

The effects of apical meristem damage on growth and defences of two *Acacia* species in the Negev Desert

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ABSTRACT

Question: Does removal of the apical meristem result in compensatory responses or overcompensation?

Hypotheses: There will be increased investment in axillary meristems and lateral branches and reduced investment in defences. There will be trade-offs between investment in different types of defence and trade-offs between defence and growth.

Organisms: Young *Acacia gerrardii* and *A. raddiana* trees.

Field site: Greenhouse, Blaustein Desert Research Institutes, Negev Desert, Israel.

Methods: The treatments were: (1) a control (no removal of either the apical meristem or biomass); (2) removal of the apical meristem only; (3) removal of 75% of the biomass of the plant including removal of the apical meristem; and (4) removal of 75% of the biomass of the plant excluding removal of the apical meristem.

Conclusions: There was no sign of overcompensation or compensatory responses in the experimentally manipulated plants. Plants with the apical meristem removed did not produce more lateral branches. Protecting the apical meristem appeared to be important, although this was only apparent when 75% of the biomass was also removed. There were trade-offs between chemical defences (condensed tannins) and mechanical defences (mean number of thorns) in *A. gerrardii* but not in *A. raddiana*. There were also trade-offs between defence and growth in *A. gerrardii*. I detected several positive correlations between mechanical defences and growth parameters in both species, indicating that mechanical defences may be part of a suite of growth-related traits.

Keywords: anti-herbivore defence, compensatory responses, overcompensation, plant–animal interactions, resource availability hypothesis, secondary metabolites, tolerance, trade-offs.

INTRODUCTION

A general rule for woody savanna plants growing on nutrient-poor soils is that they are slow growing, contain relatively high concentrations of secondary metabolites such as tannins or alkaloids, and are less palatable to browsers than faster growing plants with few chemical

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defences grown on nutrient-rich soils (Bryant *et al.*, 1989; Du Toit, 1995). Thus, for such plants it is costly to replace lost material, and they defend all the material they have. In contrast, plants growing in nutrient-rich soils can replace lost material easily. This is the basis for the 'resource availability hypothesis' of plant defence (Coley *et al.*, 1985). In deserts, both soil nutrient status and water availability are low while salinity is high (Evenari *et al.*, 1982; Ward, 2009). Thus, following the resource availability hypothesis (Coley *et al.*, 1985), I predict high levels of defence and low investments in growth in desert plants.

African *Acacias* evolved as savanna trees under intense pressure by mammalian herbivores (Ross, 1979; Scholes and Walker, 1993), but they also occur in the arid zones of North Africa and the Middle East (Halevy and Orshan, 1972). *Acacia* trees have long thorns and high tannin contents, both of which have been shown to be effective in deterring herbivores (Wrangham and Waterman, 1981; Cooper and Owen-Smith, 1985, 1986; Furstenburg and van Hoven, 1994). Inducible defences to herbivory in *Acacia drepanolobium*, *A. seyal*, and *A. raddiana* (Young, 1987; Milewski *et al.*, 1991; Rohner and Ward, 1997) suggest that defences are costly in *Acacia* species, and that trade-offs with other life-history traits or among different strategies of defence may exist. It is generally assumed that defence is costly because investments in defence come at the expense of investments in growth and reproduction (Herms and Mattson, 1992; Midgley and Ward, 1996; Rohner and Ward, 1997), while compensatory responses result in the loss of plant tissue or has no cost if the plant is not eaten (Ruiz *et al.*, 2008). Furthermore, it is assumed that few plants invest simultaneously in more than one mechanism of herbivore deterrence, and that traits of different strategies are negatively correlated (Campbell, 1986; Owen-Smith and Cooper, 1987; Van der Meijden *et al.*, 1988; Rosenthal and Kotanen, 1994; Rohner and Ward, 1997; Ward *et al.*, 1997). For example, in a field study Rohner and Ward (1997) found that *Acacia raddiana* produces more tannins and longer spines where there is browsing. We also found that this species produces smaller leaves after browsing, indicating that they are protecting their small leaves among long thorns.

