THE ROLE OF INTERACTIONS BETWEEN PERENNIALS AND ANNUALS
AS DETERMINANTS OF ANNUAL PLANT COMMUNITY STRUCTURE

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BOTANY HONOURS
1985

RESUME

Competition theory, though shrouded in controversy, suggests that competitive interactions play a major role in determining community structure. This theory has been developed almost exclusively from studies on animal communities and application to plant communities has been limited, especially locally.

Arid plant communities, being relatively simple, appeared to provide a suitable system in which to study competitive interactions. Previous work has shown interplant interactions to be important in determining spacing patterns of perennial plants in such ecosystems. But no studies had considered competitive interactions betwen annual and perennial plants and this formed the basis of the first paper.

This showed that spacing patterns and reproductive output of annuals can be significantly affected by neighbouring perennials. This idea seemed to be relevant to the production of spring annuals in Namaqualand. The performance of annuals each year would be regulated by interspecific interactions with neighbouring perennial plants. Furthermore, it seemed that the intensity of such interactions would be determined by resource availability, in particular moisture availability (although nutrients may be important too).

A model was proposed to describe variations in the annual plant community of arid and semi-arid ecosystems in which moisture plays a major role. It was possible to measure plant interactions along a moisture gradient by considering two neighbouring sites, which differed only in topography (level and a slope) and thus moisture régimes. This is described in the second paper.

Although this study can only be considered a preliminary investigation, it does provide increased understanding of the annual component of arid and semi-arid ecosystems.

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PAPER A

**INTERACTIONS BETWEEN THE PERENNIAL SUCCULENT SHRUB
(LEIPOLDTIA CONSTRICTA) AND AN ANNUAL (GORTERIA DIFFUSA)**

Running head : Interactions between perennial and annual plants

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SUMMARY

(1) Plant interactions were studied within and between a perennial
succulent shrub, (Leipoldtia constricta), and an annual (Gorteria
diffusa). These two species comprised 83% of the total plant cover in the
disturbed semi-desert community studied.

(2) Correlations of plant size with distance to nearest neighbour
demonstrate that intraspecific competition occurs within both
L. constricta and G. diffusa.

(3) Interspecifically, L. constricta does not exclude the annual
G. diffusa, but significantly reduces size and flower production in
neighbouring plants.

(4) Results suggest that perennials are of major importance in determining
the structure and reproductive potential of the annual component of
arid-zone plant communities.

INTRODUCTION

Quantitative investigations of desert and semi-desert vegetation indicate that biotic interactions play an important role in determining the structure of arid plant communities (Fonteyn & Mahall 1981). Plant distributions suggestive of negative interactions have been attributed to the intensification of environmental stress(es) by neighouring plants (Woodell, Mooney & Hill 1969; Yeaton & Cody 1976; Yeaton, Travis & Gilinsky 1977; Phillips & MacMahon 1981; Nobel 1981; Fonteyn & Mahall 1981). Theoretically the concept that regular spacing of plants in areas of low rainfall is caused and maintained by root competition for available water, has become widely accepted (Woodell, Mooney & Hill 1969; Fonteyn & Mahall 1981).

Most investigations have been limited to only a single species (Yeaton & Cody 1976), despite the fact that monospecific stands are unrepresentative of the majority of plant communities (Yeaton & Cody 1976; Phillips & MacMahon 1981). More recently quantitative studies concerning the spacing of individuals in multispecies communities have been published (Yeaton & Cody 1976; Yeaton, Travis & Gilinsky 1977; Phillips & MacMahon 1981; Fonteyn & Mahall 1981; Yeaton et al. 1985). In all these works only perennial species are considered, and yet a very successful component of desert plant commnities is the annual or ephemeral one (Patten 1978). Their success depends on exploitation of resources during periods when the environment is suitable for the completion of their life-cycles and their remaining dormant when it is not.

The aim of this study was to investigate the effect of the distribution of a perennial succulent shrub Leipoldtia constricta L. Bol. (Mesembryanthemaceae) on that of a small annual Gorteria diffusa Thunb. (Asteraceae). These two species are numerically co-dominant in a disturbed semi-arid plant community. The method used was that of nearest-neighbour analysis as described by Pielou (1960). The distance between a randomly chosen individual and its nearest-neighbour is recorded, together with the sum of sizes of the nearest-neighbour pair. A statistically significant, positive linear regression of size on distance is taken as evidence of a negative interaction. The specific questions asked were:

1. Do negative interactions occur between intraspecific pairs of L. constricta and G. diffusa?

2. Do negative interspecific interactions occur between G. diffusa and L. constricta individuals?

and

3. What, if any, effect do such interspecific interactions have on the reproductive potential of the annual species?

STUDY AREA

The study area was located in the Namaqualand region of the north-western Cape, c. 3 km east of Springbok (29° 40'S, 17°53'E) at an elevation of 1 000 m on a gentle (3-4°) east-facing slope. Soils are granite derived and sandy. Namaqualand receives its rain in winter (April - September). The mean annual rainfall for Springbok over an 83-year period is 224 mm (Weather Bureau 1965).

Vegetation consisted of a low, sparse cover (39%) of both succulent and non-succulent annuals and perennial shrubs. The dominant species were a low perennial succulent shrub L. constricta and a small annual G. diffusa which account for 71% and 12% of the total plant cover respectively. Minor elements were: Aptosimum leucorrhizum, Cheiridopsis candidissima, Eriocephalus ericoides, Euphorbia dregeana, Galenia africana, Hermannia trifurca, Lampranthus suavissimus, Osteospermum hyoseroides, Pentzia incana, Pharnaceum sp., Salsola kahlii, Sarcocaulon crassicaule, Tetragonia fruticosa, and Whiteheadia bifolia.

METHODS

Measurements of plant distributions

Three sets of measurements of nearest-neighbour distances (Pielou 1960) for randomly selected individuals were made.

1. Nearest-neighbour distances of randomly chosen individuals of G. diffusa were measured as the distance from stem to stem. Measurements of G. diffusa pairs were recorded only if no other plant was growing such that its canopy intersected a straight line between their bases. For the individuals of each pair, its size was measured as its diameter and its number of flowers (including developing buds and seed heads) were counted.

