

CHAPTER 4

EFFECTS OF PRUNING BY ELEPHANTS AND DEFOLIATION BY MOPANE CATERPILLARS ON REPRODUCTION IN *COLOPHOSPERMUM MOPANE*

4.1 Introduction

Herbivory is known to have a significant impact on plant fecundity, but while some studies have reported an increase in flower and seed production with herbivory (Strauss 1991; Paige 1992; Escós *et al.* 1996; Alados *et al.* 1997; Lennartsson *et al.* 1998; Díaz *et al.* 2004) others have found either no effect (Meyer 2000) or a negative effect (Juenger & Bergelson 2000; Peinetti *et al.* 2001; Freeman *et al.* 2003). Factors responsible for the variability in response include: intensity, timing and frequency of herbivory (Maschinski & Whitham 1989; Marquis 1992); resource availability (Lennartsson *et al.* 1998); inter and intra-species competition (Tiffin 2002); and specific characteristics of each plant species. Similarly, the type of damage associated with herbivory is expected to have a significant influence on plant reproduction, yet this specifically has not yet been investigated.

In southern African, the tree species *Colophospermum mopane* (commonly known as ‘mopane’) is browsed upon by two key species that each inflict a different type of damage while feeding. Mopane caterpillars (*Imbrasia belina*) defoliate mopane trees by removing just the leaf blades (Ditlhogo 1996), while African elephants (*Loxodonta africana*) have a pruning effect by breaking off branches and/or the main stem (Lewis 1991; Smallie & O’Connor 2000). The impact that each damage type has on mopane trees is known to differ in terms of regrowth responses (Chapters 3 & 6) and while this may help the current generation’s tolerance to herbivory (Strauss & Agrawal 1999), the ability to maintain reproductive output is also an important aspect of plant tolerance to consider

(Juenger & Bergelson 2000). Determining the impact of defoliation versus pruning on reproduction would therefore improve our understanding of the overall affect each browsing type has on the species' fitness.

According to the Resource Availability Hypothesis (RAH), the extensive removal of aboveground biomass results in an increased availability of resources per shoot for regrowth (Coley *et al.* 1985). This explains the increased growth of individual shoots after elephant pruning found in Chapter 3, and likewise, an increased production of flowers and seeds may also be expected on these shoots. Such a response was reported for *Gentianella campestris*, for example, where the removal of half the plant biomass by clipping significantly increased fruit production (Lennartsson *et al.* 1998). Unlike pruning however, defoliation tends to result in a decrease in resource availability per shoot, and thus a decrease in reproduction is expected after caterpillar utilization (e.g. Zvereva & Kozlov 2001).

Apart from the type of damage inflicted by each browser, the timing of elephant utilization of mopane trees is also different to that of mopane caterpillars. Pruning by elephants takes place mainly at the end of the dry season (August; Lewis 1986), while defoliation by mopane caterpillars takes place around November/December and again in February/March (during the two brood sessions). The timing of herbivory relative to the reproductive phenology of a plant can have a significant effect on reproduction, as found for the forest shrub *Piper arieianum*. When subjected to simulated defoliation three months before flowering, seed production in *P. arieianum* decreased significantly, but when defoliated at the time of flowering, no difference in seed production was recorded (Marquis 1992). Flowering in mopane trees occurs between December and March, but mainly during January and February (Smit 1994), which is just after the first defoliation event but about four months after the main period of pruning by elephants. Timing,

together with damage type, may therefore be expected to influence the effect that each browser has on mopane tree reproduction.

An additional difference in browsing by the two species is the size of tree targeted. While elephants tend to prefer smaller trees of < 2 m in height (Smallie & O'Connor 2000), host preference by ovipositing mopane moths is positively related to tree height (Chapters 5 and 6). Considering the impact of herbivory is often size-specific, with the negative effect decreasing with increasing tree size (as larger trees also have a larger storage of resources available for recovery; Alados *et al.* 1997), any apparent difference in tolerance to defoliation versus pruning may then be partly due to a bias in tree size. Additionally, the onset of flowering in trees is often size related, as only trees with sufficient stores can afford to invest in reproduction. If true for mopane, trees capable of flowering (i.e. taller trees) may be utilised more by mopane caterpillars than elephants, and the effect of defoliation may then have a greater direct impact on reproduction at the community level than pruning. On the other hand, elephants can prevent the recruitment of trees into the reproductive size class, thereby having an indirect impact on the overall seed production. Tree size as a determinant of reproduction is therefore important to establish to fully understand the impact by each herbivore.

