Size structure analysis of the dominant trees in a South African savanna

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The population dynamics of six major tree species from the Nylsvley savanna were inferred from their present size structures. An attempt to determine age structure was prevented by confusing 'growth' rings. The two *Acacia* species and three of the dominants from the *Burkea* savanna show approximately stable age structures. Reduced numbers in some size classes, as a result of unknown past events indicate that the population of mature trees in the future will fluctuate, regardless of future conditions. *Sclerocarya birrea* has a markedly unstable structure, with no immature trees and no evidence of successful regeneration.
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Die bevolkingsdinamika van ses belangrike boomspesies in die Nylsvley-savanne is afgelei van hul huidige groottes. 'n Poging is aangewend om ouderdomstruktuur te bepaal — dit kon egter nie gedoen word nie omdat die jaarringe onduidelik gedefinieer was. Die twee *Acacia*-spesies en drie van die dominante spesies in die *Burkea*-savanne het min of meer stabiele ouderdomstrukture. Verminderde getalle in sommige klasse van groottes, as gevolg van onbekende gebeure in die verlede, dui aan dat die bevolking van volwasse bome in die toekoms sal fluktueer, afgesien van toekomstige toestande. *Sclerocarya birrea* het 'n noemenswaardige onstabiele struktuur, met geen jong bome nie en geen teken van suksesvolle regenerasie nie.
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Introduction

The South African Savanna Ecosystem project is located in the Nylsvley Provincial Nature Reserve, in the northern Transvaal. The main vegetation type is a mixed, broadleaf deciduous savanna with about a 30% canopy cover of woody species, dominated by *Burkea africana* (Hook.) and occurring on a dystrophic sandy soil 1 – 3 m deep, with a mean annual rainfall of *c.* 600 mm. The area has a fairly long history (at least several hundred years) of human occupation, and within the *Burkea* vegetation there are a number of more open patches of *Acacia* species. All these patches exhibit evidence that they were village sites at some time in the past. (B. Fordyce pers. comm.). The study site is described in Huntley and Walker (1982).

A major objective of the project is to develop an understanding of the dynamics and stability of the vegetation in the study area. Of the various approaches to achieving such an understanding, the best is undoubtedly a long-term record of known cohorts of individual plants. Although such studies have been initiated in this project, it will take many years before they are able to provide any useful insights.

A short-term alternative is to analyse the existing size or age structure of the dominant species. If the age structure is known, both past and future states of the population can be inferred. If only the size structure is known, then little can be said about the past, but future states of the population can be inferred (Harper 1977). This paper reports the results of studies on six of the more important tree species in the main study area, viz. *Burkea africana, Terminalia sericea* (Burch.ex. Dc., *Combretum molle* R.Br.ex G.Don, *Sclerocarya birrea* (A.Rich) Hochst. subsp. *caffra* (Sond.) Kokwaro, *Acacia tortilis* (Forsk.) Hayne subsp. *heterocantha* (Burch.) Brenan and *A. nilotica* (L.) Willd. ex Del. subsp. *kraussiana* (Benth.) Brenan. For ease of presentation the subspecies are not given in the remainder of this paper.

Characteristics of the species

Burkea africana occurs in various types of woodland over a wide range of altitudes and climate and always associated with sandy soils. According to Van Wyk (1972), seeds germinate poorly, growth is slow and resistance to frost and fire is low. At Nyslvley, however, frost and fire resistance in established trees is high. Heights of > 10 m may be reached, but few trees at Nylsvley are taller than 7 m, with the majority being less than 3 m in height. This may be due to frequent disturbances in the past.

Terminalia sericea likewise occurs on sandy soils, and often at vlei margins. It can grow up to 20 m in height (Coates

Palgrave 1977), but is usually between 4 and 6 m high and sometimes occurs in a scrub form around 2 m high.

Combretum molle is characteristic of open savanna woodland and grows up to 10 m high. At Nylsvley it seldom attains this height.

Sclerocarya birrea grows in medium to low altitudes in open woodland and bush, growing up to 15 m in height (Coates Palgrave 1977).

