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Interactions between megaherbivores and microherbivores: elephant browsing reduces host plant quality for caterpillars

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Abstract. Direct effects of herbivory, and indirect effects through induced responses to herbivory, can both influence the susceptibility of plants to subsequent attacks by herbivores. There has, however, been very little research (if any) to investigate how the large-scale effects of browsing by megaherbivores (>1000 kg body mass) on woody plants might influence the subsequent use of those plants by phytophagous insects. We conducted a field study in Kruger National Park, South Africa, to investigate whether browsing by elephants (*Loxodonta africana*) on mopane trees (*Colophospermum mopane*) had any influence on the subsequent selection of those trees by ovipositing mopane moths (*Imbrasia belina*). Our results showed that, after controlling for differences in canopy volume, the density of egg masses was almost halved in mopane woodlands recovering from severe elephant browsing in the previous season. This is despite the regrowth on heavily browsed trees having lower tannin:protein ratios and longer shoots. Our suggested explanation is that large monophagous caterpillars can only feed in the canopies of the trees in which they hatch and so the quantity of food in each canopy is more important than its quality. There are implications for the sustainable harvesting of mopane caterpillars, which represent an important food resource for rural communities in southern Africa. Future avenues for research include patch selection by large herbivores in response to local nutrient enrichment by frass deposited during caterpillar outbreaks.

Key words: *Colophospermum mopane*; herbivore-plant interactions; host selection; *Imbrasia belina*; southern Africa.

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INTRODUCTION

Even in highly specific plant-herbivore interactions the likelihood of a plant being attacked by an herbivore is influenced by its immediate neighborhood of plants (Agrawal et al. 2006). Much of this among-plant variation is associated with past herbivory having triggered traits for resistance involving induced chemical defense, or tolerance involving compensatory growth (Strauss and Agrawal 1999). Trees or shrubs that

have been heavily pruned by large mammals, and which express tolerance traits such as rapid shoot regrowth and reduced chemical defense, can subsequently attract increased herbivory by other mammals and also insects (Danell and Huss-Danell 1985, Fornara and du Toit 2007). Alternatively, mammalian browsing might reduce the local abundance of phytophagous insects through exploitative competition for shared food plants (Gómez and González-Me-gías 2002). Such potential interactions have never

before, to our knowledge, been explored for megaherbivores (>1000 kg body mass) and phytophagous insects sharing the same food plants.

African elephants (*Loxodonta africana*) and caterpillars of the saturniid mopane moth (*Imbrasia belina*) are the two main herbivores of mopane trees (*Colophospermum mopane*), which occur in extensive woodlands across southern Africa. In such areas mopane vegetation forms the dominant constituent of the dry-season diet of elephants, which feed by leaf stripping, debarking, branch and stem breaking, and uprooting (Smallie and O'Connor 2000). In northern Botswana, for example, >90% of randomly sampled mopane trees had been browsed by elephants (Ben-Shahar 1998), which are considered the keystone species in mopane woodlands (Caughley 1976). Furthermore, elephants are known to preferentially rebrowse the hedged, coppicing mopane trees they had pruned in previous seasons (Smallie and O'Connor 2000). In contrast mopane caterpillars consume just the leaf blades, often leaving a stand completely defoliated (Scholes et al. 2003). The caterpillars hatch from eggs laid in masses that can each consist of 30–350 eggs glued to the upper or lower surfaces of leaves, twigs, or branches, with each egg mass representing one ovipositing event by a female moth. We assume that the number of fresh egg masses in a tree is an indication of the number of moths that recently oviposited in that tree. The moths do not feed, going through mating, ovipositing, and dying with a few days. The caterpillars, however, progress through their larval stage in about six weeks during which they feed voraciously and grow rapidly, with the fifth instars reaching a length of about 80 mm.

In a previous study (Hrabar et al. 2009a) we found that mopane trees displayed enhanced shoot regrowth after browsing by elephants and we replicated the effect with manual pruning. In addition, simulated browsing of mopane plants in greenhouse experiments (Kohi et al. 2009) found that intermediate levels of defoliation induced a response of elevated foliar condensed tannin concentrations, whereas high levels of defoliation (75% and 100%) did not. We thus conducted a field investigation into whether ovipositing mopane moths are attracted to the

enhanced nutritional quality of regrowth on mopane trees previously subjected to heavy browsing by elephants.

