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EFFECTS OF LARGE MAMMALIAN HERBIVORES AND ANT SYMBIONTS ON CONDENSED TANNINS OF *Acacia drepanolobium* IN KENYA

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Abstract—Condensed tannins have been considered to be important inducible defenses against mammalian herbivory. We tested for differences in condensed tannin defenses in *Acacia drepanolobium* in Kenya over two years among different large mammalian herbivore treatments [total exclusion, antelope only, and megaherbivore (elephants and giraffes) + antelope] and with four different ant symbiont species on the trees. We predicted that (1) condensed tannin concentrations would be lowest in the mammal treatment with the lowest level of herbivory (total exclusion), (2) trees occupied by mutualist ants that protect the trees most aggressively would have lower levels of tannins, and (3) if chemical defense production is costly, there would be a trade-off between tannin concentrations, growth, and mechanical defenses. Mean tannin concentrations increased from total exclusion treatments to wildlife-only treatments to megaherbivore + antelope treatments. In 1997, condensed tannin concentrations were significantly lower in trees occupied by the ant *Crematogaster nigriceps*, the only ant species that actively removed axillary buds. Contrary to our prediction, trees occupied by ant species that protect the trees more aggressively against mammalian herbivores did not have lower overall levels of condensed tannins. There was no consistent evidence of a trade-off between tannin concentrations and growth rate, but there was a positive correlation between mean thorn length and mean tannin concentrations across species of ant inhabitants and across herbivore treatments in 1997. Contrary to our expectation, trees had higher tannin

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concentrations in the upper parts of the canopy where there is little herbivory by mammals.

Key Words—Induced defenses, condensed tannins, *Acacia*, mammalian herbivory, ants, mutualism.

INTRODUCTION

Plants show a wide variety of defenses against herbivory, including physical responses (such as thorn production; reviewed by Myers and Bazeley, 1991), chemical defense (e.g., McNaughton and Tarrants, 1983; Du Toit et al., 1990; Bryant et al., 1992; Ward et al., 1997), growth strategies (e.g., growing too tall for the leaves to be eaten, e.g., Milewski et al., 1991; Palo et al., 1993), and low nutrient content (Lundberg and Astrom, 1990). Of increasing interest to the ecologist are inducible defenses against herbivory. When the cost of defense is high and levels of herbivory are variable, plants are predicted to have inducible defenses (Rhoades, 1979; Young, 1987; Herms and Mattson, 1992; Karban et al., 1997), i.e., they produce the defense only when herbivory is initiated so as not to commit resources prior to the need for defense. Chemical defenses are important inducible defenses because they can be produced quickly or at least transported quickly from one part of the plant to another (Bryant et al., 1983; Karban and Baldwin, 1997). There is little consensus as to the general importance of plant secondary metabolites as inducible defenses (Herms and Mattson, 1992; Karban and Baldwin, 1997) because, by definition, inducible defenses are costly to produce, yet costs of production of these chemicals have not always been detected (Bryant et al., 1983; Herms and Mattson, 1992; Simms, 1992).

Most current theories of inducible plant defenses against herbivory are based on the notion that plants will produce defenses when the benefit to be derived from them outweighs the cost of their production (e.g., Rhoades, 1979; Van der Meijden et al., 1988; Herms and Mattson, 1992; Rosenthal and Kotanen, 1994). It is generally assumed that defense is costly because investments in defense come at the expense of investments in growth and reproduction (Briggs and Schultz, 1990; Palo et al., 1993; reviewed in Herms and Mattson, 1992). Due to the costs of defense, it is also frequently assumed that few plants invest simultaneously in more than one mechanism of herbivore deterrence and that defense traits are negatively correlated (reviewed by Zangerl and Bazzaz, 1992; Silvertown and Dodd, 1996).

African Acacias as Model Organisms for Tests of Inducible Defenses. African acacias evolved as savanna trees under intense pressure by mammalian herbivores (Ross, 1979; Scholes and Walker, 1993). *Acacia* trees have long thorns and high polyphenol (especially condensed tannin) contents, both of which are effective in deterring mammalian herbivores (Wrangham and Waterman, 1981; Cooper and

Owen-Smith, 1985, 1986; Furstenburg and van Hoven, 1994). Condensed tannins are generalized digestion inhibitors in mammals (Robbins et al., 1987; Waterman and Mole, 1994). Although condensed tannins may also be effective against insect attack, the importance of these organisms as agents of selection on defenses of African *Acacia* species is generally considered to be low (Cooper and Owen-Smith, 1985; Du Toit et al., 1990; Owen-Smith, 1993; Gowda, 1997; Rohner and Ward, 1997). Inducible thorn defenses against herbivory in *A. drepanolobium*, *A. seyal* (Young, 1987; Milewski et al., 1991), *A. tortilis* (Gowda, 1996a; Rohner and Ward, 1997), and *A. raddiana* (Rohner and Ward, 1997), as well as inducible polyphenol defenses in *A. raddiana* (Rohner and Ward, 1997), suggest that defenses are costly in *Acacia* species. This conclusion is reinforced by the experimental evidence that investment in thorn defenses in *A. drepanolobium* declined following removal of mammalian herbivores (Young and Okello, 1998). Thus, *Acacia* species may be model organisms for investigating the inducibility of defenses against mammalian herbivory. Furthermore, because they frequently have long thorns and high tannin concentrations, they may be suitable species for testing for the presence of possible trade-offs between investments in different types of defense.

