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Diet Quality Modifies Germination of *Dichrostachys cinerea* and *Acacia nilotica* Seeds Fed to Ruminants

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Abstract

The pods of many woody plants form an important part of the diet of livestock during the dry season due to their high nutritive value. However, the dispersal of seeds that remain intact and can potentially germinate after excretion is of particular concern when animals consume seeds of encroaching or invasive woody plants. The objectives of this study were to determine the effects of animal species in two experiments (experiment 1: goats, sheep; experiment 2: goats, cattle), diet quality (*Medicago sativa* hay, *Digitaria eriantha* hay) and seed characteristics (size, hardness) on the effectiveness of animal seed dispersal and germination of *Dichrostachys cinerea* and *Acacia nilotica* seeds. Owing to a limitation on the availability of seeds, the two experiments were done separately at different times. Each animal in both experiments received 1 000 *A. nilotica* seeds and 1 000 *D. cinerea* seeds mixed with either a low-quality diet (*D. eriantha* hay) or a high-quality diet (*M. sativa* hay). In experiment 1, we found a significant interaction effect of animal species (goats, sheep), diet (high-quality hay, low-quality hay), and seed species (*A. nilotica* seeds, *D. cinerea* seeds) on germination ($P < 0.0001$). There was also a higher seed recovery ($P < 0.009$) when animals were offered high-quality hay (47.4% ± 4.65) compared to low-quality hay (30.2% ± 3.24). In experiment 2, animal species affected seed recovery ($P < 0.0325$; goats 32.0% ± 6.44; cattle 50.3% ± 4.27) and germination percentage ($P < 0.055$; goats 14.1% ± 1.48; cattle 9.3% ± 0.94). The diet quality fed to the animals may affect dispersal and germination. However, animal species and seed characteristics also had important effects on germination of *D. cinerea* and *A. nilotica* seeds. Thus, all three of these factors play a major role in dissemination of viable seeds.

Key Words: associated diet quality, endozoochory, germination percentage, seed characteristics, seed dispersal, seed viability, woody plant encroachment

INTRODUCTION

Seed dissemination by livestock involves a number of phases from seed ingestion to seedling establishment and survival (Gardener et al. 1993). Many seeds may be destroyed during passage through the digestive tract of herbivores, while others are defecated undamaged in the feces (Rohner and Ward 1999; Or and Ward 2003). This may frequently be related to seed hardness. Consumption of hard seeds by livestock may facilitate seed germination by scarifying the seed coat and thereby increasing water uptake during passage through the digestive system (Hoffman et al. 1989; Miller 1995; Tjelele et al. 2012). Several factors such as animal species, body size, and associated diet quality (e.g., *Medicago sativa* hay and *Digitaria eriantha* hay) play a significant role in seed recovery, seed germination, or seed viability (Janzen 1984; Rohner and Ward 1999; Pakeman et al. 2002; Or and Ward 2003; Myers et al. 2004).

The survival or digestion of seeds during passage through the digestive tract of animals has vital implications for the population dynamics of plant species (Gardener et al. 1993; Nathan and Muller-Landau 2000). If seeds survive the digestive system, they may subsequently be dispersed. There tends to be a positive correlation between body size and percentage germination, but this relationship is influenced by other factors (Bodmer and Ward 2006) such as diet quality (Jones and Simao Neto 1987) and hardness of the seed coat (Gardener et al. 1993; Whitacre and Call 2006). Thus, seed recovery and germination may be correlated with diet quality, animal species, body size, and seed species (Simao Neto et al. 1987; Shayo and Uden 1989; Whitacre and Call 2006). Associated feed of high digestibility, high crude protein, and low fiber passes more quickly through the digestive tract of animals (Robbins 1993; van Soest 1994), presumably carrying more seeds with less feces (Huston et al. 1986; Simao Neto and Jones 1987; McGregor and Whiting 2013). Faster passage rate may result in low scarification and low germination percentages (Brown and Archer 1987; Or and Ward 2003; Bodmer and Ward 2006).

