CHAPTER 6

ELEPHANTS AND MOPANE CATERPILLARS: INTERACTION THROUGH A SHARED RESOURCE

6.1 Introduction

An important determinant of an ecosystem's structure and dynamics is the interaction between species for food (Brown & Davidson 1977). In the past, most studies looking at such interactions tended to focus on taxonomically related species, as they were the most obvious to compare due to their similarities. In reality, however, it is the functional similarity (i.e. species from the same guild) rather than the taxonomic similarity of species that is relevant. Additionally, while ecologists have long recognised the importance of direct interactions (such as competition and predation) in determining the distribution and abundance of organisms, the role of indirect interaction pathways has not been as well documented (Davidson *et al*. 1984). More recently, however, a growing number of examples have illustrated that indirect effects, such as habitat modification, may exceed the direct consequences of herbivory. For example, two taxonomically different herbivores, namely beavers (*Castor canadensis*) and leaf beetles (*Chrysomela confluens*), have been shown to interact indirectly through a common food source, cottonwood (*Populus* sp.; Martinsen *et al*. 1998).

In the mopane (*Colophospermum mopane*) woodlands of Southern Africa, the two main browsing species are a megaherbivore, the African elephant (*Loxodonta africana*), and an insect, the mopane caterpillar (*Imbrasia belina*). Despite its abundance, mopane is selected for by elephants and can form the dominant constituent of their diet in certain areas (Lewis 1991; Smallie & O'Connor 2000). Woodlands dominated by mopane are therefore susceptible to elephant induced damage through leaf stripping, branch/stem breaking and uprooting (Ben-Shahar 1993). In northern Botswana, for example, only 8.3% of mopane trees sampled had never been damaged by elephants (Ben-Shahar 1998). Elephants are therefore considered to be a 'keystone' species in these woodlands (Timberlake 1995), as they are a prominent agent of structural change to mopane (Caughley 1976). Similarly, mopane caterpillars can also have a significant impact on mopane trees. Well known for their episodic population outbreaks within mopane woodland, they often completely defoliate vast stands of trees (Ditlhogo 1996). Styles (1994), for example, found that in just six weeks, the mopane caterpillar population within his study area in northern South Africa consumed 9.4 times the amount of leaf material than the elephant population could have processed in a year. Clearly, these two species therefore not only both utilize mopane, but are also both capable of having a significant impact on the trees. It is thus to be expected that the feeding actions of one species should have a significant influence on the other.

A key difference between the two browsers is the type of damage they inflict upon mopane trees. While elephants utilise mostly branches and the main stems, thereby having a pruning effect on the trees (Smallie & O'Connor 2000), mopane caterpillars defoliate trees by removing just the leaf blades. While this differential use of plant parts might reduce direct competition between the two species, an indirect interaction may still result due to the different changes in plant morphology and chemistry known to occur after pruning and defoliation. In my study on mopane exposed to both simulated and natural elephant browsing and mopane caterpillar defoliation, plants were found to respond to pruning by producing longer shoots with larger leaves, while defoliation resulted in regrowth with shorter shoots and smaller leaves (see Chapter 3). These results were in accordance with numerous other studies on mammalian (Danell *et al*. 1994; Duncan *et al*. 1998; Bergström *et al*. 2000; Lehtilä *et al*. 2000) and insect herbivory (Gadd *et al*. 2001;

Anttonen *et al*. 2002; Piene *et al*. 2002). Unlike many woody plant species, however, the foliar nutritional value (measured as tannin/protein ratio and total polyphenolic content) was found not to change after pruning by elephant, yet increased after defoliation by mopane caterpillars.

Browsing behaviour of both mammals and insects is influenced by morphological and chemical plant characteristics (reviews by: Bryant *et al*. 1991; Coley & Barone 1996), so changes in these traits may have a significant impact on the subsequent feeding behaviour of each species. Pruning, for example, often improves the quality of browse for ungulates (du Toit *et al*. 1990), thereby attracting further browsing. Bergström *et al*. (2000) found that browsing by ungulates increased on previously clipped *Combretum apiculatum* trees and similarly, elephants tend to prefer mopane trees previously damaged by elephants, as the coppicing response provides a greater availability of their preferred branch size (Smallie & O'Connor 2000). Pruning also tends to increase the susceptibility of plants to insect herbivores, as regrowth often improves host suitability. Danell and Huss-Danell (1985), for example, found that the density of insect herbivores on moderately browsed birch trees was greater than on slightly browsed trees, due to the increase in leaf size and nitrogen content. Similarly, Martinsen *et al*. (1998) found an increase in leaf beetles on cottonwoods cut down by beavers, as coppice growth had a higher nutritional value and lower toughness. Pruning may, however, also have a negative influence on insect herbivory. For example, elk (*Cervus canadensis*) browsing on aspen (*Populus tremuloides*) was found to have a negative effect on the distribution and abundance of sawflies (*Phyllocolpa bozemanii*), due to a decrease in leaf size after browsing (Bailey & Whitham 2003).

