

**INTERACTIONS BETWEEN ACACIAS
AND GIRAFFE IN ITHALA GAME
RESERVE; A STUDY IN LANDSCAPE
CHANGE.**

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**ABSTRACT**

The effects of giraffe browsing on acacia communities of Ithala Game Reserve, KwaZulu-Natal (South Africa) were examined in this study. Acacia mortality and browsing intensity were assessed in detailed "wandering quarter" transects, and in a road-side survey of the reserve. Most *Acacia* species occurring in regions of the reserve with high densities of giraffe (ca. 1.8 giraffe per km²) had high levels of mortality. Mortality due to giraffe browsing for *Acacia davyi* was ca. 100%, and *A. caffra* and *A. karroo* were also heavily affected. No or very low mortality rates were recorded in other *Acacia* species (e.g. *A. tortilis*) existing in high giraffe-density areas. Species that grow below the height of maximum giraffe reach are generally more vulnerable to giraffe, as are species that have a greater proportion of leaf area positioned on the distal portions of their branches. The differential mortality that is occurring as a consequence of these and other factors appears to be altering the species distributions and compositions in the landscape.

INTRODUCTION

African savanna plant communities are one of the few systems that still contain to any significant extent the herbivores with which they co-evolved. Directly through settlement of the land and removal of local biota and indirectly through the formulation of managed 'conservation' areas, the structure of natural communities is being altered by man. Herbivorous animals are removed from ecosystems of which they are an integral part. Herbivores are also being added in excessive numbers to ecosystems (eg Dublin *et al*, 1990), and (in some cases) to ecosystems to which they do not belong. Seemingly small changes to a 'natural' system that alter its processes or states of equilibrium in the short run, can result in the system changing until an entirely new equilibrium (whether temporary or permanent) is reached. Thus, alterations of the normal herbivore densities of a system may be expected to instigate a change in the plant communities with which they interact.

Ithala Game Reserve, situated in the North of KwaZulu-Natal, South Africa, contains about 180 giraffe (*Giraffa camelopardalis*) that appear never to have existed in this region before (Goodman and Tomkinson, 1987). Observations within Ithala Game Reserve suggested that certain species of acacia were undergoing unexpected mortality, and this mortality appeared to be linked to giraffe browsing. Giraffe have previously been shown to affect the *structure* of woodlands in the Serengeti (Pellew, 1983), but have not previously been recorded to alter the distribution of species in space.

Physical gradients in the environment and competitive interactions between species are factors ordinarily assumed responsible for changes in the distribution of plant communities in space (Begon *et al*, 1992). That the distribution of different acacias in African savannas may be determined largely by the presence of a megaherbivore, and not by intolerance of environmental variations or competition, is a novel concept. The interesting situation occurring in Ithala Game Reserve, where *Acacia* species (or genotypes) that have not before been exposed to giraffe are coexisting with ca 1.8 giraffe per square kilometre, affords the opportunity to study the effect that giraffe browsing can have on acacias and their distributions in the landscape.

The current study aimed to determine the effects of giraffe browsing, if any, on *acacia* demography and possible implications for the distribution and composition of acacias in savanna landscapes.

MATERIALS AND METHODS

STUDY SITE

The study was carried out in July 1999 in Ithala Game Reserve (IGR) and in an adjacent private game farm to the South West of IGR, situated in the north of Kwazulu-Natal province, South Africa (27°30'S; 31°17'E). IGR consists of 29 653 Ha of farmland, to the south of the Phongola River, which was acquired between 1972 and 1982. Altitude varies from a minimum of 335 m above sea level at the Phongola River valley in the north of the reserve, to 1450 m above sea level at the Louwsburg massif in the South. Land rises steeply between the narrow valley systems of the Phongola-tributary catchments (Porter, 1985), resulting in 5 884 Ha (ca. 20%) of the reserve experiencing gradients greater than 40° (Le Roux, 1985). Annual rainfall is 743.6 mm (ten-year mean) with 77% occurring during summer (October to March). Three general rainfall areas are recognised: the southern high altitude region which experiences over 900 mm pa, the central plateau area of lower altitude which experiences between 800 and 900 mm pa, and the northern dry valley lowland which experiences less than 800 mm p/a. Summer temperature-range for the reserve is generally from 18° C to 30° C, but maximum temperature is 32° C during berg-wind conditions. Winter temperatures range from 15° C to 25° C. Cooler temperatures occur in the southern high altitude region, and warmer temperatures in the Northern valley of the Phongola river (Porter, 1984).

Occurring in the reserve are three veld types (as defined by Acocks (1975)). 'Lowveld' (type 10), which is a tropical bush and savanna type (51% of the reserve); 'Northern Tall Grassveld' (type 64), which is a false grassveld type comprising 45% of the reserve; and 'North-Eastern Mountain Sourveld' (type 8), which is an inland tropical forest type comprising 4% of the reserve. (Porter, 1984). In 1984 Lowveld comprised 51%, North-Eastern Mountain Sourveld 4%, and Northern Tall Grassland 45% of the area of the reserve.

Sample Site location

Twelve sites, ten within the reserve and two on the neighbouring farm, were examined to determine the impact of giraffe browsing on the acacia tree-species present. Sites were chosen to represent high or low giraffe density occurring in the area, and according to altitude. Sites of high and low altitude were chosen to control for temperature and precipitation gradients. Information about giraffe distribution was obtained from direct observations by research and field staff at IGR, and from aerial census records of 1997. Six sites with high giraffe-densities were selected for sampling (sites 1, 2, 3, 4, 5, 6,) and six sites with low or no giraffe occurrence were selected for sampling as controls (sites 7, 8, 9, 10, 11, 12) (fig. 1). In the study 'High giraffe-density' sites are those areas in which the giraffe occur in high frequencies (often sighted in the area). 'Low giraffe-density' sites are those areas where giraffe occur in low frequencies, or not at all. Two of the control sites occurred on the neighbouring farm (sites 10 and 11), where no giraffe occur, and site 8 occurred within a disused elephant 'boma' (a natural area surrounded with game-proof fences, previously used to contain elephants). The fencing of the boma is still in place and keeps giraffe out. Giraffe occur in high densities in the area surrounding the boma (site 5). Eight of the sites (including within the tourist camp – site 10) were located at high altitude (higher than 680 m above mean sea level). Four of the high altitude sites experienced high densities of giraffe, and four sites experienced low or no occurrence of giraffe. The remaining four sites were located at low altitudes (below 600m above mean sea level). Two low altitude sites had high densities of giraffe, and two sites had low densities of giraffe. All sites were accessible by road, or by tracks suitable for four-wheel drive vehicles.

HISTORY OF GIRAFFE

Introductions of giraffe into IGR were begun in 1977 with five animals, and a further 48 were introduced between then and 1984 (the area utilised by the giraffe in 1984 is indicated in figure 1). An aerial census recorded a population of ca. 157 animals in 1997, utilising the same area utilised by the 59 giraffe of 1984 (Wolf, pers. comm. 1999). Inferred population growth rates (fig. 2) indicate that this is an underestimate

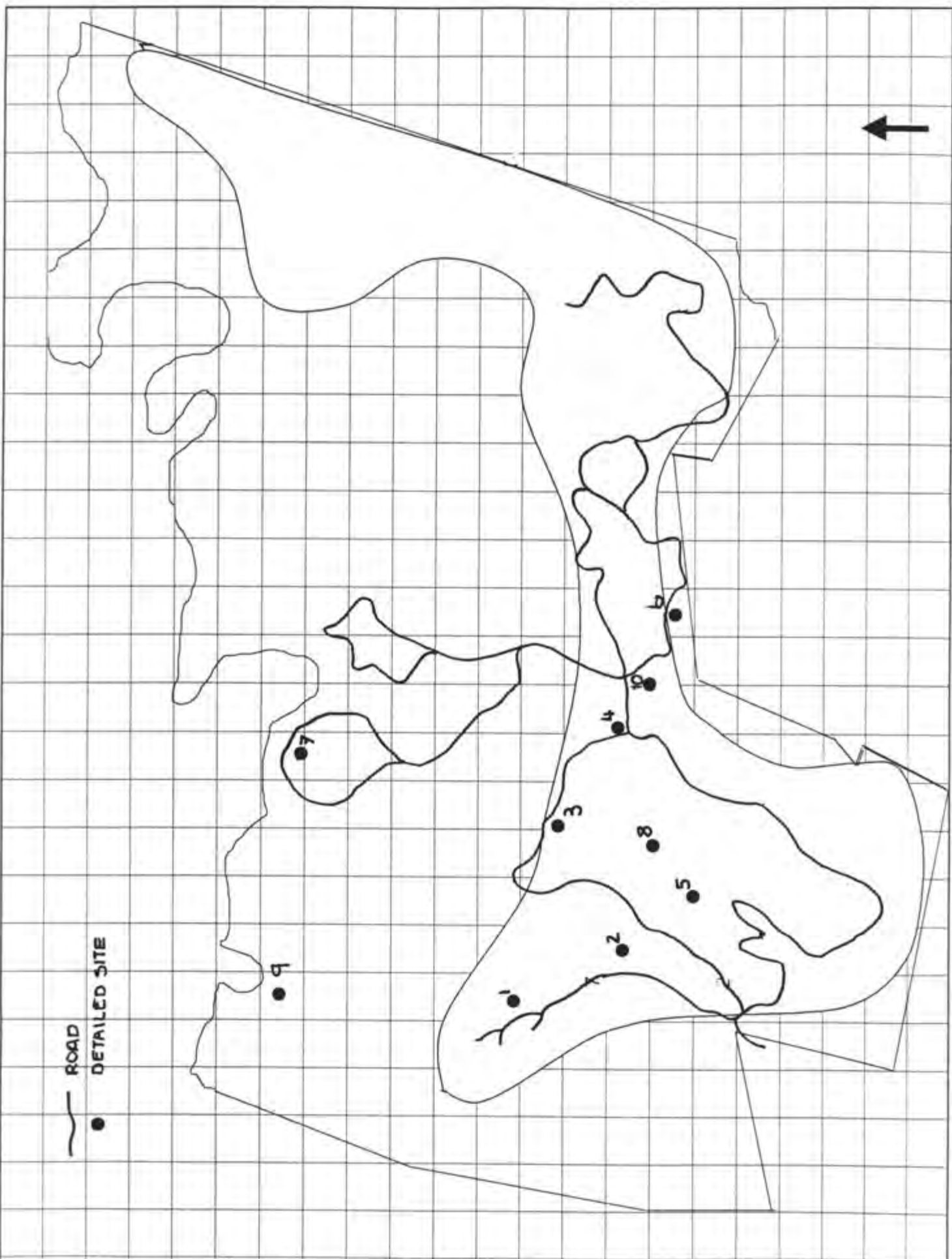


Figure 1: Area of high giraffe-densities (ca. 1.8 giraffe km⁻²) in Ithala Game Reserve, and the localities of detailed transects. Site 8 occurred within the elephant boma, and site 10 occurred within the rest camp. Sites 11 and 12 occurred on a neighbouring game farm to the south-west of Ithala Game Reserve.

