis*. He found that the average germination level of unsorted *A. raddiana* seeds increased from 1 to 13% after ingestion by gazelles (*Gazella dorcas*). Lamprey *et al.* (1974) found the germination of *Acacia* seeds ingested by impala, Thomson's gazelle (*Gazella thomsoni*), dikdik (*Madoqua kirkii* Günther), elephant and dorcas gazelle to range from 11 to 28%. Miller (1995) found that the cumulative germination of ingested seeds of both indehiscent and dehiscent *Acacia* exceeded that of uningested seeds and differed between herbivore species. *A. tortilis* and *A. nilotica* seeds retrieved from the stomach of kudu exhibited greater germination (48 and 22%, respectively) than control uningested seeds (7 and 3.5%, respectively), but lower germination than seeds retrieved from kudu's dung (60% for *A. tortilis* and *A. nilotica*) (Miller, 1995). Furthermore, *A. tortilis* and *A. nilotica* seeds chewed by the multimammate mouse exhibited greater germination than control, unchewed seeds. Hauser (1994) found 4% germination in early season uninfested and unscarified seeds and 2% germination in late season. Germination of seeds scarified using a hand file increased from 4% early in the season and 2% late in the season to 100%. Intact unscarified seeds found in cow dung had germination levels of 4–6%, whereas germination of scarified seeds rose to 98%. Rohner & Ward (1999) showed that the germination levels of intact *A. raddiana* and *A. tortilis* seeds from gazelle (*Gazella dorcas*) faeces were significantly higher than those of uningested seeds (29.8% vs. 13.5%). Furthermore, seeds ingested by Arabian oryx (*Oryx leucoryx* Pallas) showed a higher germination level than uningested seeds (51% for *A. raddiana* and 34% for *A. tortilis*). Coe & Coe (1987) showed an

Table 1 Effects of ingestion by large mammals* and artificial scarification on *Acacia* seed germination

Acacia species	Ingestion	Germination level (%)	Bruchid infestation	Remarks	Source
Acacia drepanolobium, A. brevispica, A. xanthophloea, A. clavigera, A. senegal, A. lahai, A. polyacantha, A. kirkii	Uningested	0–27	?	Dehiscent species	Lamprey (1967)
Acacia sieberiana, F. albida, A. tortilis, A. nilotica	Uningested	1–2	?	Indehiscent	Lamprey (1967)
Acacia raddiana	Uningested	4	Unsorted	Experiment duration 30 days	Halevy (1974)
Acacia pachyceras (=A. gerrardii)	Uningested	31	Unsorted	Experiment duration 30 days	Halevy (1974)
Acacia tortilis	Uningested	1	Unsorted	Experiment duration 30 days	Halevy (1974)
Acacia heteracantha	Uningested	17.6	?	Collected from tree	Coe & Coe (1987)
Faidherbia albida	Uningested	4, 2	–	Early- and late-season seeds, respectively	Hauser (1994)
Acacia tortilis	Uningested	1.5	–		Miller (1994a)
Acacia tortilis	Uningested	7	?	Seeds from tree and ground	Miller (1995)
Acacia nilotica	Uningested	3.5	?		Miller (1995)
Acacia tortilis	Uningested	7	?		Miller (1995)
Acacia tortilis	Uningested	0	Unsorted	Germination in dung	Miller (1996)
Acacia raddiana, A. tortilis	Uningested	13.5	–		Rohner & Ward (1999)
Acacia raddiana	Dorcas gazelle	21	Unsorted	Experiment duration 30 days	Halevy (1974)
Acacia tortilis ssp. *spirocarpa* (Hochst. ex A. Rich.) Brenan, *A. tortilis* ssp. *tortilis, A. raddiana*	Impala, dikdik, elephant, Dorcas gazelle, Thomson's gazelle	11–28	Unsorted		Lamprey *et al.* (1974)
Acacia tortilis	Giraffe, impala, grey duiker, steenbok, ostrich, kudu	49, 27.7, 17.9, 15.1, 60, 23	–	Respectively	Miller (1994a)
Acacia tortilis	Giraffe, impala, grey duiker, steenbok, ostrich, kudu	6.6, 2.9, 2.5, 1, 10.9, 7.7	Infested	Respectively	Miller (1994a)
Acacia tortilis	Ostrich crop	28	?		Miller (1995)
Acacia tortilis	Ostrich dung	86	?		Miller (1995)
Acacia tortilis	Kudu stomach	48	?		Miller (1995)
Acacia tortilis	Kudu dung	60	?		Miller (1995)
Acacia nilotica	Kudu stomach	22	?		Miller (1995)
Acacia nilotica	Kudu dung	60	?		Miller (1995)
Acacia heteracantha	Greater kudu, eland	8.3, 8.6	?	Opposite trend	Coe & Coe (1987)
Acacia raddiana, A. tortilis	Dorcas gazelle	29.8	Uninfested		Rohner & Ward (1999)

