Oecologia (1991) 86:70–75

Oecologia

Thorns as induced defenses: experimental evidence

A.V. Milewski*, Truman P. Young, and Derek Madden*****

School for Field Studies, 16 Broadway, Beverly, MA, 01915, USA

Received April 9, 1990 / Accepted in revised form September 24, 1990

Summary. We report evidence from controlled experiments that long straight thorns deter herbivory by browsers. Cut branches of three woody species that had their thorns removed suffered significantly greater herbivory by a tethered goat than did paired intact branches. Branches on living *Acacia seyal* plants that had their thorns removed suffered significantly greater herbivory by a wild population of free-ranging giraffes than did intact branches on the same plants. These differences in herbivory resulted in long term losses of branch length in clipped as opposed to control branches. In addition, branches within reach of giraffes produced longer thorns and a greater density of thorns than did higher branches. These results imply that increased thorn length is an induced defense.

Key words: Induced defense – Spinescence – Thorns – Giraffe – Herbivory

The presence of spines on plants is widespread. Although thorns, spines, and prickles on plants are often assumed to be anti-herbivore defenses, it has been suggested that the extent of plant spinescence is attributable to evolutionary causes other than herbivory (heat balance: Nobel 1980; liana defense: Maier 1982; drought resistance: Cole 1986, pp 50–51; refs. in Janzen 1986). Potter and Kimmerer (1988) failed to demonstrate increased herbivory on holly leaves after the removal of thorns, and experimental evidence in support of thorns as defenses is rare. Experimental removal of prickles from *Carduus keniensis* (Young and Smith 1991) and thorns from *Acacia* spp. (Cooper and Owen-Smith 1986) did increase herbivory, but neither of these studies used living plants and wild free-ranging herbivores. When the amounts of spines or stinging hairs varied locally, mammalian herbivores fed preferentially on the less well defended individuals (Supnick 1983; Pollard and Briggs 1984).

Thorns effective against medium-sized herbivores may not deter large mammals specialized for dealing with thorns. Megaherbivores (> 750 kg) may critically affect vegetation structure and function (Caughley 1976; Pellew 1983; Janzen 1986). Yet the effectiveness of plant defenses against megaherbivores is not known (Dagg and Foster 1982; Owen-Smith 1988).

If thorns are defensive structures, it is possible that these defenses can be induced; particularly, one may expect longer and more densely distributed thorns on those plants and plant parts that have been subjected to herbivory. Actual and simulated herbivory has been correlated with longer thorns (Abrahamson 1979; Myers 1987; White 1988; Myers and Bazely 1991) and a greater density of stinging hairs (Pollard 1989; Pullin and Gilbert 1989). Branches of *Acacia drepanolobium* within reach of goats had significantly longer thorns than higher branches on the same plants or branches at all heights on nearby plants protected from ungulate herbivory (Young 1987). A similar pattern has been reported qualitatively on trees eaten by giraffes (Foster and Dagg 1972). Using controlled and natural experiments, we studied the defensive effects of long straight thorns against both goats and free-ranging giraffes, and how herbivory may induce this defense.

Study site and methods

Study site and species

This research was carried out in June-August 1987 at Wildlife Ranching and Research, Inc. on the Athi Plains 40 km southeast of Nairobi, Kenya. At an elevation of 1800 m, the ranch is covered by a mixture of grassland and *Acacia* woodland in a semi-arid environment. Cattle and game animals (giraffes, Grant's gazelles,

Offprint requests to: T.P. Young

Present addresses: * Division of Mammals, Department of Zoology, Field Museum of Natural History, Roosevelt Road at Lake Shore Drive, Chicago, IL, 60605, USA; ** Department of Botany, University of California, Davis, CA, 95616, USA; *** Department of Biology, Modesto Junior College, Modesto, CA, 95355, USA

No significance should be attached to order of authorship

Thomson's gazelles, hartebeests, wildebeests, impalas) are managed on the ranch, and sold for meat.

Acacia xanthophloea and *A. seyal* ssp. *seyal* (Mimosaceae) are thorny savanna trees up to 20 m tall found at the lower (moister) end of soil catenas. *Acacia drepanolobium* occurs on impeded drainage ('black cotton') soils. Although it can grow to several meters, giraffe browsing often keeps individuals below 2 m tall. In addition to simple woody thorns it produces swollen thorns that house aggressive ants. *Balanites glabra* (Simaroubaceae) is an evergreen tree to 10 m tall with stout green thorns that occurs at low densities in *A. drepanolobium* savanna.

