

Interspecific Variation in the Reproductive Response of *Acacia* Species to Protection from Large Mammalian Herbivores

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ABSTRACT

We quantified the fruit set of four *Acacia* spp. inside and outside of long-term experimental exclosures in order to examine the fitness consequences of herbivory by large mammals. We found a considerable interspecific variation in the reproductive fitness costs of herbivory in four African *Acacia* spp. *Acacia nilotica* and *A. brevispica* respond to protection from large mammalian herbivores by greatly increasing their seed set. In contrast, there was little or no increase in seed set in *A. mellifera* and *A. etbaica*. The reasons for these differences are not known, but may be related to armament morphologies.

Key words: Laikipia; East Africa; pods; fruit set; prickles; thorns; recurved spines.

HERBIVORY CAN AFFECT POPULATIONS OF TREES AND SHRUBS NEGATIVELY through increased mortality and decreased reproduction and recruitment. Herbivory has been correlated with reduced fruit set in many woody species, but experimental evidence is less abundant (Dominguez & Dirzo 1994, Fernandez-Calvo & Obeso 2004, Parra-Tabla *et al.* 2004; see reviews by Marquis 1992, Obeso 1993), and there is a particular shortage of studies of the effects of herbivory on reproduction in acacias, despite their dominance in many of the world's semi-arid biomes, and their reputation as favored food plants of many wild and domestic herbivores. Multiple species comparisons are similarly rare.

Here we present controlled replicated experimental evidence that protection from large mammalian herbivores increases the reproductive output of some acacia species, but not others.

This research was carried out at the Mpala Research Centre in Laikipia, Kenya (0°17' N, 37°52' E, 1800 m asl). Rainfall at this site averages 500–600 mm/yr in a weakly trimodal pattern. Two soil types predominate: moderately deep, well-drained red sandy soils, and deep clay “black cotton” vertisols soils of impeded drainage (Ahn & Geiger 1987). Vegetation is semi-arid *Acacia* bushland and bushed grassland. The property is managed for livestock production and for the maintenance of a wide variety of native mammals, including zebras (*Equus burchelli* and *E. grevyi*), impalas (*Aepyceros melampus*), elephants (*Loxodonta africana*), giraffes (*Giraffa camelopardalis*), elands (*Tragelaphus oryx*), greater kudu (*Tragelaphus strepsiseros*), Grant's gazelles (*Gazella granti*), and dik-diks (*Madoqua kirkii*). The latter seven are herbivores on *Acacia* spp. See Auguotone and McNaughton (2004) for ungulate denoities in the study area.

In 1999, six 0.5-ha (70 × 70 m) exclosures were erected in the red soil habitat. Each was surrounded by an 11-strand, 3-m-

tall electrified fence that excluded all herbivores larger than 10 kg. Fences followed the design of Young *et al.* (1998), with additional mesh and electrified wires from 0–0.5 m in height. These fences have proven effective barriers to larger mammals (Augustine & McNaughton 2004).

In July and August 2004, we surveyed the reproductive status of all four common acacia species that occurred in the vicinity of these six exclosures. *Acacia brevispica* Harms is armed with scattered short recurved prickles (*cf.* Myers & Bazely 1991), *A. nilotica* Benth. with a pair of long, straight stipular spines at each node, *A. mellifera* (Vahl) Benth. with a pair of short, strongly recurved stipular spines at each node, and *A. etbaica* Schweinf. with a mixture of long, straight and short, recurved stipular spines, also paired at the nodes.

We counted the total number of seedpods on up to five individuals of each species both inside and outside each exclosure. We only surveyed trees tall enough to be reproductive and measured the heights of these individuals. No *Acacia* species was found at all exclosures; each was found both inside and outside exclosures at either three or four sites.

Fruit numbers were log transformed for normality and regressed against tree height for all trees surveyed, separately by species. Mean tree heights and numbers of pods were calculated for each species at each site, with exclosure site being the experimental unit (sample sizes 3–4 sites per species, and [2–]5 individuals per site for each herbivore treatment, for a total of 126 individuals). The numbers of pods per tree (log transformed) were analyzed with two-way ANCOVA, with site and exclosure treatment as main effects, and tree height as a covariate.

A total of 42,418 fruits were counted on 146 trees. Individuals inside exclosures tended to produce more fruits than those exposed to herbivory by large mammals, but this response differed among species (Fig. 1). It was strongest in *A. nilotica* (nearly tenfold, $F = 4.99$, $P = 0.035$) and *A. brevispica* (nearly fivefold, $F = 6.34$, $P = 0.022$), and virtually nonexistent for *A. etbaica*.

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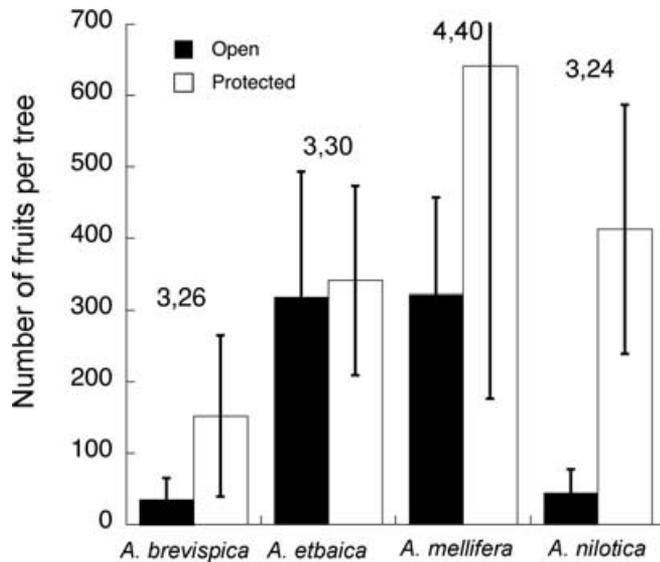


FIGURE 1. Mean fruit set in *Acacia* individuals either exposed to herbivory by large mammals or protected from them in exclosures. Bars represent one standard error, based on the number of independent sites. Samples sizes are above each bar (number of sites, number of individual trees). Statistical analyses were done on log transformed data, and controlled for variation among sites.