Goats, sheep, and cattle are possible seed dispersal agents affecting germination of *Dichrostachys cinerea* and *Acacia nilotica* seeds in African savannas. Goats are mixed feeders that are flexible in their dietary choices, whereas sheep and cattle are mainly grazers, preferring to eat herbaceous material. However, in situations where there are many bushes available, sheep and cattle may also be browsers (El Aich and Waterhouse 1999). Large-bodied animals such as cattle do not chew seeds as completely as small ruminants, e.g., goats and sheep, which

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may result in greater passage of viable seeds from cattle with less damage (Simao Neto et al. 1987; Shayo and Uden 1989). However, another consequence of large body size is longer seed retention than in sheep and goats, especially when offered diets with lower digestibility (Bodmer and Ward 2006). Bodmer and Ward (2006) found that there is a positive correlation between germination rates in *Acaci*a seeds and size of the herbivore that ingests the seeds. This correlation is most likely due to allometric scaling of digestion time (passage rate) to herbivore body mass (Robbins 1993), resulting in greater germination and viability of seeds that have passed through the digestive tract of large herbivores. Thus seed size, seed hardness, associated diet quality, and body size can influence retention times in the digestive tract and subsequently influence seed recovery, scarification, and seed germination success (Simao Neto et al. 1987; Gardener et al. 1993; Or and Ward 2003; Bodmer and Ward 2006).

The objectives of this study were to determine how seed characteristics, diet quality, and animal species influence seed recovery and germination of *D. cinerea* and *A. nilotica* to better understand the influence of seed dispersal by animals. Both *D. cinerea* and *A. nilotica* are known to be encroaching tree species, so factors that exacerbate their dispersal are likely to be of major concern to ranchers attempting to limit woody plant encroachment. We hypothesized that animals consuming a low-quality (*Digitaria eriantha* hay) diet will have longer seed retention than when consuming a high-quality (*Medicago sativa* hay) diet, and this will result in lower seed recovery and lower germination due to seed damage.

MATERIALS AND METHODS

Seed Collection

Dry mature pods of *D. cinerea* and *A. nilotica* were collected from under trees in KwaMhlanga, Mpumalanga province (lat 28°30′E, long 25°15′S) and the Agricultural Research Council Farm, Gauteng province (lat 28°19′E, long 25°35′S), respectively. Undamaged seeds were removed by hand from pods. The seeds were immersed in fresh water, and any floating seeds were discarded because they were either unripe or damaged by bruchid beetles (Or and Ward 2003). The tetrazolium viability tests of *D. cinerea* and *A. nilotica* seeds prior to feeding them to animals indicated that they had 95% and 91% viability, respectively. The length and width of 100 *D. cinerea* seeds and 100 *A. nilotica* seeds were measured using Vernier calipers. The densities for *A. nilotica* and *D. cinerea* seeds were measured using a Micro-focus X-ray Computed Tomography scanner.

Animal Feeding and Sample Measurement

Due to logistical constraints on the availability of seeds, experiments 1 and 2 were done in February 2011 and 2012, respectively. We replicated the goat treatment to ensure comparability of results.

The studies were done at the Agricultural Research Council's Irene Farm, Pretoria, South Africa. All animals were kept in the metabolic cages for 5 d to acclimate them to the experimental conditions and for 11 d during the seed recovery study. In both experiments, each animal was fed the experimental diet and seeds, individually in pens (1.2×0.73 m). All animals were fed ground *Medicago sativa* and *Digitaria eriantha* hay and water ad libitum throughout the experiment (i.e., during acclimatization and seed recovery). Each animal received 1 000 *A. nilotica* or 1 000 *D. cinerea* seeds once at the beginning of the experiment mixed with the feed in the feeding trough.

Each day during the 11 d of seed recovery, a random grab sample of each feed was taken and bulked in a sealed bag pending the analysis. For each feed, the bulked sample was analyzed for crude protein using the Kjeldahl block digestion method (AOAC 2000) and neutral detergent fiber using the Tector Fibertec system (Van Soest et al. 1991). In vitro digestibility of organic matter was done using the method based on Tilley and Terry (1963) as modified by Engels and Van der Merwe (1967). *D. cinerea* and *A. nilotica* seeds were analyzed for crude protein and metabolizable energy using the methods by AOAC (2000) and Robinson et al. (2004), respectively.

