CHAPTER 3

DIFFERENTIAL EFFECTS OF DEFOLIATION BY MOPANE CATERPILLARS AND PRUNING BY AFRICAN ELEPHANTS ON THE REGROWTH OF *COLOPHOSPERMUM MOPANE* FOLIAGE

3.1 Introduction

Plant responses to herbivory depend on the timing, type and extent of damage, the availability of resources in the environment to support regrowth, and the herbivory history of the plant (Maschinski & Whitham 1989; Paige 1992; Hawkes & Sullivan 2001; Wise & Abrahamson 2005). All responses are attempts by plant species to maximise occupancy of as many sites in the ecosystem with as much biomass as possible for as much time as possible and to achieve this, trade-offs in investments often need to be made (e.g. resprouting versus seeding; Bellingham & Sparrow 2000). In the face of herbivory, for example, trade-offs between different kinds of plant resource allocation occur, such as between resistance (the ability to reduce or prevent further herbivory) and tolerance (the ability to minimise losses in fitness following herbivory; Herms & Mattson 1992; Strauss & Agrawal 1999; Agrawal 2000; Messina *et al*. 2002). This differential allocation of resources affects shoot regrowth morphology and/or chemistry that then may, in turn, influence subsequent herbivory (Strauss 1991; Danell *et al*. 1994).

A key factor determining a plant's response to browsing is the type of damage inflicted, namely, shoot/branch/stem damage by mammalian browsers (hereafter referred to as 'pruning'), versus leaf consumption by folivorous insects (hereafter referred to as 'defoliation'). Studies have shown pruning and defoliation to affect plant responses quite differently, as pruning tends to result in an increase in the growth rate of the remaining or resprouting shoots (Messina *et al*. 2002) and the production of fewer but longer shoots with larger leaves (Danell *et al*. 1994; Duncan *et al*. 1998; Bergström *et al*. 2000; Lehtilä *et al*. 2000), while defoliation tends to result in regrowth with smaller shoots and leaves and an increase in leaf density (Gadd *et al*. 2001; Anttonen *et al*. 2002; Piene *et al*. 2002). Additionally, changes in foliar chemical composition may occur and although some studies have shown that leaves often become less chemically defended after mammalian browsing (du Toit *et al*. 1990), in general the responses to defoliation are variable (as found by Bryant *et al*. 1991 after manual defoliation of six southern African woody species). The variability in responses therefore suggests that plants have adapted different 'strategies' with which to deal with each type of browsing, and many theories attempt to explain these responses. Proposed hypotheses are not necessarily mutually incompatible, however, as while the resource availability hypothesis (RAH) is based on the premise that regrowth is related to the quantity of nutrient reserves in the plant (Coley *et al*. 1985), for example, the sink-source hypothesis (SSH) explains how sink/source relationships determine resource allocation among organs, with sink strength determining the degree of resource accumulation (Honkanen & Haukioja 1994; Stowe *et al*. 2000).

Despite the numerous studies on plant responses to herbivory, the true comparative effect of defoliation versus pruning is, however, not yet fully understood, as even though much work has looked at the effects of intensity, frequency and timing of pruning and defoliation (Lennartsson *et al*. 1998), few studies have made comparisons within an individual tree species. Consequently, results would not vary due to damage type alone but also due to other factors, such as plant functional type (e.g. deciduous versus evergreen; Krause & Raffa 1996). By considering just a single species, we could therefore significantly improve our understanding of the differential effect each browsing type has, and *Colophospermum mopane* (commonly know as 'mopane', see details in Chapter 2) provides the opportunity to carry out such an investigation in a natural system.

This deciduous, xeric savanna woodland species dominates over vast areas of land in southern Africa and is browsed upon by two key species, namely mopane caterpillars (*Imbrasia belina*) and African elephants (*Loxodonta africana*).

Despite its chemical defences, mopane is selected by elephants and can form the dominant constituent of their diet within certain areas (Lewis 1991; Smallie & O'Connor 2000), thereby making woodlands dominated by mopane susceptible to elephant induced damage (Ben-Shahar 1993). Smallie and O'Connor (2000) found that for shrub-height trees, the preferred tree size by elephants, utilization was mainly of branches, foliage and the main stem, while bark utilization was mainly from trees > 4 m high. Elephants therefore have a pruning effect on mopane trees and even though, on average, individual mopane trees are only lightly utilized, stem breakage can result in the loss of 51 –75% of above-ground biomass, and the occurrence of such utilization is known to increase under conditions of limited resources (caused by drought, high elephant densities etc.). Additionally, elephants have a preference for trees previously utilised by them, which have a greater availability of the preferred branch size due to damage-induced coppicing (Smallie & O'Connor 2000). The breakage of branches and stems, together with the continuous browsing of the same trees (hedging), can therefore have a significant impact on mopane trees.

Similarly, mopane caterpillars are well known for their impact on mopane trees, as they tend to experience population outbreaks within mopane woodland, resulting in large stands of trees being completely defoliated. Additionally, while population numbers may vary quite considerably from year to year, under favourable conditions (sufficient rainfall etc.) two brood sessions can take place within one wet season, firstly in November/December and again in February/March. Trees may hence undergo complete defoliation twice within a single growing season and this accumulative effect of defoliation events (Strauss 1991; Kaitaniemi *et al*. 1999), together with the differential timing of leaf herbivory (Tiffin 2002), is expected to have a significant effect on mopane regrowth responses.