Few studies have measured several anti-herbivore traits in the same individuals, and little is known about how *Acacia* trees allocate resources to different strategies of defence under varying levels of herbivory. I report the results of a greenhouse experiment carried out in Midreshet Sede Boqer in the Negev Desert of Israel, testing for induced responses in trees that had been exposed to different levels of herbivory. Specifically, I examined the importance of apical meristem damage on the growth and defences of *Acacia gerrardii* and *A. raddiana* trees. Both *A. gerrardii* and *A. raddiana* have a dominant apical meristem, but use their axillary meristems when the apical meristem is damaged. There is no apparent difference in the ecology of these two species and they may hybridize in some areas.

Plants may invest in chemical defences such as tannins to protect their apical meristems (Ehrlén, 1995). Should the apical meristem be removed, plants may reduce their investment in chemical defences and adopt a growth strategy instead, focusing on lateral growth. I performed an experiment with the following treatments: (1) removal of the apical meristem only, (2) removal of the apical meristem plus 75% of the biomass of the tree, (3) removal of 75% of the biomass of the tree without removing the apical meristem, and (4) a control, where no biomass or apical meristem was removed but all other conditions were the same.

Each treatment was applied to 20 trees of each species. I removed large proportions of biomass in treatments 2 and 3 to avoid the problem that compensatory responses to herbivory could be confused with Type II statistical error. That is, if there is high inherent variance in growth and defence patterns of these trees, a non-significant result could be claimed to indicate compensatory responses to herbivory (Belsky *et al.*, 1993; Stowe *et al.*, 2000).

Furthermore, some theoretical models (e.g. Tuomi *et al.*, 1994; Nilsson *et al.*, 1996; Lehtilä, 2000) predict a curvilinear response rather than a linear decline in regrowth potential. According to these theoretical models, it is only at higher levels of damage that regrowth potential declines in a linear manner. For these two reasons, I performed the rather extreme damage to the trees in this experiment.

In the light of the resource availability hypothesis of plant defence, I predicted that plants would protect their apical meristems and thus invest heavily in defence. Where trees have had the apical meristem removed, they should invest heavily in growth and most of this growth will be lateral via the axillary meristems. Because of the physiological limitations to plant productivity, there should be increased lateral branching following damage to the apical meristem (Fornoni *et al.*, 2003; Rautio *et al.*, 2005). Plants that have had 75% of the biomass plus the apical meristem removed may grow in a similar manner to those that have had only the apical meristem removed except that the loss of biomass should further reduce their investment in regrowth. Plants that have had 75% removed *excluding* the apical meristem should continue to grow vertically and will invest similar amounts in defence to control plants. These predictions are consistent with the 'compensatory continuum hypothesis' of Maschinski and Whitham (1989). Finally, I examine the possible trade-offs between several traits of anti-herbivore defence and growth among individuals of each of these two *Acacia* species, and discuss the results in the context of ecological adaptations in desert environments.

METHODS

Study area and field methods

The study site is located at Midreshet Sede Boquer, 45 km south of Beer Sheva, Israel (30.8N, 34.5E), 400 m above sea level. Average annual precipitation is 90 mm, with rain most frequent between November and March. High temperatures occur in summer with a mean of 25.7°C and humidity at 25–60% for the hottest month, while temperatures are lower during winter, with a mean of 10.8°C for the coldest month (Evenari *et al.*, 1982). The two *Acacia* tree species used in the study grow in ephemeral riverbeds (called *wadis* in Arabic) and near oases where groundwater is more accessible than in other parts of this desert (Halevy and Orshan, 1972; Evenari *et al.*, 1982). *Acacia gerrardii* is found in the Negev Desert highlands only (600 m above sea level), while *A. raddiana* is more widespread, occurring in both the highlands and in the Syrian-African Rift Valley (as low as 400 m below sea level). Large herbivores that feed on these *Acacia* species are dorcas gazelles *Gazella dorcas*, Nubian ibex *Capra nubiana*, Asiatic wild asses *Equus hemionus*, and the domestic camels and goats owned by Bedouin pastoralists.

