CHAPTER 1

INTRODUCTION

Colophospermum mopane (commonly known as 'mopane') is a xeric savanna woodland species that dominates over vast areas of land in southern Africa, where it out-competes most other woody species within its range and generally forms monospecific stands (Timberlake 1995; O'Connor 1999). Its foliage is an important browse for many mammalian herbivores such as eland (*Taurotagus oryx*), kudu (*Tragelaphus strepsiceros*), and impala (*Aepyceros melampus*; Styles 1993; Styles & Skinner 2000), as well as a number of invertebrates such as puss moth larva (Family: Notodontidae, Order: *Epicerura*) and the mopane psyllid (*Retroacizzia mopanei*; Picker *et al*. 2002). The two main herbivore species associated with mopane, however, include a megaherbivore, the African elephant (*Loxodonta africana*), and an invertebrate, the mopane caterpillar (*Imbrasia belina*).

Elephants utilize mopane predominantly through branch stripping and stem breakage (thereby having a 'pruning' affect) and show a preference for the species, despite it's availability (Smallie & O'Connor 2000). Consequently, their browsing can have a significant impact on the vegetation structure (similar to that caused by fire, Kennedy & Potgieter 2003), thereby making them a keystone species in these woodlands (Timberlake 1995). Although not agents of such structural change, mopane caterpillars are also well known for their utilization of mopane trees, as large population outbreaks are common within mopane woodland, often resulting in vast stands of trees being completely defoliated (Ditlhogo 1996). These two browsers therefore not only share the same food resource, but also both have a significant impact on the vegetation. Hence, it is expected that feeding by the one species could have a significant influence on feeding by the other.

Considering the interaction between these two browsers is unique to most other intra-guild studies, as here the two key species sharing the same resource are taxonomically so different. Other examples of inter-taxon studies include the interaction between birds and mammals (Brown *et al*. 1997), and ants and rodents (Davidson *et al*. 1984), yet both these studies looked at seed utilization, not browsing. The interaction between browsers feeding on different plant parts has also been documented, such as pocket gophers (*Thomomys talpoides*) feeding on below-ground root material and insects feeding on above-ground foliage (Ostrow *et al*. 2002). Furthermore, interactions between browsers utilising the same resource have been documented, yet these studies have tended to focus on taxonomically similar species (Bryant 2003). This study, however, adopts a novel approach and considers interactions within a functional group (the above-ground browsing guild), instead of the more traditional similar-species approach.

Defoliation by mopane caterpillars takes place only once or twice a year during November/December and possibly again in February/March, depending on the rainfall. Branch breakage by elephants, however, occurs mainly at the end of the dry season (August) when other resources are most limited (Lewis 1986). A direct interaction between the two browsers is hence not likely, as their timing of mopane utilization is different. Instead, an indirect interaction could occur, through the impact on plant responses by each species.

Woody species respond differently to herbivory according to the frequency, intensity, timing and type of damage (Maschinski & Whitham 1989; Riba 1998; Tiffin 2002). The most dramatic difference between elephant and mopane caterpillar browsing, however, is the type of damage inflicted, namely: pruning versus defoliation. Studies have shown that trees respond differently to each type of damage, due to the difference in the type and quantity of plant tissue removed. Pruning, which removes branch ends, tends to result in an increased production of side shoots, as lateral meristems are no longer kept dormant by the dominant apical mersitem (Honkanen & Haukioja 1994). Additionally, an increase in shoot length and leaf size tends to occur, as according to the resource availability hypothesis, the reduction in tree size caused by branch removal results in a greater availability of stored resources for regrowth on remaining branches (Danell *et al*. 1994; Duncan *et al*. 1998; Bergström *et al*. 2000; Lehtilä *et al*. 2000). Defoliation on the other hand, which has no effect on plant size but potentially a negative effect on stored resources (if resources used for the initial flush are not yet replenished), characteristically results in regrowth with smaller and/or fewer shoots and leaves (Gadd *et al*. 2001; Anttonen *et al*. 2002; Piene *et al*. 2002). In addition, the chemical composition of foliage can be differentially affected by defoliation and pruning. Often associated with the increased growth of leaves after pruning, is a decrease in the production of defensive secondary compounds, as these are expensive to produce and slow down growth (Herms & Mattson 1992). Defoliation, however, has a variable effect on foliage quality, which tends to be related to plant growth rate (Bryant *et al*. 1991).

Despite the numerous studies on plant responses to herbivory, the true comparative effect of defoliation versus pruning is not yet fully understood, as responses to herbivory also vary between species according to their growth strategy (deciduous versus evergreen; Krause & Raffa 1996) and few studies have made comparisons within an individual tree species. By determining the differential impact of pruning and defoliation on mopane regrowth alone, we could therefore significantly improve our understanding of how an individual species has adapted to persist while exposed to two such different damage types. For example, does the species display tolerance and/or resistance to herbivory (Rosenthal & Kotanen 1994; Mauricio *et al*. 1997; Purrington 2000; Stowe *et al*. 2000)?

