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# Herbivore population crashes and woodland structure in East Africa

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## Summary

1. Between 1985 and 1991, bush encroachment was serious in Lake Manyara National Park, northern Tanzania. Shrub cover increased by *c.* 20%. The increase was independent of initial (1985) shrub cover.
2. Since 1987 there has been a steep decline in the number of African elephant in the Park due to poaching. Elephant density decreased from about 6 km<sup>-2</sup> to about 1 km<sup>-2</sup>. However, shrub establishment, as determined from counting tree-rings, preceded poaching.
3. Shrub establishment in two areas of the Park coincided with anthrax epidemics that drastically reduced the impala population. In the northern section of the Park this was in 1984, in the southern section in 1977.
4. The diameter increment of *Acacia tortilis* was 5.24 mm year<sup>-1</sup>, irrespective of the size of the trees. Size measurements indicated an even-aged stand of *Acacia* established in 1961, which coincided with another anthrax outbreak among impala.
5. Size measurements of old *Acacia tortilis* trees indicated another even-aged stand established at the end of the 1880s. The size of trees of this stand was not significantly different from a stand in Tarangire National Park, nor from a stand near Ndutu (on the boundary between Serengeti National Park and Ngorongoro Conservation Area), also northern Tanzania. All three stands are likely to have originated from bush establishment caused by the rinderpest pandemic at the end of the 1880s.
6. It is suggested that seedling establishment of *Acacia* is a rare event under the prevailing conditions of high browsing pressures by ungulates such as impala. Punctuated disturbances by epidemics among these ungulates create narrow windows for seedling establishment, which may explain the occurrence of even-aged stands.

*Key-words:* *Acacia tortilis*, bush encroachment, elephant, epidemics, impala

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## Introduction

Even-aged stands of *Acacia tortilis* and of other tree species occur in many parts of East and Southern Africa. Fire seems to play a role (Norton-Griffiths 1979) although many *Acacia* saplings, and older trees, are quite resistant to fire (pers. obs.), so it alone cannot explain the absence of many cohorts in the *Acacia* woodland structure. Moreover, the reports on the interaction between bush such as *Acacia tortilis* and grass and fire are contradictory. Seeds of *Acacia* do not germinate well under adult *Acacia* trees (Douglas-Hamilton 1972), so in a mature *Acacia* woodland young *Acacias* are generally absent. Caughley (1976) proposed a cyclic interaction between trees and elephant *Loxodonta*

*africana*, in which the cycle was driven by elephant overutilizing trees so that the trees died, the elephants moved off to other areas, and young trees could establish themselves (see also Pellew 1983). In Lake Manyara National Park, northern Tanzania, there has been a dramatic decline in elephant numbers since 1987 due to poaching. The density was reduced from about 6 elephants km<sup>-2</sup> (Prins & Douglas-Hamilton 1989) to <1 km<sup>-2</sup> in 1991 (personal observation). Concurrent with this decline in elephant, the cover by young *Acacia tortilis* and other shrubs has increased conspicuously since the early 1980s, apparently confirming the hypothesis of Caughley (1976). This is further supported by the fact that adult *Acacia* trees suffered from bark-stripping by

elephant at the times of their high density, which resulted in an annual tree mortality rate of 8–10% (Weyerhaeuser 1982).

Although Pellew (1983) showed that giraffe *Giraffa camelopardalis* play a substantial role in *Acacia* mortality, the high mortality attributed to elephant caused especially great concern at the end of the 1960s, partly because it was thought that elephant would damage the environment irrevocably (e.g. Myers 1973; Croze 1974). In the special case of Manyara, there was concern that death of adult *Acacia* trees would also deprive tourists of the sight of lions *Panthera leo* reclining in trees (Douglas-Hamilton 1972). At present, bush encroachment (and reduced elephant numbers) poses a likewise perceived threat, as tourists cannot see lions because scrubs screen them.

In this paper the causal factors for bush establishment are investigated and the age structure especially of *Acacia tortilis* is studied in order to find out what role elephant play in it. Bush establishment is frequently described as bush encroachment. This is often the result of overgrazing by herbivores, especially by domestic stock. The most likely cause appears to be increased sub-surface water availability for shrubs and trees due to the extermination of perennial grasses (Werger 1983). Proper studies are scarce (Werger 1983) but the results reported by Nulsen *et al.* (1986) and Walker *et al.* (1986) seem to confirm this mechanism. The results presented here do not point at the same mechanism of bush encroachment, but form a parallel to those reported by Austin & Williams (1989). These authors describe massive establishment of the conifer *Callitris glaucophylla* in Australia in 1876 and 1877, when, during a drought, livestock numbers declined drastically, and again in the 1950s when myxomatosis eradicated rabbits.

