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VEGETATION CHANGES SINCE WITHDRAWAL OF FIRE FROM CATCHMENT IX, CATHEDRAL PEAK, NATAL DRAKENSBERG

Karyn Adcock

A Dissertation Submitted to the Faculty of Science, University of the Witwatersrand, Johannesburg in fulfillment of the requirements for the Degree of Masters of Science

1980

DECLARATION

I declare that this dissertation is my own, unaided work. It is being submitted for the degree of Masters of Science in the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination in any other University.

[signature]

[signature] 1989.

ABSTRACT

Catchment IX at Cathedral Peak in Natal has been protected from fire since the 1950s. In 1986 its vegetation changes were studied, primarily by resurveying Granger's 1973 belt transects and woody plots.

In 1973 the main species and plant community gradient was from stream areas to ridge-tops. Detrended Correspondence Analysis of joint 1973-1986 data showed that overall, compositional shifts in C IX were small. Communities on shallow soil and containing bracken were the most dynamic, but succession was generally not uni-directional in areas of similar composition. Some individual species changed consistently, with *L.sericea* increasing most in frequency and *T.triandra* decreasing most, but many changes (eg *Pteridium aquilinum*) varied with locality.

Philippia evansii stands had spread in extent, but thinned out, with older stands facilitating *L.sericea*. Bird-dispersed woody species established near suitable perch trees, but their subsequent success differed under different canopy species. Evidence suggests that most communities in C IX will eventually converge to forest.

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ACKNOWLEDGEMENTS

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CHAPTER 1

INTRODUCTION

1.1 OVERALL OBJECTIVES

The overall objectives of this study were to
- determine the nature and extent of vegetation changes in catchment IX (Cathedral Peak) from 1973 to 1986, and
- determine patterns of woody plant recruitment, growth and mortality after withdrawal of fire in the catchment.

1.2 BACKGROUND TO THE STUDY

In the 1950s, the protection from fire of catchment IX (C IX) at Cathedral Peak in the Natal Drakensberg was initiated. C IX was situated in a region of catchments whose vegetation was influenced by a frequent fire regime. This protection of C IX allowed vegetation changes to occur, and provided the opportunity to document and examine the changes. Studies in the area were done in 1953 by Killick (1963); and around 1973, Granger (1976) surveyed permanent transects in the catchment. These provided the basis for part of this study. From 1950 up to 1985, occasional burns occurred in C IX, but by 1986 it had been totally free of fire for at least 15 years.

Research catchment areas of the Cathedral Peak area are managed by the Forestry Research branch of the Department of Environment Affairs,* their goals being 1) the production of high quality water and preservation of the soil mantle; 2) the maintenance of faunal and floral species diversity within communities; and 3) the prevention of accelerated extinction of any component species (Bainbridge and Scott, 1981). Research is directed toward determining the effects of management actions on the hydrology and vegetation of the catchments.

Fire is the chief management tool, but the long term effects of different burning regimes on the vegetation are not well understood. Fire has of course long been a dominant influence on the vegetation. Before man, spring and summer lightning fires would have created a burning regime of varying extent and regularity (Manry 1983), unlike the extensive, regular regime currently imposed.

* Note: Administration of this area changed to the Natal Parks Board after writeup.

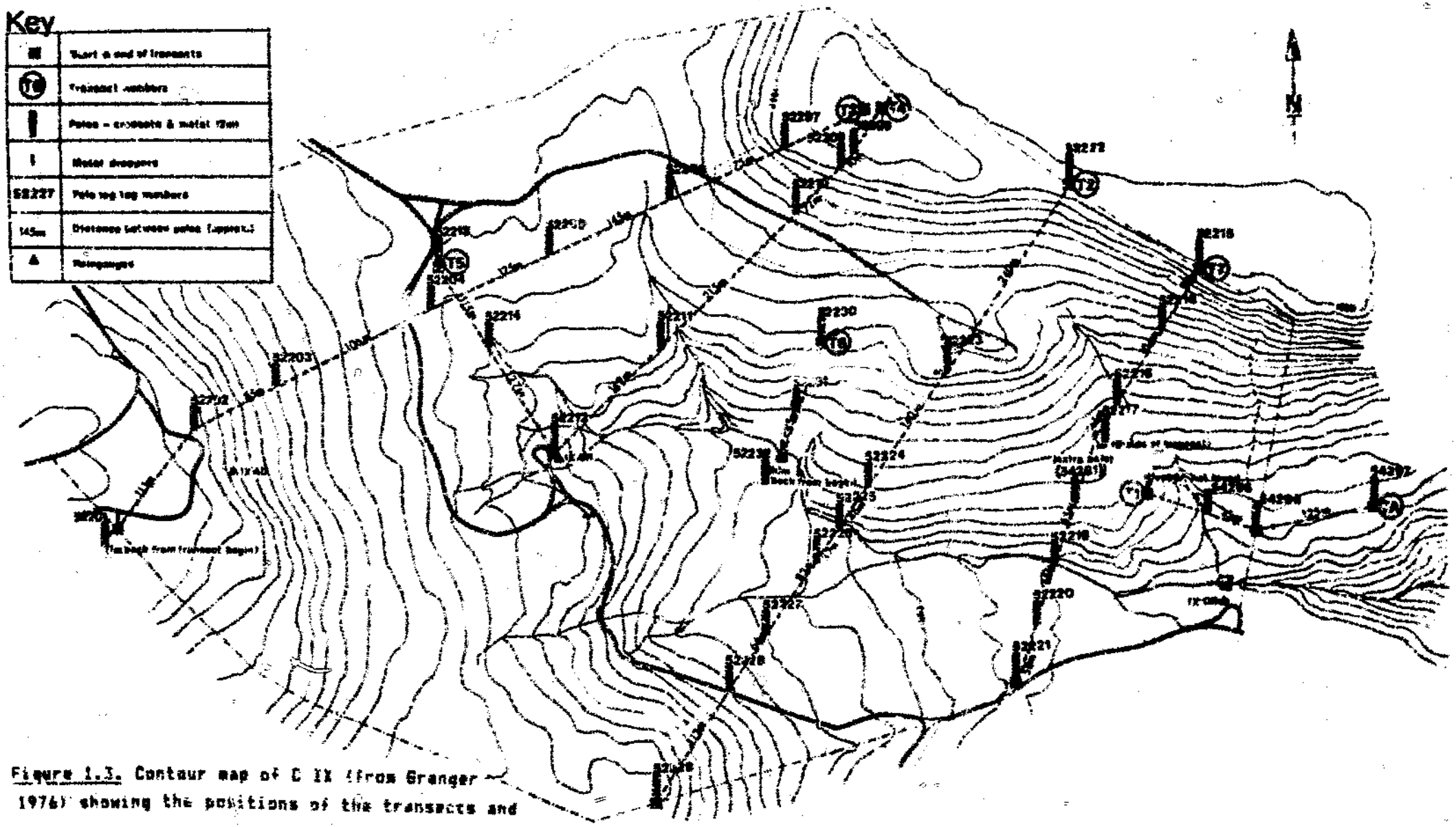


Figure 1.3. Contour map of C IX (from Granger 1976) showing the positions of the transects and the permanent markers placed in 1987.

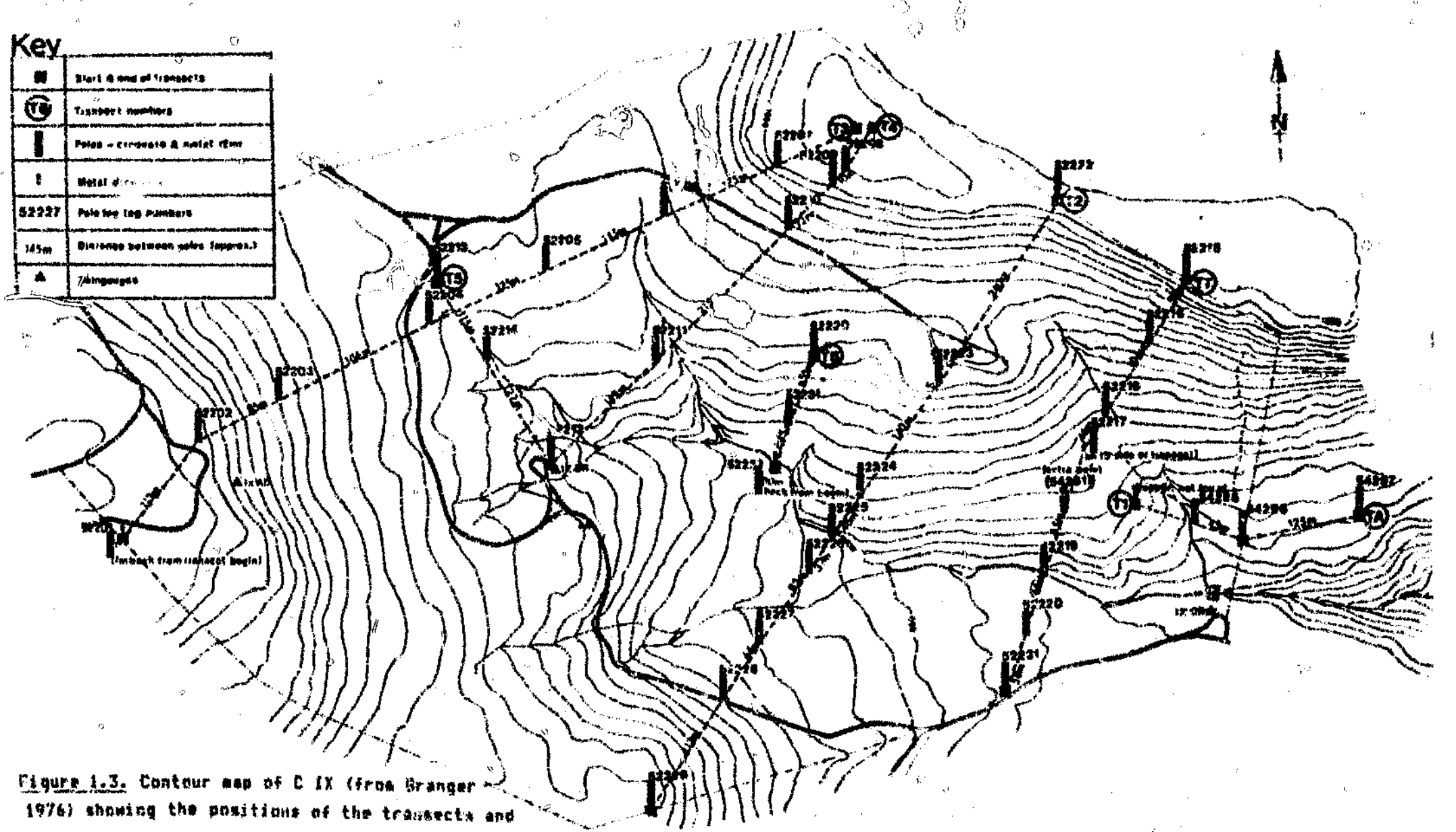


Figure 1.3. Contour map of C IX (from Granger 1976) showing the positions of the transects and the permanent markers placed in 1987.

The greatest effects of this burning have been to maintain grassland over most of the region, with forests and woody plants being restricted to altitudes below 1800m asl, or to isolated protected valleys or rocky outcrops. Given the withdrawal of fire from these catchments, the extent and type of vegetation which would result is open to question.

1.3. APPROACH

1.3.1. CHAPTER AIMS

In meeting the overall study objectives, a number of different aims were set up, each presented in separate chapters. The first aim was to use Granger's data to provide an overview of the "baseline" vegetation of 1973 (chapter 2). Granger's 1976 thesis did not provide this information in an easily digestible form. The second aim was to describe the actual vegetation changes along the transects since 1973 (chapter 3). The third aim was to investigate in more detail the patterns of recruitment, growth and mortality among "pioneer" woody plants such as *Leucosidea sericea* and *Philippia evansii*. and among "later" successional (forest precursor and forest) woody species (chapter 4). The final chapter aimed to summarize the general features of succession in C IX and examine the extent to which the observed patterns of change followed those predicted from various successional theories.

Finally it should be noted that this study was mainly at the descriptive level, which does not provide detailed insight into the mechanisms of successional change (Finegan 1984). Instead, it was hoped that by examining the patterns of change, hypotheses about the likely underlying processes could be put forward.

1.3.2. GRANGER'S 1973 BASELINE SURVEY

Granger's sampling design of 1973 formed the basis of much of this study - essentially a resurvey of C IX. Granger surveyed the catchment by placing a number of 1m wide transects across it (see Fig 1.3), and recorded the presence of species in 1m quadrats placed continuously or alternately along them. Unfortunately most transects were not clearly marked in the field, due to few marker poles being placed along them or poles having vanished in the intervening period.

In this study only part of transect 1 could be found, and the first stretch of transect 4 was probably not located in the same place as in 1973.

Granger used Normal Association Analysis, separately on each of the transects, to identify the plant communities through which the transects passed. The result was that the communities defined in one transect bore no direct relationship to those in another.

He also placed 25m² woody plots at some places along the transects, and recorded the species, height and basal diameter of woody plants in them. These plots were not permanently marked, but (for most) descriptions of their locations were provided in his thesis.

Granger used maps of the catchment soils, radiation levels and topography to interpret his findings. Although he studied species in relation to soil type at soil sampling points using Principle Components Analysis, he did not formally relate the species distribution along the transect to soils, radiation or topography.

Some inconsistencies were found in the 1973 data set when relating Granger's descriptions of communities to his raw data, and his portrayal of community positions to the contour map and the field situation. Each inconsistency was dealt with and mentioned where necessary in the text.

1.3.3. THE 1986 RESURVEY

In this study, the transects were resurveyed at a reduced sampling intensity due to time constraints. The original aim was to achieve 1/2, or at least 1/3, the 1973 intensity (see appendix 1.1). The final sampling intensities varied from this because of field conditions, and ended up at overall 41% of Granger's.

Those woody plots that could be relocated were re-measured. Because most sections of the transects, and all plots were not permanently marked, their relocation over the thickened vegetation was not always very accurate. Additional woody plots were set up in some areas of C IX, representing a greater range of woody stand ages.

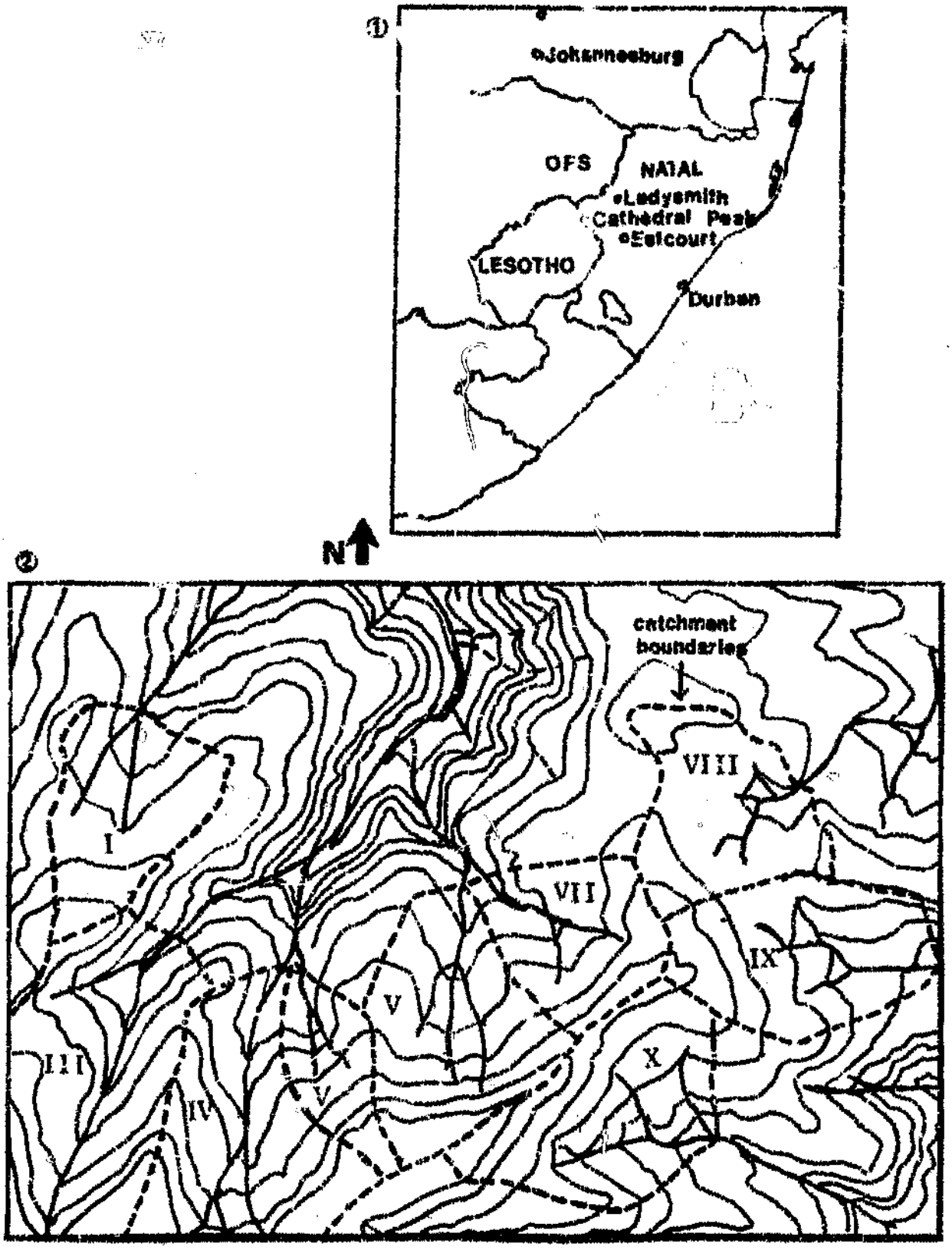


Figure 1.4. Maps showing 1) the location of the Cathedral Peak area in Natal, South Africa; and 2) the position of Catchment IX among the drainage basins of the Little Berg at Cathedral Peak Forestry Research Station.

Problems occurred with species identifications in this re-survey. Many forb and sedge species in the seedling and immature stages w ere difficult to identify, and consequently did not form part of the quantitative analyses. A list of species identified in 198' in each community along the transects is given in appendix 1.2. The names obtained from the Botanical Research Institute for sedges in this study, are not similar to those given by Granger. *Koeleria cristata* and *Festuca caprina* could not be distinguished in 1986, appearing to grade into each other morphologically (and being without flowers). These were analysed together as *F.caprina*. Granger did not record *Diheteropogon amplectens* in C IX. It is possible that his *Andropogon shirensis* was this species.

1.4 STUDY AREA

1.4.1. GEOLOGY AND CLIMATE

The mountains of the Cathedral Peak a·ea were formed from Drakensberg basaltic lavas underlaid by Karoo sandston· and shales. Prolonged river valley incision and scarp erosion sculptured the basalt escarpment of the High Berg (3000m asl) and the basalt-capped sandstone terraces of the Little Berg (King 1972). The Little Berg forms many first and second order drainage basins, one of which is catchment I/ (see fig. 1.4).

Rainfall occurs in summer and varies with altitude, from an annual average of 1200mm at 1200m asl to 2000mm at 2500m asl. Summit rainfall is 1600mm/annum. Snow falls occasionally on the Little Berg during winter. For a full description of the Little Berg climate and conditions in C IX, see Everson (1985) and Granger (1976) respectively.

1.4.2. CHARACTERISTICS OF VEGETATION IN THE C IX AREA

Killick (1963) identified three vegetation belts (climax communities) in the Cathedral Peak area. These were situated along the altitude gradient, but subject to the modifying influences of local soil type, moisture status and fire regime. The vegetation belts were:

1. the Montane belt - *Podocarpus latifolius* forest, 1280-1829m asl, generally lying below the sandstone cliffs,

2. the Sub-alpine belt - *Passerina-Philippia-Widdringtonia* fynbos, 1830-2865m asl, encompassing the basalt-capped terraces and catchment IX,

3. the Alpine belt - *Erica-Helichrysum* heath, 2865-3350m asl, including the basalt scarp.

Catchment IX lies between 1800 and 2000m asl and contains four dominant vegetation types: *Leucosidea sericea* scrubland, *Philippia evansii* shrubland, *Pteridium aquilinum* (bracken) veld, *Themeda triandra* grassland and *Protea* savanna. From observations, Killick had proposed a general sequences of community change after withdrawal of fire in the Sub-alpine areas like C IX which ended in *Passerina-Philippia-Widdringtonia* fynbos or *L.sericea-Buddleia salvifolia* scrub in moist sites (see appendix 1.3). He considered the soil characteristics and harsher climate at this altitude to be hostile to the development of *Podocarpus latifolius* forest which usually predominated at lower altitudes (below the sandstone cliffs in the area). A successional scheme was also developed by Granger, incorporating many of Killick's ideas but allowing for the possible development of forest, or more likely *L.sericea*-scrub forest (see appendix 3.2.3).

The actual vegetation changes occurring in C IX would depend on the properties of the constituent species. Species responses to fire and its withdrawal are relevant to the interpretation of successional changes in C IX, and some studies on the subject have been made (Smith 1982, Everson 1979 and Everson, Everson and Tainton 1984):

Woody species

Smith (1982) found that four common shrub species, *L.sericea*, *B.salvifolia*, *Widdringtonia nodiflora* and *P.evansii*, were adversely affected by fire. However, by one year of age, the first three were able to re-sprout after fire. *P.evansii* was more sensitive to being burned, but was able to persist at a site by seed germination which was enhanced by fire. Provided fire was less frequent than the time *P.evansii* took to reach maturity, or the other species to recover by re-sprouting, these shrubs could remain in an area. In the absence of fire their populations could increase.

L.sericea, *P.evansii* and *B.salvifolia* are wind dispersed species which persist in moist sites even in frequently burned areas. They may be expected to invade areas ahead of bird dispersed species, and can be regarded as pioneer woody species. Such established wind dispersed species may act as foci for the arrival of bird dispersed species in an area, resulting in patches of vegetation different in structure and composition to the surrounding vegetation (McDonnell and Stiles 1983). This process is called nucleation (Yarranton and Morrison 1974).

Herbaceous species

The response of herbaceous species to fire depends on its season and frequency: Summer burns and no fire for some seasons cause a decrease in grasses such as *Themeda triandra*, *Trachypogon spicatus* and *Heteropogon contortus*, while *Tristachya leucothrix*, *Harpechloa falx*, *Alloteropsis semialata* and *Rendlia altera* increase (Scotcher and Clarke 1981).

The response of these grasses to absence of fire may be caused directly, for example where *T.triandra* shows reduced secondary tillering if not burned (Everson, Everson and Tainton 1984). They may also be an indirect response to altered conditions after withdrawal of fire, for example changes in soil nutrient availability or moisture; shading from persistent moribund grass tissue, or a change in the relative competitive ability of a species whose neighbouring species are declining in response to absence of fire. The influences on grass growth and mortality of fluctuating weather appear to be small (Everson 1985).

Other herbaceous species include bracken (*Pteridium aquilinum*); many vernal aspect forbs whose life-histories seem geared to flower after spring fires; autumn flowering forbs and some semi woody 'fynbos-associated' species (Killick 1963). *P.aquilinum* occurs on deep, moist soils (Killick 1963) and is fire resistant, having underground rhizomes. It can invade grassland in the absence of fire. Everson and Breen (1983) found some evidence that *P.aquilinum* reduced the growth of *P.evansii* and restricted its invasion of bracken veld.

1.4. LITERATURE REVIEW : THEORIES OF PLANT SUCCESSION

After a disturbance (such as fire), several plant populations may progressively come to dominate a site. This directional change with time of species composition and/or vegetation physiognomy at a site (where climate remains effectively constant), is called succession (Finegan 1984). The underlying similarities of successional patterns in many parts of the world have led to a search for the underlying mechanisms controlling it. Two main but seemingly conflicting theories have been proposed to explain succession.

The first theory is that the species and growth form changes that occur during succession are a result of influences which the vegetation progressively develops over site conditions (Odum 1969). This is a holistic viewpoint, embodied in Clement's (1916) theory that when plant species establish themselves at a site, they alter site conditions which then favour the establishment of other species. The successive occupation of a site by different species, resulting from plants' influences which alter the local environment, are termed relay floristics (Egler 1954) and autogenesis (Finegan 1984).

The second, reductionist theory, is that succession is merely the sequential dominance at a site of species with different life histories, growth forms and sizes at maturity (eg Gleason 1917, Grime 1973, Egler 1954). Autogenic changes are seen as inhibiting succession, not facilitating change.

Arguments against the holistic theory stem partly from Egler's (1954) observation that (in contrast to successive occupation) the initial floristic composition of a site was important in determining the direction of vegetation changes, and that these changes could be

viewed purely as the result of the presence of species with different heights at maturity. It was also thought that the holistic view implied a predictable sequence ending in a stable "climax" vegetation, maximally adapted to the prevailing climate. Much available evidence highlighted the non-uniformity of the successional process, and shifting mosaic and cyclical nature of changes occurring in so-called stable climax vegetation.

The existence of these alternative pathways and cyclic phenomena are not accounted for by holistic theory. However, one of its most important features has been accepted in current thinking on succession: The influences that plants have on their neighbour's environment is seen as interacting with the species' life-history properties to determine succession (Watt 1947, Woods and Whittaker 1981). For example, Drury and Nisbet (1973) recognised that most of the phenomena of succession can be understood as a consequence of the growth, differential survival, and perhaps also the different colonizing abilities of species adapted to growth at different points on an environmental gradient, which varies (autogenically?) over time.

Connell and Slatyer (1977) have modeled succession at the community level using the interactions between plants' influences on their environment and their life-history properties. They proposed three interactions which lead to successional change (Pickett *et al* 1987). In all three "mechanisms", the initial stages of succession are dominated by species with copious propagules, good powers of seed dispersal, and the ability to establish and grow quickly to maturity in unoccupied sites. They modify the site to make it unsuitable for further recruitment of "early" species. After this, the mechanism of change varies:

In the Facilitation model, early species also modify the environment making it suitable for other "later" species to invade and grow to maturity. These in turn facilitate the invasion of yet other species.

In the Tolerance model, earlier species do not affect the rate of recruitment of later species, which are simply those with less rapid

dispersal or slower growth. Only those species tolerant of the increasing environmental stress caused by other plants' presence, will grow. These species can grow at lower levels of resource availability than earlier ones, and so persist to form the next stage in succession (although any effects of competition lowering the growth rates of "tolerant" species apparently nullifies this model). Many (eg Finegan 1984, Huston and Smith 1987) criticize pure tolerance as an unreasonable mechanism, and rather view it as a special reaction to competition. Tolerance implies that turnover is really the outcome of plant/plant influences on differences in species' life-history characteristics and patterns of resource use, with earlier species being less effective competitors.

In the Inhibition model, earlier species inhibit the invasion and growth of later species. Only those able to persist in the presence of earlier species (as seed or suppressed seedlings) will form the next stage in succession, when the earlier species die. Since earlier species are shorter-lived, they will gradually be replaced by longer lived species.

The three models differ in the cause of death of the earlier colonists: In facilitation and tolerance models, they are killed by competition with later species, while in inhibition they are killed by old age, or outside influences such as extreme environmental conditions, herbivores and pathogens.

Evidence of these models does exist, but as Finegan (1984) emphasized, all three may affect the same individual successively or simultaneously during its life. For example the humus conditions under a canopy tree may facilitate a seedling's establishment, but the low light conditions may inhibit its growth. Any one mechanism cannot solely explain the change from one successional stage to the next.

Noble and Slatyer (1980) adopted an approach to model successional sequences which focuses on the outcome of species' properties, and is less explicit about plant interactions. The approach requires a knowledge of the "vital attributes" of species: A successional sequence is explained in the model by the relative

a) abilities of the species to arrive or persist at a site after a disturbance such as fire,

b) abilities of the species to establish and/or grow to maturity after the disturbance; and

c) time taken for them to reach reproductive maturity; for their propagules to be lost from the area; and the relative life-spans of the individuals.

The effect of interactions such as allelopathy or shading is to modify another species' vital attributes (Huston and Smith 1987) - the exact interaction method need not be identified, only it s outcome.

Alternative theories have concentrated on a resource based approach, previously only implicit in other ideas. It uses the logical premise that species differ in their resource allocation strategies, "each one having its costs in terms of physiological and morphological trade-offs that prevent any species from being optimally adapted to all conditions" (Huston and Smith, 1987, see also Drury and Nisbet, 1973).

An example is from Tilman (1985), who proposed that a major trade-off was in allocation to below versus above-ground functions: The soil resource/light resource ratio represents a major gradient along which species have differentiated, and the initial dynamics of secondary succession may depend on the changing ratios of these limiting resources. Species adapted to maximizing soil-resource capture early on in succession, are replaced by species adapted to maximizing light capture, as light levels deteriorate during succession - the replacement process therefore depends on plants' (relative) competitive abilities for limiting resources, evident in the different forms and geometries of plant organs (eg Horn 1971).

This explanation of succession neglects many other aspects of resource-allocation trade-offs which obviously constrain a species' position in a successional sequence. Trade offs in plant maintenance, defense, growth rate, storage and reproduction (Grime 1979), along with the responses to temporal pattern of resource availability (Price 1984), all act to determine a species' position in succession. A

general scheme reflecting species' overall resource allocation strategies, and also the properties of species from early, middle and late successional stages, is the r and K continuum.

At one extreme, characteristics that confer success soon after a disturbance has cleared a site, are high rates of dispersal and copious seed production, fast growth, small sizes and short life-spans (r-selected), while those conferring success later in succession, are large sizes at maturity and shade tolerance, which accompany slow rates of dispersal, fewer seeds, slow growth, and long life spans (K-selected).