Eighty trees of each species (*A. gerrardii* and *A. raddiana*) were grown in 50-litre pots. The trees were 8 months old at the start of the experiment. In the appropriate treatment, the top 5 cm of trees were lopped off to remove the apical meristem. For the removal of 75% of the biomass treatment, estimates were done by eye. We ended these experiments after 3 years. All plants were obtained from the nursery of Keren Kayemeth L'Israel in the Negev Desert. All plants were maintained in the greenhouse with adequate water and nutrients (Osmocote).

This study focuses largely on *A. gerrardii* but includes reference to a limited number of parameters measured for *A. raddiana*. Both species have twice- or bi-pinnately compound

leaves. A leaf on these trees is divided into a petiole and a number of leaflets, and within each leaflet there are many pinnae. The parameters I measured for *A. gerrardii* were tree height, trunk diameter, growth in trunk diameter, growth in tree height, number of primary branches, mean branch length, branch diameter, number of bifurcations of branches, mean length of new branch growth, condensed tannins, number of thorns, mean thorn length, leaf length, petiole length, number of pairs of pinnae, mean pinna length, mean pinna width, numbers of pairs of leaflets, mean leaflet length, and mean leaflet width. The parameters I measured for *A. raddiana* were tree height, trunk diameter, growth in trunk diameter, growth in tree height, condensed tannins, and mean thorn length. I counted leaves >3 mm and measured length and width of the five largest to the nearest 1 mm. On the same leaves I also measured petiole lengths, numbers of pairs of pinnae, and mean pinna length and width. I took thorn measurements to the nearest 1 mm from the distal 0.5 m of three branches for each tree. Throughout this paper, I follow the morphological definitions in Ross (1979), using the term 'thorns' (thorns of any shape or length) to indicate 'spines' (straight thorns >5 mm) that have a vascular supply, and not 'prickles' (curved epidermal thorns, usually <5 mm).

Chemical analyses

From each tree, leaves were removed from the branches, oven-dried at 40°C, and ground for chemical analyses. Condensed tannins were determined by the acid-butanol assay (Waterman and Mole, 1994). Quebracho tannin was used as a standard (Hagerman and Butler, 1989), and the results were calculated as quebracho equivalents (%Q.E.).

Data analysis

Conventionally, tolerance is measured as either the difference between damaged and undamaged plants or as the ratio of damaged to undamaged plants (Simms and Triplett, 1994; Strauss and Agrawal, 1999). Usually, tolerance is recorded for related plants (Strauss and Agrawal, 1999). Here, because I was uncertain of the relatedness of the plants, I analysed the data in both their forms and noted whether compensatory responses occurred. To protect against Type I error, I performed multivariate analysis of variance (MANOVA) across all variables tested for each species to test for overall significance ($P < 0.05$), and where these results were significant I considered the significance of individual variables.

Taxonomic note

Acacia raddiana is considered by Ross (1979) to be a subspecies of *A. tortilis*. However, in the Middle East, *A. raddiana* is sufficiently morphologically and ecologically differentiated from *A. tortilis* to consider them separate species (Zohary, 1972; Shrestha *et al.*, 2002). For the sake of brevity, I refer to *A. raddiana* until further taxonomic research resolves this issue.

Acacia pachyceras Swartz in the Negev was previously identified as *A. gerrardii negevensis* (Zohary, 1972). However, on the basis of morphological characteristics, I find no reason to warrant this split and retain the name *A. gerrardii*.

RESULTS

MANOVA revealed that there was a significant overall difference between the two *Acacia* species (Wilks' $\lambda = 0.392$, $F = 5.248$, $P < 0.001$, error d.f. = 174). Condensed tannins were 1.1 times higher on average for *A. raddiana* (mean $\pm$ s.e. = $19.61 \pm 5.27\%$ Q.E.) than *A. gerrardii* (mean $\pm$ s.e. = $17.88 \pm 4.01\%$ Q.E.). In contrast, *A. gerrardii* grew 1.52 times taller on average (mean $\pm$ s.e. = 184.16 ± 65.58 cm) than *A. raddiana* (mean $\pm$ s.e. = 120.95 ± 43.49 cm) and had 1.63 times thicker trunks on average (mean $\pm$ s.e. = 25.36 ± 7.76 mm) than *A. raddiana* (mean $\pm$ s.e. = 15.53 ± 4.49 mm).