In addition, knowledge of regrowth responses is necessary to be able to understand the interaction between mopane caterpillars and elephants, as induced morphological and chemical characteristics of regrowth can influence the subsequent feeding behaviour by browsers (Bryant *et al*. 1991; Coley & Barone 1996; Cooper *et al*. 2003). The preference by moose (*Alces alces*) for previously browsed birch trees (*Betula pendula* and *B. pubescens*) is, for example, thought to be due to the greater long-shoot size on these trees, which facilitates a higher cropping rate (Danell *et al*. 1985). Similarly, elephants tend to prefer mopane trees previously utilised by them, as the damage-induced coppicing shoots provide a greater availability of their preferred shoot size (Smallie & O'Connor 2000). Insects also tend to select host plants according to their regrowth characteristics, and in the few studies looking at mammal-insect browser interactions, insect abundance was indeed influenced by previous mammalian browsing. Here, changes in leaf nutritional value is often an important host choice determinant, as this can potentially influence offspring performance, either through an increased growth rate or a decrease in predation by the sequestering of biologically active chemicals into their own tissue or glands (Karban & Agrawal 2002). For example, the abundance of leaf-eating insects was greater on birch (*Betula pubenscens*) trees previously browsed by moose to a moderate degree, which had a higher nitrogen content than leaves on lightly browsed trees (Danell & Huss-Danell 1985); while leaf beetles (*Chrysomela confluens*) were more abundant on the regrowth of cottonwoods (*Populus fremontii* and *P. angustifolia*) previously cut by beavers (*Castor Canadensis*), that had increased levels of defensive chemicals (which they sequestered for defensive purposes; Martinsen *et al*. 1998).

Any elephant induced changes to mopane trees, particularly the leaves, is therefore expected to have an influence on ovipositing behaviour by mopane moths. Similarly, the predicted decrease in shoot and leaf size after mopane caterpillar defoliation and a possible decrease in leaf quality may have a negative effect on elephant browsing, yet an increase in leaf quality could have a positive effect. Even though it is clearly possible for a two-way interaction to exist between these two browsers, it is however unfortunately beyond the scope of this project to investigate the interaction in both directions. Consequently, only the effect of elephant browsing on mopane caterpillar abundance is addressed here.

In addition to plant regrowth responses, another factor affected by herbivory is reproduction. Similar to regrowth, factors influencing reproductive responses include: the intensity, timing, type and frequency of herbivory (Maschinski & Whitham 1989; Doak 1992, Marquis 1992); resource availability (Lennartsson *et al*. 1998); inter and intra-species competition (Tiffin 2002); and the characteristics of the plant species. Timing may be important, as the period of time between when damage occurs and the onset of flowering could affect the amount of stored resources utilised for regrowth rather than reproduction. When the forest shrub *Piper arieianum* was subjected to simulated defoliation three months before flowering, for instance, seed production decreased significantly, but when defoliated at the time of flowering, no difference in seed production was recorded (Marquis 1992). Similarly, the type of damage also influences the allocation of resources towards reproduction within plants. For example, Strauss (1991) found that the number of smooth sumac (*Rhus glabra*) stems producing fruits increased after pruning by whitetail deer (*Odocoileus virginianus*), but decreased after leaf damage by a specialist chrysomelid beetle (*Blepharida rhois*). The response to each damage type is variable, however, as decreased reproduction after pruning (Peinetti *et al.*

2001) and no change in reproduction after defoliation has also been reported (Meyer 2000). Clearly, plant tolerance of herbivory is therefore not only determined by regrowth responses, but also by the ability to maintain a certain reproductive rate and invest in future generations.

Flowering in mopane takes place predominantly in January and February (Smit 1994), which is just after the first defoliation event by mopane caterpillars in November/December, but about four months after the main period of pruning by elephants in August. Timing, together with damage type may therefore be expected to influence the degree of impact elephant and caterpillar utilization have on reproduction in mopane trees. Determining this differential impact would then help our understanding of the impact each browser has on mopane tree fitness. Ultimately, this could also reveal the long-term interaction between the two browsers, as changes in reproduction could affect plant recruitment and consequently, tree density and resource availability.

While measures of regrowth and reproduction indicate how a plant has adapted to withstand different types of herbivore damage, the difference in response to pruning and defoliation makes it difficult to determine the actual comparative stress on the plant. Compensatory responses could, for example, mask the more long term detrimental effects of browsing, as damaged plants could initially perform as well as or better than non-damaged controls. Instead, developmental instability (DI) is therefore often used as an indicator of stress. Fluctuating asymmetry (FA), which reflects small random deviations from symmetry in otherwise bilaterally symmetrical characters (Palmer & Strobeck 1986), is the most commonly used measure of DI. Since the development of the right and left sides of a bilaterally symmetrical morphological character are controlled by the same genes, the degree of FA is thought to represent the inability of an individual to control developmental processes under given environmental conditions (Møller 1995; Møller &

de Lope 1998). FA is therefore considered a useful and objective tool for measuring stress levels in both plants and animals, where in most cases, an increase in asymmetry is directly related to a decrease in growth, fecundity and survival (Møller 1997; Møller 1999).

Plants are considered highly suitable organisms for studying developmental instability, due to their modular structure that results in repeated structures that reflect developmental performance (Freeman *et al*. 1993). In perennial woody plants, the character most commonly used to measure stress is foliar FA (e.g. Zvereva *et al*. 1997; Martel *et al*. 1999), for which mopane is particularly suitable, as leaves are pinnate, with two large leaflets. The level of leaf FA in mopane trees previously utilised by elephants and mopane caterpillars could therefore be a useful indicator of which browsing type causes the most stress on the trees. Furthermore, developmental instability is sometimes associated with increased leaf nutritional value (due to accelerated growth in response to browsing, Martel *et al*. 1999), and plants with a higher degree of FA may therefore be more susceptible to further herbivory (Møller 1995). Leaf FA may then also be used as an indicator of mopane leaf chemistry, which in turn could indicate whether host tree preference by ovipositing mopane moths is related to leaf chemistry (i.e. plant stress).

The objective of this study was therefore partly to investigate the differential effect of defoliation by mopane caterpillars and pruning by elephants on mopane trees, determined by measures of: (1) regrowth responses, (2) reproduction and (3) leaf fluctuating asymmetry. Additionally, the interaction between elephants and mopane caterpillars through this shared food resource was investigated, by looking specifically at whether browsing by elephants has an effect on mopane caterpillar abundance.

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