In the absence of high elephant utilization of mopane trees, oviposition by mopane moths is primarily dependant upon tree size, with egg mass abundance increasing with increasing tree size (see Chapter 5). Elephant utilization, however, has the potential of significantly reducing tree size, and hence oviposition, as stem breakage can reduce a plants' biomass by 50-75% (Smallie & O'Connor 2000). On the other hand, pruning by elephants also results in a significant increase in leaf size and shoot length, which, according to other insect-host studies, may then have a positive influence on mopane moth oviposition. Similarly, caterpillar defoliation could have a negative influence on browsing by elephants through the resultant smaller shoot and leaf size (i.e. less biomass available) or alternatively, a positive influence due to the higher nutritional value of the leaves.

Unfortunately, it was beyond the scope of this project to look at the interaction between elephants and mopane caterpillars in both directions, and hence only the effect of elephants on mopane caterpillars was considered here. The aim of this study was therefore to investigate whether mopane caterpillars are influenced by elephants indirectly through their shared food resource, mopane. I tested for three alternative scenarios by which elephant impact on mopane trees could influence the oviposition behaviour of mopane moths: (1) a negative influence, due to reduced tree size; (2) no influence at all; (3) a positive influence, due to increased leaf size and nutritional value of resprouting mopane foliage.

6.2 Methods

The study was carried out within mopane woodland in the Shingwedzi area of the Kruger National Park, South Africa (see Chapter 2 for details).

In December 2003, when egg laying by mopane moths was complete and caterpillars were beginning to emerge (i.e. defoliation was still minimal), 14 transects of 50 x 5 m were set out within the mopane woodland surrounding Shingwedzi. Seven transects were situated in areas of heavy elephant utilization (HE), and the other seven were partners to these, in nearby areas of low elephant utilization (LE). Pairing of transects minimised the effects of spatial variability in rainfall and soil. HE transects were generally situated near man-made water holes and LE transects were chosen to resemble the corresponding HE areas (judged visually), in tree density and population structure (number and size of stems). While trees in the HE transects are also likely to have been more heavily utilised by other mammalian species (due to the close proximity to water), elephants would still have been largely responsible for any branch breakage, which is of primary concern here.

6.2.1 Area description

To quantitatively describe each area, the following information was recorded for all mopane trees within each transect: live tree height (m), basal stem diameter (cm), canopy width at the widest point (m), canopy height (m) and elephant utilization. An index of canopy volume was calculated for each tree as the volume of a cylinder, using canopy height and width values. For each transect, mean tree height, stem diameter and total canopy volume/ha were then determined. Tree density/ha was also calculated, by counting the total number of trees within the transect. Additionally, mature leaves were collected randomly from around the canopies of at least 5 trees per transect. Leaves from each transect were combined to assess the overall nutritional value of foliage in the area. Protein, tannin and total polyphenolic content was determined (see Chapter 3 for details), as these chemical characteristics commonly influence herbivory (Zucker 1983; Cooper & Owen-Smith 1985; Cooper *et al.* 1988; Coley & Barone 1996; Villalba *et al.* 2002).

Using data from the Venetia-Limpopo Nature Reserve (Venetia), where elephant impact on mopane is still relatively low (see Chapters 2 & 3), tree height and the diameter of the largest living stem per tree were found to be significantly correlated for mopane (Spearman-Rank, $P < 0.01$). The diameter of the largest stem may therefore be used as an indicator of a trees' potential height, without the negative effect of elephant utilisation. Hence, to assess whether LE and HE transect pairs would be similar in population structure (i.e. potential tree height), mean largest living stem diameters were compared.

6.2.2 Utilisation by elephants

The degree of elephant utilisation was measured for each tree as the proportion of canopy biomass removed by elephants, rated on the following seven point scale: 1 = 1-10%, 2 = 11-25%, 3 = 26-50%, 4 = 51-75%, 5 = 76-90%, 6 = 91-99%, 7 = 100% (Walker 1976). Utilization was categorised according to the type of damage, namely stem, branch or foliage, and the proportion of biomass removed was visually estimated from an imaginary intact plant. This was judged by the diameter of the broken stems/branches compared to those remaining, or the by the area of canopy without leaves. Additionally, the age of utilization was recorded, either as old, medium or new. New damage included that which occurred since the previous rainy season, and was characterised by the yellowish appearance of bark from freshly broken branches (Ben-Shahar 1993). Medium age damage was grey in colour with 'fairly young' coppiced branches around the damaged section (one to two years growth, estimated from personal observation after known age damage). Old damage was grey and weathered looking, with older coppiced branches.

To compare the degree of elephant utilization on trees, an index of utilization was calculated for each tree. Firstly, the accumulative impact was determined by adding the midpoints of relevant utilization classes (e.g. from medium and new browsing events; MacGregor & O'Connor 2004). Because canopy removal estimates were made according to the expected canopy volume at the time of browsing, accumulative values could exceed

100%. Therefore, to account for this, index values were calculated by giving the highest accumulative value a value of one, and all other values were worked out relative to this, on a scale of 0-1. Using these index values, the mean degree of elephant utilisation was calculated for each transect.