Growth and anti-herbivore defence traits in *A. gerrardii* and *A. raddiana*

In the case of *A. gerrardii*, there was a significant overall difference in parameters among treatments (MANOVA, Wilks' $\lambda = 0.028$, equivalent $F = 3.248$, $P < 0.001$, error d.f. = 75). There were significant differences in tree height ($F = 33.786$, $P < 0.001$, error d.f. = 63) (Fig. 1a), with the control condition having the tallest plants and the 75% biomass + apical meristem removal the shortest. All plants showed undercompensation relative to the control.

Trunk diameter showed significant differences ($F = 31.116$, $P < 0.001$, error d.f. = 62) (Fig. 1b), with the two 75% biomass removal treatments having the narrowest trunk diameters. But there was no significant difference between control and apical meristem removed only. Thus, removal of the apical meristem indicated compensatory responses, with undercompensation occurring for both 75% biomass removal treatments.

The number of lateral branches, which is an index of the number of axillary meristems, also differed significantly, with the control having the most lateral branches ($F = 19.277$, $P < 0.001$, error d.f. = 61) (Fig. 1c). Surprisingly, removing the apical meristem did not result in more lateral branches in either treatment where this was done. No other significant differences were recorded for *A. gerrardii*.

Acacia raddiana exhibited a significant overall effect in parameters among treatments (MANOVA, Wilks' $\lambda = 0.392$, equivalent $F = 477.563$, $P < 0.001$, error d.f. = 148). There were significant differences in mean tannin values among treatments ($F = 4.047$, $P = 0.011$, error d.f. = 59) (Fig. 2a). The removal of the apical meristem + 75% of the biomass in *A. raddiana* caused a significant decline (i.e. undercompensation) in condensed tannins in this species. Interestingly, there was no significant difference between the control and the treatment with 75% of biomass removed without removal of the apical meristem in this species, indicating that the effect was due to apical meristem removal.

Similarly, there were significant differences among treatments in mean thorn (= spine) length ($F = 3.068$, $P = 0.034$, error d.f. = 69) (Fig. 2b), with thorns being significantly longer for control and apical meristem removed compared with either of the two treatments where 75% of the biomass was removed. Removal of the apical meristem resulted in compensation, with undercompensation being displayed for the two 75% removal of biomass treatments.

There were also significant differences in tree height ($F = 11.177$, $P < 0.001$, error d.f. = 69) (Fig. 2c), with the treatment with 75% biomass plus apical meristem removed being shorter than all the other treatments. There was also a significant effect of growth in trunk diameter ($F = 6.902$, $P < 0.001$, error d.f. = 56) (Fig. 2d). Trunk diameter growth was least where 75% of the biomass plus the apical meristem were removed, followed by 75% of