Experiment 1 (Goats and Sheep)

Twenty female indigenous goats (South African veld goats) and 20 female Dorper sheep were used in this study, with mean weights of 22 kg ± 0.9 and 23 kg ± 0.9, respectively. The 20 animals of each species were divided into two treatments of 10 each, then each treatment of 10 was further divided into two treatments of five per treatment, and each animal was fed high-quality alfalfa (*Medicago sativa*) hay (23% CP, 44% NDF, and 70% in vitro digestibility organic matter [IVDOM]) mixed with either *D. cinerea* or *A. nilotica* seeds. The other treatment of 10 animals was divided similarly, and each animal of this treatment was fed low-quality *Digitaria eriantha* (grass) hay (3% CP, 72% NDF, and 62% IVDOM) mixed with either *D. cinerea* (five animals) or *A. nilotica* seeds (five animals). Each animal received 1 000 *A. nilotica* or 1 000 *D. cinerea* seeds once at the beginning of the experiment mixed with the feed described above.

Experiment 2 (Cattle and Goats)

Twenty Bonsmara heifers and 20 female indigenous goats were used, with mean weights of 215 kg ± 4.8 and 24 kg ± 0.9, respectively. The 20 animals of each species were divided into two treatments of 10 each. Then each treatment of 10 was further divided into two treatments of five per treatment, and each animal was fed *M. sativa* hay (16.4% CP, 59.4% NDF, and 57.9% IVDOM) mixed with either *D. cinerea* or *A. nilotica* seeds. The other treatment of 10 animals was also divided similarly, and each animal with this treatment was fed *D. eriantha* hay (5.5% CP, 72.0% NDF, and 54.3% IVDOM) mixed with either *D. cinerea* or *A. nilotica* seeds.

Seed Recovery From Feces

All experimental animals in both experiments were allowed to consume seeds within 24 h, after which the remaining seeds were collected and counted. Fecal collection commenced immediately after the 24 h seed feeding period and continued until no seeds were found in the feces (about 11 d). Feces from goats and sheep were collected from fecal bags, whereas feces from cattle were collected from the concrete floor once a day for the duration of the trial. Feces were immersed in cold water until soft and then washed with tap water through a wire strainer until the water was clear. A cabinet with a light source below a glass surface was used to separate seeds from fecal remains. Seeds recovered from each animal for the day were counted and stored in brown bags in a cool dry place pending the germination trial.

Germination Tests

Germination tests were done at the Agricultural Research Council, Roodeplaat Forage Genebank (International Seed Testing Association 1985). Germination tests were subjected to a completely randomized experimental design. The germination test used Petri dishes containing one disk of germination paper and 5 mL of distilled water. Each petri dish contained a maximum of 50 seeds from each animal for each day. Germination tests were run in germination chambers kept at 20–30°C with a 16 h dark period and 8 h light period. The germination trial was monitored daily for 21 d, and all germinated seeds were recorded. The percentage germination was calculated at the end of germination tests as the number of seeds germinated divided by the total number of seeds placed in a Petri dish multiplied by 100 (Armke and Scott 1999). All seeds that did not germinate at the end of 21 d were counted and subjected to a viability test. *D. cinerea* and *A. nilotica* seeds were scarified using sand paper and soaked in distilled water for 18 h. Seeds were then soaked in 1% tetrazolium solution (2,3,5-triphynyl chloride) for 18 h in an incubator at 30°C. Each seed was cut longitudinally through the endosperm to expose the embryo through a microscope to evaluate viability (International Seed Testing Association 2012).

Statistical Analysis

A 2×2×2 factorial analysis of variance with the following factors: animal species (goats and sheep [experiment 1]), goats and cattle [experiment 2]), diets (low-quality hay and high-quality hay), and seed species (*D. cinerea* and *A. nilotica*). The experiments were done at different times, due to the limited availability of seeds. Hence, the analyses were done separately. Each animal in both experiments was considered an experimental unit. A fixed group of 20 animals ($n=20$ of each animal species) were selected according to age and weight, and treatments were randomly assigned to the animals (seed species and diet were fixed effects). Seeds recovered from each animal for that day were planted separately. Repeated measurements were included in the analysis as a subplot factor (Little and Hills 1972). Differences between means were considered significant at the 5% level using Fisher's protected LSD (least significant difference). The standardized residuals were tested for normality using Shapiro-Wilks test (1965). All data were analyzed by analysis of variance using SAS statistical software (SAS Institute 2002) for a completely randomized design.