METHODS

Fieldwork was based at Shingwedzi in the Kruger National Park, South Africa (du Toit et al. 2003). The vegetation is dominated by mopane trees in virtually monospecific stands that may vary in structure from short scrubland to tall riverine woodland. Elephant density is about 1.2 animals/km².

Sampling was conducted over several weeks in December, in the middle of the October-May wet season, when ovipositing was complete and caterpillars were beginning to emerge but defoliation by caterpillars was still minimal. Mopane foliage at heavily browsed sites was regrowth after intensive elephant browsing in the preceding dry season. Seven sites, all centered on artificially placed (pumped) watering holes within mopane woodland, were selected for having both heavy and light elephant browsing in close proximity of each other. At each site, one 50 m × 5 m transect was positioned within the piosphere of heavy browsing (HB) and another identical transect was positioned outside the piosphere in an area of light browsing (LB). Piosphere radius varied greatly among sites depending on topography and in some cases heavy browsing extended for at least 1 km from the watering hole, but the two transects at each site were positioned so they were generally 500 m apart. Replicating transect pairs across seven sites minimized site effects caused by factors other than elephant browsing. Transect sampling was adopted because browsing was high within the piosphere and low without, making it impossible to use individual trees as units of replication due to non-independence. In each transect, all mopane trees were counted and each was measured by live tree height (m), basal stem diameter (cm), canopy width at the widest point (m), and canopy height (m). A total of 419 trees were measured across all transects. Canopy volumes were estimated from canopy heights and widths. Undamaged mopane tree height is correlated with largest living stem diameter and so means of the latter dimension were compared within HB and LB transect pairs to confirm

uniformity in tree population structure.

We measured foliar concentrations of total phenols, condensed tannin, and crude protein (calculated from N). In each transect, handfuls of leaves were grabbed at random from around the canopies of at least five trees and then bulked together. Leaf samples were air dried, then oven dried at 50°C for at least four days until dry weight (DW), then milled through a 1-mm screen. Crude protein content was determined using the Dumas method (AOAC 2000), total phenols using the Prussian blue assay, and condensed tannin using the acid butanol method for proanthocyanidins (Hagerman 1995). Leaf material in samples of ~0.05 g DW each was extracted with 3 ml of 70% aqueous acetone by sonicating in an ice-water bath for 30 min and centrifuging at 2000 g for 10 min. Standards were sorghum tannin for condensed tannin and Gallic acid for total phenols.

Elephant browsing was visually classified for each tree as the proportion of potential canopy volume removed, scored on a seven-point scale: 1 = 1–10%, 2 = 11–25%, 3 = 26–50%, 4 = 51–75%, 5 = 76–90%, 6 = 91–99%, 7 = 100%. Each tree was allocated the mid-point of the range of its score; i.e., a tree scored 2 had lost 18%, or 0.18 of its potential canopy volume.

We considered all trees with mopane moth egg masses from the current season as host trees. Egg mass abundance per tree was recorded on a scale of 0–3, indicating 0, 1, 2, and 3 or more egg masses. Two measures of oviposition were calculated for each transect: percentage of mopane trees that were host trees, and egg mass density (egg masses/ha). No trees were too big for their canopies to be thoroughly searched and only 6 out of 69 host trees had an egg mass abundance score of 3. To determine if oviposition preference was influenced by elephant browsing, host tree percentage and egg mass density were compared across paired transects (HB vs. LB) over all seven sites. Then, to determine which variables might influence oviposition preference, host tree percentage and egg mass density were each regressed against the following for each transect ($n = 14$ transects): tree density (for all trees and also just trees > 3 m); canopy volume / ha; mean shoot length; mean leaf length; mean leaf tannin:protein ratio.

Selection is use/availability, so we treated each

transect individually to determine the relative distribution of egg masses among the larger and smaller trees (based on both tree height and canopy volume) available in that transect. Within each transect we used mean height of all trees to divide them into large and small; in the same way we further divided those into small or small-medium, and medium-large or large height classes. Four canopy volume classes were derived for each transect in the same way. For each transect the number of egg masses was calculated for each tree height and canopy size class, and then all transects were combined. The observed overall distribution of egg masses across relative size classes was compared against the distribution expected if (H_0) oviposition simply reflects tree size availability.