Plants may concentrate their defenses in those structures or life-history stages that are most likely to be affected by herbivory (e.g., Palo et al., 1993). The most clear-cut division between accessible and nonaccessible parts of trees depends on the height of the tree relative to the maximum browsing height of nonarboreal herbivores (Palo et al., 1993; Gowda, 1996a). Younger *Acacia* trees have higher levels of mechanical defense and chemical defenses than older trees (Palo et al., 1993; Brooks and Owen-Smith, 1994; Gowda, 1996b; Rohner and Ward, 1997), and within trees, lower branches have longer thorns than higher branches (Young, 1987; Milewski et al., 1991; Young and Okello, 1998). This suggests that plants and plants parts that are more exposed to mammalian browsers will invest more in defense, while larger trees normally escape mammalian herbivory and can allow for more varied and flexible investments (including reproduction) and only produce stronger defenses when necessary (see also Brooks and Owen Smith, 1994; Rohner and Ward, 1997). Here, we investigate the effects of mammalian herbivory on condensed tannins in a common African *Acacia*, *A. drepanolobium*, and determine whether the level of defense is related to the probability of herbivory.

Ants as *Acacia* Defenses. Ants that live in the swollen thorns of *Acacia* species are frequently assumed to provide a form of defense against large mammalian herbivores because they swarm over the herbivores and bite them when they come into contact with the trees (e.g., Hocking, 1970; Coe and Beentje, 1991). Madden and Young (1992) showed that *A. drepanolobium* with more active ants had more foliage than did trees with less active ants and were less heavily browsed by immature (but not mature) giraffes.

Although several African *Acacia* species produce swollen thorns and are occupied by ants, *A. drepanolobium* is the only species known to be an obligate ant

TABLE 1. ANT SPECIES COMMONLY RESIDENT ON *Acacia drepanolobium* AND THEIR ROLES,^a SUCCESSIONAL STAGE, AND EFFECT ON PLANT

Species	Interaction with tree	Successional stage	Ant behavior	Feeds on
<i>Crematogaster mimosae</i>	Mutualist	Late	Aggressive	
<i>C. sjostedti</i>	Non-Mutualist	Late	Timid	
<i>C. nigriceps</i>	Non-Mutualist	Early	Aggressive	Axillary shoots
<i>Tetraponera penzigi</i>	Non-Mutualist	Early	Timid	Extrafloral nectaries

^a Data from Young et al. (1997).

host (Ross, 1979). Several ant species on *A. drepanolobium* are mutually exclusive (Hocking, 1970), and certain ant species appear to replace others in a successional process (Young et al., 1997) (Table 1). Two of the ant species found on *A. drepanolobium* respond aggressively when their branches are disturbed (*Crematogaster mimosae* and *C. nigriceps*). Because aggressive ants may reduce the threat of herbivory to the trees (Madden and Young, 1992), we predicted that there would be a reduction in tannin concentration in trees occupied by more aggressive ants. Two less aggressive ant species on *A. drepanolobium*, *C. sjostedti* and *Tetraponera penzigi*, may be less effective at protecting their trees from herbivory (Table 1) (Young et al., 1997). In addition, two species of ants have unusual behaviors. *C. nigriceps* ate virtually all of the axillary shoots at nodes with unswollen thorns on trees they occupied (Young et al., 1997). Unlike *A. drepanolobium* inhabited by other ant species, few trees occupied by *C. nigriceps* flower or set fruit. Trees occupied by *T. penzigi* were 2–9 times more likely to have at least some leaves with their nectaries eaten compared to trees without *T. penzigi*. Most of the nectaries were eaten on these trees and more than 90% of them lacked any active nectaries, whereas only 26–38% of other trees lacked active nectaries (Young et al., 1997).

The potential interactions between the effects of mammalian herbivory and ant occupancy on *A. drepanolobium* provide a unique opportunity to examine the relative effects of mammalian herbivores and ant mutualists on plant chemical defenses. We simultaneously examined the relative effects of mammalian herbivory and ant occupancy on tannin production in an experimental design with replicated 4-ha plots that either allowed (1) the entry of all large mammalian herbivores, (2) all large mammalian herbivores except megaherbivores (elephants *Loxodonta africana* and giraffe *Giraffa camelopardis*) to enter, or (3) excluded all large herbivores (Young et al., 1998). Within each of these plots we sampled trees with each of the different ant occupants listed in Table 1.

We made the following predictions about condensed tannin concentrations in *A. drepanolobium*:

1. Trees from plots with higher levels of mammalian herbivory should have higher concentrations of condensed tannins in their leaves to defend themselves

against herbivory. Thus, the highest tannin levels should be found in the megaherbivores + antelope plots, followed by the antelope plots, and then the total exclusion plots.