Together with seed number, the successful germination and establishment of seedlings is also an important determinant of plant fitness, and a parameter influencing seedling survival is seed mass. Larger seeds generally have a higher probability of emergence and develop into seedlings with a better competitive ability than small seeds, as they have a larger store of resources (Stanton 1984). For mopane, a previous study by Smit (1994) showed tree thinning to have a significant positive effect on seed mass (presumably because resource availability per tree was improved), yet no relationship between seed mass and germination potential was found. The effect of seed mass on

seedling survival is, however, still unknown and seed size could therefore also be a possible measure of plant fitness in mopane.

Considering the various tree and pod characteristics capable of influencing a plant's reproductive success, this study set out to determine the impact that defoliation by mopane caterpillars and pruning by elephants have on mopane reproduction. The following key questions were addressed: (1) Is the leaf:pod ratio affected by previous caterpillar defoliation or elephant pruning in the same season? (2) Does pruning or defoliation affect seed mass? (3) Is the likelihood of a tree flowering affected by prior defoliation in the same season? (4) Is the occurrence of reproduction in mopane trees related to tree height?

4.2 Methods

4.2.1 Field work

The study was carried out within the Venetia Limpopo Nature Reserve, South Africa (see Chapter 2 for details). Initially, the plan was to look at the effect of defoliation and pruning on reproduction by measuring pod production on experimental trees subjected to simulated defoliation and pruning (same trees as in Chapter 3). However, none of the experimental trees or trees within the experimental area flowered. Therefore, due to the unpredictability of flowering in mopane trees, only trees already flowering were used in this study.

Twelve flowering trees that had been defoliated by mopane caterpillars in December 2003 were identified (they had not yet re-flushed) and marked in January 2004, together with 12 flowering but non-defoliated trees. In a separate area, seven flowering trees previously utilised by elephants were then marked, together with seven flowering but unutilised trees. The lower number of pruned versus defoliated trees was due to their

low availability. Control and utilised trees of a visually similar size (or potential size) were chosen in each case, but live tree height (m) and stem diameters (cm) were recorded to test this quantitatively. Due to the negative effect elephant damage can have on tree height, the potential similarity in tree size for elephant utilised and unutilised trees was determined by comparing the largest stem diameter from each tree, as tree height and largest stem size are correlated in mopane (Chapter 6).

Measures of flowering were not used to assess reproduction, as the timing of flowering within and between trees is highly variable for mopane. Branches were observed to be producing pods while others were just beginning to flower for instance. For accurate comparisons, trees would therefore have had to be monitored regularly over a number of weeks, which was not feasible here. Instead, pod production was therefore recorded, as this was more stable over time.

In March 2004, once pods had developed, marked trees were revisited and their reproductive effort recorded. Firstly, on the tree level, the percentage of canopy volume made up of leaves versus pods was estimated. Secondly, the number of pods and leaves on the terminal 50 cm of a branch were counted, for five branches per tree. Branches were chosen at random from around the canopy, but only those with pods were used. This was because the lack of pods could have been due to a lack of flowers and the aim was to assess how defoliation affected pod production, where pods could potentially develop. Similarly, only trees with more than 10% pods were measured in this way, as sufficient branches with pods were required. As a result, the sample size of defoliated and non-defoliated trees was reduced to seven and pruned and non-pruned trees were reduced to five and six trees respectively.

For trees with enough accessible pods, 10 pods were collected at random from around the canopy. Pods were kept in brown paper bags and were first air-dried and then

oven dried at 70°C for 5 days, until a constant mass. Each pod was then weighed, at an accuracy of 0.001 grams, after which the seed was removed from the pod and weighed separately. Some seeds had been parasitised by beetles and could not be used, as the consumption of part of the seed would have reduced the mass. However, the percentage of seeds parasitised per tree was recorded to determine if previous utilization influenced a tree's vulnerability to seed parasitisation.

To investigate whether defoliation influences a tree's likelihood of flowering in the same season, an additional 40 defoliated and 40 non-defoliated trees were marked in January 2004. As before, trees of similar size were selected and their height was measured. At the end of the month, the presence of flowering was then recorded for each tree. From this, the relationship between tree height and flowering could also be tested. Unfortunately this same study could not be carried out for pruned trees, as the availability of elephant damaged trees was too low.