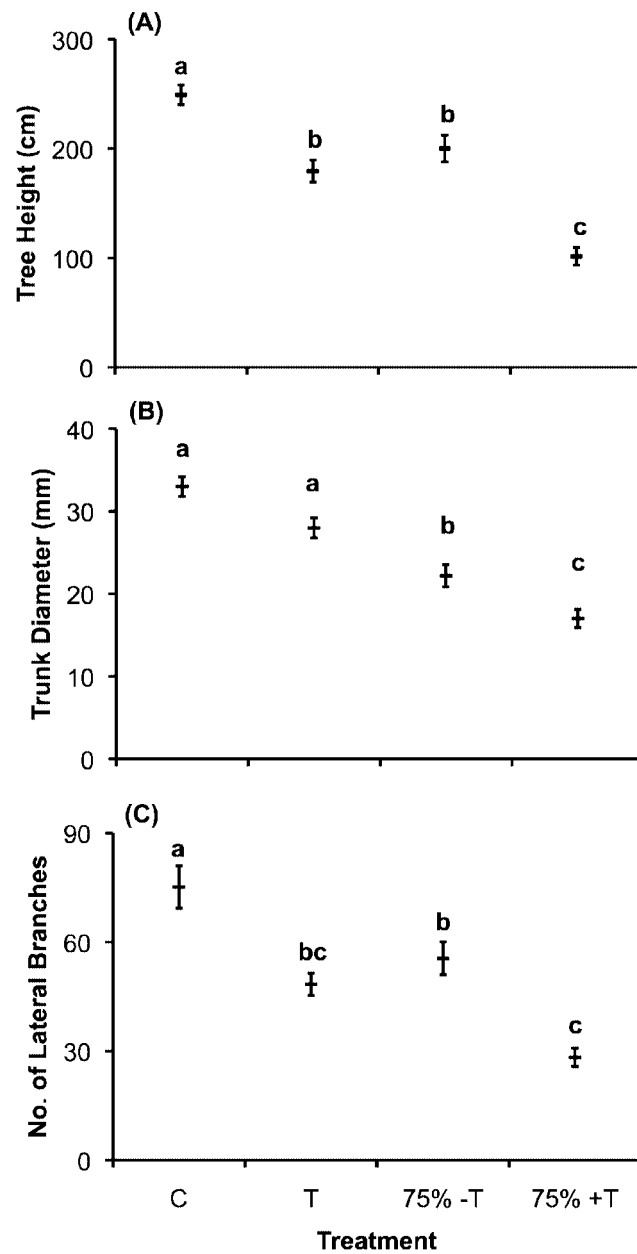


Fig. 1. Responses of *Acacia gerrardii* to different treatments. C = control (no clipping), T = tip (apical meristem) removed, 75%-T = 75% of biomass but no tip (apical meristem) removed, 75% + T = 75% of biomass plus tip (apical meristem) removed. Mean values are shown $\pm$ 1 s.e. Letters above bars indicate significant differences. (A) Tree height. (B) Trunk diameter. (C) Number of lateral branches (indicating degree of growth from axillary meristems).