### Study areas

The study was conducted in northern Tanzania, mainly in the Lake Manyara National Park (3°30'S, 35°45'E) at about 1000 m a.s.l.; fire has been absent from the Park since at least 1958 (Wardens' Reports), and probably since 1934 (personal communication from A. Seif, professional hunters' guide in Manyara between 1934 and 1958). Ground cover by bushes in 1985 and 1991 was compared in the following vegetation types (see Loth & Prins 1986): *Acacia tortilis*–*Chloris virgata* community (a rather open *Acacia* woodland), *Capparis tomentosa* communities (dense riverine vegetations), the *Croton macrostachyus*–*Phoenix reclinata* and *C. macrostachyus*–*Acacia albida* communities (woodlands characterized respectively by palms and large *Acacias*) and the *Croton macrostachyus*–*Cordia africana* community, which is a groundwater forest. Nomenclature of plants follows Greenway & Vesey-FitzGerald (1972).

Circumference measurements of old *Acacia tortilis* trees were carried out in three different geographical areas:

1. in Lake Manyara National Park in three near-adjacent locations: south of Msasa River, near Korongo N'dilana River, and north of Ndala River;
2. in Tarangire National Park: between Tarangire Gate and the Tarangire Lodge (3°45'S, 35°59'E); south of the Engelhard Bridge (3°47'S, 36°00'E); and along the Silala Swamp (3°56'S, 36°08'E); and
3. around Ndotu Camp on the southern boundary of the Serengeti and the Ngorongoro Conservation Area, south of Lake Magadi (3°02'S, 35°03'E).

### Methods

#### GROUND COVER BY BUSHES

Horizontal visibility (in m) was estimated in a number of vegetation structure types (defined by Loth & Prins 1986) in 1985 and 1991 (both during the wet season in March and May, respectively). Visibility estimates were made from a slowly driven vehicle. The average of 10 estimates, stratified per vegetation structure type, along 500-m road transects was taken as the single estimate for those particular transects. The vegetation structure types were defined from aerial photographs and mapped in 1982 (Loth & Prins 1986). These were wooded bush grassland (WBG), bushed grassland (BG), wooded bush (WB), bush (B), dense wooded bush (WBd), forest (F), dense bush (Bd) and bush thicket (Bt). The structure types are defined by percentage ground cover of both trees and shrubs (Fig. 1).

There was a good correlation between percentage cover by shrubs (as determined from the aerial photographs) and horizontal visibility in the different

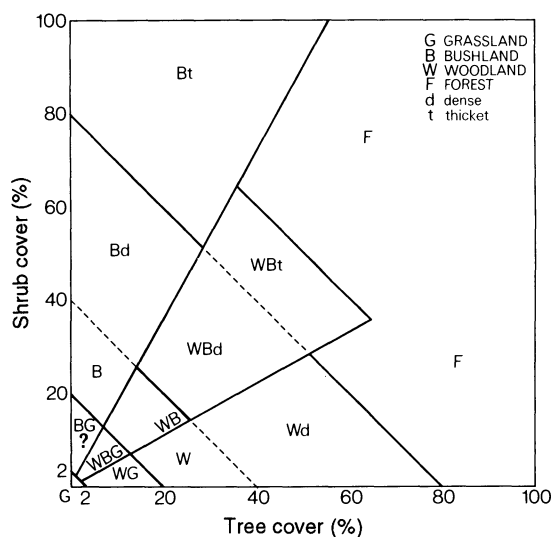


Fig. 1. Vegetation structure types as defined by percentage ground cover of trees and shrubs (after Loth & Prins 1986).

vegetation structural types at the end of the rainy season (Fig. 2;  $\log(\text{visibility (in m)}) = 2.297 \times (\% \text{ shrub cover}) - 0.0207$ ,  $R^2 = 98.2\%$ ,  $P < 0.001$ ). This formula was used to estimate the percentage shrub cover from the 1991 horizontal visibility estimates. Differences in shrub cover between years were tested with a paired  $t$ -test after arcsine-transformation of the percentages.

#### TREE-RINGS

One branch was cut from a number of shrubs with a fine saw at ground level. Tree-rings were counted for ageing (dark and light rings indicate dry and wet seasons; annually there is one long dry season and one wet in Manyara; Prins & Loth 1988). Branch diameters were measured with callipers to the nearest mm at the base; the average of the widest dimension and the narrowest was used as branch diameter. In a number of randomly chosen small areas, 25 shrubs each were measured. Only shrubs with a diameter smaller than 50 mm or a height less than 250 cm were sampled; the initial shrub was taken at random. Species from which tree-rings could not be counted (i.e. *Salvadora persica*, *Solanum incanum* and *Vernonia cinerascens*), or which were considered to be woody herbs according to the annotated checklist of the Park by Greenway & Vesey-FitzGerald (1972) (i.e. *Sida ovata*, *Sphaeranthus ukambensis* and *Abutilon mauritianum*) were ignored. The next shrub measured was the nearest neighbour of the initial shrub, etc. In the north of the park (the Ndala area) a total of 100 shrubs were measured, and 101 in the south (the Endabash area; Table 1). Tree-rings were counted independently by two observers, sometimes three, and compared afterwards. In about 65% of the cases there was perfect agreement, and in about 25% the difference