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Acacia raddiana, A. tortilis	Oryx	51	Uninfested		Rohner & Ward (1999)
Faidherbia albida	Cow dung	4–6	Uninfested		Hauser (1994)
Faidherbia albida	Cow dung, scarified by hand file	98	Uninfested		Hauser (1994)
Faidherbia albida	Scarified by hand file 100, 100		Uninfested	Early- and late-season seeds, respectively	Hauser (1994)

See Table 2 for herbivore species list.

inverse trend where the germination level of *A. tortilis heteracantha* (Bruch.) Brenan seeds collected from the tree was 17.6%, as opposed to 8.3 and 8.6% from dung of greater kudu (*Tragelaphus strepsiceros* Pallas) and eland (*Taurotragus oryx*), respectively. All experiments except that of Coe & Coe (1987) showed that ingestion by herbivores causes an increase in germination.

Acacia pods are readily consumed by large herbivores. Up to 92% of *A. tortilis* pods and 76.2% of *A. nilotica* pods are consumed by herbivores (Miller, 1994b). Rohner & Ward (1999) found that the number of *A. tortilis* seeds accumulated on the ground after 12 weeks of pod maturation in the absence of herbivores was 460 times greater than the number of seeds accumulated in the presence of herbivores.

Coe & Coe (1987) suggested the following mechanism for increased germination by chewing: The herbivore's teeth cause extensive testa surface erosion. The testa of *Acacia* seeds acts as a barrier to the entry of water, thereby preventing the seed's subsequent germination until this outer layer is scarified. From scanning electron microscopic studies, Coe & Coe (1987) deduced that the closely packed palisade cells in the testa could collapse laterally when a shearing force was applied to the seed coat. Testa erosion allows water to enter the seed and hence stimulates germination. Seed survival tends to increase with herbivore body size (Miller, 1995) because large herbivores swallow larger percentages of the pods unchewed. However, retention time also increases with the herbivore's body size; therefore, the seeds stay longer in the herbivore's gut and suffer greater testa damage. Ruminants may separate seeds and pods in the buccal cavity, eliminate the seeds from the sides of the mouth and thus increase seed survival. However, they might cause further damage by chewing seeds again (Coe & Coe, 1987). After swallowing, seeds experience further damage in the herbivore's stomach. Seed survival through the herbivore's gut varies between both *Acacia* species and herbivore species. Lamprey *et al.* (1974) observed that, after ingestion of the *Acacia* pods, the seeds are normally passed out in the mammal's faeces. Wickens (1969) estimated that 66% of the seeds of *Faidherbia albida* fed to a steer in Sudan were voided undamaged after ingestion. Halevy (1974) was among the first to conduct germination experiments after ingestion by gazelles, and his observations were that most of the seeds eaten are broken during the digestion process. Later experiments also showed lower survival than that

estimated by Wickens (1969). Coe & Coe (1987) used X-ray analysis to show that up to 16% of seeds are completely digested during their passage through the gut of large herbivores. Seed survival of *A. tortilis*, *A. nilotica*, *A. hebeclada*, *A. karroo* Hayne, *A. robusta* Burch. and *A. caffra* (Thumb.) Willd., through the gut of elephant, giraffe, kudu and impala ranged from 2.1 to 50.4%. *A. caffra* seeds suffered a greater loss than any other species (93.7–97.9%) (Miller, 1995).