Apart from an improved understanding of plant-herbivore interactions, determining the differential influence of defoliation and pruning on mopane regrowth responses will also enable an investigation into how this megaherbivore and insect may interact through their shared resource, a novel approach for intraguild studies. The aim of this study was therefore to investigate the comparative effects of pruning by elephants and defoliation by mopane caterpillars on mopane trees (i.e. the effect of the different nature and timing of damage), by addressing the following main questions: (1) Are there quantitative differences (structural and chemical) in the regrowth of mopane following caterpillar defoliation versus elephant pruning? (2) Does timing of caterpillar defoliation (early versus late season) affect regrowth? (3) Does the frequency of caterpillar defoliation (once versus twice) affect regrowth? (4) Does the first flush of regrowth after caterpillar defoliation and elephant pruning differ to the second flush i.e. the following season?

3.2 Methods

The study was initiated in August 2002 and continued until March 2004 in the Venetia-Limpopo Nature Reserve (refer to Chapter 2 for details).

3.2.1 Treatment transects

Six 80 m transects were set out within a flat and uniform area of mopane woodland, with a mean tree height of 2.17 m (sd. = 0.637, n = 144). Three transects were on each side of the road, positioned parallel, perpendicular and at 45° to the road. Along each transect, a tree was marked every 20 m with a metal tag nailed into its base (5 trees per transect i.e. n = 30). Around each marked tree, six additional trees, positioned roughly 60° apart and 2 – 8 m away from the central tree, were marked. Trees of similar size and with minimal elephant utilization were chosen. This orderly layout of experimental trees was necessary to ensure they could be found again in the dense, homogenous mopane woodland.

To test the comparability of transects, soil samples were collected from five points along each transect (i.e. at each tree group). Samples were taken from the top 10 cm of soil and air-dried in brown paper bags. Analyses were carried out to determine the water pH and soil P, Ca, K, Mg, Na and N content (according to the methodology stated by The Non-Affiliated Soil Analysis Work Committee 1990). Mineral results were expressed in mg/kg.

In August 2002, at the time of year when utilization of woody plant parts by elephants is highest (Lewis 1986), one tree from each tree group was subjected to simulated elephant browsing. Stems and branches were broken off at 1 – 1.5 m (the preferred browsing height of elephants; Smallie & O'Connor 2000), until about 75% of the original biomass was removed (estimated visually). In August 2003 the same treatment was applied to a second tree in each group.

To simulate the two successive mopane caterpillar defoliation events, one tree in each group was artificially defoliated in November 2002; one in February 2003; one in November 2002 and again in February 2003 and one in November 2003. Trees were at least 90% defoliated, by removing the entire leaf lamina by hand while taking care to leave behind the leaf petiole, to best mimic true caterpillar defoliation. The seventh tree in each group was left as a control. Treatments are hereafter referred to as follows: (1) Elephant 2002 = E'02, (2) Elephant 2003 = E'03, (3) Caterpillar November 2002 =

CN’02, (4) Caterpillar February 2003 = CF’03, (5) Caterpillar November 2002 and February 2003 = CN&F, (6) Caterpillar November 2003 = CN’03 and (7) Control = Con.

The validity of using simulated herbivory to mimic natural damage has been questioned in recent years (Baldwin 1990; Tiffin & Inouye 2000). Hjältén (2004) summarises the problems and possibilities of simulated herbivory and concludes, however, that mechanical damage is acceptable in the following circumstances: (1) when used to evaluate the direct effects of herbivory on basic plant processes such as growth, reproduction and general physiological responses (e.g. plant allocation to secondary compounds and changes in nutrient concentrations); and (2) for insect herbivores that inflict well-defined damage to plants that is easy to mimic with accuracy (e.g. external leaf-feeding insects). This study fulfils both these requirements and simulated herbivory was therefore expected to provide reliable results. Additionally, simulated herbivory has a number of advantages over natural herbivory, namely: the ability to control the magnitude and timing of damage, and avoiding any bias resulting from biotic and abiotic affects.

There are, however, still three main problems with simulated herbivory that may influence the results of this study. First, is the length of time over which the damage is inflicted. Mechanical defoliation took a maximum of two hours per tree, while naturally it would be a continuous process over about three weeks. Secondly, some insect herbivores have been found to alter plant physiology by injecting salival components while feeding (Alborn & Turlings 1997; McCloud & Baldwin 1997). This has also been found for mammalian browsers, such as moose (Bergman 2002) and goats (Rooke 2003). Lastly, urine and faeces of mammals and insects can have a strong effect on soil processes (nutrient recycling), which can then influence plant communities (Hobbs 1996; Reynolds & Hunter 2001).

3.2.2 Natural mopane caterpillar and elephant browsing

To check the reliability of the simulation results, for reasons outlined above, the effects of natural elephant and mopane caterpillar browsing were also assessed. In January 2004, when an outbreak of mopane caterpillars had just taken place, three transects were set out within defoliated areas. Along each transect, five defoliated trees were marked and for each of these, the nearest non-defoliated mopane tree of similar size was marked as the trees' partner (total n = 15 for each 'utilization'). An area with a high degree of elephant utilization was also identified and 13 elephant-utilized trees were marked, along with 13 non-utilized 'partners'.