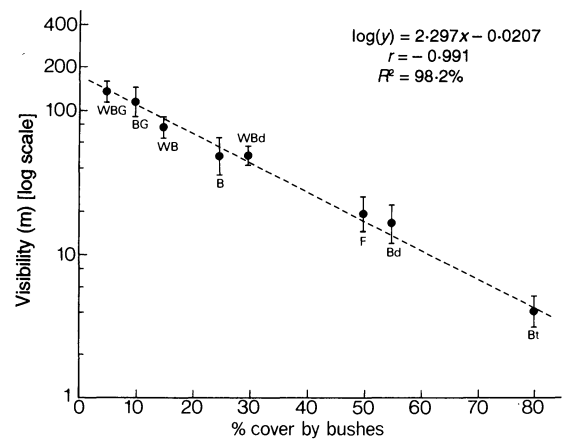


Fig. 2. Correlation between horizontal visibility at the end of the wet season (1985) and percentage shrub cover as determined from aerial photographs of Manyara.

was 1 year. In the latter situation a short discussion resulted in agreement. In the 10% of the cases where the disagreement was more than one year, the observers re-counted independently again until there was agreement.

#### DIAMETER INCREASE, GROWTH RATE AND AGE

It was not acceptable to cut down *Acacia* trees thicker than 50 mm and yet it was necessary to establish their age. Tree-rings of *Acacia* smaller than 50 mm were counted, and diameter was correlated with inferred age to establish the growth rate. A stand in the south of the Park, in the so-called Magara Extension, that was measured by Weyerhaeuser (1982) in 1981 was remeasured. The measured diameter divided by age yielded growth rate, and diameter divided by growth rate yielded

Table 1. Shrub species in which tree-rings have been counted to determine when they were established in two different areas in Lake Manyara National Park (Tanzania). The figures represent the number of individual shrubs in the two samples

Species	Ndala area	Endabash area	Total	Percentage
<i>Maerua triphylla</i>	12	27	39	19.4
<i>Acalypha fruticosa</i>	27	12	39	19.4
<i>Ocimum suave</i>	17	20	37	18.4
<i>Gardenia jovis-tonantus</i>	6	19	25	12.4
<i>Acacia tortilis</i>	10	3	13	6.5
<i>Justicia cordata</i>	8	5	13	6.5
<i>Cordia ovalis</i>	8	1	9	4.5
<i>Acacia sieberiana</i>	2	5	7	3.5
<i>Cassia didimobotrya</i>	6	0	6	3.0
<i>Balanites aegyptiacum</i>	0	6	6	3.0
<i>Phyllanthus sepialis</i>	2	0	2	1.0
<i>Cordia sinensis</i>	1	0	1	0.5
<i>Lippia javanica</i>	1	0	1	0.5
<i>Capparis farinosa</i>	0	1	1	0.5
<i>Dovyalis xanthocarpa</i>	0	1	1	0.5
<i>Kigelia africana</i>	0	1	1	0.5
Total	100	101	201	100.1

age. Because of differences in growth rate between individuals, this method of age-determination is not reliable for individual trees, but for a sample it results in the maximum likelihood estimate of the age of a stand. Stands were classified visually as 'juvenile', 'old', and 'very old'. Juvenile trees have no flattened crown, their branches still grow upright, and hardly any produce pods; it is difficult to drive a car under these trees. Old trees nearly always have a flattened crown, the bark is corrugated, and the trees produce pods; their circumference is usually less than 250 cm. Very old trees have very thick horizontal branches, while their circumference is usually more than 250 cm.

## Results

### BUSH ENCROACHMENT

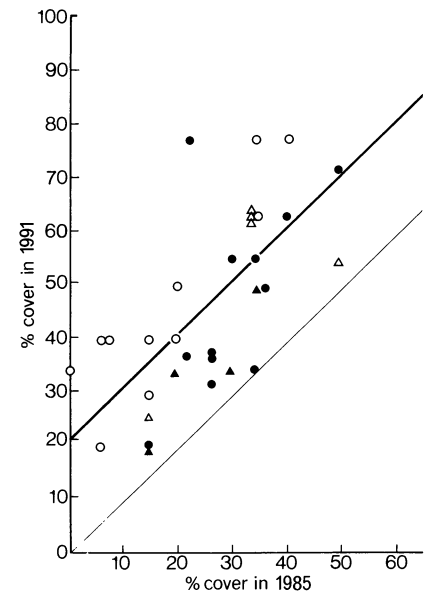
A significant increase in shrub cover occurred in many communities, but not in the *Croton macrostachyus*–*Cordia africana* community and in the *Croton macrostachyus*–*Acacia albida* community (Table 2). Both mentioned communities are dominated by large trees; the first type even has a closed canopy, being a groundwater forest. Shrub increase was most noticeable in the *Acacia* woodlands, where the cover nearly doubled in 6 years (Table 2). The percentage shrub cover in Manyara increased by nearly 21 per cent points between 1985 and 1991 (Fig. 3). The increase was not related to the initial shrub cover as measured in 1985.