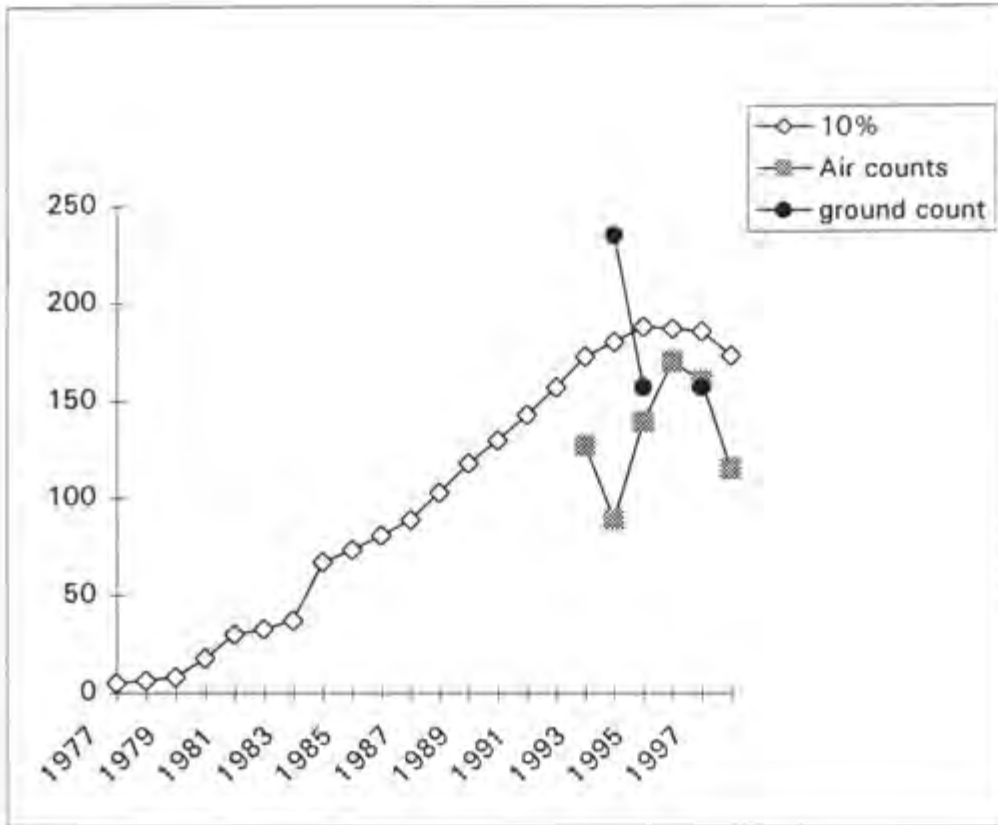


Figure 2: Projected population growth (10% pa) of giraffe in Ithala Game Reserve, KwaZulu-Natal, and census records from 1994 to 1998.

by ca. 20%. 180 Giraffe in a reserve of 29 653 Ha is a reserve-wide stocking rate of about 0.6 giraffe per km². Much of the reserve area is too steep or otherwise impenetrable to giraffe. It is roughly estimated from the 1997 aerial census and from observations by reserve staff that giraffe currently utilise a third of IGR. The actual stocking rate in the landscape is thus about 1.8 giraffe per km² (fig. 1)

METHODS

Roadside Survey

An over view of the acacia species occurring in the entire reserve was obtained from a park-wide transect along the internal roads. All accessible roads within IGR (public and residential) were traversed, and details of the acacia communities occurring on both sides of the road for 0.5 to 1 kilometre sections were recorded. Relative densities of acacias were recorded by estimating distance of visibility perpendicular to the road (Prins and van der Jeugd, 1993). A total of 86 sections occurred in the survey. Acacia species present in each section and the relative abundances of each species were determined by observation from the vehicle. An average was taken from the assessment of three independent observers. The proportion of apparent mortality for each species was similarly recorded. Browsing intensity was assessed on an overall basis for all species and individuals in each section. The browsed-branch-ends method could not be used as observations were made from the vehicle; other browse-related features were utilised instead to assess browse intensity. The absence of any apparent browse in trees was recorded as no browsing, apparent yet not very distinct browse-lines were recorded as light browsing, distinct browse-lines were recorded as moderate browsing, and the presence of 'half alive' individuals in the section - with no foliage below the browse-line - was regarded as heavy browsing.

Detailed Transects

Acacia trees at 12 sites were sampled using the 'Wandering Quarter' transect method (Bond, pers. comm. 1999) - which reduces sampling biases. A line is walked from a starting point through the study area on a fixed direction towards a chosen marker on the horizon. The nearest tree individual, within 45° either side of the 'line' of progress,

is approached for sampling. The sampled individual then becomes the new starting point and the closest individual, 45° either side of a new 'line' is sampled next. Of each acacia encountered in the transects, several aspects were recorded: species; height determined to the nearest 0.5 m (using a one-meter rule); total browse-damage to the canopy (method described in detail below); total canopy leaf-area (assessed by estimating the number of a reference branches in the canopy by two independent observers); presence of pods; above-ground mortality status of all aerial portions (alive or dead); the 'browse-line' height (a horizontal division through the tree canopy at a constant height, created by differing browsing pressure on the upper and lower portions of the canopy) was assessed where present. Individuals that were completely defoliated below the browse-line were categorised as 'half alive'. In each transect, trees were sampled until ca. 50 individuals of the predominant species had been encountered.

Browse-damage assessment

To assess damage by browse, the status of the 'branch-ends' of the entire-canopy was recorded for each individual. Branches that were undamaged possessed a tapering form. Consequently, undamaged branches ramified into many fine twigs of narrow diameter (less than 1 cm). Branches that had undergone mechanical damage, such as the pruning action of browsing herbivores, had the finer tips removed. Such truncated branches ended abruptly, having broader terminal diameters (fig. 3). A terminal twig diameter of 1 cm, or greater, was taken to indicate severe damage by browsing. The proportion of each canopy showing severe browse damage, was carefully visually assessed. Individual trees were placed into classes of browse-damage, according to the proportion of the canopy showing browsed branch-ends. The browse-damage represented by each of the six categories is represented in table 1.

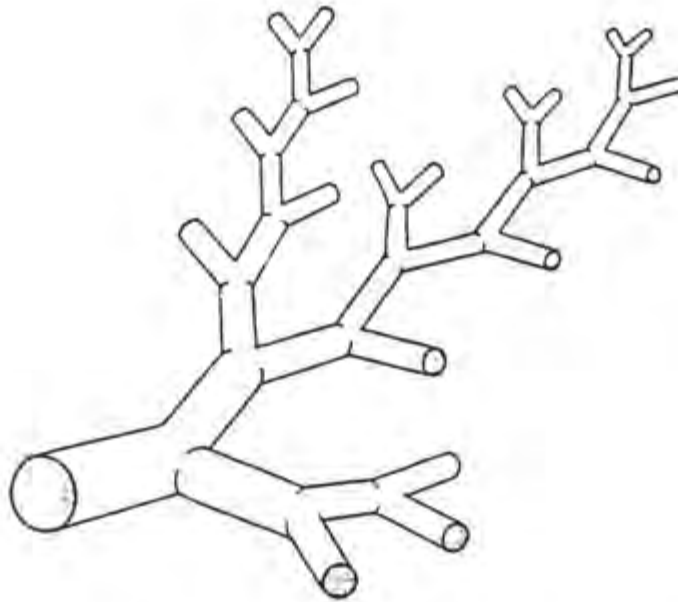


Figure 3: Schematic representation of a tree branch showing tapering ramifications. Tapering form is truncated by pruning action of herbivores. Broad terminal diameters (>1 cm diameter) of branch-ends indicates browsing has occurred.

Table 1. Categories of 'browsed branch-ends' indicating proportion of giraffe browse-damage to entire canopies.

Rank	Percent of canopy, with branch-ends greater than 1 cm diameter	Browse damage
1	0 - 10 %	Light to no browse
2	10 - 25 %	Light browse
3	25 - 50 %	Moderate browse
4	50 - 75 %	Heavy browse
5	75 - 90 %	Very heavy browse
6	90 - 100 %	Extremely heavy. Tree usu. dead

Seedling Transects

Line transects of 50 m x 20 m were placed at 11 of the sites sampled by Wandering Quarter transects. All acacia juveniles (individuals below 2 m height) within the transects were recorded. Species were recorded and placed into height classes of ≤ 0.5 m, >0.5 m and ≤ 1 m and >1 and ≤ 2 m. (Data not shown.)

Analysis

Differences in mortality between species were tested using Chi-squared analysis, within and between high and low giraffe-density sites. Regression analyses were made on the correlation between survival and browse intensity category. Browsing intensity and related mortality of species on a reserve wide basis (roadside survey) was analysed using Spearman's Rank Correlation Coefficient. All analyses were performed using STATISTICA for Windows (StatSoft, Inc. 1995).

RESULTS

Road side transects

Eleven different *Acacia* species were encountered in the park-wide roadside survey. These species are assumed to be representative of acacias occurring in IGR, as no further species were encountered at other points during the study. Figure 4 indicates the relative occurrence of each species within IGR. *A. nilotica* and *A. karroo* occurred in over 50% of the survey, whereas *A. ataxacantha*, *A. brevispica*, *A. robusta* and *A. sieberana* occurred in less than 10% of the survey. Only 10% of the road-sections surveyed contained no acacias at all.

Mortality in detailed transects

Significantly higher acacia mortality was found in the "high giraffe-density" areas (fig. 5) than in "low giraffe-density" areas. Different amounts of overall mortality were recorded for different *Acacia* species. Mortality occurred to a greater extent in species such as *A. davyi* and *A. caffra* than in species such as *A. karroo* and *A. nilotica*. Almost 100% mortality was observed in *A. davyi*. A single living individual was found, overhanging a river and closely surrounded by other tree species, where it was presumably inaccessible to giraffe. *A. gerardii* and *A. tortilis* were the only species recorded with no mortality in both high and low giraffe-density areas. All species had no or significantly lower mortality in the low giraffe-density sites. Mortality was only apparent in *A. caffra* and *A. karroo*, in the absence of giraffe (9% and 2% respectively).

Browsing in detailed transects.

To test whether survival is related to intensity of browsing experienced by the trees (browsing categories qualified in table 1), survival rate for the trees was correlated with browse intensity class (fig. 6). Data points were generated from the mean browsing category for all individuals of each species in all high giraffe-density sites, and separately for all individuals of each species in all low giraffe-density sites. The same was done for the relative survival values, and these were then correlated with browsing intensity. The correlation was significant at the 95% level ($R^2 = 0.69$, $P < 0.01$, $n = 11$). Removing *A. gerardii*, (a species with naturally thick branch ends) from the analysis further strengthens the correlation, $R^2 = 0.84$, $P < 0.001$. To test whether mortality was due to giraffe browsing and not due to browsing by other herbivores, the height of the browsing lines between the high and low giraffe-density areas was compared. The browse-lines in high-giraffe (avg=4.9 m) density areas were significantly higher than low giraffe-density areas (avg=2.6 m) ($t = 4.86$, $p < 0.001$), above the maximum reach of all other herbivores (except elephant). Browsing also significantly reduced the occurrence of pods on trees (table 3). Trees in high giraffe density areas had pods significantly more often ($df = 5$, $t = -2.597$, $p < 0.05$) than trees in low giraffe density areas.