Giraffes (*Giraffa camelopardalis* L.) are restricted to African thorn savanna and scrub (Kingdon 1979; Dagg and Foster 1982). They are the largest extant ruminant megaherbivore. Their exceptional height allows giraffes to feed as high as 6 m above the ground, but they often forage at browse heights within the reach of co-existing herbivores (Wyatt 1969; Leuthold and Leuthold 1972; Young and Isbell 1991). Giraffes have mouths designed to bite very selectively, and rely partly on taking growing shoots before their thorns harden (Pellew 1984). However, they can ingest fully mature, hard thorns with apparent indifference (Hofmann 1973).

Thorn removal experiments

Tethered goat. Three spinescent tree species were used for this experiment- *Acacia drepanolobium*, *A. seyal* and *Balanites glabra*. Six to eleven individual trees were sampled from each species in June 1987. From each tree, a single pair of branches was collected, chosen within each pair for similarity in thorn density, thorn length, leaf density, and leaf length. On each branch collected, the length of the branch was measured, the total numbers of new and old leaves were counted, and the ten longest leaves measured. One of each branched pair was then randomly chosen, and all of its thorns removed to within 0.5 cm of their bases.

A domestic goat was kept at the research camp, and used in this experiment to test the effects of thorns on herbivory by a small ungulate browser. In a grassy area devoid of browse, the goat was tethered near a large log for each experiment. One pair of branches at a time was offered to the goat. The two branches were nailed to the log, 30 cm apart and 40 cm above the ground. Left-right orientation of the experimental and control branches was randomized among all branch pairs. The goat was allowed to feed until its first pause in feeding; the bites taken on each branch were counted as the goat fed. The branches were then collected, and the above measurements made again.

The differences between measurements before and after goat herbivory represented the following: length of branch tip eaten, number of new leaves eaten, number of old leaves eaten, and reduction in largest leaf size. For each branch pair, the difference between each of these values was calculated, as was the difference in the number of bites taken. For each species, experimental and control branches were compared with a one-tailed t-test against the null hypothesis that the thornless branches experienced no more herbivory than the thorny branches.

Thorn removal experiments

Free-ranging giraffes. In an area approximately 0.5 km from the camp, living branches of *Acacia seyal* had their thorns removed in July 1988. Fifty individuals were chosen in an area of approximately one hectare. Two branch pairs were chosen from each tree, based on similarity in the traits listed above, and also for similar height (2.0–3.0 m) from the ground. The only browsing animals in the study area other than giraffes during the experiment were impalas. During many hours of observation, impalas were never observed to feed at heights above 1.5 m (pers. obs., see also Du Toit 1990).

One of each branch pair was randomly selected, and all of its thorns removed to within 1.0 cm of the stem for the terminal 30–40 cm. A numbered tag was placed at the base of this thornless section, and at a similar position on the control branch. The trees were resurveyed at three weeks, one month, two months, three months, and sixteen months. Only 24 tagged branch pairs could be relocated for the latter survey.

In addition to taking entire branch tips, giraffes stripped branches of their bark, leaves, and thorns, leaving the woody stem cores. Too few control branches were eaten to compare the amount of stem stripped on browsed control and experimental branches. Therefore, 34 unclipped branches were located on which giraffes had fed, and the lengths of stem stripped were measured and compared to values on experimental branches on which giraffes had fed.

Thorn lengths on branches subject to differing levels of giraffe browsing. Two natural experiments give insight into the induced nature of *Acacia* thorn length. First, there is a limit to how high giraffes can feed. Although the tallest giraffes occasionally feed as high as 6 m, browsing is rare above 4.5 m (Wyatt 1969; Du Toit 1990; Young and Isbell 1991). If browsing by giraffes induces the production of longer thorns, then thorns on browsed trees should be shorter above the limit of giraffe browsing and longer below, and thorns on unbrowsed trees should be short at all heights. There exist *Acacia* trees in Nairobi, 40 km away, from which giraffes have been excluded for many years.