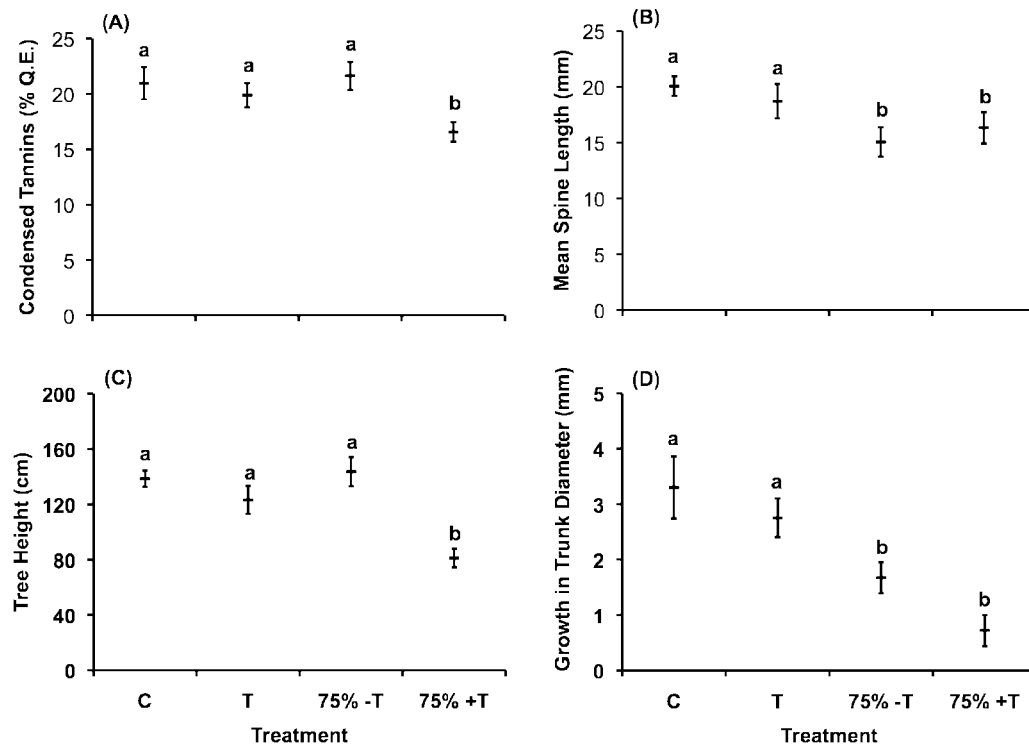


Fig. 2. Responses of *Acacia raddiana* to different treatments. C = control (no clipping), T = tip (apical meristem) removed, 75%-T = 75% of biomass but no tip (apical meristem) removed, 75%+T = 75% of biomass plus tip (apical meristem) removed. Mean values are shown $\pm$ 1 S.E. Letters above bars indicate significant differences. (A) Condensed tannins [measured in % quebracho equivalents (%Q.E.)]. (B) Mean spine (thorn) length. (C) Tree height. (D) Growth in trunk diameter.

the biomass without the apical meristem being removed. There were no significant differences in trunk diameter growth between control and apical meristem removal (compensation). No other significant differences were recorded for *A. raddiana*.

Correlations between categories of defence and growth

Acacia gerrardii showed a significant negative correlation (i.e. trade-off) between condensed tannin concentration and the number of spines ($r = -0.24$, $P = 0.004$, $n = 137$) and between the number of spines and new branch growth ($r = -0.26$, $P = 0.003$, $n = 138$). There was a weak but significant trade-off between condensed tannin concentrations and the number of bifurcations in branches ($r = -0.18$, $P = 0.038$, $n = 137$). There was a significant positive relationship between the number of spines and branch length ($r = 0.72$, $P < 0.001$, $n = 138$) and branch diameter ($r = 0.20$, $P = 0.020$, $n = 138$). There was no significant correlation between condensed tannin concentrations and mean length of spines ($P > 0.05$).

For *A. raddiana*, there were no trade-offs between investments in different forms of defence (chemical and mechanical) or between defence and growth. There was a significant positive correlation between mean thorn length and tree height ($r = 0.34$, $P = 0.005$, $n = 68$),

between mean thorn length and trunk diameter ($r = 0.29$, $P = 0.018$, $n = 68$), and between condensed tannins and tree height ($r = 0.26$, $P = 0.035$, $n = 68$).

DISCUSSION

As experience in Christmas tree selection can attest, outward appearance of bushiness can be deceiving. A short plant with the same number of branches as a tall plant will appear bushy because of shorter internodes. (Cline, 1997)

I found no evidence of compensatory responses to herbivory in either *Acacia* species, with the exception of removal of the apical meristem only in some cases. There were clear differences in regrowth of both *Acacia* species, with the plants that suffered removal of the apical meristem and 75% of the biomass usually showing the greatest change in growth patterns (undercompensation).

Similarly, Bast and Reader (2003) examined the regrowth of 5-year-old *Picea mariana* (black spruce) trees when 25%, 50% or 75% of the uppermost buds of a tree were removed and compared them to the growth of undamaged plants. They found that shoot growth did not differ significantly among trees in the meristem removal treatments, regardless of resource supply. They considered that the absence of overcompensation most likely reflected the relatively small supply of dormant meristems on treated trees.

At low to moderate levels of damage, the regrowth of an injured plant is predicted to exceed the normal growth of an undamaged plant (Tuomi *et al.*, 1994; Lehtilä, 2000; Stowe *et al.*, 2000; Stevens *et al.*, 2007). This was termed 'overcompensation' by McNaughton (1983). Perhaps the most convincing example of overcompensation was in *Ipomopsis aggregata* (scarlet gilia), where removal of a single inflorescence resulted in the production of an average of five more lateral shoots (Paige and Whitham, 1987). Similar results have been shown for the field gentian *Gentianella campestris* (Huhta *et al.*, 2000), with the highest level of overcompensation being at intermediate levels of simulated herbivory. The biological basis for overcompensation predicted by the models of Tuomi *et al.* (1994) is that damage to the plant stimulates shoot growth from meristems that, because of apical dominance, would normally remain dormant on an undamaged, non-injured plant.