3.2.3 Measuring regrowth

In November 2003, an outbreak of puss moth caterpillars (Family: Notodontidae, Order: *Epicerura*; Picker *et al*. 2002) defoliated most trees along three of the six transects. These transects were therefore excluded from the experiment, reducing the sample size of each treatment to 15 trees.

In February 2004 trees were revisited and the following information on the regrowth was recorded: leaf size, shoot length, shoot density and foliar nutritional value. Leaf length was used as an indicator of leaf size (as leaf length and width are correlated, see Appendix A), measured (in mm) from the growth point to the tip of the right leaflet. Fifteen mature undamaged leaves were measured for each tree and were chosen randomly from all sides of the canopy, between a height of 0.5 – 2 m. The length of the current years growth (which was clearly identifiable) was measured for 15 shoots per tree (to the nearest cm), chosen randomly from pruned and unpruned parts of the tree. Shoot density was measured as the number of shoots on the terminal 50 cm of a branch, for five branches per tree.

To determine foliar chemical composition, mature leaves were collected randomly from around the canopy of each tree. A detailed chemical analysis of secondary metabolites was not in the scope of this project, especially seeing as mopane is well known for its complex chemical make-up (Ferreira *et al*. 2003). Secondary metabolites such as tannin, that accumulate in high concentrations and are often stable end products, are most likely to be directly correlated with total allocation to secondary metabolites (Herms & Mattson 1992). Total polyphenolic and condensed tannin content were therefore determined, together with the protein (N) content.

Leaves were first air dried in brown paper bags and later oven dried at 50°C for at least four days. Samples were then milled through a 1mm screen. The crude protein content was determined according to an AOAC (2000) method, namely the Dumas method. Total phenols and condensed tannins were analysed in accordance with Hagerman (1995). Total phenols were quantified using the Prussian blue assay for total phenols and condensed tannins were assayed using the Acid butanol method for proanthocyanidins. Dried leaf material weighing about 0.05 g 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. A 0.1 ml aliquot of the supernatant was used in both assays. *Sorghum* tannin that was previously extracted and purified as described in Hagerman (1995) was used as the condensed tannin standard while Gallic acid was used to standardize total phenols. Quantities were calculated as mg/gDW (dry weight).

I appreciate that chemical composition values obtained in this study are not absolute leaf concentrations, as these were not possible to obtain with the field methods used. Samples should ideally have been freeze dried in dry ice soon after collection instead of being air dried, for example, but this was not possible due to the long period of time spent in the field. Values were, however, used only as relative measures for comparative purposes within the study, and are therefore suitable for this purpose.

To investigate the effect of treatment on seasonal leaf carriage, trees were inspected in June and August 2003 for leaf retention into the dry season and in October and November 2003 for the timing of leaf flush. Trees were given a leaf carriage score (LCS) where: LCS = 0 means no leaves, LCS = 1 means 1-10% of full leaf carriage, LCS = 2 means 11-40% of full carriage, LCS = 3 means 41-70% of full leaf carriage, and LCS = 4 means 71-100% of full leaf carriage. This leaf score was then subdivided into the phenological states of the leaves, using the same scoring system (Smit 1994). Leaf phenological states were classified as: (i) newly formed leaf buds (LB), (ii) immature green leaves (IL), (iii) mature green leaves (ML), (iv) yellowing, senescing leaves (YL), and (v) dry, senescing leaves retained on the tree (DL). For example, a tree could have a total LCS = 3, consisting of 80% IL (LCS = 4) and 20% ML (LCS = 2).

In March 2004, once the regrowth on the naturally defoliated trees had stopped growing (see Appendix B, Fig. B.1), all control and utilised trees (elephant and caterpillar) were revisited and information on the current years growth recorded. Leaf size, shoot length and shoot density were measured as described above. Leaf samples were also collected for chemical analysis.

3.2.4 Statistical analysis

For simulated treatments, I first tested whether there was significant variation in the regrowth (shoot length, leaf length, shoot number/50cm, and foliar tannin: protein ratio and polyphenolic content) and soil characteristics across the three transects, using one-way ANOVAs and Kruskal-Wallis ANOVAs. Then, due to the data not being normally distributed, Kruskal-Wallis ANOVAs were used to test for differences between the seven treatments, for each variable individually. Where results were significant, multiple comparison tests were used to determine which treatments were different.

Data from the naturally utilised trees were also not normally distributed, so Wilcoxon matched-pairs tests were used to test for differences between the regrowth on elephant-utilized trees and control trees, and between caterpillar defoliated trees and control trees (Zar 1999). All statistical analyses were conducted using STATISTICA (Statsoft 1991).

3.3 Results

3.3.1 Simulated treatments

There was no significant variation across the three treatment transects with respect to any of the regrowth characteristics or soil properties, except the soil Mg content (see Appendix C for soil details). It was therefore assumed that no 'transect' effect was influencing the regrowth of the trees and trees from all three transects were then grouped for analyses.

