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Woody vegetation change in response to browsing in Ithala Game Reserve, South Africa

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Abstract

Wildlife populations in southern Africa are increasingly forced into smaller areas by the demand for agricultural and residential land, and many are now restricted by protective fences. Although numerous studies have focussed on the impacts of elephants and other browsers on vegetation in large, open areas, less is known of their effects in restricted areas. The woody vegetation in Ithala Game Reserve, a fenced conservation area of almost 30 000 ha, was monitored annually from 1992 to 2000 to assess the impact of browsers on vegetation structure and composition. Three categories of tree were identified: those declining in abundance (e.g. *Aloe marlothii* and *A. davyi*), those increasing in abundance (e.g. *Scolopia zeyheri* and *Euclea crispa*), and those with stable populations (e.g. *Rhus lucida* and *Gymnosporia buxifolia)*. Species declining in abundance were generally palatable and showed low recruitment and high mortality rates. Species increasing in abundance were characterised by high recruitment, low mortality and low herbivory levels. A change in species composition towards a less palatable community is predicted. Should browsing lead to an increase in the herbaceous fuel load, fire and herbivory could change areas of woodland to grassland. Environmental factors such as moisture stress, and browsers other than elephants were responsible for approximately three times as much damage to trees as elephants were. It is therefore suggested that other browsers be considered for removal along with elephants when browsing pressure is deemed to threaten vulnerable tree species with local extirpation.

Introduction

As human populations increase and the demand for residential and agricultural land escalates, African wildlife is increasingly forced into restricted areas (Ben-Shahar, 1993; Barnes, Barnes & Kapela, 1994). Consequently, many of the formally conserved wildlife populations in southern Africa are now restricted by protective fences, and are unable to migrate or roam freely as in the past. This has implications for both the herbivore populations and the vegetation found within these closed areas (Guy, 1976). Nature reserves should be established to conserve both plant and animal diversity (Buechner & Dawkins, 1961), and it is therefore important to gain an understanding of the effects of herbivores on plant life in restricted systems. Although many studies have focussed on the impacts of elephants and other browsers on woody vegetation in large, open areas (e.g. Croze, 1974; Ruess & Halter, 1990), less is known of their effects in restricted areas. Successful conservation of both plant and animal resources in these reserves depends on informed decision-making by managers.

Elephant and other browsers are known to have altered, sometimes drastically, the abundance and composition of their food resources (e.g. Croze, 1974; Field, 1976; Ben-Shahar, 1998). Baobab (*Adansonia digitata*) populations have decreased in Ruaha National Park, Kenya (Barnes *et al*., 1994) and Tsavo National Park, Tanzania (Leuthold, 1996), and the authors cite elephants as being the agent responsible for this decline. Elephants were also responsible for decreases in *Commiphora* woodlands in Tsavo National Park (Leuthold, 1996) and *Acacia gerrardii* population vitality in Kidepo Valley

National Park, Uganda (Harrington & Ross, 1974). Giraffe caused severe mortality patterns in *Acacia davyi* populations and heavily affected *A. caffra* and *A. karroo* in Ithala Game Reserve (Loffell, 1999). Giraffe also reinforced woodland changes made by elephants, by restricting tree regeneration in heavily browsed areas in the Serengeti National Park, Tanzania (Pellew, 1983). Even small herbivores such as impala affect the abundance of woody species through their impact on recruitment (Prins & Van der Jeugd, 1993). An understanding of browsers' effects on browse resources in restricted areas is therefore key to the continued protection of biodiversity in these areas. Although the reintroduction of megaherbivores into a closed system is likely to have an effect on the vegetation, woodland change rarely depends on one factor alone. Fire is commonly identified as a synergistic factor for changes induced by elephant (Dublin, Sinclair & McGlade, 1990; Leuthold, 1996). Factors such as soil nutrient status also affect the response of woodlands to agents of change (Lewis, 1991). Not all patterns of vegetation change, therefore, can be accredited to a single factor.

Changes in plant abundance are brought about by changed recruitment and/or mortality (Silvertown & Lovett Doust, 1993). In order to examine plant population dynamics and predict further change, it is therefore important to determine the nature of recruitment and mortality patterns. Recruitment and mortality are dependent on, amongst other things, fire, rainfall and herbivory (Dublin *et al.*, 1990; Prins & Van der Jeugd, 1993). Different conditions therefore cause episodic recruitment (Silvertown & Lovett Doust, 1993; Higgins, Bond & Trollope, 2000) and differing mortality over time. While actual recruitment and mortality rates are difficult to determine, size class distributions of the population can give insight into their dynamics (Silvertown & Lovett Doust, 1993). A high density of young individuals each year suggests that recruitment is high, while the presence of a large number of the biggest individuals each year indicates that mortality is fairly low. A population exhibiting these characteristics can be assumed to be fairly healthy while one showing high adult mortality and/or low recruitment rates will probably decrease in number if this pattern persists.

Ithala Game Reserve, situated in northern KwaZulu-Natal, South Africa, is an example of a system where large browsers were exterminated and excluded for approximately a century before being reintroduced and restricted by fences after establishment of the reserve in 1972 (Johnson, 1990). The vegetation in this area was thus free from browsing pressure for a lengthy period before again being browsed. The nature and extent of changes brought about by the introduced browsers on the woody vegetation of Ithala over the past few years is of consequence for its management. In response to concern over the state of the browse resource in Ithala Game Reserve, a long-term study was set up in 1992. Elephants had recently been introduced to the reserve and it was hoped that the extent of their impact, along with that of other browsers, would be determined by continuous monitoring.

In this study, I set out to answer the following questions: 1) How are tree species dynamics in Ithala changing in response to herbivory? 2) Are there any differences between tree species that account for their different responses to herbivory? 3) To what extent do browsers in Ithala have the ability to change the composition and structure of woody communities? 4) Is the effect of herbivory on woody vegetation affected by other environmental factors? 5) Does the debate on elephant removal need to be expanded to consider other browsers?

Study area

Ithala Game Reserve, a Category II Protected Area (Wahl & Naudé 1996), is situated in northern KwaZulu-Natal. It measures 29 653 ha in area, with geographical co-ordinates 27°30'S, 31°25'E (Figure 1). Rainfall is seasonal, with the majority falling in the summer months, September to March. Annual rainfall ranges between 500 and 1200 mm, with a 25-year average of 791 mm. (Figure 2). The large altitudinal range (350 to 1550 m a.s.l.) causes rainfall to vary within the reserve. Rainfall is lowest in the northern valley lowland and highest in the southern high altitude area (Porter, 1983), but rainfall values from the Thalu office complex in Ithala (approximately 800 m a.s.l.) and Louwsberg town (approximately 1200 m a.s.l.) are significantly correlated ($p < 0.01$). Summer temperatures are warm to hot (average daily temperatures range from 18 to 30°C), while winter temperatures are generally warm to mild (daily average 15 to 25°C) (Porter 1983). Maximum temperatures can reach up to 40°C and, while frost does not occur, temperatures can reach freezing point on some winter nights (Porter, 1983).

Five main rivers and streams dissect the reserve, and topography varies from undulating grassland to steep rocky cliff faces. Approximately 20% of the reserve is located on gradients in excess of 40° (Le Roux 1985), making access to approximately 5 884 ha of the reserve difficult, if not impossible, for large animals. Porter (1983) describes the geology of the reserve. Turner (1980) produced a soil-geology map of the area. Shallow, rocky Mispah soils dominate the reserve. Soils at higher elevations tend to be leached, while relatively more fertile soils with higher clay content occur in the valley bottoms (Porter 1983). Sandy acidic soils are found in areas underlain by granite (Porter 1983).

Three major veld types dominate the reserve: Natal Central Bushveld (Granger 1996a), North-eastern Mountain Grassland (Bredenkamp, Granger & Van Rooyen 1996) and Natal Lowveld Bushveld (Granger 1996b). Porter (1983) has described the vegetation types of Ithala Game Reserve in detail (see Appendix 1 for summary of Porter's (1983) vegetation types). Balcomb (1994) has done a similar survey.

Before the reserve was established in 1972, indigenous animal populations had been largely exterminated from the area. Since 1884, Ithala had been under the ownership of white farmers, and the Rinderpest epidemic of 1896, intense hunting and the anti-nagana campaign, waged between 1919 and the early 1950s, had a severe effect on the game populations (Johnson 1990). Most of the farms in the Ithala area consisted of labour and tenant farms (Johnson 1990), and maize and cotton were grown on the flatter areas. By the time the Natal Parks Board (now KwaZulu-Natal Wildlife) took control of Ithala in 1973, overgrazing by livestock was widespread and very little game existed, with 25 species being locally extinct (Johnson 1990).

Since its proclamation as a reserve, Ithala has had a number of indigenous browsing herbivores, including black rhinoceros (*Diceros bicornis* L.), impala (*Aepyceros melampus* Lichtenstein) and kudu (*Tragelaphus strepsiceros* Pallas), and later eland (*Taurotragus oryx* Pallas) and elephant (*Loxodonta africana* Blumenbach) reintroduced. Giraffe (*Giraffa camelopardalis* L.), never previously recorded in the area (Goodman & Tomkinson 1987), were introduced. A total of 50 juvenile elephants were introduced between 1990 and 1994, and numbers reached 56 in 2000 (Table 1). Other browsers have increased in number, with black rhino, giraffe, kudu and impala having bred so successfully that part of their populations needed to be removed to relieve browsing pressure. Total animal unit equivalents of browsers have increased since 1973, becoming relatively stable at approximately 1050 AU from 1996 (Figure 3). Although animal units (or large stock units) are not a reliable measure of herbivore habitat use (Dekker, 1997), they give a consistent indication of the biomass of browsers present from year to year. No reliable estimates of nyala (*Tragelaphus angasii* Gray), bushbuck (*Tragelaphus scriptus* Pallas) or duiker (*Sylvicapra grimmia* L.*)* numbers were available.

Materials and Methods

Vegetation sampling

Transects were set up in the reserve in September 1992 and 1993, and thereafter every April up to and including 2000. They were randomly placed within the fairly accessible western sector of the reserve, within the Ngubhu basin. The vegetation type sampled by each transect was recorded, based on Balcomb's (1994) unpublished map. Most transects were 50 m long, and width was adjusted so that, where tree density allowed, 15 or more individuals of the most common tree species in the transect were measured. For each tree, the species was identified, and the state of the individual was recorded as normal growth, coppice growth, senescent or dead. The number of live and dead stems per tree was recorded, as well as stem diameter just above ground level, above any buttress swelling. From 1998 on tree height was recorded. If the tree had been damaged by herbivores, utilisation measures were recorded. In the event that a tree had been severely affected and had begun to coppice, both old and new stem diameter was recorded. The type of damage (damage to canopy, bark or roots, or accidental damage) was recorded, as well as the age of damage (greater or less than 6 months) and agent responsible. Utilisation indices were determined for canopy (Table 2) and bark use. Analysis revealed that very few bark utilisation events were recorded; only canopy utilisation measures were therefore used in analyses. Finally, growth responses (coppice growth, no effect on vigour or death) were recorded for each tree. Nomenclature of species follows Arnold & De Wet (1993).

Each year up to and including 2000, transects were again randomly sited and recorded. The number of transects measured per year ranged from 54 to over 150. All transects analysed in this study were situated within the Ngubhu basin in the western half of the reserve, in the *Acacia nilotica-Combretum zeyheri* woodland vegetation type.

A number of anomalous transects were identified within the data set; these comprised species which were not characteristic of *Acacia nilotica- Combretum zeyheri* woodland, and were excluded from analyses. Of the 153 different tree species recorded in the area over the ten year period only 31 of the most common species were included in the analyses. These made up approximately 80 % of the total density and 99 % of the total basal cover in 1992 and 80 % and 88 % respectively in 2000.

Size structure of population

A Kolmogorov-Smirnov goodness of fit test for grouped data (Zar 1999) was used to determine whether the individual tree species had changed in the population size structure of live trees between 1992 and 2000. Expected frequencies were calculated using species' 1992 distributions. Only those species with a sample size (number of trees) greater than six in both 1992 and 2000 were tested. Tree height and diameter were significantly correlated ($p < 0.01$, $R^2 = 42.41$). Diameter was assumed to give an indication of tree age. The size class distributions of those species showing a significant change were plotted. Those species which appeared to be growing through into larger size categories were then examined for relationships between average diameter and density.

Recruitment

Due to wide ranging differences in density brought about by differences in sampling intensity over the years, recruitment was not determined using absolute density values. Instead, recruitment was measured as the proportion of all live trees made up by those with a diameter of less than 0.7 cm. This size class was based on Prins and Van der Jeugd's work in 1993. The authors recorded the highest rate of growth of *Acacia tortilis* to be 0.64 cm per year. Ithala experiences a similar rainfall regime to Lake Manyara National Park (Tanzania), where Prins and Van der Jeugd carried out their work. The size class of 0 – 0.7 cm diameter was therefore assumed to include the youngest cohort of tree seedlings, i.e. those having germinated since the previous year's sampling period. Proportions of each species made up by this recruitment class, each year, made up the dependent variable data set. Tree species were pooled in order to obtain a suitable sample size. In order to approximate a normal distribution, proportions were transformed using the Freeman and Tukey (1950) arcsine transformation suggested by Zar (1999).

Agents which could influence recruitment patterns include fire, herbivory and rainfall during the study period. Fire patterns during the study period were such that not all transects were burned during any one season. Recruitment data were pooled over all transects for each species, making it impossible to assign a particular species to a 'burned' or 'unburned' category in any one year. Fire was thus not included in the analysis of recruitment. The effects of herbivory and rainfall on recruitment were examined using multiple linear regression. Rainfall figures from Thalu camp (July - June inclusive) were used as one predictor variable. Herbivory was calculated as the average percentage of each tree species' canopy utilised by herbivores every year, as recorded during the annual field excursions. Multiple linear regression was run using Statistica® 5.5 (Copyright Statsoft, Inc. 1984-2000).

Mortality

A Chi-square test was carried out to test for differences between the observed proportion of dead trees per species and the expected proportion, based on their number of live individuals. Only those species with records from seven or more years were tested. Trees were then tested to see whether large or small individuals were subject to greater mortality (G test, Sokal & Rohlf, 1981). To examine the effect of herbivory and rainfall on proportions of dead trees, multiple linear regression was used. Again, pooling of transects made it impossible to analyse the effects of fire on mortality patterns. The proportion of all trees made up by dead individuals was transformed, using the arcsine transformation suggested by Freeman and Tukey (1950, cited in Zar, 1999). All trees were tested together first. Later, trees were split into those which appeared to show a decline in abundance, and those which appeared to increase in abundance between 1992 and 2000, and tested against herbivory. A G test was conducted to test for differences between average proportions of dead trees in decreasing and increasing species. Species that showed anomalous patterns of increase or decrease were omitted from the latter analyses.