Huston and Smith (1987) conclude that although the approaches outlined above describe many aspects of succession, they fail to reveal the complex life-history traits and competitive mechanisms operating. They also tend to attribute individual properties (such as height advantages in light competition) to the population. Because succession is a plant-by-plant replacement process, the importance of life-history attributes are relative and depend on the specific environmental conditions resulting from competition with other individuals, as well as the life-history attributes of the other individuals. An in-depth understanding of vegetation change will only come from viewing processes at this level.

CHAPTER 2

PATTERNS OF SPECIES AND COMMUNITY DISTRIBUTION IN C IX IN 1973

2.1. INTRODUCTION

The objectives of this chapter were to

1) describe the distribution of key species in relation to soil type, altitude and average annual radiation levels in C IX;

2) identify vegetation groups or groups of NAA communities with similar species composition;

3) determine the variation due to reduced sampling intensity of community (site) ordination scores in species space.

The transect data from 1973 provided a baseline against which to view vegetation changes in C IX. Where Granger's thesis did not give adequate or easily summarized descriptions of the 1973 vegetation, aspects of these baseline data needed additional analysis to help in identifying and understanding the patterns of subsequent vegetation change. Three aspects of the 1973 data were investigated in this chapter.

2.1.a) Species distributions in relation to environmental factors

Granger used no formal statistical techniques to examine the distribution of species or communities occurring along the transects in relation to underlying environmental features. He did, however, provide information on the catchment soils, altitude and radiation levels. The relationships between these environmental factor complexes in catchment C IX, and species distributions along the transects, were therefore objectively described here, using Binary Discriminant Analysis (Strahler 1978).

This analysis helped to interpret the baseline distribution of species and of plant communities identified by Granger (using Normal Association analysis), and to interpret the subsequent vegetation changes in C IX (in chapter 3). Soil, altitude and radiation levels were used because each reflects in some way the soil moisture gradient in the catchment - a feature most likely to be the primary determinant of species composition (eg Dix & Smeins 1967, Killick 1964).

Because overall distribution patterns were being sought, scattered, infrequent species which were unlikely to contribute to the these patterns, were not included in this analysis. The choice of key species included those of >20% frequency in any transect, but also those which Granger had found to characterize different areas of vegetation, as opposed to those (such as many forbs) which occurred at a low frequency throughout most of C IX.

2.1.b) Similarities in species composition between 1973 plant communities

The second aspect of the 1973 data investigated, was the similarities between the NAA communities from different transects. (As explained in chapter 1, communities had been identified separately in each transect, and communities from one transect bore no direct relationship to those in another (Granger 1976) - it was not the task of this study to re-do Granger's classification, especially as the communities were in most cases quite justified). Community similarities, determined using Detrended Correspondence Analysis (DCA), were used to identify broader vegetation types for use in chapter 3. Chapter 3 looked at the patterns of vegetation change at a variety of scales, ranging from those in individual communities, to those in vegetation types, to patterns in the catchment as a whole. DCA also revealed the main gradients in species and community distribution which could be interpreted using [illegible] mation from the Binary Discriminant Analysis, and provided an ecological basis for identifying the patterns of vegetation change in C IX. Again this section used 'key' species, but including others which were frequent enough in some "communities" to permit Chi-squared or equivalent testing for changes in species frequency from 1973 to 1986.

2.1.c) Variation in the DCA score of communities with reduced sampling intensities

The third aspect of the 1973 data investigated was the effect of variations due to a reduced sampling intensity: The 1986 resurvey of C IX used an average of 41% of the 1973 sampling intensity. Because DCA was used in the following chapter to determine successional trends, it was necessary to estimate the sampling variation in the DCA scores of communities. These estimates provided a basis for identifying significant differences in the ordination scores, and therefore in the species compositions of communities at different times after withdrawal of fire (i.e. in 1973 and 1986).

2.2. METHODS

2.2.1 DISTRIBUTIONS OF KEY SPECIES IN RELATION TO CATCHMENT SOIL TYPES, ALTITUDE AND ANNUAL RADIATION LEVELS IN 1973

Binary Discriminant Analysis (BDA, Strahler 1978) was used to describe species environment relationships in the 1973 data. This technique uses presence-absence data and Factor Analysis (FA), or Principle Components Analysis, to identify the major trends of variation in species composition between environmental groups (eg different soil types), and to identify groups of species with similar patterns of presence-absence response to the environmental groups. BDA involved a number of steps, given in appendix 2.2.1 and outlined below.

Using Granger's maps, the transects (excluding TA and T1, for which full data were not available at the time of the BDA analysis) were divided into sections according to the above environmental groups (quadrat groupings are given in appendix 2.2.2). Three data sets resulted, one for each environmental parameter. Species frequencies in each group of an environmental parameter were determined, and converted into standardized residuals. Factor Analysis was conducted on the matrix of standardized residuals for each parameter. Q-mode FA discriminated between groups of an environmental parameter on the basis of vegetation trends, and R-mode FA with varimax rotation discriminated between groups of species with similar distributional responses to the parameter.

The environmental parameters (groups) used here (soil, altitude and radiation) were interrelated, in that soil type and radiation often varied with topography and altitude. No attempt was made to statistically determine their unique effects on the vegetation, but this was kept in mind during interpretation of the results. Because most levels of the environmental groups were replicated at different positions in C IX where other environmental features also differed, some variability could be expected in the species composition of these replicate sites. This in turn could result in variability in the BDA factor pattern obtained with different sampling of the replicate sites. Aspects of this variation in factor pattern were investigated:

Variability in the factor pattern of replicate sites for radiation and altitude

Gotfryd and Hansell (1985) found that observer error (reflected as differences in replicate field measurements in one site) resulted in significantly different variable weights being obtained on PCA axes, when replicates were analysed separately. In the same way, because each section of Granger's transects on one group of environmental parameter was considered as a replicate for that group, it was necessary to asses the variability of the factor patterns obtained with BDA.

An indication of overall variability was obtained by sub-sampling all levels of an environmental parameter (radiation); and in addition, the variation in the factor patterns of individual species was estimated by, holding other species constant and sub-sampling three "test" species only (*Themeda triandra, Alloteropsis semialata and Pteridium aquilinum*) using the altitude data.

Time limitations did not permit the variability in soil patterns to be tested, but the principles derived from the other tests could be applied to interpret the resulting patterns.

Sub-sampling

Two randomly chosen sections from each radiation level were omitted (by ordering the sections in a level and omitting those corresponding to two random numbers). Levels 1 and 6 were represented by one section only, and no data were omitted from them. Data for the

three test species from randomly chosen replicate sections were omitted from the altitude data set. Altitudes 1, 2, 13, 14 and 15 were represented on one site only, therefore no replicates could be omitted from them. The data sets that resulted after omitting replicate sections of transects were as follows:

RADIATION LEVEL	NUMBER OF QUADRATS OMITTED	NUMBER OF QUADRATS INCLUDED
1:	0	80
2:	97	228
3:	34	319
4:	44	966
5:	102	785
6:	0	115
ALTITUDE		
3:	12	146
4:	94	154
5:	194	63
6:	74	105
7:	80	117
8:	160	360
9:	106	133
10:	58	96
11:	37	80
12:	22	47

2.2.2. SIMILARITIES IN SPECIES COMPOSITION BETWEEN 1973 NAA COMMUNITIES

Detrended Correspondence Analysis (Hill and Gauch, 1980) was used in chapter 3 to examine the trends of vegetation change in C IX (Austin 1977), so it was used here to identify similarities between NAA communities from different transects for use in chapter 3. NAA communities had to be modified slightly to eliminate communities with too few quadrats for statistical analysis. These were assigned to adjacent communities with the most similar species composition, determined from Granger (1986). The modified communities are given in appendix 2.2.3. For selected species (see below) the frequency data for each community was arcsine transformed for DCA analysis. Although the sample sizes, and therefore the variances, were not equal in all communities, the data were considered adequate for use in DCA, which

uses chi-squared distances (Hill 1979) and not sum-of-squares or any form of analysis of variance

The selected species for this section were 'key' species plus several less frequent ones. These were ones of sufficient frequency in some communities for use in chi-squared or Fisher's exact probability testing for differences in species frequency at different times after withdrawal of fire. *Senecio dregeanus* and *Trachypogon spicatus* were left out, because the DCA downweighted them strongly (Hill and Gauch 1980).

Groups of communities with similar species compositions were identified from the community scores on the first two DCA axes. The criterion used to identify group members, was that any two member communities should not be more than half a standard deviation (ie 50 units on each DCA axis, or approximately one quarter of a species turnover, (Gauch 1982) from each other. This criterion ensured that the vegetation groups would not have too few members for statistical analysis in Chapter 3, but would still represent types with distinct species compositions. The resulting vegetation groups would also reflect the effects of the main environmental features governing gradients in species distribution.

2.2.3. VARIATION IN ORDINATION AXIS SCORES DUE TO SAMPLING

The variation in DCA site (community) axis scores derived from lower sampling intensities were determined so that significant differences between the community scores on 1973 and those of 1986 could be identified. To do this, replicate DCA scores from 5 communities in 1973 were used in a one-way ANOVA to calculate the Standard Error of such scores (for axis 1 and 2 separately), and then to derive the Least Significant Difference (Rayner 1967) between community scores on an axis.

In transect 3, quadrats from five randomly chosen communities (T3.5, T3.9, T3.14, T3.15 and T3.16) were systematically sub-sampled three times. This produced four sets of frequency data (3 subsets and the full set, arcsine

transformed) to provide replicate DCA scores for the ANOVA.

2.3. RESULTS

2.3.1. DISTRIBUTIONS OF KEY SPECIES IN RELATION TO CATCHMENT SOIL TYPES, ALTITUDE AND ANNUAL RADIATION LEVELS.

2.3.1.1 Species distributions on soil types

During Q-mode PCA (see table 2.3.1.1), species responses to the eight soil types present in C X distinguished six "groups" of soils from four factors (retained by the eigen criterion > 0.5, Statistical Analysis System, Helwig and Council 1979).

Table 2.3.1.1. SDA factor loadings of soil types on four factors, accounting in total for 88.9% of the variation in the SR matrix.

SOIL TYPE	FACTOR 1	FACTOR 2	FACTOR 3	FACTOR 4	GROUP
Hutton Wet*	.9479	.0526	-.0183	-.0695	1
Katspruit	.9310	-.0479	.0411	-.24	1
Hutton	-.7776	.0782	.2147	.493	2
Griffin Shallow	-.7234	.2693	-.4477	-.1236	2
Griffin Deep	.2130	.8608	-.2486	.231	
Mispah	-.4329	-.7241	-.3768	-.2991	4
Clovelly Shallow	-.0398	.1337	.8062	-.3143	5
Clovelly Deep	.3265	-.5918	.1011	.6412	6.(4)
EIGEN VALUE	3.3911	1.7169	1.1125	.8928	
% variation explained	42.39	21.46	13.91	11.16	

The wet soils Hutton wet* phase and Katspruit, were very similar in species composition, and were most dissimilar to the intermediate soils Hutton and Griffin shallow phase (factor 1).

* Granger (1976) often used the term Hutton form, Farningham series, hydromorphic phase for this soil, which is a misnomer. This Hutton is in a footslope position, and is wet, rather than hydromorphic.

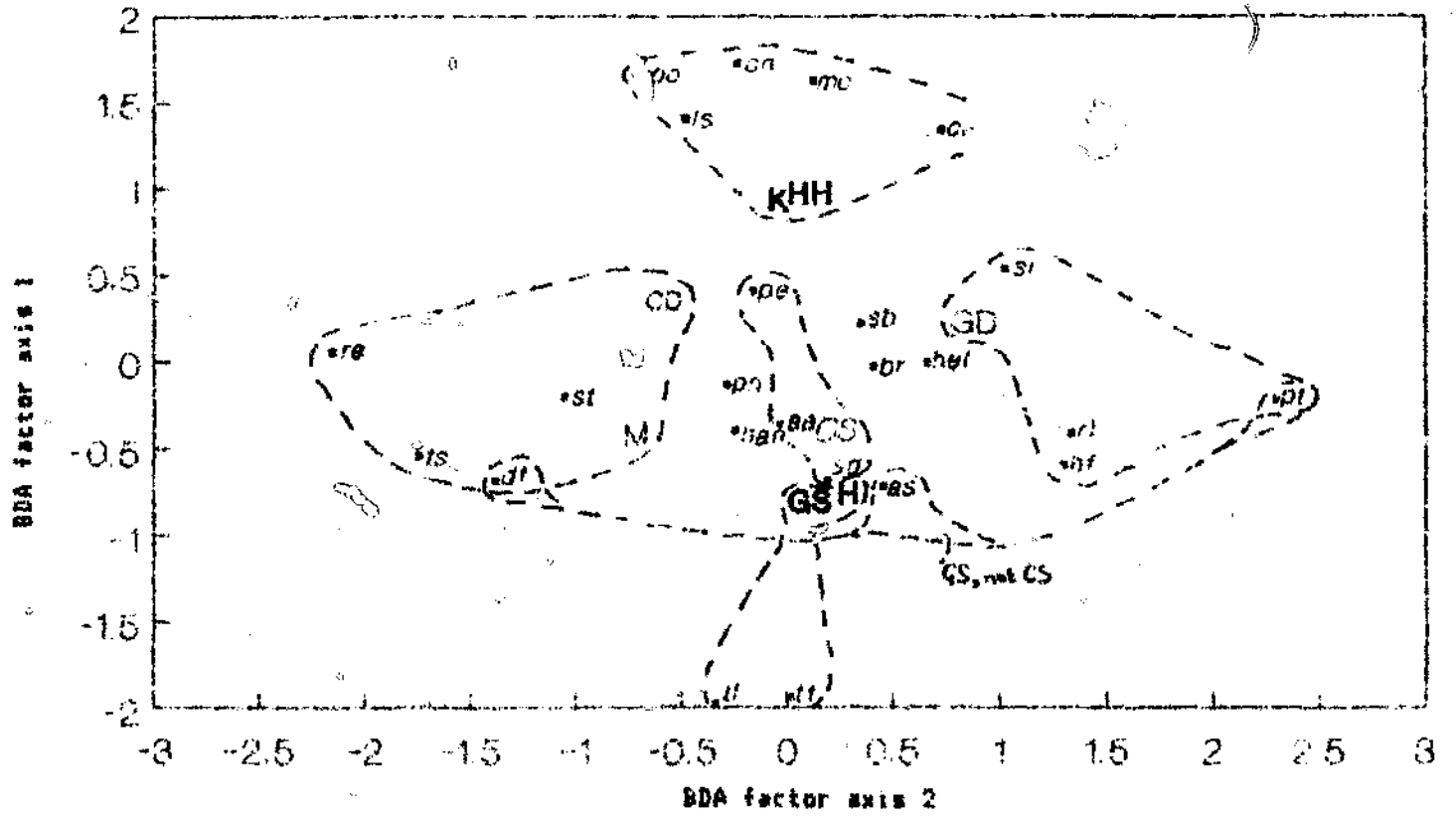


Fig. 3.1.1 Species and soil-type scores on soil factors. Soil t[illegible] Kat[illegible]uit, HH=Hutton [illegible] ; GS=Griffin Shallow, H[illegible] (i[illegible]old) are correlated with factor 1; GD=Griffin Deep, M=Mi[illegible], CD=C[illegible]lly Deep (in normal type) are correlated with factor 2; and the soil CS=Clovelly Shallow (in italics) is correlated with other factors. Groups of species with similar responses to the soil factors are enclosed in dashed lines.

Alloteropsis semialata (as), Andropogon appendiculatus (aa), Berkheya rhapontica (br), Clutia natalensis (ca), Cannabis africana (ca), Diheteropogon filifolius (df), Harpochloa falx (hf), Helichrysum aureo-nitens (han), Helicotrichon turgidulum (hel), Leucosidea sericea (ls), Miscanthus capense (mc), Panicum natalense (pa), Philippia evansii (pe), Polygala ohlendorfiana (po), Pteridium aquilinum (pt), Rendlia altera (re), Rubus ludwigii (rl), Senecio bupleuroides (sb), Senecio dregeanus (sd), Senecio isatideus (si), Stiburus alopecuroides (st), Themeda triandra (tt), Trachypogon spicatus (ts), Tristachya leucothrix (tl).

The soil Factor 2 distinguished the species composition of Griffin deep phase soils from that of stony, shallow Mispah soils, while Factor 3 and 4 further distinguish Clovelly shallow from Clovelly deep soils.

Species scores on the first two factors are shown in fig. 2.3.1.1, indicating species preferences for the respective soil groups. Groups of species with similar responses to soil were determined from their scores and their loadings after varimax rotation in R-mode PCA (not shown). These were

Katspruit (k) and Hutton Wet (HW) soils - *Polygala chlendorffiana (po), Clutia natalensis (cn), Miscanthus capense (mc), Leucosidea sericea (ls).* Hutton (H) and Griffin shallow (GS) soils - *Themeda triandra* (tt) and *Tristachya leucothrix* (tl). Griffin deep (GD) soils - *Senecio isatideus (si), Rubus ludwigii (rl), Harpechloa falx (hf), Pteridium aquilinum (pt).* Clovelly shallow (CS) soils - *Phillippia evansii (pe), Andropogon appendiculatus (aa), Senecio dregeanus (sd).* Griffin shallow, not Clovelly shallow - *Diheteropogon filifolius (df), Alloteropsis semialata (as), Pteridium aquilinum (pt).* Clovelly deep (CD) and Mispah (M) soils - *Rendlia altera (re), Trachypogon spicatus (ts), Diheteropogon filifolius (df), Stiburus alopecuroides (st).*

2.3.1.2. Species distributions in relation to altitude

Four different altitude groups were distinguished by their species compositions. Although the fifteen levels of altitude were grouped into seven 'factors' (eingen criterion > 0.5), they showed high correlations (> 0.5) with only the first three factors, accounting for 70.97% of the variance in the SR matrix of altitude. Factor 1 showed that the low altitudes 1 to 4 were most clearly distinguished from the higher altitudes 10 to 15, and factor 2 also separated altitudes 12 and 13 clearly from 8 and 9. Factor 3 represented altitudes 5 to 7 (see table 2.3.1.2).

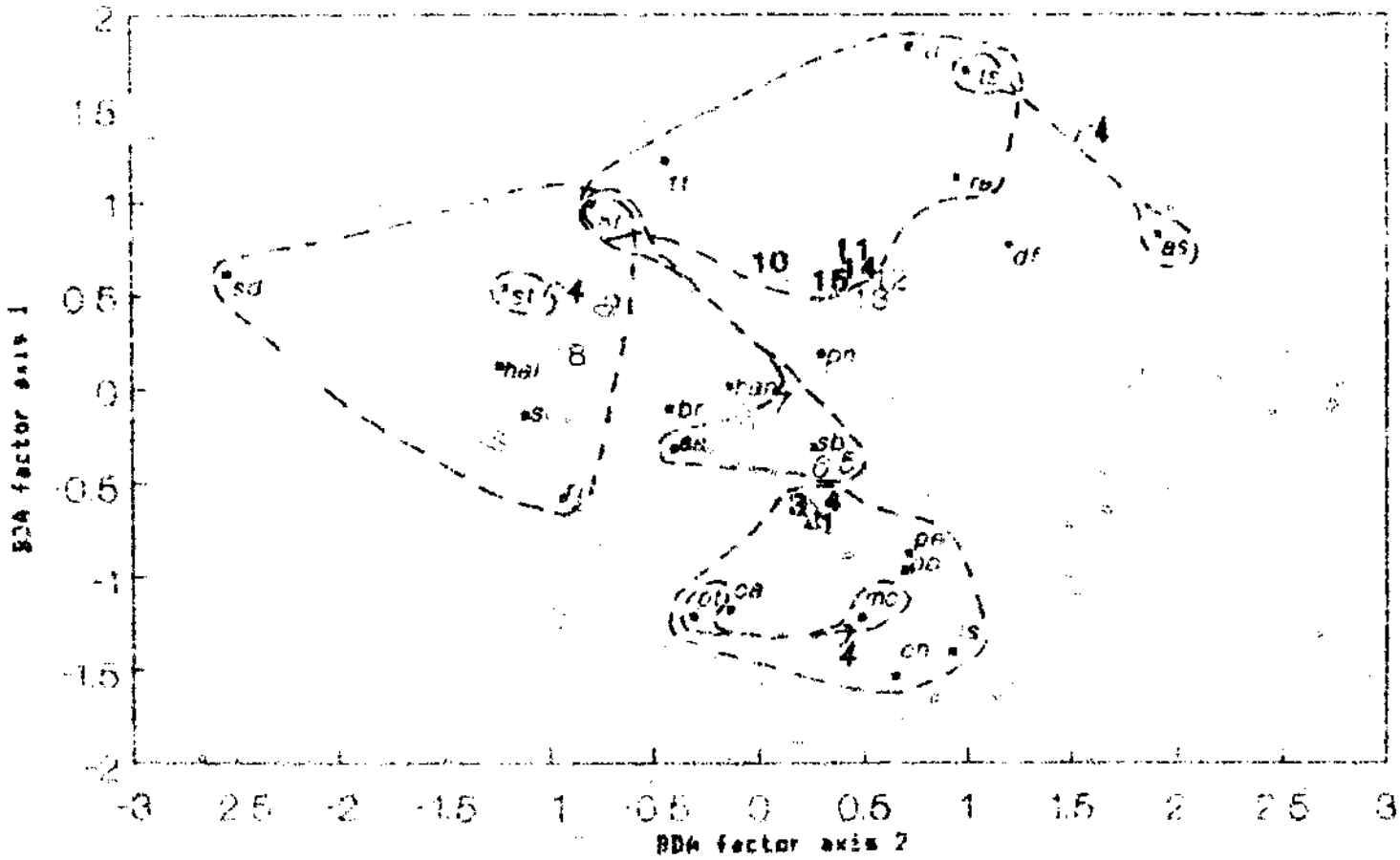


Figure 2.3.1.2. Species and altitude scores on altitude factors. (Altitude levels - 1, 2, 3 etc - in bold are correlated with factor 1; in normal type are correlated with factor 2; and in italics are correlated with other factors). Groups of species with similar responses to the altitude factors are enclosed in dashed lines.

Table 2.3.1.2. BDA factor loading of altitudes on three factors.

ALTITUDE	FACTOR 1	FACTOR 2	FACTOR 3	GROUP
1	-.787	.301	-.356	1
2	-.732	.241	-.318	1
3	-.669	.174	-.452	1
4	-.690	.315	-.020	1
10	.748	.022	.256	2
11	.807	.425	.001	2
12	.646	.606	-.008	3
13	.527	.531	-.232	3
14	.731	.451	-.232	2
15	.661	.337	-.048	2
8	.197	-.878	-.021	3
9	.494	-.708	-.117	3
5	-.424	.418	.509	4
6	-.446	.282	.659	4
7	-.062	.097	.815	4
EIGENVALUE	5.6194	2.9664	2.0595	
% variation explained	37.46	19.78	13.73	

Species scores on the first two altitude factors, and groups of species with similar responses to altitude are given in fig. 2.3.1.2. These were:

Low altitudes - *P.aquilinum , C.africana, M.capense, P.evansii ,P.ohlendorfiana, C.natalensis , L.sericea.* High altitudes - *H.falx (hf), T.triandra (tt), T.leucothrix (tl), T.spicatus (ts), R.altera (re).* Lower-mid altitudes - *A.appendiculatus (aa), H.falx (hf), S.bupleuroides (sb).* Mid altitudes - *S.dregeanus (sd), S.elopecuroides (se), H.falx (hf), H.turgidulus (hh), S.isatideus (si), Rubus ludwigii (rl).* Higher-mid altitudes - *R.altera (re), D.filifolius (df), A.semialata (as), L.sericea (ls).*

2.3.1.3 Species distributions in relation to radiation

Three different groups of radiation were distinguished by two factors (eigen criterion, > 1.0) during PCA. Factor 1 represented low radiation levels, R1-R3. Factor two represented a gradient from

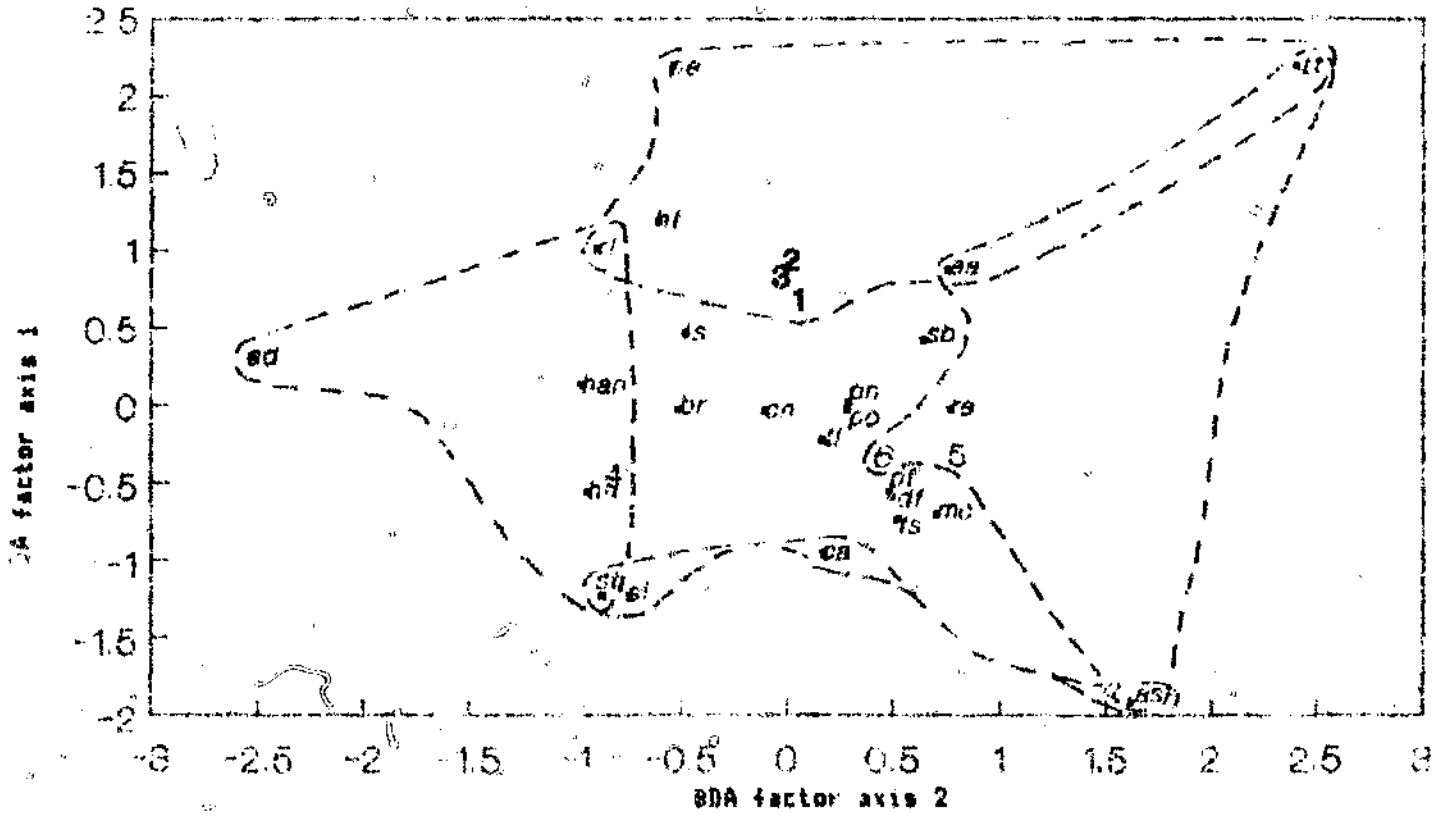


Figure 2.3.1.3. Species and radiation scores on radiation factors (Radiation levels - 1, 2, 3 etc - in bold are correlated with factor 1; in normal type are correlated with factor 2; and in italics are correlated with other factors). Groups of species with similar responses to radiation levels are enclosed in dashed lines.

radiation level 4 to radiation levels 5 and 6 (see table 2.2.1.3), although R6 was not highly correlated with this second factor.

Table 2.3.1.3. Loadings of radiation on two factors, accounting for 66.8% of the variation in the SR matrix.

RADIATION	FACTOR 1	FACTOR 2	GROUP
R1	.672	.051	1
R2	.900	.005	1
R3	.858	-.024	1
R4	-.467	-.836	2
R5	-.333	.788	3
R6	-.351	.464	3
EIGENVALUE	2.4715	1.5389	
% variation explained	41.19	25.65	

Species scores on the factor axes, and groups of species with similar responses to radiation, are given in fig. 2.3.1.3. These were

Low radiation levels - *P.evansii (pe), P.ludwigii (rl), H.falx (hf), A.appendiculatus (aa), T.triandra (tt).* Not low radiation levels - *S.alopecuroides (st), S.isatideus (si), C.africana (ca), A.semialata (as).* High radiation levels - *R.altera (re), A.appendiculatus (aa), T.triandra (tt), A.semialata (as), also P.aquilinum (pt), D.filifolius (df), M.capense (mc),* and *T.spicatus (ts)* . Not high radiation levels - *S.dregeanus (sd), R.ludwigii (rl), H.turgidulus (hh), S.alopecuroides (st).*

2.3.2. VARIABILITY IN FACTOR PATTERNS

Radiation

When some samples were removed from the radiation data, three factors were obtained. Table 2.3.2.1. shows the variable loadings and the difference between these and the loadings found from the full data set.