Simulated treatments had a significant effect on shoot length ($\chi^2 = 42.0$, df = 6, $P < 0.01$) and leaf length ($\chi^2 = 28.4$, df = 6, $P < 0.01$). Shoots were generally longer on pruned trees than defoliated trees (Fig. 3.1a). Trees flushing for the first time since pruning (E'03 trees) produced shoots significantly longer (mean ± SE: 15.8 ± 0.693 cm) than pruned trees flushing for the second time (E'02 trees; 11.1 ± 1.04 cm), whose shoots were not significantly longer than control tree shoots (6.99 ± 0.221 cm). Shoots on most defoliated trees (but not CN'03 trees) were significantly shorter than shoots on pruned trees, but not control trees. Although not significantly different, trees defoliated in February tended to have slightly shorter shoots than trees defoliated in November (5.23 ±

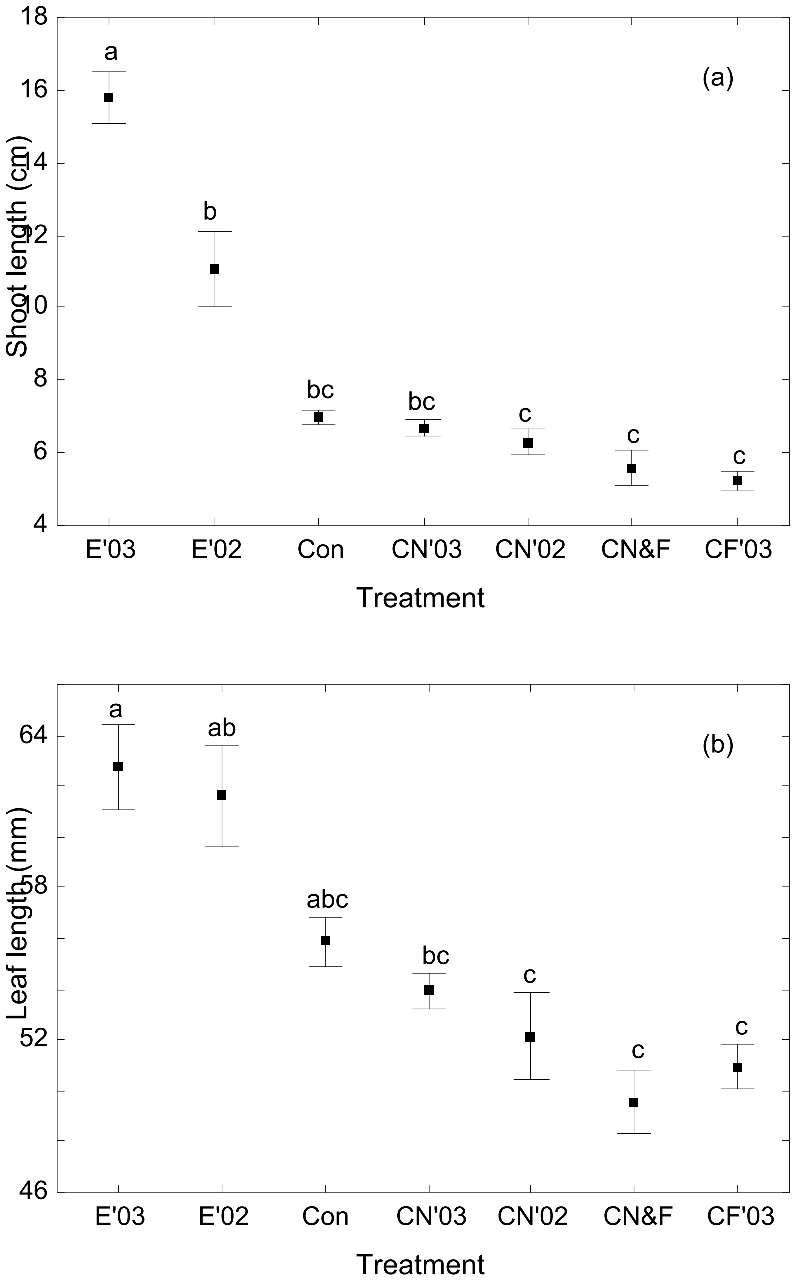

Figure 3.1 A comparison of the effects of various elephant pruning and caterpillar defoliation treatments on (a) mean (± SE) shoot length and (b) leaf size of mopane regrowth. Unlike letters (a, b and c) indicate significant differences. Treatments included: simulated elephant pruning in August 2002 (E'02) and August 2003 (E'03), controls (Con), and simulated caterpillar defoliation in November 2002 (CN'02), February 2003 (CF'03), November 2002 and February 2003 (CN&F), and November 2003 (CN'03).

0.270 and 5.57 ± 0.485 cm versus 6.30 ± 0.350 and 6.67 ± 0.223 cm). Similarly, leaves on pruned trees were significantly longer than leaves on defoliated trees, except for CN’03 trees (Fig. 3.1b, pruned: E’03 = 62.8 ± 1.67 and E’02 = 61.6 ± 1.98 mm versus defoliated: CN’02 = 52.1 ± 1.70, CN&F = 49.5 C 1.27 and CF’03 = 50.9 ± 0.875 mm). As with shoot length, leaves on trees defoliated in February tended to be smallest. Late season defoliation therefore appears to have the greatest negative impact on regrowth in mopane.

Shoot number did tend to be greater after defoliation treatments than pruning treatments ($\chi^2 = 12.2$, df = 6, $P = 0.057$; the two extreme measures being: CN = 14.45 ± 0.67 and ET = 11.60 ± 0.48) and even though this difference was not quite significant at the 5% level, it is still considered a real trend (see Stewart-Oaten 1995). There was, however, no difference in the tannin:protein ratio or total polyphenolic content of the foliage ($\chi^2 = 3.59$, df = 6, $P = 0.732$; $\chi^2 = 2.00$, df = 6, $P = 0.92$ respectively).