Acacia tortilis and *Acacia nilotica* occur in various types of woodland, wooded grassland and scrub. *A. tortilis* varies in height from 5 to 20 m, while *A. nilotica* reaches 10 m, but is usually smaller. At Nylsvley these two species are found in homogenous microphyllous thorn patches, together with *Dichrostachys cinerea* subsp. *africana*. Soils of these patches have higher nutrient levels than do soils of the surrounding savanna. Since both species are generally regarded as early successional invaders, it was considered important, in terms of the Nyslvley study objectives, to know whether their populations in the *Acacia* patches were increasing, decreasing or stable.

Burkea africana and *Combretum molle* are just two of many savanna trees which exhibit cryptogeal germination, a characteristic which is thought to have arisen as a result of evolution in a habitat that has long been subjected to frequent burning (Jackson 1974). The burial of the plumule results in the development of the root crown well below the soil surface and buds upon it will be protected from fire or frost. The part of the true stem which is underground bears buds in the axils of scale leaves. These buds are thus protected and give rise to new shoots when the shoots above ground are burnt off or damaged in any other way. *Burkea africana* does sprout at Nylsvley, as observed 3 to 4 months after an experimental burn. Other trees and shrubs at Nylsvley, which also sprout, include *Terminalia sericea, Ochna pulchra* Hook., *Dombeya rotundifolia* (Hochst.) Planch. and *Combretum molle.* Although fire appears to be the most important cause of sprouting, other possible causes could be frost and defoliation during arthropod outbreaks.

Methods

Stem basal area was chosen as the most appropriate single measure of tree size, since height may have been modified by fire or chopping. Unless otherwise noted, circumference was measured mid-way between the ground and the first major branch and, within species, this provided a consistent and repeatable measure. The species were sampled in different years, in different projects, and the sample sizes were determined individually. Sampling was carried out between March and June, and each species was sampled on one occasion only.