4.2.2 Statistical analyses

For tree height and stem diameter, as well as for each measure of reproduction (e.g. pods/50 cm and pod mass), differences between utilised and non-utilised trees were determined using either Student's t-tests for normally distributed data, or Mann-Whitney U tests for data not normally distributed. The difference between tree height of flowering and non-flowering trees was also tested using a Mann-Whitney U test (Zar 1999).

4.3 Results

Defoliated and non-defoliated trees on which pod production was measured did not differ in height or largest stem diameter (Mann-Whitney U tests: $Z = -1.27$, $P = 0.203$ and $Z = -0.231$, $P = 0.817$ respectively). Similarly, the height and largest stem diameter of

elephant utilised and non-utilised trees did not differ significantly ($t = 1.93$, $df = 9$, $P = 0.086$; $t = 0.413$, $df = 9$, $P = 0.689$ respectively). Trees were therefore comparable, as reproduction would not have been influenced by tree size.

As observed by Smit and Rethman (1998), some trees produced very few pods even though they had flowered. This was not related to previous utilization however, as four defoliated and four non-defoliated trees produced <10% pods, as did one pruned and two non-pruned trees. For trees with >10% pods, the mean (\pm SE) number of leaves/50 cm of branch was significantly less on defoliated than non-defoliated trees (28.5 ± 2.11 and 47.5 ± 2.11 respectively), while the mean number of pods did not differ (Table 4.1). The leaf:pod ratio was consequently higher in non-defoliated trees (6.64 ± 1.94), but not significantly different to that of defoliated trees (3.09 ± 0.41). There was also no difference in the leaf:pod ratio in elephant pruned trees compared to non-pruned trees, as the number of leaves or pods/50 cm of branch were no different (Table 4.1). The leaf:pod ratio per branch was often highly variable within a tree, especially for defoliated trees. One tree, for example, had a branch with 44 pods and no leaves, and another with 4 pods and 68 leaves. Mean values per tree would hide this branch-level variability, which is perhaps a better indicator of the relationship between regrowth and reproduction. Therefore, leaf and pod production was also considered at the branch level, while bearing in mind that no real conclusions can be made from these analyses, as branches from the same tree were not independent of each other. When all branches were considered individually, the leaf:pod ratio was significantly lower in both defoliated and pruned trees compared to unutilised trees. The response in leaf and pod number was, however, different for the two utilization types. Defoliated trees had a significant reduction in leaf number/50 cm of branch and no increase in pod number, while pruned

Table 4.1 Pod and leaf production in mopane trees previously defoliated by mopane caterpillars or pruned by elephants, compared to unutilised trees (mean \pm SE values).

Utilization type	Control trees		Utilised trees	<i>t</i> or <i>Z</i> [#] value	<i>P</i> - value
<i>Leaves/50cm</i>					
Caterpillar	47.5 \pm 3.43	>	28.5 \pm 2.11	4.72	< 0.010
Elephant	53.6 \pm 8.84	=	44.5 \pm 2.61	0.365 [#]	0.715
<i>Pods/50cm</i>					
Caterpillar	13.1 \pm 2.79	=	18.2 \pm 2.81	- 1.28	0.223
Elephant	16.0 \pm 2.29	=	23.6 \pm 3.69	- 1.80	0.106
<i>Leaves/pods</i>					
Caterpillar	6.64 \pm 1.94	=	3.09 \pm 0.41	1.99	0.070
Elephant	6.50 \pm 1.95	=	3.34 \pm 1.03	1.35	0.211
<i>Pod mass (g)</i>					
Caterpillar	0.328 \pm 0.017	=	0.281 \pm 0.020	1.77	0.095
Elephant	0.305 \pm 0.025	=	0.336 \pm 0.039	0.67	0.514
<i>Seed mass (g)</i>					
Caterpillar	0.077 \pm 0.014	=	0.074 \pm 0.013	0.148	0.884
Elephant	0.079 \pm 0.012	=	0.089 \pm 0.016	0.575 [#]	0.565

The symbol [#] indicates a *Z* value from a Mann-Whitney U test (for non-normally distributed data), as apposed to a *t*-value from a t-test (for normally distributed data).

trees produced the same number of leaves but significantly more pods than non-pruned trees (Fig. 4.1).