6.2.3 Oviposition by mopane moths

Within each transect, all trees with mopane egg masses from the current season were identified as host trees. Egg mass abundance per tree was recorded on a scale of 0-3, where 0 = 0 egg masses, 1 = 1 egg mass, 2 = 2 egg masses and 3 = 3 or more egg masses. Two measures of oviposition were calculated for each transect, firstly as the percentage of trees with egg masses (i.e. percentage of host trees) and secondly, as the number of egg masses/ha. Count estimates are expected to be fairly accurate, as most trees were small enough to search thoroughly and only 6 out of 69 trees had a score of 3.

To determine whether oviposition in an area is influenced by elephant utilization, the percentage of host trees and egg mass density in HE transects were compared to that in the corresponding LE transects. Then, to determine what elephant induced changes may influence oviposition behaviour, the percentage of host trees and egg mass density values were compared to the following descriptive variables for each transect: tree density (for all trees and only trees > 3 m), canopy volume/ha, mean shoot length, mean leaf length and mean leaf nutritional value (see Chapter 3 for data collection method details).

In Venetia, where elephant utilization was low, the number of egg masses per tree was positively related to tree size (Chapter 5). Therefore, the effect of tree size (which may be negatively affected by elephant utilization) on host preference was specifically investigated here too. Data from all 14 transects could not simply be combined, however, as the availability of tree sizes, and therefore host preference, could have varied between transects. Hence, transects were first made comparable by calculating relative size classes (see Fig. 6.1). To do so, the mean height of all trees within each transect was first determined (mean 1). All trees with a height above and below this mean value were then grouped separately, and the mean height of each of these two groups was calculated (mean 2 and 3). This resulted in three mean values, dividing tree height into four classes, namely: (a) small, (b) small-medium, (c) medium-large and (d) large. Canopy volume classes were calculated in the same way. To test for oviposition preference between classes, the total number of egg masses on trees within each height and canopy class was determined (for all transects combined) and compared to the number expected. Both tree height and canopy volume were used as measures of tree size, as even though one would expect the two to be autocorrelated, variability in canopy size tends to increase with tree size in mopane (see Appendix D). The expected number off egg masses was calculated both according to the number of trees within each canopy volume and height class, and the total canopy volume available within each canopy class.

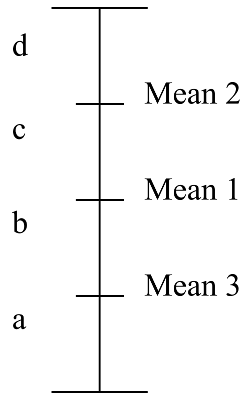

Figure 6.1 A graphic representation of how tree height and canopy volume classes (a-d) were calculated.

6.2.4 Statistical analyses

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 HE and LE areas.

Chi-squared goodness-of-fit tests were used to determine whether tree height or canopy volume classes were used disproportionately to their availability, both in terms of tree number and total canopy volume (Zar 1999). Where necessary, Bonferroni confidence intervals were used to determine which classes were preferred or avoided (Miller 1966; Neu *et al*. 1974; Byers & Steinhorst 1984).

6.3 Results

Designation of HE and LE areas was confirmed, as both the percentage of trees utilized by elephants, and the degree of elephant utilization per tree were higher in HE than LE areas (Table 6.1). In contrast, the percentage of trees with egg masses was significantly greater in LE transects, as was the egg mass density (Table 6.1, Fig. 6.2). There is therefore a negative association between mopane caterpillar abundance and elephant utilization of mopane trees within an area.

Total tree density did not differ between HE and LE areas, yet the density of tall trees (> 3 m) in LE areas was significantly greater than in HE areas. There was, however, no significant difference in the mean ‘largest stem diameter’. The reduced abundance of tall trees was therefore most likely due to elephant utilization, as the tree structure (tree height) of transect pairs was potentially the same. Similarly, the total canopy volume/ha was significantly greater in LE areas (Table 6.1).

Table 6.1 The mean ± SE values for variables describing areas of mopane woodland with high and low elephant impact, and the presence of mopane moth egg masses within these areas. The relationship between areas is also shown for each variable (Wilcoxon matched-pairs tests).