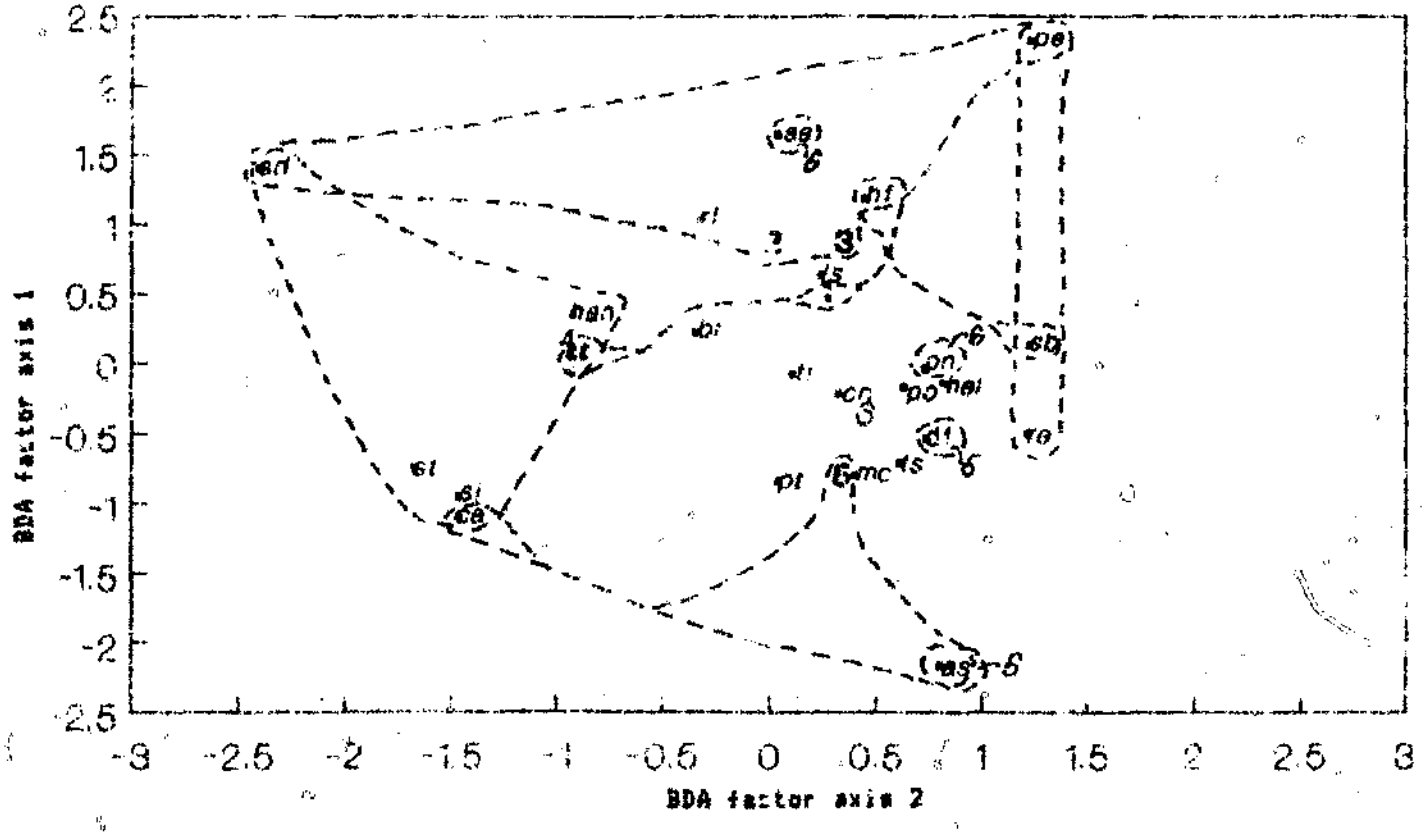


Figure 2.3.2.1. Species scores on radiation factors for the partial radiation data set (Radiation levels - 1, 2, 3 etc - in bold are correlated with factor 1; in normal type are correlated with factor 2, and in italics are correlated with other factors). Groups of species with similar responses to radiation levels are enclosed in dashed lines.

Table 2.3.2.1. Variable loadings on factors obtained from the reduced data set, and the differences between them and those obtained using the full data set.

EIGENVALUE	FACTOR 1 2.5886		FACTOR 2 1.4300		
VARIABLE	FACTOR 1	difference	FACTOR 2	difference	ANGLE
R1	0.569	-0.104	0.254	0.203	13.8°
R2	0.848	-0.054	0.358	0.354	22.7°
R3	0.854	-0.004	0.034	0.058	3.2°
R4	0.[illegible]79	0.525	-0.962	-0.133	61.5°
R5	-0.8[illegible]6	-0.483	0.335	-0.454	44.8°
R6	-0.389	-0.038	0.429	-0 035	5.1°
% variation explained	43.14	1.95	23.83	-1.8	

R5 was no longer correlated with factor 2, but became highly correlated with factor 1. R4 lost its negative correlation with F1. A third factor represented a gradient in species composition from R1 to R6 (loadings on F3 for R1 were -0.539; for R6, 0.638, and F3's eigenvalue was 1.0077, explaining 16.8% of the matrix variation).

The factor pattern obtained from the data was variable. That is, sites on similar radiation levels did not always have very similar species compositions: other environmental features were distorting the influences of radiation. Species which appear sensitive to radiation levels were *H.falx, R.ludwigii, P.evansii, L.sericea* (lower levels); *S.isatideus, Senecio bupleuroides, S.alopecuroides, H.aureo-nitens* (intermediate); *A.semialata, C.africana, R.altera, H.capense, D.filifolius, P.aquilinum, T.spicatus* (higher levels).

Species groups obtained from the reduced data set were: Low radiation levels - *T.triandra (tt), H.falx (hf) S.bupleuroides (sb);* also *S.dregeanus (sd), A.appendiculatus (aa), P.evansii (pe), H.falx (hf)* and *R.ludwigii* (rl). High radiation levels - *C.africana (ca), A.semialata (as),* also *P.aquilinum (pt), H.capense (hc), T.spicatus (ts),* and *D.filifolius (df), P.natalensis (pn)* (and *A.appendiculatus (aa)*). Intermediate radiation levels - *S.dregeanus (sd), H.aureo-nitens (han), T.triandra (tt), S.alopecuroides (st),*

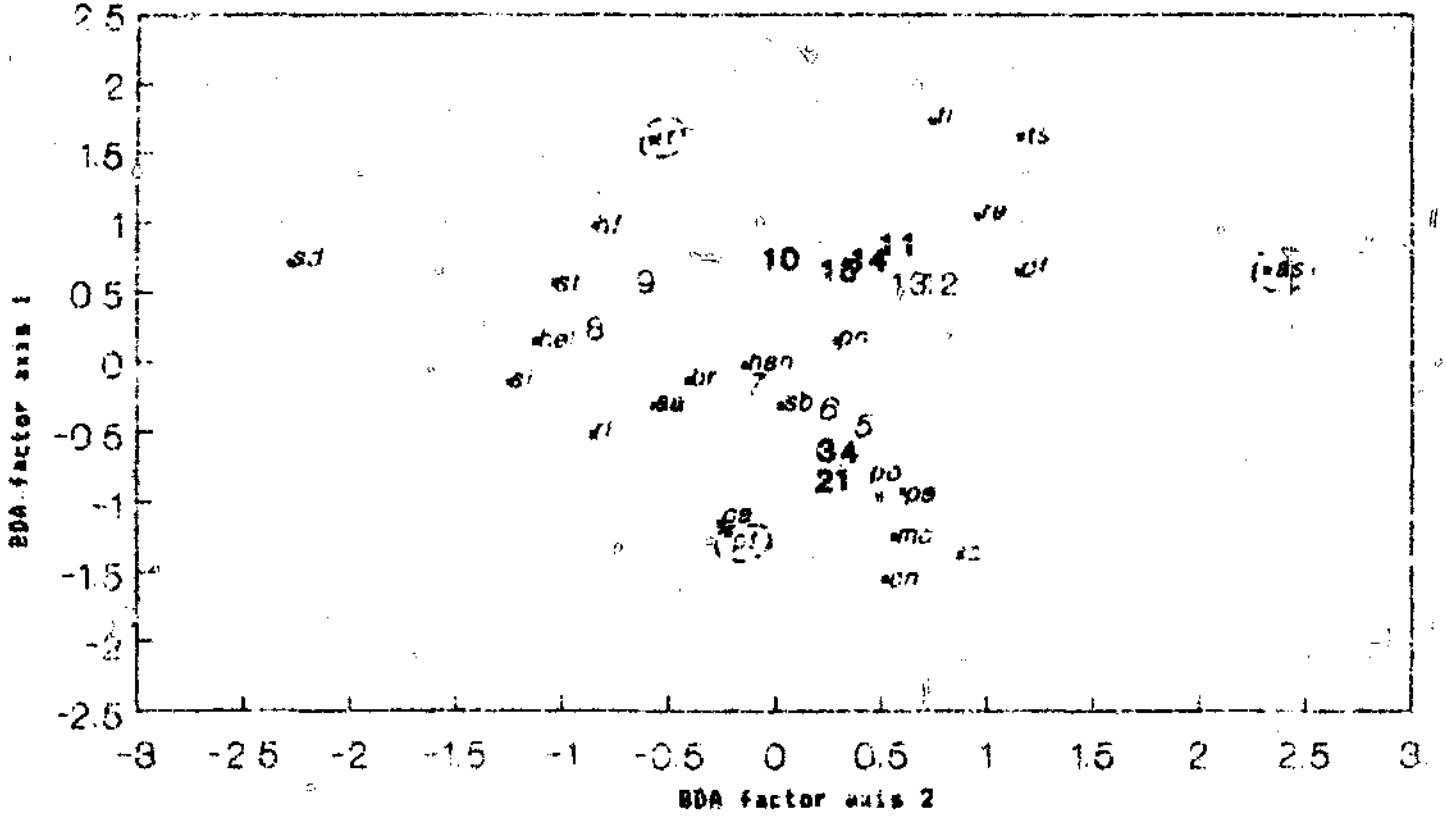


Figure 2.3.2.2. Species scores for the reduced altitude data set, showing positions of test species *Nesaea triandra*, *Alloteropsis semialata* and *Pteridium aquilinum* in factor space.

S.isatideus (si), C.africana (ca); and *P.evansii, E.bupleuroides, R.altera (re).* (see fig. 2.3.2.1, and the species standardized residuals for radiation in appendix 2.2.2).

Altitude

The scores of the three test species on the factor pattern from the sub-sample and full data set are given in table 2.3.2.2. The position of these species in factor axes space is shown in fig. 2.3.2.2 Despite the differences in scores, the species have retained their overall positions relative to the other species, so that the interpretation of the analysis remains the same.

Table 2.3.2.2. Scores of *T.triandra, A.semialata* and *P.aquilinum* on Factors 1, 2 and 3 (Q-mode BDA) obtained from the full data set and the data set reduced for these species

SPECIES	DATA SET	FACTOR 1	FACTOR 2	FACTOR 3
T.triandra				
	FULL	1.2151	-0.4425	0.5772
	SUBSAMPLE	1.5948	-0.5839	1.5111
A.semialata				
	FULL	0.8186	1.6959	-0.9748
	SUBSAMPLE	0.6580	2.3147	-0.5748
P.aquilinum				
	FULL	-1.2185	-0.3144	-1.1734
	SUBSAMPLE	-1.2271	-0.2239	0.5832

In R-mode FA, removal of samples from the test species resulted in reversal of factor 1 (table 2.3.2.3). Except for *T.triandra* the test species had not substantially altered their relative positions. However, after varimax rotation to maximize the distinction between groups of species, the test FA had more differences. The main species gradient (factor 1) along altitude remained similar, with low altitude species *L.sericea, P.evansii, C.africana, C.natalensis, P.ohlendorfiana, M.capense;* and high altitude species *A.semialata, H.falx, T.leucothrix, T.spicatus. T.triandra, D.filifolius,* and *R.altera* became included in this high altitude group. Factor 2 was substantially different, but groups defined by factors 3, 4 and 5 were the same. A seventh factor was not retained, and *Panicum natalensis* transferred from it, to became associated with factor 6.

Table 2.3.2.3. Loadings obtained for the test species on factors 1 and 2 (R-mode BOA) using the full data set and data set reduced for these species.

	DATA SET	FACTOR 1	FACTOR 2
EIGENVALUE:	full	8.2345	5.0074
	subsample	8.5162	5.0137
SPECIES			
T. triandra	full	-0.637	0.307
	subsample	880	0.214
A. semialata	full	265	-0.658
	subsample		-0.701
P. aquilinum	full	0.791	0.372
	subsample	-0.867	0.402

These changes reflect the wide range of many species' response to altitude, so that small changes in species abundances caused larger changes in species groups. This implied that the varimax rotation group-seeking process could not be realistically applied to these species distribution patterns. In fact, as in the case of radiation, the best understanding of species distributions could be gained from studying the standardized residuals of each species, given in appendix 2.2.1-3

2.3.3 SIMILARITIES IN SPECIES COMPOSITION BETWEEN 1973 COMMUNITIES

The scatter plot of community scores on the first two DCA axes is shown in fig 2.3.3.1. Ten groups of communities, called vegetation groups, were identified. The greatest differences between the axis scores of any two group members is shown in table 2.3.3.1. Members of seven of the groups differed by not more than half a standard deviation. Of the rest, groups 7 and 8 were allocated outliers, communities 2.3 and 3.16 respectively. Group 10 consisted of a mixture of plots with high axis 2 scores, but were more varying in axis 1 scores.

Miscanthus capense was confined to moist soil types at the lower altitudes (Katspruit, Huttor Mat and to some extent Griffin deep phase soils). It appeared to do well under high radiation levels, although it was also found in shaded *L.sericea* woodland areas. *Clutia natalensis, Commelina africana, Polygala ohlendorfiana* and *L.s[illegible]* share its distribution, but have slightly wider tolerances of radiation and soil moisture conditions.

P.aquilinum clearly favoured Griffin soils, and was more abundant in areas of lower radiation and l[illegible]er altitude. Granger (19[illegible]) note that *P.aquilinum* seemed confined to soils not shallower than 60cm conditions mostly found low[illegible] the topography of C IX. *H.falx* shared its preference for Griffin so[illegible] (and low radiation), but also occurred at higher altitudes. While *A.semialata* also favored these soils, it also occurs on other soil types and at high altitudes and radiation levels.

T.triandra, Rendlia alter[illegible] Panicum natalense, Diheteropogon filifolius and *T.spicatus* w[illegible] a abundant on shallow stony Hispah soils, at higher altitudes and radiation levels. *Stiburus alopecuroides, Helictotrichon turgidulum* and *Helichrysum aureo-nitens* all favoured average radiation and altitude levels with soils of intermediate moisture and depth.

The standardized residuals of BDA provided better descriptions of species responses than the Factor Analysis and varimax rotation. The species groupings derived after rotation were sensitive to relatively small alterations in species data, as shown when *P.aquilinum*, *T.triandra* and *A.semialata* were sub-sampled. This may be because while the rotation attempted to maximize the distinction between the species groups (a more arbitrary process when species show gradual changes in abundance), the standardized residuals emphasized the continuum nature of species distributions. Presumably rotation is best suited to use with vegetation where species strongly prefer or avoid the different groups of an environmental parameter.

The use of factor analysis in vegetation ecology has been criticized for its assumptions of linearity in species' responses to

CHAPTER 3

VEGETATION CHANGES AFTER WITHDRAWAL OF FIRE IN C IX

3.1. INTRODUCTION

This chapter looked at the vegetation changes along transects since 1973, attempting to identify successional trends, measure the extent of changes, and evaluate hypotheses about the types of species changes occurring after withdrawal of fire.

Vegetation changes can be defined and measured in a number of ways. First, when viewing species composition and abundance together, changes include increases and decreases in amount and the loss or gain of species (termed overall change). These types of overall change can be identified from the shifts of sites (eg vegetation types and communities) from two different times in ordinated site space. Austin (1977) outlined the aspects of site-time ordination which would reveal successional features. If the majority of sites show parallel or similar trajectories, then a general (successional) trend is evident. If the site trajectories are oriented at random, there may be divergence, or different trends at different sites. The extent of overall change is indicated by the distance between sites from successive years in ordinated site space.

Second, floristic change (Bornkamm 1981) involving actual species turnover is another aspect of vegetation change. The proportion of species not common to a site at both times (after accounting for sampling error) indicates floristic dissimilarity and measures changes in floristic composition.

Third, taking species individually, their increases or decreases in frequency (termed species frequency changes) represents a finer scale of viewing vegetation change. The significance of frequency changes are testable with chi-squared or equivalent tests.

(calculated in chapter 2) to detect significant changes in the site score between 1973 and 1986.

2) The detrending in DCA (though over zealous, Pielou 1984) is better than other methods at producing a meaningful second gradient when this is smaller than the first, as is the case with these data.

3) DCA can break down when a gradient is too long or too short; but this does not apply in this case.

4) An adequate general model of species response does not yet exist (Kent and Ballard, 1988), so that techniques alternative to DCA still have their peculiar limitations. As this thesis was not an exercise is technique comparison, it is the ecological interpretation of the results that matter. There is no "best" technique. However, Ter Braak's (1987) CANOCO computer program, unavailable at the time of write-up, may prove more than useful.

Aspects of the DCA ordination, corresponding to the above-mentioned levels of vegetation groups and communities, were examined as outlined below. Additional aspects, relating to the even higher level of overall catchment, were also looked at.

3.2.1.1. General trends in the catchment vegetation

To determine whether there existed a general trend of vegetation change in C IX, the trajectories of the vegetation group means were examined. Parallel trajectories of group means implied a consistent trend throughout the C IX vegetation, whereas non-parallel ones implied multi-directional changes.

3.2.1.2. Trends and the extent of overall changes within vegetation groups

To determine whether a trend occurred within an individual vegetation group, the trajectories of the member communities were examined. Again, many near parallel trajectories within a vegetation group indicated that it was showing a consistent trend. As a measure

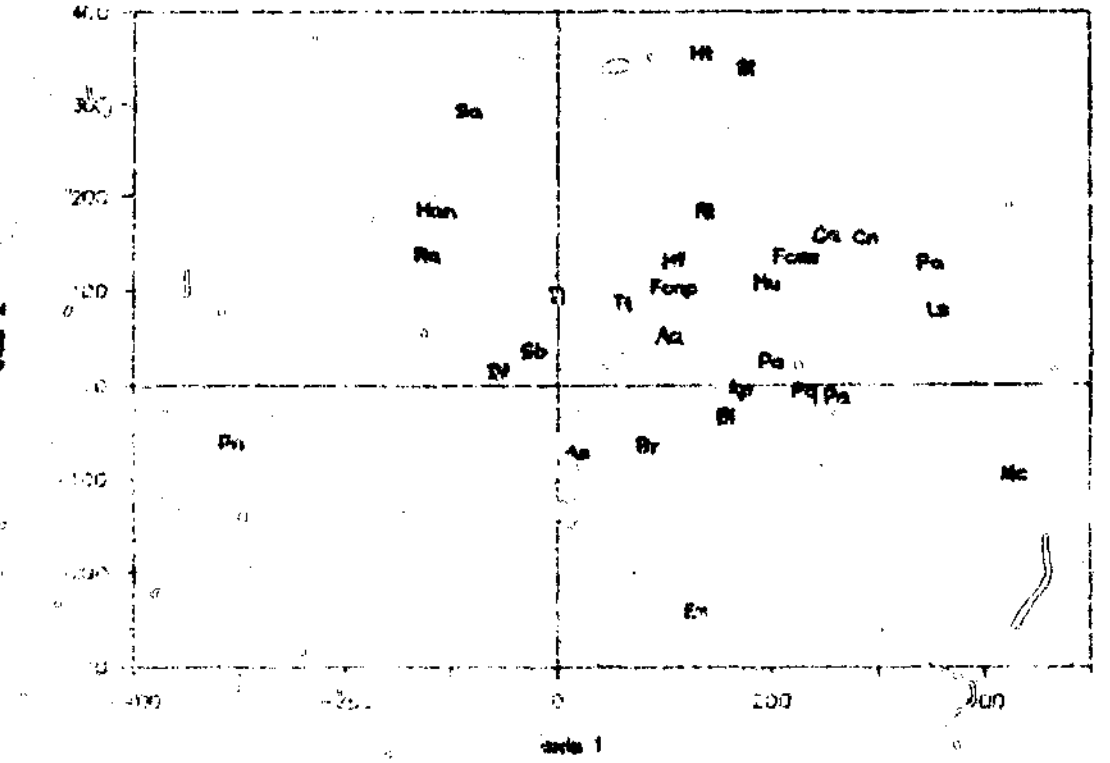


Figure 2.3.2.2. Scatterplot of species scores on DCA axes 1 and 2 from the ordination of 1973 NAA community data. See fig.3.3.1.1 for species names.

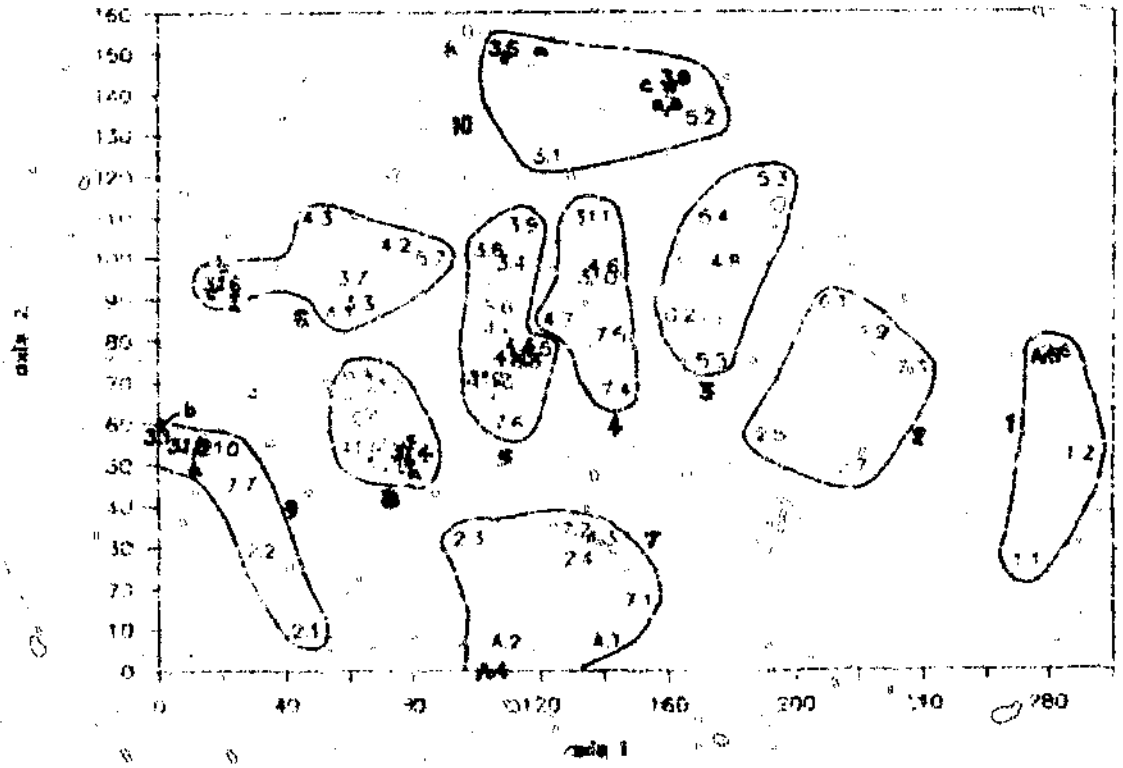


Figure 2.3.3.1. Scatterplot of the community (site) scores on DCA axis 1 and 2, from the ordination of 1973 NAA community data. Ten "vegetation groups" are demarcated by solid lines. Also shown are variations in axis scores of communities sampled at 1/3 the 1973 intensity; these are the scores for the three subsets of data (a, b and c) taken from communities 3.4, 3.9, 3.14, 3.15 and 3.16 (see section 2.3.4).

Table 2.3.3.1. Maximum difference in axis score between members of a vegetation group.

VEGETATION GROUP	AXIS 1	AXIS 2
1	17	41
2	44	40
3	29	44
4	18	42
5	15	48
6	66	23
7	54	17
8	15	22
9	46	45
10	62	26

Fig. 2.3.3.2 shows the relationships of species to the DCA axes. The results of the BDA's were used to interpret the axes as follows: The distribution of species along the DCA axis 1 was from higher altitude and radiation, shallow soiled areas with *S.alopecuroides*, *P.altera*, *D.filifolius*, *S.bupleuroides*, *T.leucothrix*, and *P.natalensis*; through species occurring over a wider range including middle altitude areas (*T.triandra*, *H.falx*, *R.ludwigii*, *A.appendiculatus*, *F.caprina*, *A.semialata*, *Berkheya rhapontica*, *Buchenroedera lotononoides*, and *Acalypha punctata*); then species of lower-mid altitude with deeper soils, (*P.aquilinum*, *Festuca caprina*, *Helichrysum umbraculigerum*, *Pellaea quadripinnata*), down to species of lower altitude, deep, moist soils, (*H.capense*, *P.ohlendorfiana*, *L.sericea*, *P.evansii*, *C.natalensis*). This was shown by the trend in vegetation groups 1 through 6 to follow the transects from the drainage line up the slopes toward the 'rim' of the catchment basin, as shown in fig. 2.3.3.3.

DCA axis 2 appeared to be a gradient from the head of the catchment to the mouth. This is shown by the greater prevalence of vegetation groups 3 and 10 toward the head of the catchment, as opposed to group 7 toward the catchment mouth, but this is not easily interpreted (fig. 2.3.3.3).

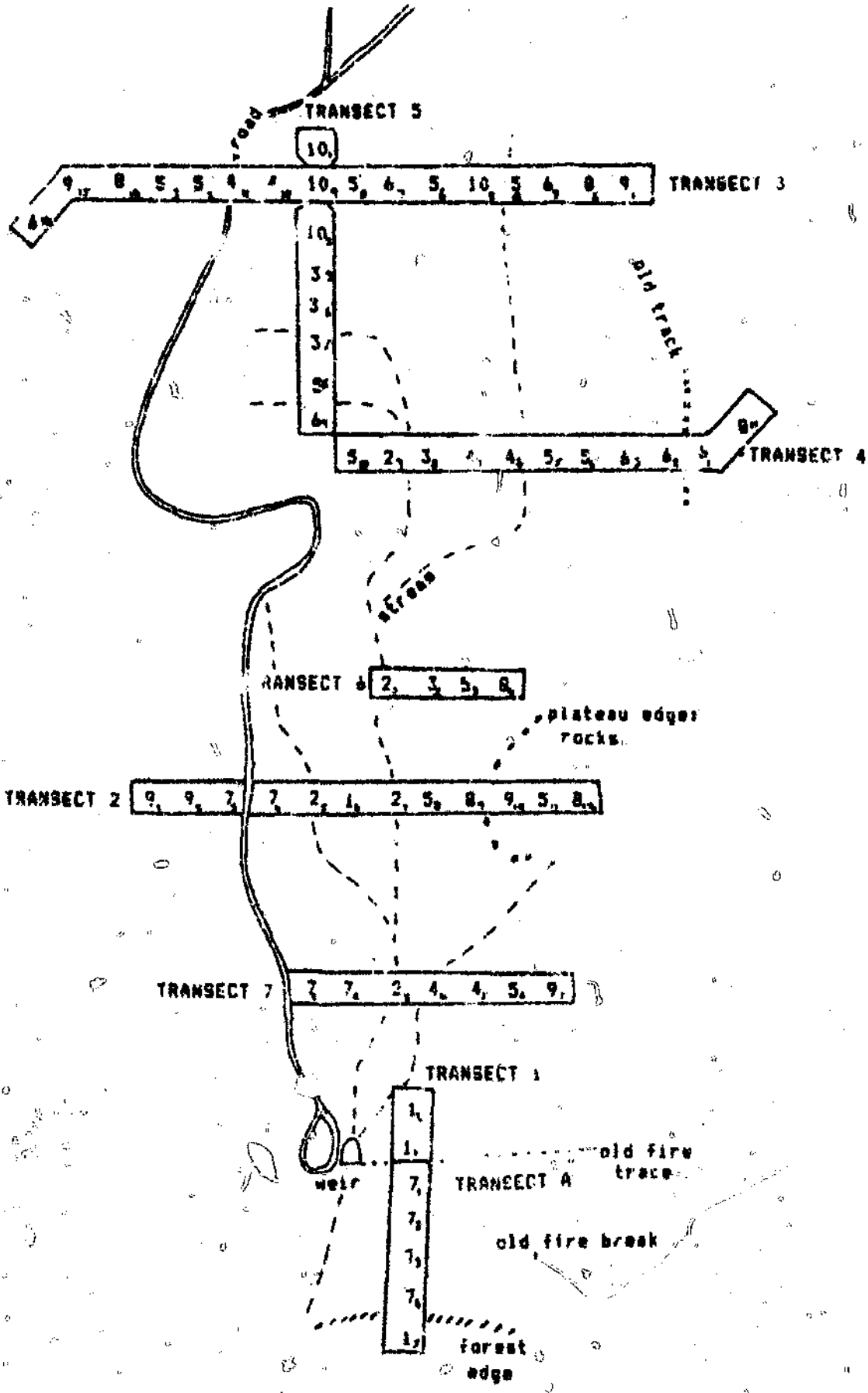


Figure 2.3.3.3. A stylised diagram of C IX, showing the positions of transects, the position of communities along the transects, and the vegetation group (1-10, obtained from DCA) to which each community belongs. (Communities are numbered from start to finish along each transect, indicated with small numbers).

Species characteristic of the vegetation groups are given below. They are listed in order of their importance in characterizing the vegetation group (ie species found more in that group than in any others), with frequency being a second criterion:

1: Leucosidea sericea, Miscanthus capense, Pellaea quadripinnata, Philippia evansii, Helichrysum umbraculigerum, Pteridium aquilinum, Commelina africana, Polygala ohlendorfiana.

2: Pteridium aquilinum, Miscanthus capense, Leucosidea sericea, Clutia natalensis, Helichrysum umbraculigerum, Philippia evansii, Polygala ohlendorfiana.

3: Andropogon appendiculatus, Acalypha punctata, P.aquilinum, M.capense, T.triandra, H.umbraculigerum, L.sericea, C.africana, Harpechloa falx.