Differential mortality

Different levels of mortality among the *Acacia* species may be due to different levels of giraffe browsing on each species or different sensitivities to browsing. Figure 7, obtained from the park wide survey data, indicates differing trends in the mortality related to browse-pressure for different species. Some species had lower amounts of mortality with the same amount of browsing pressure, than others. *A. nilotica* and *A. karroo* appear more able to survive the same amounts of browsing (medium to high levels) that causes high mortality (above 50% in some cases) in *A. caffra*, *A. davyi* and *A. gerardii*. The results of mortality trends throughout the reserve represented in figure 7 are less robust than those represented in figure 5.

The differential mortality of acacias in IGR may be a consequence of different abilities to survive browsing so that, for example, the mean level of browsing will cause the death of one species but not another. This varying tolerance may be modified by availability (accessibility and desirability) of a species to giraffe. The proportion of foliage allocated to the terminal branches (branches less than 1 cm diameter) is shown in figure 8 to be a factor influencing abilities of the species to survive browsing. Those species with a higher proportion of their leaves situated on the distal (narrow diameter)

branches, which are easily bitten off, have lower survival rates than those with more of their leaves located on internal (broader diameter) branches.

Height and differential survival

Tree height may be a factor in differential survival, with trees >6 m emerging above giraffe browsing height. Reserve-wide observations indicated that taller trees (greater than 6 m) survived more frequently than shorter individuals where browsing was intense. This observation is not reflected in figure 9 except to a small extent for *A. caffra* (fig. 9a). *A. caffra* individuals which are in the height zone accessible to giraffe (2 - 6 m) have a 20 % higher mortality rate than individuals that are taller than 6 m. Short individuals, less than 2 m, had mortality rates similar to individuals of all sizes existing in low giraffe-density areas. Mortality for *A. davyi* (fig. 9) is the same as that represented for this species in figure 5 (ca. 100% mortality in high giraffe-density areas, irrespective of height. No mortality occurred in low giraffe areas, again irrespective of height). Little difference in mortality rates occurred between size classes of *A. karroo* and *A. nilotica*, and no mortality was encountered for *A. gerardii* (which only occurred in low giraffe-density sites) or *A. tortilis* (which only occurred in high giraffe-density sites). Individuals of *A. karroo*, *A. nilotica*, *A. gerardii* and *A. tortilis* of all heights are thus indicated to be equally vulnerable to browse related mortality.

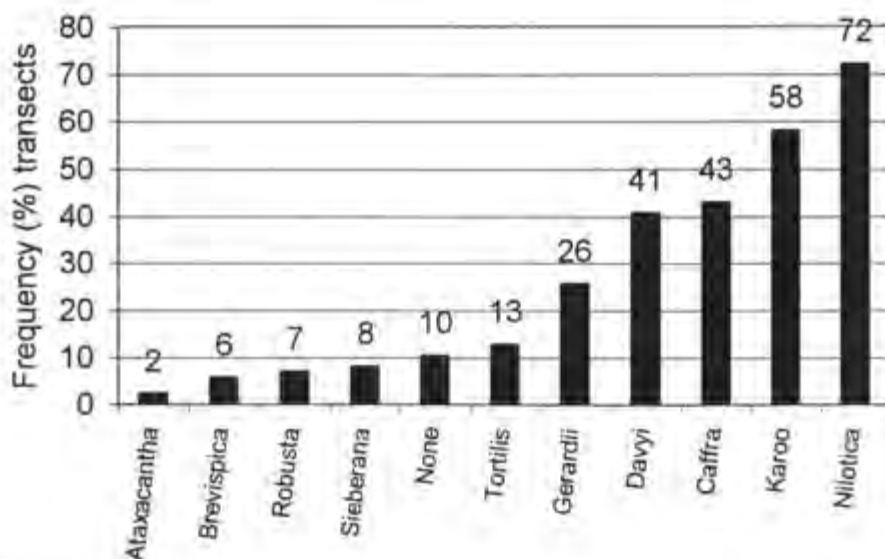


Figure 4: Frequency of occurrence of all *Acacia* species in roadside transect, Ithala Game Reserve, Northern Kwazulu-Natal. 86 transect units were sampled, varying in length from 0.5 - 2 km

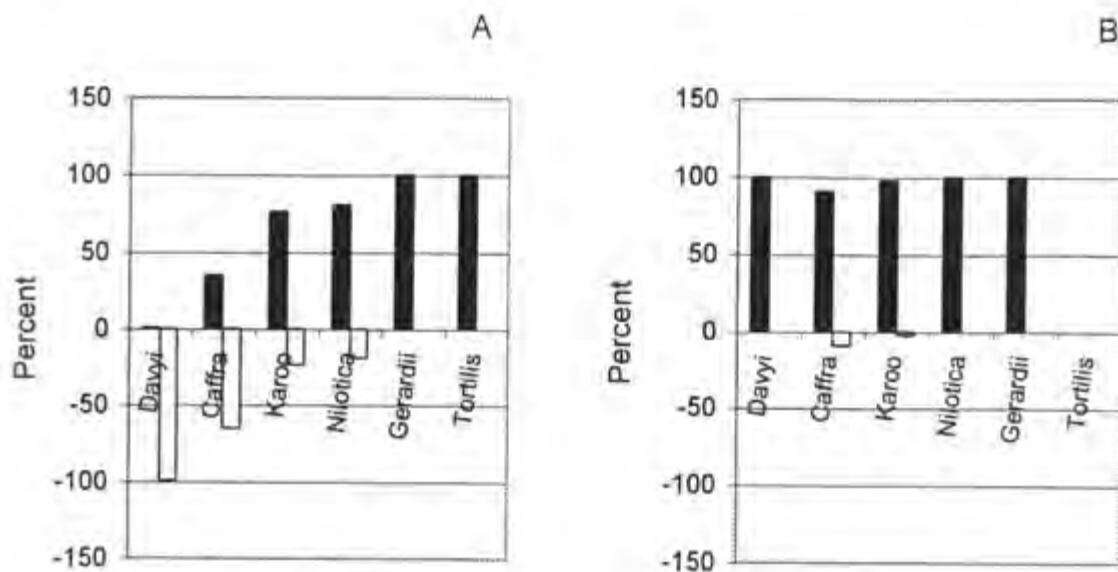


Figure 5. Differential mortality of *Acacia* species in (A) all sites with high giraffe density, and (B) all sites with low giraffe density. Letters on bars show significant differences between species and between sites. (■) Alive, (□) dead.

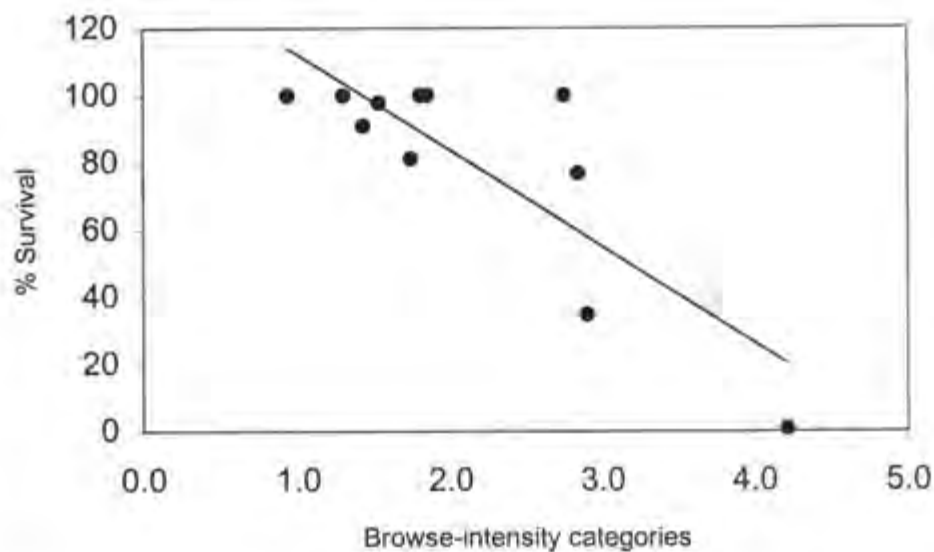


Figure 6: Average browse-intensity experienced by each *Acacia* species in high giraffe-density area and in low giraffe density areas, correlated ($R^2=0.68$, $p<0.01$) with percent survival. With the thick-branched *A. gerardii* removed from the analysis $R^2=0.82$.

Table 2: Browe-line height for individual *Acacias* in high giraffe-density low giraffe-density areas, showing mean and median values of browse-line height for each site. Browse-line height is significantly higher (Student's t-test: $df=10$, $t=4.86$, $p<0.001$)

		High Giraffe density sites					
Site		1	2	3	4	5	6
mean (sd)		4.7 (1.6)	6.2 (0.5)	5.3 (1.5)	4.4 (1.6)	5.1 (1.4)	3.8 (2.1)
median		5.75	6	6	5	6	3.5
		Low giraffe density sites					
Site		7	8	9	10	11	12
mean (sd)		2	4	3	2.4	1.6	2.5
median		2	4	3	2	2	2.5

Table 3: Percent of *Acacia* individuals bearing pods in high giraffe-density and low giraffe-density areas. Significantly fewer trees bear pods in high giraffe-density areas (Student's t-test: $df=5$, $t=-2.59$, $p<0.05$)

		High Giraffe density sites					
Site		1	2	3	4	5	6
Percent with pods		1.3	29	10	14	12.5	6.5
		Low giraffe density sites					
Site		7	8	9	10	11	12
Percent with pods		21.3	21	63.8	57.5	23.8	27.5