### BUSH ESTABLISHMENT 1977 AND 1984

Sixteen woody species that yielded good (countable) tree-rings were sampled for ageing. The most important species were *Ocimum suave*, *Maerua triphylla*, *Acalypha fruticosa* and *Gardenia jovictonantus* (Table 1). Species composition of the samples from the Ndala area was different from the Endabash area ( $\chi^2_{10} = 41.776$ ,  $P < 0.005$ ); species with a frequency of only 1 were pooled to avoid small cell figures in the  $\chi^2$  analysis (Everitt 1972).

**Table 2.** Horizontal visibility at the end of the wet seasons of 1985 and 1991 and the corresponding ground cover of shrub (%) in a number of vegetation communities in Manyara. Differences were tested after arcsine-transformations of the fractions

Vegetation community	Number of sample	Visibility (m)		Shrub cover (%)		Change in shrub cover		
		1985	1991	1985	1991	Mean $\pm$ 95% CL	<i>t</i>	<i>P</i>
<i>Acacia tortilis</i> – <i>Chloris virgata</i>	31	70.6	30.4	24.9	45.6	20.7 $\pm$ 4.8	$t_{30} = 8.432$	<0.0001
<i>Capparis tomentosa</i>	18	23.3	14.6	53.0	64.0	11.0 $\pm$ 6.6	$t_{17} = 3.190$	<0.01
<i>Croton macrostachyus</i> – <i>Phoenix reclinata</i>	16	117.9	78.9	27.8	32.0	4.2 $\pm$ 6.3	$t_{15} = 2.088$	<0.05
<i>Croton macrostachyus</i> – <i>Acacia albida</i>	7	55.7	52.9	35.1	40.1	5.0 $\pm$ 6.2	$t_6 = 1.191$	NS
<i>Croton macrostachyus</i> – <i>Cordia africana</i>	9	19.1	16.9	56.4	57.4	1.0 $\pm$ 4.0	$t_8 = 0.646$	NS



**Fig. 3.** Bush cover increase in Manyara between 1985 and 1991 was about 20%: (○) wooded bush; (●) dense wooded bush; (△) bushed grassland; (▲) wooded bush grassland.

However, it cannot be concluded that any one species is under- or over-represented in any of the two areas, because for each species the  $\chi^2$  value contribution is too small to be different at 10% level (required  $\chi^2 = 7.88$  according  $\alpha' = \alpha/2(c-1)$ , in which  $c = 11$  and probability  $\alpha = 0.1$ ; Everitt 1972). Hence, the two areas can be compared directly.

Comparison between the areas would be complicated if the species in the same area had a different mean age, because over- or under-representation of species in any of the two areas might affect conclusions. The four most abundant species (*Ocimum*, *Maerua*, *Acalypha* and *Gardenia*) were tested. In the Endabash area, the mean age of these species was not significantly different (ANOVA:  $F_{3,74} = 0.366$ ). In the Ndala area, however, mean shrub ages were not equal ( $F_{3,58} = 5.397$ ,  $P < 0.05$ ). A subsequent Scheffé multiple-comparison test showed that the mean age of *Maerua* and *Ocimum* were two extremes of a sliding scale ( $S = 5.005$ ,  $P < 0.05$ ), but because

the differences between the other combinations were not significant (e.g. *Maerua* and *Acalypha*,  $S = 2.326$ ; *Gardenia* and *Ocimum*,  $S = 1.031$ ) the different species of the Ndala area were also treated as one statistical population.

The statistical populations of both areas were not normally distributed (test for normality: Endabash  $\chi^2_3 = 22.155$ ,  $P < 0.01$ ; Ndala,  $\chi^2_3 = 13.218$ ,  $P < 0.01$ ). However, a  $\log_{10}$ -transformation of the skewed age distribution made the populations normal (Ndala,  $\chi^2_3 = 4.735$ , NS) or nearly normal (Endabash,  $\chi^2_3 = 9.512$ ,  $P > 0.01$ ). Because the variances of the log-transformed populations were not equal ( $F = 2.810$ ), the  $t$ -test for unequal variance was used (Pollard 1977), which resulted in  $t_{199} = 3.946$ ,  $P < 0.01$ , which showed that shrub establishment in the Ndala area occurred significantly later in time than in the Endabash area.

Shrub establishment in Ndala (Fig. 4a) became vigorous in 1984 (the year of an anthrax outbreak that killed 92% of the impala *Aepyceros melampus*; Prins & Weyerhaeuser 1987), peaked in 1985, and subsequently diminished again to a very low shrub establishment from 1989 to 1991, concurrent with a sharp increase in the number of impala when the population recovered from anthrax (Table 3). In the Endabash area (Fig. 4b) vigorous shrub establishment took place immediately after the anthrax outbreak of 1977 and stayed high till 1986; apparently since that time impala have recovered to some extent in the Endabash area (in 1985  $< 1$  impala  $\text{km}^{-2}$ , but in 1991 c.  $4 \text{ km}^{-2}$ , pers. obs.).