2. Nearest-neighbour distances were measured for randomly chosen L. constricta individuals as the distance from canopy centre to canopy centre. Seedlings and immature individuals were ignored as potential nearest neighbours. Measurements of L. constricta pairs were not recorded if any other perennial was situated such that its canopy intersected a striaght line between the canopy centres. The size of each plant was measured as its diameter.

3. Measurements were made of the G. diffusa plants growing around randomly chosen L. constricta individuals. Only G. diffusa individuals growing within a 1 m radius from the centre of each L. constricta bush and with no intervening plants of any species, were considered. For these individuals size, number of flowers and distance from the shrub canopy centre were recorded.

Plant canopy cover data were measured by the line intercept method for five randomly placed 5 m lines.

Data analysis

For pairs of both L. constricta and G. diffusa individuals linear regressions of the sum of sizes against nearest-neighbour distance were calculated. In addition a linear regression of sum of flowers against nearest-neighbour distance was calculated for G. diffusa pairs.

In order to investigate interspecific interactions linear regressions of first size and second number of flowers of G. diffusa individuals against the ratio, distance of G. diffusa individual from L. constricta centre to size of L. constricta shrub, (R) were calculated. In addition histograms were drawn of (a) number of individuals, (b) number of flowers and (c) the number of flowers per plant, for G. diffusa individuals at various distances from the edge of L. constricta canopies.

RESULTS AND DISCUSSION

Evidence for competition between plants is given by nearest-neighbour distances being greater for pairs of larger combined size (Pielou 1960, 1962). Reviewing studies utilizing nearest-neighbour analyses it becomes quite obvious that biotic interactions are potentially of major functional importance in the structuring of arid-zone plant communities. In this study linear regressions calculated for sum of plant sizes against nearest-neighbour distance for pairs of both G. diffusa ($P < 0,0005$) and L. constricta ($P < 0,0005$) indicate that intraspecific competition is occurring for both species (Fig. 1). A further indication of negative interaction between G. diffusa pairs is provided by the positive correlation ($P < 0,0005$) between combined number of flowers and nearest-neighbour distance (Fig. 2).

Interspecific negative interactions between the annual and perennial are indicated by positive correlations for both size of annual ($P < 0,0005$) and number of flowers of annual ($P < 0,005$) against the ratio R of distance of annual from perennial centre to perennial size (Fig. 3).

Further evidence of interspecific interaction is provided by analyzing the distribution and performance of the annuals relative to the positioning of the perennials (Fig. 4). The decrease in number of annuals with increasing distance from the perennial canopy edge (Fig. 4a) can be attributed to interference by other plants. Most flowers are produced by annuals between 30 and 40 cm from the perennial canopy edge (Fig. 4b) despite the small contribution of this group in terms of number of plants. The number of flowers per annual individual at different distances from the perennial canopy edge are shown in Fig. 4c. Low values for annuals less than 30 cm from the canopy edge are indicative of competitive interaction, whilst the low values more than 70 cm beyond the canopy edge can be attributed to the effects of neighbouring plants. Thus although G. diffusa annuals are not excluded from beneath the canopies of L. constricta perennials, nor their immediate vicinity, their productivities (size and number of flowers) are adversely affected by proximal L. constricta individuals.

This study represents the initial phase of detection and analysis of distribution patterns of these two species. While such descriptions and inferences are valuable they do not test for controlling mechanisms or directly 'measure' the extent of interactions (Fonteyn & Mahall 1981). For this reason it would be desireable to supplement this work with experimental data such as removal or relative yield experiments. Nevertheless indications are that perennials are of prime importance in determining the structure and function of the annual component in arid-zone communities. We suggest that this effect is manifested primarily through the intensification of root competition for available water.

ACKNOWLEDGEMENTS

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A

LEGENDS TO FIGURES

Fig. 1.   Relationships between nearest-neighbour distances and the sum of sizes for (a) pairs of G. diffusa, $y = 59,29 + 0,52\ x$, (b) pairs of L. constricta, $y = 38,28 + 0,58\ x$.

Fig. 2.   Relationship between nearest-neighbour distance and the sum of flower numbers for pairs of G. diffusa, $y = 4,53 + 0,12\ x$.

Fig. 3.   Relationships between ratio R (distance between G. diffusa and L. constricta individuals to size of L. constricta individuals) and (a) size of G. diffusa individuals, $y = 8,26 + 17,43\ x$, and (b) number of flowers of G. diffusa individuals, $y = 0,34 = 2,72\ x$.