Mean values of pod and seed mass were both slightly lower after defoliation and greater after pruning, but masses were not significantly different (Table 4.1). On the tree level, reproductive investment (measured as pod density per branch and pod or seed mass) was therefore unaffected by either defoliation in the same season or recent pruning by elephants.

Pods on trees previously utilised by elephants tended to be less parasitised than pods on unutilised trees (17.1 % and 38.6 % respectively), and this difference was nearly significant (Mann-Whitney U test, $Z = -1.85$, $P = 0.064$). A similar trend was found for the mean values from defoliated (7.78 %) and non-defoliated trees (18.9 %), yet these values were not significantly different due to the high degree of variability between trees (ranging from 0-60% in control trees; Mann-Whitney U test, $Z = 1.23$, $P = 0.216$).

For the 80 defoliated and non-defoliated trees identified, the proportion of defoliated trees that flowered was nearly equal to that of non-defoliated trees (24 % versus 21 % respectively; total N of flowering trees = 18). Defoliation therefore had no influence on a tree's likelihood of flowering in the same season. Flowering was, however, related to tree height, as flowering trees were significantly taller than non-flowering trees ($\bar{x} = 4.49$ m \pm SE 0.30, $\bar{x} = 3.29$ m \pm SE 0.17 respectively; Mann-Whitney U test: $Z = -3.24$, $P < 0.01$).