The effects of large mammalian herbivores on bruchid infestation

Infestation levels of *Acacia* seeds by bruchid beetles vary between *Acacia* species (Table 2). It has frequently been claimed (Coe & Coe, 1987; Miller, 1996) that one of the effects of mammalian herbivory is to reduce bruchid infestation by consumption of the pods while still on the tree. This assumes that the bruchids' main infestation takes place on the ground. However, Miller (1994b) and Rohner & Ward (1999) found infestation levels on the tree and on the ground to be the same, indicating that the mammals may not control bruchid infestation levels in this manner. Miller (1996) found the infestation levels of seeds from the tree canopy to be lower than those on the ground. This may imply secondary infestation on the ground, a fact that stresses the importance of herbivory by large mammals because of their ability to lower the infestation level by removing the pods from the vicinity of the tree.

Coe & Coe (1987) found the infestation level of indehiscent *Acacia* species from the ground to be 28.9% for *A. erioloba* E. May and 35.0% for *A. sieberiana*. The dehiscent species, *A. elatior* Brenan showed an infestation level of 25.3%. Uningested *A. nilotica* and *A. karroo* seeds had 36.5 and 40% infestation levels, respectively (Miller, 1994a). *Acacia tortilis* infestation level did not differ according to the presence or absence of herbivores, or according to whether the pods were on the tree or on the ground (Rohner & Ward, 1999). *A. nilotica* had an infestation level of 31.0–58.0% on the ground in the absence of herbivores (Miller, 1994b). Halevy (1974) described infestation levels of 72% for *A. raddiana*, 99% for *A. tortilis* and 64% for *A. pachyceras*. Recently, Rohner & Ward (1999) described high infestation levels of 97.6% for *A. raddiana* and 96.2% for *A. tortilis* in the same populations studied by Halevy (1974). Infestation levels of *Acacia* seeds that were ingested by herbivores are lower

Table 2 Effects of ingestion by large mammalian herbivores *on bruchid infestation

Acacia species	Ingestion	Infestation (%)	Remarks	Source
Acacia raddiana, A. tortilis, A. pachyceras	Uningested	72, 99, 64	Respectively	Halevy (1974)
Acacia elatior	Uningested	25.3	Dehiscent, from ground	Coe & Coe (1987)
Acacia erioloba, A. sieberiana	Uningested	28.9, 35	Indehiscent, from the ground	Coe & Coe (1987)
Acacia nilotica, A. karroo	Uningested	36.5, 40	Respectively	Coe & Coe (1987)
Acacia tortilis, A. nilotica, A. karroo	Uningested	68, 36.5, 40	Respectively	Miller (1994a)
Acacia nilotica	Uningested	31–58	Herbivores absent	Miller (1994b)
Acacia raddiana, A. tortilis	Uningested	97.6, 96.2	Respectively	Rohner & Ward (1999)
Acacia spp.	Impala, Thompson's gazelle, dikdik, elephant, Dorcas gazelle	0–45	Seeds found in faeces	Lamprey et al. (1974)
Acacia tortilis heteracantha	Eland, greater kudu	0.01, 1.9	In dung, respectively	Coe & Coe (1987)
Acacia tortilis spirocarpa	Sheep	2.4	Seeds found in dung	Coe & Coe (1987)
Faidherbia albida	Elephant	3.3	Seeds found in dung	Coe & Coe (1987)
Acacia tortilis	Giraffe, impala	3, 2	Respectively	Miller (1994a)
Acacia tortilis	Kudu, steenbok, duiker	0, 0, 0	Respectively	Miller (1994a)
Acacia nilotica, A. karroo,	Giraffe, impala, kudu, steenbok, duiker	0, 0, 0, 0, 0	Respectively	Miller (1994a)

*Herbivore species list: Dorcas gazelle *Gazella dorcas*, impala *Aepyceros melampus*, dikdik *Madoqua kirkii*, African elephant *Loxodonta africana*, Thomson's gazelle *Gazella thomsonii* Günther, giraffe *Giraffa camelopardalis*, common duiker *Sylvicapra grimmia* Linnaeus, steenbok *Raphicerus campestris*, greater kudu *Tragelaphus strepiceros*, oryx *Oryx gazella* Linnaeus, eland *Taurotragus oryx*, sheep and cow.