Description of herbivory

Herbivory was calculated per tree species as the average percentage canopy removed per recorded tree, over the entire study period. The relative contribution of four agents of utilisation to overall canopy utilisation of all trees was calculated, both as frequency of utilisation and as amount of damage to the individual trees. These agents were elephant, black rhinoceros, other browsers (it was difficult to distinguish between other browsers) and other agents. 'Other' agents included humans, moisture stress, flooding, shading, fire, frost, wind, accidents and unknown causes of damage. Elephant damage was considered to be that most reliably identified; patterns of elephant damage over time were thus examined. A Kolmogorov-Smirnov goodness of fit test for discrete data was conducted to test whether the distribution of elephant-damaged trees in different damage categories had changed between 1992 and 2000. The 1992 distribution of damaged trees comprised the expected distribution pattern for 2000. Relationships were sought between the amount of herbivory, rainfall and number of herbivores (expressed as animal unit equivalents) per year.

Change in frequency and abundance

Simple tests were used to detect general patterns in woody vegetation change over the sampling period. A G test (Sokal & Rohlf, 1981) was used to test for changes in frequency of occurrence of the most common tree species between 1992 and 2000. Frequencies were recorded as the number of transects in which the tree species occurred in 1992 and 2000.

Change in abundance over the study period was measured using the nonparametric Mann-Whitney U test (Zar 1999) on both density (individuals per hectare) and basal area (cm^2 per hectare) data from 1992 and 2000. Many species' data were non-normally distributed due to a high incidence of transects where the species did not occur. Density and basal cover values included all transects (excluding aforementioned anomalous transects), even those where the species was not present.

Results

Reliability of data

On examination of results, it was evident that some aspects of the data were anomalous, and were probably due to sampling error rather than biological variation. Density values varied substantially over the years for some species, especially for those with small sample sizes. The extent of this variation was often greater than could be accounted for by even extreme shifts in environmental conditions. Examples include species that were not recorded at all in 1992, but were present in high densities in subsequent years, with even the largest size class (diameter greater than 100 cm) being represented. *Olea europea*, for example, was not recorded at all in 1992, but was found in all seven size classes in 1994. Similar, if less remarkable, patterns were shown by *Diospyros lycioides* and *Coddia rudis.* This is highly improbable, and could only have been an artefact of sampling. *Euclea divinorum* showed a similarly unlikely disappearance between 1999 (when both density and recruitment were high) and 2000. The aforementioned species were excluded from all analyses. Table 6 highlights further anomalies in the abundance data, in that a number of species are absent in 1992, but present in 2000 (e.g. *Pyrostria hystrix*), or vice versa (e.g. *Ziziphus mucronata*). Further examples of anomalies caused, most probably, by sampling error are given in the text to follow. Results such as these suggest that frequency, density and basal area data were unreliable in many instances, probably due to misidentification of species, different transect sizes over the years, different sampling intensity and placement of transects in anomalous areas such as drainage belts or animal pathways. The abundance values displayed in Table 6 should therefore be viewed with caution.

Although density and frequency values were affected by sampling errors, other measures were considered to be more reliable. These included proportions of individuals which were in the recruitment category or had died (mortality), as well as proportions of trees occurring in different size classes. These three measures gave valuable insights into the patterns shown by some tree species. Measures of herbivory were assumed not to be unduly biased by transect placement either.

It is suggested that future field research be concentrated on a number of fixed transects with constant dimensions and known geographic locations. Although not always practicable, misidentification of tree species could be limited by increased constancy of field assistants. It is further suggested that nesting for rare tree species be avoided, or these nested transects analysed separately. Walker (1976) provides guidelines for successful monitoring of change in vegetation composition and utilisation in savannas.

Size structure of population

Size class structure of the woody population was less likely to be affected by placement of transects than were measures of abundance. The patterns observed, then, are likely to be more accurate indicators of population dynamics. Those species with significant Kolmogorov-Smirnov test results (Table 3) showed a change in size class distribution between 1992 and 2000. Species showing no significant size class structure change included *Acacia caffra, Ormocarpum trichocarpum, Peltophorum africanum, Rhus rehmanniana* and *Ziziphus mucronata.* Although *P. africanum* showed no significant change, it had individuals in fewer size classes in 2000 than in 1992; a number of species shared this trend. Of the species with significant Kolmogorov-Smirnov test results, *Euclea crispa* and *Scolopia zeyheri* showed an increase in the number of size classes represented, between 1992 and 2000. The other species, excluding *Acacia karroo* and *Euclea racemosa* (which showed no change in size class number) declined in the number of size classes represented in 2000, when compared with 1992 (Table 3). *Aloe marlothii* was excluded from this analysis as no live individuals were sampled in 2000.

No individuals of *Acacia gerrardii* (Figure 4 a) were found in size classes five, six or seven in 2000, whereas these classes had been well represented in 1992. *Scolopia zeyheri* and *Euclea crispa* had individuals in more size classes in 2000 than 1992. A number of species, including *Euclea natalensis, E. racemosa, E. crispa, Acacia nilotica, Rhus lucida, R. pentheri* and *Scolopia zeyheri*, had a large number of small individuals in 1992 which appeared to have grown through into the larger size classes in 2000 (Figure 4 b, d, e, h, j, l & m respectively). These species showed a non significant relationship between density and average size of the individuals, indicating that self-thinning relationships (Zeide, 1995; Xue *et al.*, 1999) had not occurred. Although multi-species communities, such as occur at Ithala, are unlikely to follow the –3/2 self-thinning law documented for monocultures (Yoda *et al.*, 1963), a negative relationship between density and average size of individuals might be expected. Sample sizes of *Acacia nilotica, Euclea natalensis, E. racemosa* and *Rhus lucida* were deemed sufficient (n>=40 individuals) in intermediate years to be examined more closely (Figure 5 a-d). *Rhus lucida* showed evidence of being a maturing population, with individuals in the smaller size classes in 1992 slowly growing through to the larger size classes in 2000 (Figure 5 d). *Euclea natalensis* showed a similar pattern (Figure 5 b), although this species still had a considerable proportion of all individuals in the two smallest size classes (0-1 and 1-3 cm diameter respectively) in 1998 and 2000. *Acacia nilotica* also showed an ageing process, as a greater proportion of individuals occurred in larger size classes in the latter years of the study; very few individuals were present in the larger size classes from 1996 onwards, though (Figure 5a). *Euclea racemosa* (Figure 5c) did not appear to be ageing as much as was suggested when only 1992 and 2000 were considered. It is noteworthy that, apart from *Acacia nilotica*, those species with an ageing population were those which are less favoured by browsing ruminants and elephants (Owen-Smith & Cooper, 1987; De Boer *et al.*, 2000).

A second pattern shown by those species with significant changes in size class structure is one of loss of large individuals between 1992 and 2000. No *Acacia gerrardii* individuals larger than 10 cm in diameter were recorded in 2000. When intermediate years were examined, this pattern was still evident, though a small number of individuals larger than 30 cm in diameter were recorded in 1998. 1999 showed a low density of individuals in size class five (10-30 cm diameter), although no larger individuals were recorded. *Acacia karroo* showed a similar pattern. Size classes between five and ten cm, and greater than 100 cm, were increasingly poorly represented from 1992 to 2000.

Combretum apiculatum indicated a large increase in the smallest size class (0-1 cm) in 2000. Patterns in intermediate years indicate that this species had high recruitment rates, with higher proportions of individuals in the smallest size classes (<=3 cm diameter) than in others. High recruitment in 2000 is thus consistent with previous years. Average herbivory rates on *C. apiculatum* were not high (on average 10 % canopy removed), making it unlikely that herbivory in 1999 caused a reversion of many larger individuals to this size class in 2000.

Although statistically significant, changes in size class structure of *Gymnosporia buxifolia* and *Dichrostachys cinerea* between 1992 and 2000 were not dramatic.

Recruitment

Recruitment, as indicated by the proportion of all trees made up by those with a diameter equal to or less than 0.7 cm, did not range widely between 1992 and 2000. The average percentage of live trees made up by these individuals increased slightly between 1994 and 1995 (Figure 6) before becoming stable at approximately 25 %.

Rainfall figures from the previous year had a significant effect on recruitment ($p < 0.000$), while rainfall figures with a lag of one year had no significant effect ($p < 0.401$). Rainfall appeared to affect recruitment in 1995 and 1996, when two years of fairly high rainfall, interspersed by one year of only slightly below average rainfall (Figure 2), coincided with increased recruitment rates of approximately 36 - 38 % in 1995 and 1996 (Figure 6). Low rainfall between 1997 and 1999 (Figure 2) preceded a fall in mean recruitment to approximately 26 % in 1999 (Figure 6).

Herbivory had a significant negative effect ($p < 0.000$). Recruitment could thus be predicted by

Arcsine (Proportion recruitment) = 0.003 x (rainfall in previous year) -0.006 x (mean % canopy herbivory) + 0.470

($F_{2,312} = 22.862$, $p < 0.000$, $R^2 = 0.128$), where proportion recruitment refers to the proportion of total live trees made up by those with a diameter of 0.7 cm or less.

As the percentage canopy utilisation in the previous season increased, the proportion of all live trees comprised by the recruitment size class decreased. This could be due to browsing of the young seedlings, causing mortality. The combined effects of rainfall and herbivory explain only 13 % of the variance in recruitment. It is possible, then, that the most important factors affecting recruitment have not been included in the model; fire could be one of these factors.

Mortality

Proportions of dead trees per species were found to be significantly different to those expected, based on proportions of live trees present ($p < 0.001$). Those species exhibiting the greatest difference in number of dead trees compared with expected proportions were, in rank order, *Aloe marlothii*, *Acacia nilotica* and *Acacia davyi*. All exhibited more dead trees (45.2 %, 21.5 % and 7.5 %, respectively - Table 4) than one would expect based on the number of live trees present. Four percent of all sampled *Acacia gerrardii* individuals were dead (Table 4).

Of those species that showed fewer dead trees than expected, *Euclea crispa*, *E. racemosa*, *Hippobromus pauciflorus* and *Rhus lucida* contributed most to the Chi-square value. All four of these species displayed less than 1.5 % mortality (Table 4). Decreased mortality is one factor which, among others, could cause an increase in abundance of these species. The contribution of these species to the Chi-square value was negligible, however, as was that of all other species (excluding *Aloe marlothii*, *Acacia nilotica* and

A. davyi), suggesting that most species' mortality patterns were consistent with patterns of live tree numbers.

There were significantly more large dead trees (diameter >=10 cm) than was expected based on the number of large live trees ($G = 269.116$, $p < 0.001$). *Aloe marlothii*, *Acacia nilotica* and *Acacia davyi*, the three species exhibiting greater mortality than expected, also had more large dead trees than expected ($G = 40.264$, $p < 0.001$). This indicates that large trees (diameter >=10 cm) died more often than did smaller ones. Although this could be an artefact of sampling - small dead trees might be overlooked or difficult to identify - it suggests that large trees were often the specific target of mortality agents. Rainfall did not have a significant effect on mortality per year ($F_{1,7} = 0.051$ $p < 0.828$, $R^2 = 0.007$). There was no lag effect of rainfall either ($F_{1,7} = 0.984$ $p < 0.354$, $R^2 = 0.123$).

As herbivory increased, so did the proportion of dead trees ($F_{1,27} = 24.605$ $p < 0.000$, $R^2 = 0.477$) when all trees were considered together:

Arcsine (Proportion mortality) = 0.015 x (mean % canopy utilisation) -0.036

Herbivory's effect on the proportion of dead trees suggests that it was an important cause of mortality, accounting for 48% of the variation in mortality figures.

Species were grouped according to apparent patterns of change in abundance. For those species that showed a decrease in abundance between 1992 and 2000, increased herbivory caused an increase in the proportion of dead trees ($F_{1,12} = 14.136$ $p < 0.003$, $R^2 = 0.541$).

Arcsine (Proportion mortality of 'decreasing' species) = 0.017 x (mean % canopy utilisation) -0.038

Herbivory caused greater mortality in these 'decreaser' species than when all species were grouped together. This implies that these 'decreaser' species are less well adapted to severe herbivory than are those that increased in abundance, which did not show a significant relationship with herbivory ($F_{1,8} = 1.079$ $p < 0.330$, $R^2 = 0.119$). The decreaser species also had a higher average mortality than did the increasers ($p < 0.01$) (Figure 7). Herbivory thus causes greater mortality in decreaser species such as *Aloe marlothii* than for increaser species such as *Euclea racemosa*. Increased herbivory rates therefore have greater implications for decreaser species than for others.

Description of herbivory

Aloe marlothii, *Cussonia natalensis* and *C. spicata*, *Coddia rudis*, *Acacia nilotica* and *A. gerrardii* are among those species with the highest herbivory rates, indicating that they are preferred by browsers in the Ngubhu basin (Table 5). By identifying the herbivore responsible for the greatest amount of damage to each tree species, it is evident that *Aloe marlothii* was browsed most heavily by black rhino (Table 5). *Euclea* and *Rhus* species were not favoured by browsers in the current study; neither were *Diospyros lycioides*, *Acacia tortilis* and a number of others (Table 5). The high percentage of canopy removal of *Aloe marlothii* could be a factor driving a decrease in abundance. This species, along with *Cussonia natalensis*, could be seen in the field to be heavily utilised by browsers.

It is evident from Table 5 that, for many tree species, black rhinos and other herbivores were responsible for as much damage as, or more than, elephants.

Browsers together were responsible for over 60 % of the number of utilisation events over the study period. It was interesting that 37 % of all damage was caused by agents other than herbivores (Figure 8). Of the identified browsing agents, elephants were responsible for 16 % of all damage events over the study period, while black rhinos accounted for 13 % of damage frequency (Figure 8). Other browsers utilised woody individuals approximately as often as the former two species together. Elephants were responsible for 37.6 ± 16.76 % (mean ± standard deviation) of all tree mortality, while black rhinos were responsible for 7.1 ± 14.09 %. In 2000, the combined animal unit equivalent mass of elephants and black rhinos was approximately one third of that of the rest of the combined browsers. The impact that these two megaherbivores had on their browse resource was thus disproportionately large compared with the number of individuals and biomass that they represented.

Frequency of utilisation by elephant fluctuated over the years, while black rhino accounted for fewer utilisation events in later years (Figure 9). Figures 9 and 10 show similar patterns. Predictably, frequency and percentage of total damage were correlated ($R^2 = 0.81$, $p < 0.01$). Both frequency and amount of utilisation by browsers other than black rhino and elephant increased over the study period, despite culling of species such as giraffe, kudu and impala during this time. Black rhino utilisation fluctuated over the study period but appeared to be declining in later years. Reduction of their numbers by reserve officials could account for this trend. Two black rhinos were removed in both 1993 and 1995, and 11 (20% of the population) were removed in 1998. Three more individuals were removed by officials in 2000. Both frequency and amount of elephant utilisation of woody species fluctuated between 1992 and 2000. Elephant numbers increased from 30 to 56 individuals over the study period, and the size of the animals increased as the introduced orphans grew. One might expect this to cause increased amounts of herbivory. Elephant movement throughout the reserve increased with time (B. Page, pers. comm., Senior Lecturer, University of Natal, Durban). Before release, elephants were held in a boma within the Ngubhu basin (I. Rushworth, pers. comm., Regional Ecologist North, KwaZulu-Natal Wildlife). Natal Parks Board (now KwaZulu-Natal Wildlife) yearbooks noted that, in 1994/1995, most sightings of the elephants were still within this basin. In 1995/1996, elephants were again seen most often in the Ngubhu basin, but sightings were also recorded in the Dakaneni River basin. By 1996/1997, elephants had been sighted in both the Ngubhu and Dakaneni river basins, as well as in the eastern half of the reserve. Barnes (1983) mentioned that patterns of elephant movement differed between years. Elephant movement throughout the reserve could therefore account for some of the fluctuations in damage occurring in the Ngubhu basin. Other browser species in comparison are more sedentary, and in the case of black rhino even territorial. Elephants are preferential grazers (Guy, 1976). Differential availability of grass could therefore be another factor causing fluctuations in browse usage by elephants over the years, with lowered grass quality or quantity causing increased browse utilisation. It is evident that, while frequency and amount of damage were closely correlated, elephant damage was greater than one might expect based on frequency values alone. On a tree per browsed tree basis, it is apparent that, when elephants utilised trees, they did so to a greater extent than did black rhinos and other browsers (Figure 11).