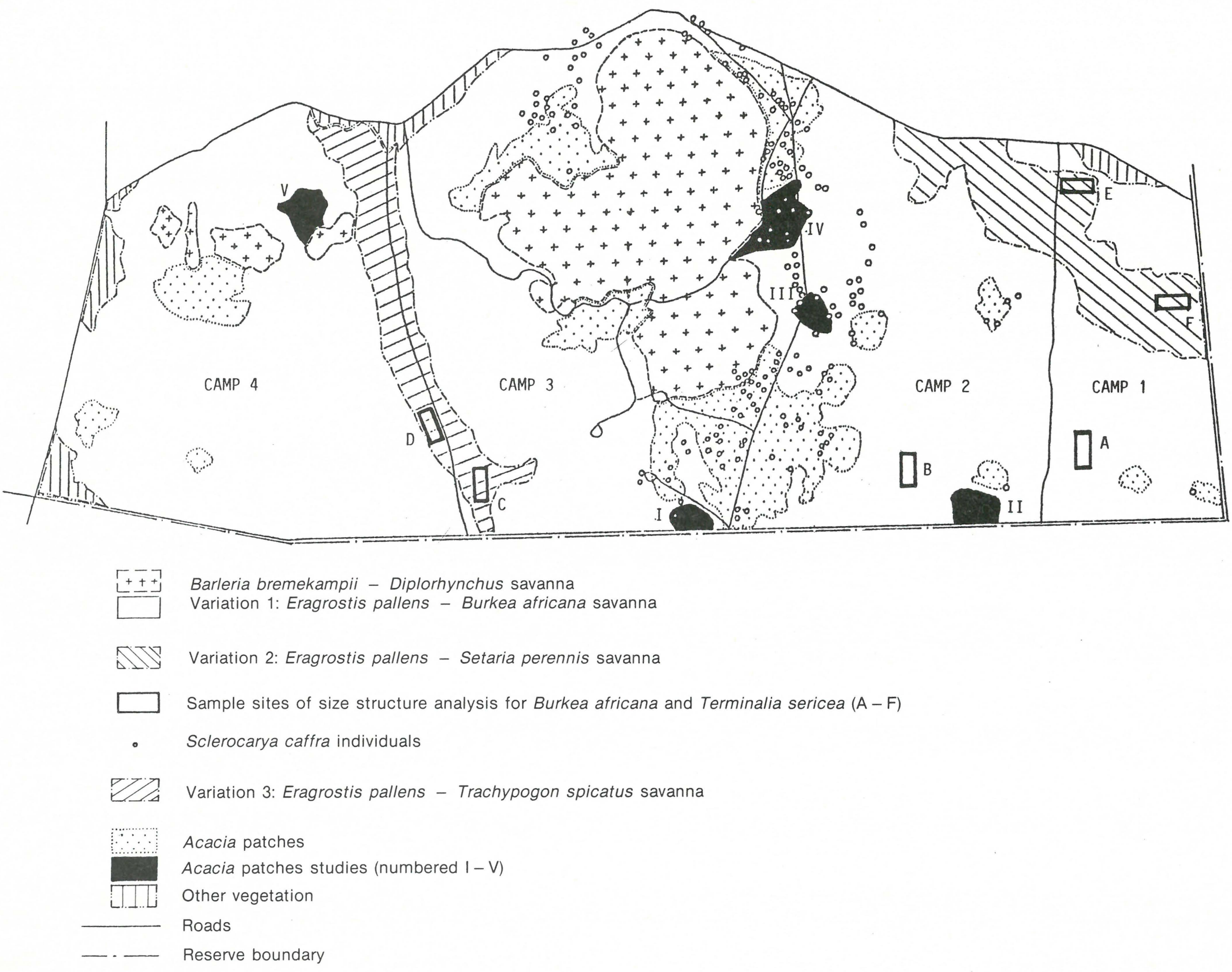

Figure 1 Nylsvley Study Area (Adapted from Coetzee *et al.* 1977).

Burkea africana

Information for the circumference distribution was obtained from each of the 4 camps at Nylsvley. Two sites were located within each of the three variations of the *Burkea* savanna and, where possible, they were made to coincide with the permanently marked sites set up by Lubke (1976). The positions of the sites are indicated in Figure 1. In each site a total area of 0,5 ha was sampled by setting up five, 10 × 100 m transects placed at intervals of 50 to 75 m, and measuring the circumference of each *Burkea africana* within each transect.

Terminalia sericea

Circumference data were obtained from the same sites that were used for the *Burkea* study (Figure 1), but using only four 10 × 100 m transects, again laid out in each of the three variations of the *Burkea* savanna.

Combretum molle

Twenty-two 10 × 100 m transects were established in camps 1, 2 and 3 in the *Eragrostis pallens* (Hack.) – *Dombeya rotundifolia* community of Coetzee *et al.* (1977), where *Combretum molle* occurs in the highest frequencies. Circumferences of each *Combretum molle* individual were measured, as before, in each transect.

Sclerocarya birrea

The frequency of occurrence of this species was not high enough to warrant transect establishment. Colour aerial photographs were used to locate *Sclerocarya birrea* individuals. The trees were then located on foot and their circumferences measured just above the buttress swellings. The area between the individual trees was searched, systematically, for seedlings and saplings.

Acacia tortilis and *Acacia nilotica*

The circumferences of all individuals of both species, measured below the first major branches, were obtained within each of five separate *Acacia* patches.

Problems

Sprouting

Because of the sprouting habits of *Burkea africana* and *Terminalia sericea*, difficulties were encountered in distinguishing individuals. Where stems were very close together and appeared to share the same root system, they were counted as one individual and the largest stem was measured. Where small plants occurred in the immediate vicinity of the base of a large tree, all the plants were measured separately. Where small stems were in close proximity to a large dead stem, the circumference of the largest, living stem was recorded, and it was noted as being a sprouter from a dead tree.

Multi-stemmed bushes growing in clumps caused the greatest problems and were very common in sites D, E and F. The whole clump was treated in the same way as coppice, by measuring the largest stem of the largest bush in the clump.

Seedlings

All individuals of each species in the transects were sampled, regardless of size. However, because the current year's seedlings of *Burkea africana* were extremely small they could not be counted accurately over the same area as were the larger individuals. Instead, two 5 × 5 m quadrats were set up within each transect in predetermined positions, and seedlings within the quadrats were counted. During the survey it was noted that a far greater density of seedlings occurred beneath the canopies of large trees, than in the open. An additional two 5 × 5 m quadrats were then placed specifically beneath large trees in each transect.

Recognition of age by growth rings

The original objective of these studies was to determine the age structure of each of the species concerned. The formation of growth rings in the wood of deciduous, or markedly seasonal evergreen trees, allows for ageing by means of a ring count of a core or cross-section of the trunk. Major problems, however, arose in the determination of growth rings for these species.