than those of uningested seeds. Lamprey *et al.* (1974) showed that the bruchid-damaged *Acacia* seeds found in mammalian faeces in Tanzania ranged from 22 to 45%. Coe & Coe (1987) found the infestation level of *Acacia* seeds ingested by mammalian herbivores to range from 0.01% in *A. tortilis heteracantha* to 3.3% in *F. albida*. Miller (1994a) found that seeds of *A. tortilis* ingested by giraffe and impala exhibited a significantly lower bruchid infestation than uningested seeds. All other indehiscent *Acacia* seeds ingested by a variety of large herbivores were uninfested, whereas uningested seeds showed 36.5–68.0% bruchid infestation.

In general, infestation levels of *Acacia* seeds that were ingested by herbivores are lower than those of uningested seeds. The infestation levels described in various experiments for uningested *Acacia* seeds ranged between 25.3 and 99%, whereas the infestation levels for ingested seed ranged between 0 and 45%.

Coe & Coe (1987) suggested that ingestion may kill bruchid larvae at early stages of development within the seed through the effect of stomach acids, without destroying the seed. They further suggested that reduction in infestation could occur via removal of the pectic layer surrounding the seed, which might aid seed location by adult beetles. However, Ernst, Decelle & Tolsma (1990) found the opposite trend; the degree of bruchid infestation for *A. burkei* Benth. seeds that were deprived of their seed testa increased from 8 to 60%.

Bruchid larvae at a late stage of development can be selectively destroyed by chewing or breakdown in the buccal cavity or in the alimentary canal because tunneling larvae may weaken the seeds (Janzen, 1971; Halevy, 1974; Lamprey, Halevy & Makacha, 1974; Coe & Coe, 1987). Seeds with exit holes made by bruchids are partly hollow, depending on the size of the beetle or on the number of beetles developed in one seed, and thus are easily destroyed by the herbivore's teeth or by gut peristalsis (Miller, 1994a). Ingestion by herbivores reduces infestation first by dispersion of the seeds prior to their infestation (or reinfestation) on the ground and second by selectively destroying infested seeds.

The effects of bruchid infestation on *Acacia* seed germination

Different studies found contrasting effects of bruchid infestation on seed viability (Table 3): Halevy (1974) found the germination percentage of infested *A. raddiana* and *A. pachyceras* to be lower than that of intact seeds. Germination levels were 1 and 6%, respectively, for the infested seeds, in contrast to 25 and 68% for intact seeds. Halevy (1974) further found that gazelle ingestion raised the germination percentage of unselected seeds from 4 to 21%. Because of the fact that uningested seeds showed an infestation percentage of 72%, he deduced that some of the infested seeds did germinate.

Rohner & Ward (1999) also found a lower germination level for infested *A. raddiana* seeds, viz. 2.1% for infested versus 15.6% for intact seeds. Hauser's experiments (1994) revealed the opposite trend. The germination level of early season *F. albida* seeds with bruchid holes in Hauser's study was 100%, although most of them died shortly after germination. Late-season seeds with bruchid holes showed a lower germination level of 10%,

Table 3 Effects of bruchid infestation on *Acacia* seed germination.

Acacia species	Germination level (%), intact seeds	Germination level (%), infested seeds	Remarks	Source
Acacia raddiana, *A. pachyceras*	25, 68	1, 6		Halevy (1974)
Faidherbia albida	4	100	Early in the season Most seedlings died shortly after germination	Hauser (1994)
Faidherbia albida	2	10	Late in the season All seedlings died shortly after germination	Hauser (1994)
Acacia hebeclada, *A. tortilis*, *A. nilotica*	5.5, 1.5, 0.5	1.4, 2.5, 0.5	Non-significant differences between infested and uninfested seeds	Miller (1994a)
Acacia raddiana	15.6	2.1		Rohner & Ward (1999)

and all of them died shortly after germination, possibly because of fungal attack or other seed pests. Early- and late-season intact seeds showed 4 and 2% germination, respectively. Miller (1994a) found that differences in germination between infested ingested seeds and infested uningested seeds of *A. tortilis* depended on the herbivore's body size. That is, the germination level of infested ingested seeds exceeded that of infested uningested seeds when ingested by the large giraffe, ostrich and kudu, and did not differ when ingested by the smaller impala, duiker and steenbok (Miller, 1994a).