In 1987, *Acacia xanthopholea* and *A. seyal* thorns at varying heights were measured on the ranch. For each height on each tree, two to three branches were surveyed and three representative thorns and leaves measured on each branch. The density of thorns along each branch was also measured. Measurements on higher branches on the ranch were taken from trees or branches that had blown down, within two days of their fall. Several *A. xanthophloea* trees were similarly surveyed for thorn length in Nairobi town.

A second natural experiment was provided by the reluctance of giraffes to feed in the vicinity of the three-year-old research camp, located in *Acacia* woodland. Seven 200 m line transects were run from the middle of the camp, in all directions from the camp. One or two branches 1.7–2.0 m off the ground were surveyed on each *Acacia* tree encountered within 5 m of each transect. Three representative thorns and three representative leaves were measured on each branch.

In addition, giraffe dung was recorded for 1 m on either side each 10 m section of each transect. An index of giraffe presence was calculated as the sum of the rankings of mean number of dung piles per section and the percent of sections with dung.

Results

Thorn removal experiments

The tethered goat preferred to feed on *Acacia* branches with thorns experimentally removed (Table 1). The difference between control and experimental plants was greatest for new leaves eaten and branch tips lost. The two *Acacia* species lost three times as many new leaves from the experimental branches as from the control branches. Of the 17 *Acacia* control branches (combining both species), only one lost a shoot tip, whereas over half of the 17 experimental branches had their shoot tips eaten. The goat always ate entire leaves of *Balanites*. In addition, there were no new leaves on *Balanites* at this time, so only three of the five comparisons were made (Table 1). The goat also preferred *Balanites* branches without thorns.

The results from the free-ranging giraffes were even more striking (Table 2). In the three weeks between clipping the thorns and the first resurvey of the trees,

Table 1. The percent increase in herbivory by a tethered goat associated with thorn removal in paired trials. Mean values are given for "Cm of shoot tip eaten" rather than reporting infinite increases in herbivory. Sample sizes are the number of branch pairs tested. Tested with one-tailed *t*-test against the hypothesis of no increased herbivory on de-thorned branches

Effect	*Acacia seyal* $N=11$	*Acacia drepanolobium* $N=6$	*Balanites glabra* $N=5$
Number of bites taken	+28% ($p<0.01$)	+33% ($p<0.10$)	+16% ($p<0.05$)
Length of shoot tip eaten (cm)	70 vs 5 ($p<0.02$)	11 vs 0 ($p<0.05$)	7 vs 0 ($p\sim0.20$)
Number of new leaves eaten	+300% ($p<0.01$)	+300% ($p<0.01$)	---
Number of old leaves eaten	+72% ($p<0.001$)	+48% ($p<0.10$)	+25% ($p<0.005$)
Leaf length lost	+34% $p<0.001$	+65% $p<0.01$	---

Table 2. Herbivory by free-ranging giraffes on control and experimentally de-thorned branches of *Acacia seyal*. $N=50,50$ for all tests, unless otherwise noted

	Thorns removed	Control	*p*
Percent of branches eaten after:			
3 weeks	52	8	<0.006
1 month	64	10	<0.005
2 months	70	13	<0.005
3 months	74	16	<0.005
Percent of initial branch length eaten after 3 months:			
All branches	39	5	<0.001
Eaten branches only ($N=34,8$)	52	30	<0.01
Percent of length stripped:			
Eaten branches only ($N=34,34$)	18	13	<0.05
After 16 months ($N=24,24$):			
Number of shoots per branch	0.9	1.3	<0.005
Length of new shoots (cm)	4.9	5.2	<0.005
Total change in branch length (cm)	−12.9	+1.5	<0.05