#### *Acacia* GROWTH AND BUSH ESTABLISHMENT 1961

The rate of increase in diameter of young *Acacia* trees was  $5 \text{ mm year}^{-1}$ , because a regression of inferred age on diameter (mm) (being the error-free measurement) was  $-14.711 + 5.053 \text{ years}$  ( $n = 21$ ,  $r = 0.905$ ,  $P < 0.001$ ). A residual analysis on a

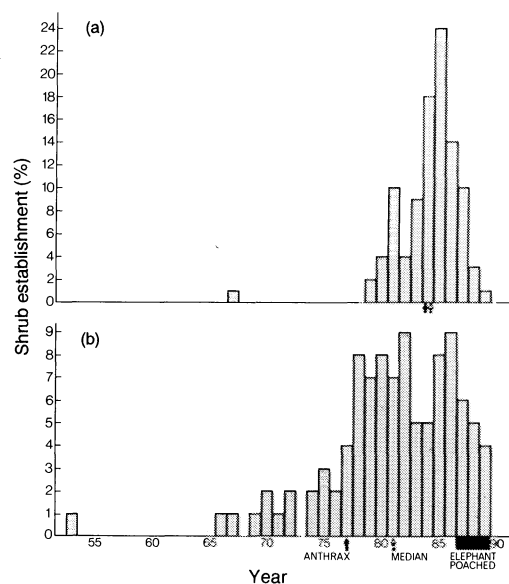


Fig. 4. Establishment of shrubs smaller than 50 mm diameter or shorter than 250 cm in the northern part of Manyara: (a) the Ndala Area and (b) the Endabash Area in the south. Solid arrows indicate years with severe anthrax outbreaks affecting the impala population; the black bar gives years with severe elephant poaching.

forced regression through zero showed that the data distribution did not allow for this regression, apparently because the growth rate of very young *Acacia* seedlings is lower than for those between 4 and 14 years (Prins & Van der Jeugd 1992).

The increase in diameter of the *Acacia* trees in the Magara Extension was calculated from the difference between the mean ( $\pm$ SD) stand diameter in 1991 ( $\phi = 33.0 \pm 9.6 \text{ cm}$ ,  $n = 20$ ) and 1981 ( $\phi = 28.7 \text{ cm}$ ,  $n = 270$ ; Weyerhaeuser 1982), yielding a rate of diameter increase of  $4.3 \text{ mm year}^{-1}$ . This corresponds quite well with  $6.4 \text{ mm year}^{-1}$  for Manyara's *Acacia* trees of the replacement class (recalculated from Fig. 18 in Mwalyosi 1977), and with an estimate for old trees in the Serengeti of  $5.0 \text{ mm year}^{-1}$  (Herlocker

Table 3. Population estimates of impala and years of anthrax outbreaks in Manyara, Tanzania

Year	Impala population estimate and anthrax occurrence	Source
1959	1500–2000	Warden's Reports (1960)
1961	severe outbreak in the whole park	Warden's Reports (1961)
1965	285	Watson & Turner (1965)
1967	300	Vesey-FitzGerald (1969)
1968	451	Makacha & Schaller (1969)
1975	985	Mwalyosi (1977)
1977	outbreak S of Ndala River	Weyerhaeuser (1982)
1981	1332	Prins & Weyerhaeuser (1987)
1982	1436	Prins & Weyerhaeuser (1987)
1983	1576	Prins & Weyerhaeuser (1987)
1984	212 (outbreak N of Ndala River)	Prins & Weyerhaeuser (1987)
1985	300	Prins & Weyerhaeuser (1987)
1991	1500	unpublished estimate, this study

**Table 4.** Relationship between the diameter of *Acacia tortilis* and the annual increase. All measurements were done in Manyara, Tanzania except Herlocker's from the Serengeti

Approximate diameter (d.b.h.)	Annual diameter increase (mm)	Source
25 mm	5.0	this study – tree-rings
185 mm	6.4	Mwalyosi (1977) – recalculated
310 mm	4.3	this study – Magara Extension
570 mm	5.0	Herlocker (1976)
720 mm	5.5	Weyerhaeuser (1982)
Mean	5.24	

1976). Weyerhaeuser (1982) reported an annual diameter increase of  $5.5 \text{ mm year}^{-1}$  for mature known individual trees ( $n = 16$ ) measured in 1969 and again in 1981. Because there is no relation between age and diameter increase (Table 4), the mean of these five estimates ( $5.24 \text{ mm year}^{-1}$ ) is the best estimate of the diameter increase rate of *Acacia tortilis*.