4: P.aquilinum, T.triandra, Acalypha punctata, Andropogon appendiculatus, L.sericea, P.evansii, Iristachys leucothrix, Festuca caprina, Harpechloa falx.

5: T.triandra, P.aquilinum, H.falx, T.leucothrix, Acalypha punctata, A.appendiculatus, Rubus ludwigii, H.umbraculigerum.

6: T.triandra, T.leucothrix, Senecio bupleuroides, Stiburus alopecuroides, Rendlia altera, Diheteropogon filifolius, A.appendiculatus, H.falx.

7: P.aquilinum, Elionurus muticus, Acalypha punctata, Alloteropsis semialata, T.triandra, T.leucothrix, A.appendiculatus, H.umbraculigerum.

8: P.evansii, T.triandra, T.leucothrix, S.bupleuroides, Diheteropogon filifolius, A.appendiculatus, H.falx. (Elionurus muticus, P.aquilinum).

9: D.filifolius, T.leucothrix, T.triandra, S.bupleuroides, Alloteropsis semialata, Elionurus muticus, A.appendiculatus.

10: Senecio isatideus, A.appendiculatus, T.triandra, P.aquilinum, Rubus ludwigii, Helictotrichon turgidulum, S.bupleuroides, Acalypha punctata, H.falx.

2.3.4 VARIATION IN DCA COMMUNITY SCORE WITH REDUCED SAMPLING INTENSITY

The maximum difference between two sample axis scores was 0.3 standard deviations on the DCA axes (table 2.3.4.1, also see fig. 2.3.3.1).

Table 2.3.4.1. Full data set and subset DCA axis scores for the five communities tested for variation in axis score with reduced sampling intensity.

COMMUNITY	FULL DATA SET	SUBSET 1	SUBSET 2	SUBSET 3
T3.5				
axis 1	109	112	91	110
axis 2	151	151	144	149
T3.9				
axis 1	163	163	162	154
axis 2	144	144	151	144
T3.14				
axis 1	79	74	79	78
axis 2	53	52	45	57
T3.16				
axis 1	9	12	0	28
axis 2	55	59	44	60
T3.16				
axis 1	20	25	19	17
axis 2	94	98	88	92

The 95% confidence intervals about a single estimate of community score were calculated from the ANOVA as + or - 13.258 units on the DCA axis 1, (Std. error = 6.6769), and + or - 14.749 on DCA axis 2 (Std. error = 9.8793).

2.4. DISCUSSION

Of the three environmental factors examined, soil type provided the best description of species distributions in C IX. Along with altitude, it reflected the overall moisture gradients which have patterned species distributions in the catchment.

While radiation's influence on the vegetation also acts through determining the moisture regime, only some species showed a clear response to it, especially *Philipoia evansii*, *Harpochloa falx* (low levels), and *Diheteropogon filifolius*, *Panicum natalensis*, *Alloteropsis semialata* and *Rendlia altera* (higher levels). The fact that the radiation analysis did not produce a clear gradient from low to high levels, further indicates that radiation's influence is modified by other factors.

P.evansii's response to radiation has been examined by Everson and Breen (1983), who concluded that its distribution in south facing, low radiation sites is probably because it experiences more favourable water relations there. *H.falx*'s distribution under conditions of lower radiation, is likely related to its ability to survive the low light intensities of shading, as shown by Everson (1985). He also found *T.leucothrix* and *A.semialata* to be more shade tolerant, but this was not reflected (at this scale of examination) in their distributions in C IX (*T.leucothrix* did not show clear tolerance of lower radiation levels, while *A.semialata* appeared to avoid sites with less radiation - see appendix 2.2.1.3). Also, Everson's findings are not reflected in the distribution of *T.triandra*, which showed no avoidance of low radiation levels as would be expected, being more sensitive to low light than *H.falx*. However, *Trachypogon spicatus* did favour high radiation levels, and so more closely reflects its sensitivity to low light levels in its C IX distribution (see appendix 2.2.1.3).

environmental gradients. The resulting distortion of factor axes has deterred ecologists from using FA, but the manner in which Strahler employs it (by having environmental groups as observations) alleviates the major problem, which is relating distorted factor axes to environment. Also, the standardized residuals were invaluable in reflecting directly the species' responses to environmental groups; and helped achieve a form of direct gradient analysis. This is currently best achieved only using environmentally constrained ordination with the new Canonical Correspondence Analysis package of ter Braak (1987), a method not available at the time of write-up.

Finally, it should be noted that the results of the multivariate techniques used here did not differ greatly from the "intuitive" findings of previous researchers (Killick 1963, Granger 1976). If these lengthy procedures are being used purely for hypothesis generation, the time could be better spent in the field using direct techniques which give insight into particular hypotheses about species' responses, and are generated far more quickly by "subjective" field observations.



Using the above measures of vegetation change, the main objective of this chapter was to describe the patterns of change in C IX at different spatial scales, ranging from the whole catchment (viewing the data from all areas in C IX together), to changes in areas of the same vegetation type (these areas are termed vegetation groups, defined in chapter 2), to those changes occurring in local sites or communities (derived from 1973 NAA communities).

The work of Granger (1976) and Everson (1985) resulted in some predictions about which species would increase or decrease in dominance after withdrawal of fire. A subsidiary objective of this chapter was therefore to test their predictions.

3.2. METHODS

3.2.1. SUCCESSIONAL TRENDS AND THE EXTENTS OF OVERALL CHANGES IN C IX

To determine trends and extents of changes in species composition and abundance since 1973, the change in position of "sites" in ordinated site space were examined (eg Austin 1977, Foran et al 1986). Sites were defined at different levels of organization or scale of plant association; the lower level being individual plant communities (NAA communities, see chapter 2), and the higher level being vegetation groups means, derived from groups of communities with similar species compositions (identified using DECORANA on arcsine transformed frequency data from 1973 only).

DCA was performed on the 1973 and 1986 data sets *together*, using the transformed data of species frequencies in communities in the two years. Its use was thought appropriate for a number of reasons (drawn from Ter Braak and Prentice 1988):

1) Unlike Correspondence Analysis, DCA includes non-linear re-scaling of the axes, which equalizes the within-site variance at all points along the axes. A change of one unit should measure the same difference in composition anywhere on the axis. This feature enabled the uniform application of the least significant difference measures

of the extent of change in a vegetation group. ANOVA was used to calculate the 95% least significant difference between years in each group mean, on each axis. In addition, as a comparison with the use of DCA, chi-squared tests were used on vegetation group data to measure overall change in each group.

3.2.1.3. The extent of overall change within plant communities

The extent of change in an individual community was measured using the differences in axis score of a community (ie a site defined at the community level) between the two years. Tests for significant differences between years were made using the least significant differences established for each axis in chapter 2. The LSD for axis 2 was interpreted at the 99% level, to account for differences in axis 'direction' and spread in species space resulting from ordination of the joint 1973-1986 data, as opposed to the 1973 data alone (ie, the distance between two 1974 communities on axis 2 was more variable in the joint ordination than the 1973-only ordination).

3.2.2. CHANGES IN SPECIES FREQUENCIES

The changes in individual species' frequencies were also examined at three scales, using different groupings of the frequency data. The scales were a) species frequency changes in the catchment, b) changes within different vegetation types (groups), and c) "localized" species frequency changes, within individual plant communities. The corrected G-statistic (Sokal and Rolf, 1981) was calculated to test for significant differences (ie increases or decreases) in frequencies between the two years. With small sample sizes, Fisher's exact probability test was substituted. The corrected G is slightly less conservative than chi-squared corrected for discontinuity, and is otherwise equivalent. Species tested were ones frequent enough for Fisher's or chi-squared, as mentioned in chapter 2.

3.2.2.1. Species frequency changes in the whole catchment

To determine which species had increased and which had decreased their frequency for the catchment as a whole, their presence-absence frequencies in each transect were summed. Additional species, not included in the RDA or DCA in chapter 2 or 3, were tested for overall frequency change in the summed data from all transects. These species were infrequent throughout the most parts of the transects, but tests for change could be made on their summed data.

3.2.2.2. Species frequency changes in vegetation groups

Individual species frequency changes within vegetation groups were determined using the summed species frequencies of communities belonging to the groups.

3.2.2.3. Species frequency changes in communities

Changes within communities were tested using the frequency of each species in that community. Because the sample sizes of the various communities were not the same, the amount of change that could be identified as statistically significant (and therefore the power of the test) varied. For each community (each sample size), the percentage change in species frequency that would give a significant G-statistic at P = 0.05 level is provided (Appendix 3.2.3b). A common sense estimate of the amount of change that is *biologically* significant is perhaps around 10% of the 1973 value, but some sample sizes did not always permit this level of difference to be tested.

3.2.3. THE EXTENT OF FLORISTIC CHANGE WITHIN COMMUNITIES

Species turnover within communities was estimated from their floristic similarity in 1973 and 1986 - the proportion of species shared between the two years. Again, only the major species as used in this chapter, were used in this test. The 1973 floristic similarity of different vegetation groups was used to show the range of differences in species composition then present in the catchment. Floristic change over time in one site could therefore be viewed in relation to catchment-wide floristic differences.

Sørensen's (1948) community coefficients (CC) were calculated, with CC = *2a/b+c; a* = the number of species in the community in both 1973 and 1986, *b* = the number of species in the community in 1973 only; and *c* = the number of species in the community in 1986 only.

CC was interpreted as a rough estimate of species turnover, because some species which were present at very low frequencies in 1973 would not have been recorded (even if present) with the lower sampling intensities of 1986, and because not all species in a community were used. Potencially, the change in DCA axis score of a site as measured by the number of average standard deviations of species turnover (SD) it represents, could be used to measure species turnover. However, Olsvig *et al* (1983) compared measures of turnover and concluded that Hill's eigenvector estimate of half change (HC-(EV)) and SD units were unreliable estimates of this parameter.

3.2.4. EVALUATION OF HYPOTHESIZED SPECIES DOMINANCE SEQUENCES

Some of Granger's (1976) hypothesized sequences of species dominance in the vegetation of C IX were tested. The tests were restricted to particular temporal species sequences because Granger did not distinguish clearly between these and supposedly spatial ones.

The hypothesis that species A would "replace" species B in dominance was tested by summing the frequencies of each pair of species in the two years in communities where both were present, and calculating the G-statistic. This tested the significance of a difference in the proportion of the two species between 1973 and 1986.

Although Granger's hypotheses applied to specific site conditions only, hypothesized trends involving species in different areas were the same, so that all communities which contained the initially dominant species were used to make the tests. Where two co-occurring species were said to be replaced by some others, not all combinations were tested (eg if *T.triandra* and *A.appendiculatus* were to replace *E.muticus* and *A.semialata*, only the changes in proportion of *T.triandra* and *E.muticus*, *A.appendiculatus*

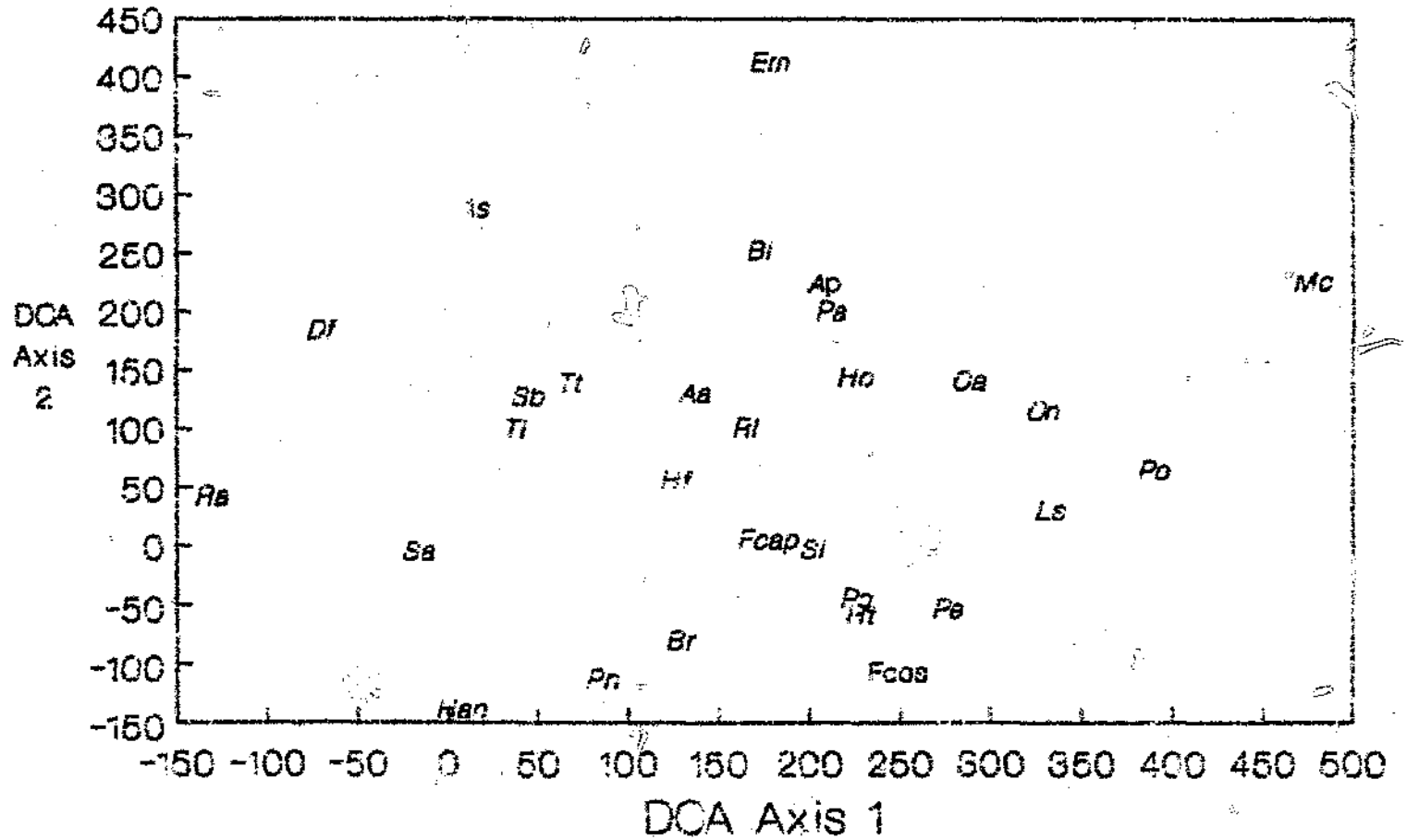


Figure 3.3.1.1 Species ordination showing species scores from the DCA of joint 1973-1986 data.

Ap=*Acalypha punctata*; An=*Alloteropsis semialata*; Aa=*Andropogon appendiculatus*; Br=*Berkheya raphontica*; Si=*Buchnerodera lotononoides*; Cn=*Clutia natalensis*; Ca=*Commelina africana*; Df=*Diheteropogon filifolius*; En=*Elionurus muticus*; Fcap=*Festuca caprina*; Fcos=*Festuca costata*; Hf=*Harpechloa falx*; Hau=*Helichrysum aureo-nitens*; Hu=*Helichrysum umbraculigerum*; Ht=*Helictotrichon turgidulum*; Ls=*Leucosidea sericea*; Mc=*Miscanthidium capense*; Pn=*Panicum natalense*; Pq=*Pellaea quadripinnata*; Pa=*Philippia evansii*; Po=*Polygala ohlendorfiana*; Pa=*Pteridium aquilinum*; Rs=*Rendlia altera*; Rl=*Rubus ludwigii*; Sb=*Senecio pupleuroides*; Si=*Senecio isatideus*; Sa=*Stiburus alopecuroides*; Tt=*Themeda triandra*; Tl=*Tristachya leucothrix*;

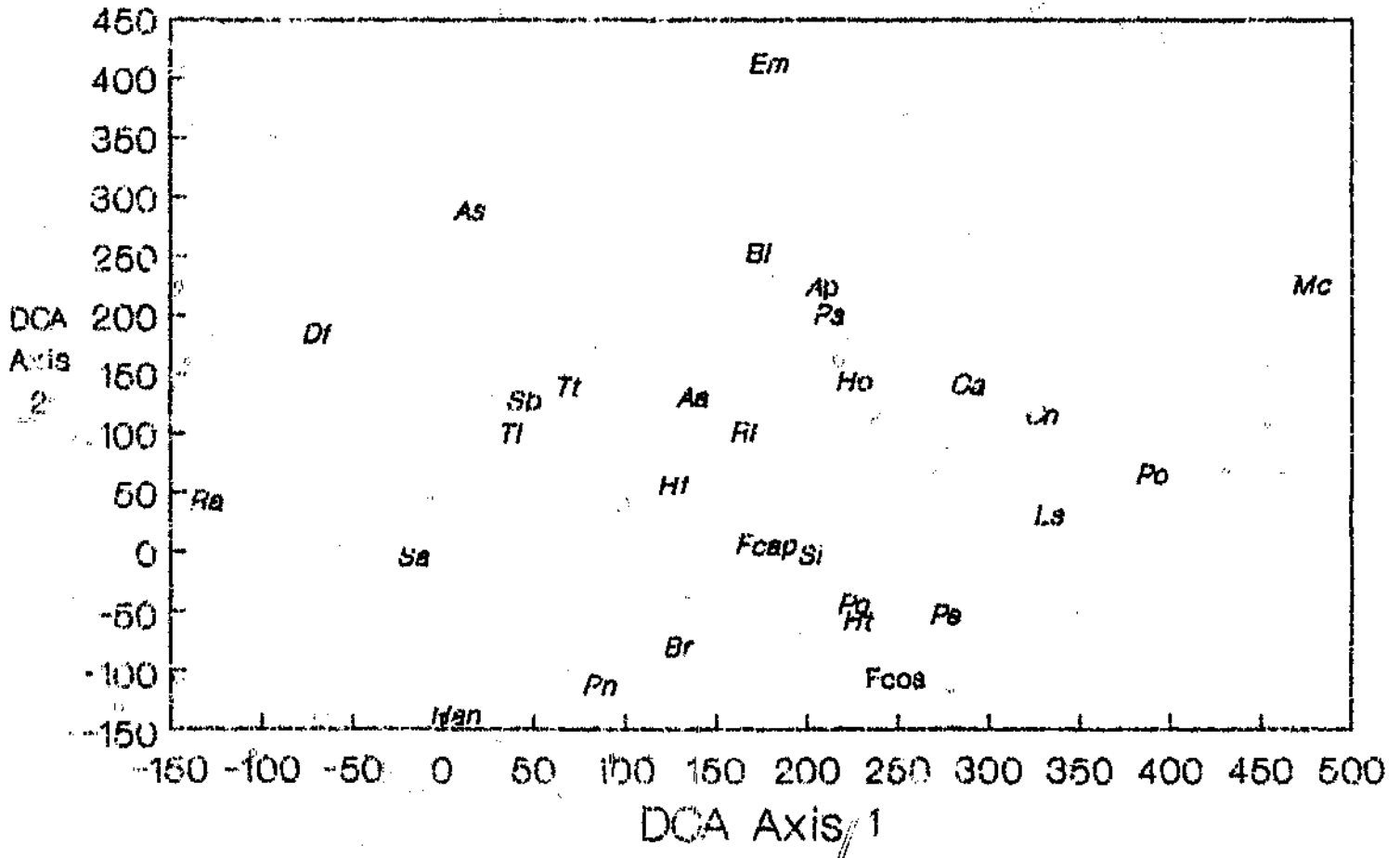


Figure 3.3.1.1 Species ordination showing species scores from the DCA of joint 1973-1986 data.

Ap=*Acalypha punctata*; Aa=*Alloteropsis semialata*; Ad=*Andropogon appendiculatus*; Br=*Berkheya rephenticae*; Bl=*Buchnerodera lotononoides*; Cn=*Clutia natalensis*; Ca=*Cynodon africana*; Df=*Diheteropogon filifolius*; Em=*Elionurus muticus*; Fcap=*Festuca caprina*; Fcos=*Festuca costata*; Hf=*Harpochloa falx*; Han=*Helichrysum aureo-nitens*; Hu=*Helichrysum umbraculigerum*; Ht=*Helictotrichon turgidulum*; Ls=*Leucosidea sericea*; Mc=*Miscanthidium capense*; Pn=*Panicum natalensis*; Pq=*Pellaea quadripinnata*; Pe=*Philippia evansii*; Po=*Polygala ohlendorfiana*; Pa=*Pteridium aquilinum*; Re=*Rendlia altera*; Rl=*Rubus ludwigii*; Sb=*Senecio bupleuroides*; Si=*Senecio isatideus*; Sa=*Stiburus alopecuroides*; Tt=*Themeda triandra*; Tl=*Tristachya leucothrix*;

and *A.semialata*, and *A.appendiculatus* and *E.muticus* were tested.

Granger's hypotheses (given in full in appendix 3.2.3) were as follows:

On shallow soils, *T.triandra* replaces *Diheteropogon filifolius* and *Rendlia altera*.

On steep, cool, south-facing slopes with deep soil, *T.triandra* replaces *E.muticus*, while *A.appendiculatus* replaces *E.muticus* and *A.semialata*. *Philippia evansii*, *Helichrysum aureo-nitens*, *P.aquilinum*, *Rubus ludwigii* and *Leucosidea sericea* replace *T.triandra*, and *Pellaea quadripinnata* replaces *A.semialata*. *L.sericea* replaces *A.appendiculatus*.

On steep, cool, south-facing slopes with shallow soil, *Berkheya rhapontica* replaces *Rendlia altera*, *T.triandra* replaces *Diheteropogon filifolius*, and *P.evansii* and *L.sericea* replace *T.triandra*.

On marshy areas and moist soils, *P.evansii* replaces *Senecio isatideus* and *Miscanthus capense*. *R.ludwigii* replaces *P.aquilinum*, and *L.sericea* replaces *A.appendiculatus*, *M.capense* and *P.aquilinum*.

Other replacements tested were that *H.falx*, *A.appendiculatus* and *T.leucothrix* replace *T.triandra* (from Granger, 1976 and Everson 1985).

3.3 RESULTS

3.3.1. SUCCESSIONAL TRENDS AND THE EXTENT OF OVERALL CHANGES IN C IX

Joint 1973--1986 DCA

DCA of the joint 1973-1986 data resulted in the species ordination shown in fig 3.3.1.1. The first axis showed a gradient from *Miscanthus capense*, *Polygala ohlendorfiana*, *Leucosidea sericea* and *Clutia natalensis* to *Stiburus alopecuroides*, *Diheteropogon filifolius* and *Rendlia altera*. This gradient is essentially similar to that obtained with

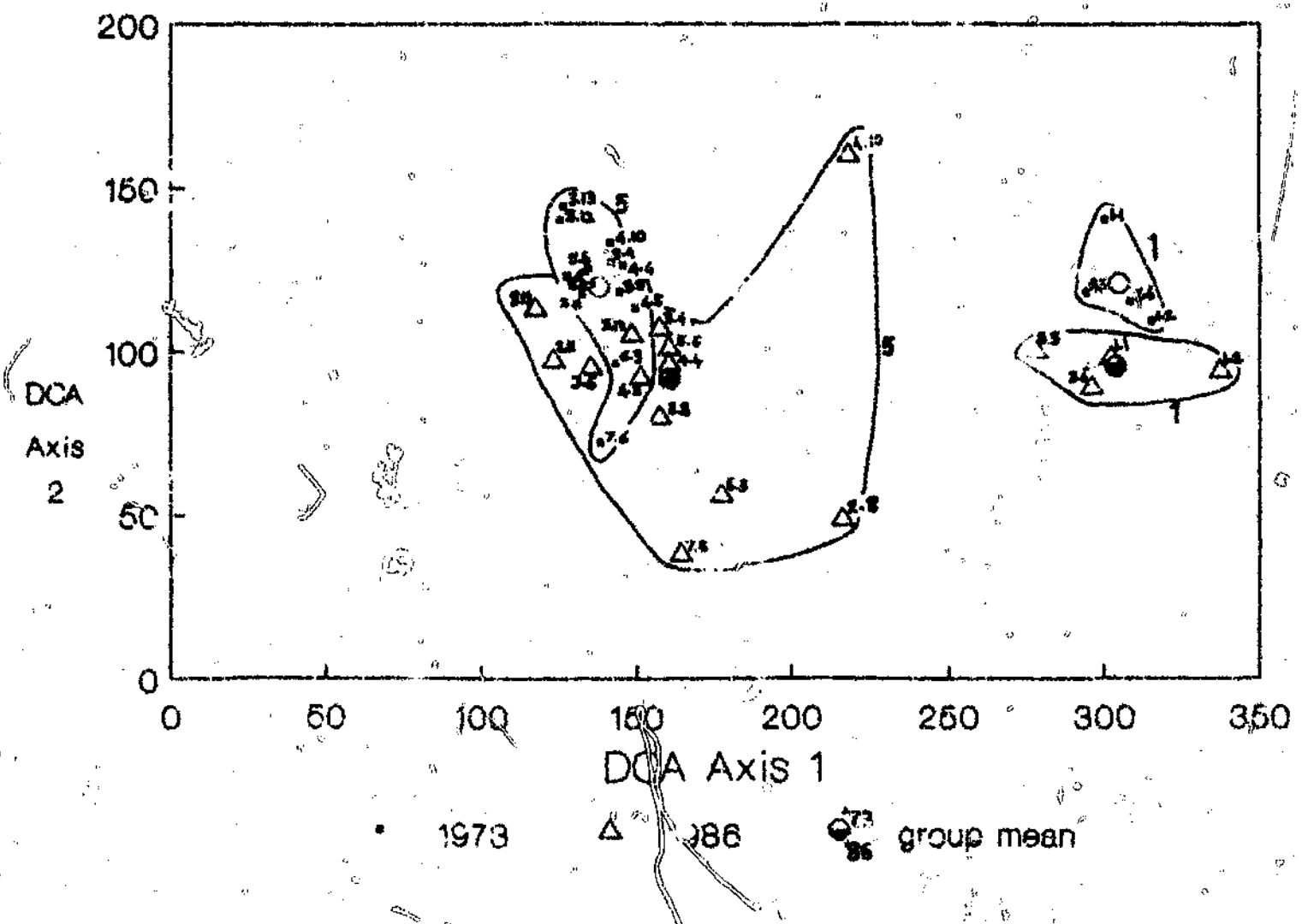


Figure 3.3.1.2 a) Site ordination for the DCA of the joint 1973-1986 data set, showing the change in site scores of communities in vegetation groups 1 and 5. The mean scores for the vegetation groups are also given (group mean).

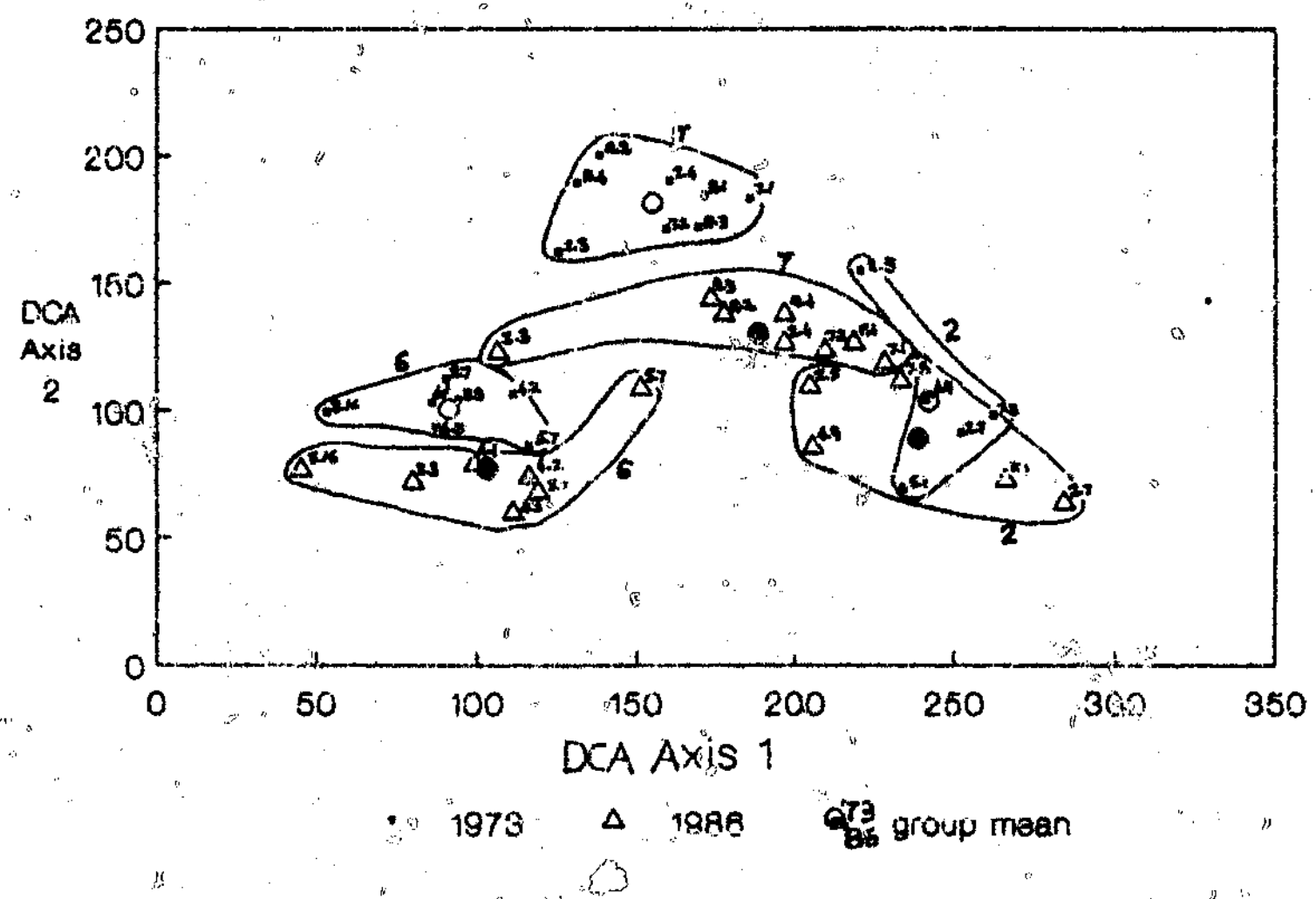


Figure 3.3.1.2 b) Site ordination for the DCA of joint 1973-1986 data, showing the change in site scores of communities in vegetation groups 2, 6 and 7. The mean scores for the vegetation groups are also given (group mean).

