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Increased thorn length in *Acacia depranolobium* – an induced response to browsing

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Summary. I report here longer thorns induced by large mammal herbivory on the tree *Acacia depranolobium.* I compared trees that had been browsed by domestic goats to trees protected from goat browsing. Thorns on browsed branches within the reach of goats (<125 cm above the ground) were significantly longer than thorns from higher branches on the same browsed trees, and significantly longer than branches at similar heights on unbrowsed trees. It appears that increased thorn length was an induced response to large mammal herbivory in *Acacia depranolobium*, both among and within individual trees.

Key words: Induced defense – Herbivory

A growing body of descriptive and experimental evidence indicates that individual plants subjected to herbivory increase their defenses. Induced resistance to insect attack has been inferred from increased production of chemical or physical defenses, or reduced fitness of herbivorous insects (Rhoades 1983; Schultz and Baldwin 1982; McNaughton and Tarrants 1983; Karban 1983; Karban and Carey 1984). Such plasticity in plant defenses allows plants to divert resources to defense only when they are needed, increasing overall efficiency of resource allocation.

Several lines of evidence indicate that thorns and prickles are effective deterrents of herbivory. A) An examination of feeding rates on various armed and unarmed African savannah trees showed that thorns reduced the rate of browsing by large mammals (Cooper and Owen-Smith 1986). B) Rates of feeding by mammalian herbivores were greatly increased by the experimental removal of thorns from *Acacia* species (Cooper and Owen-Smith 1986) and prickles from the thistle *Carduus keniensis* (Young and Smith 1987). C) Abrahamson (1975) noted that thorns on *Rubus* shrubs in browsed sites were longer and sharper than thorns on shrubs from unbrowsed sites. This latter was probably an induced response.

I recently had the opportunity to examine the effects of browsing by domestic goats on *Acacia depranolobium* in Kenya. *Acacia depranolobium* is small African savannah tree. The branches of *A. depranolobium* are armed at each node with a pair of straight thorns up to 7 cm long. *Acacia depranolobium* is an ant-acacia: petiolar nectaries are present, and some thorns are swollen, often containing ant colonies. I present here data on an induced increase in thorn length on branches accessible to goats.

Study Sites and methods

I examined a population of *A. depranolobium* trees near Naro Moru, Kenya (0 10′S, 37 00′E, elevation 2,000 m) in October 1984. A road bisects the population, which is on ± level black cotton soil. The land south of the road is privately owned (by the Naro Moru River Lodge) and grazing by domestic stock has been prohibited for the last thirty years. Common land lies north of the road, and is heavily grazed by domestic stock. Acacias here are browsed mainly by goats. Goats rarely feed higher than 125 cm from the ground (personal observation). Levels of herbivory by large wild mammals (bushbuck, eland, giraffe, impala, waterbuck) have been low since settlement of the area by European farmers and ranchers in the 1920′s.

All trees were sampled 10 m north and 10 m south of the road for a 150 m stretch of road. The height of each tree was measured. Three branches were examined on each tree: the lowest branch (always less than a meter above the ground), the branch nearest to one meter from the ground, and the highest branch (or, in the tallest trees, the branch nearest to two meters from the ground). On each branch, the length of four representative unswollen thorns were measured: one each pointing up, down, left, and right (when facing the tree). Thorn lengths on each branch were averaged to give a single value for each branch, and differences among trees and among branch heights were compared. Forty-four trees were sampled on the north (browsed) side of the road, and 35 trees on the south (unbrowsed) side.

Results

Browsed branches produced longer thorns than unbrowsed branches. The average thorn lengths on branches are shown in Fig. 1. Thorns on the lower branches (within reach of goats) of browsed trees were 26–27% longer than thorns from a similar height on unbrowsed trees ($P<0.001$ for both lower branch height classes). These thorns on lower branches from the browsed sites were also 36–44% longer than thorns on the higher branches (out of reach of goats)

Table 1. Mean length in cm (±one standard error) of thorns either pointing up or pointing down on branches various heights above the ground in browsed *Acacia depranolobium*. Sample sizes in parentheses