Fig. 4.   The effects of L. constricta on G. diffusa: (a) number of G. diffusa individuals; (b) total number of G. diffusa flowers; and (c) the number of flowers per G. diffusa individual, against distance from L. constricta canopy edge.
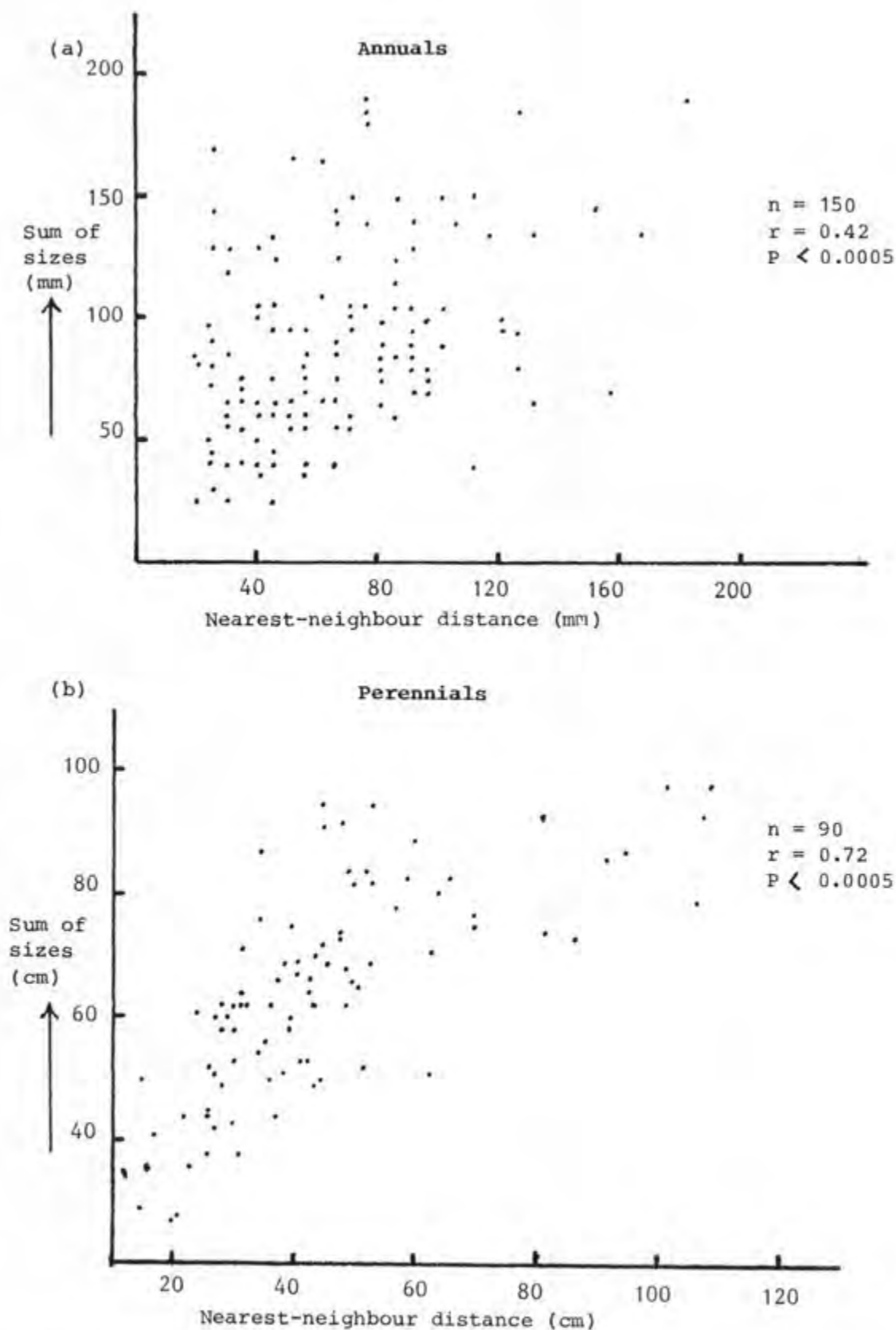
Figure 1. Relationships between nearest-neighbour distances and the sum of sizes for:
(a) pairs of $\underline{G}$. $\underline{diffusa}$, $y = 59.29 + 0.52x$
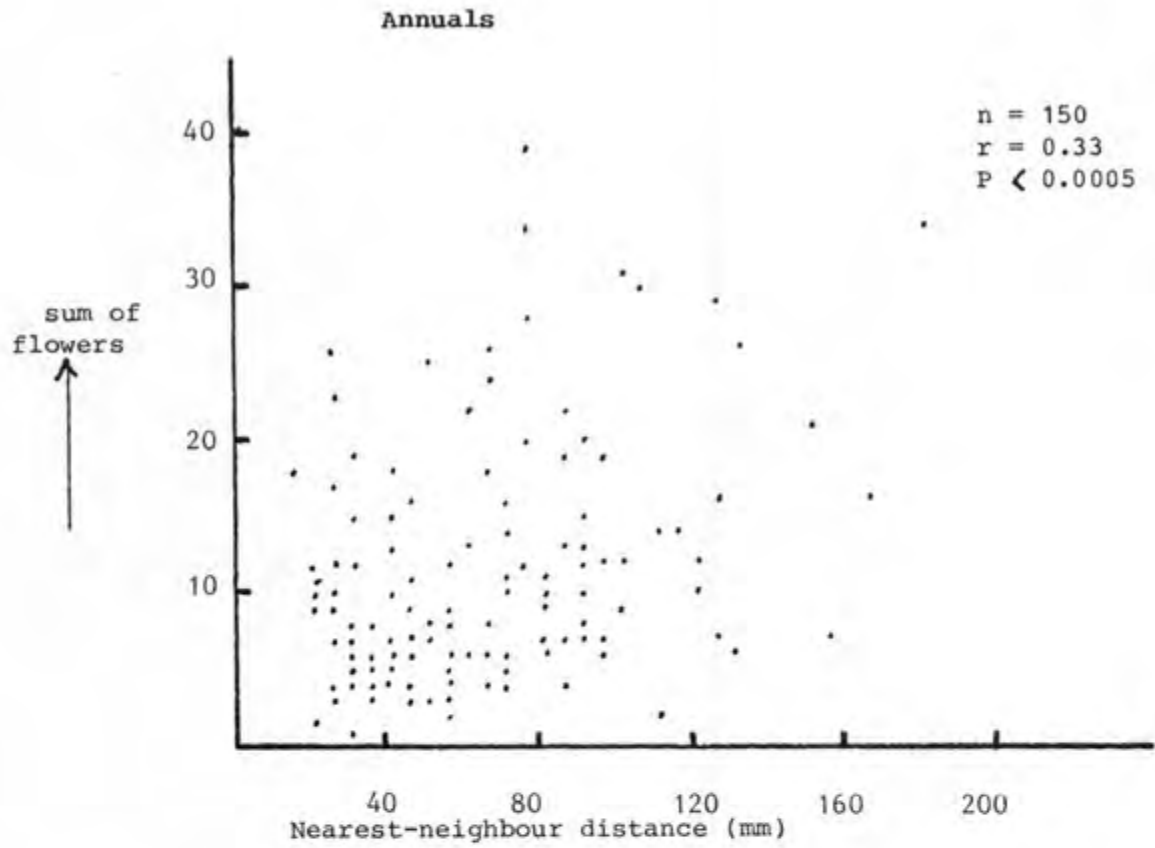(b) pairs of $\underline{L}$. $\underline{constricta}$, $y = 38.28 + 0.58x$.