On average, elephants removed 36.5 ± 11.01 % of the canopy of every tree that they browsed. This was greater than that removed by black rhinos and other browsers (27.5 ± 8.56 % and 16.2 ± 8.49 % respectively). Considering the size of the elephants, this phenomenon is not surprising. A further consideration is that elephants often remove a lot more vegetative matter than they actually consume. Elephants, particularly bulls, are often noted to push trees over for display rather than for feeding purposes (Guy, 1976). This does not generally apply to other browser species.

All tree species were pooled in order to increase sample size for elephant damage over time. There was no pattern in the percentage of trees showing elephant damage over time; approximately four to ten per cent of all trees were browsed by elephants each year. This was surprising, as the elephant population almost doubled during the study period. Again, this could be due to elephant movement out of the Ngubhu basin, which increased in later years. The frequency distribution of elephant damage events over the different damage categories was examined. Results of the Kolmogorov-Smirnov test indicate that elephant-damaged trees were significantly differently distributed over the damage categories in 2000 than they were in 1992 ($p < 0.001$). In 1992, most elephant damage to trees was minimal (0-10 % of the tree's canopy utilised) (Figure 12). No trees damaged by elephants had more than 75 % of their canopy removed, and almost none had more than 50 % removed. In 2000, however, trees displayed greater damage by elephants more often. Almost 35 % of elephant-browsed trees had between 24 and 50 % of their foliage removed, while approximately four per cent of all trees browsed by elephants had 100 % of their canopy removed (Figure 12). Damage over the years evidently accumulated as trees were revisited by elephants. Individual tree species with adequate sample sizes in most years, for example *Rhus lucida*, *Acacia nilotica*, *Dichrostachys cinerea* and *Euclea racemosa*, showed similar patterns of increased elephant damage over time.

Based on Field's work (1971), a negative relationship might be expected between rainfall and herbivory; rainfall was not, however, significantly correlated with either animal numbers (expressed in animal unit equivalents) or the percentage herbivory per year ($p > 0.05$). Surprisingly, the correlation between herbivory and herbivore numbers was not significant. This could be due to the inadequacies of expressing browsers as animal unit equivalents (Dekker, 1997). Alternatively, the increase in animal numbers, calculated for the reserve as a whole, might not adequately predict herbivory in the Ngubhu Basin, which could have reached browser saturation at an early date.

Change in frequency and abundance

Although the sampling strategy prevented accurate estimates of change in density it is still possible to detect patterns. *Acacia gerrardii*, *Aloe marlothii* and *Rhus lucida* showed a significant decline in frequency between 1992 and 2000, while *Acacia karroo, Berchemia zeyheri, Combretum molle, Dombeya rotundifolia, Euclea racemosa, E. crispa, Pappea capensis* and *Scolopia zeyheri* showed significant increases (Table 6). Other changes in frequency were not statistically significant.

Most common tree species showed a consistent increase or decrease in both basal area and density per hectare, between 1992 and 2000. Five species, however – *Combretum molle, C. apiculatum, Acacia karroo, Pappea capensis* and *Dombeya rotundifolia* - showed conflicting patterns of basal area and density change (Table 6).

Euclea natalensis, E. divinorum, Acacia gerrardii, Aloe marlothii and *Rhus lucida* showed consistent patterns of decline in frequency, basal area and density per hectare, with one or more indicator of abundance indicating a significant decrease from 1992 to 2000. Others such as *Euclea racemosa, E. crispa, Scolopia zeyheri* and *Berchemia zeyheri* increased consistently in frequency of occurrence, basal area and density (Table 6), with at least one of these indicators showing a significant increase in abundance between 1992 and 2000. While not showing significant changes in abundance, species such as *Peltophorum africanum*, *Dichrostachys cinerea, Rhus pentheri* and *Ziziphus mucronata* indicated patterns of decline. Similarly, species such as *Rhus rehmanniana* and *Acacia tortilis* did not show significant results ($p > 0.05$), but indicated possible increases in abundance. *Gymnosporia buxifolia* showed a significant decrease in basal area.

Discussion

Patterns of change in woody species

Heavy browsing and low rainfall in the year preceding establishment were predicted to reduce recruitment increase adult mortality. This has negative consequences for population size. Different tree species responded differently to herbivory and other environmental variables, however, causing populations to vary considerably in their patterns of increase or decrease.

The apparent decrease in frequency of *Acacia gerrardii*, *Aloe marlothii* and *Rhus lucida* is interesting. *Aloe marlothii* was browsed, on average, approximately twice as heavily as *Acacia gerrardii* and more than four times as heavily as was *Rhus lucida* during the study period. It is evident that *Aloe marlothii* suffers heavy browsing and appears to be undergoing widespread mortality and decrease in abundance in Ithala Game Reserve. *Acacia gerrardii*, a favoured source of browse for game species (Van Wyk & Van Wyk, 1998), also appeared to have suffered a decline in abundance since the study began. The decline of *Rhus lucida* did not appear to be linked to browsing pressure, which was relatively light; other factors including, possibly, sampling error could be responsible for its apparent decline.

The significant increase in frequency of four species (*Pappea capensis, Combretum molle, Berchemia zeyheri* and *Dombeya rotundifolia*) is somewhat anomalous, as they are not generally known to increase in response to browsing pressure. The former three species are noted by Van Wyk and Van Wyk (1998) to be favoured browse species, while Owen-Smith and Cooper (1987) note that *Dombeya rotundifolia* is favoured during the dry season. Differences in the geographic position of transects in 1992 and 2000 could have rendered some species more likely to be sampled in 2000, and possibly caused their apparent increase in frequency. Transects in 2000 were on average 74.3 ± 16.3 m^2 larger than those in 1992. This would cause an increased probability of a species' occurrence in transects in 2000, possibly explain some anomalous increases in frequency. It does, however, strengthen the likelihood that species indicating a decrease were showing a true decline in abundance. Patterns in size class change in *Pappea capensis, Combretum molle, Berchemia zeyheri* and *Dombeya rotundifolia* between 1992 and 2000 were investigated. While the largest size classes represented in 1992 in both *Pappea capensis* and *Combretum molle* were missing in 2000, both of these species showed an apparent increase in recruited individuals in 2000. This pattern supports implications of an increase in abundance, but the absence of the largest size class in 2000 should be noted. The largest size class sampled in 1992 was also absent in 2000 for *Dombeya rotundifolia.* There was an increase in density of all the other size classes, though, indicating a seeming increase in abundance and high recruitment.

The increase shown by *Berchemia zeyheri* appeared to be an artefact of sampling. While only one size class (1-3 cm diameter) was represented in 1992, six were present in 2000. Only an exceedingly high growth rate of 3.4 cm (in diameter) per year would allow individuals in this size class to reach the largest size class (30-100 cm diameter) recorded in 2000. The highest average growth rate cited by Prins and Van der Jeugd in East Africa (1993) was a 6.4 mm per year diameter increase for *Acacia tortilis.* Although the species are bound to differ in growth rates, it seems unlikely that *B. zeyheri* would achieve a growth rate of 3.4 cm per year. If anything, *Berchemia zeyheri,* with hard heartwood

(Van Wyk & Van Wyk, 1998), is likely to grow more slowly than *Acacia tortilis,* a species associated with early successional stages (Smith & Shackleton, 1988) and hence likely to grow more rapidly. It is probable that observer bias and differences in geographical location of transects between the years were responsible for the changes in abundance seen in this species.

A pattern of increased adult mortality and low recruitment appeared to be responsible for the general decline shown by *Aloe marlothii* and *Acacia gerrardii.* Of those species which showed a significant increase in basal area or density, *Euclea racemosa, E. crispa* and *Scolopia zeyheri* showed increased densities of individuals in the smallest size class in 2000. *Euclea crispa* showed an exceptionally high density of small individuals (<1 cm diameter) in 2000 compared with the same size class in 1992.

The size class distribution of *Acacia karroo* was similar in 2000 to 1992, although densities were higher in 2000. This calls into question the apparent decrease in density indicated in Table 6, although indications of a decline in the larger size classes of this species could indicate that it is not entirely unlikely to decline in abundance in future.

The significant increase in basal area of *Gymnosporia buxifolia* is supported by evidence of a decrease in density of individuals in the largest size class, which exhibit the greatest basal area per individual.

Patterns of herbivory on woody species

Indicators of the level of browsing experienced by different tree species yield further insight into patterns of abundance, as species with high levels of browsing could have increased mortality and dampened recruitment. Although plant traits of palatability are dependent on the specific animal species in question, it is enlightening to consider evidence of acceptance or rejection of plants provided by other authors. Findings are to a large extent in agreement with De Boer *et al.* (2000), who noted that elephants preferred *Combretum* species, *Dichrostachys cinerea* and *Ziziphus mucronata* (favoured species in Ithala – Table 5). De Boer *et al.* (2000) also noted that elephants avoided *Euclea* and *Rhus* species, which corresponds with the findings of this study. Guy (1976) also noted *Dichrostachys cinerea* and *Acacia* species to be preferred by elephant, while *Euclea divinorum* was avoided. Kudu and impala preferred *Dichrostachys cinerea*, *Acacia nilotica*, *A. karroo* and *Ziziphus mucronata*, while avoiding *Euclea natalensis* (Owen-Smith & Cooper, 1987). Again, these findings were similar to those of this study. Differences arose in that *Peltophorum africanum* and *Dombeya rotundifolia* were rejected by goats, kudu and impala(Owen-Smith & Cooper, 1987); the current study found that these species were eaten fairly extensively. Other animal species in Ithala Game Reserve could be responsible for this apparent discrepancy. *Diospyros lycioides* was said to be a preferred species (Owen-Smith & Cooper, 1987), whereas it was not found to be so in the present study. *Acacia tortilis* was apparently avoided in the Ngubhu basin. Loffell (1999) also noted the low utilisation of *Acacia tortilis* by giraffe in Ithala Game Reserve. This species, however, is noted by Pellew (1983) to be browsed heavily by elephant and giraffe in the Serengeti, and is also noted by Van Wyk and Van Wyk (1998) to be a well utilised browse species. Discrepancies such as these could be attributed to seasonal and environmental factors such as different soil nutrient status (Owen-Smith, 1993), as well as a different mix of herbivores and tree species. Differences in browsing pressure could also be responsible for different browsing patterns, however. Rushworth (unpublished monitoring data) notes that *Protea caffra* and *Protea comptonii*, both avoided by browsers in other reserves, are heavily browsed by kudu and eland in Ithala game reserve. *Lantana camara*, a noxious alien (Pooley, 1998), is also heavily browsed in Ithala. Patterns such as these could indicate high browsing pressure in the reserve, or else that seasonal movement of browsers can no longer take place due to restrictive fences. Indications of heavy browsing on other species make Acacia nilotica's low utilisation rates in Ithala even more anomalous.

The high levels of damage caused by agents other than herbivores concur with high levels of wind and lightning damage to trees noted in the absence of elephants in Rwanda (Spinage & Guiness, 1971). Although Akagera National Park, where their study was carried out, experiences a high number of lightning days per year, it is important to note that elephants and other herbivores are not the only agents that make a noteworthy contribution towards overall tree damage.

Examination of the patterns of change shown by different species, as evidenced by recruitment and mortality levels, size class structure and changes in density, enable us to return to the original aims of the study. In particular, insight can be gained into the five main points outlined earlier.

Effect of herbivory on the dynamics of woody species

There is evidence that three broad categories of tree exist in Ithala Game Reserve: those showing an increase in abundance, those showing a decrease in abundance, and those whose abundance has remained largely unaltered over the study period.

A number of species appeared to have fairly stable populations, exhibiting non-significant changes in abundance. Changes in size class structure were either non-significant or represented few dramatic changes between 1992 and 2000. These species experienced average to high recruitment rates, low to average mortality rates (0 – 2.9 % of all trees made up by dead individuals – Table 4), and, while being utilised by herbivores, were not browsed extensively (average 8 to 15 % canopy removed – Table 5). Species considered to be stable within the Ngubhu basin include *Rhus lucida, R. pentheri, R. rehmanniana, Peltophorum africanum, Combretum apiculatum, C. molle, Gymnosporia buxifolia, Acacia caffra, Pappea capensis, Dichrostachys cinerea, Maytenus nemorosa* and *Dombeya rotundifolia. Acacia karroo* appeared to be stable but fairly high mortality rates (4.4 % - Table 4), combined with average to high herbivory rates (15 ± 6.3 % - Table 5) could render this species vulnerable to increased herbivory and a decline in density. Loffell's study (1999) concurs, predicting the eventual demise and perhaps disappearance of *A. karroo* from areas of high giraffe abundance, of which the Ngubhu basin is one. This species could be benefited, however, by its ability to germinate and establish successfully under the canopy of other species (O'Connor, 1995). This characteristic, in contrast with most other Acacia species, allows it to establish even when surrounding bush and shrubs are fairly dense. Loffell (1999) also predicts the decline of *Acacia caffra*. This is possible but not apparent from results of the present study.

Species which appear to have increasing populations include *Euclea natalensis, E. racemosa, E. crispa* and *Scolopia zeyheri*. These species generally exhibited significant increases in abundance measures (frequency, basal area and density), although *Euclea* *natalensis* did not show this pattern. These species all appeared to be maturing populations on the basis of size class structure (Figure 4), and, in the case of *Euclea crispa* and *Scolopia zeyheri*, had individuals in more size classes in 2000 than in 1992. All showed average to high recruitment rates and low mortality rates (< 1.2 % mortality – Table 4). Most species indicating an increase in abundance were not often selected by herbivores (herbivory rates of < 8% - Table 5), excluding *Scolopia zeyheri*, which had, on average, 15 ± 8.2 % of its canopy removed by browsers (Table 5). This species was one of those which did not show a significant relationship between herbivory and mortality, however, indicating that this herbivory rate did not have a detrimental effect on the species' survival.