RESULTS

Seed Size, Density, and Nutritive Value

The length and width of *D. cinerea* seeds were 4.2 ± 0.1 mm and 1.7 ± 0.1 mm and for *A. nilotica* seeds were 6.9 ± 0.1 mm and 5.7 ± 0.1 mm. The density of *A. nilotica* seeds (1.6 g cm^{-3} ± 0.01) was lower than that of *D. cinerea* seeds (1.7 g cm^{-3} ± 0.07). The two seed species (*D. cinerea* and *A. nilotica*) used in both experiments (goats, sheep and cattle, goats) have relatively high crude protein (CP), with *D. cinerea* having a higher mean value (19.3% ± 0.06) than *A. nilotica* (14.1% ± 0.06). *Dichrostachys cinerea* seeds (15.7 MJ/kg ± 0.20) had slightly less energy than *A. nilotica* seeds (16.5 MJ/kg ± 0.12).

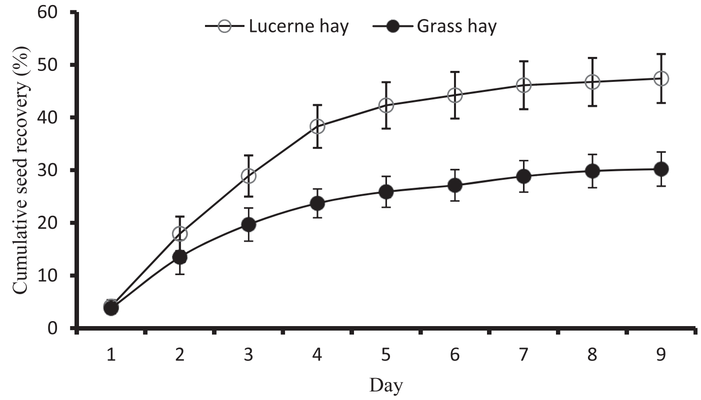

Figure 1. Significant effect of diet (high-quality hay and low-quality hay) on mean cumulative percentage seed recovery from experiment 1. Bars represent standard errors (SE).

Seed Recovery

Experiment 1 (Goats and Sheep). Both goats and sheep consumed all 1 000 *D. cinerea* seeds offered. However, sheep consumed more *A. nilotica* seeds (940 ± 17.24 seeds) than goats did (628 ± 26.15 seeds). There were no significant interactions or main effects for cumulative percentage viable seed recovery in respect to animal and seed species. However, sheep and goats had a higher cumulative percentage seed recovery when they ate the high-quality hay (47.4% ± 4.65) compared to low-quality hay (30.2% ± 3.24) ($P < 0.01$; Fig. 1).

Experiment 2 (Goats and Cattle). Cattle consumed more (1 000 ± 0.00 seeds) *A. nilotica* seeds than goats did (820 ± 25.12). There was no significant difference in the number of *D. cinerea* seeds consumed by cattle (1 000 ± 0.00) and goats (961 ± 4.78). No significant effects of diet or seed species or the interaction of diet, seed species, and animal species were found on cumulative percentage recovery. However, significantly more seeds were recovered from cattle than from goats (cattle 50.3% ± 4.27; goats 32.0% ± 6.44; Fig. 2).

Germination Trial

Experiment 1 (Goats and Sheep). Combining for goats and sheep, there were more viable *A. nilotica* and *D. cinerea* seeds (83.9% and 92.2%, respectively) than dead seeds after 21 d of seed germination tests. The interaction of animal species, diet quality, and seed species had a significant effect on cumulative percentage germination ($P < 0.05$).

For goats fed low-quality hay, *A. nilotica* seed germination (9.4% ± 3.66) was higher ($P < 0.05$) than *D. cinerea* seed

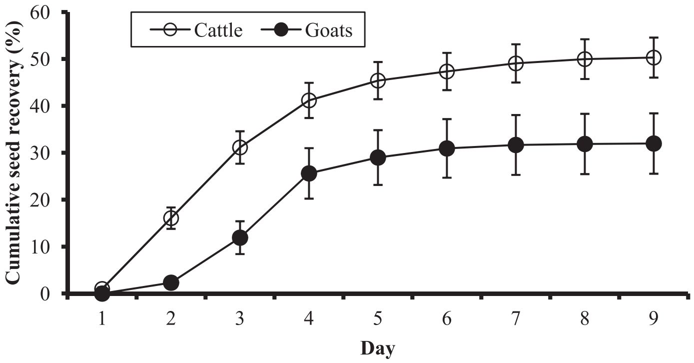

Figure 2. Significant effect of animal species on mean cumulative percentage seed recovery from experiment 2. Bars represent standard errors (SE).