2. More aggressive ant species (*C. nigriceps* and *C. mimosae*) may protect their trees from herbivory more than less aggressive species (*C. sjostedti* and *T. penzigi*). This should result in reduced tannin concentrations in the leaves of trees occupied by mutualist ant species.

3. Because inducible defenses are hypothesized to be costly to produce (Herms and Mattson, 1992; Zangerl and Bazzaz, 1992), there should be a trade-off between investments in chemical (tannins) and physical (thorn) defenses. Similarly, there may be a trade-off between growth rate and chemical defenses.

4. If *A. drepanolobium* is capable of investing differentially in different parts of the canopy according to the probability of being eaten, we should find lower tannin levels high in the upper canopy where mammalian herbivory is low, with this effect being reduced in the megaherbivore plots.

METHODS AND MATERIALS

Research was conducted at the Mpala Research Centre in the Laikipia ecosystem (36°50'E, 0°15'N) in north-central Kenya. *Acacia drepanolobium* is the dominant tree species in the wooded grasslands on "black cotton" soils in this ecosystem, comprising approximately 95% of woody individuals (Young et al., 1997, 1998). There are 18 experimental plots (fenced in September 1995), each 4 ha in size and located in three blocks. Within each block, different forms of barriers and control of individual cattle herds create six mammalian herbivore treatment levels. The treatment levels are: (1) total exclusion, (2) cattle only, (3) nonmegaherbivore wildlife (antelope) only, (4) nonmegaherbivore wildlife (antelope) + cattle, (5) all wildlife, including megaherbivores (= elephants + giraffe) and antelope, and (6) all wildlife (megaherbivores and antelope) + cattle. This design has one replicate per block. Because cattle do not eat *Acacia* leaves (Young and Okello, 1998), we collapsed the treatment levels into three wild mammalian herbivore levels, allowing two replicates per block. The treatment levels we considered here were total exclusion, antelope, and antelope + megaherbivores (elephants and giraffes). Browsing species that occurred in the antelope plots were: Grant's gazelle (*Gazella granti*), eland (*Taurotragus oryx*), steinbuck (*Ramphiceros campestris*), and oryx (*Oryx beisa*). Antelope plots also included zebras, buffaloes, and hartebeests, but these grazers do not eat *Acacia* leaves and will not concern us here. Densities of large mammals were not controlled within the plots other than by restricting access (Young et al., 1998). Dung counts suggest that the antelope barriers reduce the presence of antelopes by 90% and that the megaherbivore barriers reduce the presence of elephants and giraffes by >80% (Young et al., 1998).

In July 1997, within each of the 18 plots we collected undamaged leaves over a short time period approximately 1 m above the ground of one tree for each of the four ant species mentioned above. We sampled leaves at two heights (1 and 2 m) on trees occupied by the mutualist ant species, *C. mimosae*. In all but two cases, these were different trees. This procedure was repeated in 1998 on 90 new trees, each paired with a nearby tree from 1997 with respect to ant occupant and branch height. These 1998 trees also served as control trees for a leaf removal experiment.

The branches from which we sampled leaves in 1997 were also the basis of a leaf removal experiment. Each branch selected was randomly chosen from a simple forked pair of branches of similar length. After collecting leaves for our tannin analysis, we removed all remaining leaves from the leaf removal branch, while keeping its paired branch as a control.

In combination with the new trees sampled in 1998, this experiment had three levels: leaf removal, leaf control on the same tree, and (a separate) control tree. If trees invest preferentially in sections that have had leaves removed, then tannin concentrations should be highest in the leaf removal treatments in the following year. If tannins are invested at the level of the tree as a whole, leaf removal and leaf controls should have similar tannin concentrations that will be higher than in the control trees.

We also attempted to ascertain whether there were trade-offs between tannin production and investments in thorns and in growth. Mean thorn (=spine) lengths across multiple trees occupied by different ants species in these plots were taken from Young and Okello (1998). We also had mean thorn length measurements from a small number of thorns on each sampled tree. Growth rates of individual branches were measured as the difference between branch lengths in surveys in 1997 and 1998.

Leaves were air-dried prior to measurement of condensed tannins. All analyses were done simultaneously. We measured condensed tannins in the leaves using a standard acid-butanol protocol (Waterman and Mole, 1994). Following the recommendation of Hagerman and Butler (1989), quebracho was used as a standard (quebracho supplied by A. E. Hagerman, Miami University, Ohio, USA). All results are expressed as percent dry weight in quebracho equivalents (QE).

The data were analyzed in a randomized block ANCOVA with mammal treatment as a fixed factor and ant species and branch height class as random factors (error terms as for model III ANOVA). Height of tree and length of new growth on the sampled branch were used as covariates.