A

Figure 2. Relationship between nearest-neighbour distance and the sum of flower numbers for pairs of G. diffusa, y = 4.53 + 0.12x.
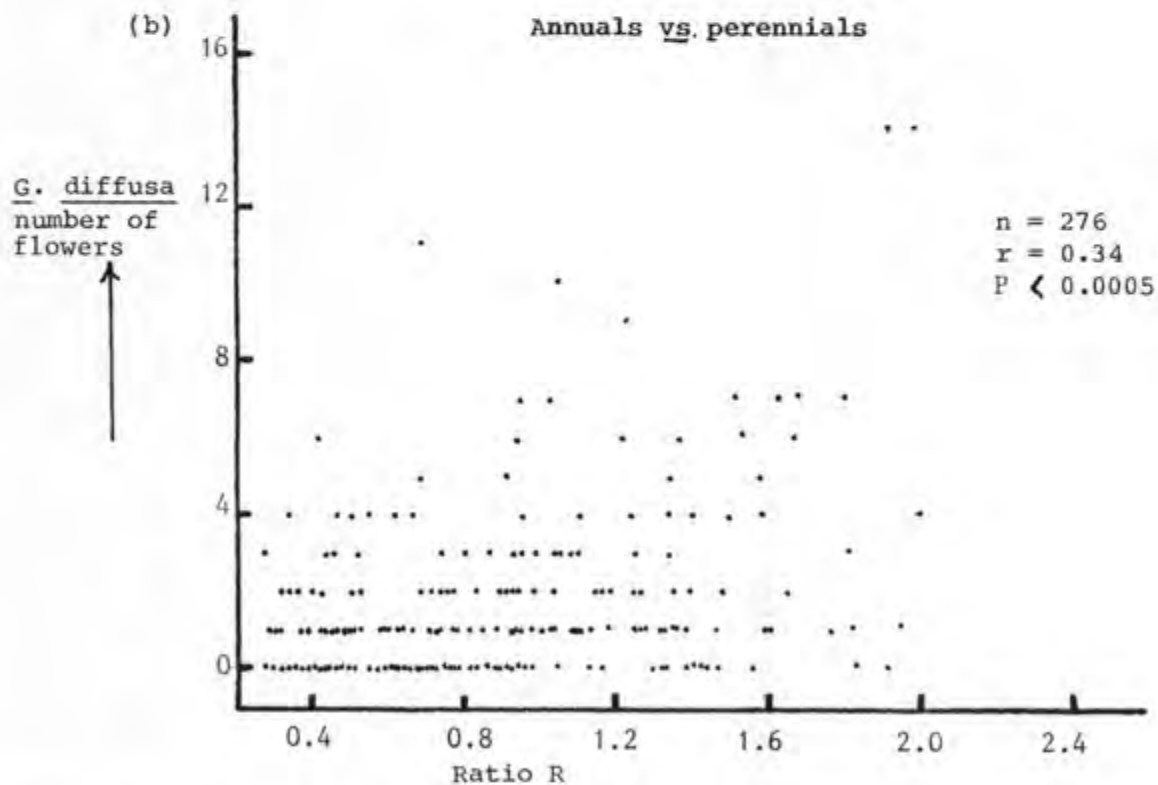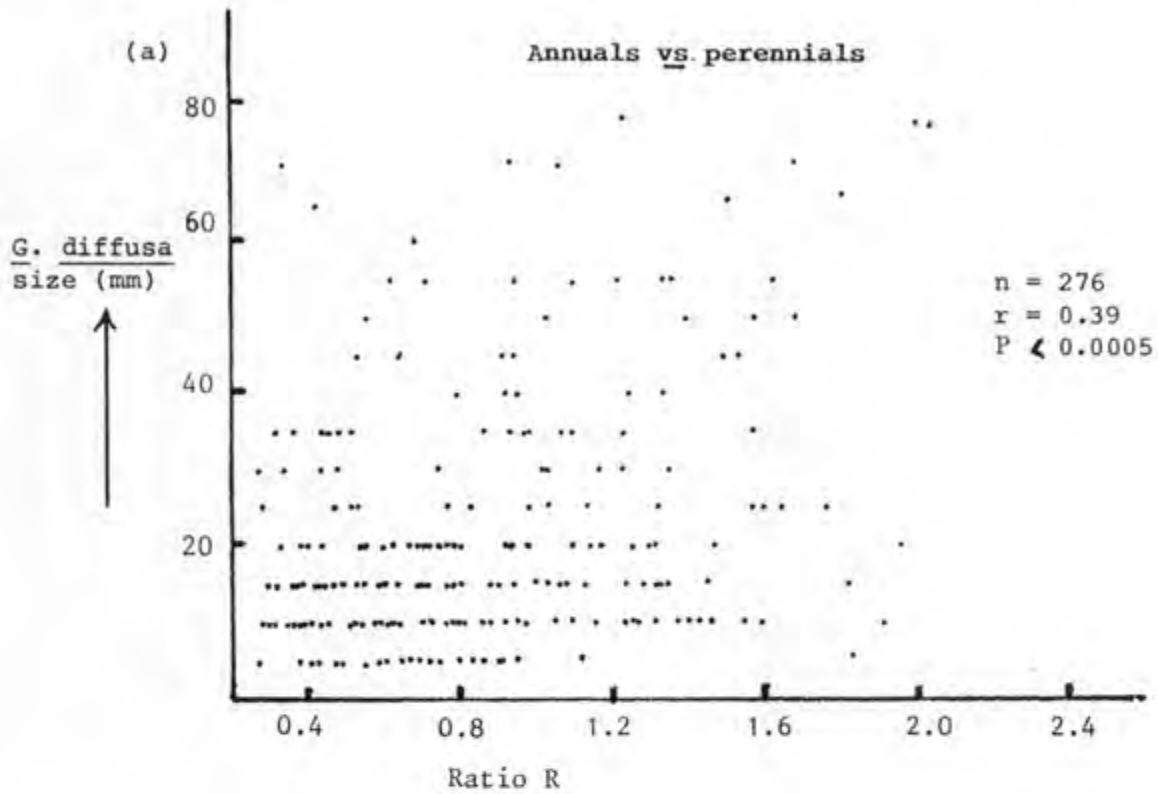
Figure 3. Relationships between ratio R (distance between G. diffusa and
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and (a) size of G. diffusa individuals y = 8.26 + 17.43x and
(b) number of flowers of G. diffusa individuals,
y = 0.34 + 2.72x.
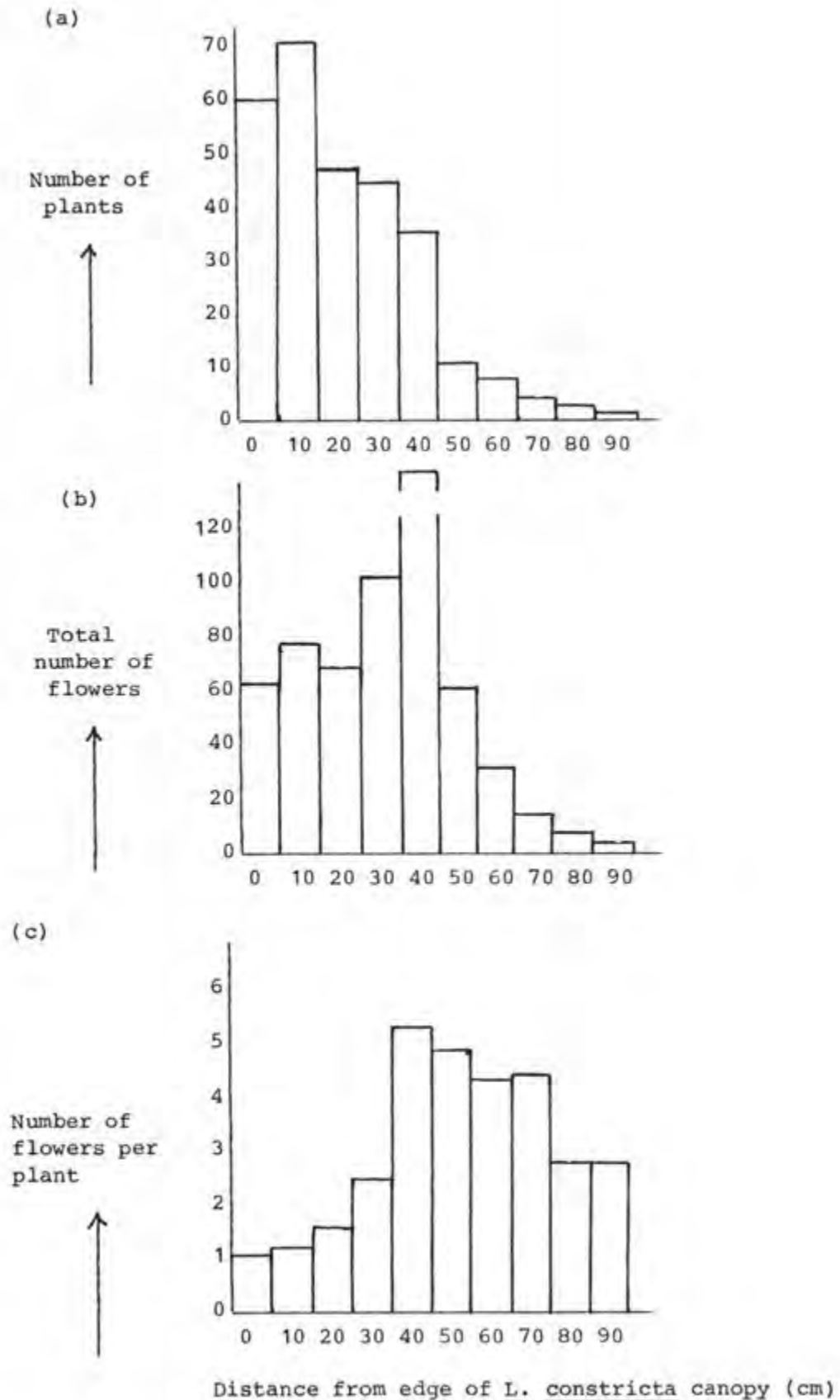
Figure 4. The effects of L. constricta on G. diffusa:
            (a) number of G. diffusa individuals;
            (b) total number of G. diffusa flowers; and
            (c) the number of flowers per G. diffusa individual
                against distance from L. constricta canopy edge.