Angiosperm ring margins can usually be delineated by one or more of the following features: boundary parenchyma, ring-porosity, dense latewood lines, semi-ring porous structures, and other growth-related variations in parenchyma pattern (Lilly 1977). In many cases, these variations are only visible if the wood is sectioned and then studied under a microscope. For all of the species studied, cores were taken, sectioned and viewed in this manner.

Despite various attempts using unstained and stained cores, no definite growth ring structures could be found that could be reliably related to age. Features which, superficially, appeared to delineate growth rings, were either discontinous or, on close examination, turned out to be rows of fibres which, being laid down in response to stress, do not necessarily demarcate a single growing season. The best results were obtained with *Burkea africana*, which agrees with Lilly's (1977) assessment of some South African trees, but even with this species there was no assurance that ring count could be used directly to infer age. Because of these problems the analysis of population structure and dynamics had to be based only on the sizes of the trees.

Results

The stem circumference of *Burkea africana, Terminalia sericea, Combretum molle, Acacia tortilis* and *A. nilotica* trees were grouped into 100 mm size classes. To achieve approximately the same number of size classes, the class interval for *Sclerocarya birrea* was 250 mm.

For *Acacia tortilis* and *A. nilotica*, seedlings were not included in the size structures. There was a disproportionately large number of seedlings, very few of which appear to survive.

The size structures for the individual species and the quotients between successive size classes are shown in Figures 2 – 7. The quotients are a measure of movement from one size class to the next (Meyer 1952). In a stable population the quotient between the numbers of trees in successive size classes approaches a constant value (q).

Discussion

Burkea africana

The number of trees in two size classes (the 5th and 8th) reflect an uneven size distribution (Figure 2). The uneveness may either be an artefact of the class intervals, or it may be due to some historical event. Inappropriate class intervals could be a result of misinterpreting the shape of the growth curve (i.e. assuming a linear relation between age and size when in fact it is sigmoidal). This would be possible if there had been only a single depression of a size class (for example, class 5), but two depressed classes make it most unlikely.

The historical effect could be due either to reduced regeneration and/or increased mortality. An increase in the loss of above-ground growth at some times in the past is supported