Table 1. Interaction effect of animal species (goats, sheep), diet (grass hay, alfalfa hay), and seed species (*A. nilotica*, *D. cinerea*) of mean ± SE percentage seed germination.

Interaction effect	% Seed germination[1]
Sheep × grass hay × *A. nilotica* seeds	10.58 ± 1.84 a
Goats × grass hay × *A. nilotica* seeds	9.38 ± 3.66 a
Goats × grass hay × *D. cinerea* seeds	6.78 ± 1.13 abc
Goats × alfalfa hay × *D. cinerea* seeds	6.71 ± 1.53 abc
Sheep × alfalfa hay × *D. cinerea* seeds	6.05 ± 0.91 abc
Sheep × grass hay × *A. nilotica* seeds	5.42 ± 1.12 bc
Sheep × alfalfa hay × *A. nilotica* seeds	4.13 ± 1.32 c
Goats × alfalfa hay × *A. nilotica* seeds	2.50 ± 0.97 c

[1]Percentage seed germination followed by a different letter indicates a significant difference ($P < 0.05$).

germination (6.8% ± 1.13). Greater germination percentage of *D. cinerea* seeds (6.7% ± 1.53) was observed in goats fed high-quality diet than for *A. nilotica* seeds (2.5% ± 0.97; $P < 0.05$).

In sheep, germination percentages for animals fed low-quality hay and *D. cinerea* seeds (10.6% ± 1.84) were higher ($P < 0.05$) than for sheep fed low-quality hay and *A. nilotica* seeds (5.4% ± 1.12; Table 1). There were no differences ($P > 0.05$) in germination percentages between sheep fed high-quality hay and *A. nilotica* versus *D. cinerea* seeds (Table 1).

Experiment 2 (Goats and Cattle). Combining data for goats and cattle, there were more viable *A. nilotica* and *D. cinerea* seeds (64.7% and 57.7%) than dead seeds after 21 d of seed germination tests in this experiment. Animal species was the only significant effect on mean cumulative germination percentage (goats 14.1% ± 1.48; cattle 9.3% ± 0.94) ($P < 0.01$). Unlike results for experiment one (goats, sheep), there were no effects of diet and seed species on cumulative germination percentage ($P > 0.05$). There were no differences in germination percentages ($P > 0.05$) between goats fed high-quality hay and *A. nilotica* seeds versus *D. cinerea* seeds. In cattle, there were no differences ($P > 0.05$) in germination percentages between those animals fed low-quality hay and *A. nilotica* versus *D. cinerea* seeds; the same absence of difference ($P > 0.05$) occurred with high-quality hay.

DISCUSSION

Seed Recovery and Germination Trial

Effect of Diet Quality. Seed recovery and survival after passage through the gut depends on hardness and size of the seeds, number of seeds consumed, and animal species and size (Gardener et al. 1993; Bodmer and Ward 2006; Varela and Bucher 2006; Whitacre and Call 2006; Castro et al. 2008). It must also be noted that variable feed intake could contribute to variability in passage rate and therefore, seed recovery. These factors may singly or jointly influence seed recovery and germination. The quality of the associated diet is one of the most important determinants of success of livestock fecal seed dispersal (Simao Neto et al. 1987; Miller and Coe 1993; Miller 1995; Whitacre and Call 2006). Seeds ingested when animals are consuming higher quality forage tend to pass faster through the digestive tract with less damage to the seed coat (Jones and Simao Neto 1987; Shayo and Uden 1989; Whitacre and Call 2006). Consequently, such seeds tend to germinate better than seeds that reside in the gut for longer and consequently have more seed damage. This may explain the significant effect of diet observed on cumulative percentage seed recovery in experiment 1.