Four species indicated a decline in abundance over the study period. These included *Aloe marlothii*, *Acacia gerrardii*, *A. nilotica*, and *A. davyi*. These species should be the subject of continued monitoring. Most of these species showed significant decreases in one or more measure of abundance, and indicated a decrease in large individuals. Recruitment was low, while mortality was often high (4 % - 45 % - Table 4). These species were heavily browsed (average percent canopy utilisation > 17 % – Table 5), with *Aloe marlothii* having an average of 39 ± 27.9 % of its canopy removed by browsing agents. *Acacia davyi* was not heavily browsed, although Loffell (1999) indicated that they were indeed targets of heavy herbivory by giraffes. Field observations suggest that this species is declining (B. Page, pers. comm.). *Aloe marlothii* is a species which is unmistakably declining in abundance, as evidenced by the present study as well as field observations. An increasing number of dead individuals, fewer live specimens with time and very high herbivory rates make this species a conservation priority in this reserve.

Two more species, *Cussonia natalensis* and *C. spicata*, were not adequately sampled and therefore did not show significant results, but displayed high rates of average herbivory (30 ± 39.0 % and 17 ± 24.5 % respectively – Table 5). These species showed evidence in the field of being heavily browsed and are suspected to be declining (B. Page, pers. comm.).

Although a decline in abundance of the aforementioned six species was recorded within the Ngubhu basin, reserve-wide extirpation may not be inevitable, due to the existence of refuges. Both *Cussonia spicata* and *C. natalensis* are noted by Van Wyk and Van Wyk (1998) to occur often in rocky outcrops. *Aloe marlothii* also occurs often on rocky slopes (Van Wyk & Van Wyk, 1998). As mentioned above, approximately 20 % of Ithala Game Reserve is too steep for most large herbivores (Le Roux, 1985). The presence of many steep, rocky valleys and hillsides, then, could provide refugia free from large herbivores, where remnant populations of these species could persist. *Acacia gerrardii*, often found in river valleys (Van Wyk & Van Wyk, 1998), could also maintain individuals in riverine vegetation which was dense enough to discourage access by large herbivores. This species, along with *Acacia davyi* and *A. nilotica*, could also be afforded a degree of refuge on steep slopes.

Differential tree response to herbivory

The acceptability of foliage to browsers can be influenced by many factors. These include nutrients and secondary metabolites, physical defence mechanisms such as thorns, growth stage of the tree and its leaves, soil nutrient and light availability and previous defoliation history (Owen-Smith & Cooper, 1987). Those species found to be decreasing in abundance were all browsed heavily. *Cussonia natalensis* and *C. spicata* are both undefended by thorns, and their leaves are borne in clusters at the end of branches, making them easy to browse. This phenomenon is shared by *Acacia davyi* and *A. caffra*, which have their leaves at the distal ends of narrow branches. This offers an efficient bite for a large herbivore because of the amount that can be collected in one bite. *Acacia nilotica* and *A. gerrardii* have a lower percentage of their leaflets on narrow branches (78 % and 62 %, respectively) (Loffell, 1999). *Acacia karroo* and *A. tortilis* are also species which present less of their foliage in terminal clusters, and, along with *A. nilotica*, have their foliage distributed down the stem, making it more difficult for herbivores to harvest. *Acacia davyi* and *A. caffra* are further poorly defended by thorns in comparison with *A. karroo*, *A. nilotica* and *A. tortilis*. *Acacia nilotica* nonetheless remains fairly heavily browsed (Table 5). Owen-Smith (1993) discussed the palatability of *Acacia nilotica* leaves to kudu, concluding that this species is highly palatable despite high levels of hydrolyzable tannins. Du Toit, Bryant and Frisby (1990) found that high levels of browsing on *Acacia nigrescens* caused an increase in nutrients and lower condensed tannin levels in the foliage; this suggests that a feedback loop exists whereby herbivory increases palatability of some species. This could be the case in the *Acacia* species browsed heavily in the reserve. Unpalatable species such as *Euclea natalensis* and other *Euclea* species were found by Owen-Smith (1993) to be high in condensed tannins, possibly accounting for their unpalatability.

The difference in species' response to herbivory prompts one to investigate the underlying cause of these response patterns. Most species which were increasing in abundance displayed low levels of browsing (*Euclea natalensis*, *E. racemosa* and *E. crispa*), while those which showed signs of decrease (e.g. *Aloe marlothii*, *Cussonia natalensis*) were heavily browsed. It was therefore unclear as to whether the apparent increases and decreases were due to different responses to herbivory, or were simply caused by different levels of herbivory. If the changes evident were simply due to different levels of browsing, it follows that species such as *Aloe marlothii* and *Cussonia natalensis* would not decrease in abundance if they were less heavily browsed, while heavy browsing of *Euclea* species would cause their decline. This seems reasonable in the case of *Aloe marlothii*, which displayed high levels of mortality, apparently due to heavy browsing. *Scolopia zeyheri*, however, does not conform to this pattern. This species was fairly heavily browsed (15 ± 8.2 % - comparable to browsing levels experienced by *Acacia gerrardii*), and yet *S. zeyheri* appeared to be increasing in abundance. Certain characteristics of this species allowed it to thrive in spite of being browsed. *S. zeyheri* was noted to coppice after browsing; so did *Acacia karroo*, *A. nilotica*, *Cussonia natalensis* and *A. gerrardii* (among many others), however, so this factor alone did not account for *Scolopia*'s success. A factor that set the 'increasers' apart from all other species (apart from *Combretum apiculatum*) was a high rate of recruitment. All four species which increased in abundance either devoted a fair proportion of their resources to reproduction, or else had more successful recruitment from the same reproductive effort as decreasing species. This could be due to two factors. First, being unpalatable, seedlings of these species would be less vulnerable to being browsed, and so would have increased chances of survival. A possible second reason for their successful recruitment is that, unlike most *Acacia* species, which are associated with early successional stages and do not establish or grow well under adult canopies (Smith & Shackleton, 1988), *Euclea* seedlings do (Smith and Goodman, 1986). *Scolopia zeyheri* could possibly share this characteristic with the *Euclea* species.

A further property of all 'increasers' was a low mortality rate. All four increaser species showed mortality rates which were lower than expected, based on proportions of live trees. Even *Scolopia zeyheri*, browsed a similar amount to *Acacia gerrardii*, had a mortality rate less than one third as high as that of *A. gerrardii*. While it is not known what caused this lowered mortality rate, this, along with high recruitment, seemed to account for the differences in response to herbivory.

The role of herbivores in changing vegetation composition and structure

The changes in population of the species mentioned above indicate that herbivores play an important role in changing the composition and structure of woody communities. If browsing continues at present rates and the elephant population continues to expand, it is likely that a change in community composition of the trees in Ithala will occur. Based on evidence presented by this study, it seems likely that a number of the more palatable species will become rarer, with larger individuals being heavily browsed (and eventually killed), and poor recruitment rates. One might predict that many palatable species, such as *Acacia davyi* and the *Cussonia* spp., will lack a sizeable recruitment class, as well as the larger size classes, and a number of years could thus see further significant decline in these species' populations. *Aloe marlothii* is another species that seems doomed in areas other than steep refuge sites if present herbivory rates continue. In place of these palatable, decreasing species, one would expect unpalatable species with high recruitment rates (e.g. *Euclea* spp.) to increase in density. Smith and Goodman (1987) similarly predicted a succession in dominance from *Acacia nilotica* to *Euclea divinorum* in nearby Mkuzi Game Reserve. Although these authors predict that the reintroduction of elephants to Mkuzi would open up the *Euclea* canopy allowing increased *Acacia* seedling establishment, the present study predicts that herbivory (by species including elephants) is one of the agents driving this succession towards dominance by unpalatable species. Herbivore browsing thus has the potential to alter community composition.

Herbivores could also affect community structure. Large trees (diameter >=10 cm) died more often than did smaller ones. Elephants were not singled out as the agent most likely to kill mature trees in Ithala. Okula and Sise (1986) and Tchamba (1995) found, however, that more mature trees were killed by elephants in Waza National Park (Cameroon) than trees in smaller size classes. Their results suggest that elephants may be important agents of mortality for large trees in Ithala. Ruess and Halter (1990) also noted increased mortality of mature *Acacia tortilis* and *A. xanthophloea* trees due to large herbivores in the Serengeti National Park (Tanzania). The structure of the vegetation community in the Ngubhu basin could thus possibly be altered in future, in that large individuals (e.g. *Acacia gerrardii* and *A. nilotica*) would gradually be replaced by small, shrubby individuals with many seedlings and few, if any, large trees (Smith & Goodman, 1987). This has implications for tourism (Prins & van der Jeugd, 1993), reducing visibility from vehicles and detracting from the overall appearance of the landscape.

Interactions between environmental factors and herbivory

Herbivory is not the only causal factor in woodland change; rainfall and fire are also important factors to consider (Buechner & Dawkins, 1961; Dublin *et al.*, 1990). As evidenced in the current study, rainfall at Ithala had a significant impact on recruitment rates. The effects of heavy herbivory on tree recruitment could thus be mitigated by higher-than-average rainfall, but low rainfall enhanced the detrimental effects of herbivory on seedling growth. Rainfall was not a significant cause of mortality in Ithala, although a few trees were reported to have died from moisture stress. Herbivory was therefore responsible for approximately as many tree deaths in dry years as in wetter years. It was unfortunate that the effects of fire on woodland change could not be examined in the current study. A number of studies predict that regular fire, combined with elephant browsing, will lead to a change from woodland to grassland in savanna areas (e.g. Buechner & Dawkins, 1961; Pellew, 1983; Dublin *et al.*, 1990). Conflicting patterns emerge as to the mechanism of woodland change, and the maintenance of the vegetation in its changed state (i.e. as a grassland). Buechner and Dawkins (1961) and Pellew (1983) cite elephants as the destructive force behind woodland degeneration. They hold that, once woodlands were disturbed and their structure changed (mature trees were broken or killed, so that smaller individuals remained), fire prevented regeneration and recruitment of smaller trees. Pellew (1983) also cited giraffe as agents preventing woodland regeneration. Dublin *et al.* (1990), on the other hand, wrote that an external perturbation (such as fire) was necessary to change the vegetation from woodland to grassland. Their model showed that elephants were unable to cause such a change, but that once grassland was formed, elephants were able to hold it in that state.

This study indicates that there is currently no major decline in the overall density of woody species in the Ngubhu basin, which is currently fairly dense woodland. Although a number of tree species indicate a decline in abundance, other species are increasing, and yet others appear to be fairly stable. At present, the Ngubhu basin has low herbaceous fuel, causing fires to spread sporadically and to be fairly cool (I. Rushworth, pers. comm.). Very few trees were recorded as being damaged by fire. There is little indication, therefore, of how fire and herbivores together would influence the proportions of trees and grass in this system. The data do suggest, however, that if the number of browsers is not limited somehow, either naturally because of resource limitation or by removal, that a decline in woody cover, and an increase in the cover of grass, is likely.

Other browsers and the debate on elephant removal

As in most nature reserves where elephants are present, managers of Ithala Game Reserve are likely to be faced with the question of whether to control elephant numbers in order to conserve vegetation species and biomass. The 'elephant problem', as it has been called in the literature (Ben-Shahar, 1993), highlights the conflicting aims to conserve both plant biodiversity and elephant populations, which are under pressure in certain areas due to poaching (Prins & Van der Jeugd, 1993). At present, the overall density of elephants in Ithala is approximately 0.19 elephants per square kilometre. This is lower than the recommended stocking rate of 0.4 elephants km^{-2} for Valley Bushveld (Penzhorn, Robbertse & Olivier, 1974), and below the 0.5 elephants km^{-2} noted by Fowler and Smith (1973) to cause serious damage to dry savanna habitat. However, the effective density of elephant is much higher as large parts of the reserve are not utilised because of topography, vegetation type and the apparent behavioural response of these orphans of avoiding open areas (I. Rushworth, pers. comm.). Rushworth (pers. comm.) estimates that approximately 50 % of the reserve is unutilised by elephants, and calculates the effective density to be approximately 0.38 elephants km^{-2}. For the Kruger National Park, Eckhardt, Van Wilgen and Biggs (2000) mention a threshold of potential concern which, if reached, should precipitate corrective action. This threshold was set at an 80% change in the cover of any component of the vegetation in any given landscape. This seems a fairly high threshold, and it does not appear that woody vegetation cover changed to nearly this extent in Ithala. Elephant densities therefore do not appear to be high enough at present to warrant removal. The impact of browsers on the vegetation is, however, of concern. Although five of the six tree species apparently in decline were most heavily browsed by elephants, the impact of other browsers should not be overlooked (Lock, 1993). *Aloe marlothii*, for instance, the species showing the greatest decline, was most heavily browsed by black rhinos. *Acacia davyi* was considered by Loffell (1999) to be under greatest threat from heavy giraffe browsing. *Cussonia natalensis*, *C. spicata*, *Acacia gerrardii* and *A. nilotica* were all most heavily browsed by elephants. Damage to vegetation by browsers excluding elephant, as well as that caused by factors such as lightning and moisture stress, contributed approximately three times as much to overall tree utilisation as did elephants. It is therefore pertinent, in this case, to consider incorporating other browsers into the 'elephant problem'. Although species other than elephant are not generally capable of pushing over or pollarding large trees, their utilisation of browse species should nonetheless not be overlooked. Of the 35 species listed in Table 5, thirteen were most heavily damaged by animal species other than elephants and black rhinos, while a further ten species were utilised as heavily by other browsers as they were by elephants or black rhinos. Authors such as Pellew (1983) and Prins and Van der Jeugd (1993) have highlighted the effects that browsers other than elephants can have on vegetation structure and composition. Goodman and Tomkinson (1987) noted that giraffe, being an alien species to Zululand and one which is not endangered, should be carefully monitored, if not removed altogether. Loffell's (1999) findings on giraffe impact on *Acacia* species provide support for Goodman and Tomkinson (1987), and reiterate the considerable impact that species other than elephants have had on Ithala's browse resource. Managers at Ithala have recognised this, and have removed black rhino, giraffe, kudu, impala and nyala at varying stages during the reserve's history (I. Rushworth, unpublished data). Appropriate stocking rates for browsers other than elephants can be calculated following guidelines suggested by Dekker (1997) and others. Elephants and their impact on vegetation should be seen within the broader context of the browser community within which they occur. Although strong evidence exists that they are important determinants of vegetation dynamics, they are not the only – or even necessarily the greatest – agent involved.

The browsers at Ithala Game Reserve have had a significant impact on the woody vegetation in the Ngubhu Basin since 1992. While present browsing pressure does not appear to threaten the abundance of some tree species, others more vulnerable to herbivory could become locally extinct if increases in browsing pressure occur. The situation is a delicate one and needs to be carefully considered because, as Buechner and Dawkins (1961) maintain, both animal and vegetation biodiversity need to be preserved if the reserve is to be developed in the broadest sense for conservation of nature.