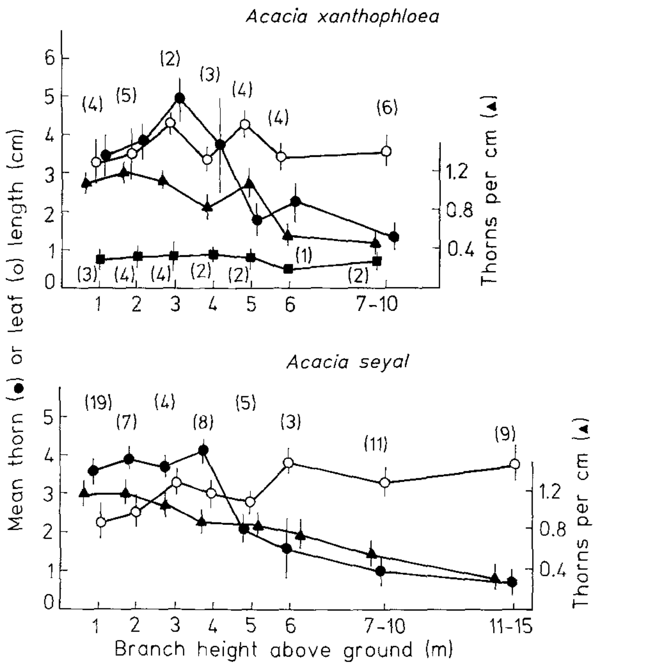

Fig. 1. Changes in thorn and leaf length with branch height in *Acacia xanthophloea* and *Acacia seyal*. *Closed circles* = thorns on trees growing in the presence of giraffes; *open circles* = leaves on trees growing in the presence of giraffes; *squares* = thorns on *A. xanthophloea* trees growing in the absence of giraffes; *triangles* = thorn density (number of thorns per cm of branch) on trees growing in the presence of giraffes. Sample sizes shown are the number of trees sampled at each height. Bars are one standard error

giraffes fed upon 26 of the experimental branches, but only 4 of the control branches. This difference continued through three months of surveys. Not only were giraffes more likely to feed on experimental branches, but for those branches on which they did feed, experimental branches suffered significantly greater branch tip loss and greater stripping damage than did control branches. Preference for branches whose thorns had been experimentally removed was therefore expressed both as a greater tendency to feed on experimental branches, and greater relative damage to experimental branches. In total, branches whose thorns had been removed lost an average of 39% of their original length in the first three months after clipping, whereas control branches lost an average of only 5%.

Both experimental and control branches exhibited growth during the study period. However, experimental branches averaged fewer shoots per branch and less total regrowth than control branches (Table 2). Even 16 months after clipping, experimental branches were on average 12.9 cm shorter than at the beginning of the experiment, whereas control branches were on average 1.5 cm longer.

The clipping experiment described here followed a preliminary clipping experiment that was carried out a year earlier. The results of that less extensive experiment showed similar significant increases in giraffe herbivory on branches whose thorns had been removed.

Acacia thorniness relative to herbivory

Increased thorn length and thorn density accompanied increased giraffe herbivory. On *Acacia seyal* and *A. xanthophloea* trees accessible to giraffes, thorns were consistently long at heights up to 4 m, but were significantly shorter at 5 m and above (Fig. 1). This was paral-

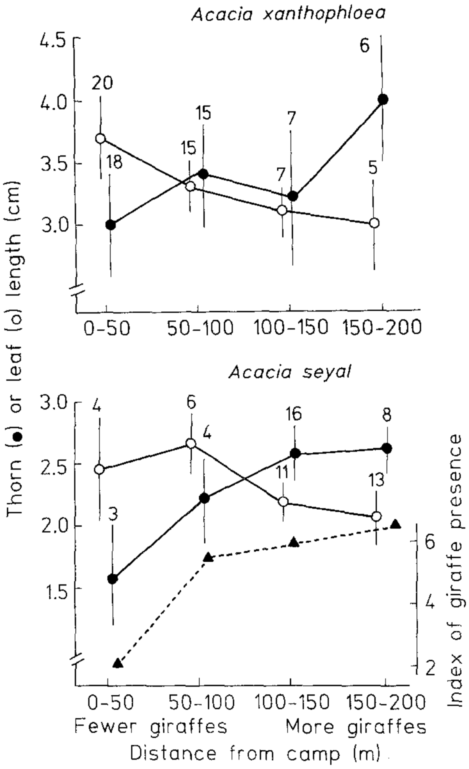

Fig. 2. Changes in thorn and leaf length in *Acacia xanthophloea* and *Acacia seyal* along a gradient away from the research camp (increasing giraffe density). *Closed circles* = thorn length; *open circles* = leaf length. Sample sizes shown are the number of trees sampled. Bars are one standard error. *Triangles* the index of giraffe dung presence

leled by differences in thorn density. On the other hand, mean leaf length remained constant *(A. xanthophloea)* or increased *(A. seyal)* with increasing height. Leaves were shorter than or equal to thorns low on the trees, but were significantly longer than thorns above giraffe feeding height. Unbrowsed *Acacia xanthophloea* trees in Nairobi had consistently short thorns at all heights. Interestingly, branches on Nairobi trees that had been pruned often produced long thorns.

