

SUCCESSIONAL DYNAMICS IN AN *ACACIA NILOTICA*-*EUCLEA DIVINORUM* SAVANNAH IN SOUTHERN AFRICA

T. M. SMITH*†§ AND P. S. GOODMAN†‡

*Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, Tennessee, U.S.A.; †Centre for Resource Ecology, University of Witwatersrand, Johannesburg, and ‡Natal Parks Board, Pietermaritzburg, Natal, South Africa

SUMMARY

(1) Three sites were chosen to examine the relationships in time and space between *Acacia nilotica*, a microphyllous, deciduous tree and *Euclea divinorum*, an evergreen shrub. The succession in dominance from *Acacia nilotica* to *Euclea divinorum* was a function of differences in the timing and distribution patterns of seedling establishment.

(2) Establishment of *Acacia nilotica* seedlings was restricted to open areas with no woody canopy covers, whereas both the distribution of seed and seedling establishment of *Euclea divinorum* was limited to areas beneath the canopies of established *Acacia* individuals.

(3) The spatial pattern of established *Acacia nilotica* was a function of within-species competition. Individuals were regularly dispersed, and there was a significant positive correlation between the nearest-neighbour distance and the combined size of the nearest-neighbour pair.

(4) *Euclea divinorum* individuals were aggregated, with patches corresponding to the area over which *Acacia nilotica* projected canopy cover. However, there was a positive correlation between the nearest-neighbour distance and the combined size of the nearest-neighbour pair for within-species comparisons, suggesting the importance of competition (within species) on the spacing pattern of *Euclea* within patches.

(5) *Euclea divinorum* shrubs were found to be regularly dispersed within patches when the dispersion index (R) was recalculated with density based only on the area of *Acacia nilotica* canopy cover.

(6) There was no significant correlation between nearest-neighbour distance and combined size for mixed-species nearest-neighbour pairs of *Acacia nilotica* and *Euclea divinorum*.

(7) The role of disturbance in species replacement in time is discussed.

INTRODUCTION

Examination of the distribution of woody seedling establishment in the *Acacia* savannah of southern Africa (Smith & Walker 1983; Smith & Goodman 1986) has revealed a marked absence of *Acacia* seedling establishment under the canopies of established trees, whereas many other woody species are 'tolerant' of tree cover. The distribution of seedling establishment for these species is either clumped (associated with under-canopy environments) or independent of the established trees. Unlike the microphyllous, deciduous *Acacia* spp., the species that become established in under-canopy environments are either broadleaf-deciduous or evergreen. Smith & Walker (1983), and Smith & Goodman (1986) have hypothesized that the observed spatial and temporal differences in

§ Present address: Department of Environmental Biology, Research School of Biological Sciences, Australian National University, Canberra, ACT, Australia.

seedling establishment result in a transition of the microphyllous *Acacia* spp. community to a stand dominated by evergreen and deciduous-broadleaf species.

This study examines the effects of differential spatial and temporal patterns of seedling establishment on the dynamics of a savannah community, and focuses on the interactions of *Acacia nilotica*, a microphyllous-deciduous tree species, and *Euclea divinorum*, an evergreen shrub.

THE STUDY SITES

The study was conducted in Mkuzi Game Reserve (27°30′–27°45′S, 32°05′–32°25′E; altitude 30–480 m) situated on the coastal plain in northeastern Natal, South Africa, approximately 40 km west of the coast.

The Reserve is located in the summer rainfall region and has a median annual rainfall of 610 mm and a range (1952–83) of 316–1048 mm. There is a single wet season lasting, on average, from October to March with the highest rainfall occurring in February. The mean annual temperature is 23.2 °C with maximum summer temperatures reaching 45 °C. Winters are warm with a mean daily temperature of 18.8 °C and absolute minimum of 5.5 °C.

The soils vary widely from sands to heavy clays. The geology and soils of the Reserve have been described by Goodman (1985).

Three sites were chosen to represent a successional sequence from *Acacia nilotica* to *Euclea divinorum*. Site 1 was a mature stand of *Acacia nilotica* in which *Euclea divinorum* seedling establishment was occurring. Site 2 was transitional with mature *Acacia nilotica* and *Euclea divinorum*. Site 3 was a stand of mature *Euclea divinorum* interspersed with standing dead *Acacia nilotica*. The sites were similar in soil properties and slope position, minimizing variation due to site factors. Within each site, a 60 m × 60-m sample plot was established for vegetation analyses.