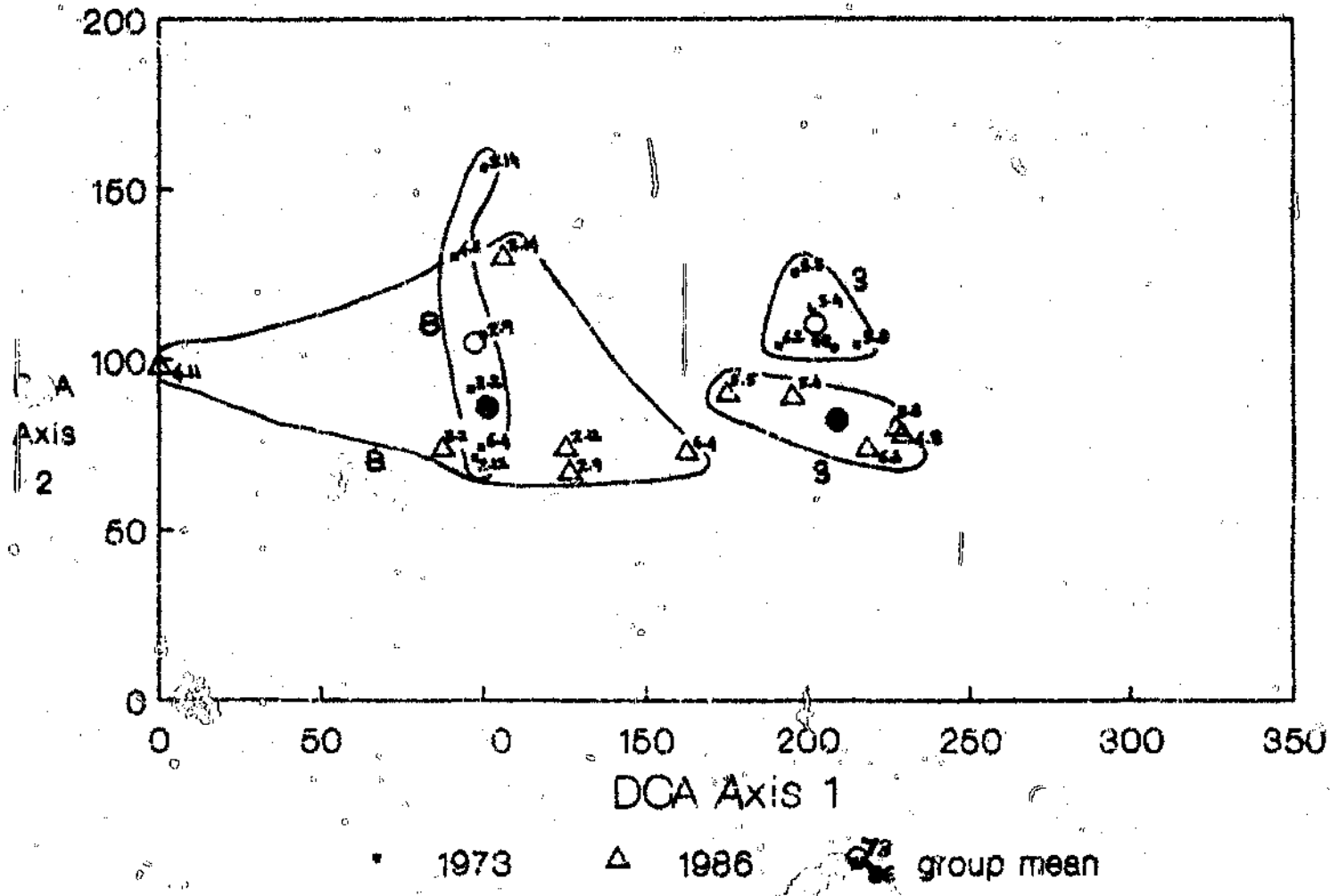


Figure 3.3.1.2 c) Site ordination for the DCA of the joint 1973-1986 data set, showing the change in site scores of communities of vegetation groups B and G. The mean scores for the vegetation groups are also given (group mean).

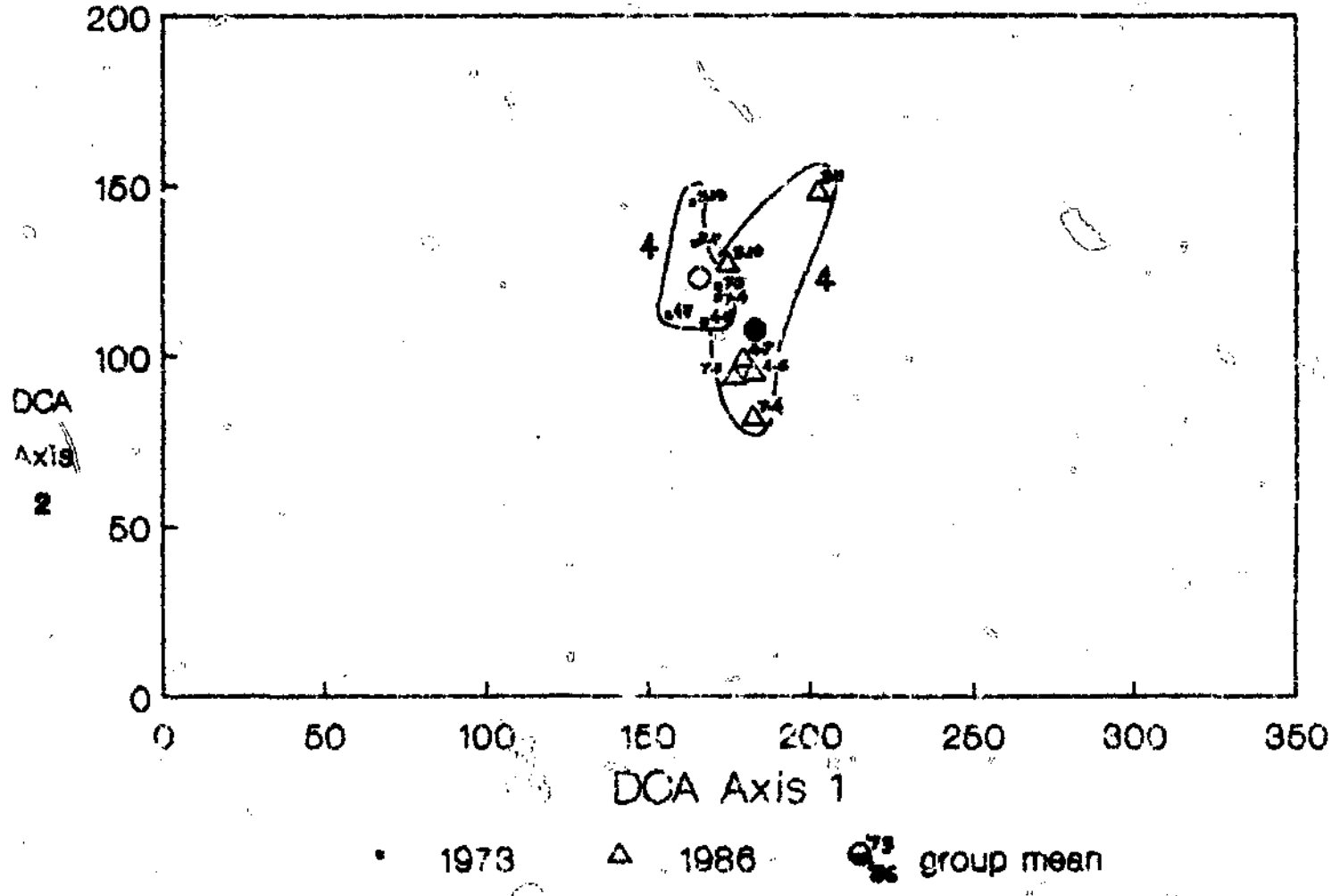


Figure 3.3.1.2 g) Site ordination for the DCA of the joint 1973-1986 data set, showing the change in site scores of communities in vegetation group 4. The mean scores for the vegetation groups are also given (group mean).

the 1973-only data, only *Panicum natalense* and *Helichrysum aureo-nitens* had markedly increased their scores and altered their positions relative to the other species. Other differences were small and the species had retained their overall placings along the gradient.

The second DCA axis was reversed in the joint data ordination. Although there were more differences to the 1973 axis 2, the overall gradient was similar, with *Ellionurus muticus*, *Alloteropsis semialata* and *H.caprinus* having positive axis scores at one extreme and *H.aureo-nitens*, *H.turgidulum* and *S.isatideus* having negative scores at the other. Many species altered their relative positions on the axis, especially *P.natalense*, *Berkheya rhapontica* and *Rubus ludwigii* .

The above differences in species positions resulted in communities being condensed in species space, compared to the 1973-only ordination. Also on axis 2, inter-site (community) distances were more variable than the equivalent distance in 1973 ordination, indicating that species were ordered differently along this axis. This made interpretation of changes more difficult.

3.3.1.1 General trends in the catchment vegetation

The most obvious overall trend in the data was the decrease in axis 2 scores of the 1986 vegetation group means (Fig 3.3.1.2, a) - e)). This implied a move in species composition away from *E.muticus*, *A.semialata*, *Acalypha punctata* and *Buchenroedera lotononoides* towards more *P.natalense*, *H.aureo-nitens*, *Festuca caprina*, *B.rhapontica*, *H.turgidulum* and *Pellaea quadripinnata*. Trends on axis 1 were not consistent, and appeared to depend on the vegetation group. Groups 1, 2, and 3 at one extreme of the axis showed very little change, groups 4 - 7, with non-extreme scores on axis 1, showed some increases in score, group 8 again showed little change, while groups 9 and 10 showed a decrease in axis 1 score.

3.3.1.2. Trends and the extent of overall changes within vegetation groups

Trends of change within individual vegetation groups reflected the consistent decrease in the axis 2 scores, with some exceptions (T4.10 in group 5, T7.7 in group 9, 5.1 in group 10, T2.12 and T6.4 in group 8, T5.7 in group 6, and T8.1 and T7.3 in group 2). Trends on axis 1 were again relatively inconsistent, with similar communities in a vegetation group diverging. However, the bigger trend was toward an increase in axis 1 score (see fig 3.3.1.2 a) – e)).

Only vegetation groups 5 and 7 showed significant differences in group mean axis 1 scores between the two years. Groups 3, 5, 6, 7 and 9 showed significant differences in axis 2 scores (table 3.3.1.2). The greatest changes in axis 2 score were in vegetation groups 7 (-51.37), 9 (-30.83) and 5 (-28.15). All other significant changes in vegetation group mean scores were small, partly a reflection of divergence in species composition within groups.

Table 3.3.1.2. Vegetation group mean axis scores in 1973 and 1986 for DCA axis 1 and 2, showing least significant difference levels and significant differences in scores for the group means.

VEGETATION GROUP	YEAR	MEAN	S.E.	L.S.D	P< 0.05
AXIS 1					
1	1973	304.2[illegible]			
	1986	303.25	12.6886	35.7	NS
2	1973	241.80			
	1986	238.40	11.3491	31.9	NS
3	1973	202.20			
	1986	208.80	11.3491	31.9	NS
4	1973	165.33			
	1986	182.50	10.3602	29.2	NS
5	1973	137.48			
	1986	160.23	7.0384	19.8	S
6	1973	91.00			
	1986	103.00	9.5717	26.9	NS
7	1973	114.75			
	1986	167.87	8.9722	25.2	S
8	1973	97.17			
	1986	101.00	10.3602	29.1	NS
9	1973	53.57			
	1986	41.33	10.3602	29.1	NS
10	1973	174.25			
	1986	187.75	12.6886	35.7	NS
AXIS 2					
1	1973	120.50			
	1986	95.25	10.9293	30.8	NS
2	1973	103.40			
	1986	89.00	9.7755	27.5	NS
3	1973	110.20			
	1986	82.20	9.7755	27.5	S
4	1973	122.83			
	1986	107.50	8.9238	25.1	NS
5	1973	119.62			
	1986	91.46	6.0605	17.1	S
6	1973	100.43			
	1986	77.00	8.2618	23.2	S
7	1973	181.38			
	1986	130.00	7.7282	21.7	S
8	1973	104.83			
	1986	86.00	8.9238	25.1	NS
9	1973	130.83			
	1986	100.00	8.9238	25.1	S
10	1973	103.00			
	1986	87.00	10.9293	30.8	NS

Table 3.3.1.3. Significant changes at P < .05 level in the DCA axis score of individual communities, with least significant differences calculated from ANOVA.

VEGETATION GROUP	COMMUNITY	SCORE 1973	SCORE 1986	CHANGE IN SCORE
AXIS 1	L.S.D at P< .05 = 27, at P< .001 = 32*			
2	T2.7	253	284	31
2	T4.9	241	205	-36*
2	T6.1	234	266	32*
2	T7.3	262	233	29
3	T6.2	191	218	27
4	T3.11	164	202	38*
5	T2.8	135	216	81*
5	T4.10	141	218	77*
5	T6.3	143	177	34*
6	T3.7	90	119	29
6	T5.7	116	151	35*
7	T2.4	160	196	36*
7	T7.1	185	228	43*
7	T7.2	159	209	50*
7	TA.1	171	218	47*
7	TA.2	138	177	39*
7	TA.4	131	196	65*
8	T2.12	97	125	28
8	T4.11	91	0	-91*
8	T6.4	99	162	63*
9	T2.1	81	20	-61*
9	T7.7	62	0	-62*
AXIS 2	L.S.D. at P< .05 = 30; at P< .001 = 36*			
1	T1.1	140	98	-42*
2	T2.5	155	110	-45*
3	T5.5	125	90	-35
5	T2.3	120	49	-71*
5	T3.8	118	80	-38*
5	T3.12	140	105	-35
5	T3.13	144	113	-31
5	T4.4	126	96	-30
5	T6.3	96	56	-40*
5	T7.6	72	38	-34
6	T3.3	104	72	-32
6	T3.7	112	68	-44*
6	T4.2	106	74	-32
6	T4.3	93	60	-33
7	T2.3	162	123	-39*
7	T2.4	190	127	-63*
7	T7.1	183	119	-64*
7	T7.2	171	124	-47*
7	TA.1	184	127	-57*
7	TA.2	200	138	-62*
7	TA.4	189	138	-51*
8	T2.9	107	67	-40*
8	T4.11	130	98	-32
9	T2.1	178	96	-82*
9	T2.2	160	113	-47*
9	T3.1	106	46	-60*
10	T3.9	105	62	-43*

Chi-squared tests for overall change in species frequency within vegetation groups were more sensitive than the test done for DCA group means. In order of decreasing difference between years, groups 3, 7, 10, 4, and 5 showed significant changes (Chi-squared = 17.6, 8.9, 8.62, 6.9 and 5.89 respectively). The changes in group 10 and 4 were "undetected" by the test on the DCA, and group 9 showed no difference using chi-squared, but was different on DCA axis 2 with the other test.

3.3.1.3. The extent of overall change within plant communities

Table 3.3.1.3 shows the axes scores of communities significantly different at $P < 0.05$. The biggest changes on axis 1 occurred in T4.11 (-91), T2.8 (81) and T4.10 (77). The biggest changes on axis 2 were in T2.1 (-82) and T2.8 (-71). Most of the axis 1 and 2 changes were significant at the $P < 0.001$ level. For axis 2, those not significant at this level were considered unchanged because of the 'distortion' in this axis. More communities changed in vegetation group 7 than in any other vegetation group, while communities in vegetation groups 1, 3, 4 and 10 showed few significant changes.

3.3.2. CHANGES IN SPECIES FREQUENCIES IN C IX

3.3.2.1. Species frequency changes in the whole catchment

There were no extreme changes in the frequency (catchment-wide) of any species in C IX (see table 3.3.2.1). *L.sericea*, *Wahlenbergia krebsii*, *Diheteropogon amplectens*, *H.turgidulum* and *P.quadripinnata* showed the biggest increases (22.1%, 21%, 19.9%, 17.9% and 15.7% respectively) and *T.triandra*, *A.appendiculatus* and *D.filifolius* showed the biggest decreases in frequency (18.5%, 12.9% and 12.3% respectively). Table 3.3.1.2.1 shows the species with significant frequency changes since 1973. *P.aquilinum*, *C.natalensis*, *B.rhapontica*, *Festuca costata*, *Stiburus alopecuroides*, *Polygala ohlendorfiana*, *M.capense*, *T.spicatus*, *Gunnera perpensa* and *Aster perfoliatus* remained unchanged.

Table 3.3.2.1. Changes in species' frequencies in the whole of C IX since 1973, significant at p<0.05..

SPECIES Frequency:	% in 1973	% in 1986	% CHANGE
INCREASES			
L.sericea	8.5	30.6	22.1
Wahlenbergia krebsii	0.5	21.5	21.0
D.amplectens	2.4?	22.3	19.9?
H.turgidulum	3.3	21.3	17.9
P.quadripinnata	5.6	21.3	15.7
P.natalense	0.4	10.0	9.6
C.africana	16.5	24.2	7.6
P.evansii	6.1	8.3	2.2
H.aureo-nitens	2.9	9.9	6.9
H.falx	38.4	45.4	6.9
R.ludwigii	28.4	32.2	3.9
R.altera	10.5	13.9	3.5
Vernonia hirstuta	12.9	15.3	2.4
Myrsine africana	1.9	3.8	1.9
Schistostephium crataegifiorum	2.5	3.7	1.2
DECREASES			
T.triandra	78.1	59.6	-18.5
A.appendiculatus	42.3	29.2	-12.9
D.filifolius	21.4	9.2	-12.3
S.bupleuroides	31.5	23.1	-8.4
Helichrysum glomeratum	10.1	3.0	-7.1
A.punctata	37.0	30.2	-6.8
H.contortus	13.1	6.3	-6.8
A.semialata	17.2	12.2	-5.0
E.muticus	10.6	6.0	-4.6
T.leucothrix	60.3	56.1	-4.17
H.umbraculigerum	37.8	34.4	-3.39
S.isatideus	7.41	5.47	-1.94
B.lotononoides	3.8	2.26	-1.54

3.3.2.2. Species frequency changes in vegetation groups

The most widely occurring changes involved *L.sericea*, *P.quadripinnata*, *H.turgidulum*, *T.triandra*, *A.appendiculatus*, *P.natalense* and *D.filifolius*. Figs 3.3.2.2 a) — e) show changes in the % frequencies of some species in each of the ten vegetation groups, and in conjunction with fig 2.3.3.3 show how species are distributed in C IX with respect to these vegetation groups.

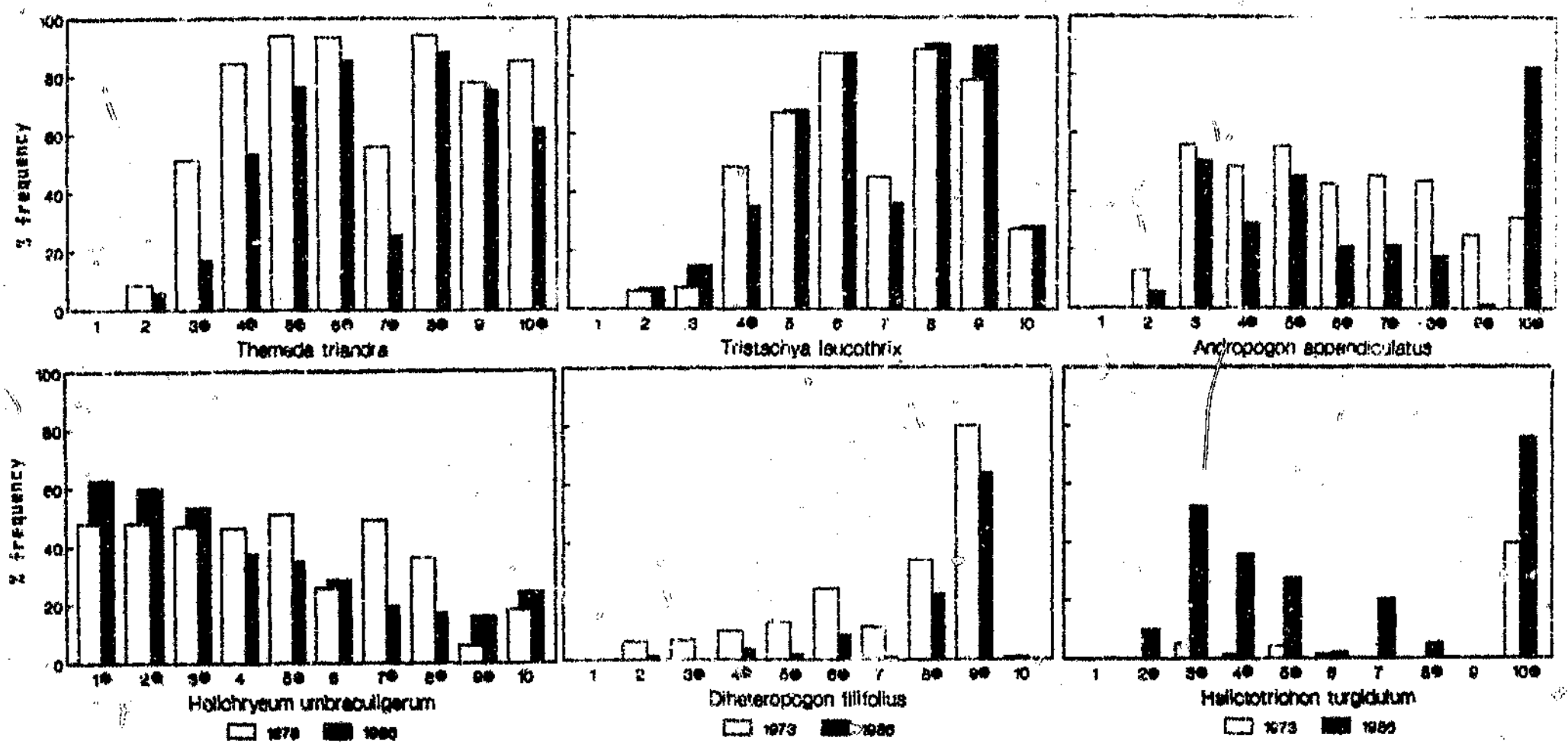


Figure 3.3.2.2 a) Changes in the % frequency of species in vegetation groups 1 to 10 (numbered on the bottom axis). Those vegetation groups showing significant changes in species frequency (using the G-statistic) at P < .05, are marked with a dot (•).

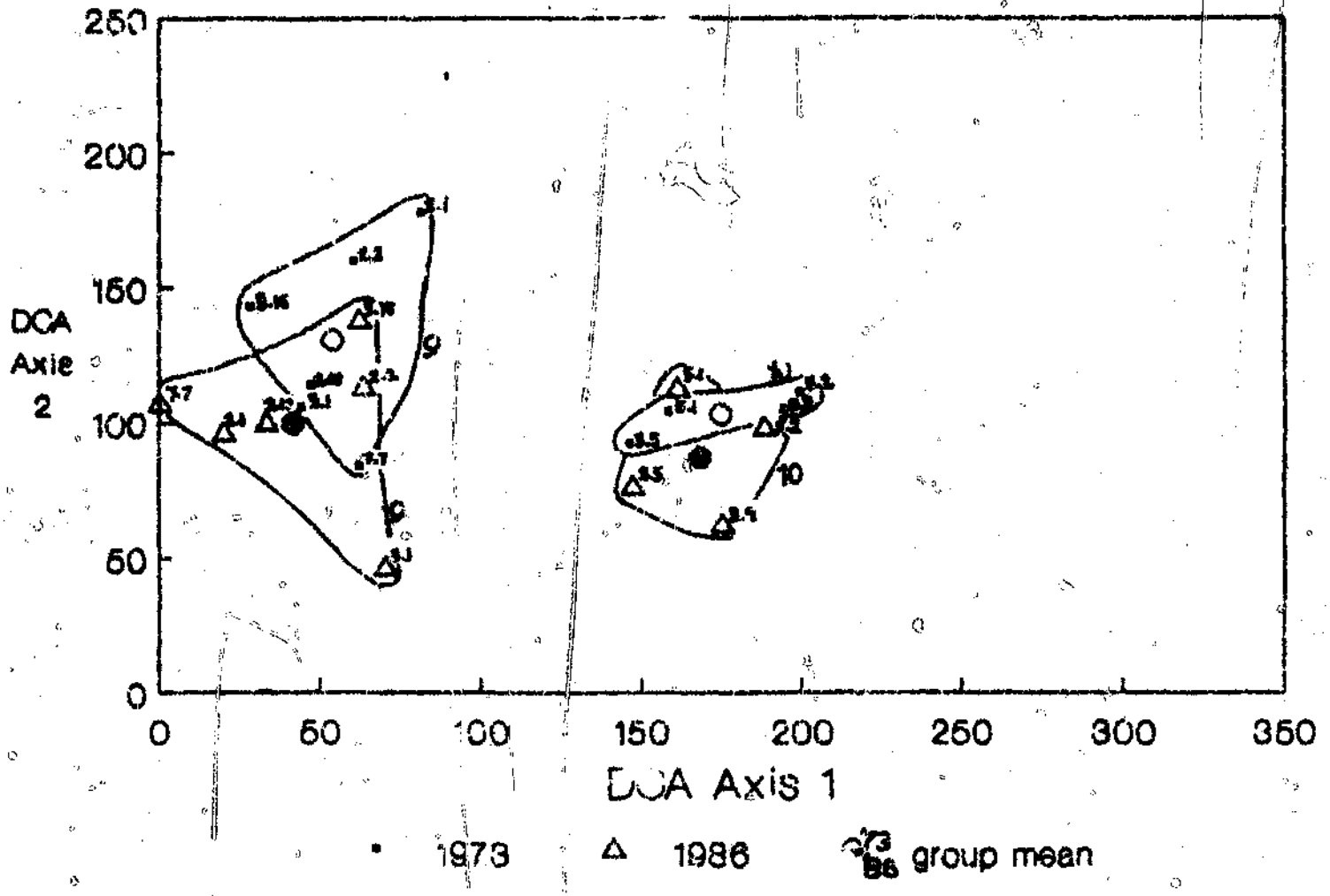


Figure 3.1.1.2 a) Site ordination for the DCA of the joint 1973-1986 data set showing the change in site scores of communities in vegetation groups 9 and 10. The mean scores for the vegetation groups are also given (group mean).

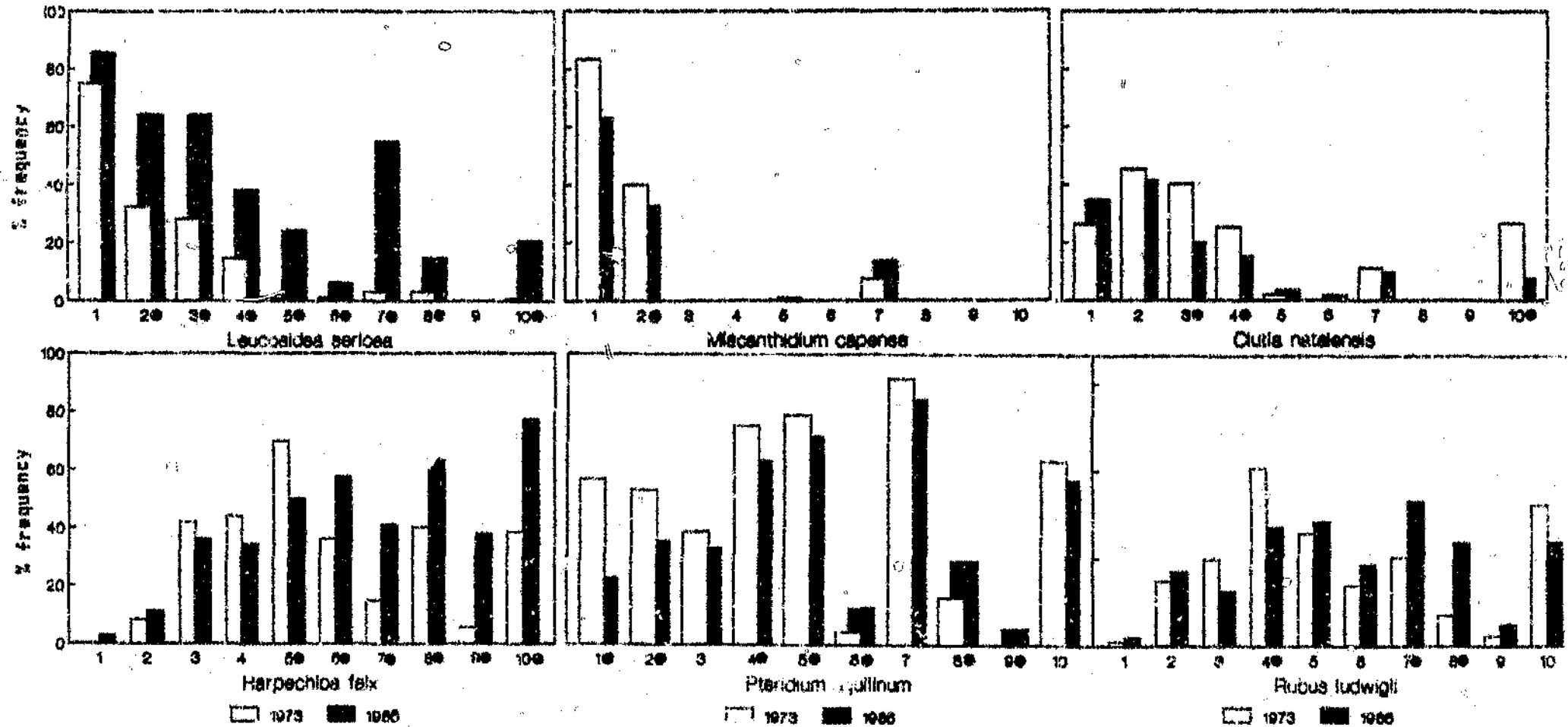


Figure 3.3.2.2 b) Changes in the % frequency of species in vegetation groups 1 to 10 (numbered on the bottom axis). Those vegetation groups showing significant changes in species frequency (using the G-statistic) at $P < .05$, are marked with a dot (•).