Variable	High elephant impact		Low elephant impact	*P* - value
Utilization				
% trees utilized by elephant	95.7 ± 1.58	>	60.6 ± 11.2	0.02*
Degree of elephant impact (index)	0.45 ± 0.06	>	0.16 ± 0.03	0.02*
% host trees (i.e. with eggs)	11.2 ± 2.77	<	22.9 ± 5.31	0.05*
Number of egg masses/ha	137 ± 35.8	<	440 ± 104	0.03*
Area description				
Largest stem diameter/tree (cm)	7.08 ± 1.09	=	7.09 ± 0.75	0.74
Total tree density/ha	982 ± 111	=	1411 ± 180	0.12
Density of trees > 3 m high	117 ± 37.9	<	394 ± 69.5	0.04*
Total canopy volume/ha (m^3)	7804 ± 797	<	14579 ± 2781	0.04*
Shoot length (cm)	115 ± 8.66	>	89.0 ± 12.6	0.04*
Leaf length (mm)	59.0 ± 1.47	=	56.6 ± 1.41	0.40
Tannin/protein ratio	0.48 ± 0.02	<	0.55 ± 0.02	0.02*
Total polyphenols (mg/g)	57.1 ± 1.69	=	59.3 ± 1.72	0.50

* Indicates significant differences at the 5% level

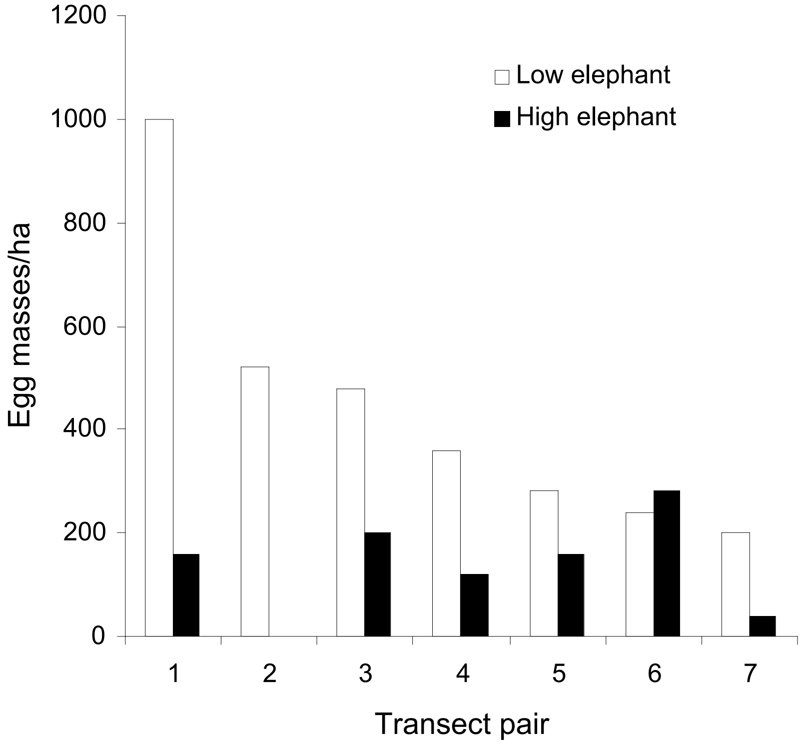

Figure 6.2 The density of mopane moth egg masses in areas of mopane woodland with high and low elephant impact (Wilcoxon matched-pairs test, $P < 0.05$).

As expected for pruned trees, shoot length was significantly longer in areas of high elephant utilization, yet unlike previous results (see Chapter 3), leaf length did not differ. Additionally, the total polyphenolic content of leaves was no different in HE and LE areas, yet the tannin:protein ratio was significantly lower in HE areas. This increase in foliar nutritional value with high levels of elephant impact also differs from results of my study in Venetia, where no change was observed (Chapter 3). The reduction in tannins and the lack of increase in leaf size is most likely an indication of the higher degree of stress in Kruger trees, which would have been subjected to elephant utilization for a more prolonged period compared to Venetia, where elephants were only reintroduced in 1991 after a minimal 50-year absence.

Considering only those variables that did differ between HE and LE transects, egg mass density was negatively related to shoot length and leaf nutritional value, yet was positively related to the density of tall trees and the total canopy volume/ha (Fig. 6.3). Elephant utilization therefore appears to have a negative impact on the density of mopane caterpillars in an area by reducing the number of tall trees and the total canopy volume/ha.

Similarly, based on tree number, ovipositing females were found to prefer the tallest trees and those trees with the largest canopy volume within an area, while shorter trees and trees with a smaller canopy volume were avoided (Table 6.2). When considering the actual resource availability within each canopy size class, however, no class was utilised more or less than expected in relation to its availability ($\chi^2 = 1.97$, df = 3, $P = 0.579$).