RESULTS

There was no significant correlation in condensed tannin concentration within trees between years ($r = 0.15$, $F = 2.14$, $P = 0.15$). For 89 unmanipulated trees for which we had data in both 1997 and 1998, we found no difference in tannin

TABLE 2. TANNIN CONCENTRATIONS IN 1997 AND 1998 ON TREES INHABITED BY *C. mimosae*^a

Branch height	Mammalian treatment	Herbivory	Tannin concentration (% QE)
AU: 1 m 2 m OK? Low (1m)	Control	None	16.27 ± 1.63
	Antelope only	High	10.96 ± 1.83
	Megaherbivores + antelope	High	13.44 ± 2.43
High (2m)	Control	None	19.29 ± 1.59
	Antelope only	None	17.56 ± 2.12
	Megaherbivores + antelope	Low	17.12 ± 1.07

^a Estimates of herbivore presence are based on dung counts of herbivores that can reach reference branches.

concentration between years (paired *t* test, *t* = 0.76, *P* = 0.45). In no analysis were there significant year effects. There were also no block effects. Overall, there was tremendous variation in tannin concentrations among samples (range 2–30% QE, coefficient of variation = 37%).

We only sampled higher branches on trees occupied by *Crematogaster mimosae* (*N* = 47 trees) Tannin levels from upper branches were 33% higher than on lower branches, even after controlling for the identity of ant occupant by using only trees occupied by *C. mimosae* (Table 2). This was true for both years, for all herbivore treatments, and in both experimental and control trees and branches. For all of the analyses that follow, upper and lower branches were analyzed separately, or only lower branches were analyzed.

Among lower branches, there were no differences in condensed tannin concentration among trees occupied by different ant species. However, there was a difference in condensed tannins among 1997 trees with different occupant ant species (*P* = 0.03, Table 3). Contrary to prediction 2, the lowest tannin levels were found in trees with a nonmutualist species, *C. nigriceps*, while trees with *C. mimosae*, a mutualist species, had the highest tannin levels (Figure 1). Scheffé post hoc tests revealed that there was a difference in tannin concentrations between

TABLE 3. PARTIAL TABLE FROM RANDOMIZED BLOCKS ANCOVA FOR SUMMER 1997 DATA^a

Source	<i>d.f.</i>	<i>F</i>	<i>P</i>
Block	2	1.20	0.31
Herbivores	2	0.36	0.87
Ant species	3	3.08	0.03
Herbivores × ant species	6	1.03	0.44
Tree height	1	3.87	0.05
Branch height	1	15.24	<0.001

^a Dependent variable is condensed tannin concentration.

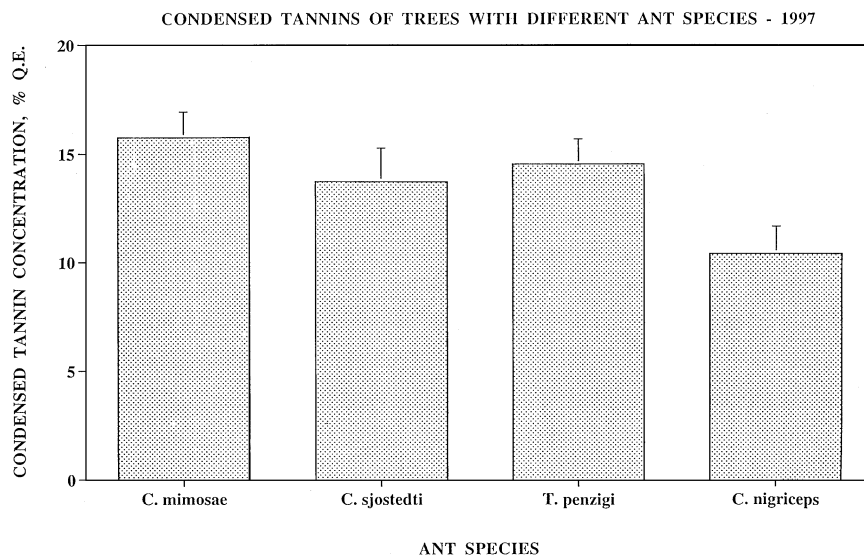


FIG. 1. Differences in mean condensed tannin concentrations (+SE) in *A. drepanolobium* among ant occupants for unmanipulated trees in 1997.

trees occupied by *C. nigriceps* and *C. mimosae* ($P = 0.03$) only. These two species swarmed more aggressively than *Tetraponera penzigi* or *C. sjostedti*. In 1998, there was no difference in condensed tannins among trees with different occupant ant species ($F = 0.67$, $P = 0.58$).

We found no effect of our leaf removal treatments ($F = 1.71$, $P = 0.18$). Paired t test comparisons that either controlled for within-tree variation (leaf removal vs. leaf control) or paired leaf removal vs. control tree or leaf control vs. control tree were not significant (range of $t = 0.22$ – 1.20 , $P = 0.83$ – 0.23). Condensed tannin concentration in control tree leaves was 14.80 ± 0.64 (S.E.) % QE ($N = 89$), in leaf controls was $13.65 \pm 0.74\%$ QE ($N = 74$), and in the leaf removal treatment was $12.87 \pm 0.83\%$ QE ($N = 75$). There were no interactions between leaf removal treatments and either herbivore treatments ($F = 0.41$, $P = 0.80$) or ant treatments ($F = 0.67$, $P = 0.67$).