PAPER B

A PROPOSED MODEL OF YEAR-TO-YEAR VARIATION
IN ANNUAL PLANT COMMUNITY STRUCTURE

Running head : A model of annual plant community structure

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SUMMARY

(1) A model is proposed which describes the year-to-year variation in the structure of the annual species component of arid and semi-arid communities. Variation is described in terms of total annual rainfall which determines both the availability of space and the intensities of intraspecific and interspecific plant interactions.

(2) In order to test this model spacing patterns and plant interactions were quantified in a recently disturbed semi-arid community at two neighbouring sites which differ in topographies and moisture regimes. Dominant species at both sites were a perennial succulent shrub (Conicosia capensis) and an annual (Adenogramma glomerata).

(3) Foliage projected cover data indicates that more space is available to annuals at the drier site on the slope.

(4) Comparisons of nearest neighbour pairs of C. capensis indicate that intraspecific interactions are important in determining the size and spacing patterns of these perennials, at both sites.

(5) Intraspecific comparisons of nearest neighbour pairs of A. glomerata indicate that intraspecific interactions are not important in determining the structure of the annual plant community, at either site.

(6) Interspecific nearest neighbour comparisons provide no evidence for interspecific interactions between the perennial C. capensis and the annual A. glomerata at either site.

(7) Results are interpreted with respect to the proposed model and possible reasons for incompatibilities are discussed.

(8) Implications of this model to the management of the annual species component of arid and semi-arid ecosystems are suggested.

INTRODUCTION

Quantitative studies of plant distribution patterns indicate that biotic interactions can play an important role in determining the structure of arid and semi-arid plant commmunities. Evidence of intraspecific and interspecific competition has been inferred from correlations between nearest neighbour distances and plant sizes (Yeaton & Cody 1976; Yeaton, Travis & Gilinsky 1977; Phillips & MacMahon 1981; Fonteyn & Mahall 1981; Yeaton et al. 1985). It is suggested that these patterns are caused by root competition for available water. Investigations have largely been confined to perennial shrubs, despite the fact that annuals are known to be a successful component of these communities (Patten 1978). Recently Cunliffe & Yeaton (in preparation) have shown significant interactions between a perennial shrub and an annual, which suggests that perennials may be of major importance in determining the structure of the coexisting annual community. In this study we propose a model (Fig. 1) which describes the year-to-year variation in the structure of the annual species component of arid and semi-arid communities.