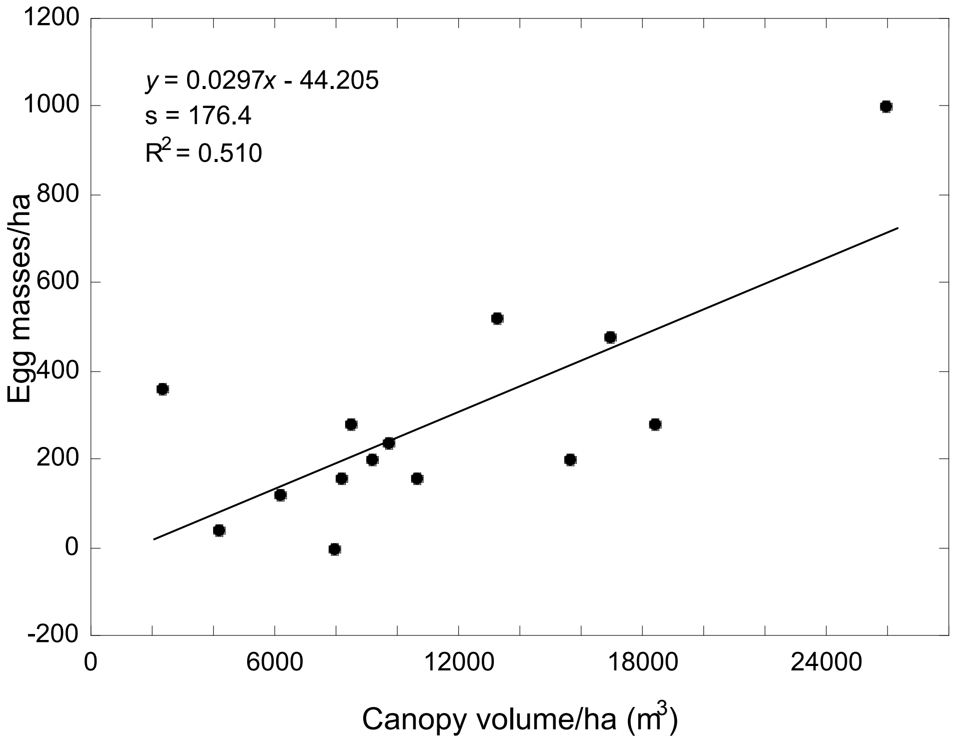

Figure 6.3 The relationship between the number of mopane moth egg masses/ha and mopane tree canopy volume/ha in mopane woodland ($F_{1,12} = 14.5$, $P < 0.01$, $R^2_{adj} = 0.510$).

Table 6.2 The selection of different size mopane trees by ovipositing mopane moth females, based on the number of trees within each size class and using canopy volume and tree height as two measures of tree size.

Class	Proportion of trees	Observed egg masses	Proportion of observed egg masses	Bonferroni intervals	Selection[#]
Canopy volume					
Small	0.437	9	0.090	$0.018<p<0.162$	-
Small-medium	0.269	17	0.170	$0.076<p<0.264$	-
Medium-large	0.173	30	0.300	$0.185<p<0.415$	+
Large	0.121	44	0.440	$0.316<p<0.564$	+
Tree height					
Small	0.283	6	0.060	$0.001<p<0.119$	-
Small-medium	0.296	13	0.130	$0.046<p<0.214$	-
Medium-large	0.234	15	0.150	$0.061<p<0.239$	0
Large	0.187	66	0.660	$0.542<p<0.778$	+

Symbols indicate classes used significantly more (+), less than (-), or equal to their availability (0), determined by Bonferroni confidence intervals.

6.4 Discussion

This study found that a high level of elephant utilization on mopane trees has a negative impact on the density of *Imbrasia belina* egg masses in an area, even though trees previously browsed by elephants had longer shoots and were of a higher nutritional value than unutilised trees. This negative relationship with leaf nutritional value found here may suggest that oviposition is influenced by leaf quality, yet results from previous work showed an opposite trend (Styles & Skinner 1996; Chapter 5), thereby indicating this not to be the case. A result that is consistent for all three studies, however, is the decrease in egg mass density with decreasing tall tree density (associated with high elephant impact). This therefore confirms tree size, measured both as tree height and canopy volume, to be the primary determining factor of mopane moth oviposition behaviour. When considering resource availability on larger trees versus egg abundance, however, no preference for larger trees was found. The greater utilization of large trees was therefore probably due to the greater chance of moths intercepting the larger bodies, rather than actual preference (but see discussion in Chapter 5).

The lack of preference for previously browsed plants is unlike results from many other studies on insect-mammal herbivore interactions, where plants tend to become more vulnerable to insect damage after pruning (Danell & Huss Danell 1985). Most previous studies have, however, only considered species that are likely to be dependant upon resource quality for larval performance, due to their feeding behaviour and relatively low population densities i.e. minimal resource competition. Densities of sap sucking (Schowalter & Ganio 1999; Ostrow *et al*. 2002) and galling (e.g. sawflies, Hjältén & Price 1996) species have, for example, been found to increase with increasing leaf/shoot size and/or nutritional value. Some studies on leaf-chewing species have also shown this trend, such as that by Martinsen *et al*. (1998) who found an increase in leaf beetle densities on cottonwoods previously felled by beavers. Where mopane moths differ to most other species studied, however, is that its' larvae are relatively immobile (confined to one or a few trees) and tend to reach outbreak proportions. During such outbreaks the population may become density dependent due to resource competition, thereby making resource quantity, rather than quality, the primary limiting factor for the species. Interestingly, Schowalter and Ganio (1999) found a similar trend of reduced defoliator insect numbers in recovering hurricane-damaged forest patches, which is likely to resemble elephant damage in its severity. The species of insect was not given, however, and unfortunately no other studies on the effect of pruning on an outbreak defoliator species could be found for comparative purposes.