When both years were combined (180 different trees, no tree measured twice), there were no year or ant species effects, but there was a significant mammalian herbivore effect (Table 4). There appears to be a difference in these data between the confirmed mutualist (*C. mimosae*) and the other ants in terms of how tannin concentrations respond to mammalian herbivore treatments, resulting in a significant ant $\times$ herbivore treatment interaction ($F = 2.35$, $P = 0.006$). This interaction means that for trees without *C. mimosae*, the differences between mammalian herbivore treatments are consistent with prediction 1 ($P = 0.05$;

TABLE 4. PARTIAL TABLE FOR REDUCED ANOVA MODEL FOR ALL DATA FOR BOTH YEARS USING UNMANIPULATED TREES ONLY^a

Source	<i>F</i>	<i>P</i>
Year	0.95	0.33
Herbivores	3.11	0.05
Ant species	2.08	0.13
Ant × year	1.89	0.16

^a Dependent variable is condensed tannin concentration. The interaction term was included in this analysis because in the full ANOVA model with all interaction terms, this was the only interaction with $P < 0.25$. There were also no significant block effects ($P = 0.91$) in the full model.

Control = $12.03 \pm 0.89\%$ QE, antelope only = $12.98 \pm 1.07\%$ QE, megaherbivores + antelope = $15.24 \pm 0.88\%$ QE). Data for each of the three ant species separately show this trend.

Within *C. mimosae* trees, the results are essentially reversed. Tannin levels are high on branches exposed to little or no herbivory (i.e., contra prediction 4), and low on branches subject to high herbivory (Table 2). We identified dung piles according to mammalian herbivore species and grouped these species according to whether they were tall enough to either reach the 1-m or 2-m branch height classes. Among individual plots, tannin levels were negatively correlated with the number of dung piles of species capable of reaching either the 1-m or 2-m branch height classes ($F = 5.82$, $P < 0.02$).

There was no correlation between tree height and tannin concentrations ($r = 0.11$, $F = 1.08$, $P = 0.30$) in 1997, although there was a positive correlation between branch height and tannin concentrations ($r = 0.37$, $F = 14.22$, $P < 0.001$).

Trade-Offs. Tannin concentration and thorn length were not correlated in 1997 ($r = 0.20$, $F = 2.61$, $P = 0.11$) or 1998 ($r = 0.074$, $F = 0.78$, $P = 0.38$). There was also no interaction effect between tannin concentration, thorn length, and either ant species (1997: $F = 0.29$, $P = 0.83$; 1998: $F = 0.39$, $P = 0.76$) or herbivore treatment (1997: $F = 0.51$, $P = 0.60$; 1998: $F = 0.15$, $P = 0.86$). When data for each ant species were analyzed separately, there was no correlation between tannin concentration and thorn length in 1997 and 1998 (range of $F = 0.06$ – 0.85 , range of $P = 0.81$ – 0.25). However, contrary to prediction 3, greater mean tannin concentration was associated with greater mean thorn length across ant species in 1997 ($r = 0.99$, $F = 202.6$, $P = 0.005$) (Figure 2), but not in 1998 ($r = 0.15$, $F = 0.04$, $P = 0.85$).

For low branches (height = 1 m), and with data for each ant occupant species treated separately, we found a significant correlation between tannin concentration

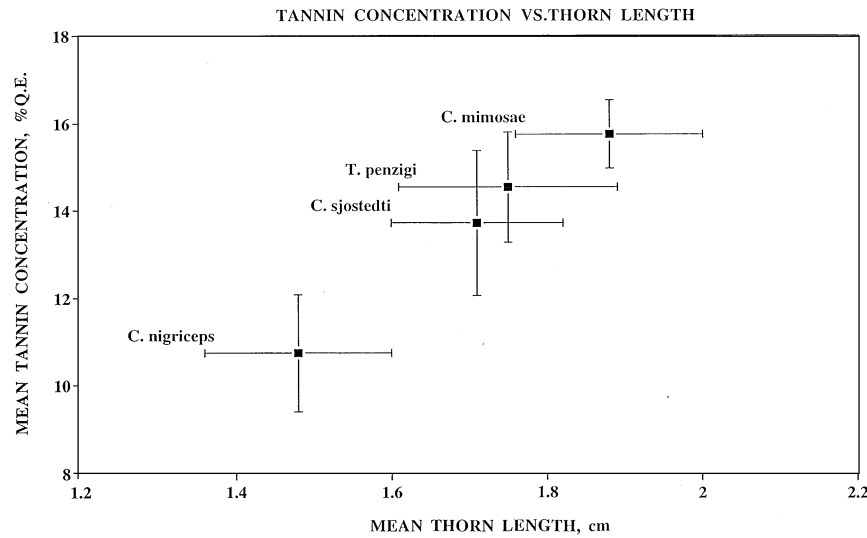


FIG. 2. Relationship between mean condensed tannin concentration and mean thorn length per tree averaged across ant treatments. Error bars represent ± 1 SE for both tannin concentration (ordinate) and thorn length (abscissa).