Effect of Seed Species. The morphology of the two seed species (*D. cinerea* and *A. nilotica*) may explain the consumption, seed recovery, and germination percentages obtained in this study. The two seed species differed in size and hardness. *D. cinerea* seeds may have been easier to swallow with less chewing due to their relatively small size compared to *A. nilotica* seeds. The higher crude protein (despite lower energy levels) in *D. cinerea* seeds than in *A. nilotica* seeds may have been a reason why this seed species was consumed to a greater degree. Furthermore, the larger the animal the less likely it is to be a selective feeder (van Soest 1994), which may be the reason why all *D. cinerea* and *A. nilotica* seeds in experiment two (goats vs. cattle) were consumed irrespective of seed size. Small seeds of less than 2.5 mm in width are more likely to escape mastication and rumination than large seeds (Russi et al. 1992; Gardener et al. 1993; Whitacre and Call 2006). In addition, if small food particles are able to pass through the reticulo-rumen orifice to the lower parts of the digestive tract faster than large particles (Minson 1990), then small seeds may also pass faster (Bodmer and Ward 2006; Whitacre and Call 2006). Hard-coated seeds usually have high seed recovery due to their resistance to damage during chewing and rumination (Gardener et al. 1993; Whitacre and Call 2006), although this may depend on the herbivore species (Rohner and Ward 1999). Hard-coated seeds have higher chances of passing through the gut without substantial damage to the seeds (Brown and Archer 1987; Archer and Pyke 1991; Gardener et al. 1993; Miller 1995; Tjelele et al. 2012). Even though density of *A. nilotica* seeds was lower than that of *D. cinerea* seeds, its density was reasonably higher than some legumes such as *Trifolium semipilosum* and *Stylosanthes hamate* (Simao Neto et al. 1987). Some seeds that have a very hard seed coat and insufficient seed scarification during passage through the gut may have a low germination in the feces (see also Simao Neto and Jones 1986; Simao Neto et al. 1987; Schupp et al. 1997).

Effect of Animal Species. The high mean cumulative percentage seed recovery for cattle compared to that of goats in experiment two may be attributed to the large difference in size of the animals. Cattle in this study conferred potentially higher seed recovery of *D. cinerea* and *A. nilotica* seeds compared to goats and are therefore more likely to promote woody plant encroachment, provided that the seeds are adequately scarified. Miller (1995) and Bodmer and Ward (2006) found that seed survival through the digestive tract and seed germination increased linearly with body size. Goats and sheep chew food thoroughly (Shayo and Uden 1989; McGregor and Whiting 2013), which may result in seed damage and reduced seed recovery. However, some seeds may escape damage from chewing and rumination (Jones and Simao Neto 1987; Thompson et al. 1990; Miller 1995). Furthermore, Simao Neto and Jones (1987) and Thompson et al. (1990) have shown that large differences in seed recovery and seed germination between cattle and small ruminants (goats and sheep) may be related to initial mastication and rumination. Even though seed type did not significantly affect seed recovery, the relatively high seed recovery may be in part a function of the hard coats of both *A. nilotica* and *D. cinerea* seeds compared to other legume species previously recorded (Brown and Archer 1987; Simao Neto et al. 1987; Miller 1995; Shayo and Uden 1998).

The relatively high viability of *A. nilotica* and *D. cinerea* seeds from experiment 1 and experiment 2 shows that passage through the digestive system of these livestock did not greatly compromise germination potential. However, under natural conditions, seed dispersal does not guarantee seed germination, which depends on appropriate environmental and seed survival conditions (Ward and Rohner 1997; Rohner and Ward 1999; James et al. 2011; Grellier et al. 2012).

MANAGEMENT IMPLICATIONS

In experiment 1, the effect of diet quality influenced both seed recovery and germination percentages in goats and sheep. This suggests that animals fed seeds mixed with high-quality diet are most likely to pass through the digestive tract intact and remain viable. Results from experiment 2 also showed that more seeds were recovered from cattle than goats, which is attributed to animal body size and quality of diet consumed, both of which influence retention time in the gut (Miller 1995; Bodmer and Ward 2006). The relatively high seed recovery and germination percentages in this study may be due to the morphology (size, hardness) of the two seed species (Whitacre and Call 2006; Tjelele et al. 2012).

Acacia nilotica and *D. cinerea* seeds remained in the gut of goats, sheep, and cattle for about 9 d in this study. Thus, seeds can be transported and potentially germinate in areas far removed from were consumed. The interaction animal species and size, diet quality, and seed characteristics (size, hardness) all play a major role in dissemination of viable and scarified seeds either alone or in combination. Animals consuming *D. cinerea* and *A. nilotica* seeds during the dry season should be restricted to fenced paddocks to reduce the possibility of woody plant encroachment.

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