In arid and semi-arid ecosystems moisture stress inhibits the formation of a dense cover of perennials (Harper 1977; Hickman 1977; Klemow & Raynal 1983). Annual plants "fit" into the spaces between perennials and it is suggested that their productivity is limited by the amount of available space. Intraspecific and interspecific plant interactions will also be important and these are related to the availability of resources and thus to environmental variables such as the amount and timing of rainfall. In addition, space may be created by disturbances such as grazing, trampling, ploughing or severe drought.

Assuming abundant seed availability, immediately after a disturbance which has eliminated all perennial plants, the potential productivity of annual species is at a maximum (p max) and is a function of area (see Fig. 1). The extent to which this is achieved is determined by both environmental variables (particularly rainfall) and plant interactions which are themselves influenced by rainfall. Some establishment of perrenial plants will also occur, which again will be determined by rainfall. In the

second year after the disturbance the amount of space available to annuals is less than during the previous year since a portion is now occupied by perennials. The degree to which the available space is utilized is once again determined by the current year's rainfall and plant interactions.

In order to test this model, community structure and plant interactions were investigated at two sites which differed only in topography, the one being on level terrain and the other on a moderate (23°) slope. Communities at both sites (separated by less than 100m) were composed of the same species and in particular co-dominated by Conicosia capensis N. E. Br. and Adenogramma glomerata (L.f.) Druce. It was assumed that due to different topographies the two sites would differ in moisture regimes, with more moisture being available at the level site than on the slope. The level site was therefore considered to simulate high rainfall conditions for both year 1 and year 2 (ie R_1 and R_2 on Fig. 1); the site on the slope represents low rainfall conditions for both years (ie r_1 and r_2 on Fig. 1). Two seasons ago, the area was ploughed, totally destroying all existing plants. Measurements were made towards the end of the growing season in the second year after the disturbance. On the basis of the model it was predicted that:

(1) In the drier situation on the slope, more space would be available to annuals (PS_2) since perennial establishment would have been more limited than at the level (moister) site (PL_2) (See Fig. 1).

(2) Productivity of annual species would be greater on the slope (AS_2) because more space would be available at this site, than on the level (AL_2) (See Fig. 1).

(3) Intraspecific interactions between perennials would occur, which would maintain space between the perennials at both sites.

(4) Both intraspecific, and in particular, interspecific interactions with neighbouring perennials would be important in determining spacing patterns of the annual species community at both sites.

STUDY AREA

The study area was located in the winter rainfall region of the south-western Cape, South Africa, near Ysterfontein (32° 07'S, 17° 28'E). Soils are deep sands on a smoothly undulating coastal plain. The mean annual rainfall at Ysterfontein over a 25 year period is 368 mm (Weather Bureau 1965). The vegetation at the study area is West Coast Strandveld (Moll et al. 1984), although the actual study site was located in a 15 m strip which had recently been ploughed. At the time of measurements vegetation was 15 months old, and had already experienced two growing seasons. The community on this disturbed strip was co-dominated by C. capensis, either a biennial or perennial low growing succulent shrub, and A. glomerata, a stringy ground-dwelling annual herb.

METHODS

Foliage projected cover

The point sampling technique was used to measure plant foliage projected cover. Vegetation was assessed at both sites for 1000 points which were located at 10 cm intervals over 10 x 10 m lines. The lines were placed parallel to one another at one metre intervals. Vegetation was recorded as a 'hit' (any living plant matter) or a 'miss'. 'Hits' were placed into one of three categories according to the species: Conicosia, Adenogramma or 'others'. The latter category was composed almost entirely of annuals. Foliage projected cover was calculated for each category as the percentage of 'hits' out of the 1000 points at each site.

Plant interactions

The general method used was that of nearest-neighbour distances (Pielou 1960). The distance between a randomly chosen individual and its nearest neighbour is recorded together with the sum of sizes of the

nearest-neighbour pair. A statistically significant linear regression of size on distance is taken as evidence of a negative interaction.

Three sets of measurements concerning plant distributions were made at both sites.

(1) For C. capensis nearest-neighbour distances of randomly chosen individuals were measured as the distance from stem to stem. Measurements were recorded only for those pairs for which no other perennial plant was growing such that its canopy intersected a straight line between their bases. For individuals of each pair, size was measured as half its greatest diameter, and its number of flowers (including developing buds and seed heads) was counted.

(2) Plant distributions of A. glomerata were quantified by measuring nearest-neighbour distances for randomly chosen individuals, as the distance from base to base. Measurements were recorded only if no other plant was growing such that its canopy intersected a straight line between the two A. glomerata individuals. The size of an individual was measured as its greatest radius.

(3) Measurements were made of A. glomerata individuals growing around randomly chosen C. capensis individuals. In each case only those A. glomerata individuals growing such that no other plant intervened between it and the C. capensis were measured. For these individuals their size and distance from the C. capensis were recorded. In addition the size of the C. capensis plant was measured.

For pairs of both C. capensis and A. glomerata linear regressions of sum of sizes against nearest -neighbour distance were calculated. In addition linear regressions of sum of flowers against nearest-neighbour distance was calculated for C. capensis pairs. Evidence for interspecific interactions were sought by linear regressions of size of A. glomerata individuals against the ratio distance of A. glomerata individual from C. capensis centre to size of C. capensis.

RESULTS

Total plant cover was higher on the level where more moisture is available (Fig. 2). Here C. capensis formed 74% of the total plant cover as opposed to 35% on the slope. Results of Median tests (P< 0.0005) indicated that C. capensis individuals on the level were smaller, bore fewer flowers and were closer together than on the slope. Linear regressions calculated for nearest-neighbour distances against (i) sum of sizes and (ii) sum of flowers for C. capensis pairs indicate that intraspecific competition was occurring on both the level and the slope (Table 1). Correlation coefficients for the two sites are not significantly different for either sizes or numbers of flowers (Z =0.12, p =0.42; z = 0.11, p = 0.46, respectively). This suggests that a similar intensity of intraspecific interaction was occurring amongst C. capensis pairs in both situations, despite the considerable differences in plant sizes and spacing.