Browsing treatment appeared to affect leaf carriage in a number of ways. Firstly, trees defoliated in February had a very low total leaf carriage in June and August (Fig. 3.2), indicating they were unable to flush again before the onset of the dry season. Pruned trees, however, tended to have a greater leaf carriage later into the dry season (August), suggesting that pruning aids leaf retention in remaining foliage. Secondly, all defoliation treatments resulted in trees producing leaf buds earlier in the growing season than control and pruned trees (October). By November, trees from all treatments had flushed nearly 100%, with roughly half of the buds already having grown into immature leaves.

3.3.2 Naturally browsed trees

Regrowth on trees naturally damaged by elephants was similar to the simulated treatment trees. Shoots and leaves were significantly longer than on control trees (Wilcoxon

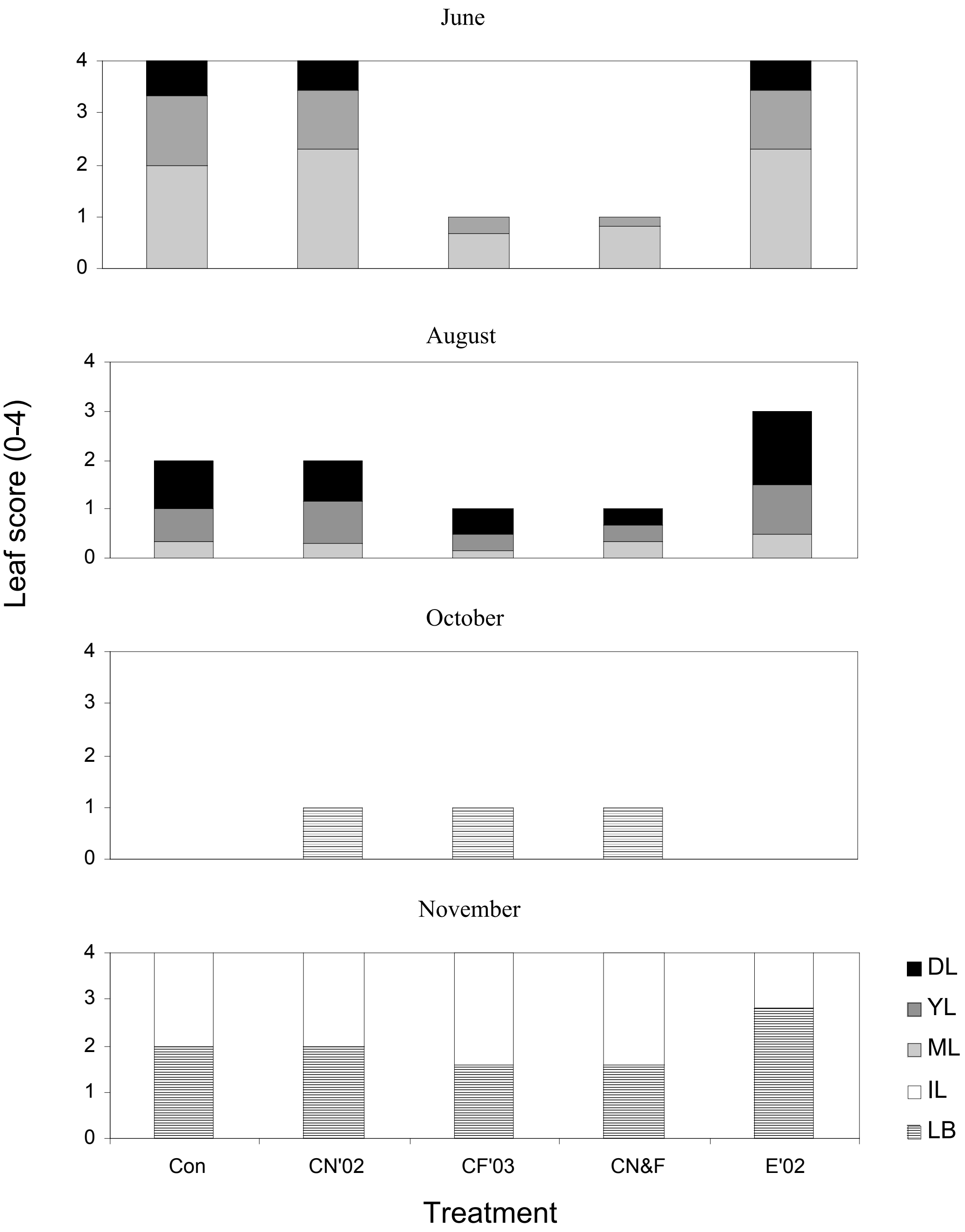

Figure 3.2 Seasonal leaf carriage of mopane trees after simulated caterpillar and elephant utilization treatments (refer to in Fig. 3.1 for treatment code details and the text for score details). DL = dead leaves, YL = yellow leaves, ML = mature leaves, IL = immature leaves, LB = leaf buds.

matched-pairs test: $P < 0.01$; shoots: 18.2 ± 1.34 versus 7.03 ± 0.341 cm; leaves: 62.6 ± 1.65 versus 49.6 ± 1.07 mm), while there was no difference in the number of shoots/50 cm length of branch ($P = 0.859$), nor in the tannin:protein ratio and total polyphenolic content of the foliage ($P = 0.507$, $P = 0.249$ respectively; Fig. 3.3).