METHODS

A census of all woody plants was taken in each sample plot. In all cases, more than 95% of the individuals were of the two species under study. Therefore, all further sampling and analyses refer to data on *Acacia nilotica* and *Euclea divinorum* only. Individuals were classified as either trees (*Acacia nilotica* > 1 m height), shrubs (*Euclea divinorum* > 1 m height) or seedlings (all individuals ≤ 1 m height). To save repetition, *Acacia nilotica* and *Euclea divinorum* will be referred to by their generic names only.

Seedling establishment

To examine the patterns of seedling establishment by *Acacia* and *Euclea* relative to the canopy cover of trees, the species, height and distance to the bole of the nearest tree were recorded for each seedling on Site 1. The relative position of each seedling with respect to canopy cover was calculated by dividing the distance from the bole by the radius of the canopy (nearest-neighbour tree). The seedlings were divided into two groups: beneath tree canopy (values ≤ 1.0) and areas with no tree canopy cover (values > 1.0). The under-canopy observations were then further subdivided (0.0–0.2, 0.2–0.4, 0.4–0.6, 0.6–0.8, 0.8–1.0) to examine position relative to canopy cover which may represent gradients of light, moisture or nutrients from the bole of the tree to the outer edge of the canopy. The number of individuals of each species within each group was expressed as a percentage of

the total observations (> 1.0) and under-canopy sampling from an equal area.

The seeds of *Euclea divinorum* and *Acacia nilotica* were used to examine the distribution of seeds on the *Euclea* fruits. The seeds of *Euclea* trees was examined using a quadrat, the soil to a depth of 5 cm. The distribution of seeds was tested using a chi-square sta-

The importance of canopy cover was examined using a chi-square test (Smith & Grant 1987; Fuentes 1979; Phillips 1991).

For each tree and shrub, the size was calculated as if the tree were a cylinder and the minor axes of the canopy cover of the nearest neighbour species comparisons were made for opposite species. The results were correlated (Pearson product-moment correlation; Pielou 1960, 1962) to determine the significance of the relationship.

The nearest-neighbour distance was used to determine the significance of the relationship between shrubs (Sites 2 and 3).

The size (i.e. height) of the trees was measured in modes corresponding to the height classes (1–2 m, 2–3 m, 3–4 m, 4–5 m, 5–6 m, 6–7 m, 7–8 m, 8–9 m, 9–10 m).

In contrast, *Euclea* is represented in the 1–2-m class on Site 1 and in the 2–3-m class on Sites 2 and 3.

Acacia seedlings were classified as either beneath canopy (relative positions > 1.0) or above canopy (relative positions < 1.0) (Fig. 1).

There was a significant difference ($P < 0.0001$), with seedlings beneath canopies rather than above.

the total observations for that species. Percentages were corrected for differences in open (> 1.0) and under-canopy (≤ 1.0) areas sampled; therefore, each of the groups represents sampling from an equal area.

The seeds of *Euclea* are dispersed by birds and small mammals, and the canopies of *Acacia* trees are used as perching and roosting sites by many of the bird species that feed on the *Euclea* fruits. The distribution of seeds relative to the canopy cover of established trees was examined using one hundred 25 cm \times 25-cm quadrats (Site 1) randomly located both under canopies of *Acacia* trees and in areas with no tree canopy cover. In each quadrat, the soil to a depth of 2.5 cm was collected and sifted for *Euclea* seed. The distribution of seeds between under-canopy and open areas of the site was compared using a chi-square statistic.

Spatial pattern of trees and shrubs

The importance of competition in the distribution of trees and shrubs on the study sites was examined using both dispersion analysis (Cottam 1955; Phillips & MacMahon 1981; Smith & Grant 1987) and nearest-neighbour analysis (Pielou 1960, 1962; Gutierrez & Fuentes 1979; Phillips & MacMahon 1981; Smith & Goodman 1986).

For each tree and shrub, height and stem diameter(s) were measured. Canopy cover was calculated as if the canopy were an ellipse: $C = 0.25 ab\pi$, where a and b are the major and minor axes of the canopy. For within-species comparisons, the distance to and canopy cover of the nearest-neighbour of the same species were recorded. For between-species comparisons the same data were collected for the nearest-neighbour of the opposite species. The sum of the canopy areas of the nearest-neighbour pair was then correlated (Pearson product moment) with the corresponding nearest-neighbour distance (Pielou 1960, 1962) for both within and between-species comparisons.