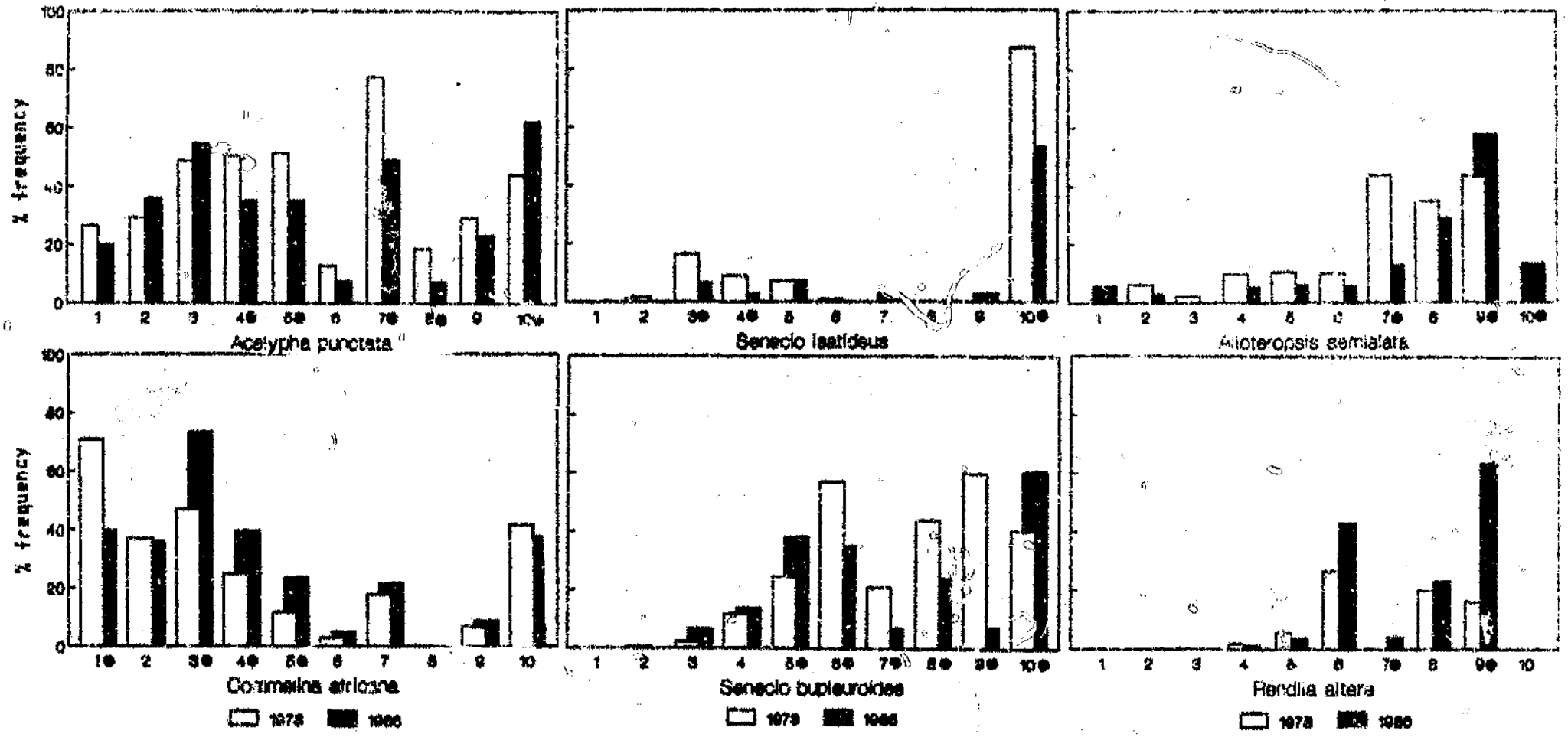


Figure 3.3.2.2 c) Changes in the % frequency of species in vegetation groups 1 to 10 (numbered on the bottom axis). Those vegetation groups showing significant changes in species frequency (using the G-statistic) at P < .05, are marked with a dot (•).

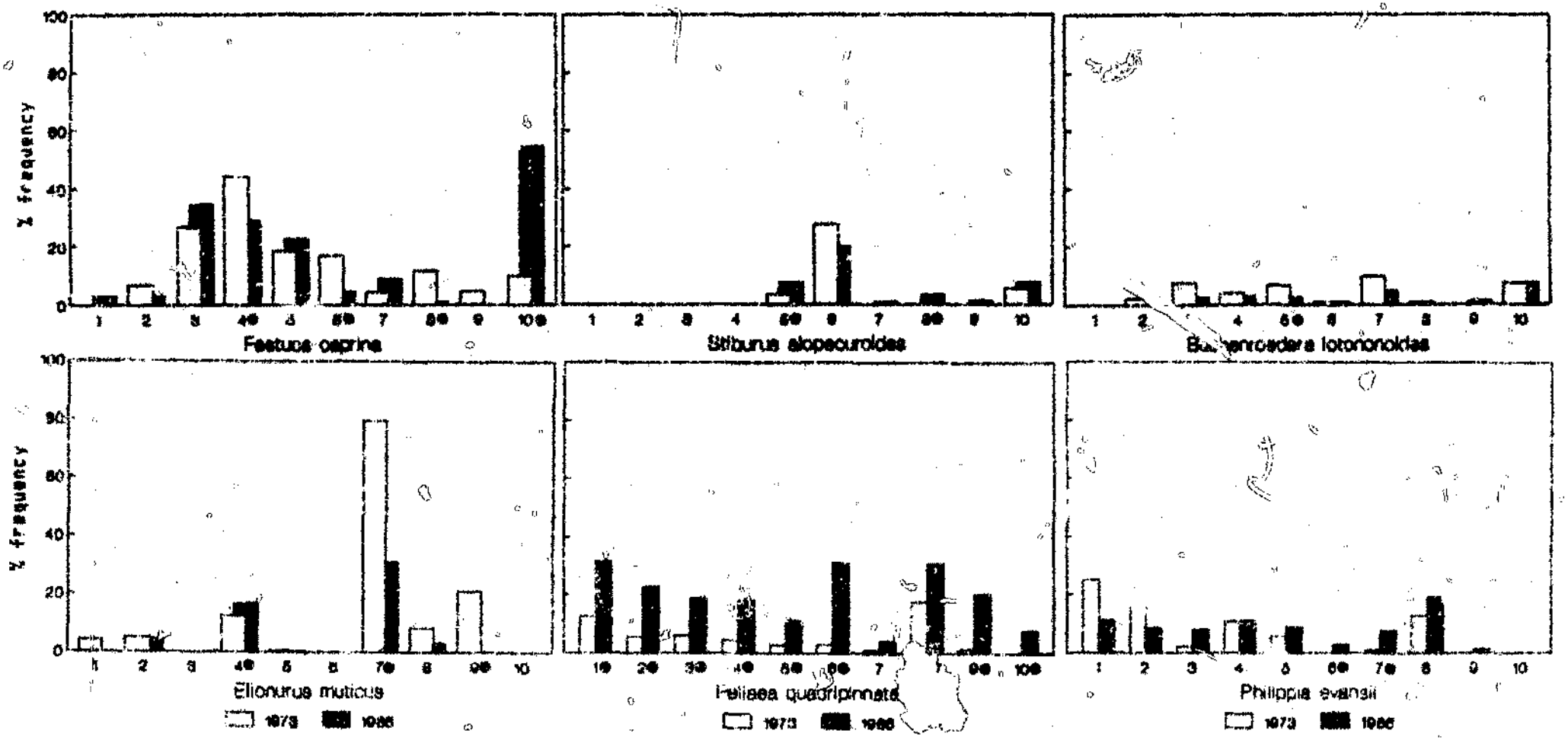


Figure 3.3.2.2 d) Changes in the % frequency of species in vegetation groups 1 to 10 (numbered on the bottom axis). Those vegetation groups showing significant changes in species frequency (using the B-statistic) at $P < .05$, are marked with a dot (•).

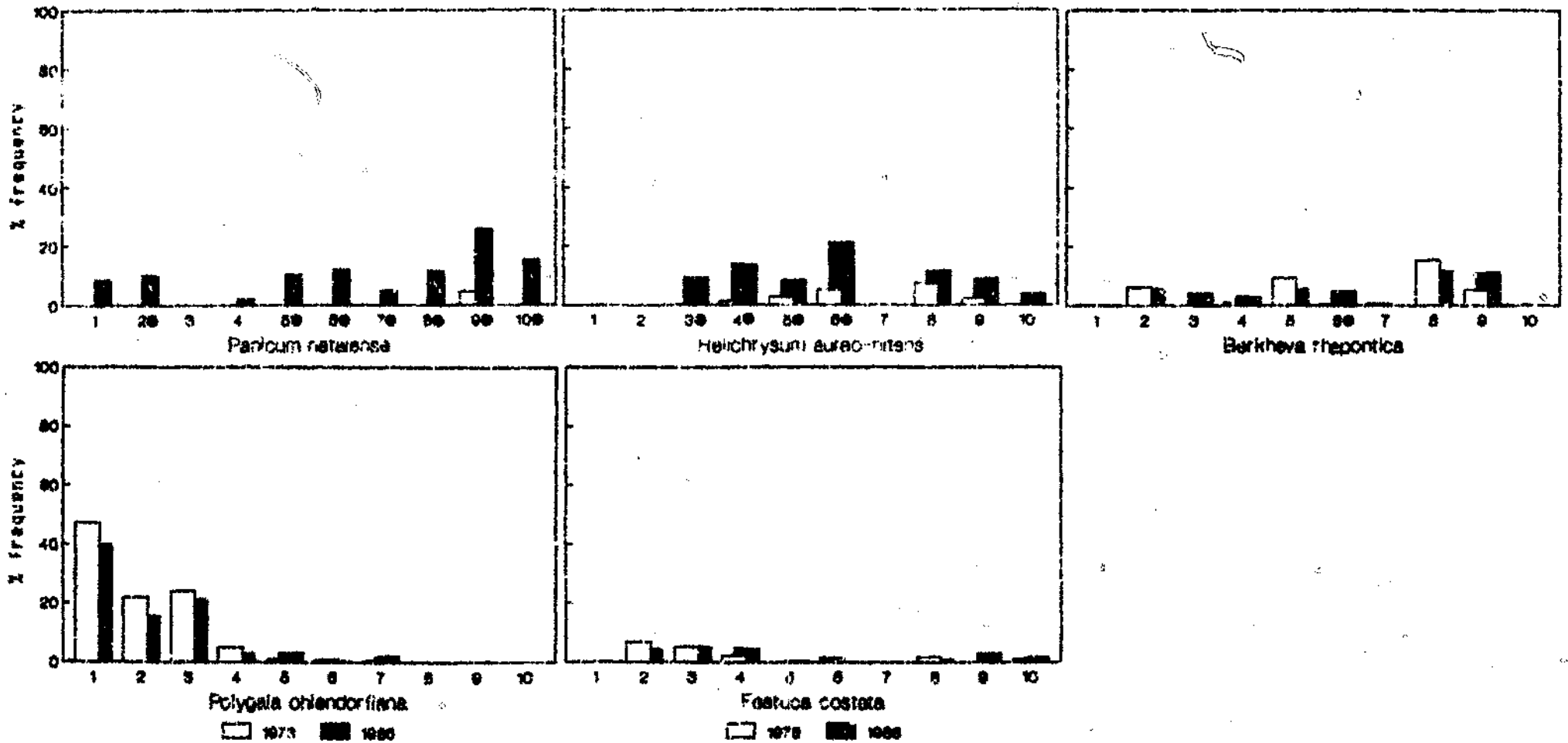


Figure 3.3.2.2 a) Changes in the % frequency of species in vegetation groups 1 to 10 (numbered on the bottom axis). Those vegetation groups showing significant changes in species frequency (using the G-statistic) at P < .05, are marked with a dot (•).

L.sericea increased the most in vegetation group 7, which was dominated by *P.aquilinum* and included the old fire-break area east of the weir. Areas least invaded were in vegetation group 6 and 8 where *P.aquilinum* was infrequent, and *T.triandra* dominated. Vegetation group 9, on shallow dry soils where *D.filifolius* was most frequent, still lacked *L.sericea*. *C.natalense* increased in mature areas of *L.sericea* (vegetation group 1), but decreased in other areas, especially in those vegetation groups occurring toward the head of C IX (3, 10 and to some extent 4). *M.capense* decreased in mature *L.sericea* areas (1 and 2), and increased in vegetation group 7 where *L.sericea* was still immature and invading extensively.

P.aquilinum decreased in vegetation groups occurring lower down in C IX, and increased in groups [illegible] which occurred at higher altitudes. This pattern of change [illegible] reflects the outward clonal growth of *P.aquilinum* colonies into new areas and the degeneration of older parts of the colonies (eg Watt 1947) which originated lower in the catchment.

D.filifolius was almost lost in most vegetation groups since 1973. Only groups 8 and 9 still had >20% of quadrats containing this species. *T.triandra* decreased most in more moist vegetation groups nearer streams in the catchment (3, 4, 7 and 10), and least in drier, higher sites (9, 8 and 6). *T.leucothrix* decreased only in vegetation group 4. Although it also decreased overall, *A.appendiculatus* showed the opposite trend to *T.triandra*: It increased in some more moist sites (vegetation group 10), and decreased most in drier sites (9, 8 and 6).

H.turgidulum and *F.caprina* increased most in more moist vegetation groups (excluding *L.sericea* dominated groups 1 for *H.turgidulum* and 2 for *F.caprina*), while *H.falx* increased mostly in drier areas (9, 8, 6) but also in some more moist sites (7 and 10). It decreased in vegetation group 5. *S.alopecuroides* decreased in the relatively dry vegetation group 6, and spread to other areas (7, 8, 9). *R.altera* and *A.semialata* both increased in vegetation groups 7 and

9, but the latter also increased in 10, where *R.altera* remained absent.

P.natalense and *P.quadripinnata* appeared to increase throughout most of the catchment, though *P.natalense* more so in higher altitude sites (9, 10, 3, and 6). The "fynbos" species *Buchenroedera lotononoides* showed a slight decline in most of its range.

Changes in other species are given in fig 3.3.2.2 and appendix 3.3.2.2, which shows the average percentage frequencies of species in the vegetation groups, with species ordered as they occur along the DCA axis 1.

DCA showed that groups 5 and 7 had the greatest change in axes scores. These two groups were therefore compared in more detail. In both vegetation groups *P.aquilinum* was present at >75% frequency, and *L.sericea* was initially virtually absent, but in group 5, *T.triandra* dominated the grass layer while *E.muticus* dominated in group 7. *T.triandra*, *A.punctata*, *H.umbraculigerum*, *D.filifolius*, and *A.aspendiculatus* decreased in both, while *P.natalense*, *H.turgidulum* and *L.sericea* increased in both. Notable differences were that *H.falx* decreased in group 5 and increased in group 7, and *Senecio bupleuroides* increased in 5 and decreased in 7.

3.3.2.3. Species frequency changes within communities

All the changes in species frequencies in individual communities could not be described, but the results of tests for differences in frequencies between years are given in appendix 3.3.2.3 a) and b).

Some communities which had shown the greatest changes (from the results of DCA (3.1.3) and tests for species turnover - see below) were chosen to examine in more detail. Percentage frequencies of species in 1973 and 1986 were graphed, with species ordered from those showing the greatest decreases in overall frequency to those showing the greatest overall increases (from 3.3.2.1).

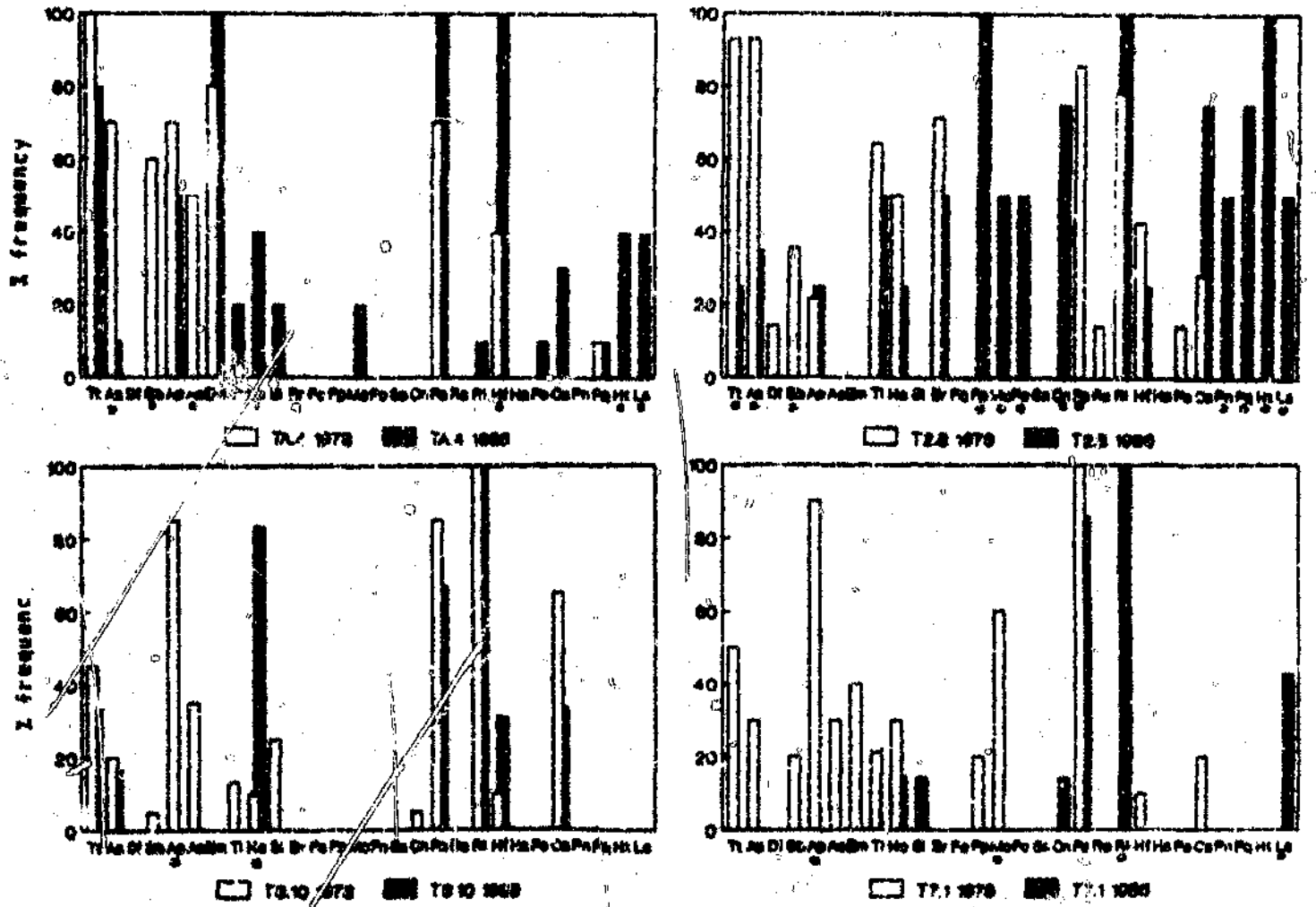


Figure 3.3.2.3 a) Species frequencies in 1973 and 1986 in certain *Pteridium aquilinum* dominated communities which showed greater turnovers or frequency changes than other such communities. Species are ordered from those showing the greatest decreases in C II to those showing the greatest increases.

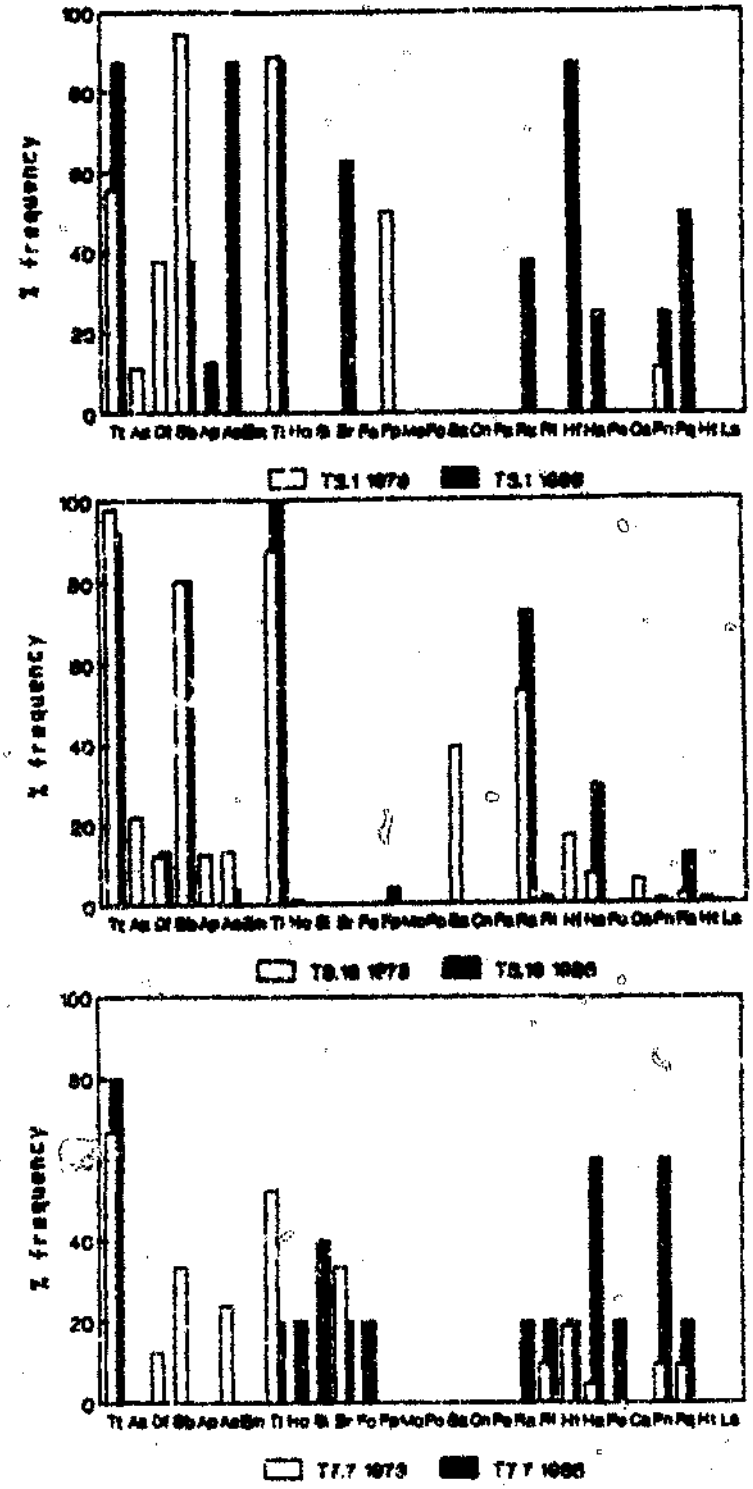


Figure 3.3.2.3 b) Species frequencies in 1973 and 1986 in certain ridge top communities which showed greater species turnovers or species frequency changes than others. Species are ordered from those showing the greatest decreases in C IX to those showing the greatest increases.

Firstly, many communities containing >50% *P.aquilinum* had large changes. These were TA.4, T2.8, T3.10 and T7.1 (see fig 3.3.2.3 a). These four communities all had low sampling intensities, which undoubtedly contributed to the apparent changes. However, they were also all quite accurately relocated in 1988, being near marker-poles left in 1973, so that these results do reflect the field situation.

The two quite similar communities TA.4 and T7.1 showed different changes, *H.falx* and *H.turgidulum* increasing in TA.4 only, and *R.ludwigii* increasing in T7.1. *Acalypha punctata* and *N.capense* decreased in T7.1, while *A.punctata* remained constant in TA.4, and *N.capense* made an appearance (not significant), along with *H.umbraculigerum*. These differences may be partly due to the different fire history of the sites: TA.4 occurred in the old fire-break which had previously had a higher fire frequency and less time since withdrawal of fire.

T2.8, which occurred on the steep bank above the stream, showed increases in *N.capense*, *L.sericea*, *Pellaea quadripinnata* and other species, but *P.aquilinum* declined along with *T.triandra* and *A.appendiculatus*. T3.10 showed an increase in *H.umbraculigerum* at the expense of *A.punctata*, and *L.sericea* did not colonize as in the other communities.

Secondly, communities occurring on the catchment ridges in drier, shallower soil had also changed, including T3.1, T3.16 and T7.7 (see fig 3.3.2.3 b). These areas lacked *P.aquilinum* and were each dominated by *T.triandra*, *T.leucothrix* and other grasses (*F.caprina* and *D.filifolius*; *R.altera*; and *A.semialata* respectively). The forb *S.bupleuroides* was also common in these three communities. T3.1 had a big increase in *H.falx* and *A.semialata* and some forb species. T3.16 maintained its dominant grasses, unlike T7.7. *H.aureo-nitens* increased in all three communities.

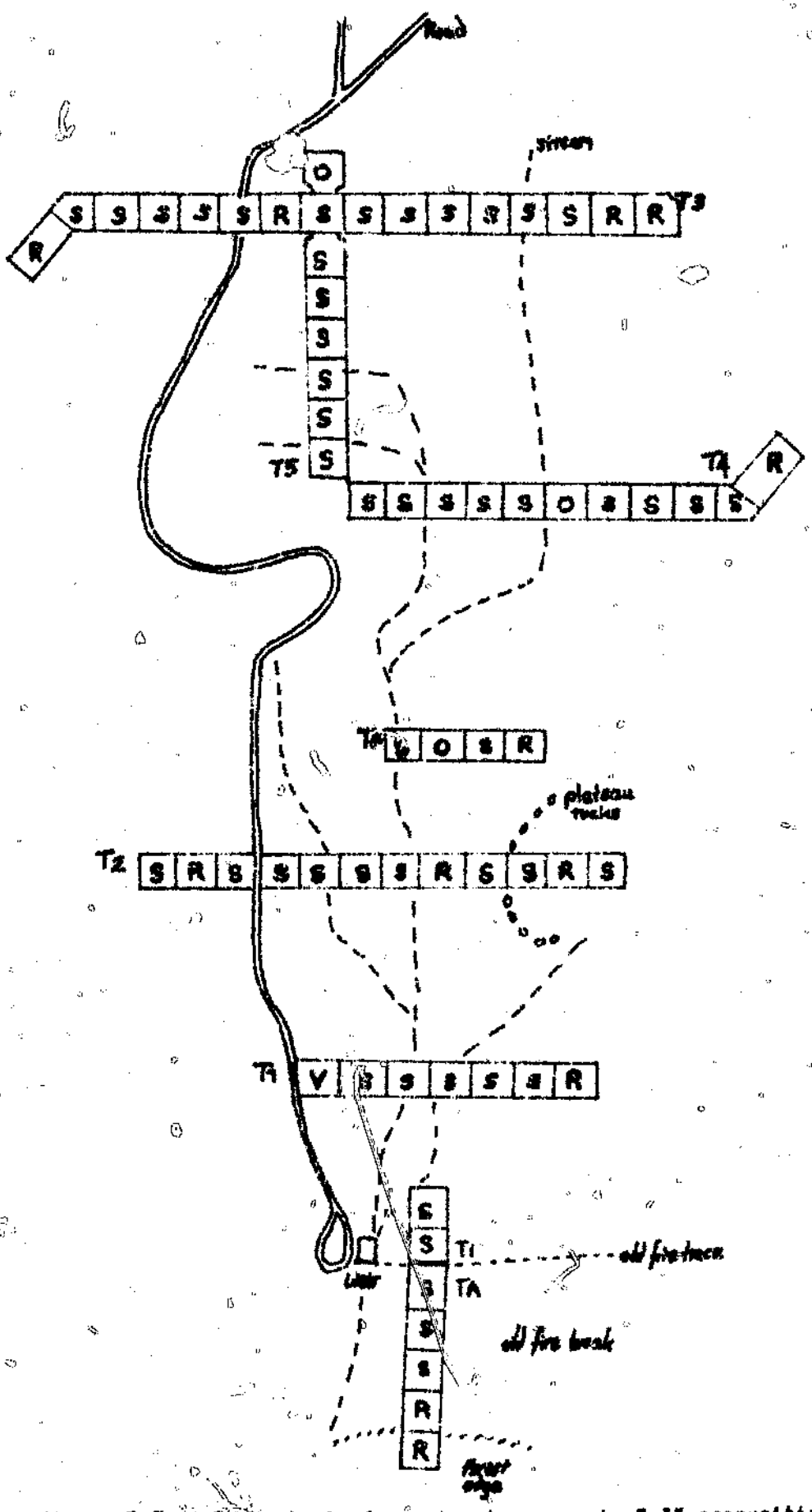


Figure 3.7.: The extent of species turnover in C II communities since 1973. O = no turnover, more than 90 % of species were present in both years; S = slow change, 65-90%; R = rapid change, 35-64%; V = very rapid, 0-34% of species were present in both years.

3.3.3. THE EXTENT OF FLORISTIC CHANGE WITHIN COMMUNITIES

To indicate the initial range of differences in species composition in C IX, the floristic similarities of vegetation groups was determined. The most different vegetation groups in C IX (groups 1 versus 10, 6 and 8) represented a total turnover of 46.7 to 50% of their (major) species. Floristically, most vegetation groups were similar, sharing more than 75% of their species, indicating that vegetation differences mainly involved the relative frequencies of species.