Juvenile trees in the Ndala and Endabash areas had a girth at breast height (g.b.h.) of  $49.3 \pm 7.8 \text{ cm}$  (mean with 95% confidence limits) ( $\phi = 15.7 \pm 8.8 \text{ cm}$ ,  $n = 50$ ), thus the best estimate for the age of the stand is  $29.9 \pm 4.7$  years (mean  $\pm 95\%$  confidence limits) and stand establishment of these juvenile trees is inferred to have taken place in 1961 (median 1963). In 1960 to 1961, again, the impala population of the park was severely reduced by anthrax (Warden's Reports 1960–61) (Table 3). The 1960–61 *Acacia* establishment does not show up in Fig. 4 because that figure represents results from branches and saplings with a diameter less than 50 mm only (see Methods).

#### OLD STANDS OF *Acacia*

Old trees were measured in three different areas in the northern part of Manyara where there are still mature woodlands (Table 5): south of Msasa River, near Korongo N'dilana and north of Ndala River.

Mean diameter values were significantly not different (ANOVA:  $F_{2,72} = 0.798$ ), so the g.b.h. of the old *Acacia* trees in Manyara was calculated for the combined samples (Table 5). The old Manyara stands were calculated to have been established in 1887, c. 105 years before the study.

Because of the coincidence of stand establishment and anthrax epidemics in 1984, 1977 and 1961, we propose that the mature, old trees originated from a similar epidemic killing off large numbers of browsing ungulates in the 1880s. Because the historical record only points at the rinderpest epidemic of the end of the 1880s (Sinclair 1977) (but does not provide data on other epidemics), we hypothesize that rinderpest was a causal factor for the establishment of the mature *Acacia* woodlands of Manyara. As this epidemic was pandemic, spreading from Somalia (1889) to Malawi (1892) and further south, apparently killing over 90% of the ungulates including cattle and small-stock (cf., e.g. Farler 1882 and Baumann 1894), it was predicted that elsewhere in northern Tanzania mature woodlands of the same age had to occur. Thus, *A. tortilis* trees in Tarangire National Park, some 100 km east of Manyara, were also measured, as were *A. tortilis* trees on the boundary between Serengeti National Park and the Ngorongoro Conservation Area 120 km north-west of Manyara (Table 5). The three samples were lumped because the means were not signifi-

**Table 5.** Data on girth at breast height (g.b.h.) for old stands of *Acacia* in seven sites in northern Tanzania. Combined ages were calculated from the g.b.h. values using the average rate of increase in diameter ( $5.24 \text{ mm year}^{-1}$ )

	g.b.h. (cm)	Diameter (cm)			Combined g.b.h. (cm) (mean $\pm$ 95% CL)	Combined age (years)	
		Mean	$\phi$	SD		$n$	Mean $\pm$ 95% CL
Manyara							
South Msasa River	173.3	55.2	8.7	25	171.5 $\pm$ 5.9	104.4 $\pm$ 3.6	105
near Korongo N'dilana	175.5	55.9	7.7	25			
Ndala River	166.6	53.0	8.4	25			
Tarangire							
Tarangire gate-Lodge	185.0	58.9	10.7	25	175.0 $\pm$ 7.4	106.3 $\pm$ 4.5	105
Engelhard Bridge	163.1	51.9	9.2	25			
Silala Swamp	176.9	56.3	10.3	25			
Ndutu	162.3	51.6	8.9	50	162.3 $\pm$ 7.7	98.6 $\pm$ 4.7	97.5
Overall total					170.5 $\pm$ 4.1	103.7 $\pm$ 2.5	



cantly different (ANOVA:  $F_{2,72} = 3.067$ ). The inferred mean age of these trees was 106.3 years (Table 5).

The inferred mean age of median trees around Ndotu Camp was 98.6 years (Table 5).

The aggregate samples of Manyara, Tarangire and Ndotu were not significantly different ( $F_{2,197} = 2.984$ ), so the hypothesis that these old stands of northern Tanzania were established simultaneously was not rejected. The mean g.b.h. of all trees was 170.5 cm (Table 5) which yielded a mean inferred age of these stands of 103.7 years. So, in Manyara, Tarangire and in the eastern Serengeti it appears that, likely due to rinderpest, vigorous bush encroachment took place around 1887 (with 95% certainty between 1885 and 1890), which resulted in the present-day mature *Acacia* trees that still dominate the landscape.