The nearest-neighbour based Clarke & Evans (1954) dispersion index (R) was used to determine the significance of departure from randomness for both trees (Sites 1 and 2) and shrubs (Sites 2 and 3).

RESULTS

Size-class distributions

The size (i.e. height) class distributions of *Acacia* on Sites 1 and 2 were bimodal with modes corresponding to seedlings (≤ 1 m height) and trees greater than 3 m height (Fig. 1). On Site 3 the *Acacia* population comprised only seedlings and standing dead trees.

In contrast, *Euclea* is represented almost exclusively by seedlings, with a few individuals in the 1–2-m class on Site 1 (Fig. 1). The size class distribution is shifted toward increasing size on Sites 2 and 3 with very little seedling (≤ 1 -m height class) recruitment.

Seedling establishment

Acacia seedlings were found almost exclusively in areas with no woody canopy cover (relative positions > 1.0), with a few individuals at the outer edge of the canopies (relative position 0.8–1.0) (Fig. 2). In contrast, *Euclea* seedlings were found only beneath the canopies of *Acacia* trees (Fig. 2).

There was a significant difference in the density of *Euclea* seeds ($\chi^2 = 218.90$, $P < 0.0001$), with seeds found almost exclusively in soil samples from beneath tree canopies rather than areas of no canopy cover.

Successional dynamics in savannah

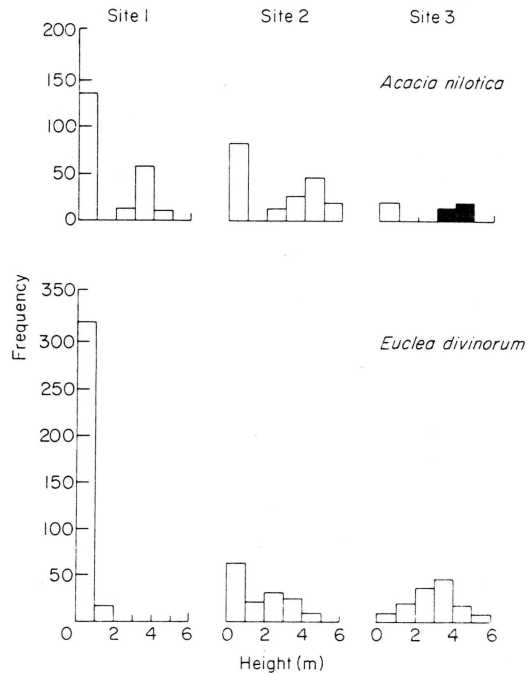


FIG. 1. Size class distributions of *Acacia nilotica* and *Euclea divinorum* on the three study sites in Mkuzi Game Reserve, South Africa. Solid bars are standing dead material

Spatial pattern of trees and shrubs

Because of the absence of *Euclea* shrubs on Site 1 and living *Acacia* trees on Site 3, between-species nearest-neighbour comparisons were possible on Site 2 only. *Acacia* trees on Sites 1 and 2 were regularly dispersed ($R=1.289$, $P<0.001$ for Site 1, and $R=1.210$, $P<0.01$ for Site 2). There were also significant positive correlations between the nearest-

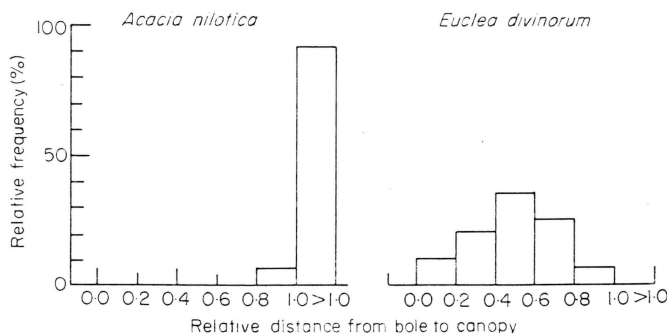


FIG. 2. Distribution of seedlings on Site 1 (Mkuzi Game Reserve, South Africa) relative to established *Acacia nilotica* canopy cover. The number of individuals is expressed as a percentage of the total number of observations. The distance is relative to the position of the seedling with respect to the bole (position 0) and outer edge of the canopy (position 1).

neighbour distance and
($r=0.68$, $n=72$, $P<0.0$

Euclea individuals c
distribution of *Euclea* :
Acacia trees. However,
neighbour distance an
($r=0.85$, $n=69$, $P<0.0$
tant role in the spatial
hypothesis, the dispers
based only on the area
Euclea was found to be

There was no signific
combined canopy cover
 $n=70$, $P=0.24$).