As expected from vegetation group differences, most communities did not have a high level of species turnover - they contain similar species in 1973 and 1986 (most estimates of %CC were from 65 to 90%). However, twelve communities had a greater degree of turnover, with %CC = 35 to 64%. Three communities shared 20% or more of their species at both times, and one community showed dramatic changes, with only 28.6% of its key species in common between the years.

Fig 3.3.3 shows the positions of the communities in C IX and their extent of species turnover. Many of the areas showing greater turnover are toward the rim of the catchment, in grasslands on shallower soils. Others are in forest margins (TA,5), or in *P.aquilinum* areas with *L.sericea* invasion (T7.1; TA,4, T2.8). Areas with no change (0) were adjacent to drainage lines. Community 7.1 which showed the greatest change, had 'lost' *T.triandra*, *A.appendiculatus*, *A.punctata*, *E.muticus* and *N.capense* and gained *L.sericea* and *R.ludwigii*. Although the sample size was [illegible], this community was located at the original marker point of its [illegible] and the samples from the two years would have been in the identical places.

3.3.4. EVALUATION OF HYPOTHESIZED SPECIES DOMINANCE SEQUENCES

Most of the hypothesized dominance sequences were supported by the data. Those not supported involved the species *A.appendiculatus*, *R.altera* and *P.aquilinum*.

Table 3.3.4. Tests for significant changes in proportion of two species in hypothesized replacement sequences. If a hypothesized replacement (of sp.B by sp.A) is supported, then the proportion (sp.A/sp.B) in 1986 will be significantly greater than in 1973. The number of communities used in each test (and which contained both species), is given in brackets.

REPLACEMENT SEQUENCE (A replaces B = A > B)		Proportion of A to B 1973	1986	p
T.triandra > *D.filifolius*	(42)	3.18	5.81	<.001
T.triandra > *R.altera*	(29)	5.37	3.06	<.001
T.triandra > *E.muticus*	(14)	2.86	3.51	NS
A.appendiculatus > *A.semialata*	(42)	1.73	1.43	NS
A.appendiculatus > *E.muticus*	(18)	1.77	1.59	NS
H.aureo-nitens > *T.triandra*	(23)	0.06	0.31	<.001
R.ludwigii > *T.triandra*	(52)	0.37	0.59	<.001
P.aquilinum > *T.triandra*	(50)	0.65	0.87	<.001
L.sericea > *T.triandra*	(43)	0.12	0.73	<.001
P.dvansii > *T.triandra*	(24)	0.18	0.33	<.001
P.quadripinnata > *A.semialata*	(29)	0.29	1.32	<.001
L.sericea > *A.appendiculatus*	(43)	0.21	1.15	<.001
R.rhapontica > *R.altera*	(14)	1.24	0.66	<.01
P.aquilinum > *M.capense*	(14)	1.95	1.84	NS
P.aquilinum > *S.isatideus*	(25)	3.5	4.73	<.01
R.ludwigii > *P.aquilinum*	(50)	0.56	0.67	<.01
L.sericea > *P.aquilinum*	(45)	0.22	0.79	<.001
L.sericea > *M.capense*	(15)	0.73	2.04	<.001
H.falx > *T.triandra*	(58)	0.49	0.79	<.001
T.leucothrix > *T.triandra*	(58)	0.77	0.94	<.01
A.appendiculatus > *T.triandra*	(57)	0.53	0.49	NS

A.appendiculatus showed an unpredicted relative decline, while *R.altera* showed an unpredicted relative increase. *P.aquilinum* did not replace *M.capense*: both species decreased their frequency in the presence of mature *L.sericea*. *P.aquilinum* did not replace *S.Isatideus* in dominance throughout its range, but did so in communities of vegetation group 10 (see fig 3.3.2.2 a) and b)). Table 3.3.4. shows the proportion of the species pairs in 1973 and 1986, and the probability of the observed difference in proportion occurring by chance.

3.4. DISCUSSION

General successional trends

The general trend of vegetation change in catchment C IX was shown using DCA, as a shift towards more of those species scoring < 100 on axis 2 of the joint 1973-86 DCA (see fig 3.3.1.1). Viewing individual species changes in the whole catchment confirmed this, showing that *L.sericea, H.turgidulum, P.quadripinnata, P.natalense, P.evansii, H.aureo-nitens, R.altera* had increased, while many species with higher scores on axis 2 had decreased (*E.muticus, A.semialata, T.triandra, A.appendiculatus, D.filifolius, A.punctata, H.umbraculigarum, S.bupleuroides*). Species not involved in this trend were *P.aquilinum, C.africana, R.ludwigii, S.Isatideus, S.alopecuroides, M.capense, F.costata, F.caprina*, and *P.ohlendorfiana*.

Axis 1 of DCA did not reveal changes in species composition as site shifts along it. This was because species which increased after withdrawal of fire occurred at either extreme of axis 1, exerting "pull" in opposite directions, (for examples, see appendix 3.3.2.2, where species are ordered along axis 1 and the differences in species frequency between years are shown). Decreases in axis 1 scores generally represented greater increases in *P.natalense* and *R.altera* and smaller increases in *L.sericea, C.africana* and *P.evansii*, as would occur in grass-dominated communities situated higher up the catchment ridges. Increases in axis 1 represent the opposite trend, with a greater increase in *L.sericea* "swaying the balance".

Conclusions

There have been few marked overall vegetation changes in C IX transects since [illegible]. The most pronounced changes have involved *L.sericea*'s invasion and *T.triandra*'s decline. Species responses after withdrawal of fire were varied, many species reacting to different site conditions in different ways. Only a few species showed consistent patterns of change irrespective of site differences. The details of succession at a site were therefore not predicted, although some general trends were discernable.

CHAPTER 4

WOODY PLANT POPULATION CHANGES IN C IX

4.1. INTRODUCTION

The main aim of this chapter is to provide a better insight into the patterns and processes of woody vegetation changes in C IX. Because time did not permit experimentation to determine the life history characteristics of species which influence their distribution and abundance during woody stand development, a more opportunistic approach was adopted instead.

The most obvious vegetation changes since withdrawal of fire from C IX, had involved the woody species *Philippia evansii* and *Leucosidea sericea* (Granger 1976). In 1953, these species were restricted to areas about watercourses, as shown in fig 4.1.1. By 1973, both had spread their populations onto the flat lower areas of the catchment. In addition, *P.evansii* had advanced on the steep south facing slopes, while *L.sericea* had spread through the moist areas around stream origins (fig 4.1.2.)

Such changes were previously observed elsewhere in the Cathedral Peak area, and had led Killick (1963) to propose that without recurrent burning, *P.evansii* (along with other fynbos species such as *Passerina filiformis* and *Widdringtonia dracomontana*), would form the dominant vegetation type in subalpine regions like C IX, with *L.sericea* forming a persistent shrubland in moist places.

Granger (1976) had a different idea of what would happen. He hypothesized that the *L.sericea* would eventually dominate most of C IX, replacing *P.evansii* shrubland and invading *Miscanthus capense* grassland, *Pteridium aquilinum* veld, and to some extent *Themeda triandra* and other grassland areas. He thought later successional (forest and forest precursor) species would be restricted to moist areas, where localized patches of *L.sericea*-scrub forest would develop. These previous postulations about woody plant succession in C

IX had been largely free of evidence of how or why these woody species should come to dominate C IX.

The approach taken in this study was to make use of 5m² woody plots from 1973 (Granger 1986) and surveys of additional wooded sites. The overall aims were then to

1. a) use available information from present and past surveys (in 1953 and 1973) to determine "qualitative" changes in the dominant vegetation of woody plots since 1953, and

1. b) determine the overall amount and type of woody population changes that had occurred in the resurveyed plots since 1973; and finally to

2. use data on the existing (1986) stand height-class structures and species compositions to identify the patterns of seedling recruitment, plant growth and mortality that occur during woody stand development. The woody population patterns were used where possible to draw inferences about processes of woody vegetation change in C IX, (eg Watt 1947, Smith and Goodman 1987), and to predict future changes.

To aid in meeting the overall aims of this chapter, a number of questions and hypotheses were posed, which examined specific aspects of the woody populations. Firstly, hypotheses about the patterns of *P.evansii* and *L.sericea* seedling recruitment (developed from field observations) were evaluated: These were that

a) *L.sericea* recruitment in some grassland areas is "facilitated" (by some unknown mechanism) in stands of *P.evansii* which are senescing and where the biomass of the grass layer is reduced; and

b) conversely, *P.evansii* seedling recruitment decreases in such stands.

Despite being useful for identifying overall change, the DCA alone could not clarify the nature of changes. The detailed approach of testing individual species in each vegetation group for frequency change could. The chief benefit of DCA, was that patterns of change in an individual species could be related back to the main vegetation gradients identified in chapter 2. In hindsight, the use of the 1973 only data to determine confidence intervals for community score changes was not justified, and the joint 1973-1986 data should have been used to give more accurate results. Alternative methods of describing overall change may have been more sensitive to changes, but also have their limitations (eg using 'weightings" from the baseline (1973) data on subsequent data (1986); or by using the species x time correlation matrices for each community (stand) in Principle Components Analysis (see Swaine and Greig-Smith 1980))

Patterns of species frequency change within vegetation groups and communities

Patterns and trends of change within one type of vegetation were partially obscured by variations in the direction of changes and the species concerned. Divergence in species composition and abundance had taken place.

There were however some general patterns of species change in the catchment. Species showing the most consistent directions of change - no matter what community they occurred in - were those which changed the most in frequency (*T.triandra*, *D.filifolius*, *P.quadripinnata*, *L.sericea*, *P.natalense*, *H.aureo-nitens*, and *D.amplectens*).

General patterns of change in vegetation groups partly reflected individualistic species responses to the influence of soil moisture and depth. Some species which showed a "preference' for relatively drier, shallower soils higher up in the catchment became increasingly restricted to these sites (*D.filifolius*, *T.triandra*, and *H.contortus*), while others increased their presence there (*R.altera*, and to some extent *A.semialata*).

Species preferring intermediate conditions of moisture, soil depth and altitude also showed some pattern to their changes. Some shifted their distribution from drier to more moist areas (*A.appendiculatus*, *A.semialata*, *S.bupleurroides*, *P.caprina*), while *H.falx* (and possibly *R.ludwigii*) spread from areas with older *L.sericea* stands, both to more moist areas with younger *L.sericea*, and to drier, higher altitude sites. *P.aquilinum*, *H.capense* and *C.africana* occurring on more moist sites with mature *L.sericea* also declined, while *H.umbraculigerum* increased in such areas.

Floristic change

Floristic change since 1973 has been slow in most communities of C IX. This suggests that so far no species will have been lost from C IX. Some of the greatest turnovers had occurred in *P.aquilinum* areas, which were also characterized by a decline in some grass species (*T.triandra*, *A.appendiculatus*, *A.semialata*), and an increase in many forbs (eg *H.umbraculigerum*, *S.isatideus*, *R.ludwigii*, but not *A.junciformis*) and selected grasses (eg *H.falx*, *H.turgidulum*, *H.capense*); and sometimes the invasion of *L.sericea*. Even within these areas, the changes varied depending on the communities' locations. The ridge top communities with greater species turnovers also showed variation in the nature of their change, with increases in *R.altera* and *H.aureonitens* being the only consistent changes. Riverine communities were the most stable.

Predictions of change from Granger (1986)

Unpredicted species declines and increases occurred in C IX, and Granger's hypothesized pathways of change were not always identifiable. Besides the general differences mentioned in the results, some events at specific sites involving other species, were not predicted (see appendix 3.2.3 for Granger's full predictions):

L.sericea did not increase at stream bank sites (eg T4.9), and *Merxmuellera macowanii* (previously *Danthonia macowanii*) persisted. In the vlei area at T4.8 which was dominated by *P.aquilinum* in 1973, this species declined while *A.appendiculatus* persisted, and *L.sericea* began

invading. On moist flat *P.aquilinum* and *H.capense* areas, *L.sericea* invaded directly without *P.evansii*'s presence (this was suggested by Granger and Killick).

On the cool south and east aspects with deeper soil, the details of actual change varied from Granger's predictions. From examining T2.9 and T7.4, *T.triandra* and *A.appendiculatus* did not replace *E.muticus* and *A.semialata*, but *T.triandra*, *A.appendiculatus* and sometimes *A.semialata*, declined, while either *H.falx* (T2.9) or *H.turgidulum* (T7.4) increased. Although *P.aquilinum* invaded in T2.9, it was still infrequent, and *P.evansii* and *L.sericea* invaded the grassland directly without the initial influence of bracken. In T7.4 where bracken was dominant, no increase since 1973 was detected in these woody species. *P.quadripinnata* and *R.ludwigii* did increase, but not in the predicted sequence.

Buchenroedera lotononoides did not decline as much as Granger predicted it would in the absence of fire. Finally on shallow soils, *T.triandra* did not replace *D.filifolius*; rather *R.altera*, *H.falx* and *A.semialata* did.

Other predictions

Everson (1985) suggested that *T.triandra*, *H.contortus* and *T.spicatus* decrease with time after fire, while *A.semialata*, *T.leucothrix* and *H.falx* increase. Although predictions about *T.triandra* (decrease), *A.semialata* (relative increase) and *H.falx* were verified in 3.3.3, additional features of some grass species changes through time were evident in other results. Although *A.semialata* increased relative to *T.triandra* as predicted, it decreased overall (see 3.3.2.1), a feature shown in Everson's work but not discussed. *T.leucothrix* also unexpectedly decreased, while *T.spicatus* remained unchanged, and did not decrease as suggested, but *Heteropogon contortus* did.

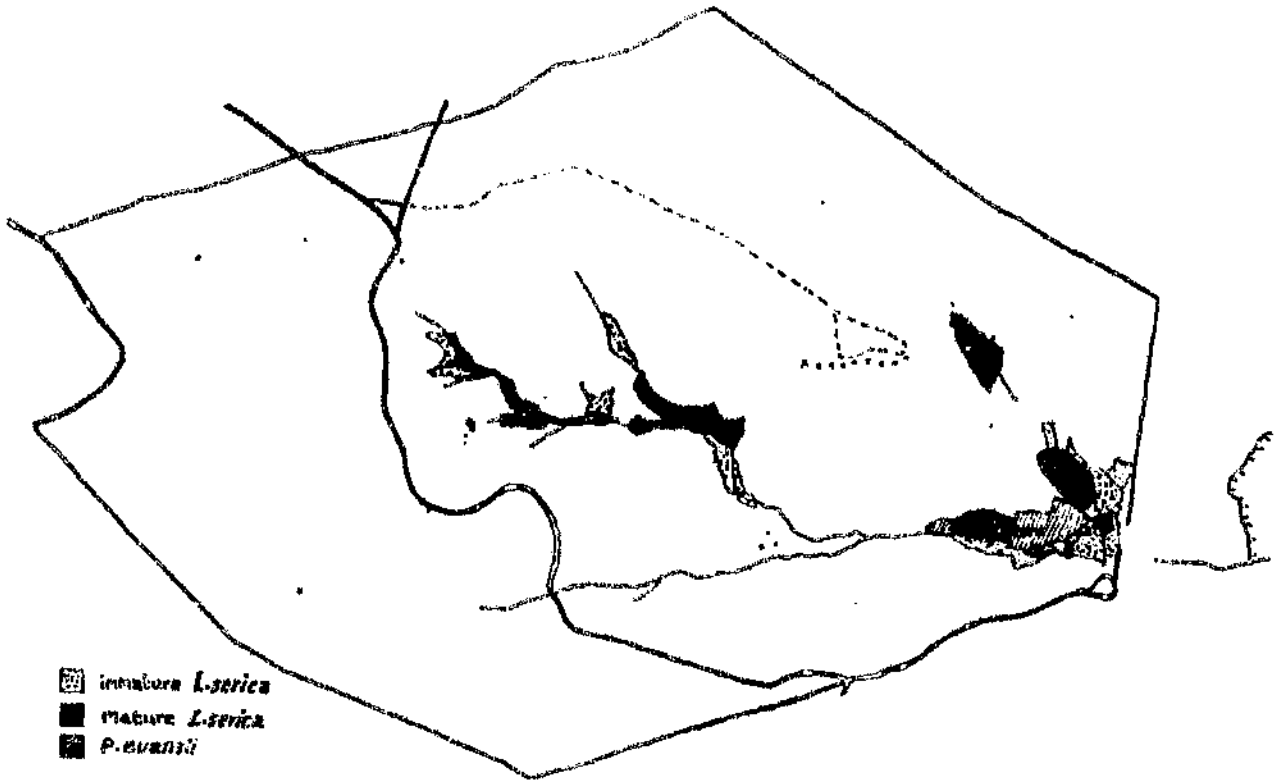


Figure 4.1.1. Map of C IX showing the distribution of *P.evansii* and *L.sericea* in 1953, after 9 years of partial withdrawal of fire (from Killick 1963).

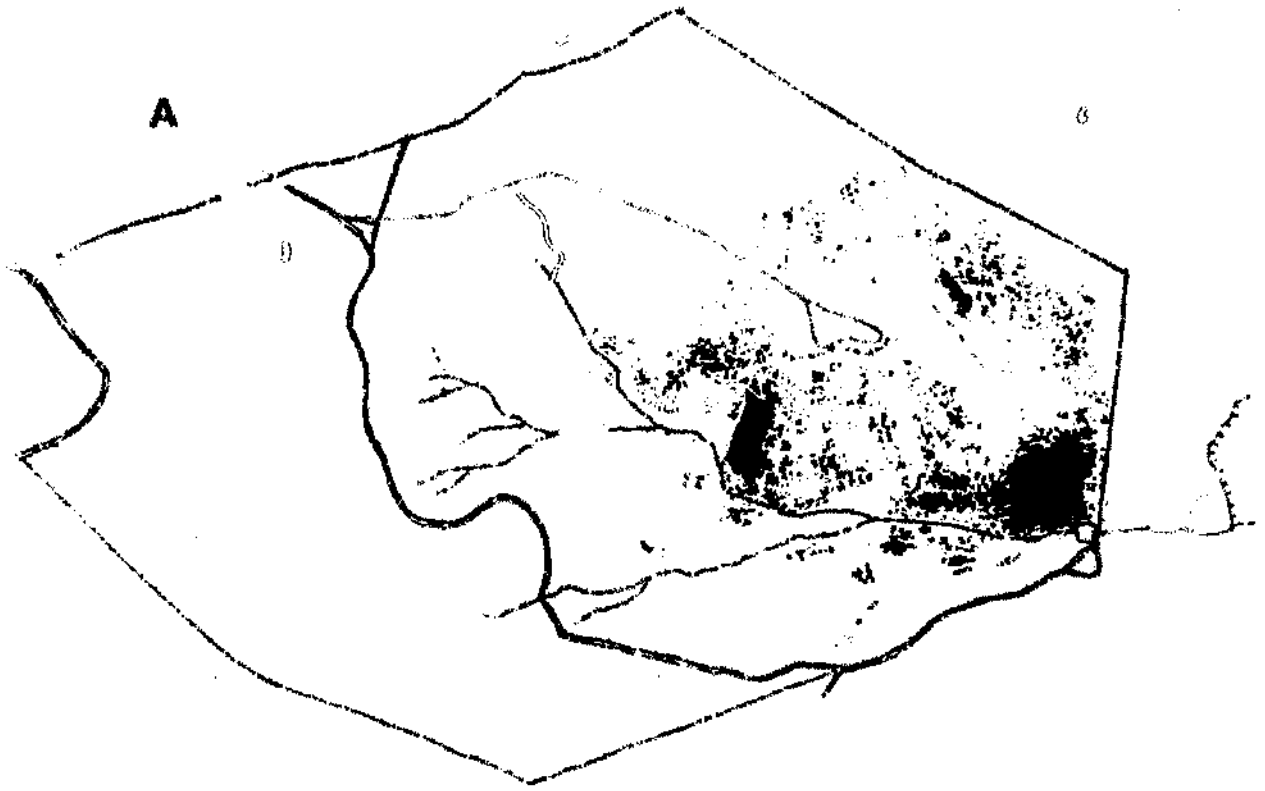


Figure 4.1.2. Maps of C IX showing the distribution of *P.evansii* (A) and *L.sericea* (B) in 1973, 8 years after total fire protection (and 29 years after partial withdrawal of fire).



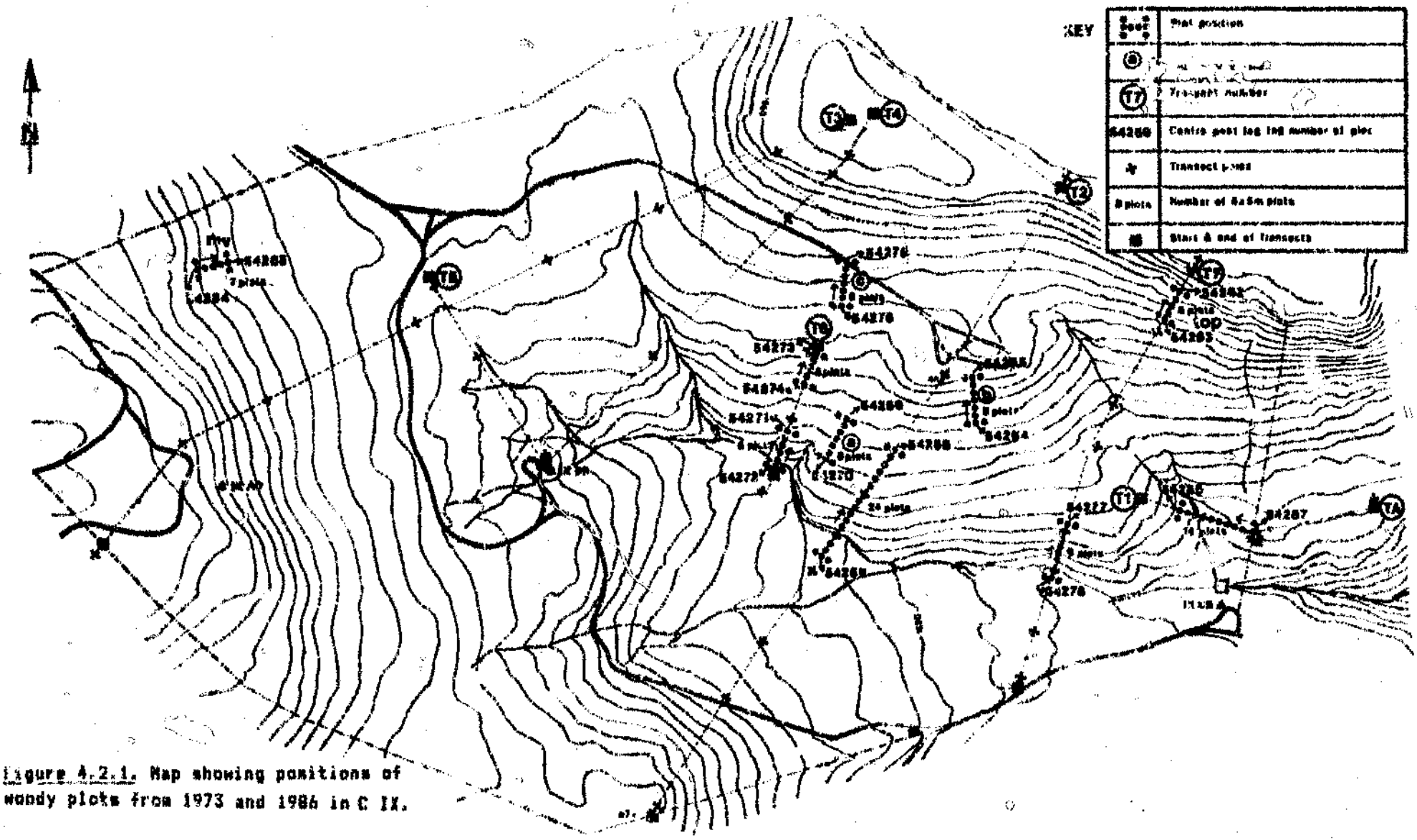


Figure 4.2.1. Map showing positions of woody plots from 1973 and 1986 in C IX.

Secondly, regarding later successional species and their relationship with current canopy dominants ("pioneer woodies" such as *L.sericea*, or other species which existed in C IX before and soon after withdrawal of fire), these questions were posed:

a) What is the potential of later successional species to replace *L.sericea* canopy plants?

b) What is *L.sericea*'s potential to be self-replacing and remain dominant in the closed-canopy situations which occur later in succession?

c) More generally, where, and under what conditions of woody stand age, canopy species composition and structure are later successional species likely to succeed in C IX?

During these investigations, the opportunity was taken to seek evidence for or against Killick's and Granger's hypotheses.

4.2 METHODS

4.2.1 CHANGES IN THE DOMINANT VEGETATION OF WOODY PLOTS SINCE 1953

Identification of the main vegetation changes since 1953 allowed the woody stands to be roughly aged for later use. Woody plot positions in C IX are shown in fig 4.2.1, and described in 4.2.2 and 4.2.3. The dominant vegetation present in the plots in 1953, 1973 and 1986 was determined from

a) Killick's 1953 vegetation map of C IX and his field notes, given in Granger (1976);

b) Granger's 1973 map and transect data, and 1973 woody plot data (in the case of resurveyed plots); and

c) 1986 transect and woody plot data for resurveyed and additional plots (see 4.2.3 for a description of additional plots).

The main trends of woody stand change were identified from diagrams of each series of plots in the three years.

4.2.2 OVERALL TRENDS OF DENSITY AND MEAN HEIGHT CHANGE SINCE 1973

The only woody plot data available from 1973 were on the densities and mean heights of species in each plot. Quantitative descriptions of woody plot changes were therefore confined to these variables.

Field techniques

The 5x5m woody plots surveyed in 1973 were re-located where possible from information provided by Granger (1975). Because he did not actually mark the plot positions there was some error associated with the resurvey measurements. The following plots from 1973 were resurveyed: transect 1, plots 1 to 14; transect 2, plots 1 to 24; transect 6 plots 1 to 5, and 7 to 10; and transect 7, plots 1 to 9. These plots were contiguous except in T6 top section, where the in-between plots were also surveyed (plots 11' and 12'), and T7, where plot 1 was not relocated but plot 1' was surveyed instead. Other plots surveyed in 1973 were left out, because either their positions were not recorded by Granger (transect 4, transect 5), or their positions could not be at all accurately relocated (transect 7, plots 10 to 16; transect 2 plots 24 to 26; transect 1, plots 15 to 25).

Within each plot, the height and species of each woody plant taller than 5cm was recorded. Plants smaller than 5cm were not included because a) *L.sericea* produced copious seedlings, most of which died before 3-5 leaves had been produced, when they were still <5cm tall; and b), *P.evansii* seedlings smaller than 5cm were extremely difficult to find in the thick sward - none were found in the 5% plots searched. Although not stated in his thesis, it seems evident from the density/ mean height data that Granger did not count seedlings below 6cm tall.

Data analysis

To test whether the mean height or density of the *L.sericea* and *P.evansii* in a group of plots had changed significantly since 1973, the Mann-Whitney U test was used. The groups of plots were based on transects and the dominant vegetation within transects (see 4.2.1.).

Because forest precursor and forest (later successional) species were still rare in 1973, any increase in abundance was so obvious that no statistical test was required.

4.2.3 LOCAL CHANGES IN WOODY SPECIES DENSITIES; AND THE PRESENT (1986) HEIGHT CLASS STRUCTURE OF WOODY PLOTS

Variations in direction and extent of density changes in the resurveyed woody plots were identified, by describing the locations of "changes" along a series of plots. No statistical tests of the differences in species densities in individual plots from 1973 and 1986 were possible.

To describe the present (1986) vertical structure of all the woody plots, the species height-class frequency distributions of the resurveyed and 37 additional plots were graphed.

The additional plot positions were designed to provide a contrast to existing plots and to test hypotheses outlined in 4.2.4, and not to provide a full record of woody changes throughout C IX. They were situated as follows:

Seven contiguous plots were placed in the north west of C IX (henceforth referred to as the NW plots), within a clump of *L.sericea* bushes that had existed at least since 1973.

Three groups of eight contiguous plots (plots A, B and C) were situated on the south facing slope of C IX, in the proximity of transect 2 and transect 6, in varying aged stands of *P.evansii*.

Six plots were situated 20m from the end of transect 7 (T7 top plots), in a mixed age stand of *P.evansii*.

The height classes used in this section, and in 4.2.4, were as follows: plants 6 to 49cm tall (<50) were classed as seedlings; plants 50cm to 150cm tall (<150) were classed as small plants; plants 151cm to 250cm tall (<250) were middle-sized, and plants greater than 250cm (>250) were tall plant, or senescing plants in the case of *P.evansii*. These height-classes were chosen to reveal the main "life stages" of the woody species. Plants less than 50cm tall were generally reproductively immature: In a survey of 90 *P.evansii* plants, all those >80cm were in flower. While 9 out of 13 plants between 60cm and 80cm tall were flowering, all 37 plants<55cm tall were without flowers. Although no survey was made, *L.sericea* was thought to show similar patterns of flowering (Smith, pers com). Small and middle-sized plants of all species were considered reproductively mature, while tall plants of *P.evansii* were senescing. Tall plants of *L.sericea* and other species were considered as exerting their influence as canopy plants.

4.2.4 PATTERNS OF RECRUITMENT, GROWTH AND MORTALITY OF L.SERICEA, P.EVANSII AND LATER SUCCESSIONAL SPECIES WITHIN WOODY PLOTS

This section attempted to identify the patterns of woody plant seedling recruitment, growth and mortality that occurred during the development of stands of woody plants. To do this, the relationships between the locations of different densities of seedlings, small, middle-sized, tall and dead plants of different species were investigated. Preliminary evaluations were made of the hypotheses derived from observations during field work, using a subsample of 24 plots (the A, B and C plots). The hypotheses were specified as follows:

In grassland on the south-facing slope of C IX,

1) *L.sericea* seedling density is positively correlated with dead and senescing *P.evansii* density, and negatively correlated with grass biomass and *P.evansii* canopy cover, and

2) *P.evansii* seedling density is positively correlated with grass biomass and canopy cover, and negatively correlated with dead *P.evansii* density).