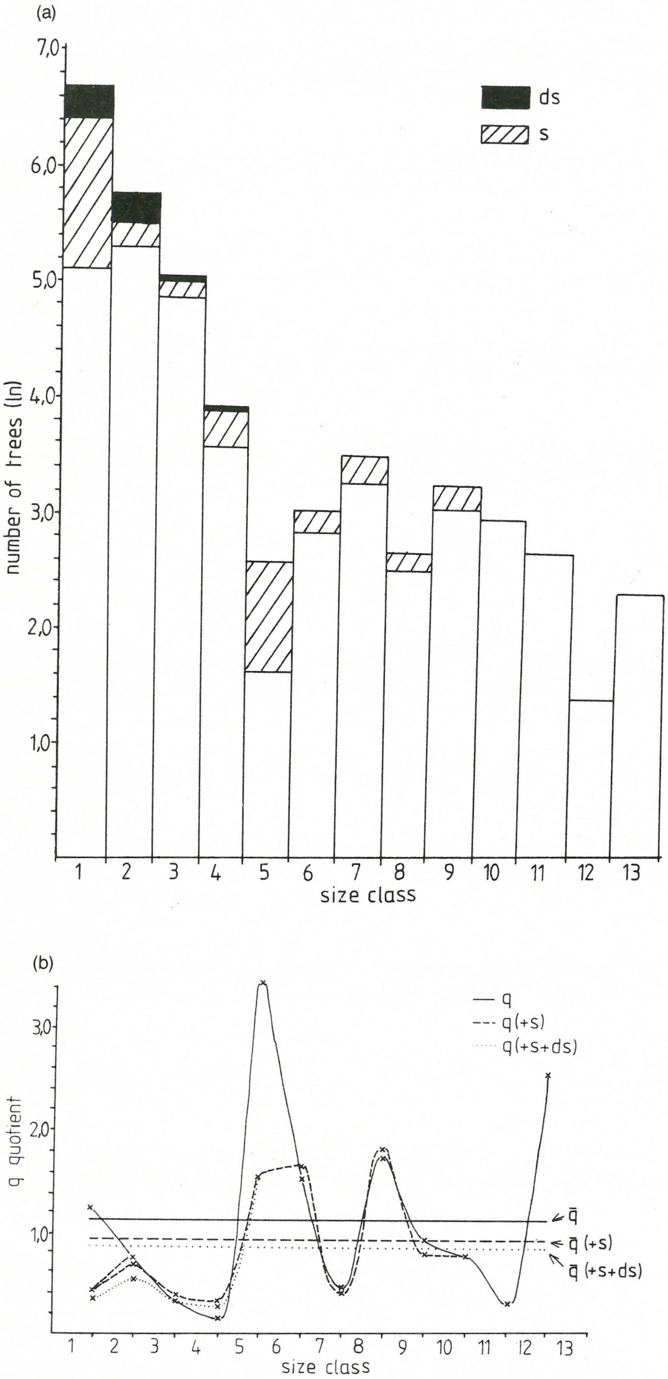

Figure 2 Population size structure of *Burkea africana* including multi-stemmed trees (s) and trees sprouting from a main, dead stem (ds). (a) Numbers of trees per size class. (b) Quotients between the number of trees in successive size classes. q is the hypothetically stable community.

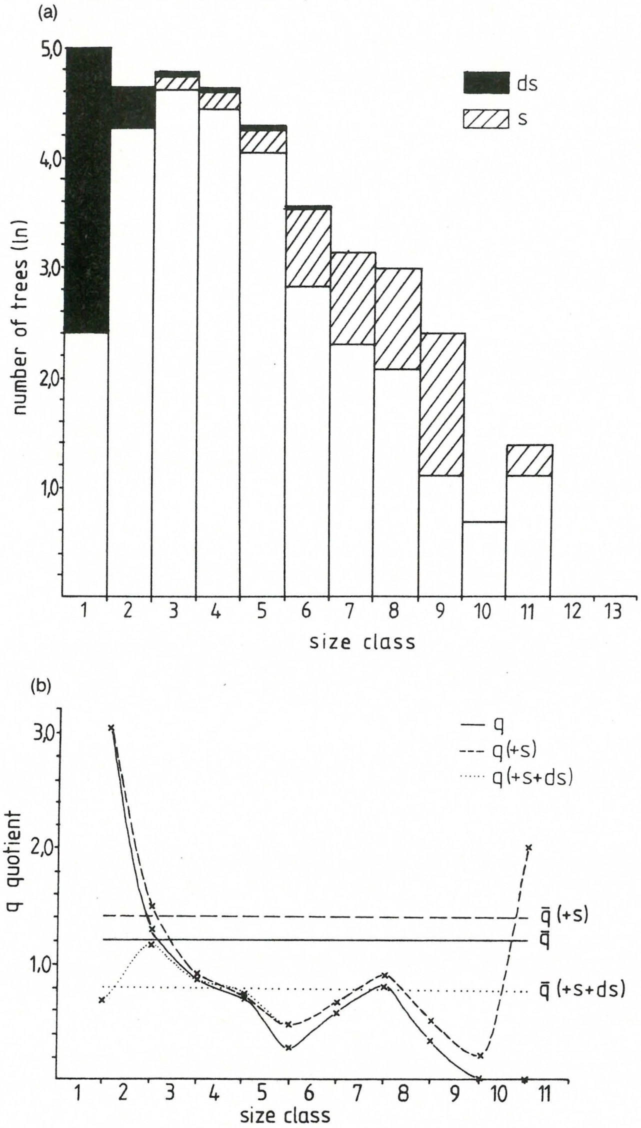

Figure 3 Population size structure of *Terminalia sericea* including multi-stemmed trees (s) and trees sprouting from a main, dead stem (ds). (a) Numbers of trees per size class. (b) Quotients between the numbers of trees in successive size classes. q is the hypothetically stable community.

by the inclusion of sprouting trees into the size distribution (Figure 2a). The high incidence of sprouting indicates widespread and frequent damage at the appropriate times (see, especially, size class 5). If the sprouted trees are not included in the size distribution, the deviation from the theoretically stable population (q in Figure 2b) is even greater. It is also conceivable that if the event causing the mortality was due to humans, regeneration could also have been affected. We have not included the results of the age/ring count analysis, because of the problems outlined earlier, but if the estimate of the oldest age (110 years) was correct, it means that two major disturbances occurred somewhere around 50 and 80 years ago.