There was a signific
the combined cover of
 $P<0.001$). As was the
 $P<0.001$). It was not p
remaining stumps and
within the original patc

The three sites can be
nilotica savannah to a
from the size-class distr
absence of temporal sl
arid environments (H
succession is associat
canopy environments.
their establishment an
canopy species (Hust
studied to resource av
observed differences in
(or lack thereof).

The distribution of
differences in seedling
broadleaf-deciduous a
Smith & Goodman (c
environments is mos
established trees (unpu
S. Taylor, personal co
germination below tre
under tree canopies co
unpublished data).

There are two poss
merely a function of
associated with under-

neighbour distance and the combined canopy cover of the nearest-neighbour pair ($r=0.68$, $n=72$, $P<0.001$ for Site 1, and $r=0.66$, $n=58$, $P<0.001$ for Site 2).

Euclea individuals on Site 2 were aggregated ($R=0.719$, $P<0.001$) because the distribution of *Euclea* shrubs was limited to patches corresponding to the canopies of *Acacia* trees. However, there was a significant positive relationship between the nearest-neighbour distance and the combined canopy cover of the nearest-neighbour pair ($r=0.85$, $n=69$, $P<0.001$), suggesting that within-species competition plays an important role in the spatial pattern of individuals within patches. To examine further this hypothesis, the dispersion index (R) was recalculated, with the density of individuals based only on the area of *Acacia* canopy cover. On the basis of the recalculated density, *Euclea* was found to be regularly dispersed ($R=1.17$, $P<0.05$).

There was no significant correlation between the nearest-neighbour distance and the combined canopy cover for mixed-species nearest-neighbour pairs on Site 2 ($r=-0.15$, $n=70$, $P=0.24$).

There was a significant positive correlation between the nearest-neighbour distance and the combined cover of the nearest-neighbour pair for *Euclea* on Site 3 ($r=0.57$, $n=101$, $P<0.001$). As was the case with Site 2, *Euclea* had an aggregated dispersion ($R=0.300$, $P<0.001$). It was not possible to reconstruct the original area of the canopy cover from remaining stumps and standing dead *Acacia* individuals, so the dispersion of *Euclea* within the original patches corresponding to the *Acacia* canopies could not be calculated.

DISCUSSION

The three sites can be interpreted as representing a successional sequence from *Acacia nilotica* savannah to a stand dominated by *Euclea divinorum*. This sequence is evident from the size-class distributions. The change in dominance observed is in contrast with the absence of temporal shifts in species composition (i.e. succession) reported from more arid environments (Hanes 1971; Noy-Meir 1973; Zedler 1981). The appearance of succession is associated with the presence of species with the ability to establish in under-canopy environments. Therefore, these species must exhibit adaptations which allow for their establishment and growth under conditions which restrict the regeneration of the canopy species (Huston & Smith 1987). The differences in the responses of the two species studied to resource availability (both above and below ground) are evident from the observed differences in their patterns of seedling establishment and spatial interactions (or lack thereof).

The distribution of seedlings relative to tree canopy cover is consistent with the differences in seedling establishment between microphyllous *Acacia* and many of the broadleaf-deciduous and evergreen species reported by Smith & Walker (1983), and Smith & Goodman (1986). The absence of *Acacia* establishment in under-canopy environments is most likely due to competition for below-ground resources from established trees (unpublished data) and reduced light under tree canopies (T. M. Smith & S. Taylor, personal communication). There are generally higher rates of *Acacia* seedling germination below tree canopies; however, there is a higher mortality of new seedlings under tree canopies compared with areas between canopies (T. M. Smith & S. Taylor, unpublished data).

There are two possible explanations for the distribution of *Euclea* seedlings: (i) it is merely a function of seed distribution, or (ii) it is a function of environmental factors associated with under-canopy sites. The differences in seed density between under-canopy

and open sites suggest that the distribution of *Euclea* seedlings is a function of seed distribution. However, this does not preclude the possibility that seedling establishment is also a function of the environmental conditions under tree canopies. Under-canopy sites are associated with higher nutrient and organic carbon concentrations, rate of water infiltration and soil water holding capacity (Kennard & Walker 1973; Olsvig-Whittaker & Morris 1982). However, under-canopy sites have a higher rate of soil water depletion. Mean surface temperatures are lower under canopy cover, and reductions in irradiance have been found to exceed 80% (Kennard & Walker 1973; T. M. Smith & S. Taylor, unpublished data). *Euclea* seedlings appear to be well adapted to the shaded conditions of the under-canopy environments. Juvenile leaves are much larger than adult leaves (on average six times the surface area) and have higher chlorophyll content. The growth rate of *Euclea* seedlings is also much lower than the more shade-intolerant *Acacia* spp. (T. M. Smith, unpublished data). These adaptations may reduce the probability of survival in open areas of high irradiance, where ground temperatures can exceed 45 °C.