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Table 1: Estimated numbers of the main browser species in Ithala Game Reserve in 1992 (onset of this study) and 2000

Browser species	1992	2000
Elephant	30	56
Black Rhinoceros	48	43
Giraffe	157	157
Eland	123	140
Kudu	498	750
Impala	1243	1701

Table 2: Canopy utilisation index for woody species in Ithala Game Reserve

Canopy Utilisation index	Description (% volume of canopy removed)
0	0
1	1-10
2	11-25
3	26-50
4	51-75
5	76-90
6	91-99
7	100

Table 3: Results of Kolmogorov-Smirnov goodness of fit test for changes in size class structure of common tree species between 1992 and 2000. Species with highly significant changes in size class distribution are presented. Only species with sample sizes greater than six trees in both years were tested.

Species	1992 Sample size	Number of size classes represented in 1992	Size class category containing greatest number of individuals (1992)	2000 Sample size	Number of size classes represented in 2000	Size class category containing greatest number of individuals (2000)
Acacia gerrardii	60	7	**Middle to ***larger class	15	3	*Smaller
Acacia karroo	71	6	Evenly distributed	125	6	Smaller
Acacia nilotica	279	7	Smaller	155	6	Larger
Combretum apiculatum	64	6	Smaller	64	5	Smaller
Dichrostachys cinerea	382	7	Smaller	267	5	Smaller
Dombeya rotundifolia	51	6	Smaller	138	5	Middle
Euclea crispa	11	2	Smaller	112	5	Smaller
Euclea natalensis	143	6	Smaller	60	5	Smaller
Euclea racemosa	71	6	Smaller	252	6	Smaller to middle
Gymnosporia buxifolia	149	7	Smaller to middle	133	6	Smaller to middle
Rhus lucida	311	7	Smaller to middle	214	6	Smaller to middle
Rhus pentheri	55	7	Smaller	25	5	Larger
Scolopia zeyheri	16	3	Smaller	103	6	Smaller

* 'Smaller' size classes refer to trees with diameters of 0 - 3 cm
** 'Middle' size classes refer to trees with diameters of 3 - 30 cm
*** 'Larger' size classes refer to trees with diameters of 30 cm or larger

Table 4: Proportion of all trees made up by dead individuals, per species, 1992-2000. Ithala Game Reserve, South Africa.

Species	Total number of individuals	Proportion dead/total:
Aloe marlothii	186	0.452
Acacia davyi	65	0.215
Acacia nilotica	2229	0.075
Acacia karroo	1199	0.044
Acacia gerrardii	320	0.038
Rhus rehmanniana	68	0.029
Combretum molle	145	0.028
Rhus gueinzii	179	0.028
Acacia caffra	732	0.027
Acacia ataxacantha	115	0.026
Dombeya rotundifolia	1063	0.024
Dichrostachys cinerea	2393	0.023
Ziziphus mucronata	46	0.022
Berchemia zeyheri	326	0.021
Gymnosporia buxifolia	1046	0.017
Pappea capensis	260	0.015
Scolopia zeyheri	735	0.012
Rhus lucida	2165	0.011
Euclea racemosa	2581	0.009
Maytenus nemorosa	229	0.009
Combretum apiculatum	371	0.008
Rhus pentheri	352	0.006
Euclea natalensis	888	0.005
Euclea crispa	1401	0.003
Hippobromus pauciflorus	910	0.002
Ormocarpum trichocarpum	221	0.000
Peltophorum africanum	142	0.000

Table 5: Average ± standard deviation of percentage canopy removed per tree for each species, 1992-2000, and browser species responsible for most damage. ('Other' refers to browsers such as kudu, giraffe, bushbuck, eland, nyala, impala and duiker). Damage was measured as the cumulative percentage of canopy removed from all trees, on a per species basis. Ngubhu Basin, Ithala Game Reserve

Tree species	Average percentage canopy removed per tree	Standard deviation (%)	Browser responsible for most damage to tree species:	Sample size (number of trees)
Aloe marlothii	39.16	27.926	Black rhino	196
Cussonia natalensis	29.82	39.034	Elephant	40
Coddia rudis (E. Mey. ex Harv.) Verdc.	20.38	13.887	Other	1196
Acacia nilotica	19.35	6.007	Elephant	2133
Cussonia spicata	16.98	24.463	Elephant	21
Acacia gerrardii	16.52	10.832	Elephant	315
Berchemia zeyheri	15.40	8.067	Elephant	309
Dichrostachys cinerea	15.08	4.371	Other/black rhino	2302
Rhus rehmanniana	15.08	9.993	Black rhino	53
Acacia karroo	14.90	6.321	All similar	1134
Scolopia zeyheri	14.89	8.218	Other/elephant	726
Acacia caffra	14.81	10.039	All similar	721
Ziziphus mucronata	14.48	10.838	Elephant/other	40
Dombeya rotundifolia	13.56	8.027	Other	1036
Gymnosporia buxifolia	12.78	4.211	Other	1361
Peltophorum africanum	11.90	13.649	Elephant	123
Ormocarpum trichocarpum	11.35	11.869	Other	221
Pappea capensis	10.96	4.109	Elephant/other	243
Hippobromus pauciflorus	10.75	20.896	Other/black rhino	812
Rhus pentheri	10.74	6.440	Other	347
Rhus gueinzii	10.61	10.225	All similar	156
Combretum apiculatum	10.01	6.579	Black rhino/other	376
Rhus lucida	9.98	2.790	Elephant	2014
Olea europea L. subsp. *Africana* (Mill.) P.S. Green	8.81	8.737	Elephant	298
Combretum molle	8.58	7.987	Other	139
Euclea crispa	8.13	9.902	Other	1586
Acacia davyi	7.92	12.286	Elephant	63
Maytenus nemorosa	7.78	8.955	Other	229
Euclea racemosa	7.33	3.179	Other	2384
Acacia ataxacantha	7.03	8.274	Other/elephant	95
Pyrostria hystrix	5.83	6.921	Other	91
Euclea natalensis	5.30	4.120	Other	836
Acacia tortilis	3.50	7.481	Black rhino	52
Euclea divinorum Hiern	2.75	2.126	Other	474
Diospyros lycioides Desf.	0.99	1.670	Other	480

Table 6: **Percentage change and G test results for change in frequency of occurrence, and t test results for change in basal area and density of tree species in the Ngubhu Basin, Ithala Game reserve, 1992 to 2000. Frequency refers to number of transects in which the species occurred in either 1992 or 2000. Negative values indicate a decline abundance, while positive values indicate an increase.**

Species name	**Frequency of occurrence in 1992 (Total 63 transects)**	**Frequency of occurrence in 2000 (Total 34 transects)**	**Percent change in frequency 1992-2000**	**Mean basal area ± standard deviation (m^2/ha), 1992**	**Mean basal area ± standard deviation (m^2/ha), 2000**	**Change in average basal area (1992-2000) as % of 1992 value**	**Mean density ± standard deviation (trees/ha), 1992**	**Mean density ± standard deviation (trees/ha), 2000**	**Change in mean density (1992-2000) as % of 1992 value**
Acacia gerrardii Benth. var. *gerrardii*	20	1	-28.8 **	1.37 ± 2.767	0.03 ± 0.179	-97.8 *	95.92 ± 194.720	27.45 ± 160.065	-71.4 *
Aloe marlothii Berger subsp. *orientalis* Glen & Hardy	21	3	-24.5 **	91.72 ± 688.344	0.19 ± 1.011	-99.8 *	59.30 ± 120.37	8.627 ± 29.153	-85.5 *
Euclea natalensis A. DC. subsp. natalensis	31	10	-19.8 NS	0.28 ± 1.350	0.03 ± 0.077	-87.8 NS	244.84 ± 462.034	63.04 ± 129.512	-74.3 *
Rhus lucida L.	57	25	-16.9 *	7.29 ± 27.196	1.42 ± 2.423	-75.5 NS	498.65 ± 427.219	233.84 ± 258.141	-53.1 **
Acacia nilotica (L.) Willd. ex Del. subsp. *kraussiana* (Benth.) Brenan	51	23	-13.3 NS	20.68 ± 83.170	2.95 ± 4.370	-85.7 NS	466.05 ± 672.711	200.48 ± 345.813	-57.0 *
Peltophorum africanum Sond.	11	2	-11.6 NS	23.00 ± 158.586	0.02 ± 0.138	-99.9 NS	40.93 ± 112.004	2.96 ± 12.279	-92.8 NS
Dichrostachys cinerea (L.) Wight & Arn. subsp. *africana* Brenan & Brumm. var. *africana*	45	22	-6.7 NS	9.03 ± 61.983	0.44 ± 0.564	-95.1 NS	590.21 ± 688.914	347.28 ± 422.210	-41.2 NS
Rhus pentheri Zahlbr.	23	11	-4.2 NS	7.83 ± 43.868	0.32 ± 0.969	-95.9 NS	83.00 ± 173.143	35.64 ± 63.210	-57.1 NS

Species name	Frequency of occurrence in 1992 (Total 63 transects)	Frequency of occurrence in 2000 (Total 34 transects)	Percent change in frequency 1992-2000	Mean basal area ± standard deviation (m^2/ha), 1992	Mean basal area ± standard deviation (m^2/ha), 2000	Change in average basal area (1992-2000) as % of 1992 value	Mean density ± standard deviation (trees/ha), 1992	Mean density ± standard deviation (trees/ha), 2000	Change in mean density (1992-2000) as % of 1992 value
Ziziphus mucronata Willd. subsp. *mucronata*	2	0	-3.2	0.00 ± 0.004	0	-100 NS	6.35 ± 39.648	0	-100 NS
Acacia davyi N.E. Br.	2	0	-3.2	0.06 ± 0.457	0	-100 NS	12.70 ± 79.295	0	-100 NS
Cussonia natalensis Sond.	2	0	-3.2	0.00 ± 0.009	0	-100 NS	4.23 ± 24.313	0	-100 NS
Acacia ataxacantha DC.	2	1	-0.2	0.16 ± 1.222	0.00 ± 0.005	-99.5 NS	3.17 ± 17.673	1.18 ± 6.860	-62.9 NS
Combretum apiculatum Sond. subsp. *apiculatum*	15	9	2.7 NS	0.91 ± 6.304	0.15 ± 0.551	-83.5 NS	95.20 ± 264.952	102.06 ± 228.943	7.2 NS
Gymnosporia buxifolia (L.) Szyszyl.	38	22	4.4 NS	10.79 ± 42.888	0.84 ± 1.449	-92.2 *	235.94 ± 326.286	195.05 ± 222.195	-17.3 NS
Ormocarpum trichocarpum (Taub.) Engl.	2	3	5.6 NS	0.01 ± 0.081	0.00 ± 0.015	-77.4 NS	12.70 ± 79.95	10.20 ± 42.679	-19.7 NS
Cussonia spicata Thunb.	0	2	5.9	0	0.00 ± 0.002	NS	0	3.80 ± 15.434	NS
Acacia caffra (Thunb.) Willd.	20	13	6.5 NS	0.86 ± 4.424	0.12 ± 0.385	-85.9 NS	158.26 ± 584.227	67.03 ± 110.511	-57.6 NS
Rhus rehmanniana Engl.	3	4	7.0 NS	0.03 ± 0.176	0.09 ± 0.322	230.36 NS	9.52 ± 53.019	12.75 ± 40.415	33.8 NS
Acacia tortilis (Forssk.) Hayne subsp. *spirocarpa*	1	3	7.2 NS	0.01 ± 0.065	0.07 ± 0.240	718.5 NS	0.91 ± 7.199	7.26 ± 24.030	699.9 NS
Pappea capensis Eckl. & Zeyh.	2	5	11.5 *	0.05 ± 0.399	0.00 ± 0.015	-90.7 NS	2.38 ± 13.995	12.75 ± 32.840	435.3 NS
Maytenus nemorosa (Eckl. & Zeyh.) Marais	0	5	14.7	0	0.01 ± 0.077	NS	0	35.39 ± 141.673	NS

Species name	**Frequency of occurrence in 1992 (Total 63 transects)**	**Frequency of occurrence in 2000 (Total 34 transects)**	**Percent change in frequency 1992-2000**	**Mean basal area ± standard deviation (m^2/ha), 1992**	**Mean basal area ± standard deviation (m^2/ha), 2000**	**Change in average basal area (1992-2000) as % of 1992 value**	**Mean density ± standard deviation (trees/ha), 1992**	**Mean density ± standard deviation (trees/ha), 2000**	**Change in mean density (1992-2000) as % of 1992 value**
Pyrostria hystrix (Brem.) Bridson	0	5	14.7	0	0.0 ± 0.016	NS	0	20.61 ± 62.966	NS
Combretum molle R. Br. ex G. Don	3	7	15.8 *	0.03 ± 0.226	0.00 ± 0.011	-89.7 NS	9.52 ± 46.539	25.20 ± 62.835	164.6 NS
Hippobromus pauciflorus (L.f.) Radlk.	0	7	20.6	0	0.05 ± 0.164	NS	0	224.90 ± 642.272	NS
Berchemia zeyheri (Sond.) Grubov	1	10	27.8 **	0.00 ± 0.004	0.50 ± 2.185	99223.2 *	1.59 ± 12.599	25.43 ± 49.076	1501.8 *
Dombeya rotundifolia (Hochst.) Planch. var. *velutina* Verdoorn	12	16	28.1 **	2.41 ± 12.781	0.41 ± 0.786	-83.1 *	81.22 ± 239.109	238.24 ± 417.258	193.3 *
Acacia karroo Hayne	10	15	28.2 **	0.77 ± 2.735	0.42 ± 1.127	-45.0 NS	114.81 ± 371.897	108.33 ± 183.567	-5.6 *
Euclea racemosa Murray	13	21	41.1 **	0.87 ± 4.251	0.90 ± 1.881	2.9 **	112.70 ± 350.802	284.90 ± 422.810	152.8 **
Euclea crispa (Thunb.) Guerke subsp. *crispa*	3	16	42.3 **	0.00 ± 0.003	0.02 ± 0.045	5171.5 **	16.93 ± 95.578	176.28 ± 323.954	941.1 **
Scolopia zeyheri (Nees) Harv.	2	20	55.6 **	0.00 ± 0.029	0.53 ± 2.589	10483.0 **	25.40 ± 177.771	166.05 ± 291.072	553.8 **
Rhus gueinzii Sond.	0	4	77.8	0	0.03 ± 0.108	NS	0	11.02 ± 32.030	NS

Species lacking percentage change values were absent in 1992
NS – no significant difference between 1992 and 2000
* significant difference between 1992 and 2000 ($p<0.05$)
** significant difference between 1992 and 2000 ($p<0.01$)

Figure legends

Figure 1: Map of South Africa showing position of Ithala Game Reserve, and magnification of the reserve. All data were collected from transects within the valley of the Ngubhu River.

Figure 2: Deviation from average rainfall 1973-2000 (Thalu Camp, Ithala) (25-year average = 791 mm)

Figure 3: Total browser animal unit equivalents per year in Ithala Game Reserve, 1973-2000

Figure 4 a-m): Proportional distribution of individuals in the seven size classes. Only species with significant differences in size class structure between 1992 and 2000 are presented ($p < 0.05$). Diameter size classes are as follows: 1) 0-1 cm 2) 1-3 cm 3) 3-5 cm 4) 5-10 cm 5) 10-30 cm 6) 30-100 cm 7) 100^+ cm

Figure 5: Proportion of individuals in different size classes, 1992-2000. Only species with maturing populations and large sample sizes included. Size classes as per Figure 3. Only even years are presented for clarity. Ngubhu Basin, Ithala Game Reserve.