Whatever the real ages might be, the size distribution of *B. africana* indicates that the population at Nylsvley is not stable and will therefore exhibit periods with greater and lesser densities of mature trees as the different cohorts move through to the largest sizes. To some extent this effect may be masked by different growth rates of trees within size classes, owing to differences in soil depth, etc.

Terminalia sericea

With all individuals (including those which have sprouted from a main dead stem — Figure 3a) the population appears to approach a stable size distribution (Figure 3b). Without the sprouters, the size distribution is decidedly uneven (size classes 1 and 2), indicating the importance of vegetative regeneration in maintaining a stable population of *T. sericea*.

Combretum molle

This shows no overall pattern. The uneveness of the size distribution (Figures 4a & b) is the sort induced by stochastic effects, and is expected in natural populations. The complete absence of individuals in class 15 is the only unexpected (and

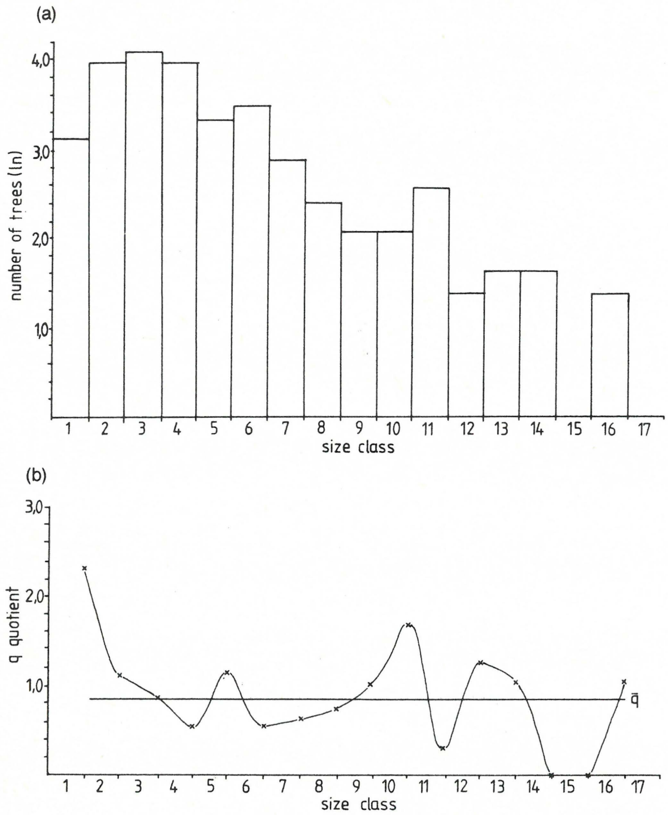

Figure 4 Population size structure of *Combretum molle*. (a) Numbers of trees per size class. (b) Quotients between the numbers of trees in successive size classes. q is the hypothetically stable community.