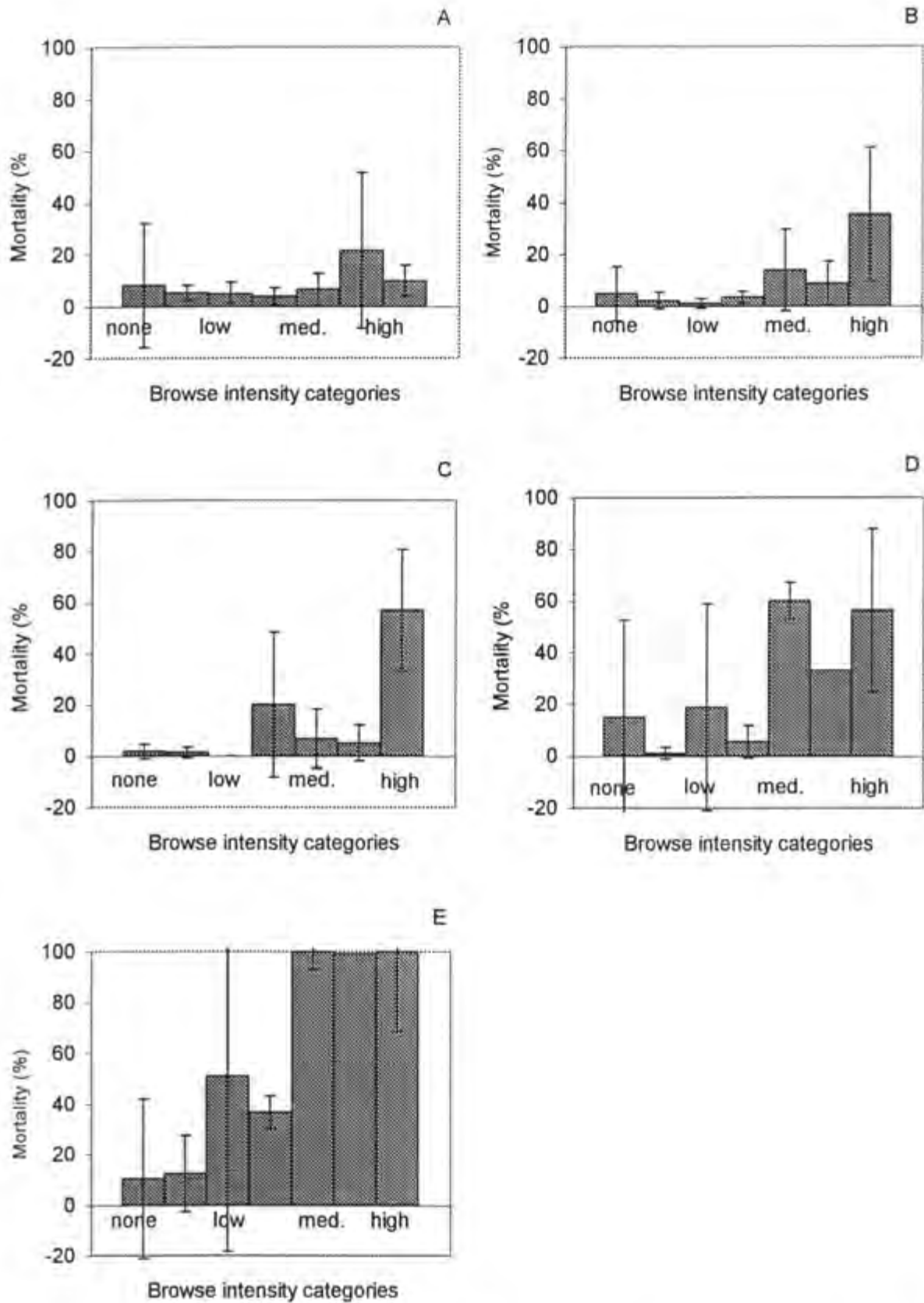


Figure 7: Browsing intensity and related *Acacia* species mortality (error bars indicate standard deviation) on a reserve-wide basis. (A) *Acacia nilotica*, (B) *Acacia karroo*, (C) *Acacia gerardii*, (D) *Acacia caffra*, (E) *Acacia davyi*. Spearman's Rank Correlation test found *A. davyi* to have significantly lower mortality in the 'none' to 'low' browse areas, than in the 'medium' to 'high' browse areas

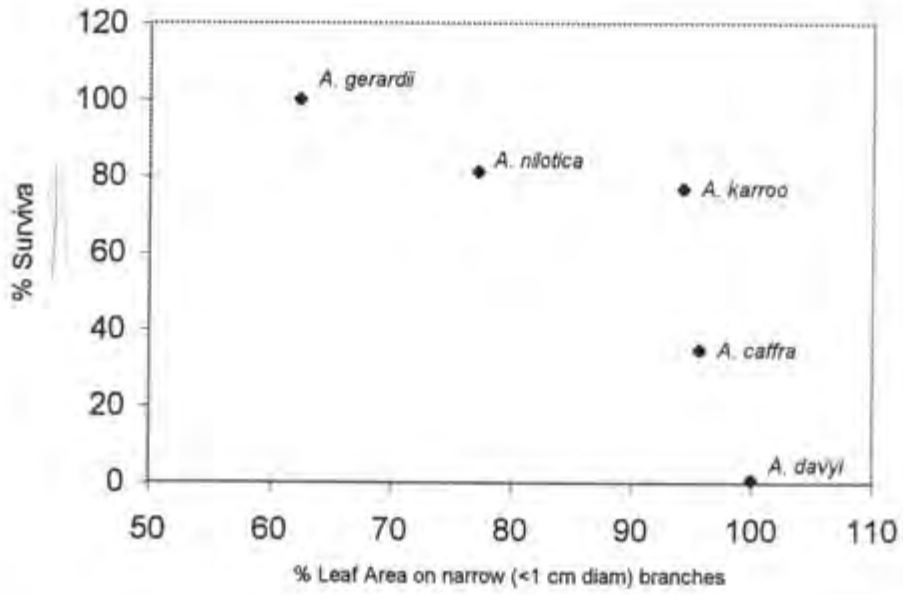


Figure 8: Foliage positioning and survival of *Acacias* in high giraffe-density areas

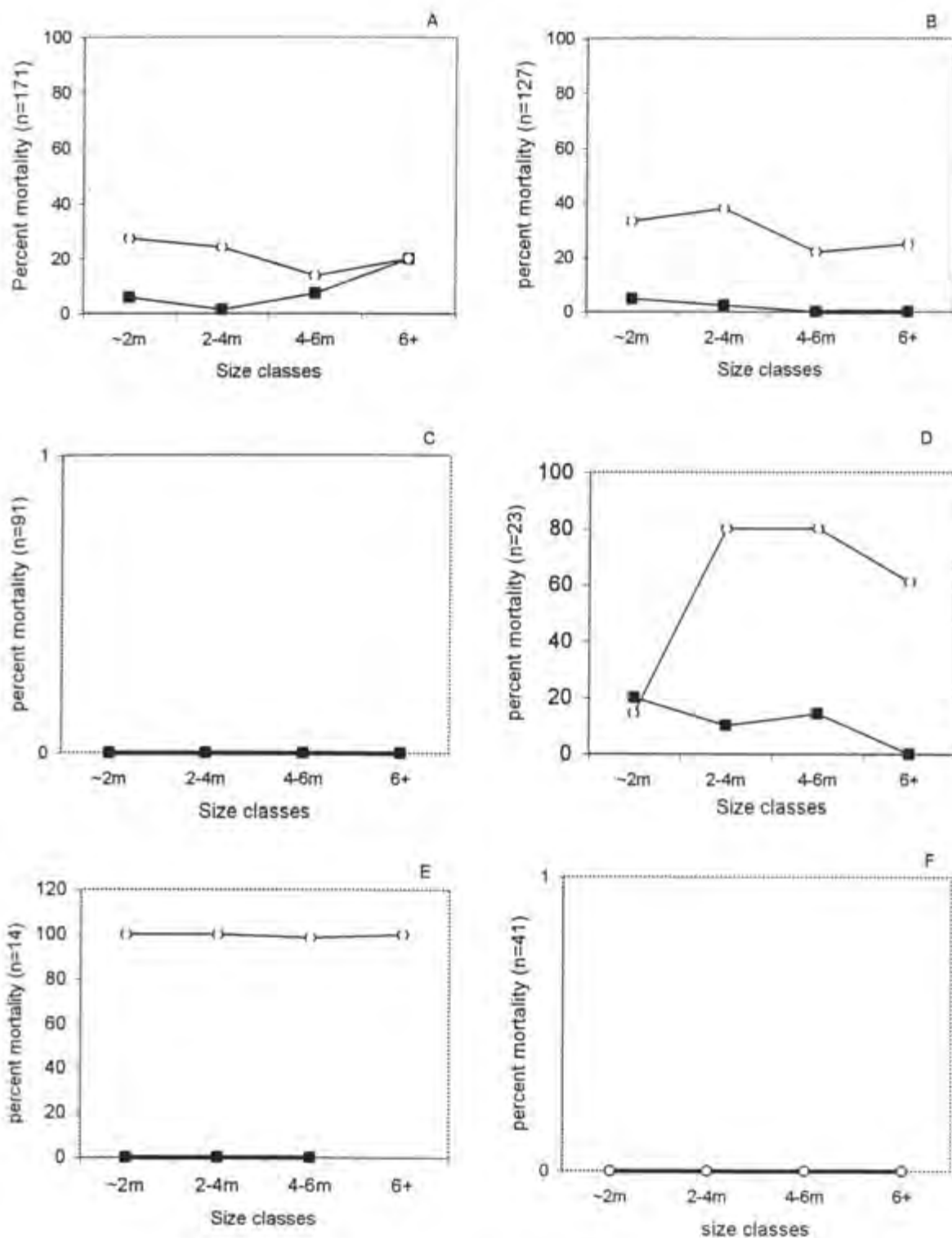


figure 9: Percentage mortality of selected *Acacia* spp in relation to height classes in Italia Game Reserve. High (○) and low (■) giraffe-density areas; (A) *Acacia nilotica*, (B) *Acacia karroo* (C) *Acacia gerardii*, (D) *Acacia caffra*, (E) *Acacia davyi*, (F) *Acacia tortilis*

DISCUSSION

The giraffe

The maintenance of biodiversity is one of the main management objectives of conservation organisations such as the Kwazulu-Natal Nature Conservation Services. During the formation of Ithala Game Reserve, nineteen mammal species were “reintroduced” into the reserve in order to return the area to its “natural” situation (Brett, 1980) and conserve biodiversity. Among the species that were introduced was the megaherbivore, giraffe (*Giraffa camelopardalis* Matschie). This is the largest extant ungulate ruminant, reaching masses in excess of 1000 kg (Smithers, 1983). According to Goodman and Tomkinson (1987), this animal did not occur historically in the ITG region. The original recommended stocking rate of 100 giraffes (Le Roux, 1985) was altered to 200 animals after a revision of carrying capacities two years later (Le Roux, 1987). The initial stocking rate recommendations were based on carrying capacity estimation techniques that utilised information of grassland types and extents (and not the woodland types and extents as is necessary for a browser). Animal-biomass carrying capacities (kg.km^{-2}) were then converted directly into various animal species per km. Giraffe are strict browsers, and never graze at all (Foster and Dagg, 1972). The revised estimates of giraffe carrying capacity was not based on biomass of available browse, but on the number of giraffe utilising a 2344 Ha region of IGR (Le Roux, 1987).