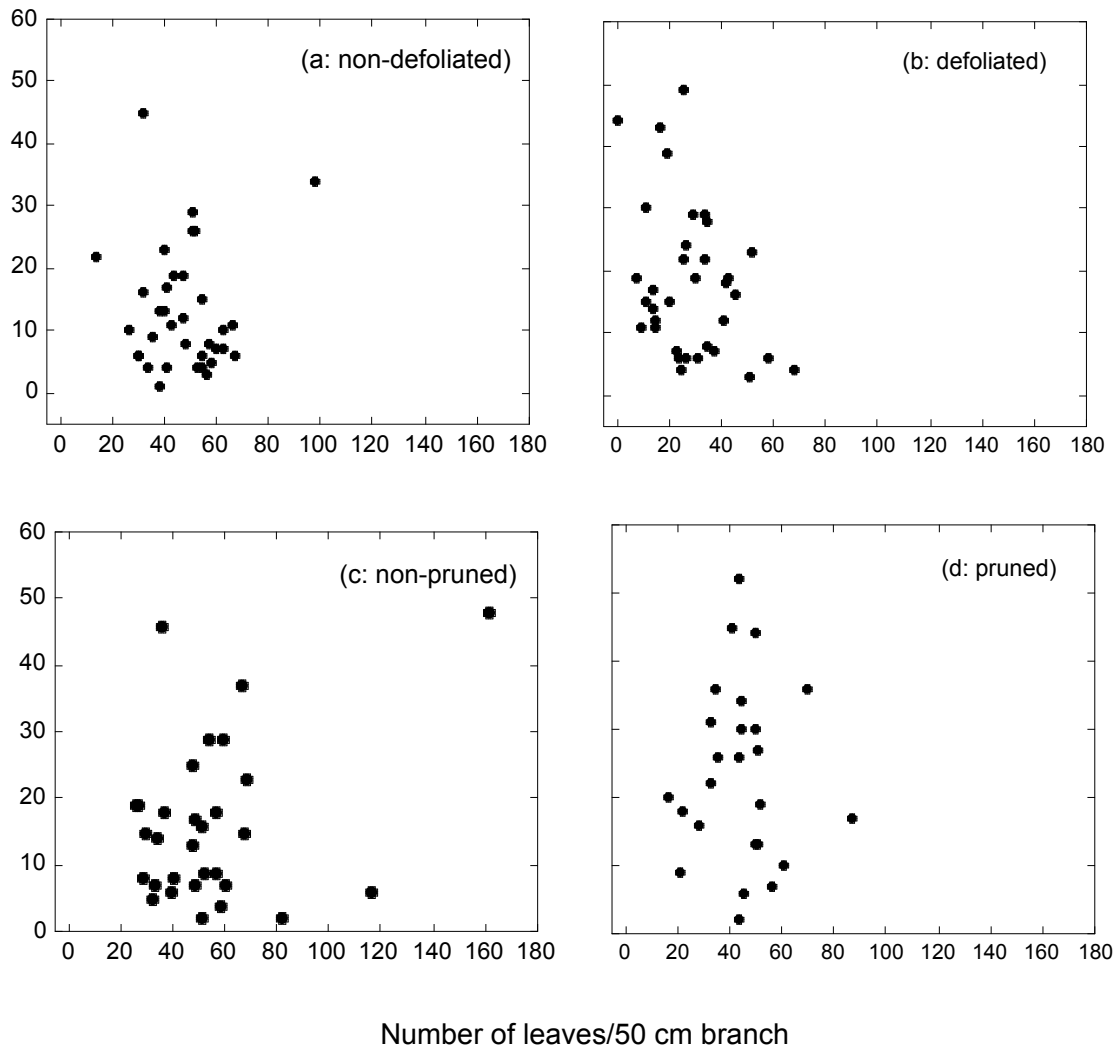


Figure 4.1 The number of leaves versus pods per 50 cm length of branch on (a) non-defoliated, (b) mopane caterpillar defoliated, (c) non-pruned and (d) elephant pruned mopane trees. Data from all branches are shown here (5 branches were sampled per tree).

4.4 Discussion

From this study, defoliation by mopane caterpillars and pruning by elephants appear to have no effect on the reproductive investment of mopane trees, as mean pod density and pod mass on utilised trees was no different to unutilised trees. Defoliation also had no influence on a plants' likelihood of flowering that season, with flowering being determined more by tree height. Unlike pod production, however, the mean leaf density was significantly reduced in the regrowth of defoliated trees.

The lack of negative impact on reproduction after herbivory found here is in accordance with results from studies on other species, such as *Ilex aquifolium* (Obeso 1998) and *Styrax obassia* (Tamura & Hiura 1998). As suggested by Marquis (1992), a possible reason for this apparent tolerance to browsing is that resources required for reproduction are not provided by current photosynthetic material, but rather by stored resources from branches or the main trunk. In mopane, flowering generally takes place shortly after the first defoliation event, before regrowth begins. Additional stored resources would therefore not yet have been utilised for regrowth, and the amount available for reproduction would remain unaffected. This would also explain why defoliation had no influence on a plants likelihood of flowering that season, nor any affect on whether a flowering plant produced pods or not.

Unlike defoliated trees, regrowth on elephant utilised trees had taken place before the onset of flowering, yet pod density and mass were still not negatively affected. Instead, pod number tended to increase on individual branches and the mean pod weight was slightly greater than on non-pruned trees. The possible negative effect that the early timing of elephant utilization could have had on pod production therefore seems to have been over-ridden by the increase in resource availability per branch (due to the increase in the root/shoot ratio caused by browsing; Danell *et al.* 1994). Similarly, the decrease in

leaf density in the regrowth of defoliated reproductive trees can also be explained according to changes in stored resource availability. Here the expending of stored resources on reproduction prior to the onset of regrowth would have resulted in fewer resources available for leaf growth. Such a cost of reproduction has also been reported in the absence of herbivory, as Miyazaki *et al.* (2002) reported a reduction in leaf size on reproductive branches of *Styrax obassia* for example, and Bauce and Carisey (1996) found flowering Balsam fir (*Abies balsamea*) trees to produce half the current-year foliage of non-flowering trees. It should be noted, however, that from this study it cannot be concluded that the decrease in leaf number was in fact due to resource allocation towards reproduction, as a comparison with leaf number on defoliated, non-flowering trees could not be made.

The ability of mopane to invest in reproduction, even in the face of a stress such as herbivory, is possibly due to the species' pre-required store of resources necessary for reproduction to take place. For example, trees only begin flowering once large enough that the cost relative to the amount of stored resources is sufficiently low and hence affordable. Additionally, reproduction in individual mopane trees is sporadic, sometimes only re-occurring after four years. This too is presumably to allow the plant time to sufficiently build up its' store of resources between each reproductive event. Plant fitness would therefore largely be determined by the rate of resource accumulation within a plant, as this would affect the frequency of reproductive years. Consequently, factors influencing the rate of resource accumulation, such as soil type and inter-plant competition, could be important determinants of plant fitness (Maschinski & Whitham 1989), together with a plants' physical characteristics, such as leaf size and number. Defoliation and pruning, which cause significant changes in leaf size and shoot length (depending on the timing and frequency of damage; Chapter 3), would therefore also have

a more long-term impact on mopane tree fitness. Ultimately, a long-term study is therefore needed to determine the true impact of herbivory on mopane reproduction (Doak 1992).