Natural caterpillar defoliation, however, had a greater effect on plant responses than simulated defoliation. Both shoot and leaf lengths were significantly shorter on previously defoliated trees than control trees (Wilcoxon matched-pairs test: $P < 0.01$; shoots: 3.70 ± 0.135 versus 7.15 ± 0.231 cm; leaves: 45.4 ± 1.36 versus 57.3 ± 1.79 mm) and foliar tannin:protein ratio and total polyphenolic content were significantly reduced (tannin:protein ratio: 0.348 ± 0.027 versus 0.443 ± 0.027; polyphenols: 52.4 ± 3.67 versus 63.9 ± 3.39 mg/gDW; Wilcoxon matched-pairs test: $P < 0.05$; Fig. 3.3). Only shoot density was unaffected ($P = 0.211$).

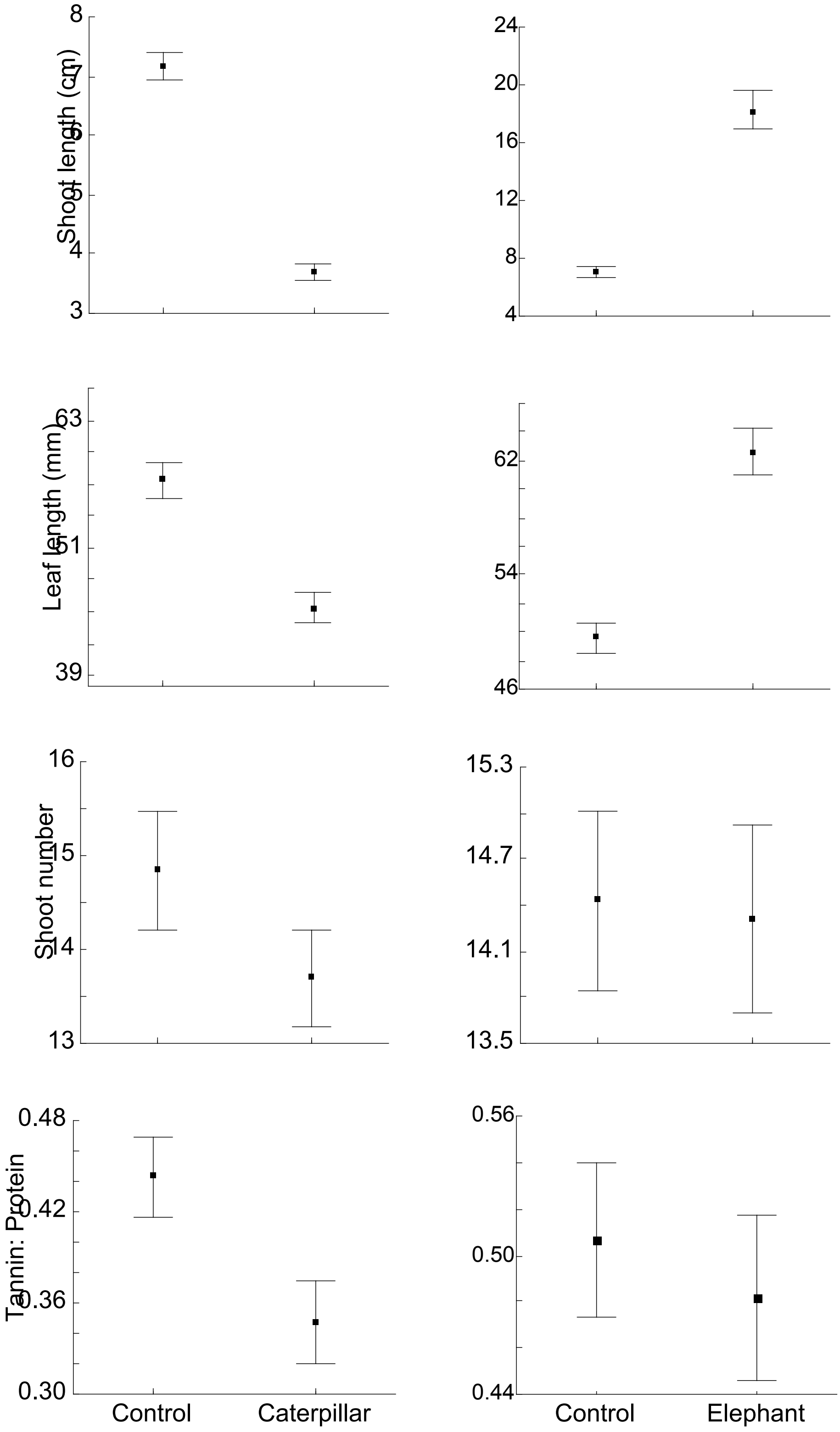

Figure 3.3 The effect of natural elephant pruning and mopane caterpillar defoliation on the regrowth of mopane trees (mean ± SE values).