A density of 1.4 giraffe per km^2 existed at the time of that study, and it was assumed that this was the carrying capacity for the region. Giraffe spread through the landscape at a very slow rate as they experience difficulty in crossing certain landscape barriers such as rivers and steep slopes. Areas within IGR with low levels of giraffe occurrence are primarily areas excluded by steep slopes. As giraffe in IGR have not colonised all areas within the reserve about 180 animals (fig. 1 and 2) currently exist in only about a third of the potentially available area (fig. 1) i.e. 1.8 giraffe per km^2 . The giraffe population growth dynamics represented in figure 2 suggest that the population growth rate was high (ca. 10% pa) but the population has stabilised in the last few years, probably having reached carrying capacity. Space limitation can be assumed the cause

of the stabilisation of population growth. Colonisation of new areas in the reserves would thus be expected to induce further population expansion

The current study examined the impact that the giraffe living in IGR are having on the acacia communities within the reserve – a snapshot survey in a continuing drama. It was found that the browsing pressure exerted by these animals is causing the mortality of several acacia species, some even to the point of local extinction of the adult trees. Mortality that occurred in areas with giraffe, occurred across all size classes of species (appendix 1), indicating that high mortality-levels are not cohort senescence. Certain species are affected more than others (fig. 5) and differential mortality rates occur between species. Mortality of adult trees is clearly shown to occur, and to be a consequence of heavy browsing by a giraffe (fig. 5 – fig. 8.). The long-term effect that this may have on the distribution of species in the landscape can be inferred from this study. *A. davyi* has already disappeared from high giraffe density areas, and observations over a greater time span are likely to show the eventual disappearance of *A. caffra*, and then *A. karroo*. The removal of adult trees from the landscape may result in a complete extinction of all individuals of the species affected, and an alteration of species composition in the landscape. Alternatively it may result in the creation of a “gulliver” system (Bond and Maze, 1998) where the species are present but exist for most of their lives as stunted individuals within the grasslayer. Lower numbers of pods on trees where giraffe occur, whether due to them being consumed, or because trees do not have enough resources to allocate to reproduction, may negatively affect acacia *recruitment* in these areas.

DIFFERENTIAL MORTALITY

Differential mortality of *Acacia* species occurring in IGR indicates that some species are being impacted by giraffe browsing more than others are. Are some species ‘worse-off’ than others are when faced with browsing by giraffe? Can one predict species extinctions where giraffe are introduced in the future? The reason behind the varying severity of browsing-effects (i.e. amount of above-ground die back of mature individuals) on different *Acacia* species may be related to characteristics of the acacias, characteristics of the browsers (giraffe), or both.


Characteristics of the trees – Browse tolerance.

Some species of acacia are seen to be more able to survive severe browsing by giraffe than others are (possibly due to evolutionary adaptation to browsing) (fig. 7). The placement of foliage within the tree canopy is shown by this study to be a species-specific characteristic influencing browse-tolerance (fig. 8). The greater the proportion of foliage allocated to the branches in the periphery of the canopy that might be stripped by giraffe, the higher the mortality related to browsing for that species. Giraffe are known to consume shoot tips as well as leaf whorls of acacias (Pellew, 1984). Feeding in this fashion removes photosynthetic material to a much greater extent in some species than in others due to the positioning of leaves. The entire leaf area of *A. davyi* is positioned on the distal branches where it can be completely removed by giraffe. It has suffered 100% mortality in the landscape where it is accessible to giraffe. *A. karroo* and *A. gerardii* have thick branches bearing fascicles of leaves. The leaves are stripped from the branches but resprout from undamaged fascicle buds. Continued heavy browsing of *A. karroo* and *A. gerardii* is likely to weaken these trees. *A. karroo*, in particular, is likely to succumb in large numbers over the next few years.

Escape by height

This study has shown that tree height may be a plant characteristic moderating the severity of effects from browsing. The importance of tree-height is not independent from the maximum browse-reach of the browser. The maximum browse reach of giraffe is 5.75 m – 6 m (Pellew, 1983), and trees attaining heights greater than this can "escape" the giraffe. *Acacia* Species with individuals above giraffe-reach could thus be expected to have survived introduction of giraffe better than species existing solely below 6 m. No specimens of *A. davyi* encountered in this study were found to occur above 6 m, and they have previously been reported to grow only up to a height of 5 m (Ross, 1979). *A. davyi* grows entirely within a 'vulnerable height' window and all but one individual of *A. davyi* occurring in high giraffe-density areas were dead. Height is an important factor affecting local exterminations of this species. The importance of tree height is further demonstrated in study by Teague (1989) in which it was shown that defoliation of the upper canopy of *A. karroo* is significantly more detrimental than defoliation of other portions of the canopy. A tall *A. karroo* tree with its upper canopy beyond the reach of giraffe can be expected to 'endure' browsing pressure better than

one below the safety height. Height was found by Pellew (1983) to be an important factor in the dynamics of *A. tortilis* woodlands in the Serengeti. The effects of elephants, fire and giraffes in this system were dependent on the height classes of the trees. Trees that were shorter, occurring within a height class susceptible of fire, were kept at this height by giraffe, which acted as a growth-retarding agent for the acacias.

A. caffra can grow to a height of 14 m (Ross, 1979), and about 15% of individuals in detailed transects attained heights of over 9 m in this study. The 65% above ground die back experienced by *A. caffra* in high giraffe-density areas is, however, not unexpected. This species is less able to cope with high levels of browsing due to the heavily distal placement of its leaves (fig. 8). In addition, although *A. caffra* has the ability to grow beyond giraffe-reach, over 50% of individuals of detailed transects occurred in the 2-6 m height class most vulnerable to giraffe, reinforcing the importance of height as an  ?

In this study only 5% of *A. nilotica* individuals were taller than 6 m, and yet there was only a 19% above ground-die back in this species, in high giraffe density areas. It occurs directly within the vulnerable height zone, yet the impact of browsing was not as severe as would be expected if height-related safety were the only factor. *A. nilotica* allocates lower proportions of foliage to peripheral branches and more resistant to high levels of browsing. Mechanisms other than height decrease the vulnerability of *A. nilotica* to giraffe browsing. This also appears to be the case for *A. tortilis*, which has very low levels of mortality despite being found in high giraffe density areas.

Choice of food-plant by browsers

Tree height and foliage-placement have been revealed by this study to be important characteristics aiding tree survival under very high levels of giraffe browsing. Other plant characteristics (such as palatability and secondary defences) are known to affect the 'desirability' of a species to herbivores (Cooper and Owen-Smith, 1986). The less desirable species is less 'available' to browsers (due to browser-choice of food plant). Plants have evolved mechanisms to make themselves 'less available', by exploiting the browsers' ability to choose. The alternative explanation for differential mortality of the *Acacia* species is that they are exposed to different levels of browsing. The more

heavily browsed species would then, presumably, be more vulnerable to browse induced mortality.

Cooper and Owen-Smith (1986) have suggested that the loss of foliage to browsers is a product of i) Frequency of plant species encountered by the herbivores, ii) Likelihood of the herbivore feeding on the species encountered, iii) Expected duration of the feeding episode, and iv) Eating rates while feeding.

The *frequency* with which an *Acacia* species is encountered will be a function several factors. The densities in which that acacia species occurs in the landscape, the densities in which giraffe occur in the landscape, and the proportion of overlap between the habitat utilised by the acacias and the habitat utilised by giraffe. If an acacia species occurs in an area never entered by giraffe, that species will not experience giraffe browsing.

The involvement of giraffe-acacia encounter-frequencies in the local extinctions of *Acacia* species in IGR is evident from figure 5. The above-ground die back of species in the low giraffe-density areas (where giraffe-acacia encounters can be assumed to be seldom or never) is significantly different from above-ground die back in high-density giraffe areas (where giraffe-acacia encounters can be assumed to be significantly higher). Other than this, the detrimental effect of browse on certain acacias may be related to the 'availability' of those species in the landscape. *A. tortilis* has been reported to be a favourable food plant of giraffe in the Serengeti (Pellew, 1984), and to be one of the 'top five' tree species selected by giraffe in the Kruger National Park, (Furstenburg and Van Hoven, 1992). In IGR no browse-related mortality was found for *A. tortilis* in high giraffe-density areas. Light to no browsing (browse category 1, table 1) was experienced by this species, according to the 'browsed branch-ends' method of browse-intensity assessment. The light browsing may be due to a low reserve-wide 'availability' of *A. tortilis* (it is found in 13% of park-wide transects, fig 4). If reduced random giraffe-*A. tortilis* encounters occurred, lower browsing rates would be expected (resulting in the lack of giraffe-related mortality of this species). However, reduced giraffe-*A. tortilis* encounters are unlikely as this species occurs in the high-giraffe density areas. The 'browsed branch-ends' method of browse-intensity

assessment may be inaccurate in the browse intensity that it shows for this species, for reasons discussed below. Direct observation is, however, needed to understand the role that 'availability' (to browsing) plays in the impact a tree-species experiences from browsers.

The likelihood of herbivores feeding on the species encountered, expected duration of the feeding episode, and eating rates while feeding, are related aspects and will be discussed together. The choice of a herbivore to feed on a species of food-plant will be determined by the 'quality' of that species. Quality as a food-source is a function of the species' chemical and physical attributes (Bergström, 1992). Different food-plant species vary in how much they benefit a browser (nutritionally), and in how much feeding on that species costs the browser (in terms of time spent feeding, or toxins ingested) (Gowda 1997). Optimal foraging theories (*inter alia* Owen-Smith and Novellie, 1982) suggest that a browser will feed preferentially on species with maximum return of nutrients for minimum time spent, and minimum 'damage' (such as that from toxins and thorns) incurred. Aspects of acacia defences in Ithala, and the effect that these have on the giraffe present were not examined in this study.

Foliage from *Acacia* species contains high concentrations of nutrients, and acacias are the preferred food-plants for many browsers (Cooper and Owen-Smith, 1986). Chemical attributes such as the production of condensed tannins, and physical attributes such as thorns, are anti-browser defences of acacias (Pellew, 1984; Cooper and Owen-Smith, 1986; Furstenburg and Van Hoven, 1992). Condensed tannin production is an inducible response, and tannins have a negative effect on the acceptability and nutritional value of dietary browse to giraffes. Giraffes are found to avoid plants with high levels of condensed tannins (Furstenburg and Van Hoven, 1992). Instead, they browse selectively on plants with low tannin-levels, and reduce their feeding duration when tannins are present. Acacias with a relatively high tannin content (ca. 9% of dry leaf weight) become more important as browse when other food-species lose their leaves in the cold or dry season (Furstenburg and Van Hoven, 1992). *Acacia nilotica* has been found to contain extremely high levels of condensed tannins (ca. 16% of dry leaf weight) (Furstenburg and Van Hoven, 1992). The negligible amount of browsing experienced by this species (fig. 7a), in spite of its

presence in the 'browse-height-zone', may thus be a consequence of high condensed tannin content.

Although it is questionable whether they are indeed 'induced defences' (Midgley and Ward, 1996), defence by thorns is important for deterring browsing or reducing tissue-loss to browsers (Cooper and Owen-Smith, 1986). *A. tortilis* has been shown to significantly increase the biomass of long spines following pruning (Gowda, 1997), and spine length and spine density of *A. seyal* and *A. xanthophloea* have been found to be greater in the landscape where giraffe-densities were higher. The higher spine density has been implicated in protecting the twig-apices of a plant, because higher spine densities are negatively correlated with twig-loss to browsing goats (Gowda, 1996). Cooper and Owen-Smith (1986) have found a similar response to spines by kudus. When unarmed specimens were presented to the kudus, their feeding rate increased and bite-size decreased. The bite size for kudus, (which have larger mouth parts) was affected more than it was for impalas and goats, in the presence of spines. Kudus were restricted to mostly taking leaves or leaf clusters when spines were present and were thus inhibited from feeding on species for which spinescence was coupled with especially small leaf size.