Figure 6: Average percentage of live trees made up by those with diameters < 0.7 cm, over all tree species, 1992-2000.

Figure 7: Proportion of all trees made up by dead individuals, by 'increasers' and 'decreasers'.

Figure 8: Overall proportion of frequency of utilisation by different agents, over all tree species, 1992-2000. 'Other' agents include humans, moisture stress, flooding, shading, fire, frost, wind, accidents and unknown causes of damage.

Figure 9: Percentage frequency of utilisation made up by each agent, over all tree species, 1992-2000. 'Other' agents include humans, moisture stress, flooding, shading, fire, frost, wind, accidents and unknown causes of damage.

Figure 10: Total utilisation by different agents over all tree species, 1992-2000. 'Other' agents include humans, moisture stress, flooding, shading, fire, frost, wind, accidents and unknown causes of damage.

Figure 11: Average per cent canopy removed by browsers per browsed tree (all tree species included), 1992-2000.

Figure 12: Percentage of elephant-damaged trees per damage category. Damage categories are as follows: 1) 0-10 % canopy removed, 2) 11-25 %, 3) 26-50 %, 4) 51-75 %, 5) 76-90 %, 6) 91-99 % and 7) 100 % canopy removed.

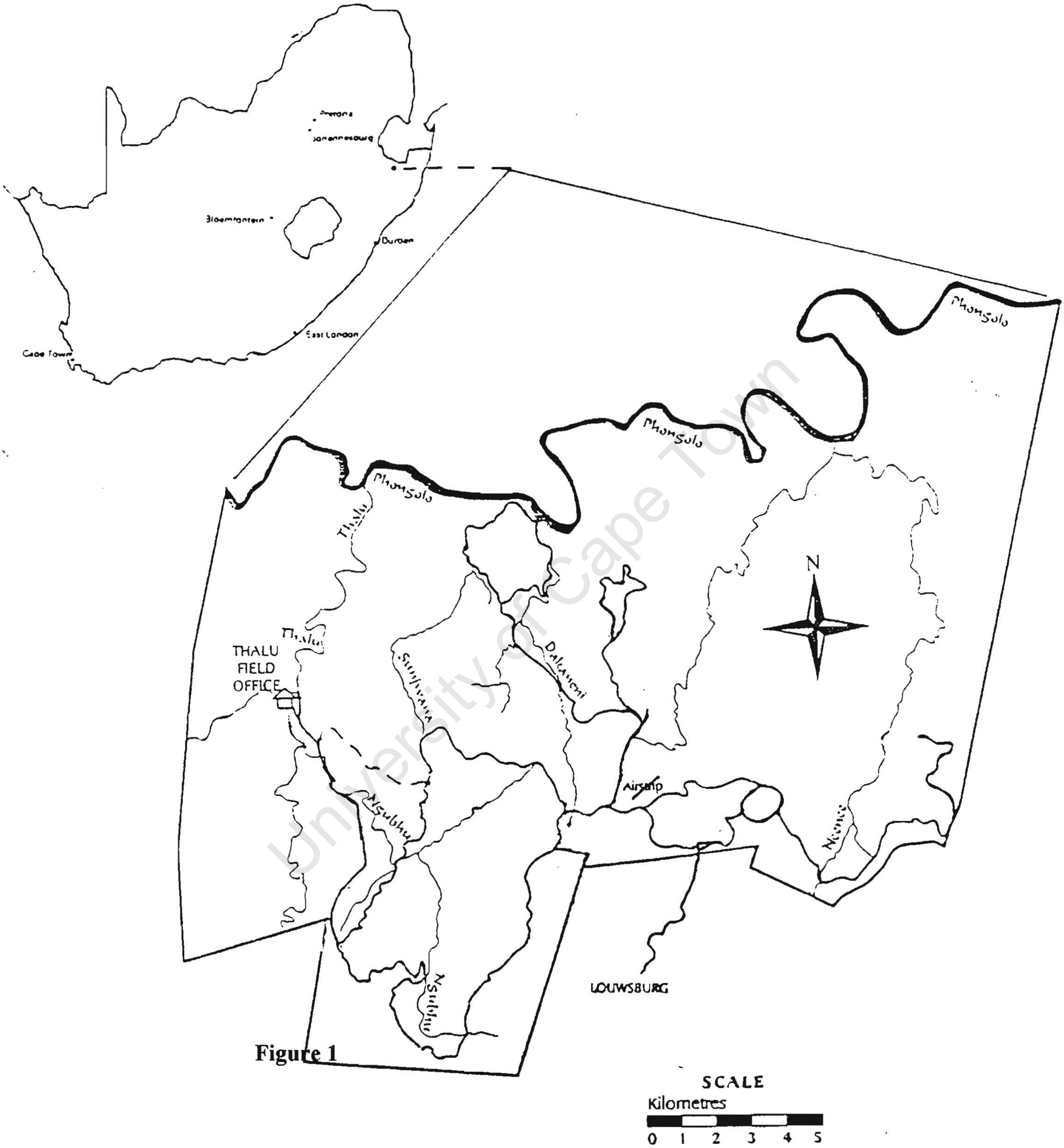

Pretoria
Johannesburg
Bloemfontein
Durban
East London
Cape Town
Phongolo
Phongolo
Phongolo
Thalu
Thalu
THALU FIELD OFFICE
Sumfwana
Dakaneni
Ngubhu
Airstrip
Ncence
Nsubhu
LOUWSBURG
N
SCALE
Kilometres
0
1
2
3
4
5

Figure 1

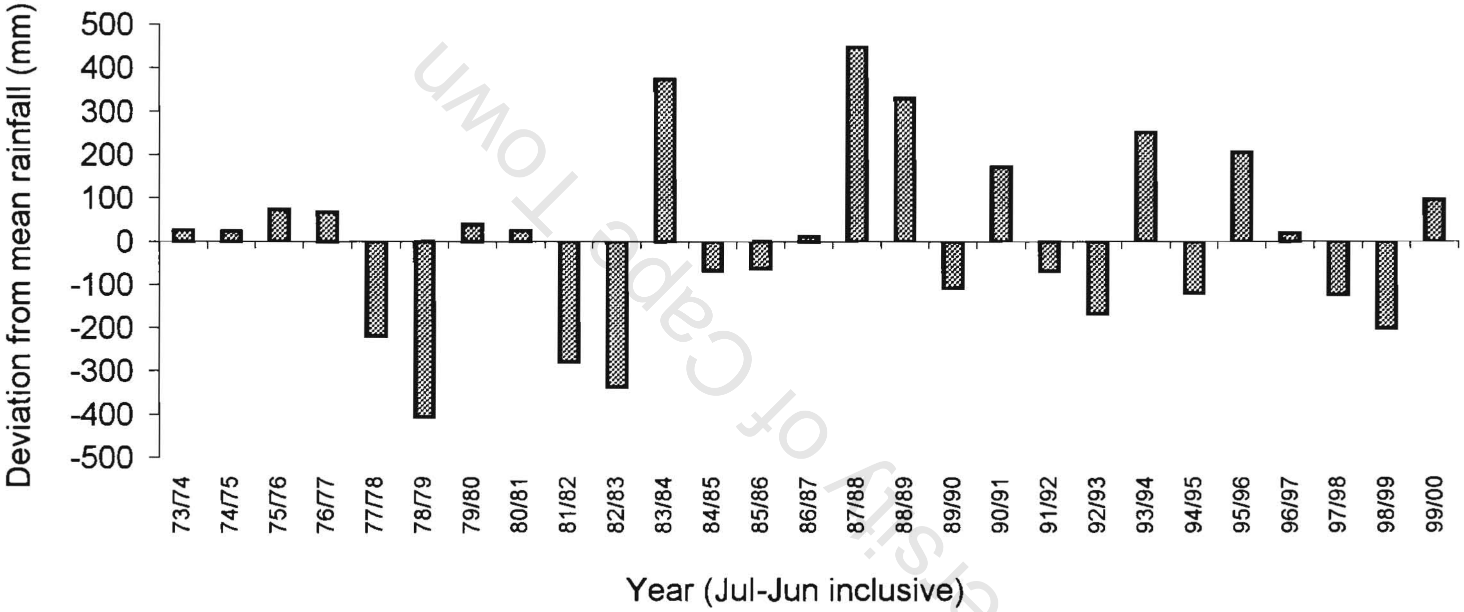

Deviation from mean rainfall (mm)
500
400
300
200
100
0
-100
-200
-300
-400
-500
73/74
74/75
75/76
76/77
77/78
78/79
79/80
80/81
81/82
82/83
83/84
84/85
85/86
86/87
87/88
88/89
89/90
90/91
91/92
92/93
93/94
94/95
95/96
96/97
97/98
98/99
99/00
Year (Jul-Jun inclusive)

Figure 2

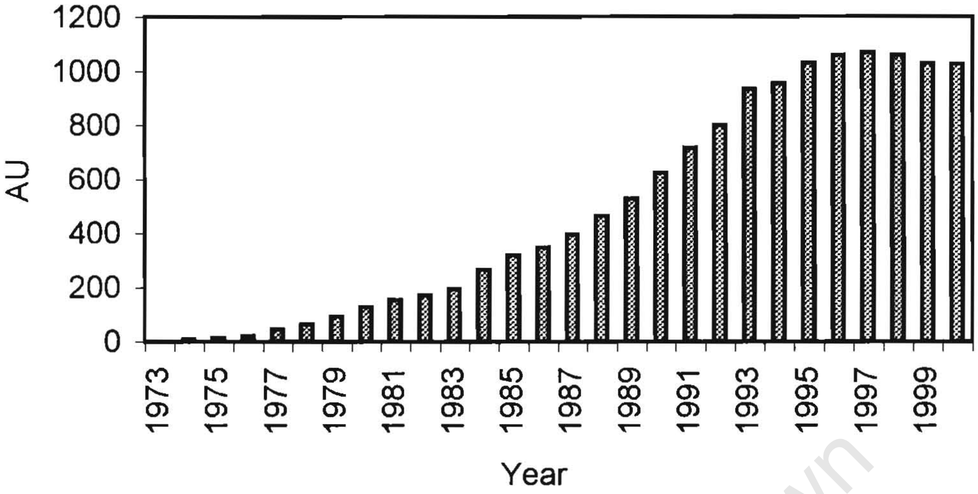
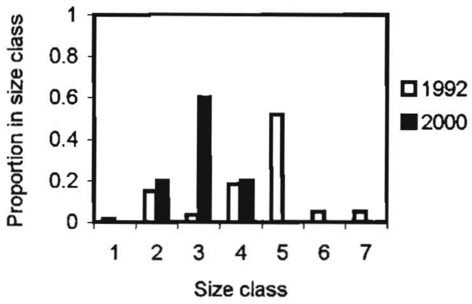
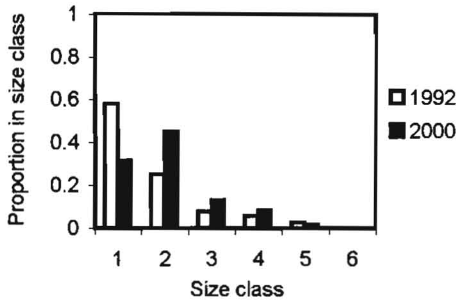

1200
1000
800
600
400
200
0
AU
1973
1975
1977
1979
1981
1983
1985
1987
1989
1991
1993
1995
1997
1999
Year