Foliage projected cover of the annual A. glomerata was greater on the slope (8%) than on the level (2,5%), as was its relative contribution to total plant cover (Fig. 2). Intraspecific interactions do not appear to be pronounced, although a weak, significant interaction (r = 0,29, P< 0,0025) was detected on the level (Table 1). This may be due to the fact that greatest radius was not a reliable indicator of plant performance, in which case intraspecific competition could have been present but was not detected.

Linear regressions for interspecific comparisons are not significant at either site (Table 1).

DISCUSSION

At the time of data collection vegetation had experienced two seasons of growth. During the first season of growth more C. capensis individuals established on the level where moisture availability was greater than on

the slope. Thus less space was potentially available to annuals on the level (58%) than on the slope (87%) during the second season's growth, and this is reflected by the lower foliage projected cover of annuals (Adenogramma and 'others' combined) on the level (15%) as opposed to the slope (24%). Significant intraspecific interactions between C. capensis pairs were detected at both sites, which would cause space to be maintained between these perennials. The space which is not occupied by C. capensis is utilized equally by annuals in both situations: ratios of Adenogramma and 'other' plants to available space are 0.34 on the level and 0.38 on the slope. This lends support to the idea that annual productivity is regulated by availability of space which in turn is a function of the coexisting perennial community.

Thus predictions from the model concerning space availability to annuals ($PS_1 > PL_1$), productivity of annuals ($AS_2 > AL_2$) and C. capensis intraspecific interactions are fulfilled. However no interspecific interactions between A. glomerata and C. capensis individuals were demonstrated either on the slope or the level. Neither are intraspecific interactions important in determining spacing patterns of A. glomerata individuals at either site. The lack of A. glomerata interspecific interactions and A. glomerata - C. capensis interspecific interactions has two possible explanations:

(1) The methods used were unsuitable to detect these interactions. For example perhaps greatest radius is not a reliable indicator of A. glomerata performance. Biomass might have provided a better index.

(2) Interspecific interactions with C. capensis might not have been of major importance in determining the spacing patterns of the A. glomerata individuals. Other biotic or abiotic factors might have been of greater importance such as seed availability or germination microsite requirements.

The proposed model assumes abundant seed availability for both annual and perennial species and that germination and establishment are proportional to rainfall. The applicability of these assumptions (see Harper, Williams & Sagar 1965; Louda 1982) will be important determinants as regards the relevance of the model. For example rainfall is not a simple factor, but rather comprises various influences such as the annual total and distribution in time through the year. Further understanding could be gained from experimental evidence such as removal experiments or by continued monitoring of changes in plant distributions in relation to space and resource availability (rainfall) at the study site.

These results have considerable management potential. The display of spring-annuals in the Namaqualand region of the north western Cape is already a considerable tourist attraction and has the potential for further expansion into a major industry. Understanding of the structure and function of the annual community will allow successful manipulation, such that maximum productivity may be attained. From the conservation aspect it is important that we develop some degree of understanding prior to extreme intervention lest irreparable degradation ensue.

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LEGENDS TO FIGURES AND TABLES

Table 1. Correlation coefficients for linear regressions of distance apart of nearest neighbour intraspecific and interspecific pairs of C. capensis and A. glomerata against various parameters.

Figure 1. Model illustrating how the potential productivity (P) of annual species (indicated by absolute sizes of circles) decreases with time (in years) after a disturbance. The degree to which potential productivity is realized each year (A) (shaded portions) is determined by that year's rainfall (▥ = high rainfall; ▤ = low rainfall) and the degree of interaction (both intraspecific and interspecific) between the annual and perennial components of the community. Rainfall, depicted as high (R) or low (r) , also influences the size of potential productivity for the following year.

Figure 2. Foliage projected cover of C. capensis ⊞ , A. glomerata ▦, and 'other' plant species ▨ (a) on level ground and (b) on a 23° slope.

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Table 1. Correlation coefficients for linear regressions of distance apart of nearest neighbour intraspecific and interspecific pairs of C. capensis and A. glomerata against various parameters.

Species pairs	Parameter	Level or slope	Number of pairs sampled	Correlation coefficient	Probability
C-C	≶ sizes	Level	100	0.47	< 0.0005
C-C	≶ sizes	Slope	100	0.37	< 0.0005
A-A	≶ sizes	Level	100	0.29	< 0.0005
A-A	≶ sizes	Slope	150	0.10	N.S.
C-C	≶ flowers	Level	95	0.52	< 0.0005
C-C	≶ flowers	Slope	100	0.44	< 0.0005
C-A	Ratio*	Level	93	-0.11	N.S.
C-A	Ratio*	Slope	166	-0.08	N.S.