and new branch growth for trees occupied by *T. penzigi* only. However, this correlation was positive ($r = 0.55$, $F = 11.34$, $P = 0.002$, $N = 28$). For high branches (height = 2 m), we had data for trees occupied by *C. mimosae* only. There was a negative trend between tannin concentration and branch growth, but this was not significant ($r = -0.33$, $F = 3.37$, $P = 0.08$, $N = 29$). Thus, there is no support for prediction 3, viz. that there is a trade-off between tannin production and growth.

DISCUSSION

Inducible Defenses. There was considerable variation in condensed tannin concentrations among *A. drepanolobium* individuals and in different parts of the canopies of individual trees. Similarly, there was high variation in thorn lengths within and among individuals (Young and Okello, 1998), which means that substantial sample sizes are necessary to reveal even moderate effect sizes. Some of the variation in tannin concentrations includes interyear differences within trees and differences among mammalian and ant treatments.

Our pooled results for 1997 and 1998 provide evidence for inducible tannin defenses across mammalian herbivore treatments in a manner that is consistent with prediction 1. However, this effect was small and was revealed only after excluding trees occupied by one of the ant species. The absence of a strong effect

of herbivore treatments may be due to the short time available for the production of inducible defenses (see also Young and Okello, 1998) or because these trees do not strongly respond to mammalian herbivory. In addition, tannin response to herbivory may be ephemeral (Furstenburg and van Hoven, 1994).

An additional consideration is that secondary compounds may not always be effective against mammalian herbivores. The condensed tannin concentrations found in *A. drepanolobium* in this study were relatively low, and it is uncertain whether they reached a threshold level necessary to deter ruminants as suggested by Cooper and Owen-Smith (1985). Further examination of the behavioral and physiological responses of local mammalian herbivores to different levels of tannin production is required to answer this question. We believe that the search for generalities regarding the inductive responses of trees to mammalian herbivory must necessarily focus on the abilities of the trees to respond in a timely manner and with tannin levels of sufficient concentration to act as a deterrent to further herbivory. Furthermore, optimal tree response strategies with regard to growth-defense relationships, as well as possible trade-offs between multiple defensive strategies (e.g., tannins and thorns), must be reconsidered (see below).

Ant occupants appeared to exert a greater effect on condensed tannins than mammalian herbivore treatments. It is possible that differences among ant treatments occurred because ants choose trees according to their tannin phenotypes. We consider this to be unlikely because ant species replace one another on trees (Young et al., 1997). Trees occupied by the two more aggressive ant species did not have lower tannin concentrations than trees occupied by the less aggressive ant species. This result is inconsistent with prediction 2. Trees occupied by one of the two aggressive species, *C. nigriceps*, did exhibit lower tannin levels (at least in 1997); this is the ant species that eats the axillary shoots of its host trees, and reduces the number of leaves per branch. One possibility is that the negative impact of the ant on the leaves reduces the resources available to the tree to invest in tannin defenses. An alternative explanation is that their destruction of axillary buds results in the production of larger, more nectariferous (observed), and physiologically younger (implied) leaves. "Younger" leaves may produce less tannin (Furstenburg and van Hoven, 1994).

There was also a significant ant $\times$ herbivore treatment interaction, with trees occupied by *C. mimosae* exhibiting a pattern in which shoots subject to less herbivory contained substantially more tannin than shoots subjected to more herbivory. This contradicts both prediction 1 and prediction 4. It is also curious that the antelope-only treatment had lower tannin concentrations than the total exclusion plots in 1998. Are there lower levels of tannins where herbivory is highest under certain circumstances because browsing causes a local decline in tannins? At first sight, such results might seem counterintuitive because it is usually assumed that tannins are produced in order to reduce herbivory and might be expected to increase in concentration under high herbivory. However, other studies of African

acacias have found that tannin concentrations decreased with herbivory. Du Toit et al. (1990) found that heavily browsed specimens of *A. nigrescens* had greatly reduced condensed tannin concentrations and may serve as "grazing lawns" (sensu McNaughton, 1983) for herbivores. They proposed the following mechanism for this phenomenon: Browsing reduces intershoot competition for nutrients through a reduction in the number of shoots and the release of apical dominance. The result is increased concentration of nutrients in the remaining shoots. Increased nutrient concentrations in the remaining shoots was recorded by them in *A. nigrescens* [but not *A. tortilis*; see also Gowda (1997)] and Teague (1989) for *A. karroo*. Du Toit et al. (1990) also showed that there was a strong positive correlation in *A. nigrescens* between leaf nitrogen concentration and the percentage of browsed shoots on a tree. This increased nutrient concentration, together with a release of apical dominance, stimulates growth. We note here that Young et al. (1997) found that *A. drepanolobium* trees occupied by *C. nigriceps* showed greater shoot growth than trees occupied by the other ant species. Furthermore, carbohydrate demands incurred by rapid regrowth cause substrate limitation of carbon-based secondary metabolite synthesis (Bryant et al., 1983, 1987; Danell and Huss-Danell, 1985). Hence, leaf condensed tannin concentrations decline. Reduced chemical defense and increased shoot nutrients increase the palatability of most woody plants (Bryant et al., 1983; Cooper and Owen-Smith, 1985; Danell and Huss-Danell, 1985; Cooper et al., 1988), thereby attracting increased browsing pressure. This hypothesis remains to be tested. We note here that another study (Rohner and Ward, 1997) found no reduction in secondary compounds in *A. raddiana* and *A. tortilis* that suffered unnaturally high levels of herbivory in Israel.