	Branch height above ground		
	<75 cm	75–125 cm	>125 cm
Pointing up	2.27±0.12 (44)	2.28±0.14 (35)	1.69±0.18 (12)
Pointing down	2.34±0.13 (44)	2.43±0.14 (35)	1.75±0.20 (12)

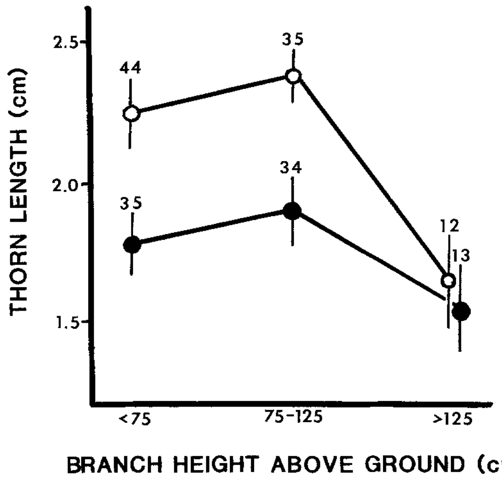

Fig. 1. Mean thorn length in cm (±one standard error) on branches various heights above the ground in browsed (o) and unbrowsed (•) *Acacia depranolobium* trees. Sample sizes are above each bar

on the same browsed trees (P<0.001). The length of thorns on higher branches in the browsed site were not significantly different from the length of thorns in the unbrowsed site.

The observed differences in thorn length were not due to a difference in overall thorn length between short and tall trees; lower thorns on tall browsed trees were no longer than lower thorns on short browsed trees (2.25 vs 2.36 cm). There was no significant difference in mean tree height between the browsed site (109.8±5.8 cm, S.E.) and the unbrowsed site (121.7±8.1, $t=1.19$, $P \sim 0.25$).

Because thorn length appears to be sensitive to herbivore pressure, it was suggested that on the lowest branches on browsed trees, the thorns pointing up might be longer, while on the higher branches, the thorns pointing down might be longer (Susan Meeks, personal communication). This would point the longest thorns in the direction of herbivore attack. However, this was not the case. There were no significant differences in thorn length on browsed trees between thorns pointing up and thorns pointing down, at any height (Table 1).

Discussion

Browsing on *A. depranolobium* branches induced increased gross morphological defenses in the form of longer thorns. It is unlikely that the thorn length differences between the browsed and unbrowsed *Acacia depranolobium* trees was due to genetic differences between the two sub-populations. The two sub-populations have been under different browsing pressures for only about thirty years, and even the smaller trees surveyed were probably not much younger than that. In addition, the two subpopulations are in close proximity, increasing the likelihood of considerable gene flow between them. Similarly, it is unlikely that the observed thorn length differences in this 30 yr natural experiment were due to site effects other than herbivory. All browsed trees were within 15 m of the nearest unbrowsed trees, and there were no obvious soil differences between the two sides of the road. Also, the within-tree differences in thorn length on the browsed site discount both edaphic and genetic explanations of the thorn length differences among trees. It is most likely that the thorn length differences between browsed and unbrowsed trees were due to phenotypic responses to differences in herbivory.

The induced increase in *A. depranolobium* thorn length varied within individuals. Unbrowsed branches on browsed trees showed no response. Karban and Carey (1984) showed that induced resistance can be expressed in plant parts other than those initially affected. In contrast, the present case shows that induced resistance can be limited to a local, within-plant response.

Several other physical plant defenses have been shown to be inducible, including structural silica (McNaughton and Tarrants 1983), tree gum (Karban 1983), and leaf toughness (Schultz and Baldwin 1982). These physical defenses are mostly irreversible. Once in place, the resources in them probably cannot be recovered (except for gum). Thorns in particular are investments in defense that cannot be called back.

Not only are thorns permanent investments, but their production is relatively slow. It takes several weeks for new thorns to grow to their final size. Therefore the induced response of increased thorn length will only be effective if fluctuations in herbivore pressure are longterm phenomena; the presence or absence of herbivores must be fairly constant. Dramatic longterm changes in herbivore densities in East Africa are not uncommon (Grimsdell 1979, Ottichilo 1986), and it appears that the slow, irreversible response to browsing of producing longer thorns by branches of *Acacia depranolobium* is adaptive.

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