According to Vance (1985), a number of possible mechanisms enable two competitors for one resource to coexist. These include: (1) the use of different body parts, (2) the use of different growing seasons and (3) spatial subdivision in the environment. Under 'normal' conditions, when elephant densities are not too high, elephants and mopane caterpillars fulfil all three of these criteria, and therefore display a degree of resource partitioning. Firstly, as already mentioned, the two species mostly utilize different plant parts. Mopane caterpillars feed only on the leaf blades and elephants feed mainly on branches (Smallie & O'Connor 2000). Secondly, the majority of branch breakage by elephants takes place in the dry season (Lewis 1986), while mopane caterpillar defoliation occurs in the summer. Elephants do also feed on leaves during this time, but the impact on individual trees is minimal compared to branch breakage. Finally, there is also a spatial separation in their use of mopane trees, both at the habitat and individual tree level. In Venetia, for example, mopane moths were found to prefer the tall riverine trees and egg masses were more abundant on tall trees (Chapter 5), while elephants preferred shorter trees of < 2 m (Smallie & O'Connor 2000) and therefore concentrated their feeding in the woodland or shrubland habitats. This minimal usage of large trees by elephants was even found in the relatively high elephant density areas of northern Botswana, as even though 43% of mopane trees were affected by elephants, the density of large trees remained largely unchanged (Ben-Shahar 1998).

The use of larger trees by elephants is, however, known to increase when smaller size classes are depleted (Lewis 1991). Such a situation could be episodic, in association with events such as fire, frost or drought (MacGregor & O'Connor 2002), which may cause high mortality of trees up to 3m in height (Chafota 1998). Alternatively, the severe impact on canopy trees could be in localised areas (Ben-Shahar 1993), caused by a high concentration of animals around permanent water sources (see Fig. 6.4), or due to elephant movements being restricted by physical barriers, such as game fencing (Cumming *et al.* 1997). Local population densities may also increase 'unnaturally' in open systems, in response to habitat loss due to an expanding human population and development (Ben-Shahar 1996). Increased utilization of tall trees by elephant, and the subsequent decline in the mopane caterpillar population, may therefore occur naturally, but has the potential to be greatly enhanced by mans' activities.

While no actual preference for large canopied trees was detected, the direct relationship between egg mass number and tree height would mean that the larger the tree felled by an elephant, the greater the impact on the mopane caterpillar population. The felling of a tall tree would not only have an immediate effect on resource availability for mopane caterpillars, but also a long term effect, as felled trees tend to be continuously browsing by elephants (Smallie & O'Connor 2000), keeping their height suppressed (termed 'hedging', Styles 1993). Additionally, hedging could have a long-term impact on tree density (and hence resource availability) by preventing the recruitment of trees into the larger, reproductive size classes (see Chapter 4), and through increased tree mortality

Figure 6.4 Mopane woodland heavily impacted by elephants, resulting in a double-tiered woodland structure consisting of tall, intact trees and coppicing damaged trees (the photo was taken in Chobe National Park, Botswana).

from the continual browsing pressure. Any negative impact of elephant utilization on tree height could therefore affect mopane caterpillar abundance indirectly in many ways, for long periods of time.

According to Bailey and Whitham (2003), the interaction between common and/or keystone species is likely to result in community-wide consequences. In their study, they showed how browsing by elk had a negative affect on the distribution and abundance of sawflies, which resulted in up to a 33% reduction in the arthropod community associated with sawflies. Additionally, browsing had a negative impact on bird foraging on galls, by altering the density of their prey. Beavers, considered as a keystone species, have also been found to affect the distribution of a common leaf-feeding beetle, which in turn affects the diversity of other taxa (Martinsen *et al*. 1998). Likewise, *Imbrasia belina* are also preyed upon by a diverse array of species. Pupae are readily dug up by jackals (*Canis mesomelas*), bat-eared foxes (*Otocyon megalotis*), warthogs (*Phacochoerus aethiopicus*) and aardvarks (*Orycteropus afer*), for example, while, larvae are eaten by mammals (mainly baboons, *Papio ursinus* and vervet monkeys, *Cercopithecus aethiops*), birds (34 species were documented by Styles 1995), and invertebrates (e.g. spiders, ants, and mantids; Styles & Skinner 1996). Moths are also taken by birds and spiders, as well as by bats while active at night (Hill & Smith 1984). The negative impact of elephants on *I. belina* could therefore also have an indirect effect on a great diversity of species from different trophic levels.

One species in particular likely to be affected by any decrease in the mopane caterpillar population, is man. The larvae forms an important food source for rural communities by providing a vital source of protein (65% of dry mass), especially during lean periods. Harvested in large numbers, it has become an important trading commodity.

In Botswana, for example, the mopane industry earns the country an estimated R46 million annually (Potgieter *et al.* 2001).