Acacia trees further from the research camp produced longer thorns and shorter leaves than trees nearer the camp (Fig. 2). Within 50 m of camp, acacia thorns were shorter than their accompanying leaves, but beyond 150 m from the camp, acacia thorns were significantly longer than the leaves they protected. Giraffe dung decreased with increasing proximity to the camp (Fig. 2).

Discussion

Doubt persists about the defensive nature of thorns (Cole 1986, refs. in Janzen 1986; Potter and Kimmerer 1988). In the only previous study involving the removal of acacia thorns, Cooper and Owen-Smith (1986) demonstrated that penned goats ate more quickly from dethorned branches, but differences in the total amount of herbivory were not reported. Cooper and Owen-Smith presented only qualitative differences between control and experimental branches exposed to tame impalas. The results presented here provide the first clear evidence that thorns do defend acacias against a wild population of an important herbivore, the giraffe.

Thorns may function as defenses in two ways. First, sharp thorns may penetrate mouth parts. Second, long stout thorns may restrict the lateral mouth movements that strip branches. Giraffes do not strip stems with their tongues, but use the tongue to draw foliage towards the front lower teeth, which function as combs for stripping branches against the toothless upper palate (AVM, pers. observ.).

Acacia leaves are more palatable than the leaves of co-occurring unarmed plant species (Owen-Smith and Cooper 1987). This may explain why giraffes prefer acacias to other species, and even eat thorny acacias with considerable skill (Wyatt 1969; Foster and Dagg 1972). Despite this skill at dealing with thorns, giraffes eat considerably more material on effectively thornless acacia branches when they encounter them. This is demonstrated not only by our controlled experiment, but also by giraffe feeding on fallen trees. When giraffes encountered fallen acacias in our study site, they quickly and completely stripped the upper branches now accessible, which had very short thorns.

Acacia species are capable of considerable regrowth after normal levels of herbivory (Pellew 1983; Du Toit et al. 1990). However, *Acacia seyal* branches whose thorns had been experimentally removed were unable to recover the branch length lost to increased herbivory, even more than a year later. In the *Acacia* species studied here, thorn pairs are produced only at the nodes. Therefore thorn density is inversely proportional to internode distance. The increased density of thorns on *A. seyal* branches within reach of giraffes could be due to a direct adaptive response, but could also be the result of reduced growth rates on browsed branches.

The relationship between thorns and giraffes in East Africa goes back at least 1–2 million years (Dagg and Foster 1982). Many browsing animal species feed upon many thorny plant species, but the interaction between giraffes and *Acacia* species is particularly strong. Giraffes are strict browsers, and acacias are their preferred food, comprising the vast majority of their diet when available (Wyatt 1969; Foster and Dagg 1972; Young and Isbell 1991). Conversely, for many acacia species, giraffes are the primary browsers. Over a wide range of foliage heights (2–5 m), giraffes are virtually the only browsers (Du Toit 1990). Exceptions are elephants, which tear down entire limbs and trees, and vervet monkeys, which eat young shoot tips, flowers and fruits. It is reasonable to suggest that thorniness in East African acacias functions today mainly as a defense against giraffes.

The two natural experiments reported here (Figs. 1, 2) indicate that giraffe herbivory induces the production of long thorns in a pattern similar to that shown elsewhere for areas now predominantly browsed by goats (Young 1987). It is unlikely that the transects away from camp coincided with any natural gradient other than giraffe herbivory. The transects radiated in all directions from the camp, and were limited to similar *Acacia* woodland.

Nairobi is wetter than the ranch, but this is unlikely to account for the very short thorns measured there. Acacias in parts of Nairobi with giraffes (Nairobi National Park) showed patterns of thorn length similar to those at the ranch. In addition, thorn length at the main study site was unrelated to habitat type or location along the soil moisture gradient (Madden 1988).