Wilcoxon matched-pairs tests were used to test for significant differences in (1) elephant utilization, (2) percentage host trees, (3) egg mass density, (4) tree density, (5) potential tree size, (6) leaf size, (7) shoot length, and (8) foliar nutritional value between HB and LB areas. Chi-squared goodness-of-fit tests were used to determine whether ovipositing mopane moths used tree height and canopy volume classes in proportion to availability, with availability quantified in terms of both tree number and total canopy volume. Bonferroni confidence intervals (95%) were constructed to identify which classes were preferred or avoided.

RESULTS

Positioning of transects in areas of heavy (HB) and light (LB) elephant browsing was confirmed by both the percentage of trees browsed by elephants and the index of elephant impact per tree (HB $>$ LB; Table 1). The percentage of trees selected as hosts by ovipositing mopane moths and the number of egg masses per woodland area were both less in heavily browsed transects (HB $<$ LB; Table 1; Fig. 1). One exception was the transect pair at Site 6 (Fig. 1) where the growth of the mopane woodland in that area is stunted, presumably by an interaction of soil type and rainfall, so there was little difference in woodland structure between the areas of high browsing within the piosphere and low browsing without. Overall, total tree density and largest stem diameter did not differ (HB = LB) across levels

Table 1. Variables describing mopane woodland, elephant browsing, and mopane moth ovipositing (mean \pm SE) at seven sites where pairs of 50 m \times 5 m transects were positioned in areas with heavy (HB) and light (LB) elephant browsing impact, respectively. Comparators (Comp) indicate the significance ($P \leq 0.05$) of differences across the seven pairs of transects for each variable (Wilcoxon matched-pairs tests).

Variable	Heavy browsing (HB)	Comp	Light browsing (LB)	<i>P</i>
Trees browsed by elephants (%)	95.7 \pm 1.58	>	60.6 \pm 11.2	0.02
Level of elephant impact (index)	0.45 \pm 0.06	>	0.16 \pm 0.03	0.02
Host trees, i.e., with eggs (%)	11.2 \pm 2.77	<	22.9 \pm 5.31	0.05
Ovipositing (egg masses/ha)	137 \pm 35.8	<	440 \pm 104	0.03
Tree basal stem diameter (cm)	7.08 \pm 1.09	=	7.09 \pm 0.75	0.74
Total tree density (trees/ha)	982 \pm 111	=	1411 \pm 180	0.12
Trees >3 m high (trees/ha)	117 \pm 37.9	<	394 \pm 69.5	0.04
Total canopy volume (m ³ /ha)	7,804 \pm 797	<	14,579 \pm 2,781	0.04
Shoot length (cm)	115 \pm 8.66	>	89.0 \pm 12.6	0.04
Leaf length (mm)	59.0 \pm 1.47	=	56.6 \pm 1.41	0.40
Tannin:protein ratio	0.48 \pm 0.02	<	0.55 \pm 0.02	0.02
Total polyphenols (mg/g DW)	57.1 \pm 1.69	=	59.3 \pm 1.72	0.50

of elephant impact, yet the density of tall trees (>3 m) was reduced in areas of high elephant impact (HB < LB). We attribute this to the effects of elephant browsing because mean potential tree height (based on largest stem diameter) did not differ while total canopy volume /ha did (HB < LB). Shoots were significantly longer in areas of high elephant impact (HB > LB) and, despite no difference in length or total polyphenolic content of leaves, a difference in tannin:protein ratio (HB < LB) confirmed a tolerance response of compensatory growth indicating higher food

quality. Egg mass density was negatively related to shoot length and leaf nutritional value, but positively related to tall tree density and total canopy volume /ha ($P < 0.05$ in each case). After controlling for differences in canopy volume across transect types (Table 1), mean egg mass density in the canopy in LB transects (0.030/m³) was almost double that in HB transects (0.017/m³). Similarly, based on tree numbers, ovipositing by mopane moths was biased towards the tallest and largest canopied trees available (Table 2).