Cooper and Owen-Smith, (1986) state that browsing rate on *A. caffra* was not as low as other acacias, because of the large leaf-size of this species. It has a leaf rachis of 5 – 22 cm long, prickles only up to 9 mm long (Ross, 1979) and is the staple food species of kudus and elands in Pilansberg Game Reserve (Gowda, 1996). The feeding rate on a species with small leaf clusters, such as *A. tortilis* (Cooper and Owen-Smith, 1986) with a leaf length of 0.2 – 2 cm and spines up to 10 cm long (Ross, 1979), will be low. An optimally foraging browser will be expected to select for species with large-leaves and relatively short thorns, on which they will have a high browsing rate. Such species will thus be more 'vulnerable' to attention from browsers.

A. davyi, the acacia most severely affected by browsing in IGR, has large leaves (rachis 8-18 cm long), and slender spines of only 0.4 – 3 cm. A high leaf-length to thorn length ratio such as this will be desirable to browsers, all other things being

equal. The extremely high mortality of this species in high giraffe-density areas may be related to increased attention from browsers.

The loss of foliage to browsers is a product of several interactive plant characteristics, in connection with characteristics of the specific browser involved (maximum reach for browsing, size of browser mouth parts). Tree-height, and foliage positioning on branches are important characteristics, but landscape occurrence-frequency, nutrient content of foliage, secondary chemical defence content of foliage, length and density of thorns, and leaf-size, are also involved. These characteristics differ between *Acacia* species, each independently affecting the foliage-loss to giraffe by different species. Consequently, they can also be expected to be playing a role in the differential mortality of *Acacia* species experiencing heavy browsing by giraffe.

Giraffe in other reserves

The effect of giraffe in Ithala Game Reserve appears not to be duplicated in many other Kwazulu-Natal game reserves. Although giraffe have been introduced into the Hluhluwe-Umfolozi Park (HUP) and Mkuzi Game Reserve (Goodman and Tomkinson, 1987), no extreme giraffe-damage has been reported for these well-studied areas (Balfour and Goodman, pers. comm. 1999). This peculiarity poses many questions. Are the browse-rates much higher in IGR? Are there fewer alternative food-plant species available for the giraffe in IGR? Are the species (or genotypes of species) that occur in IGR not historically adapted to such browsing through lack of exposure? Are environmental variables (such as temperature, soil-types or precipitation) limiting the acacias' abilities to withstand substantial defoliation?

Six giraffe individuals were introduced in to HUP in 1955, and the population has stabilised at ca. 800 animals. 80 % of the giraffe occur in Umfolozi, at a density of ca. 1 giraffe per km², and Hluhluwe giraffe-densities are ca. 1.6 giraffe per km². Giraffe in Mkuzi Game Reserve occur at a density of 0.55 giraffes per km². Giraffe densities in Hluhluwe, although not as high as IGR (which has densities of 1.8 giraffe per km²), are higher than would be expected for the lack of observed damage. This may be a function of alternative browse resources available to these animals, or a higher tolerance of the trees to high browse levels. Alternatively, since giraffe densities have

increased in Hluhluwe relatively recently from those in Umfolozi, vegetation change may yet be in a dynamic phase, and damage may become evident in the future.

Difficulties of this study

The current study has given clear indications of the effect that browsing by giraffe is having on acacias in IGR. Differences in relative mortality may be due to giraffe feeding preferences (and hence relative amounts of leaves removed from a species) or due to differences in the responses of the trees to similar browsing levels. Further exploration of giraffe feeding preferences versus tree resistance is required to understand the differential demographic effects of giraffe on *Acacia* species.

The browsed-branch ends method for assessing intensity of browsing on trees is based on the assumption that the giraffe browse predominantly by “pruning” shoots and leaves (biting off the ends of shoots and their accompanying foliage) and not by “picking” off leaves alone (Cooper and Owen-Smith, 1986). Picking by a browser would result in foliage loss and not shoots loss. The browsed branch ends method for assessing browse infers browsing intensity from amount of shoot loss. Severity of browsing experienced by species with defences that limit shoot loss, but that are still browsed upon, will consequently be underestimated.

Conclusion

The situation occurring in Ithala Game Reserve highlighted in this study has some interesting implications. Mortality of a species due to giraffe browsing was dependent on *where* individual trees were growing. Trees that were inaccessible, because landscape features (such as steep slopes and impenetrable thickets) excluded giraffe from the area in which they occurred, survived the browsing pressure. This shows that the actions of a browser may actually alter landscape scale distributions of species. *Acacia* species that are more ‘vulnerable’ to mortality when heavily browsed are being restricted to landscape refugia. Current patterns of acacia and other tree species distributions in the African landscape may be a consequence of historical browsing patterns, and the landscape distributions of species may be dramatically altered by the introduction of browsers such as giraffe to areas in the future. East African savannas are dominated by *A. tortilis* (Pellew, 1983) which is the species most resistant to

browsing by giraffe in this study. Are other *Acacia* species confined to steep slopes (and other such refugia) away from giraffe impact? Are the species that are more 'resistant' to giraffe due to defences, such as very high tannin levels, large spines or ant galls (such as those of *A. drepanolobium*) (Madden and Young, 1992), more dominant in the landscape than others? Is the distribution of other common *Acacia* species a function of herbivore (especially giraffe) browsing pressure, rather than a function of factors such as physiological determination of growth? If so, the distribution of tree species may have been profoundly affected by browser-induced extinctions of populations.

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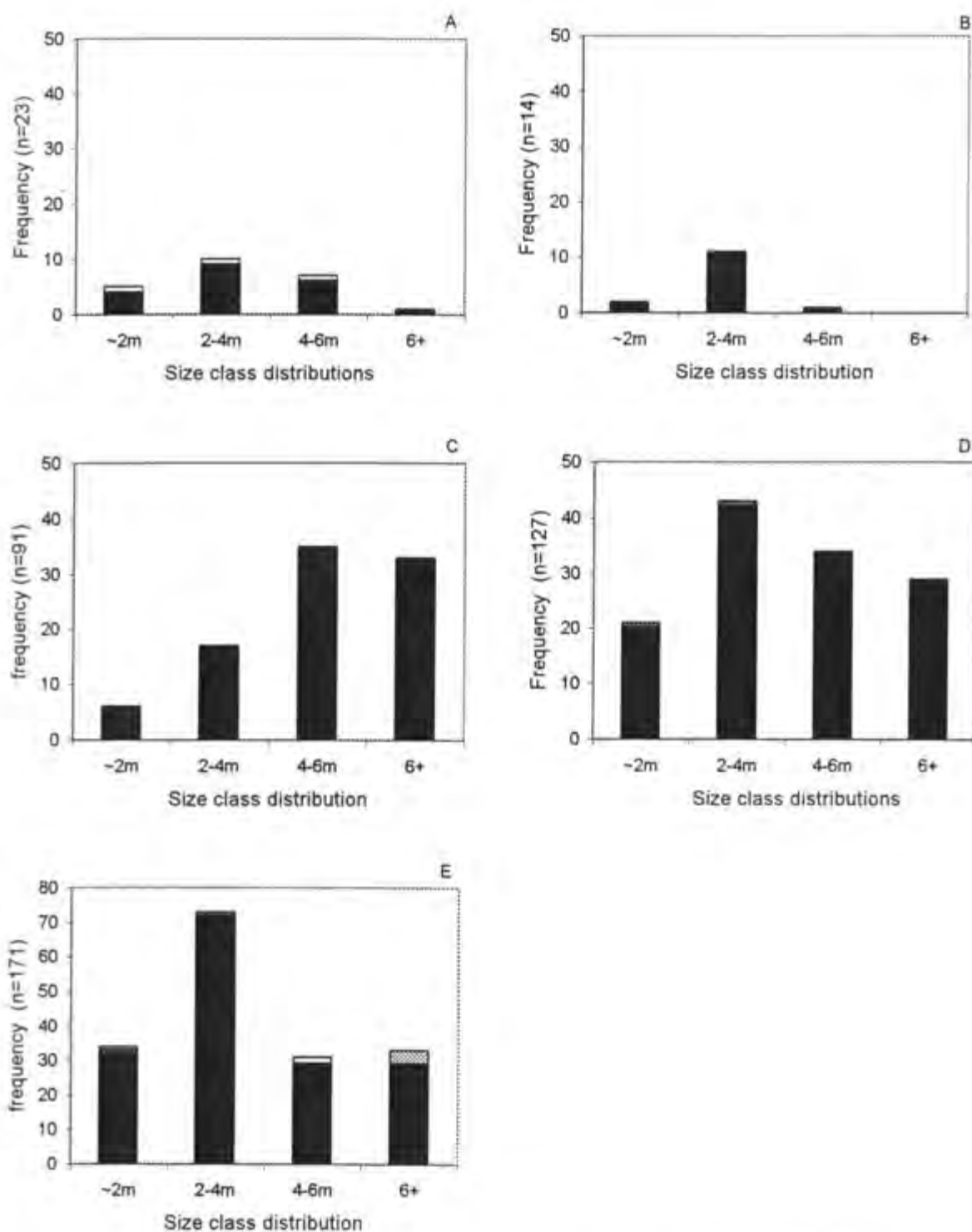
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APPENDICES