Karban and Myers (1989) suggest three criteria for a plant response to qualify as an induced defense: the response is associated with herbivory, the response actually reduces herbivory, and reduced herbivory increases the fitness of the plants. Our controlled and natural experiments appear to meet the first two criteria. In September of 1987, when taller *Acacia seyal* trees were flowering, the only shorter trees in flower were within 100 m of the camp (DM, AVM, pers obs). Controlled experiments elsewhere have demonstrated that giraffe herbivory can dramatically reduce acacia growth (Pellew 1983). These observations imply that the latter criterion is met as well.

An induced defense is only adaptive if it tracks variation in herbivory in some effective way. There must be periods of low herbivory long enough that a constant investment in defense is unprofitable, and enough herbivory at other times that some investment is necessary. Additionally, the periods of increased herbivory must be long enough that the time delay in producing the defense is relatively short in comparison. Acacias in East Africa produce new shoots and new thorns with the onset of rains, usually once or twice a year (Lamprey 1984:126, AVM unpubl data). Therefore for induced increases in thorn length to be effective, fluctuations in herbivory may need to occur on a scale of many months to years. Multi-year changes in giraffe herbivory (Pellew 1983) and herbivore numbers in general have been reported for African savannas (Hillman and Hillman 1977; Grimsdell 1979; Walker et al. 1987; Prins and Douglas-Hamilton 1990), although it is not clear how common such changes are.

On the other hand, induced changes in thorn length could have evolved without variation in herbivore numbers. Variation in browsing relative to branch height could have been sufficient for the evolution of induced defense if there were no better predictor of branch height escape from herbivory than herbivory itself. In the absence of other cues that identify the plant parts at greatest risk of herbivory, the most effective cue for the distribution of defenses might be the actual herbivory on those plant parts.

Acknowledgments. We are grateful to Dr. D. Hopcraft for his encouragement of research on his property. We thank School for Field Studies students A.S. Armoudlian, B.D. Ascher, A. Becker, L.S. Beck, K. Bowes, C.M. Brown, K. Caggiano, M. Christina, S. Coles, K.S. Dietrich, J.M. Fair, F.H. Fisher, L. Frazier, J.E. Geer, E. Gibbs, B.R. Goodbar, J.S. Goodwin, M.E. Kennedy, K.M. Leonard, C. McKay, A.B. Marghoob, T. Martini, J.C.C. Neale, D. Oksenberg, J. Phillips, S. Pilkenton, M. Schustek, J. Schreiber, A. Smith, A.D. Strauss, S.E. Tuttle, A. Weill, S.T. Willard, L. Woods and R.M. Yelland for field assistance. R. Karban, L. Isbell, J.H. Myers, R. Ruggiero, P.R. Siegel, D. Wilkie, C.H. Peterson and anonymous reviewers assisted with the manuscript. Logistical support was provided by L. Isbell, M. Stanton, K. Hutt, P. Robinson, C. Carey, M. Sommerlatte, J.B. Stelfox, P.J. Tilley, the Department of Botany of the University of California at Davis, the Field Museum of Natural History and the St. Lawrence University Kenya Program.

References

Abrahamson WG (1975) Reproductive strategies of dewberries. Ecology 56:721–726

Caughley G (1976) The elephant problem – an alternative hypothesis. E Afr Wildl J 14:265–283

Cole MM (1986) The savannas: biogeography and geobotany. Academic Press, London

Cooper SM, Owen-Smith N (1986) Effects of plant spinescence on large mammalian herbivores. Oecologia 68:446–455

Dagg AI, Foster JB (1982) The Giraffe: its biology, behavior, and ecology. Robert E. Krieger Publishing Co., Malabar, Florida, USA

Du Toit JT (1990) Feeding-height stratification among African browsing ruminants. Afr J Ecol 28:55–62

Du Toit JT, Bryant JP, Frisby K (1990) Regrowth and palatability of *Acacia* shoots following pruning by African savanna browsers. Ecology 71:149–154

Foster JB, Dagg AI (1972) Notes on the biology of the giraffe. E Afr Wildl J 10:1–16

Grimsdell JJR (1979) Changes in populations of resident ungulates. In: Sinclair ARE, Norton-Griffiths M (eds) Serengeti: Dynamics of an Ecosystem. University of Chicago Press, Chicago, pp 352–359