C-C (C. capensis - C. capensis); A-A (A. glomerata - A. glomerata);
C-A (C. capensis - A. glomerata)
*Ratio = distance of A. glomerata individual from C. capensis centre to size of C. capensis.
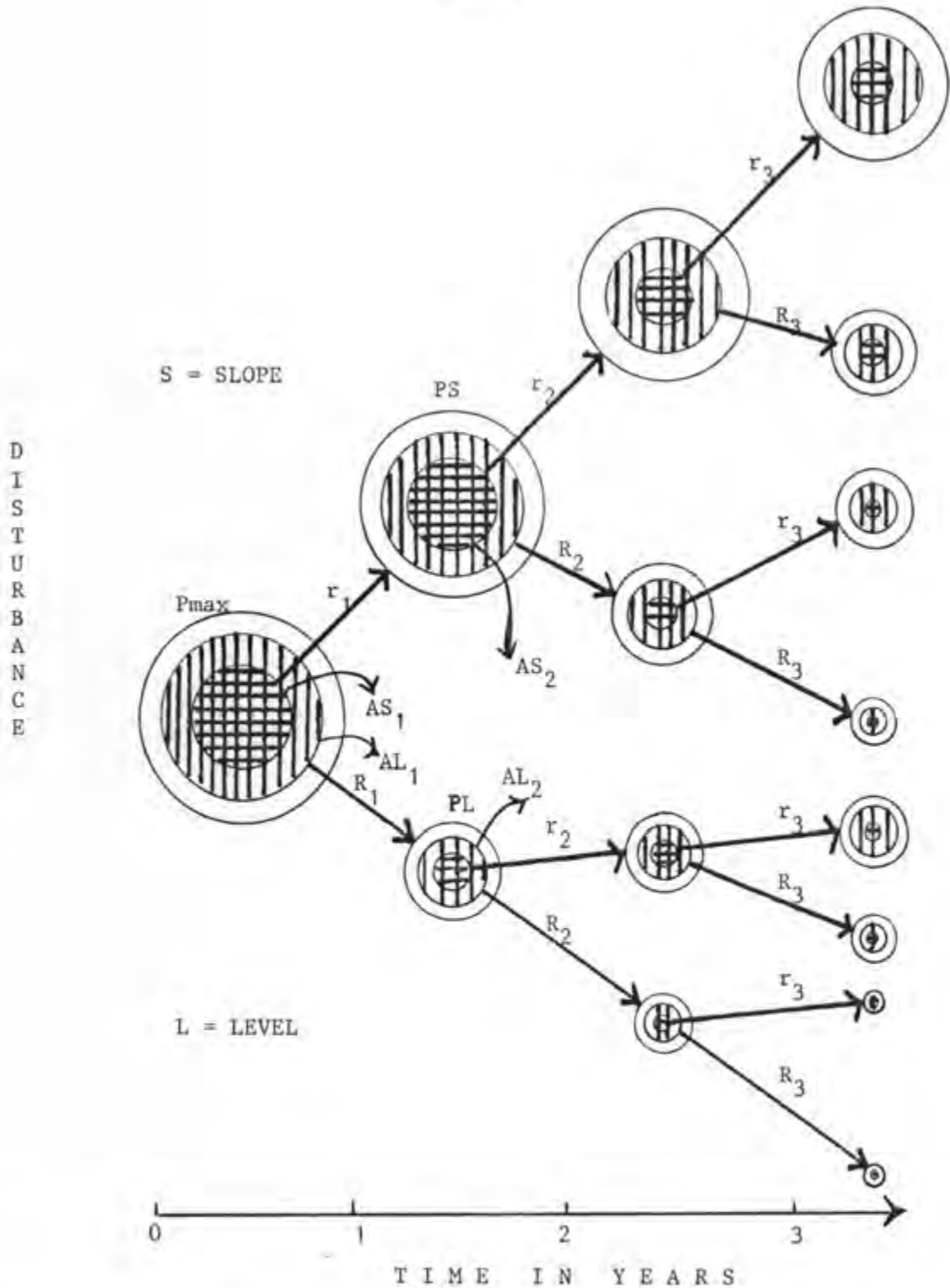N.S. = not significant (P < 0.10).

Figure 1. Model illustrating how the potential productivity (P) of annual species (indicated by absolute sizes of circles) decreases with time (in years) after a disturbance. The degree to which potential productivity is realized each year (A) (shaded portions) is determined by that year's rainfall (▥ = high rainfall; ▤ = low rainfall) and the degree of interaction (both intraspecific and interspecific) between the annual and perennial components of the community. Rainfall, depicted as high (R) or low (r), also influences the size of potential productivity for the following year.
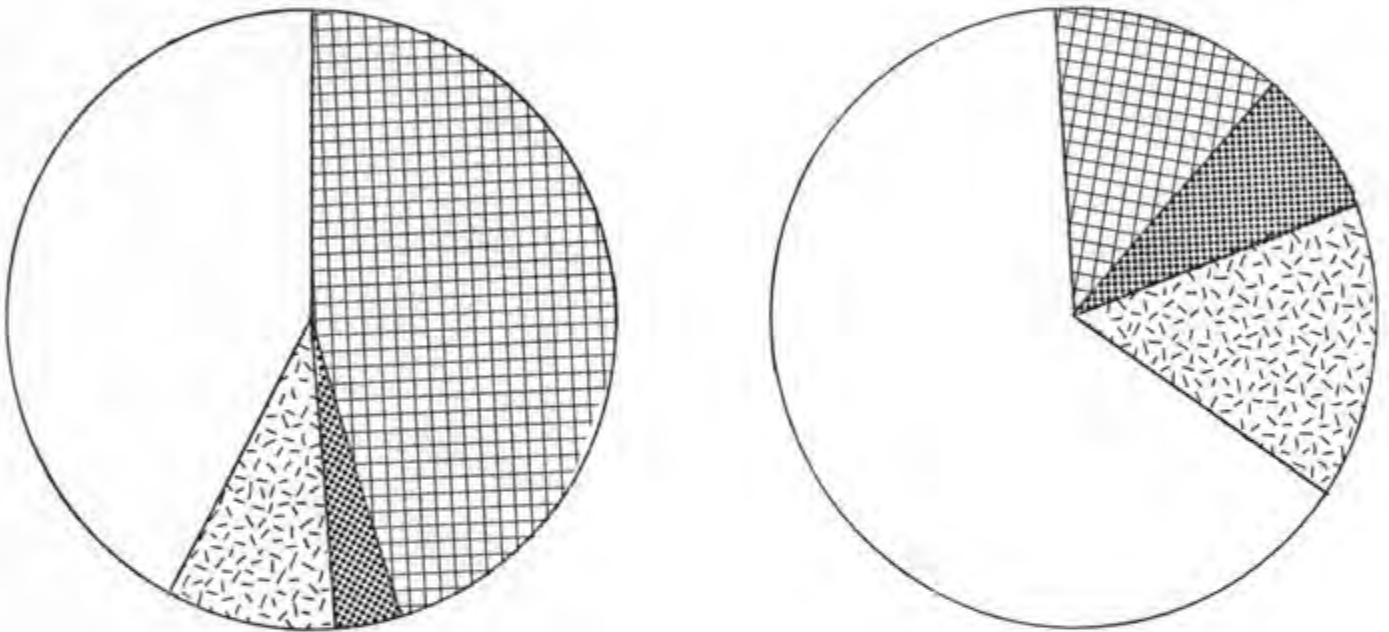
Figure 2. Foliage projected cover of C. capensis ⊞ , A. glomerata ▨, and 'other' plant species ⬙ (a) on level ground and (b) on a 23° slope.