### Discussion

In relation to the structure of African woodlands, especially those formed of *Acacia* trees but also with other dominant species, much emphasis has been put on the role of elephant (Douglas-Hamilton 1972; Croze 1974; Caughley 1976; Guy 1976; Barnes 1979; Weyerhaeuser 1982; Jachmann & Bell 1985; but see Norton-Griffiths 1979). Possibly this came about because of the apparent destructive behaviour of these animals towards adult trees, and the conspicuous effect of which perhaps led ecologists to look especially at *Acacia* mortality, which, in turn, gave rise to hypotheses about cyclic interactions between elephant and *Acacia* or other trees (Caughley 1976; Pellew 1983). However, recruitment of seedlings into the population is just as important to an understanding of the phenomenon of even-aged stands in *Acacia* as is tree mortality removing individuals from the population again (*vide* Norton-Griffiths 1979). In the study area, annual tree mortality due to elephants' destructive behaviour was *c.* 8–10% when the elephant density was high (Weyerhaeuser 1982), a figure comparable to *Acacia* mortality in the Serengeti (Pellew 1983). The present results show that recruitment has been vigorous (Fig. 3) and bush encroachment is very high (Table 2). The research was initiated by assuming that this was caused by elephant poaching, because the Manyara population has been reduced by about 90% since 1987 when poaching became rampant. However, as there is no density-dependent relationship between the initial shrub cover in 1985 and the increase in shrub cover since that time (Fig. 3), it does not seem likely that lack of consumption by elephants is the primary factor in explaining bush encroachment. Moreover, shrub establishment preceded poaching by a few years in the northern part of the park, and by 10 years in the southern part, in both cases coinciding with anthrax outbreaks specifically killing off large numbers of impala (Fig. 4, Table 3). Slightly

older stands apparently originated from a similar anthrax outbreak in 1961 (see Results). In these three historically well-documented epidemics the numbers of herbivores other than impala were hardly affected (Prins & Douglas-Hamilton 1989).

Impala consume grasses, herbs and shrubs; they often feed on *Acacia* pods and seedlings of shrubs (Hofmann 1973; Lamprey 1963; H.H.T. Prins, personal observation). Impala spend more of their time in woodlands than wildebeeste *Connochaetus taurinus* or zebra *Equus burchelli*. These are typical grazers (Hofmann 1973; De Boer & Prins 1990), so it is unlikely that these species would strongly predate upon *Acacia* seedlings. Giraffe density in Manyara is reasonably high (about  $0.8 \text{ km}^{-1}$ ) (personal observation) but giraffe especially browse trees higher than about 2 m (personal observation; Pellew 1983) and are not observed to eat seedlings (see also Hofmann 1973). Other browsing herbivores occur in much lower densities than impala (Prins & Douglas-Hamilton 1989: bush-buck *Tragelaphus scriptus*, black rhinoceros *Diceros bicornis* — locally extinct since 1988). The occurrence of anthrax outbreaks killing impala in years with apparent peak seedling establishment thus points at impala as a likely candidate to be the suppressor of seedling recruitment in the Manyara system. Anthrax outbreaks among impala have not been recorded prior to 1960; they were numerous in 1940 (Watermeyer & Elliott 1943) and also before that time (since, at least 1934 Mzee A. Seif, unpublished data), but counts are not available.

Rinderpest had a devastating impact on ungulates, both domestic and wild, at the end of the last century. It was accidentally introduced in Somalia, probably from India, in 1889 and again in 1903 (Von Ostertag & Kulenkampff 1941). Its first occurrence in northern Tanzania and southern Kenya can be dated through oral history. 'Rinderpest was the first catastrophe [which befell the Masai], and it started like this. First of all there was an eclipse of the sun and it took place at about five o'clock in the afternoon. . . It was then that the rinderpest attacked the cattle. The epidemic finished the Masai cattle. . .' (Marieni ole Kertella in interview in Hanley (1971), p.285). This eclipse took place on 22 December 1889 in the late afternoon in the Nairobi area (M. Drummen, personal communication). Rinderpest must have severely reduced the impala populations in, for example, Manyara, Tarangire and Serengeti. This could have caused widespread bush encroachment in many areas in East African at the end of the last century. Bush encroachment was observed at that time to occur (Ford 1971), and apparently the present-day mature *Acacia* stands are remnants of a cohort established during that period. This is confirmed by the inferred date of establishment of the three woodlands in northern Tanzania of 1887, with 95% confidence limits of 1885 and 1890,

which overlaps with the date for the rinderpest as remembered in oral history.

Pellew (1983) rejected the hypothesis that rinderpest had a great impact on *Acacia* at the end of the last century, because he concentrated his explanation on the population dynamics of giraffe. On the other hand, Kjekshus (1977) also presented evidence for the relationship between rinderpest and the occurrence of the present-day mature *Acacia* woodlands.