In conclusion, elephants and mopane caterpillars usually display resource partitioning within mopane woodland, yet under conditions of high elephant impact, mopane caterpillar abundance decreases. These two members of the mopane browsing guild do therefore interact indirectly through their shared resource. The negative effect of elephant utilization on mopane caterpillar abundance appears to operate through the decrease in density of tall mopane trees. This association raises implications for the conservation of mopane caterpillars as a protein source for rural people, as any factor increasing elephant impacts on mopane trees (e.g. fences and waterholes) will also influence mopane caterpillar abundance, and also probably the subsequent biodiversity in the area.

6.5 References

ANTTONEN, S., PIISPANEN, R., OVASKA, J., MUTIKAINEN, P., SARANPÄÄ, P. & VAPAAVUORI, E. 2002. Effects of defoliation on growth, biomass allocation, and wood properties of *Betula pendula* clones grown at different nutrient levels. *Canadian Journal of Forestry Research* **32**:498-508.

BAILEY, J.K. & WHITHAM, T.G. 2003. Interactions among elk, aspen, galling sawflies and insectivorous birds. *Oikos* **101**:127-134.

BEN-SHAHAR, R. 1993. Patterns of elephant damage to vegetation in northern Botswana. *Biological Conservation* **65**:249-256.

BEN-SHAHAR, R. 1996. Do elephants over-utilize mopane woodlands in northern Botswana? *Journal of Tropical Ecology* **12**:505-515.

BEN-SHAHAR, R. 1998. Changes in structure of savanna woodlands in northern Botswana following the impacts of elephants and fire. *Plant Ecology* **136**:189-194.

BERGSTRÖM, R., SKARPE, C. & DANELL, K. 2000. Plant responses and herbivory following simulated browsing and stem cutting of *Combretum apiculatum*. *Journal of Vegetation Science* **11**:409-414.

BROWN, J.H. & DAVIDSON, D.W. 1977. Competition between seed-eating rodents and ants in desert ecosystems. *Science* **196**:880-882.

BRYANT, J.P., PROVENZA, F.D., PASTOR, J., REICHARDT, P.B., CLAUSEN, T.P. & DU TOIT, J.T. 1991. Interactions between woody plants and browsing mammals mediated by secondary metabolites. *Annual Review of Ecology and Systematics* **22**:431-446.

BYERS, C.R. & STEINHORST, R.K. 1984. Clarification of a technique for analysis of utilization-availability data. *Journal of Wildlife Management* **48**:1050- 1053.

CAUGHLEY, G.C. 1976. The elephant problem: an alternative hypothesis. *East African Wildlife Journal* **14**:265-283.

CHAFOTA, J. 1998. Effects of changes in elephant densities on the environment and other species – How much do we know? *Cooperative Regional Wildlife Management in Southern Africa*.

COLEY, P.D. & BARONE, J.A. 1996. Herbivory and plant defenses in tropical forests. *Annual Review of Ecology and Systematics* **27**:305-335.

COOPER, M. & OWEN-SMITH, N. 1985. Condensed tannins deter feeding by browsing ruminants in a South African savanna. *Oecologia* **67**:142-146.

COOPER, S.M., OWEN-SMITH, N. & BRYANT, J.P. 1988. Foliage acceptability to browsing ruminants in relation to seasonal changes in the leaf chemistry of woody plants in a South African savanna. *Oecologia* **75**:336-342.

CUMMING, D.H.M., FENTON, M.B., RAUTENBACK, I.L., TAYLOR, R.D., CUMMING, G.S., CUMMING, M.S., DUNLOP, J.M., FORD, A.G., HOVORKA, M.D., JOHNSON, D.S., KALCOUNIS, M., MAHLANGU, Z. & PORTFORS, C.V.R. 1997. Elephants, woodlands and biodiversity in Southern Africa. *South African Journal of Science* **93**:231-236.

DANELL, K. & HUSS-DANELL, K. 1985. Feeding by insects and hares on birches earlier affected by moose browsing. *Oikos* **44**:75-81.

DANELL, K., BERGSTRÖM, R. & EDENIUS, L. 1994. Effects of large mammalian browsers on architecture, biomass, and nutrients of woody plants. *Journal of Mammalogy* **75**:833-844.

DAVIDSON, D.W., INOUYE, R.S. & BROWN, J.H. 1984. Granivory in a desert ecosystem: experimental evidence for indirect facilitation of ants by rodents. *Ecology* **65**:1780-1786.

DITLHOGO, M.K. 1996. Information on the biology and use of *Imbrasia belina*, and other edible moth species. Unpublished Ph.D. thesis, University of Manitoba, Winnipeg, Canada.

DUNCAN, A.J., HARTLEY, S.E. & IASON, G.R. 1998. The effects of previous browsing damage on the morphology and chemical composition of Sitka spruce (*Picea sitchensis*) saplings and their subsequent susceptibility to browsing by red deer (*Cervus elaphus*). *Forest Ecology and Management* **103**:57-67.