Our data certainly suggest that tannin responses are highly contingent effects. We tentatively suggest that some forms of browsing may sufficiently increase carbohydrate demands for regrowth and cause a trade-off with secondary metabolite synthesis and, thus, result in a subsequent decline of tannin concentrations. If browsing is not severe enough, or does not result in the release of apical dominance, intershoot competition will not be reduced and the process will not occur as outlined by Du Toit et al. (1990), and induced production of tannins may then occur in trees suffering herbivory.

Trade-Offs. There was no indication of trade-offs between investments into chemical or mechanical defense or between chemical defense and growth in *Acacia drepanolobium*. Indeed, across trees occupied by different ant species, mean tannin concentrations and thorn lengths were positively correlated in 1997 (Figure 3), in contradiction with prediction 3. Several issues arise concerning underlying assumptions when attempting to demonstrate trade-offs between thorn and tannin defenses in individuals within a population (see also Rohner and Ward, 1997):

1. Chemical and mechanical defenses may not be operating at a comparable time scale. Production of thorns is irreversible and may integrate a response over

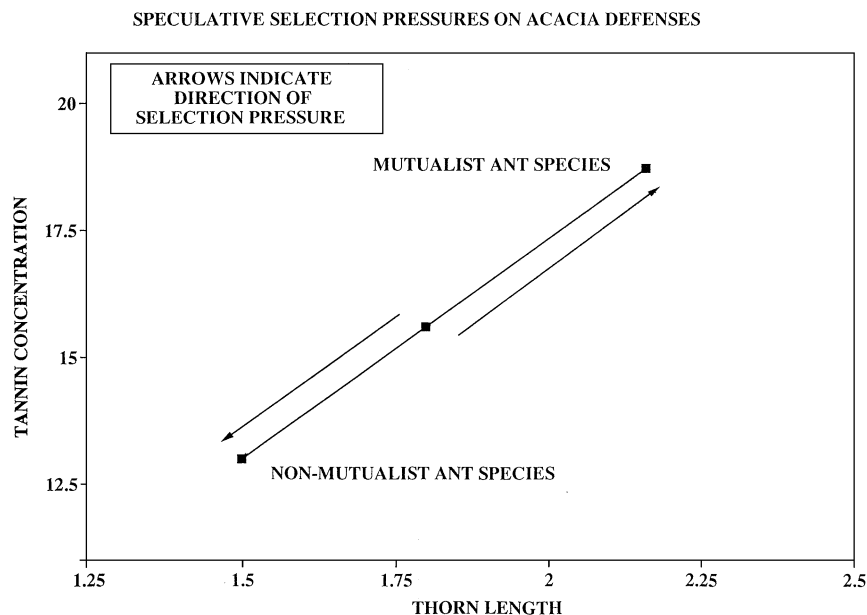


FIG. 3. Schematic diagram indicating how bidirectional selection by mutualist and non-mutualist ant species might result in a positive correlation between tannin and thorn production.

several years. Production of secondary metabolites, in contrast, is more variable on a shorter time scale (Cooper et al., 1988; Furstenburg and van Hoven, 1994). Indeed, in this study we found no significant correlations in tannin concentrations among years within trees. This difference in time scale between the production of thorn and chemical defenses may obscure correlations.

2. Phenotypic changes in response to herbivory can cause positive, rather negative, correlations. The negative impact of *C. nigriceps* on the trees (reduced leaf area and virtually eliminating reproduction) may cause the trees to be stressed, reducing their abilities to invest in both tannins and thorns. Conversely, a mutualist species such as *C. mimosae* may increase the tree's quality (e.g., by reducing herbivory), resulting in more resources being available to invest in both tannins and thorns against mammalian herbivory. These effects may result in bidirectional selection (Figure 3), causing the observed positive correlation.