Acacia trees are regularly dispersed as a function of within-species competition (see Smith & Goodman 1986). Because *Euclea* seedlings establish under *Acacia* canopies, *Euclea* individuals are aggregated at the spatial scale at which the competitive interactions between *Acacia* individuals is occurring. However, at the spatial scale corresponding to the *Acacia* canopies, within-species competition is an important factor in the spacing pattern of *Euclea*.

The lack of a significant correlation between the nearest-neighbour distance and the combined size for mixed-species pairs of *Acacia* and *Euclea* need not imply a lack of competition between the two species. The average depths of lateral root extension for *Euclea* and *Acacia* individuals excavated on Site 2 were 10 and 24 cm, respectively. Therefore, the shallower-rooted *Euclea* may reduce the water available to the deeper-rooted *Acacia*. Although *Euclea* is a shrub, they can sometimes achieve heights equal to or greater than those of the *Acacia* under which they have established. As the *Euclea* grow through and above the *Acacia* canopy, the *Acacia* canopy is shaded and senescence occurs.

With the senescence of the *Acacia* individuals, the stand changes from one of large, regularly dispersed *Acacia* to a stand dominated by patches of *Euclea*, with the position and size of patches being a function of the original distribution of the *Acacia*. Although some *Acacia* seedling establishment occurs between the *Euclea* patches, in stands where the original density of *Acacia* individuals is high (e.g. closed-canopy woodland), the *Euclea* form a closed-canopy thicket, preventing *Acacia* seedling establishment. No *Euclea* seedling establishment has been observed under the canopies of established *Euclea* individuals, and little is known about the longevity of *Euclea*. As is the case with most evergreen tree species in southern African savannas, *Euclea* is not heavily browsed; therefore, large herbivores have little effect on mortality rates. Although frequent fires can be used to limit the establishment of *Euclea* (P. S. Goodman, unpublished data), where thickets are formed, the availability of potential fuel is low and there is little mortality of established individuals.

Insight into the long-term dynamics of the vegetation of the Reserve has been gained by examining aerial photographs from 1930 to present (Goodman 1985). With the elimination of elephant in the region, there has been an increase in the density of large *Acacia* trees in the areas dominated by *A. nilotica* and *A. tortilis*, followed by an increase in the establishment of *Euclea*. At present, many of the areas once dominated by *Acacia* species are now dominated by *Euclea* thickets. It may well be that the absence of elephants

has acted as a 'disturbance' that allows seedling establishment to occur. Preliminary data suggest that the disturbance in the past may have acted as a 'disturbance' either be direct, through the interaction of reduced fire frequency, or indirectly through the interaction of reduced fire frequency (Eltringham 1979).

This hypothesized disturbance is an interpretation of the role of disturbance at the individual scale, for the individual tree. However, disturbance dynamics, such as disturbance frequency and disturbance at one level.

The results of the present study are at a larger scale of observation (the landscape scale) in savannah systems. A major question is the relative importance of various disturbance patterns in savannas in controlling the dynamics of the system.

We thank Mary Ware, Grossman, B. O'Regan and D. Upton for their assistance in the field; and D. Upton for his comments on the manuscript.

Research was supported by the U.S. National Science Foundation.