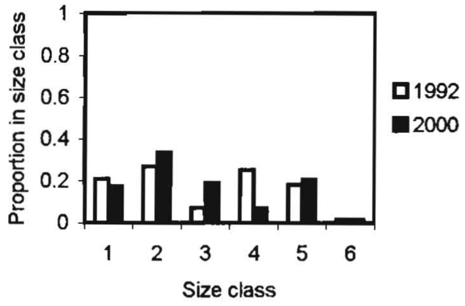
Figure 3



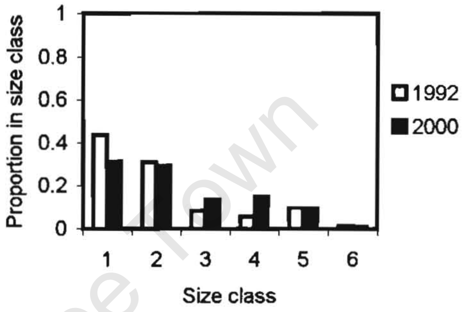
a) ***Acacia gerrardii***



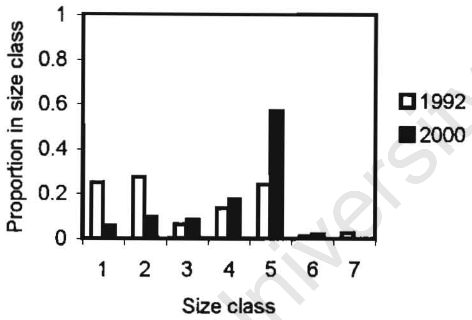
b) ***Euclea natalensis***



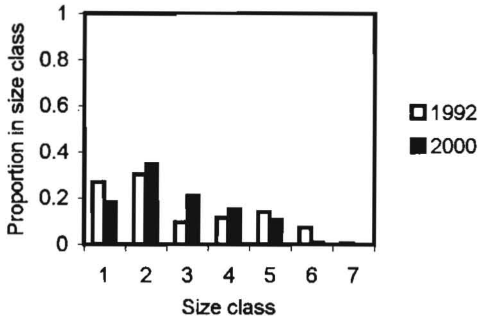
c) ***Acacia karroo***



d) ***Euclea racemosa***

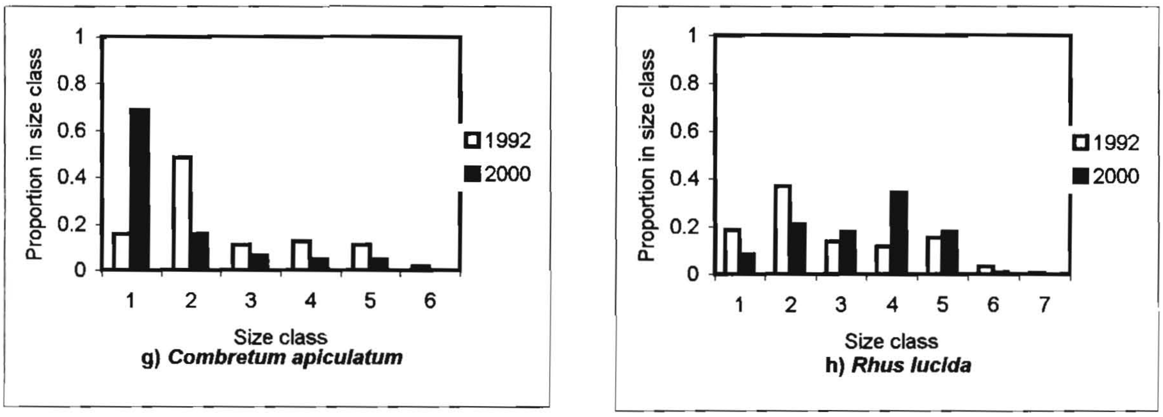


e) ***Acacia nilotica***



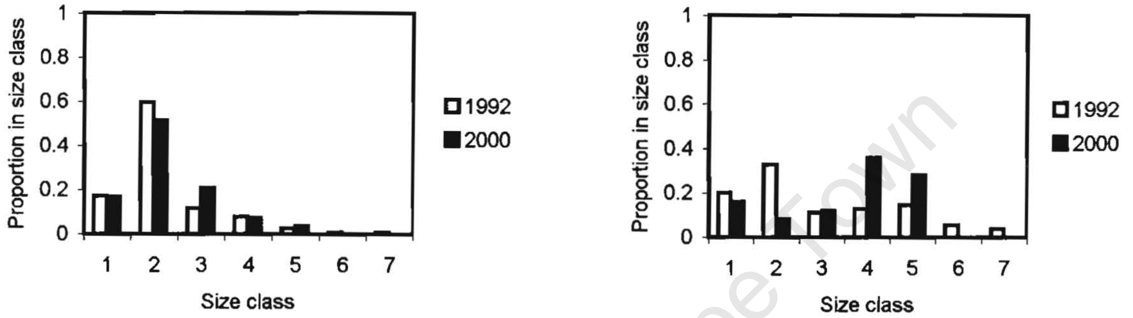
f) ***Gymnosporia buxifolia***

Figure 4 a - f



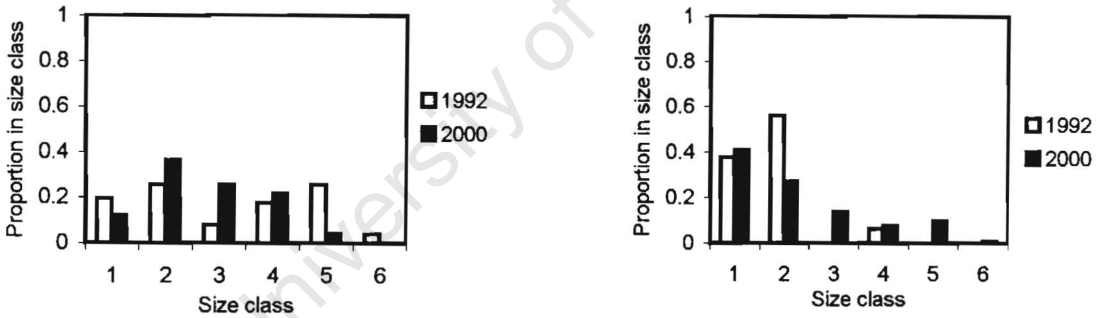
g) *Combretum apiculatum*

h) *Rhus lucida*



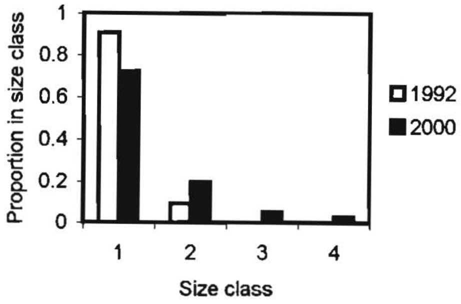
i) *Dichrostachys cinerea*

j) *Rhus pentheri*



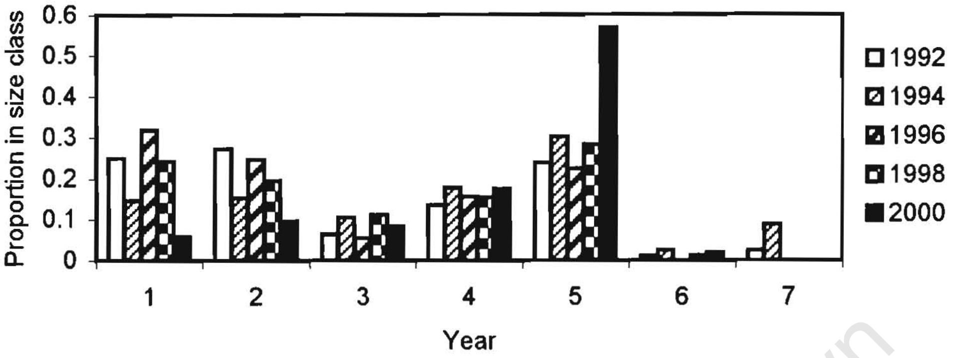
k) *Dombeya rotundifolia*

l) *Scolopia zeyheri*

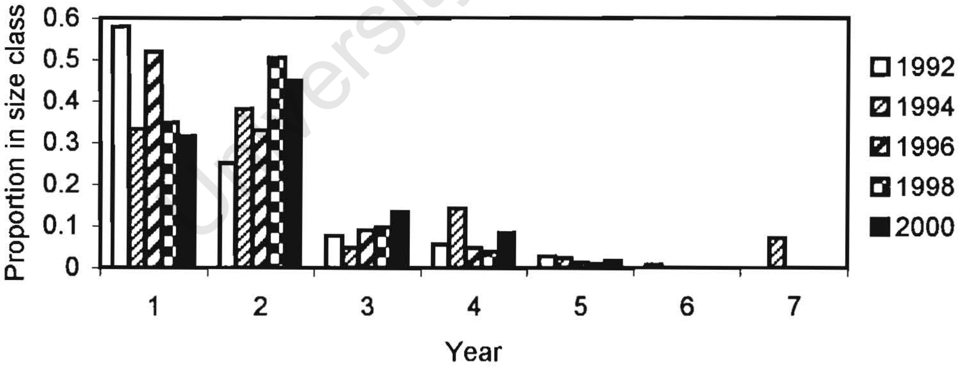


m) *Euclea crispa*

Figure 4 continued - g - m

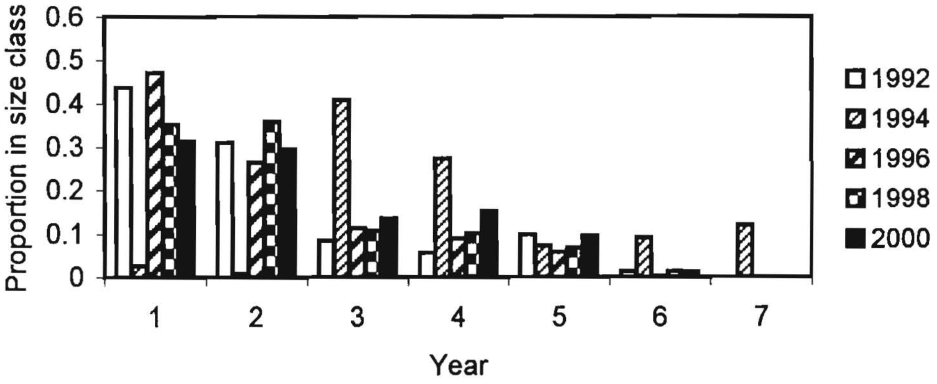


a) ***Acacia nilotica***

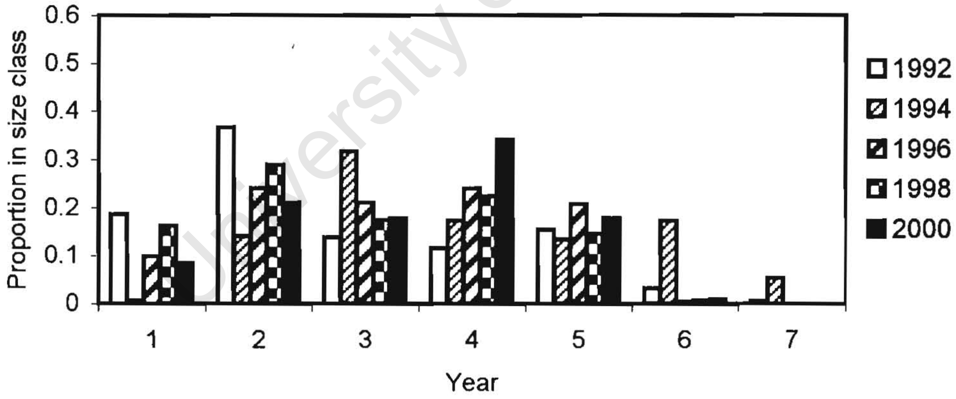


b) ***Euclea natalensis***

Figure 5 a,b



c) *Euclea racemosa*



d) *Rhus lucida*

Figure 5 continued - c,d

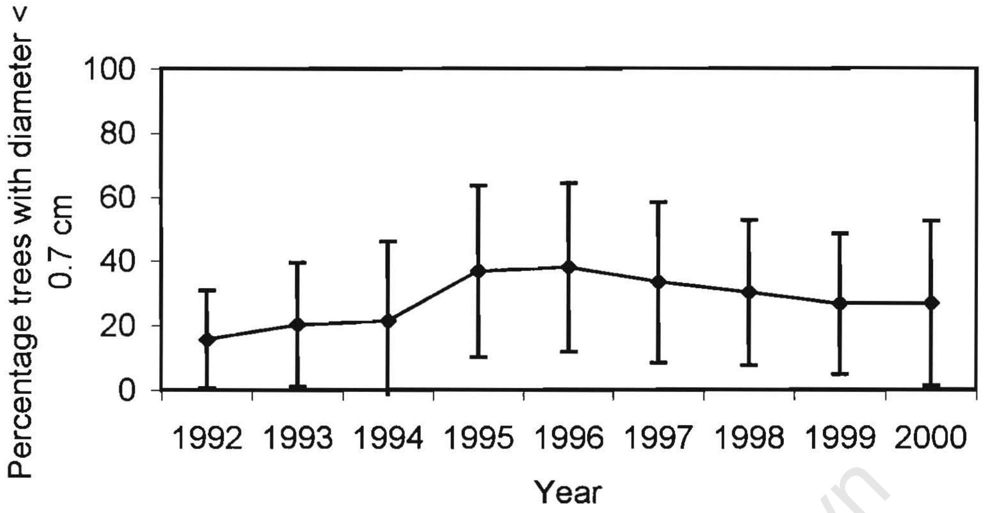

Percentage trees with diameter < 0.7 cm
100
80
60
40
20
0
1992
1993
1994
1995
1996
1997
1998
1999
2000
Year

Figure 6

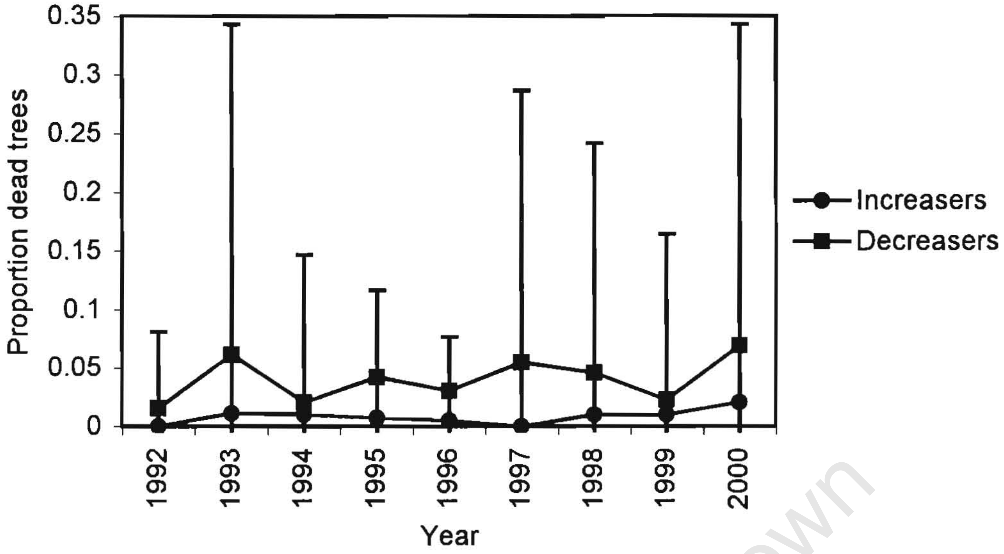

Proportion dead trees
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
1992
1993
1994
1995
1996
1997
1998
1999
2000
Year
Increasers
Decreasers

Figure 7

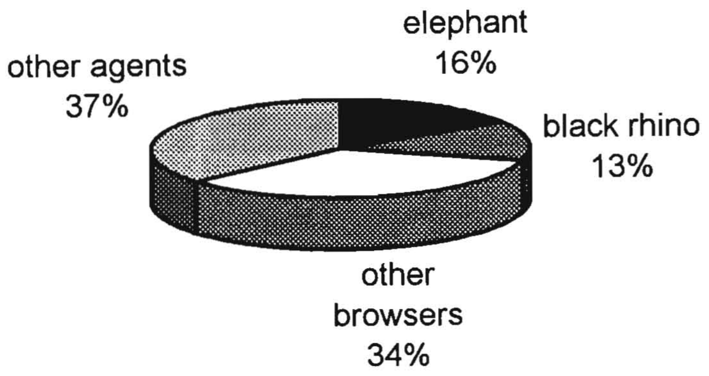

elephant
16%
black rhino
13%
other
browsers
34%
other agents
37%

Figure 8

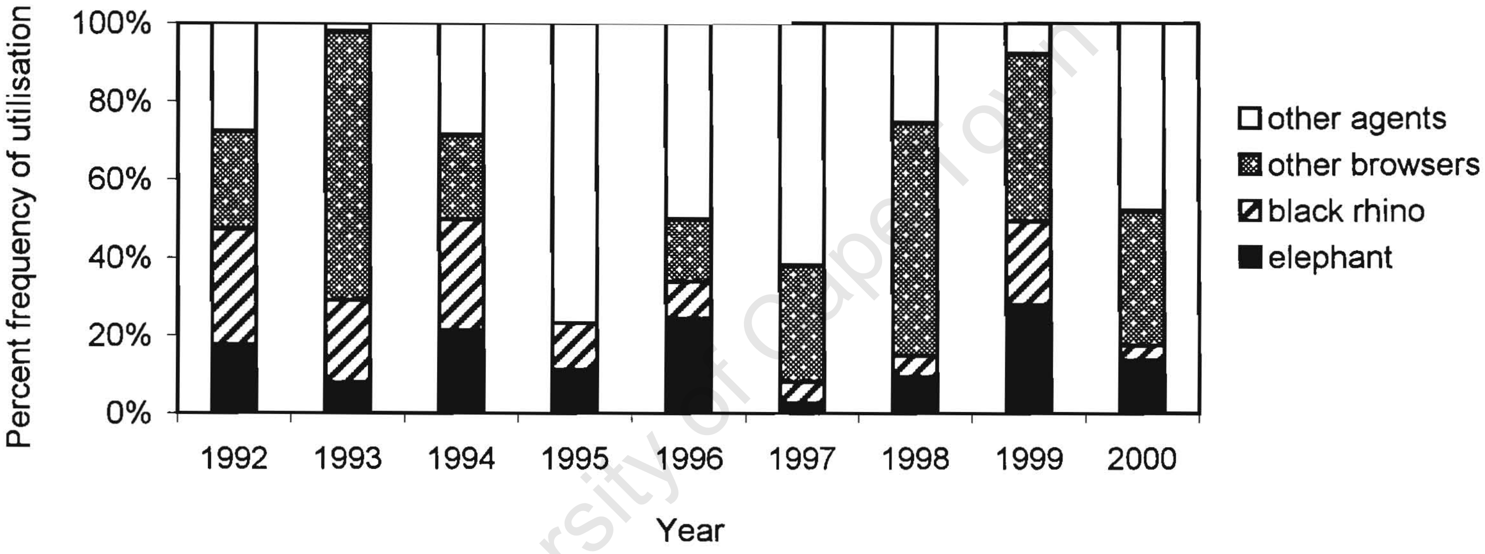

Percent frequency of utilisation
100%
80%
60%
40%
20%
0%
1992
1993
1994
1995
1996
1997
1998
1999
2000
Year
other agents
other browsers
black rhino
elephant