It is assumed that germination in dung would be beneficial to the seedlings because of the better microclimate caused by the ability of the faecal material to retain water. Also, nutrients in the dung might support the developing seedlings (Coe & Coe, 1987; Miller, 1995). Miller (1995) conducted germination experiments of ingested and uningested seeds in dung and in soil. She found that ingested *A. tortilis* and *A. nilotica* seeds germinated significantly more than uningested seeds when grown in dung and in soil. However, in contrast with other studies showing the opposite trend (Lamprey, 1967; Fenner, 1986; Mwalyosi, 1990), more ingested and uningested seeds germinated in soil than in dung.

Discussion

The central question in *Acacia* dispersal ecology is 'Is it advantageous for *Acacia* seeds to be eaten by ungulates?' (Miller & Coe, 1993). The answer arising from this review is in the affirmative. *Acacia* seeds mostly benefit from being eaten by large herbivores. This trend is even stronger when bruchid beetles infest *Acacia* seeds. In general, infestation decreased and germination levels increased when seeds were ingested by herbivores. The main effects of herbivores on bruchid-infested seeds appear to be:

1 Destruction of infested seeds by chewing.

2 Scarification of seeds in the early stages of larval development, thus enhancing germination.

However, it is not obvious that increased germination is advantageous at all times for the plant. In dry regions, where massive rainfalls are rare events, many plants have developed hard seed coats that ensure a long seed lifespan and only allow germination when sufficient water resources are available (Rohner & Ward, 1999). Rohner & Ward (1999) found that 95% of germinated seeds died within 6 months of germination in the Negev desert because of water stress. Hence, seed dormancy is preferable to germination in dry years.

The positive effect of herbivores on *Acacia* germination may be solely because of the fact that they may remove the seeds from the tree prior to infestation. The timing of pod removal by herbivores, as well as its intensity, may be crucial. Although bruchid infestation is assumed to occur mainly on the ground, it may occur while the pods are on the tree at an early developmental stage and still green (Southgate, 1979; Rohner & Ward, 1999). Further infestation and reinfestation may occur when the pods or seeds fall on the ground (depending on whether the pods split or not). The consumption of pods in an early developmental stage is considered to be an important advantage for the tree because infestation levels increase over time (Rohner & Ward, 1999). Rohner & Ward (1999) also recorded synchrony in pod maturation. Forty-eight per cent of the pods of *A. tortilis* fell on the ground within 2 weeks of pod maturation and 66% within 3 weeks of pod maturation. The synchrony in pod maturation might reduce reinfestation.

Although many experiments found the potential for large herbivores to influence infestation and survival levels of *Acacia* seeds, some of them did not find any influence (Miller, 1994b). Miller (1994b) found ungulate browsing to have no effect on bruchid infestation levels. Rohner & Ward (1999) found no indication that the presence of large herbivores resulted in reduced seed damage through competitive depression of the activity or population sizes of bruchid beetles. The spatial and the temporal scales of all experiments recorded here are relatively small, and may provide imperfect evidence of the roles of the factors affecting bruchid population dynamics (dispersal into a system may be sufficient to maintain bruchid populations in spite of local reductions caused by mammalian herbivory).

We have described some general trends that may have important implications on *Acacia* seed survival. The knowledge accumulated thus far enables one to make management decisions that should improve *Acacia* seed survival. Our main recommendation is to retain a degree of herbivory, keeping the ratio between the number of seeds produced and the herbivores consuming them small, in order to disperse most of the seeds from the natal tree before they are infested by bruchid beetles. The herbivores should have a relatively large body size, and thus large teeth, and a long gut retention time in order to reduce destruction of seeds by chewing and to

increase germination by scarification of the testa during digestion.

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