DISCUSSION

If dry-season browsing by elephants simply reduced the subsequent abundance of wet-season foliage on mopane trees without any enhancement of nutritional quality, then we would expect reduced moth ovipositing in direct proportion with reduced canopy volume. What we found, however, was a disproportionately low density of *Imbrasia belina* egg masses in heavily browsed transects even after controlling for differences in canopy volume and despite the foliage in those transects having longer shoots of higher nutritional quality. This difference in foliage quality and the tendency for more *I. belina* egg masses to be found in larger trees are both consistent with our previous manipulations and observations in a separate area of mopane woodland with a low elephant density (Hrabar et al. 2009a, b). Yet the absence of host selection for post-browsing regrowth of enhanced nutritional

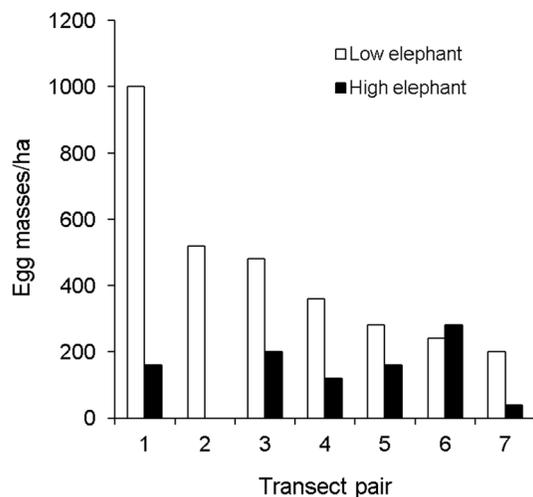


Fig. 1. Densities of mopane moth egg masses in seven pairs of transects situated in mopane woodland areas with high and low intensities of elephant browsing.

Table 2. Selection of different sized mopane trees by ovipositing mopane moths, based on proportional availability of trees within each size class and with size classified separately by canopy volume and tree height, with positive (+), negative (–), or no (0) selection determined by 95% Bonferroni confidence intervals around the proportions of observed egg masses.

Tree size class	Proportion of trees	Proportion of observed egg masses	Bonferroni intervals (95% CI)	Selection
Canopy volume				
Small	0.437	0.090	$0.018 < p < 0.162$	–
Small-medium	0.269	0.170	$0.076 < p < 0.264$	–
Medium-large	0.173	0.300	$0.185 < p < 0.415$	+
Large	0.121	0.440	$0.316 < p < 0.564$	+
Tree height				
Small	0.283	0.060	$0.001 < p < 0.119$	–
Small-medium	0.296	0.130	$0.046 < p < 0.214$	–
Medium-large	0.234	0.150	$0.061 < p < 0.239$	0
Large	0.187	0.660	$0.542 < p < 0.778$	+

quality differs from findings on phytophagous insects elsewhere (Danell and Huss-Danell 1985). We suggest the key might be that leaf-chewing insects select individual host plants offering high food quantity whereas sap-suckers and gallers select patches of host plants on the basis of food quality (Schowalter and Ganio 1999, Ostrow et al. 2002, Bailey and Whitham 2006). The large (~13 g) leaf-chewing caterpillars of mopane moths are effectively sessile in their individual natal trees, which can become totally defoliated, and so it should be adaptive for ovipositing moths to select hosts offering high foliage abundance per individual stem. Being vulnerable to multiple vertebrate and invertebrate predators (Styles and Skinner 1996) the risk—in addition to heat and desiccation—must become greatly increased if caterpillars have to disperse across the ground from a completely defoliated tree in search of another still bearing leaves.

Our results have relevance to the traditional use of mopane caterpillars as food by rural people in southern Africa who depend upon this rich source of protein, fatty acids, and minerals (Glew et al. 1999). Reducing the individual canopy sizes of mopane trees, for example by chopping live branches for firewood, is likely to reduce the caterpillar harvest despite stimulating coppicing. Similarly, where elephants are compressed by habitat-loss into shrinking patches of mopane woodland, high browsing pressure will reduce the supply of this important non-timber forest product to neighboring human communities.

Finally, the evidence we found of a mammalian megaherbivore influencing a phytophagous

insect through a shared food resource invites further research into the interactions involved. Herbivores adjust their foraging patterns in response to spatial variations in nutrient density (Pastor 2011) and even elephants can select nutrient-rich patches at scales as fine as 100 m² (Pretorius et al. 2011). Hence, an intriguing question is whether frass deposited during caterpillar outbreaks has a local fertilizing effect sufficient to attract other herbivores (Barrio et al. 2013).

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