Much larger *Acacia* trees than the ones mentioned above also occur in Manyara; these were classified as very old, and according to Mzee A. Seif, who hunted in Manyara in 1934, they had not changed at all since that time. Their g.b.h. was  $345.6 \pm 33.0$  cm mean with 95% confidence limits;  $\phi = 110.0$  cm,  $SD = 21.9$  cm,  $n = 19$ ), with an inferred age of this group of  $209.9 \pm 20.0$  years (mean with 95% confidence limits). Apparently, these trees are remnants of woodlands established around AD 1781 (confidence region 1761–1801). These old trees possibly reveal bush encroachment from when the Iraqw tribe vacated the Manyara area because of warfare associated with the advent of the Masai from the north. Clan leader succession lists coupled with oral history date this confrontation from AD 1760 to 1800, both in the case of the Masai (H.A. Fosbrooke, personal communication) and the Iraqw (personal interviews). Oral history (S. Swalleh, personal communication) records goat husbandry and limited agriculture for the Iraqw ancestors that lived in Manyara. Bush encroachment is a normal process in East Africa but goats can be used to suppress it (Pratt & Gwynne 1977; Anon. 1983). Cessation of goat presence around 1780 likely caused bush encroachment, because the Masai did not occupy the area afterwards. This 'fossilized' bush encroachment is not likely to have been caused by the desertion of the Engaruka Culture sites (north of Manyara), because this took place around 1700 (Sutton 1990). It seems too early to be an effect of the intense elephant hunting, especially by Arabs for European and American traders, because this trade really took off from the 1830s onwards (Gavin 1986).

For the impact of rinderpest on present-day woodland structure, some further evidence is found in the population structure of baobab *Adansonia digitata* trees. Barnes (1979) reported a girth increment for this species of 1 m per 40 years. Inspection of baobab size classes as reported by him for Ruaha N.P. (Central Tanzania) indicates an over-representation of trees established between 1860 and 1870. Size classes for Manyara (Weyerhaeuser 1982) show a peak in baobab establishment between 1870 and 1880. Because both authors only give size classes and not individual sizes, a more-accurate dating is not possible. Yet, for both areas, some 500 km apart, baobab establishment corresponds quite well, and more or less coincides with the inferred *Acacia* establishment in Tarangire, Manyara and Serengeti.

In Manyara, punctuated disturbances in the ungulate community created narrow 'windows' in the pressure on *Acacia* seedlings, which resulted in a few seedling establishment events over the last two centuries, i.e. 1780, 1887, 1961 and 1983. Neither intermediate cohorts of *Acacia* nor evidence for herbivore crashes other than the mentioned ones were found. These rare events resulted in even-aged stands of *Acacia tortilis*. Similar causal effects of catastrophic events on establishment have been described for tree species on the Galapagos Islands (Lawesson 1989) and for Australia, where seedling establishment of *Astrebla lapacea*, for example, occurred only twice between 1941 and 1983, and for *Callitris glaucophylla*, when livestock numbers declined drastically in 1876 and 1877, and when myxomatosis eradicated rabbits in the 1950s (Austin & Williams 1989).

It appears that in explaining the structure of the *Acacia* woodlands the effect of elephant-induced tree mortality has been overrated and that the occurrence of limited windows for recruitment plays an important role. If this is true, it is not justifiable to interpret the occurrence of even-aged stands of *Acacia* as stable limit-cycles, as was suggested by Caughley (1976), Norton-Griffiths (1979) or Pellew (1983). Austin & Williams (1989) concluded that it is risky to base conclusions about vegetation

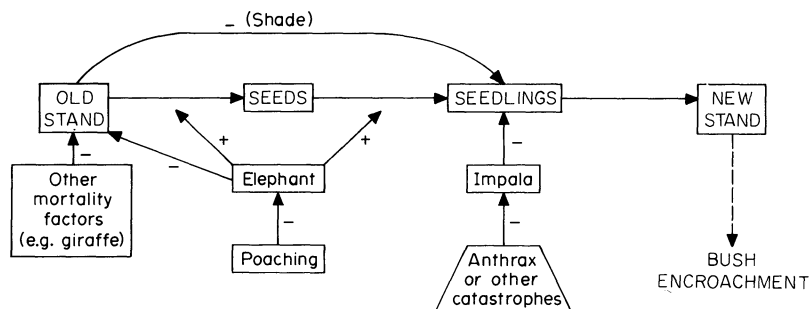


Fig. 5. Summary of interactions between *Acacia tortilis*, elephant, and impala in Lake Manyara National Park. Minus signs indicate that higher values in the preceding box result in lower values in the succeeding one, while plus signs result in higher values.

dynamics on single locations and short-term periods. The present results against the light of the elephant controversy of the 1970s (e.g. Myers 1973; Norton-Griffiths 1979) imply that it is also risky to base the management of protected areas in Africa on observations over short-term periods or single locations only. In the Serengeti, which is close to Manyara, rinderpest at the end of the last century reduced herbivores, which in turn gave rise to a high bulk of combustible grassy fuel; frequent fires then reduced bush cover and prevented *Acacia* establishment, for example. When the herbivores recovered from the rinderpest disturbance and amounts of combustible material declined, compression of elephant into the park still prevented establishment (Norton-Griffiths 1979). Contrastingly, in Manyara fire has been absent for more than 60 years, and elephant hardly seem to play a role in the establishment of bushes or *Acacia tortilis* trees, although their strongly reduced browsing pressure on larger bushes undoubtedly affects visibility in Manyara. Elephants interact with seed production (personal observation) and affect seed germination ability (e.g. Pellew 1983). However, the impala, a much smaller herbivore, seems to play a greater role (Fig. 5).

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