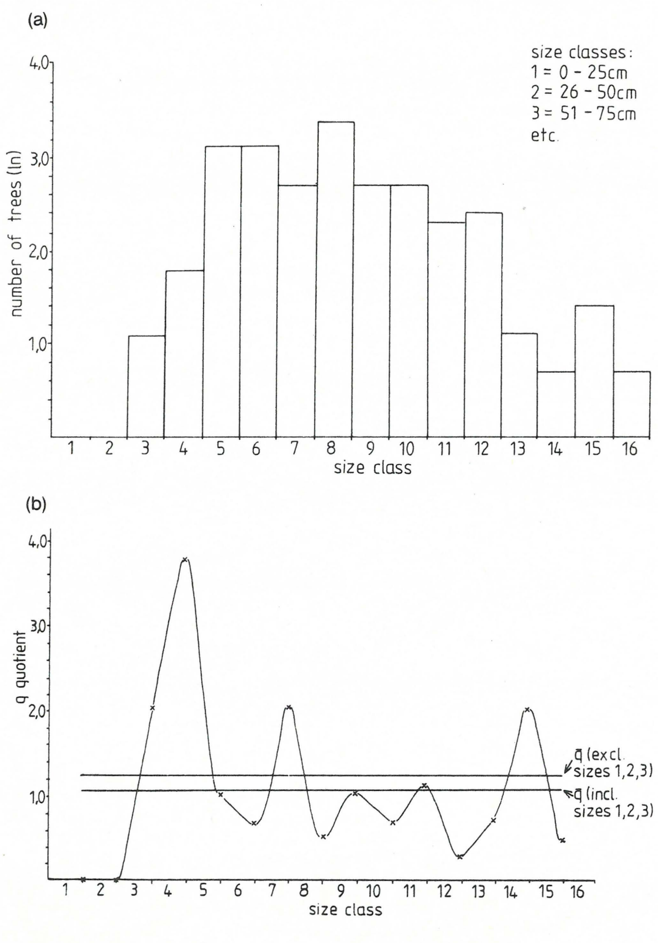

Figure 5 Population size structure of *Sclerocarya caffra*. (a) Numbers of trees per size class. (b) Quotients between the numbers of trees in successive size classes. q is the hypothetically stable community.

inexplicable) feature of the results. This could be attributable to sampling error, but is unlikely considering the numbers of trees in classes 14 and 16 (13 and 12, respectively).

Sclerocarya birrea

The population of *Sclerocarya birrea* at Nylsvley appears to have no individuals with a circumference of less than 50 cm, and very few with circumferences ranging from 50 – 100 cm (Figure 5a). Between 125 cm and 300 cm, all the size classes are approximately evenly represented. Above 300 cm circumference the number of trees drops off markedly.

Some seedlings have been found in disturbed sites where they were protected by other vegetation, (Y. Goldring pers. comm. 1982), but they have not survived beyond one or two years. It would therefore appear that successful regeneration is highly episodic, and there has certainly been no successful regeneration for many years.

Acacia tortillis and *A. nilotica*

Uneveness in the size distribution of *A. tortilis* appears to represent fluctuations around a relatively stable condition (Figure 6a & b). *A. nilotica* shows more variability, and the plot of quotients for successive size classes shows a rather

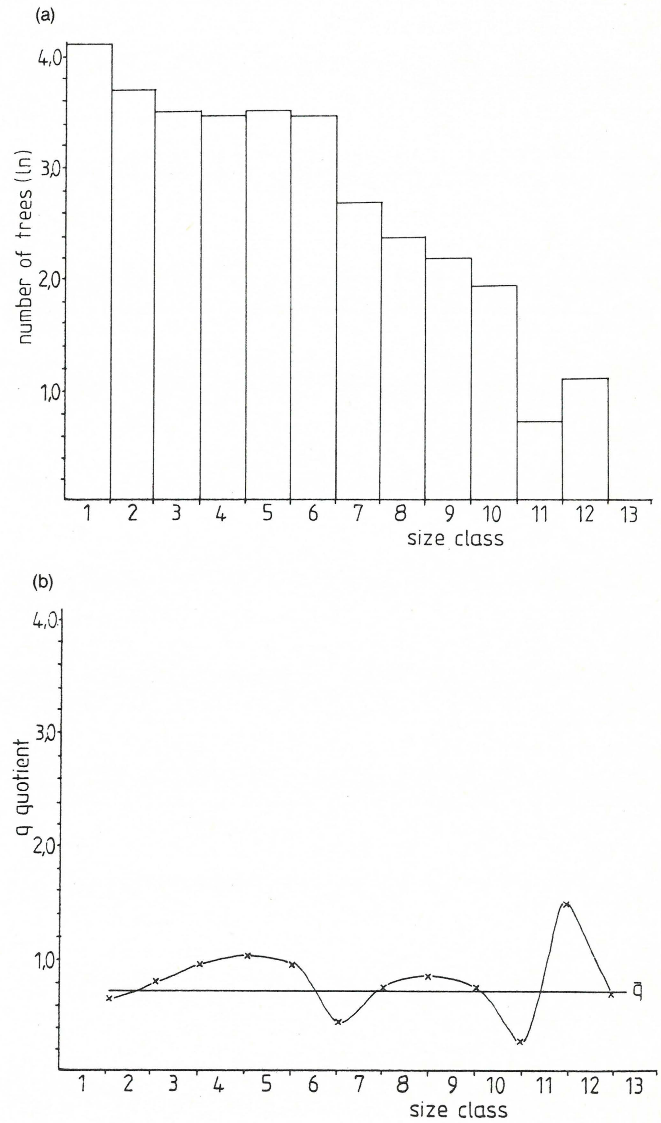

Figure 6 Population size structure of *Acacia tortilis*. (a) Numbers of trees per size class. (b) Quotients between the numbers of trees in successive size classes. q is the hypothetically stable community.