- Allen, T. F. H. & Starr, T. B. (1972). *World Wildlife and the Threat of Extinction*. Yale University Press, New Haven, CT.
- Clark, P. J. & Evans, F. C. (1954). A method of combining the nearest neighbour method with the quadrat method. *Biometrika*, **41**, 175-189.
- Cottam, G. (1955). *The Measurement of Biological Populations*. Report, Office of Naval Research, Washington, DC.
- Eltringham, S. K. (1979). *The Ecology of the Savanna*. Ph.D. dissertation, University of Cambridge.
- Gutierrez, J. R. & Fuentes, C. (1979). *Leguminosae savannas of the Puna region, Bolivia*. Ph.D. dissertation, University of Cambridge.
- Hanes, T. L. (1971). Successional dynamics of a savanna woodland in the Kruger National Park, South Africa. *Journal of Ecology*, **59**, 521-532.
- Huston, M. & Smith, T. M. (1987). *Successional Dynamics in a Savanna Woodland*. Ph.D. dissertation, University of Cambridge.
- Kennard, D. G. & Walker, L. A. (1973). The vegetation of the vicinity of Fort Victoria, South Africa. *Journal of Ecology*, **61**, 25-51.
- Noy-Meir, I. (1973). Desert and savanna. *Journal of Ecology*, **61**, 25-51.
- Olsvig-Whittaker, L. & Morris, J. (1982). *South African Journal of Botany*, **48**, 1-15.
- Phillips, D. L. & MacMahon, J. D. A. (1981). *Journal of Ecology*, **69**, 97-115.

has acted as a 'disturbance' to the *Acacia* communities. If *Euclea divinorum* seedling establishment occurs only in under-canopy environments in these communities, as preliminary data suggest, the turnover rate of large *Acacia* trees due to elephants in the past may have acted as a factor restricting *Euclea* seedling establishment. The effect could either be direct, through the reduction of establishment sites, or indirect, as a function of the interaction of reduced tree cover—increased grass production—increased frequency of fires (Eltringham 1979; Smart, Hatton & Spence 1985).

This hypothesized sequence of events points to the need for re-evaluating our present interpretation of the role of disturbance (e.g. from fire and herbivores) in savannahs. At the individual scale, fire or elephant damage has a negative effect—mortality of an individual tree. However, at the scale of the population, in the context of community dynamics, such disturbance is essential for the maintenance of species dominance. Disturbance at one level may be a stabilizing force at another (Allen & Starr 1982).

The results of the present study have shown the importance of choosing the appropriate scale of observation (temporal and spatial) when inferring process from pattern in savannah systems. A more careful consideration of scale in the interpretation of observed patterns in savannas may well shed light on the current discussions concerning the relative importance of various factors (i.e. disturbance, resource abundance, resource partitioning) in controlling the physiognomic structure of savannah systems.

ACKNOWLEDGMENTS

We thank Mary Ward for assistance with data collection; Professor B. Walker, D. Grossman, B. O'Regan, B. Page and D. Weinstein for helpful discussions over the course of the study; and D. Urban, M. Huston and M. Post for reviewing earlier drafts of the manuscript.

Research was supported by the University of the Witwatersrand, Natal Parks Board, and the U.S. National Science Foundation's Ecosystem Studies Program.

REFERENCES

- Allen, T. F. H. & Starr, T. B. (1982). *Hierarchy*. University of Chicago Press, Chicago.
- Clark, P. J. & Evans, F. C. (1954). Distance to nearest neighbor as a measure of spatial relationships in population. *Ecology*, **35**, 445–453.
- Cottam, G. (1955). *The Measurement of Regular Plant Distributions and Their Occurrence in Nature*. Technical Report, Office of Naval Research, University of Wisconsin, Madison.
- Eltringham, S. K. (1979). *The Ecology and Conservation of Large African Mammals*. Macmillan, London.
- Goodman, P. S. (1985). *Soil, vegetation and large herbivore relations in Mkuzi Game Reserve, Natal*. PhD dissertation, University of the Witwatersrand, South Africa.
- Gutierrez, J. R. & Fuentes, E. R. (1979). Evidence for intraspecific competition in the *Acacia craveni* (Leguminosae) savanna of Chile. *Oecologia Plantarum*, **14**, 151–158.
- Hanes, T. L. (1971). Succession after fire in the chaparral of southern California. *Ecological Monographs*, **41**, 27–52.
- Huston, M. & Smith, T. M. (1987). Plant succession, life history and competition. *American Naturalist*, (in press).
- Kennard, D. G. & Walker, B. H. (1973). Relationships between tree canopy and *Panicum maximum* in the vicinity of Fort Victoria. *Rhodesian Journal of Agricultural Research*, **11**, 145–153.
- Noy-Meir, I. (1973). Desert ecosystems: environment and producers. *Annual Review of Ecology and Systematics*, **4**, 25–51.
- Olsvig-Whittaker, L. & Morris, J. W. (1982). Comparison of certain Nylsvley soils using a bioassay technique. *South African Journal of Botany*, **1**, 91–96.
- Phillips, D. L. & MacMahon, J. A. (1981). Competition and spacing patterns in desert shrubs. *Journal of Ecology*, **69**, 97–115.