Individuals of *A. mellifera* protected from herbivory produced twice as many fruits on average, but this pattern was obscured by a high variance. Individuals surveyed inside the exclosures were not significantly taller than those surveyed outside the exclosures, but branch herbivory on these species would not necessarily affect total height.

For *A. nilotica*, there was a strong relationship between tree height and fruit production among both protected ($R^2 = 0.32$, $P = 0.015$) and exposed ($R^2 = 0.64$, $P < 0.001$) individuals. For *A. etbaica*, there was a significant positive relationship only among those individuals inside the exclosures ($R^2 = 0.29$, $P = 0.018$). Neither *A. brevispica* nor *A. mellifera* exhibited significant relationships between plant height and fruit production (all $P > 0.40$).

It appears that some *Acacia* spp., respond strongly to protection for herbivory by large mammals by producing more fruits. For the *Acacia* spp. that did show an increase in reproduction associated with protection from large herbivores, this evidence fulfills the third criterion of Karban and Myers (1989) for the demonstration of induced defense. First, the plant must respond in a measurable way to herbivory (Young 1987; Gowda 1996, 1997; Young & Okello 1998; Young *et al.* 2003). Second, the response induced by herbivory must reduce subsequent herbivory (*i.e.*, be a defense) (Cooper & Owen-Smith 1986, Milewski *et al.* 1991, Cooper & Ginnet 1997). Third, increased herbivory must cause a decrease in plant fitness. Surprisingly, although some descriptive studies have documented mortality of adult acacias from large mammal herbivory (Pellew 1983, Birkett 2002, MacGregor & O'Connor 2004, Birkett & Stevens-Wood 2005), there have been very few experimental studies of the effects of large mammal herbivory on the fitness of acacia

plants (Oba 1998, Bond & Loffell 2001), and none documenting reproductive costs of herbivory.

Herbivory may suppress reproduction in several ways. First, foliar herbivory may reduce the energy put into reproduction effort by removing photosynthetic biomass, or by inducing costly defences (Karban & Baldwin 1997, Young & Okello 1998, Ward & Young 2002, Gowda *et al.* 2003, Young *et al.* 2003, Huntzinger *et al.* 2004) or costly compensatory growth (Gadd *et al.* 2001). Second, if large mammalian herbivores reduce the density of adult acacias, this could affect pollination efficiency (J. Goheen, pers. comm.). However, the densities of adult *Acacia* spp. were similar inside and outside of the exclosures at the time of this study. Third, large mammalian herbivores may be eating the fruits themselves. *Acacia nilotica*, which showed the greatest response to protection from herbivory, was the one species with indehiscent pods, which are more likely to be dispersed by large mammals. However, we found no evidence of pod removal at the time of this survey (as the pods were still ripening), and no bare peduncles that would indicate removed pods.

There was a considerable variation among *Acacia* spp. in their response to herbivore exclusion. In particular, *A. etbaica* and *A. mellifera* appear to maintain high levels of fruit production even in the presence of large mammalian herbivores. Although we have only a rudimentary sense of chemical defense for these species, the pattern we observed does not appear to be related to a variation in chemical defense. In a survey of leaf tannin content, these two species had the lowest (*A. etbaica*) and the highest (*A. mellifera*) condensed tannin levels of the 10 local *Acacia* spp. tested (D. Ward & T. P. Young, pers. comm.).

It is intriguing that the two species in this study that responded least to herbivory have short recurved stipular spines, which have been shown to be particularly effective in deterring herbivory (Cooper & Owen-Smith 1986). *Acacia nilotica*, the only species producing only long-straight spines, showed the most dramatic reduction in seed set with herbivory. Similarly, individuals of *A. drepanolobium* (which are armed with long, straight spines) when protected from herbivory also show large increases in seed set (Goheen *et al.* 2007). It may be relevant that there is little evidence for the occurrence of induced response to herbivory in the form of more or longer recurved spines (see Rooke *et al.* 2004), although such an evidence is rich for long, straight spines (Young 1987, Young & Okello 1998, Young *et al.* 2003). However, the sample size in this study (four species) is too small to make broad generalizations.

These exclosures exclude all herbivores larger than 5 kg. Ninety-two percent of the acacias we surveyed were less than 5 m tall, and all had the majority of their branches within the 5 m browse heights of elephants and giraffes, but the effects of other larger ungulates (*e.g.*, elands, kudus) may also have contributed to the pattern. Several studies have documented how herbivores (and especially elephants and giraffes) affect the growth and survival of adult and juvenile acacias in Africa (Pellew 1983, Birkett 2002, Augustine & McNaughton 2004, MacGregor & O'Connor 2004, Birkett & Stevens-Wood 2005). The data presented here suggest that herbivores can also reduce seed production, with potential effects on populations that extend into the next generation.

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