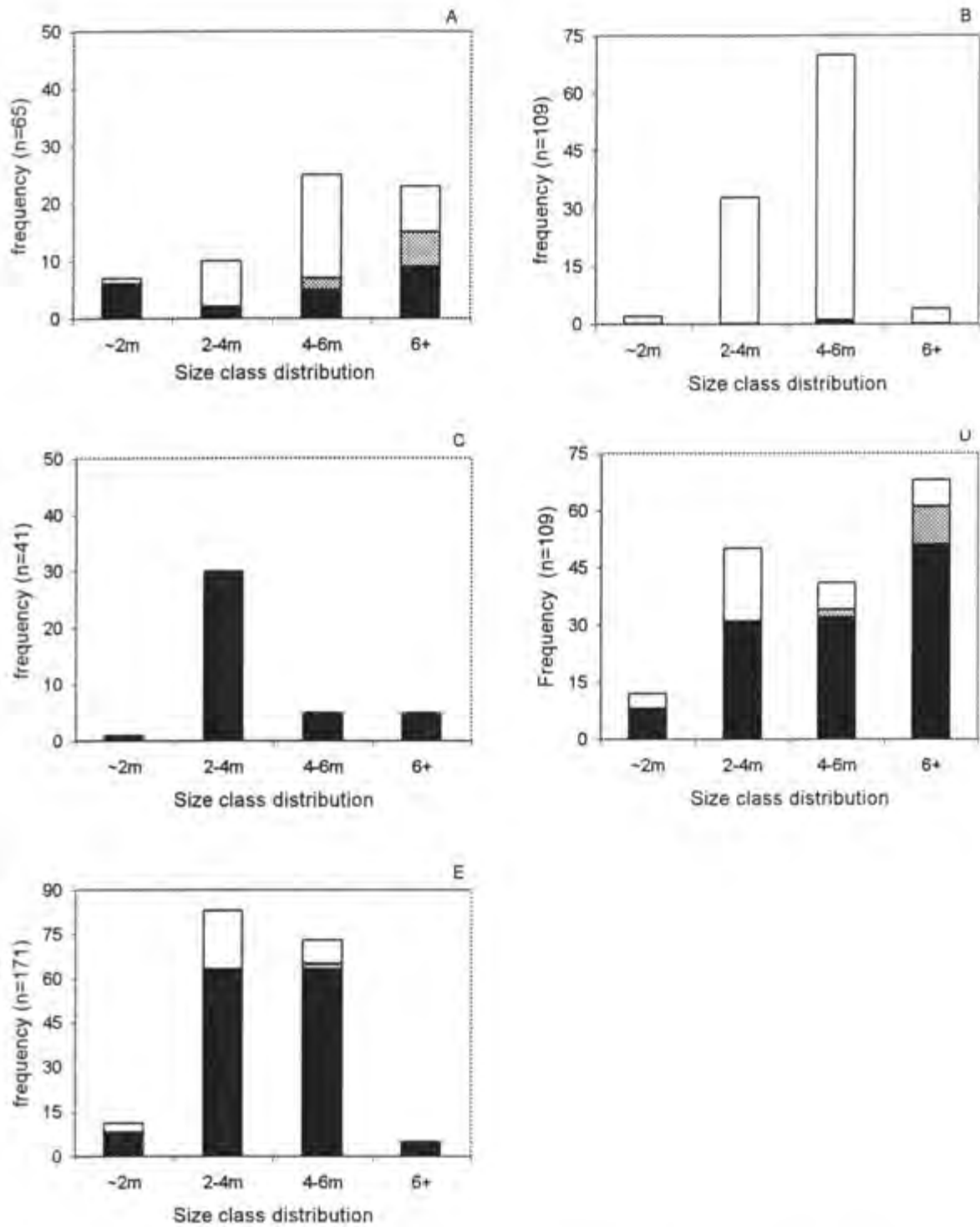
Appendix 1 displays the proportion of mortality for acacias in high (a) and low (b) giraffe density sites, Ithala Game Reserve, KwaZulu-Natal. This figure displays the size class distributions of species recorded in the detailed transects, indicating what proportion of the populations is living, 'half alive' (entirely lacking foliage below the browse line) and dead.

Appendix 2 represents the leaf area of acacia individuals of different heights, for each species. Leaf area is presented in reference-branch units unique to each site, and is not directly comparable between sites.

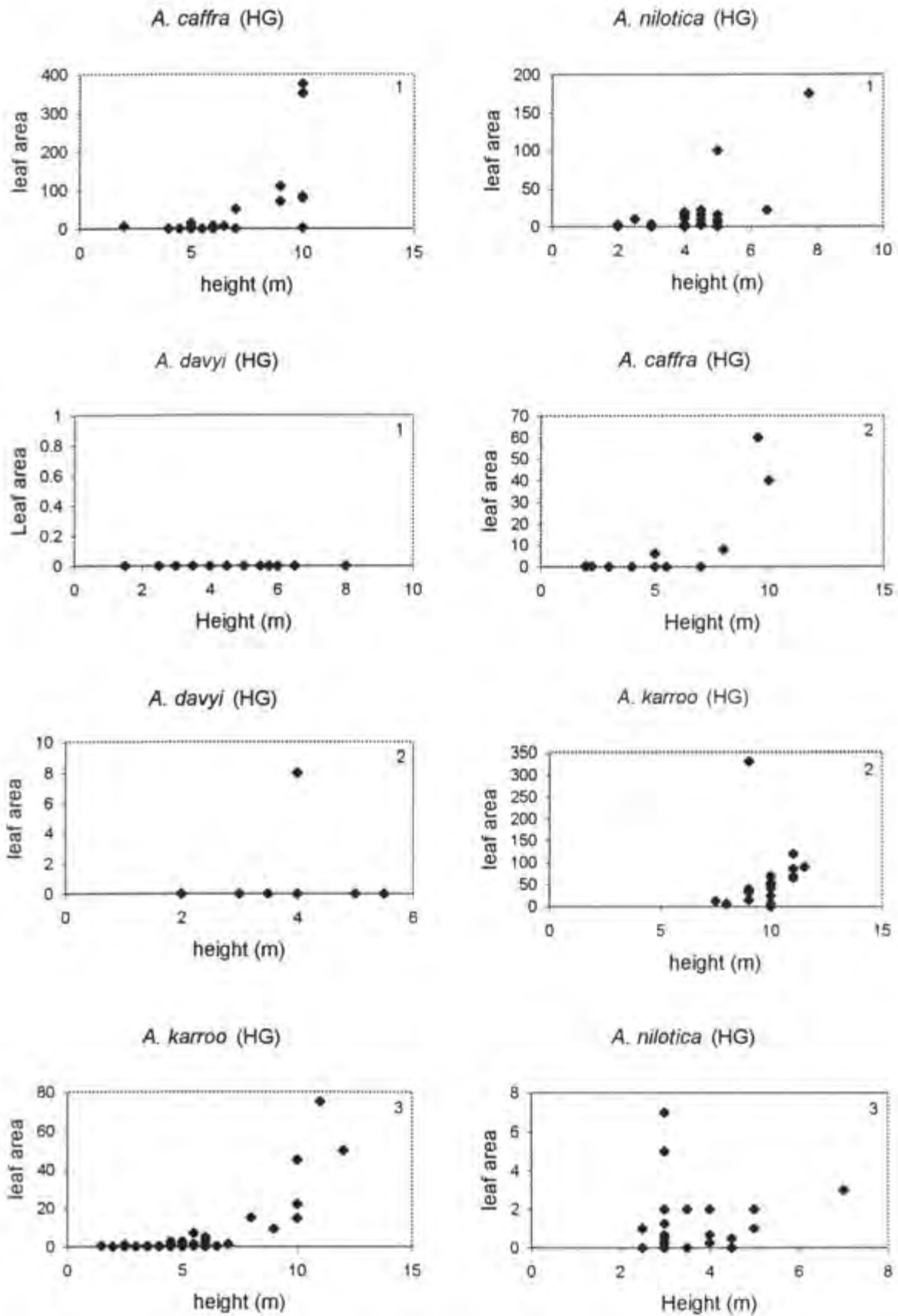


Appendix 1a: Proportion of above ground dieback for *Acacia* spp. In low-giraffe density sites, Ithala Game Reserve. (A) *A. caffra*, (B) *A. davyi*, (C) *A. gerrardii*, (D) *A. karroo*, (E) *A. nilotica*.

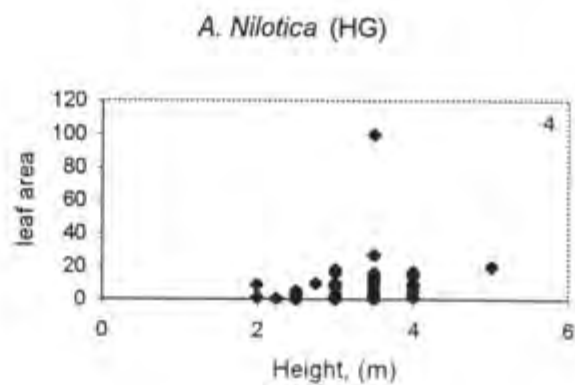
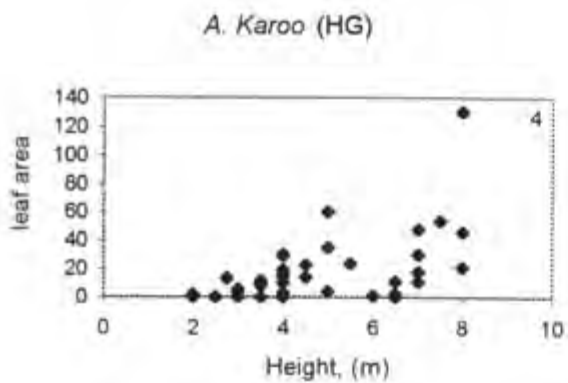
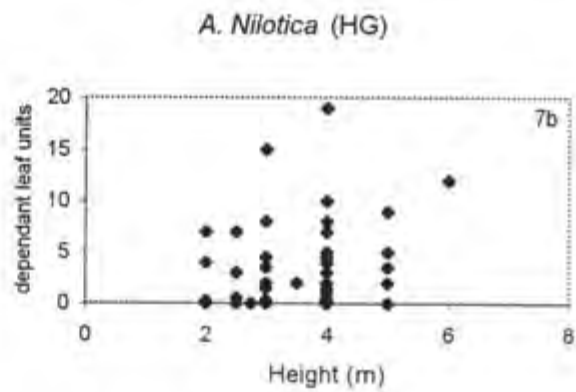
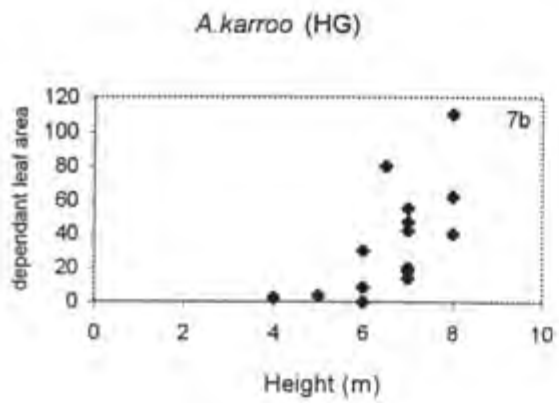
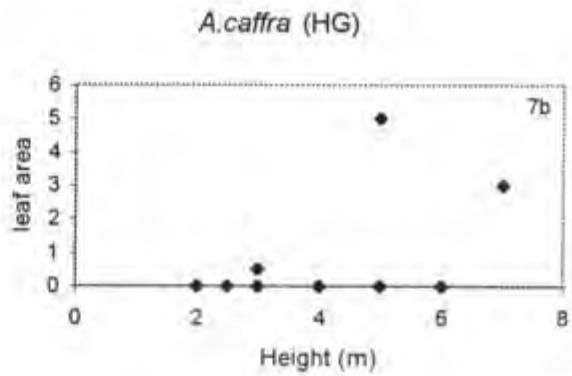
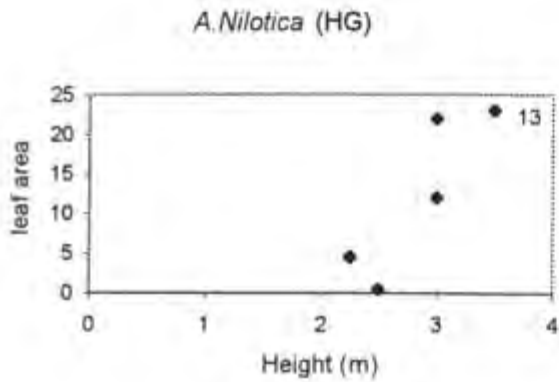
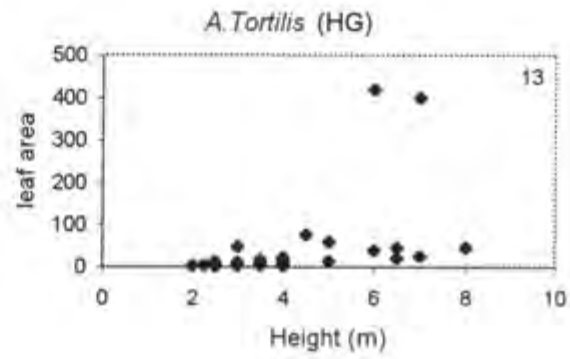
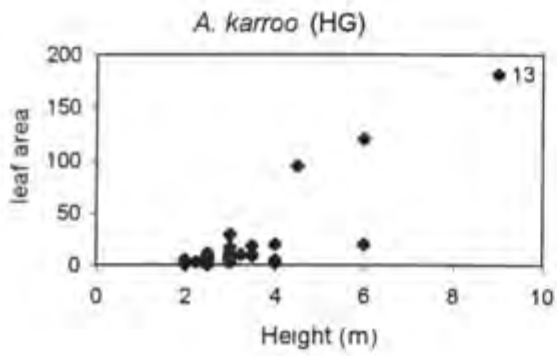
(■) Living individuals, (▨) 'half-alive' individuals, lacking foliage below browse-line in canopy, (□) dead individuals