Haukioja and Koricheva (2000) reviewed differences in tolerance between woody plants and herbaceous perennials. They concluded that differences in tolerance might be caused by differences in modular architecture (woody plants are more modular than herbaceous perennials), longevity, and the type of herbivory (most woody plants experience insect folivory) that the plants endure. They also found that the short duration of most studies might restrict the demonstration of compensatory responses in woody plants. My study plants mostly experience mammalian herbivory and my study was considerably longer (3 years) than many others in the literature.

Obeso (1993) found that all studies on woody plants published to that time showed reduced reproductive output upon herbivory (i.e. undercompensation), while herbaceous perennials showed a range of responses from undercompensation to overcompensation. Haukioja and Koricheva (2000) considered that many of the studies reported by Obeso (1993) focused on effects on a single ramet (e.g. a branch). Here, however, I report the effects of removal of 75% of the tree and find little evidence of compensatory responses.

Importantly, although Strauss and Agrawal (1999) indicated that mechanisms exist to explain the evolution of tolerance, a number of authors have indicated that there is no

mechanism to explain the evolution of tolerance (Tiffin, 2000; Stinchcombe, 2002; Fornoni *et al.*, 2003). Until such time that mechanisms are demonstrated, it is probably premature to suggest that a single mechanism exists.

Aarssen and Irwin (1991) and Aarssen (1995) have suggested that the unbranched architecture of unbrowsed plants may be associated with competition for light and other selection pressures that favour fast vertical growth through apical dominance. Quick vertical growth may be achieved by focusing resources on a single growth axis rather than by dividing resources among multiple meristems. Aarssen and Irwin (1991) and Aarssen (1995) argue that selection should favour fast vertical growth and unbranched architecture in dense vegetation and will be relaxed in open habitats. This hypothesis clearly does not explain the presence of vertical growth in *A. gerrardii* and *A. raddiana* because these plants typically grow in open habitats with little or no vegetation surrounding them (Rohner and Ward, 1997, 1999; Ward *et al.*, 2000).

There was no significant change in the production of condensed tannins in *A. gerrardii*, but there was a change in tannin production in *A. raddiana*. *Acacia raddiana* showed a reduction in the production of tannins when the apical meristem and 75% of the biomass were removed, but there were no significant changes associated with any of the other treatments. This is inconsistent with my hypothesis that the apical meristem is protected by secondary defence compounds. Nonetheless, the fact that there was a significant difference between condensed tannin concentrations in *A. raddiana* trees with 75% of the biomass removed and 75% of the biomass removed plus the apical meristem indicates that the removal of the apical meristem does have a significant negative impact on the allocation of secondary defences. My results for *A. raddiana* were similar to those of Du Toit *et al.* (1990), who found that heavily browsed specimens of *Acacia nigrescens* had reduced chemical defences and may serve as 'grazing lawns' (*sensu* McNaughton, 1983) for herbivores.

Trade-offs in chemical and mechanical defences

Trade-offs in the investments into chemical or mechanical defence occurred for *A. gerrardii* but not for *A. raddiana*. I also found that there were trade-offs between investments in mechanical defence and growth in *A. gerrardii*, as well as between chemical defences and the number of branch bifurcations.

In both *Acacia* species in the present study, there were positive correlations between mechanical defences and several plant size parameters. Similar positive correlations were obtained for *A. karroo* in populations from South Africa (Mboumba and Ward, 2008). This observation contrasts with the results comparing spinescence and chemical defence across taxa. High levels of spinescence are seldom found in combination with chemical defence, indicating that few plants invest simultaneously in more than one mechanism to deter herbivory (Campbell, 1986; Owen-Smith and Cooper, 1987; Van der Meijden *et al.*, 1988; Rosenthal and Kotanen, 1994; Rohner and Ward, 1997).

Three main questions arise concerning the underlying assumptions when attempting to demonstrate trade-offs between chemical and mechanical defence in individuals within a population.