Interestingly, when all branches were considered individually, the relationship between leaf and pod number became far more apparent, with both types of utilization resulting in a decreased leaf:pod ratio. According to Honkanen and Haukioja (1994), partial defoliations create asymmetric within-canopy competition over resources, with defoliated branches being less competitive and thereby displaying retarded growth. Additionally, the movement of resources between branches is restricted in woody plants, meaning that a defoliated branch would suffer more resource depletion after flower production than non-defoliated branches (Marquis 1992; Alados *et al.* 1997). Leaf and pod production within a single tree canopy is therefore often variable, depending on damage locality. In this study, trees were not completely defoliated (ranging from 50 to 95%) and non-defoliated sections were not marked as such. Sampled branches could therefore have been from both defoliated and non-defoliated areas, or from damaged and undamaged areas in pruned trees. Thus, it is not surprising that the leaf - pod relationship was more significant at the branch level, as branch-specific responses would then have been detected. I therefore recommend that future studies take note of the previous utilisation of specific branches within a tree to better detect the impact of herbivory, and to confirm the apparent branch-specific response in reproduction observed here.

It should be noted that pod production in this study was measured as the density of pods per branch, and was not a whole tree count. Therefore, even though mopane appears to display overcompensation in reproduction at the branch level after pruning, total pod production may still have been unaffected (or negatively affected) by a reduction in tree size.

The lack of significant change in seed mass after pruning, but the increase in seed number (at the branch level), is similar to results from studies on *Gentianella campestris* (Lennartsson *et al.* 1998) and *Ipomopsis aggregata* (Paige 1992). This suggests that the trade-off in resource allocation between seed size and number is not affected by changes in resource availability caused by herbivory (Geritz *et al.* 1999; Kiviniemi 2001; Leishman 2001). There was, however, a slight increase and decrease in pod weight after pruning and defoliation respectively, and these differences may also become significant if considered at the branch level (i.e. pods collected specifically from utilised and unutilised branches). If this does occur, and if seed size and seedling recruitment in mopane are positively related, defoliation and pruning could then have a negative and positive influence the reproductive success of mopane trees respectively.

Apart from seed size, an additional factor affecting seed viability is pre-dispersal damage caused by seed predatory insects (Igarashi & Kamata 1997). For example, infestation of *Acacia erioloba* pods by bruchid beetles was found to be the primary factor preventing seed germination under conditions of adequate water (Barnes 2001). Similarly, insect infested acorns from holm-oak trees (*Quercus ilex*) had a 15 percent decrease in viability (Leiva & Fernández-Alés 2005). While the mean percentage of damaged pods tended to be lower on browsed mopane trees, the reliability of this trend is questionable as there was a high degree of between-tree variability within each treatment. Such variability has also been reported for other species (Barnes 2001; Leiva & Fernández-Alés 2005), but the cause is not well understood. In this study, both the sample size of pods per tree and trees per treatment were relatively small, which could be responsible for the high degree of variability. Further work with larger sample sizes is therefore recommended to confirm this interesting trend, as this knowledge could help our understanding of the indirect impact of herbivory on plant fitness.

In conclusion, mopane trees appear tolerant of defoliation by mopane caterpillars and pruning by elephant (if no change in canopy size) in the short term, as the ability to invest in reproduction remained unaffected. Defoliation also had no effect on a tree's likelihood of flowering that season, which was instead determined by tree height. Furthermore, although not specifically tested in this study, production of pods and leaves appears to be dependant on damage at the branch level, indicating the lack of resource movement between branches and hence the importance of localised resource availability. Reproduction in mopane trees therefore seems to be determined by stored resources in the plant, and is not altered in response to herbivory. The only negative effect recorded here was the decrease in leaf density in regrowth after defoliation. This could potentially result in a delayed or long-term negative impact on reproduction, as the rate of resource accumulation and hence the frequency of reproduction could be affected. Similarly, elephant pruning could also have a long-term negative impact on plant fitness if trees are prevented from reaching a reproductive size.

4.5 References

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