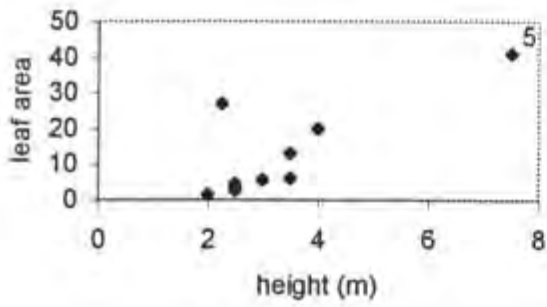
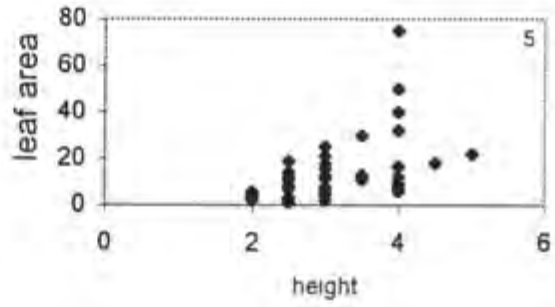
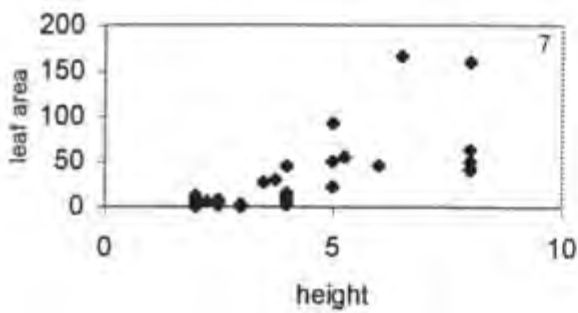
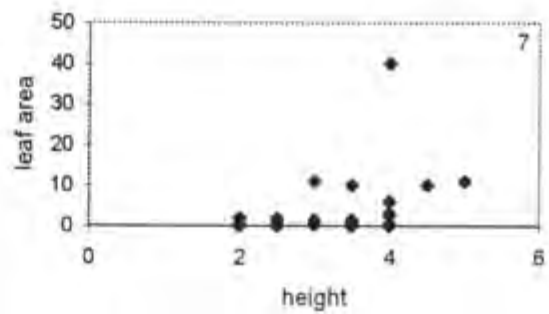
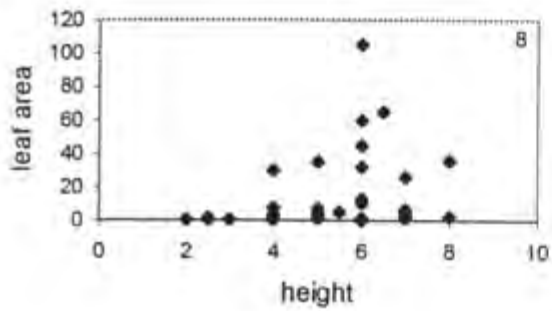
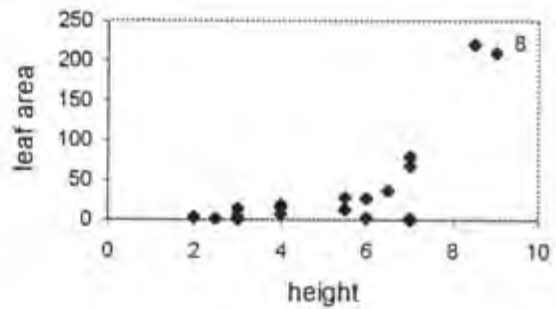
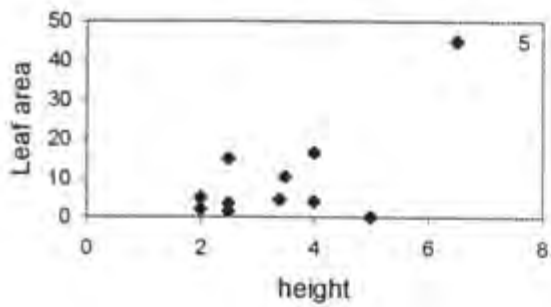
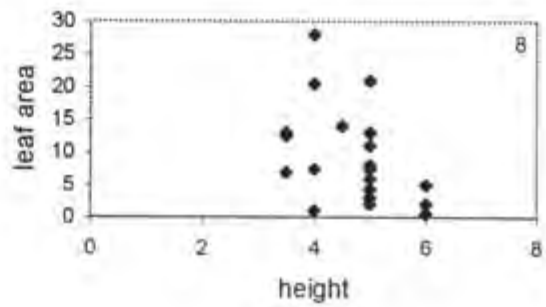


Appendix 1b: Proportion of above ground dieback for *Acacia* spp. in high-giraffe density sites, Ithala Game Reserve. (A) *A. caffra*, (B) *A. davyi*, (C) *A. tortilis*, (D) *A. karroo*, (E) *A. nilotica*
 (■) Living individuals, (▒) 'half-alive' individuals, lacking foliage below browse-line in canopy, (□) dead individuals

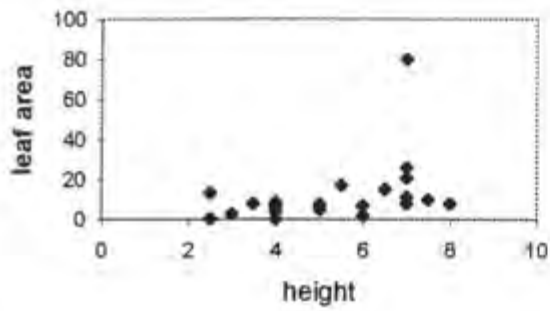


Appendix 2: leaf area represented in number of (site dependant) reference-branch units, and height (m) of individuals in all sites. HG - High giraffe density sites, LG - low giraffe density sites

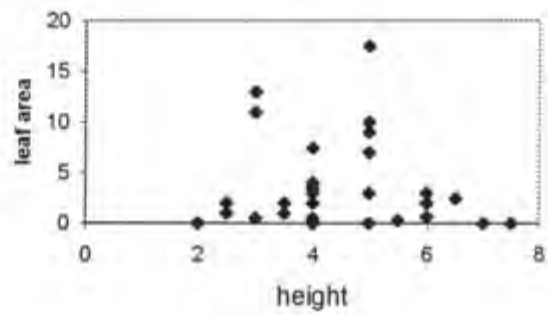
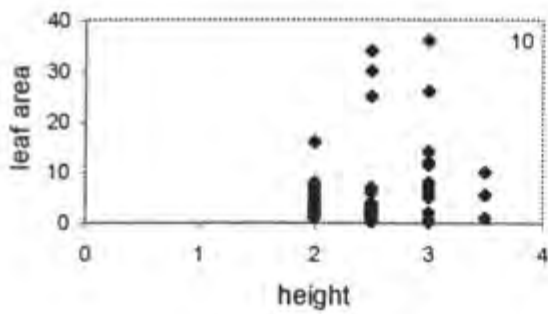
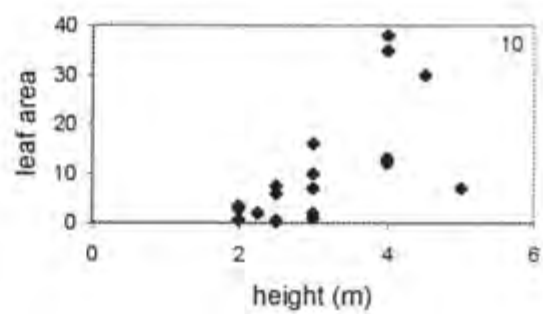
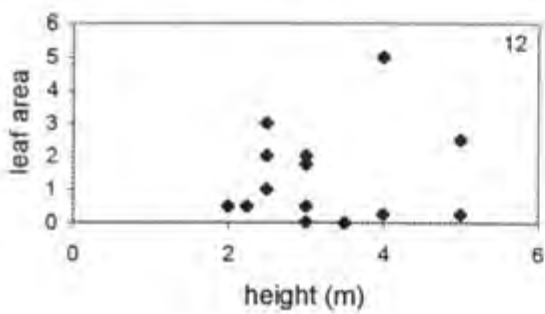
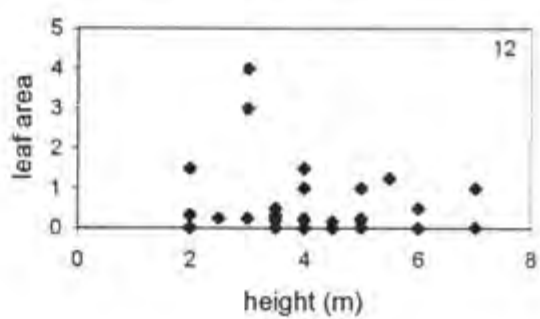
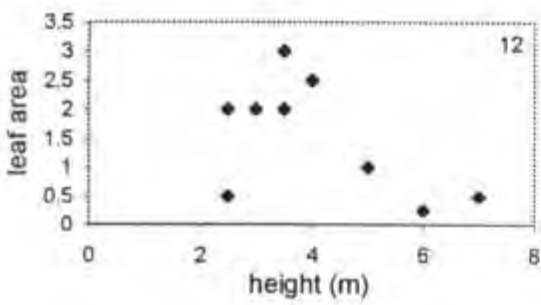


A. robusta (LG)*A. nilotica* (LG)*A. karroo* (LG)*A. nilotica* (LG)*A. gerardii* (LG)*A. karroo* (LG)*A. karroo* (LG)*A. nilotica* (LG)

karroo, LG, site 9



Nilotica site 9, LG

*A. nilotica* (LG)*A. karroo* (LG)*A. caffra* (LG)*A. gerardii* (LG)*A. karroo* (LG)*A. nilotica* (LG)