Hillman JC, Hillman AK (1977) Mortality of wildlife in Nairobi National Park, during the drought of 1973–1974. E Afr Wildl J 15:1–18

Hofmann RR (1973) The ruminant stomach. Stomach structure and feeding habits of East African game ruminants. East African Monographs in Biology, Vol. 2. East African Literature Bureau, Nairobi

Janzen DH (1986) Chihuahuan desert nopaleras: defaunated big mammal vegetation. Ann Rev Ecol Syst 17:595–636

Karban R, Myers JH (1989) Induced plant responses to herbivory. Ann Rev Ecol Syst 20:331–348

Kingdon J (1979) East African Mammals. An atlas of evolution in Africa. Vol.IIIB. Academic Press, London, New York

Lamprey H (1984) Woodland ecology. In: Lusigi WJ (ed) Final report on the implementation of the Integrated Project on Arid Lands phase III. UNESCO, Nairobi, pp 108–138

Leuthold BM, Leuthold W (1972) Food habits of giraffe in Tsavo National Park, Kenya. Oecologia 35:246–252

Madden D (1988) Examination of thorns and ants as features of defense for East African *Acacia.* MS Thesis, California State University, Fresno, CA, USA

Maier FE (1982) Effects of physical defense on vine and epiphyte growth in palms. Trop Ecol 23:212–217

Myers JH (1987) Nutrient availability and the deployment of mechanical defenses in grazed plants: a new experimental approach to the optimal defense theory. Oikos 49:350–351

Myers JH, Bazely D (1991) Thorns, spines, and prickles: are they stimulated by herbivory and do they deter herbivores? In: Tallamy D, Raup M (eds.) Herbivore-induced Phytochemical Changes in Plants. John Wiley, New York

Nobel PW (1980) Interception of photosynthetically active radiation by cacti of different morphology. Oecologia 45:160–166

Owen-Smith RN (1988) Megaherbivores. The influence of very large body size on ecology. Cambridge University Press, Cambridge

Owen-Smith RN, Cooper SM (1987) Palatability of woody plants to browsing ruminants in a South African savannah. Ecology 68:319–331

Pellew RAP (1983) The impacts of elephant, giraffe and fire upon the *Acacia tortilis* woodlands of the Serengeti. Afr J Ecol 21:41–74

Pellew RAP (1984) Giraffe and okapi. In: MacDonald D (ed) Encyclopedia of mammals. Facts on File, New York, pp 534–541

Pollard AJ (1986) Variation in *Cnidoscolus texanus* in relation to herbivory. Oecologia 70:411–413

Pollard AJ, Briggs D (1984) Geneecologial studies of *Urtica dioica* L. III. Stinging hairs and plant-herbivore interactions. New Phyt 97:507–522

Potter DA, Kimmerer TW (1988) Do holly leaf spines really deter herbivory? Oecologia (Berlin) 75:216–221

Prins HHT, Douglas-Hamilton I (1990) Stability in a multi-species assemblage of large herbivores in East Africa. Oecologia 83:392–400

Pullin AS, Gilbert JE (1989) The stinging nettle *Urtica dioica*, increases trichome density after herbivore and mechanical damage. Oikos 54:275–280

Supnick M (1983) On the function of leaf spines in *Ilex opaca*. Bull Tor Bot Club 110:228–230

Walker BH, Emslie RH, Owen-Smith RN, Scholes RJ (1987) To cull or not to cull: lessons from a southern African drought. J Appl Ecol 24:381–401

White PS (1988) Prickle distribution in *Aralia spinosa* (Araliaceae). Am J Bot 75:282–285

Wyatt JR (1969) The feeding ecology of giraffe *(Giraffa camelopardalis)* in Nairobi National Park and the effect of browsing on their main food plants. MSc Thesis, University of East Africa, Nairobi

Young TP (1987) Herbivory induces increased thom length in *Acacia drepanolobium*. Oecologia (Berlin) 71:436–438

Young TP, Isbell LA (1991) Sex differences in giraffe feeding ecology: energetic and social constraints. Ethology (in press)

Young TP, Smith AP (1991) Herbivory in alpine Mount Kenya. In: Rundel P (ed) Tropical alpine systems: Plant form and function. Springer, Berlin Heidelberg New York