3.4 Discussion

Both mopane caterpillars and elephants cause extensive damage to individual mopane trees, yet the two types of herbivory affect plant responses in significantly different ways. Pruning by elephants resulted in the production of longer shoots and leaves, while defoliation by caterpillars had the opposite effect. Foliar chemical composition was only found to change after natural caterpillar defoliation, where an increase in nutritional value occurred. The difference in plant responses found here supports results from numerous other studies on browsing (e.g. Bryant *et al*. 1991; Danell *et al*. 1994; Lehtilä *et al*. 2000), and results are as expected considering the differential affect each damage type has on resource availability and resource allocation within individual plants.

According to the sink/source hypothesis (SSH), for example, damage affects plant growth primarily by changing the ability of meristems to compete for resources (Honkanen & Haukioja 1994). In undamaged individuals, sink-source relationships determine resource allocation among organs, with sink strength determining the degree of resource accumulation. Damage through browsing often removes sinks and/or sources, however, thereby altering relationships and modifying allocation patterns (Stowe *et al*. 2000). Because defoliation and pruning affect functionally different plant tissues (physiological sources or sinks), it is hence not surprising that they have variable effects on growth. Defoliation, for example, weakens sink strength of meristems formed immediately after damage, thereby leading to poor plant growth, while branch/stem removal destroys apical meristem dominance (strong physiological sinks) of entire branches, thereby resulting in the redirection of resources towards lateral meristems, which would otherwise remain dormant.

While changes in sink/source relationships explains how damage could affect the distribution of growth activity, the overall regrowth of a plant is also dependent upon the quantity of nutrient reserves in the plant (i.e. resource availability). During summer, photoassimilates are accumulated and transferred to stems and roots, where they are stored for growth the following spring. Removal of storage organs reduces these carbon and mineral reserves, thereby reducing overall plant growth (Quiring & McKinnon 1999). In mopane woodland, the timing of the main defoliation event (November/December) is such that plants would have utilized stored resources for new shoot production (i.e. acting as sinks), but would most likely not have had sufficient time to replenish the used reserves through photosynthesis. Leaf removal at this time would therefore result in an overall decrease in resources available compared to at the start of the first flush. Enhanced by the increase in shoot number after defoliation, less resources are then available per shoot, resulting in a decrease in shoot and leaf size. A similar response has been observed for other southern African deciduous species, such as *Acacia tortilis*, *Grewia flavescens and Dichrostachys cinerea* (Bryant *et al*. 1991). The response to elephant utilization, which was opposite to defoliation, is also as expected considering the probable changes in resource availability within the plant. The high intensity of branch/stem breakage had a significant impact on the root/shoot ratio, as up to 75% of the canopy biomass was removed. When part of the photosynthetic material of a plant is removed, potentially more water and nutrients are then available for the remaining photosynthetic material, resulting in increased shoot and leaf growth (Alados *et al*. 1997). Similarly, the shorter shoot length on trees flushing for the second time (E'02) compared to those flushing for the first time (E'03) can be explained in this way, as the root/shoot ratio would have decreased after the first flush.

In accordance with results from other studies is the greater negative impact of late season (February) defoliation on regrowth found here (Maschinski & Whitham 1989; Danell *et al*. 1994). According to Tiffin (2002), early and late-season damage is more detrimental than mid-season herbivore damage for various reasons. During early season defoliation, leaves may be removed while still growing and acting as sinks, and are therefore removed before having a chance to act as sources and replenish resources used for growth. Similarly, if defoliation takes place too late in the growing season, time for regrowth and replacement of lost resources before the dry season may be insufficient (Maschinski & Whitham 1989; Lennartsson *et al*. 1998). Consequently, growth the following season is retarded. This explains the reduced growth after February (i.e. late-season) defoliation here, as very few mopane trees were observed being able to flush again before the dry season, while November-defoliated (i.e. mid-season) trees re-flushed readily. It should be noted, however, that the summer during which late-season treatments were applied (February 2003) was hot with little rainfall after February (see Fig. 2.3), resulting in a very poor mopane caterpillar crop (most died of desiccation) and minimal defoliation of trees. The following season (2003/2004) experienced good rainfall into March, however, and stands of trees were observed to re-flush each time after three complete defoliation events (once was by puss moth larva). It may therefore have been an unusual situation for mopane trees to incur defoliation and reduced resource availability simultaneously, as in more arid areas there is naturally only one generation of caterpillars (Oberprieler 1995). Growth of mopane is known to be dependant upon water availability, as nitrogen mineralistaion requires the soil to be moist (Henning & White 1974). The already short period for regrowth and nutrient replenishment after the February defoliation would then have been made even worse by the low late-season rainfall in 2003.

While the differential response of mopane trees to pruning and defoliation is consistent with current theory, it is interesting to consider how these responses may help mopane trees withstand the pressures of herbivory. The degree to which a plant is able to respond to and tolerate herbivory depends upon both the extent of damage inflicted and the amount of resources stored belowground. The interaction between resource allocation and resource availability is therefore important, as a plants 'decision' about how to invest it's accumulated resources will directly influence the amount of stored resources available for regrowth after damage (Stowe *et al*. 2000). Various factors are known to influence the size of storage organs, such as the interaction between the long-term frequency and severity of disturbance (Riba 1998), as well as site productivity (Bellingham & Sparrow 2000). In areas of low frequency disturbance, for example, the production of storage organs would not be worthwhile, as it would just constrain aboveground growth and reduce the plants' competitive ability. Site productivity can influence whether a plant invests in resprouting or seeding and, according to Bellingham and Sparrow (2000), more fertile and moist sites tend to promote seed production as compared to dry and less fertile sites. Mopane woodland, which tends to occur on resource limited sites (see review by Timberlake 1995), also experiences relatively frequent and severe disturbance events, in the form of defoliation or drought. It is therefore not surprising that this species has an exceptionally high root biomass (Smit & Rethman 1998), which allows it to regrow rapidly (Cheplick & Chui 2001). Interestingly, this high investment in root material by mopane may actually explain the decrease in leaf size after defoliation, as Papatheodorou *et al.* (1998) found that with increased browsing of *Quercus coccifera* shrubs, coarse root material increased but leaf size decreased. Mopane trees may therefore also have adapted this precautionary approach of increasing resource allocation below ground in response to browsing.