3. If there is a small difference between good and poor individuals in the amount of resources acquired (allocated to total defense) and a large difference in the relative allocation of resources to tannin and thorn defenses, then a trade-off will occur (Van Noordwijk and de Jong, 1986) (Figure 4a). If there is a large difference between good and poor individuals in the amount of resources acquired (allocated

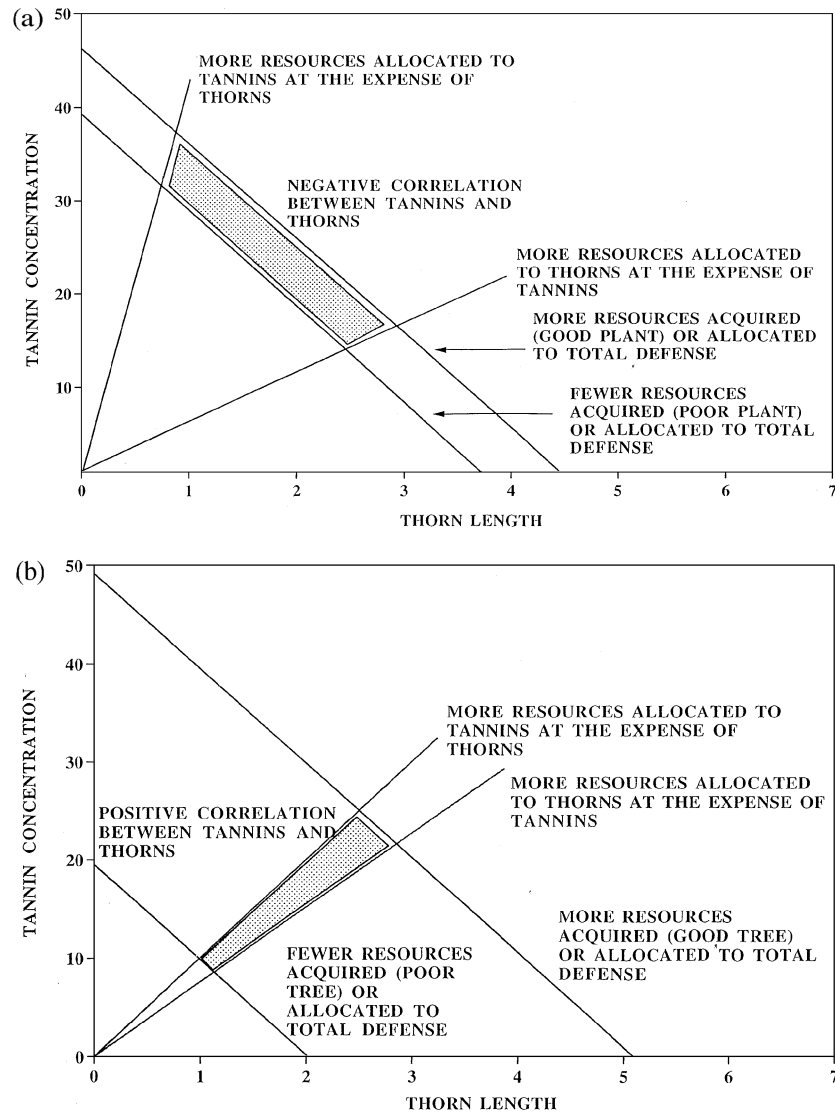


FIG. 4. (a) Schematic diagram indicating how a small difference between good and poor individuals in the amount of resources acquired (or allocated to total defense) and a large difference in the relative allocation of resources to tannin and thorn defenses will cause a trade-off (Van Noordwijk and de Jong, 1986). (b) Schematic diagram indicating how a large difference between good and poor individuals in the amount of resources acquired (or allocated to total defense) and a small difference in the relative allocation of resources to tannins and thorns will result in a positive correlation (Van Noordwijk and de Jong, 1986).

to total defense) and a small difference in the relative allocation of resources to tannins and thorns, a positive correlation will result (Van Noordwijk and de Jong, 1986) (Figure 4b).

The scenarios in Figures 3 and 4b are not mutually exclusive, i.e., large differences in resource availability may be induced by the activity of the ants which, if combined with low variability among plants in resource allocation, will result in the scenario outlined in Figure 4b. Further experimentation, such as ant removals combined with manipulation of resource availability, is needed to ascertain whether these explanations are appropriate for *Acacia drepanolobium*.

4. Defenses may not be costly to the plant. Inducible defenses were apparent for physical defenses in *A. drepanolobium*, *A. seyal* (Young, 1987), *A. tortilis* (Gowda, 1996a; Rohner and Ward, 1997), and *A. raddiana*, suggesting that thorn production is costly and resources are allocated differently when browsing levels are low. However, the results of Rohner and Ward's (1997) study on *A. tortilis* in Israel, Gowda's (1997) study on *A. tortilis* in East Africa, and the study by Du Toit et al. (1990) of *A. tortilis* in South Africa did not confirm this for secondary compounds.

Thus, it is still not clear whether condensed tannins can be considered as general defense compounds in *Acacia* species, whether they are effective inducible defenses (see review by Owen-Smith, 1993), and under which conditions such responses are likely to be expressed. Further research is needed to understand these relationships. Our original, admittedly simplistic, view of these compounds as defenses against herbivory certainly needs revision. Undoubtedly, such revision will need to incorporate more realistic models of physiological constraints to defense production and its relationship with investments in other traits such as growth.

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