Figure 9

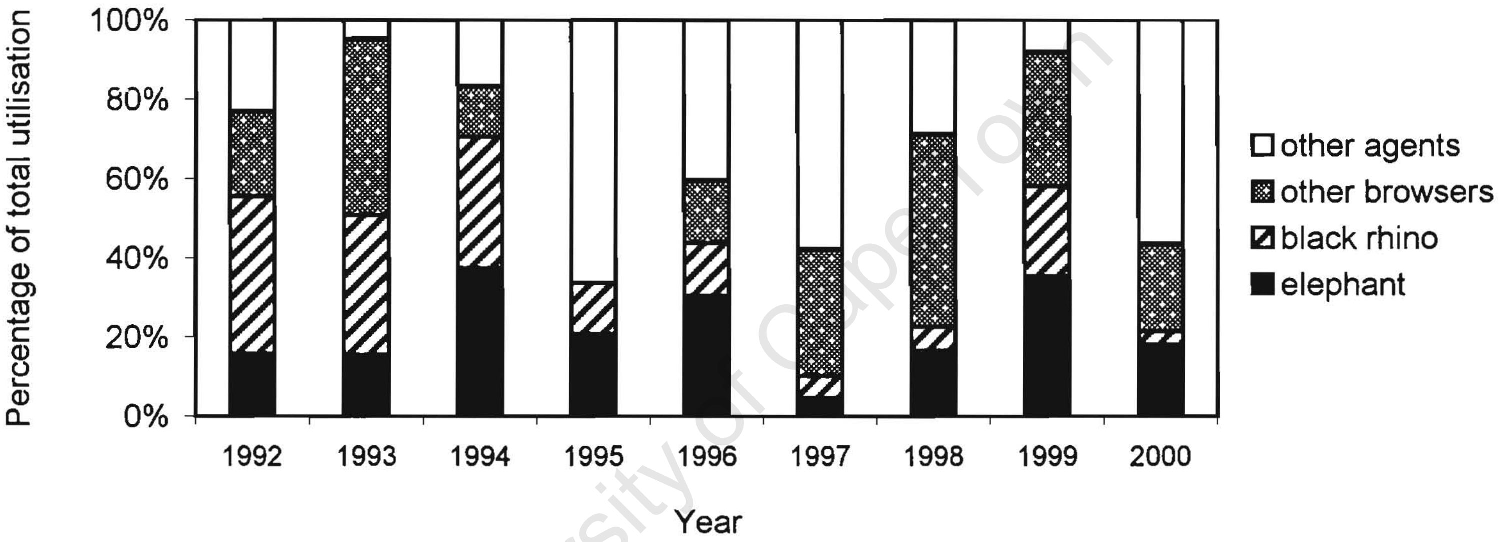

Percentage of total utilisation
100%
80%
60%
40%
20%
0%
1992
1993
1994
1995
1996
1997
1998
1999
2000
Year
☐ other agents
▩ other browsers
▨ black rhino
■ elephant

Figure 10

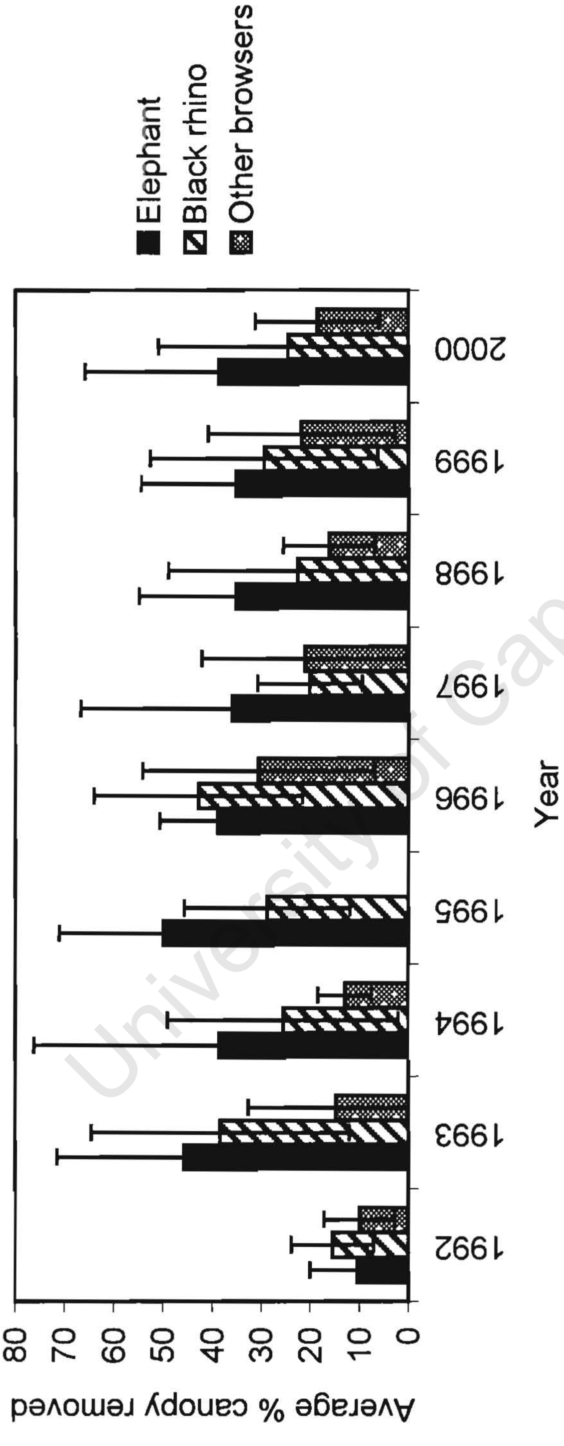

Average % canopy removed
0
10
20
30
40
50
60
70
80
1992
1993
1994
1995
1996
1997
1998
1999
2000
Year
■ Elephant
▨ Black rhino
▩ Other browsers

Figure 11

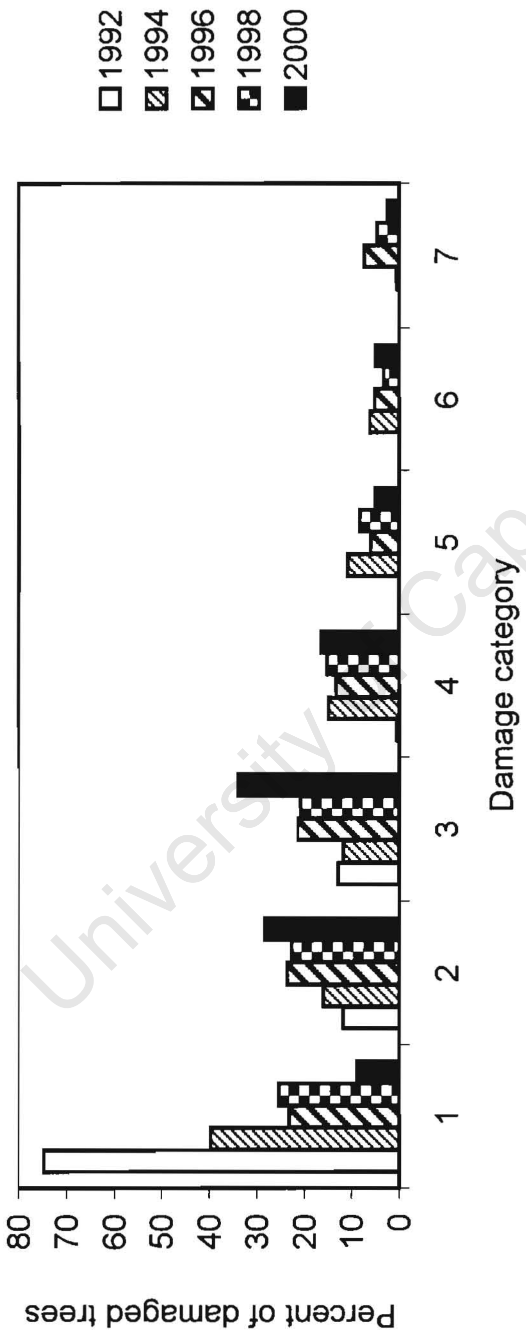

Percent of damaged trees
80
70
60
50
40
30
20
10
0
1
2
3
4
5
6
7
Damage category
1992
1994
1996
1998
2000

Figure 12

Appendix 1: Vegetation types of Ithala Game Reserve, showing underlying geology and soils, dominant woody species and rainfall regime (after Porter 1983)

Vegetation type	Geology	Soils	Dominant woody species	Rainfall regime
Themeda triandra grassland (757 ha, 2.6% of reserve). 1100-1300 m a.s.l.	Dolerite	Shallow Mispah series; Hutton form	(Present but not dominant): *Aloe vryheidensis, A. suprafoliata* (both endemic)	>900mm
Plateau grasslands (3507 ha, 11.8% of reserve). >800 m a.s.l.	Pongola shales, ironstones & sandstones	Wide range; often shallow Mispah on rock		750 - 1050 mm
Vleis (184 ha, 0.6% of reserve)	No rock present	Valsrivier, Glenrosa		>850 mm
Secondary grasslands on old lands (5428 ha, 18.3% of reserve)	Wide range	Wide range	Encroaching *Dichrostachys cinerea, Acacia* spp.	800 – 1000 mm
Ficus capensis-Euclea schimperi woodland (530 ha, 1.8% of reserve)	Dolerite	Shallow Mispah soils on rock	*F. capensis; E. schimperi; Vitex rehmanni; Acacia nilotica; A. karroo; Euphorbia ingens; Euclea crispa; F. sonderi; F. ingens; F. natalensis,* among others	>900mm

Vegetation type	**Geology**	**Soils**	**Dominant woody species**	**Rainfall regime**
Leucosidea sericia woodland (6ha, 0.02% of reserve)	Dolerite	Moderately deep Farningham soils; more rarely shallower Mispah soils	*L. sericea; Burchellia juberlina, Euclea natalensis, Cussonia spicata; Scolopia zeyheri*	>900mm
Riverine forest (1560 ha, 5.3% of reserve)	Alluvium	Deep alluvial soils – Dundee and Oakleaf on Pongola River; elsewhere Glendale, Shorrocks, Glenrosa and Portsmouth forms	*A. karroo; Breonadia microcephala; Combretum erythrophyllum; Ekebergia capensis; F. capensis; F. sycamorus; F. verruculosa; Mesa lanceolata; Phoenix reclinata; Rauvolfia caffra; Salix woodii; Syzigium cordatum; S. guineense,* among others	Variable, depending on position along river
Scrub forest (474 ha, 1.6% of reserve)	Quartzite; Pongola shale; Pongola sandstone	Shallow Mispah on rock	*Aloe arborescens; A. bainesii; Bridelia micrantha; Burchellia bubilina; Cussonia spicata; F. capensis; Halleria lucida; Maytenus acuminata; Rhoicissus rhomboidea; Scolopia zeyheri; Urera tenax,* among others	Various (found throughout reserve)
Acacia davyi-Dichrostachys cinerea woodland (350ha, 1.2% of reserve; eastern side)	Quartzite	Rocky Mispah	*Dichrostachys cinerea; A. davyi; Aloe marlothii; Acacia nilotica; Protea caffra*	>800 mm

Vegetation type	**Geology**	**Soils**	**Dominant woody species**	**Rainfall regime**
Acacia nilotica-Combretum zeyheri woodland (7885 ha, 22.6% of reserve - covers most area)	Extensive Pongola shale and sandstones which border on Ecca sandstones and shales in upper Ngubhu basin	Generally shallow Mispah on slopes; deeper Shorrocks and Muden soils in valley bottoms	*A. nilotica; C. zeyheri; C. apiculatum; Peltophorum africanum; Dombeya rotundifolia; Heteropyxis natalensis; A. caffra; A. karroo*	Ranges from 350 - 900 mm
Acacia nilotica-Aloe marlothii woodland (1285ha, 4,33% of reserve)	Dolerite	Basic, clayey soils of moderate depth belonging to the Hutton or Shortlands form	*A. nilotica; A. marlothii; M. heterophylla; S. birrea; D. cinerea; A. karroo; A. tortilis; Peltophorum africanum; Euphorbia ingens*	800 - 1000 mm
Acacia nigrescens woodland (2197ha, 7,41% of reserve)	Pongola shale and sandstone	Rocky, shallow Mispah soils on ridges and hilsides	*A. nigrescens; Combretum apiculatum; C. zeyheri; Berchemia zeyheri; Peltophorum. africanum*	< 850 mm
Combretum apiculatum-Pterocarpus angolensis Woodland (3517ha, 11,86% of reserve)	Granite in Eastern parts of reserve; elsewhere Pongola shale and sandstone	Shallow and rocky soils belonging to the Glenrosa and Mispah series	*Peltophorum. africanum; D. cinerea; Pterocarpus. angolensis; C. apiculatum; C. zeyheri; E. schimperi; A. nilotica*	750 - 900 mm

Vegetation type	**Geology**	**Soils**	**Dominant woody species**	**Rainfall regime**
Pterocarpus angolensis-Bequaertiodendron magaliesmontanum woodland (<3% of reserve)	Quartzite	Shallow Mispah soils on rock	*Pterocarpus angolensis, B. magaliesmontanum, Pavetta edentula* (selective use by humans modifies this type by eliminating *P. angolensis*)	750 – 850 mm
Faurea saligna–Protea caffra woodland (407 ha, 1.4% of reserve)	Usually Pongola shales and ironstones in western part of reserve; elsewhere on quartzite reefs	Shallow Mispah	*F. saligna, P. caffra, Acacia karroo, A. nilotica. Protea comptonii & P. roupelliae* may be plentiful on quartzite.	<800 mm
Euphorbia cooperi-Ficus ingens woodland (530 ha – 1.8% of reserve)	Exposed granite	Cartref or Glenrosa (20-90 cm deep). Sometimes shallow Mispah.	*Bequaertiodendrom magaliesmontanum, Ficus ingens, Combretum zeyheri, Pappea capensis, Acacia nilotica, Heteropyxis natalensis, Euphorbia cooperi*	750 – 900 mm
Spirostachys africana woodland (20 ha, 0.1% of reserve)	No exposed rock present	Deep alluvial	*Spirostachys africana, Dichrostachys cinerea, Commiphora neglecta, Maytenus senegalensis*	<750 mm