Additional factors that could help in mopane's tolerance to browsing are leaf life span and leaf size. Extended leaf carriage period, together with increased leaf size after pruning, for example, allow for more photoassimilates to be accumulated and resources are therefore better replenished (Nowak & Caldwell 1984; Stowe *et al*. 2000). The increase in leaf life span after elephant utilization can be explained in terms of the RAH, as not only is the plants' water status improved, but pruning can also reduce the competition between leaves for root-derived cytokinins, which have been found to delay leaf senescence (Salisbury & Ross 1985). Additionally, although not measured, an apparent increase in leaf thickness may also explain the increase in leaf life span, as the two are often positively correlated (Wright *et al*. 2002).

Defoliation did not affect leaf senescence (due to there being no change in competition between leaves), yet the nutritional value of leaves was significantly improved after natural defoliation. This could also help in the replenishment of resources, as a higher N content in leaves increases a plants' photosynthetic capacity, thereby acting as a compensatory response to the loss in leaf area (Kazda *et al*. 2004). Additionally, an apparent reduction in leaf thickness (although not measured) after defoliation would further enhance the rate of increase in photosynthetic capacity, as light intensity decreases with depth from the leaf surface (Hattori *et al*. 2004). Therefore, just as increased leaf size and life span potentially improved mopane tolerance to pruning (by increasing the rate of resource replenishment), decreases in chemical defences and leaf thickness may enhance mopane tolerance to defoliation.

Interestingly, unlike natural defoliation, no change in leaf chemistry was recorded after simulated defoliation. The apparent improvement after natural defoliation could be due to the younger leaf age (Styles & Skinner 1997), yet leaves from the regrowth of trees manually defoliated in November 2003 were also younger than from control trees, but were no more nutritional. Additionally, the difference in shoot and leaf length was notably greater after natural versus simulated defoliation, indicating natural defoliation did have a genuinely greater impact. One explanation for differences in response could be that simulated herbivory did not sufficiently mimic natural defoliation (in various ways discussed earlier). Alternatively, differences could be due to variation in individual tree history. During the study period, it was observed that mopane caterpillar abundance was very low within the area in which treatment trees were situated. Previous defoliation of treatment trees was therefore probably minimal. Naturally defoliated trees, however, were frequently observed to have a high abundance of mopane caterpillars and were frequently defoliated. The greater impact recorded on these trees may therefore be due to a long-term accumulative effect of repeated damage, such as that found for *Erica arborea* (Riba 1998). Furthermore, there may already have been differences between trees selected for oviposition by moths or browsing by elephants and the unselected partner trees, resulting in measured responses not only reflecting the effect of pruning and defoliation, but also initial differences between pairs.

The decrease in resistance with an increase in mopane caterpillar damage is unusual, as it is generally accepted that a co-evolutionary relationship exists between a plant and its primary pest (a specialist herbivore), with the frequency of resistance alleles being highest in those populations in which the pest is most common (Purrington 2000). When considering the conditions under which mopane grows, however, the negative relationship found here is not surprising, as the optimal allocation of resources (in this case defence versus growth) depends on the frequency and severity of attack (Doak 1992; Messina *et al*. 2002), both of which mopane tend to experience to a high degree. Additionally, host preference by mopane moths does not appear to be influenced by leaf nutritional value (see Chapters 5 & 6), in which case increases in chemical defences would not act as a deterrent and increased investment in costly chemical defences (Coley 1988; Bergelson & Purrington 1996; Jones & Hartley 1999; Strauss *et al*. 2002) would not be worthwhile, as the chance of further defoliation would remain high and the cost of leaf loss would be even greater. Instead, when resources are invested in growth, this helps replenish stores through increased photosynthesis (Caldwell *et al.* 1981; van der Meijden *et al*. 1988).

In conclusion, mopane trees respond differently to pruning and defoliation due to changes in sink/source relationships and resource availability. Even though no conclusions are made about the overall effect on plant fitness in this study (as this was not measured), defoliation and pruning were found to have a negative and positive effect on regrowth respectively. Time since damage (i.e. first versus second flush) also had a significant influence on regrowth after pruning, as shoot and leaf length were significantly longer on trees flushing for the first time, and within-season timing of damage was important for defoliation, as late-season defoliation had a greater negative impact than mid-season defoliation. Despite the differences in regrowth responses after defoliation and pruning, both types, however, promote the replenishment of stored resources and therefore both enhance the plant's tolerance to herbivory. This, together with the prior pattern of resource allocation to storage organs, indicates how mopane trees are adapted to deal with the impacts of herbivory, of either form.

3.5 References

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