DU TOIT, J.T., J.P. BRYANT & FRISBY, K. 1990. Regrowth and palatability of *Acacia* shoots following pruning by African savanna Browsers. *Ecology* **71**:149-154.

GADD, M.E., YOUNG, T.P. & PALMER, T.M. 2001. Effects of simulated shoot and leaf herbivory on vegetative growth and plant defense in *Acacia drepanolobium*. *Oikos* **92**:515-521.

HILL, J.E. & SMITH, J.D. 1984. *Bats. A natural history*. British Museum (Natural History), London.

HJÄLTÉN, J. & PRICE, P.W. 1996. The effect of pruning on willow growth and sawfly population densities. *Oikos* **77**:549-555.

LEHTILÄ, K., HAUKIOJA, E., KAITANIEMI, P. & LAINE, K.A. 2000. Allocation of resources within mountain birch canopy after simulated winter browsing. *Oikos* **90**:160-170.

LEWIS, D.M. 1986. Disturbance effects on elephant feeding: evidence for compression in Luangwa Valley, Zambia. *African Journal of Ecology* **24**:227-241.

LEWIS, D.M. 1991. Observations of tree growth, woodland structure and elephant damage on *Colophospermum mopane* in Luangwa Valley, Zambia. *African Journal of Ecology* **29**:207-221.

MACGREGOR, S.D. & O'CONNOR, T. 2002. Patch dieback of *Colophospermum mopane* in a dysfunctional semi-arid savanna. *Austral Ecology* **27**:385-395.

MACGREGOR, S.D. & O'CONNOR, T. 2004. Response of *Acacia tortilis* to utilization by elephants in a semi-arid African savanna. *South African Journal of Wildlife Research* **34**:55-66.

MARTINSEN, G.D., DRIEBE, E.M. & WHITHAM, T.G. 1998. Indirect interactions mediated by changing plant chemistry: beaver browsing benefits beetles. *Ecology* **79**:192-200.

MILLER, R.G. 1966. *Simultaneous statistical inferences*. McGraw-Hill, New York.

NEU, C.W., BYERS, C.R. & PEEK, J.M. 1974. A technique for analysis of utilization-availability data. *Journal of Wildlife Management* **38**:541-545.

OSTROW, D.G., HUNTLEY, N. & INOUYE, R.S. 2002. Plant-mediated interactions between the northern pocket gopher, *Thomomys talpoides*, and aboveground herbivorous insects. *Journal of Mammalogy* **83**:991-998.

PIENE, H., MACLEAN, D.A. & LANDRY, M. 2002. Spruce budworm defoliation and growth loss in young balsam fir: relationships between volume growth and foliage weight in spaced and unspaced, defoliated and protected stands. *Forest Ecology and Management* **6113**:1-17.

POTGIETER, M., MADZIBANE, J., MASHABANE, L. & WESSELS, D. 2001. Mopane-veld. Can we afford to loose this valuable veld type? *Veld and Flora* **June**: 78-79.

SCHOWALTER, T.D. & GANIO, L.M. 1999. Invertebrate communities in a tropical forest canopy in Puerto Rico following Hurricane Hugo. *Ecological Entomology* **24**:191-201.

SMALLIE, J.J. & O'CONNOR, T.G. 2000. Elephant utilization of *Colophospermum mopane*: possible benefits of hedging. *African Journal of Ecology* **38**:352-359.

STYLES, C.V. 1993. Relationships between herbivores and *Colophospermum mopane* of the Northern Tuli Game Reserve, Botswana. MSc thesis, University of Pretoria, Pretoria.

STYLES, C.V. 1994. Mopane worms: more important than elephants? *Farmer's Weekly* **July 29**:14-16.

STYLES, C.V. 1995. Notes on the bird species observed feeding on mopane worms. *Birding in South Africa* **47**:53-54.

STYLES, C.V. & SKINNER, J.D. 1996. Possible factors contributing to the exclusion of saturniid caterpillars (mopane worms) from a protected area in Botswana. *African Journal of Ecology* **34**:276-283.

TIMBERLAKE, J.R. 1995. *Colophospermum mopane*: Annotated bibliography and review. *The Zimbabwe bulletin of forestry research*, *no. 11.* Forestry Commission, Harare, Zimbabwe.

VANCE, R.R. 1985. The Stable coexistence of two competitors for one resource. *The American Naturalist* **126**:72-86.

VILLALBA, J.J., PROVENZA, F.D. & BRYANT, J.P. 2002. Consequences of the interaction between nutrients and plant secondary metabolites on herbivore selectivity: benefits or detriments for plants? *Oikos* **97**:282-292.

WALKER, B.H. 1976. An approach to the monitoring of changes in the composition and utilization of woodland and savanna vegetation. *South African Journal of Wildlife Research* **6**:1-32.

ZAR, J.H. 1999. *Biostatistical Analysis*, 4th edn**.** Prentice-Hall, Englewood Cliffs, New York.

ZUCKER, W.V. 1983. Tannins: Does structure determine function? An ecological perspective. *The American Naturalist* **121**:335-365.