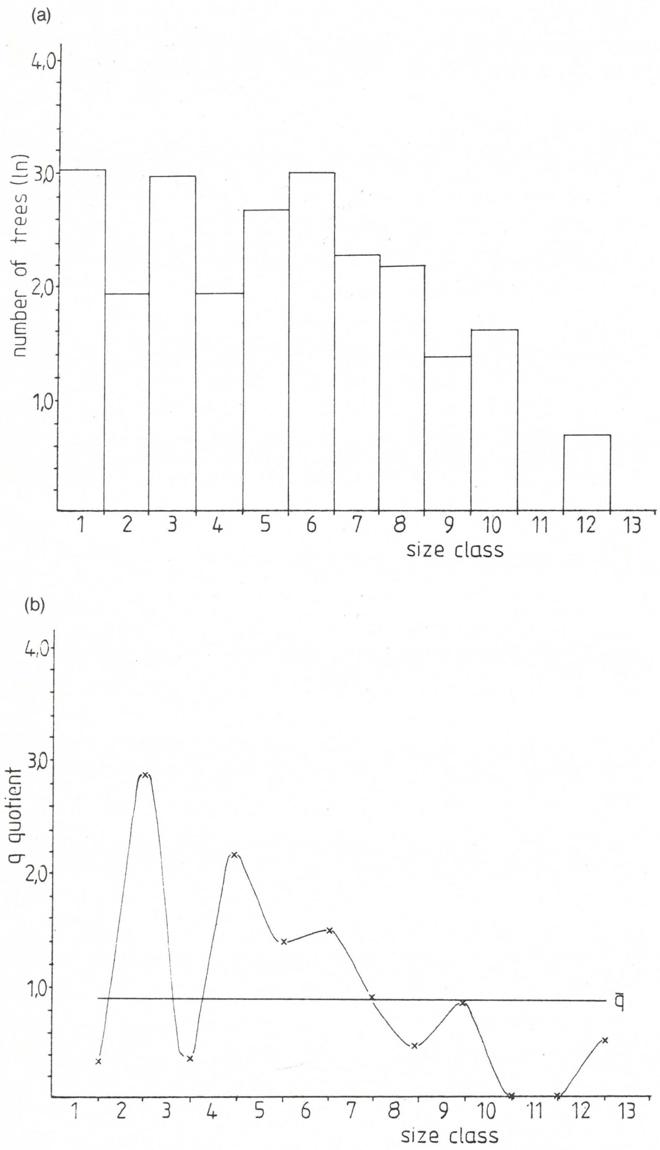

Figure 7 Population size structure of *Acacia nilotica*. (a) Numbers of trees per size class. (b) Quotients between the numbers of trees in successive size classes. q is the hypothetically stable community.

marked decline in the numbers of individuals in the larger size classes (Figure 7b). Although 57% of the seedlings were found to occur on the periphery of the patches, other data (Walker & Weighill 1981) show that *Acacia* seedlings do not establish successfully on soils which are found in the *Burkea* savanna at Nylsvley and vice versa for *Burkea* seedlings on soils in the *Acacia* patches. It is therefore unlikely that the patches will increase or decrease in size under the present soil moisture and nutrient regime.

The future population structures of all six species will vary over time, even if management and climate have no effect. The degree to which they will be different is indicated by the variability in their current size structures. Although the differences in numbers per size class will be modified by different rates of growth of individuals within cohorts of the same age, the future numbers of trees in the various classes will change. This has obvious consequences for the interpretation of vegetation monitoring programmes.

Five of the six species (the exception being *Sclerocarya birrea*) display an approximately stable size structure, in that there is no clear evidence of either an increasing or decreasing trend. Each of them demonstrates, to a greater or lesser extent, past disturbances, borne out by the inverse relationship between coppicing and the relative abundance of the size class concerned, and by the uneven plots of the quotients for successive size classes.

Sclerocarya birrea is not regenerating, and has not done so for many (15 – 20?) years. The fruits are well distributed, but the seeds are heavily parasitized. They apparently germinate and establish best in disturbed soil, but the young seedlings are highly palatable, and in recent years none that we could find have survived.

Acknowledgements

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