First, do variables of chemical and mechanical defence operate at a comparable time-scale? Production of thorns is irreversible, and on the distal 0.5 m of a branch, I would have measured the integrated response over several years (Midgley and Ward, 1996). Gowda *et al.* (2003) found that nutrient inputs affected the patterns of thorn defence in *Acacia tortilis*, such

that the relative mass of spines increased significantly more than other structural parts such as leaves and twigs. Here, too, this effect occurred after several years. Production of secondary metabolites, in contrast, is more variable (Cooper *et al.*, 1988; Furstenburg and van Hoven, 1994) and may obscure correlations.

Second, have confounding factors been controlled for? When testing for trade-offs in individuals and not across taxa, phenotypic variation in the resource acquisition of individuals can lead to an interaction that changes an underlying trade-off into a positive or zero correlation between two traits (reviewed in Roff, 1992; Stearns, 1992). For example, larger individuals of *Lotus corniculatus* also contained higher tannin concentrations (Briggs and Schultz, 1990). The confounding factor can also result from a negative correlation. For example, Palo *et al.* (1993) found that chemical defences of woody plants in East African savannas were reduced with increasing species height. And age effects may play a role. Brooks and Owen Smith (1994) showed that younger trees had higher levels of mechanical defence than older trees. The correlation suggests that small trees are more exposed to mammalian browsers and invest more into defence, whereas larger trees normally escape mammalian herbivory and can allow for more varied and flexible investments (including reproduction), larger trees growing heavier defences only when necessary (Brooks and Owen Smith, 1994). Brooks and Owen-Smith (1994) found this pattern of age effects on spinescence but not on chemical defences in *A. tortilis* and *A. nilotica* in a South African savanna. Similarly, in this study, I also found several positive correlations between mechanical defences and growth parameters in both *A. gerrardii* and *A. raddiana*, indicating that mechanical defences may be part of a suite of growth-related traits (reviewed by Watson, 1986; Geber, 1990; Juenger *et al.*, 2000). This positive correlation is consistent with the model of Ward and Young (2002), which indicates that if there are large differences in resource acquisition and relatively small differences in resource allocation – such as one might expect when there are optimal investments in growth and defence – then positive correlations may result [see Van Noordwijk and De Jong (1988) for a formal explanation of this theory with regard to growth and defence]. Few studies have correlated traits of chemical and mechanical defence for individuals, and it is unknown whether such phenotypic variation caused a problem in detecting trade-offs in the present study.

Third, are defences costly to the plant? Inducible defences were apparent for chemical and mechanical defence traits in *A. raddiana* (Rohner and Ward, 1997), indicating that condensed tannin and thorn production is costly and that resources may be allocated differently according to the part of the plant that is browsed. Other studies have indicated that inducible defences depend on the degree of herbivory. For example, in a study of *A. drepanolobium*, Ward and Young (2002) showed that there was an increase in investment in condensed tannin defences with increasing herbivory by both large mammals and ants. Therefore, this pattern may be more general than previously assumed, and lends further support to the criticism that chemical defences may not always be costly (Herms and Mattson, 1992; Koricheva *et al.*, 2004; Orians and Ward, 2010).

Plant–animal interactions in desert environments

The resource availability hypothesis predicts that plant defences will increase when growth rates are limited by resources such as water, nutrients or light (Coley *et al.*, 1985; reviewed by Orians and Ward, 2010). Interestingly, Du Toit *et al.* (1990) found that the chemical defences of *Acacia nigrescens* were lower near waterholes than at control sites. This result was related to

obvious differences in browsing levels, but could also be a consequence of differences in regrowth capacity if that capacity depends on the availability of water (but see also Teague, 1988). In contrast, Milton (1991) found that there was selection for spinescence near water sources in arid environments and suggested that this could be due to mammalian herbivory. In a meta-analysis, Hawkes and Sullivan (2001) found that woody plants grew more under low resource conditions. Further research is required on the effects of variations in water and nutrient supply on plant growth and defences.

ACKNOWLEDGEMENTS

I thank the *Keren Kayemeth L'Israel* and Nature Reserves Authority, Israel. I am grateful to Iris Musli who assisted with fieldwork and chemical analyses. Funding for this study was provided by *Keren Kayemeth L'Israel* and the National Research Foundation of South Africa. This is publication 748 of the Mitrani Department for Desert Ecology.

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