L.sericea seedlings was investigated in 4.2.3. The ground-projected canopy areas of all canopy plants, except *Protea species*', were estimated from canopy diameters measured in two directions. *Protea* plants had either sparse and discontinuous canopies, or none, having recently died. An average canopy cover of 7.07m² was presumed for these plants.

The locations of the sample trees are shown in fig 4.3.5. Sample sizes were as follows: For *L.sericea* thicket, 10 plants; for scattered *L.sericea*, 7 plants; for individual *L.sericea* among *P.aquilinum*, 10 plants, for the east ridge *Protea*, 12 plants.

Woody plots (4.2.1) with areas of closed woody canopy were also used to provide additional estimates of forest and precursor species seedling densities under canopies.

Data analysis

The mean densities of under-canopy species were calculated as:

$$\text{seedling density} = \frac{\text{total no. of seedlings for that species}}{\text{total area sampled}}$$

Questions on aspects of *L.sericea*, precursor or forest seedling distribution were analysed as follows.

a) To determine the probabilities of "later" species seedlings replacing *L.sericea* canopy plants on their death, differences in the ratio of *L.sericea* to later species seedlings were examined. The survival beneath *L.sericea* canopies, of a higher density of its own seedlings than precursor or forest seedlings, implied that there was a greater chance of *L.sericea* continuing to dominate that site. A higher density of forest or forest precursor seedlings, implied that one of these plants has a greater chance of becoming a canopy dominant (given that *L.sericea* and other species have equal seedling (>5cm) survival rates).

b) To see if *L.sericea*'s recruitment rate was maintained during stand development, (and therefore whether this species was potentially self-replacing in closed canopy situations and able to remain dominant

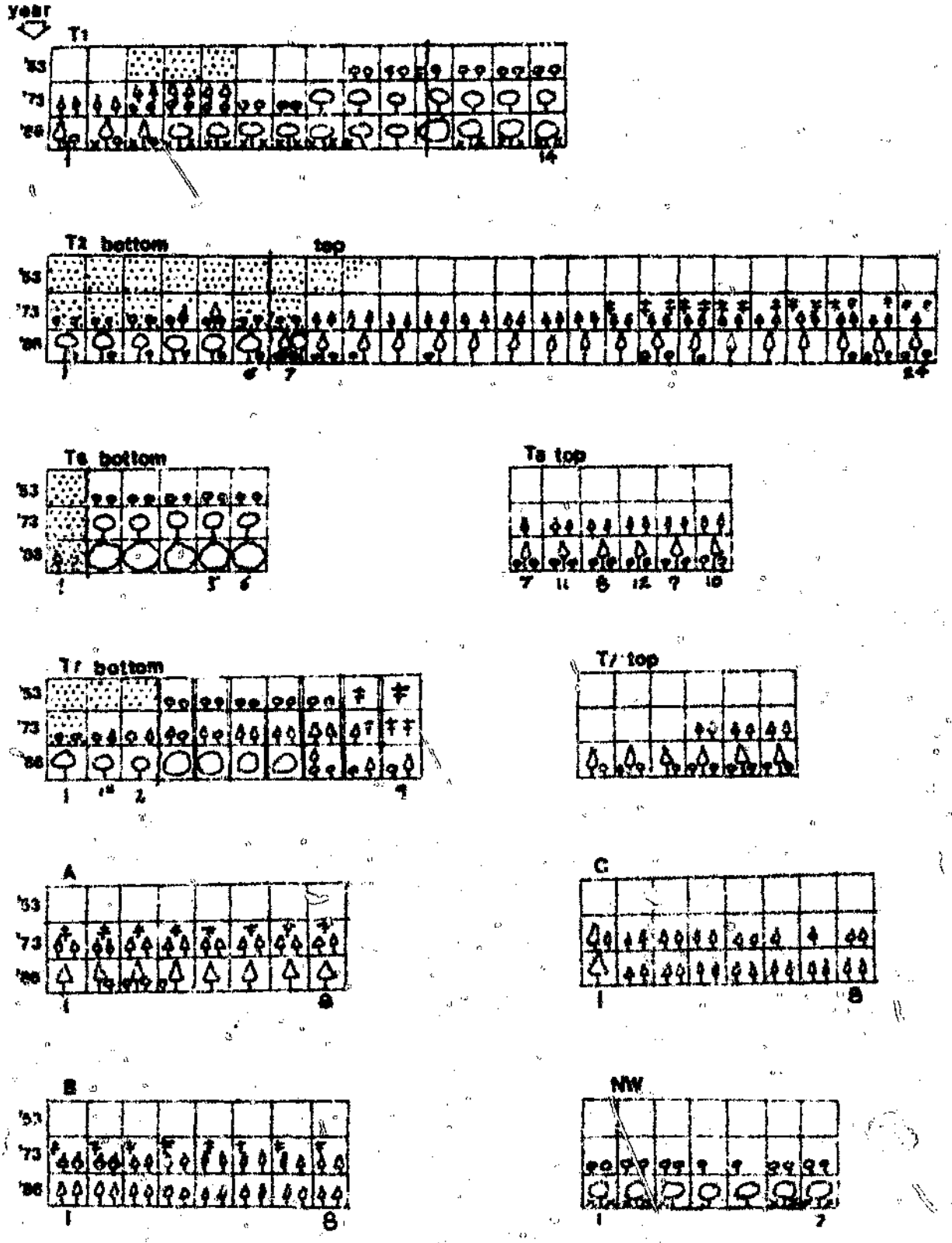


Figure 4.3.1. Dominant vegetation in re-surveyed and additional woody plots in 1953, 1973 and 1986. (☐ = *Themeda* grassland, ☐ = *Miscanthidium capense* grassland, ☐ = *Pteridium aquilinum*, ☐ = Young *P.evansii*, ☐ = young *L.sericea*, ☐ = mature *P.evansii*, ☐ = mature *L.sericea*, ☐ = very mature *L.sericea*, ☐ = later successional species

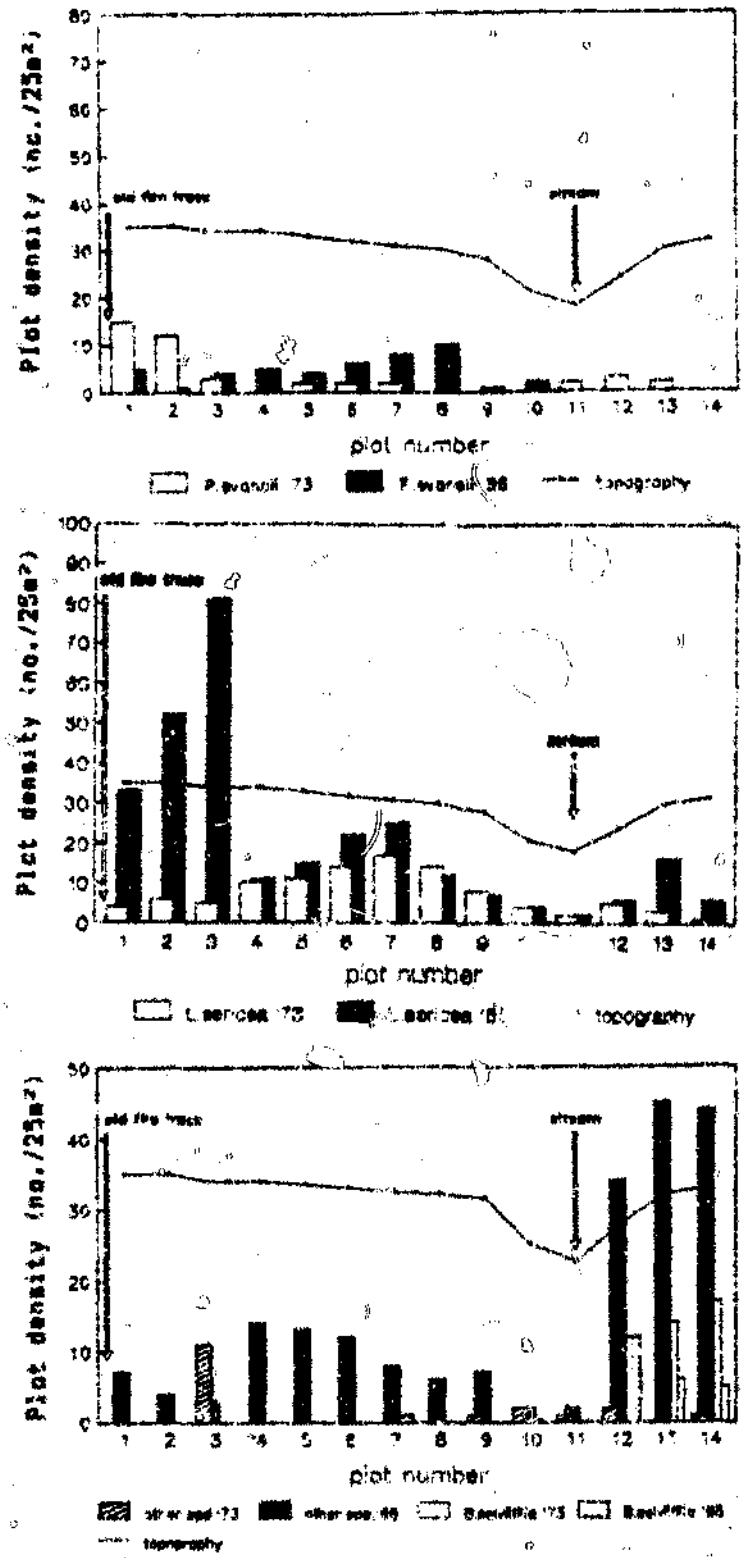


Figure 4.3.3.1. Densities of *P.evansii*, *L.sericea* and later successional woody species in 1973 and 1986, in resurveyed plots along transect 1. A topographical profile of the plots' locations (not to scale) is given.

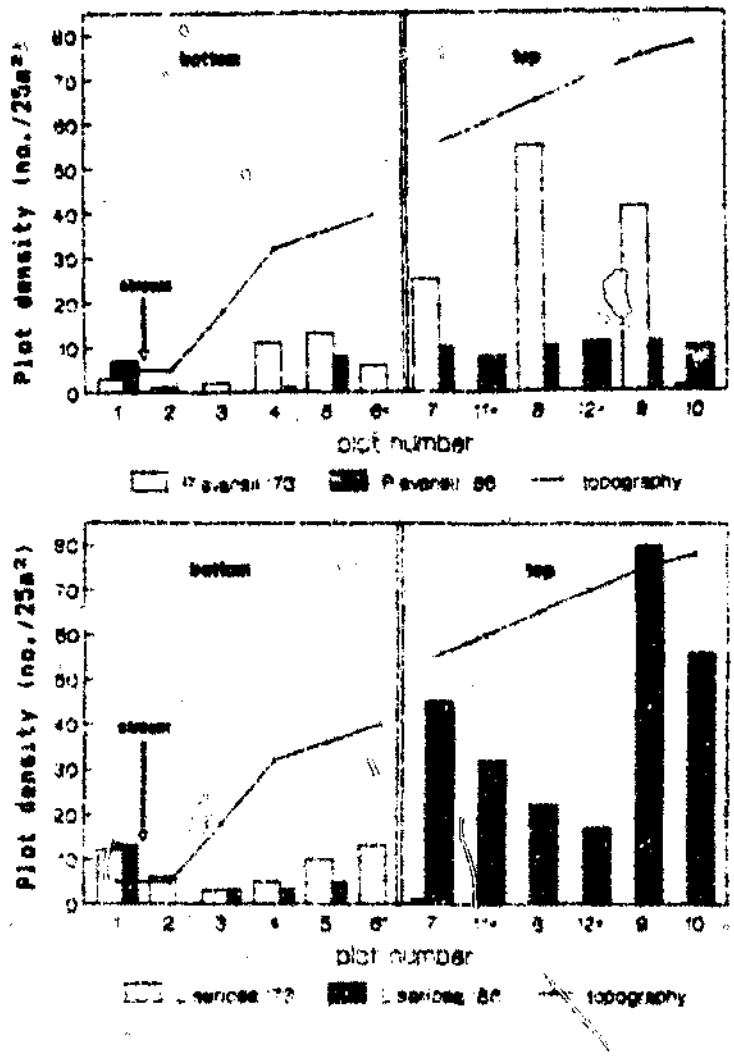


Figure 4.3.3.7. Densities of *P.evansii* and *L.sericea* in 1973 and 1986, in resurveyed plots along transect 6. Plot 6* was surveyed in 1973 only, and plots 11* and 12* in 1986 only.

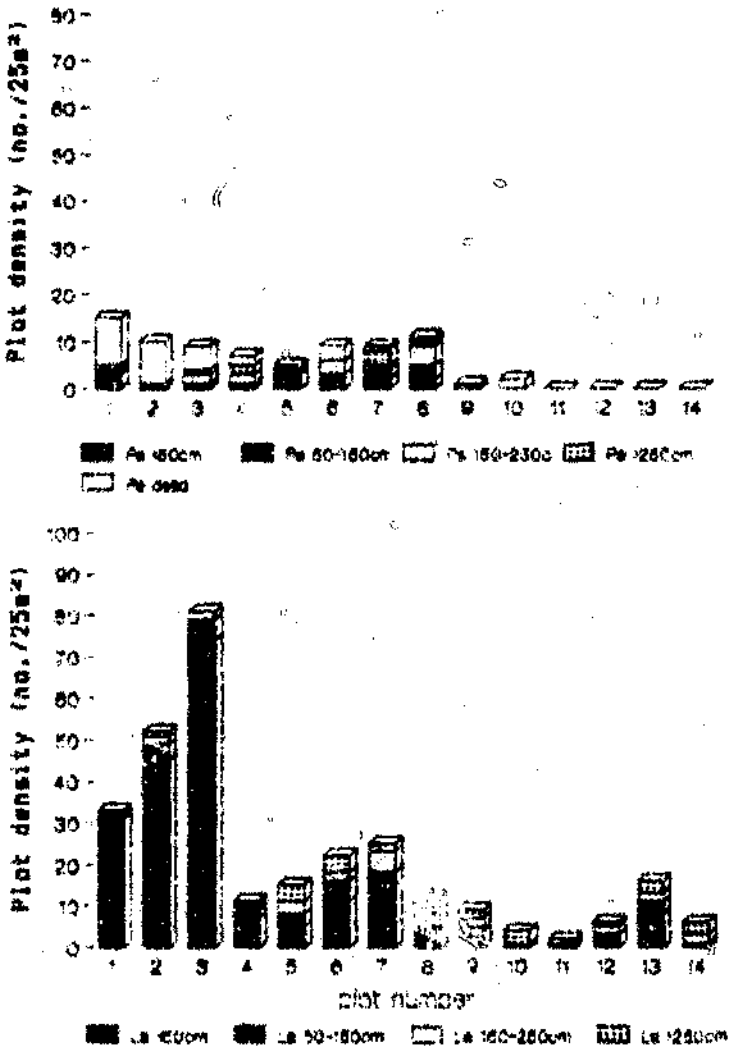


Figure 4.3.3.5. Height class structure of *P. evansii* (Pe) and *L.sericea* (Ls) in the transect 1 woody plots in 1986.

Field techniques

In all resurveyed and additional (4.2.3) plots, the height and species of each plant was recorded. Data on other aspects of stand structure were obtained in some areas: Plant basal circumferences at 20cm (for those plants greater than 5cm in circumference, and dead *P.avensii*) were measured in the A, B and C plots and the NE plots. The canopy areas of plants in the A, B and C plots were measured (by recording the canopy diameters in two dimensions at right angles to each other). The grass biomass present in each of the A, B and C plots was estimated, by harvesting all live biomass in four 0.167m² circular sample areas in each plot (Everson 1985). The samples were oven dried at 80° C for two days and then weighed. The mean dry weight of the 4 samples provided an estimate of grass biomass for each plot. Canopy cover and estimated grass biomass are given in 4.2.4.

Data analysis

Recruitment

To identify the correlation between the density of a species' seedlings (<50cm tall) and the density of other species/height-classes in the plots, the log (x + 0.1) transformed data from all woody plots were subject to the exploratory data techniques of correlation and partial correlation analysis. The log (x + 0.1) transformation was used to obtain data suitable for use in multivariate analysis: after transforming the data, the distribution of residuals of multiple regression analyses were found not to depart greatly from (the assumptions of) normally distributed data.

Once possible relationships between the plot variables had been identified, they were further characterized using multiple regression and additive elements analysis (Whittaker 1984). Additive elements aids in the interpretation of fitted statistical models, such as the generalized linear model, by full partitioning of the maximised log-likelihood ratio test statistic (effectively the residual sums of squares) into additive elements. Unlike stepwise multiple regression, which produces different regression equations depending on the order in which the variables are entered, it is effective in selecting from a number of possible variables, those with the greatest explanatory power. It also accounts for co-linearity of variables, a common

feature of biological data. The reliability of the explanatory power of variables was also tested, where necessary, using ridge traces.

For A, B and C plots, data on grass biomass and *P.evansii* canopy cover were included in a separate analysis, to test the above-mentioned hypotheses.

Population growth and mortality

Estimates of the distribution of *P.evansii* mortalities among different size classes were made, and compared between stands of different ages (as deduced from maps, 1973 aerial photographs and the stand circumference and height-class structure). The relationship between *P.evansii* basal circumference and plant height was described.

Patterns of *L.sericea* growth and mortality were deduced from stand height class structures. Further data on seedling mortality patterns were obtained from frequencies of different sized seedlings in the vacinity of 'parent' plants in various localities.

Because later successional species of taller size-classes were not yet abundant in C IX, few quantitative descriptions could be made. Descriptions of observed trends were given where possible.

4.2.5. RECRUITMENT PATTERNS OF L.SERICEA, FOREST PRECURSOR AND FOREST SPECIES SEEDLINGS BENEATH CANOPY PLANTS

The small sample sizes in this section precluded rigorous testing of the observed differences in seedling densities, but allowed the examination of some features of the spatial patterns of seedling recruitment which would reveal possible successional trends.

Field techniques

A survey was made of the woody species growing under the canopies of a sample of "canopy" trees growing in C IX. Canopy plants which had woody plants of precursor and forest species growing beneath them were of the following species: *L.sericea, Rhamnus prunoides, Protea caffra* and *P.roupelliae*, and *Buddleia salvifolia*. Evidence from 4.2.4 showed that *P.evansii* did not actively influence the recruitment of forest or precursor species, and its influence on

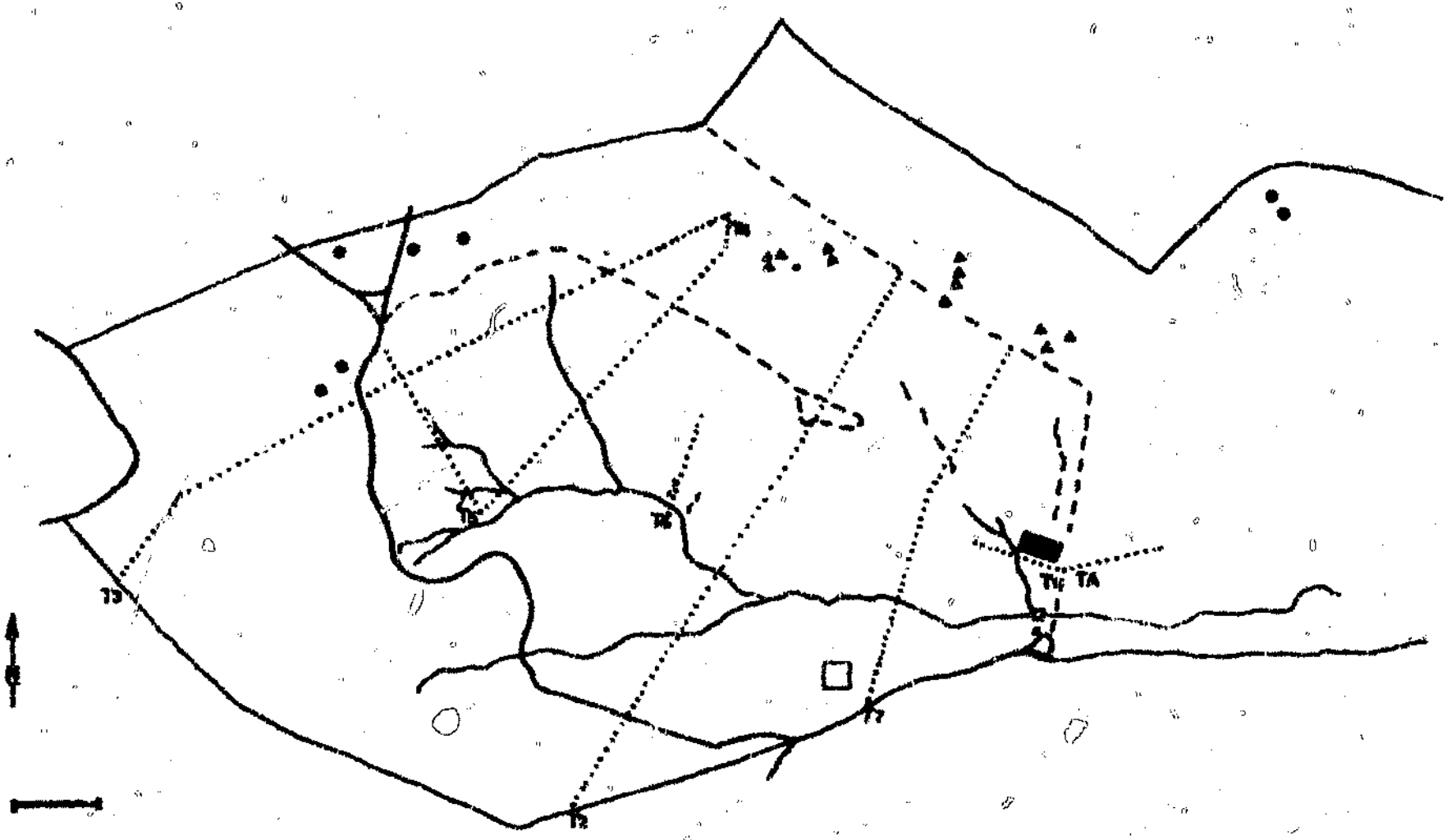


Figure 4.2.5. Location of sample sites for determining patterns of woody plant seedling recruitment in C 1X.

▲ = *Protea* species sampled on the north ridge of C 1X.
● = Individual *L.sericea* trees.
■ = *L.sericea* thicket.
□ = Scattered *L.sericea* in *P.aquilinus* veld.

in C IX during later succession), differences in *L.sericea* seedling density during stages of *L.sericea* stand development were tested in a Kruskal-Wallis one-way ANOVA. The stages of stand development were from shrubs scattered in grassland areas, to individual shrubs more closely spaced in a *P.aquilinum* area, to closed canopy *L.sericea* thicket or scrubland (data from the scattered *L.sericea*, the *L.sericea* thicket, the individual *L.sericea* and T1 (5 plots), respectively).

c) To determine where later successional species are likely to succeed in C IX, areas with different dominant canopy species were examined for differences in the density and diversity of later successional species.

4.3 RESULTS

4.3.1 CHANGES IN THE DOMINANT VEGETATION OF WOODY PLOTS SINCE 1953

Fig 4.3.1 shows the groups of woody plots and their dominant vegetation in the three years, 1953, 1973 and 1986.

Granger's woody plots had been placed in areas of taller existing woody plants, so that his samples were restricted to the lower south slope of C IX and areas about the streams, and did not represent the whole of C IX. The additional plots include some sites which were not wooded in 1973.

There were four main sequences of change: The first involved grassland areas above the main stream in C IX (see map of plot positions in fig 4.3.1), where *P.ovansii* (and sometimes *P.aquilinum* invaded and grew to produce mature stands, which were then invaded by *L.sericea*, and subsequently forest and forest precursor species. The second sequence involved *Miscanthus capense* dominated areas where *L.sericea* invaded, with or without *P.ovansii* being present. "Later" successional species then appeared. The third sequence involved the direct invasion of *Themeda* grasslands by *L.sericea*, and then later successional species. The fourth sequence occurred on the steep banks above streams, where *L.sericea* existed before 1953 (see fig 4.1.1), and continued to dominate, although some later successional woody plants appeared. Estimates of stand age are given in appendix 4.3.1.

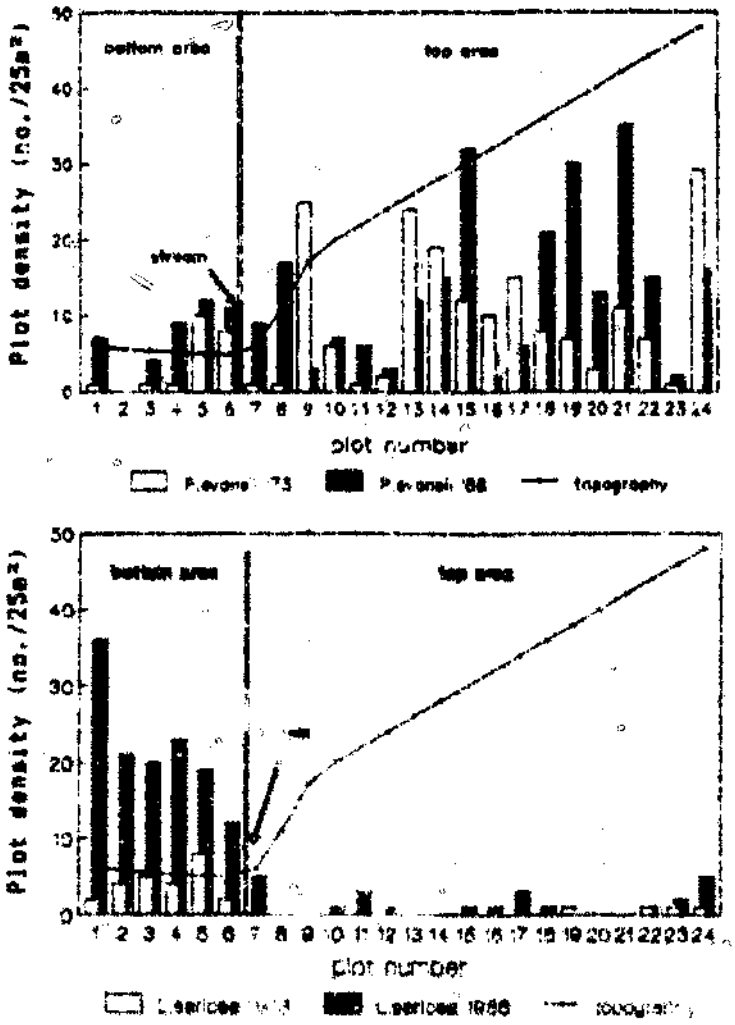


Figure 4.3.3.2. Densities of *P.evansii* and *L.sericea* in 1973 and 1986, in resurveyed plots along transect 2.

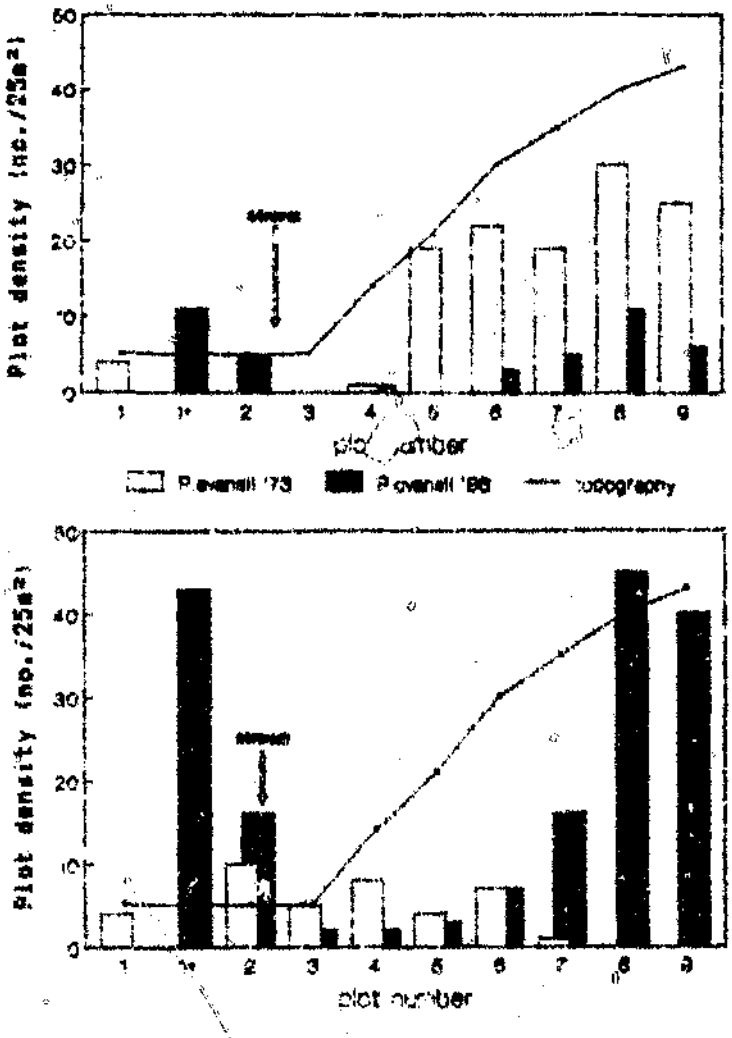


Figure 4.3.3.4. Densities of *P.evansii* and *C.serrata* in 1973 and 1986, in resurveyed plots along transect 7 (bottom section). Plot 1* was surveyed in 1986 only. Plots 1, 1* and 2 were contiguous but the rest were alternate.

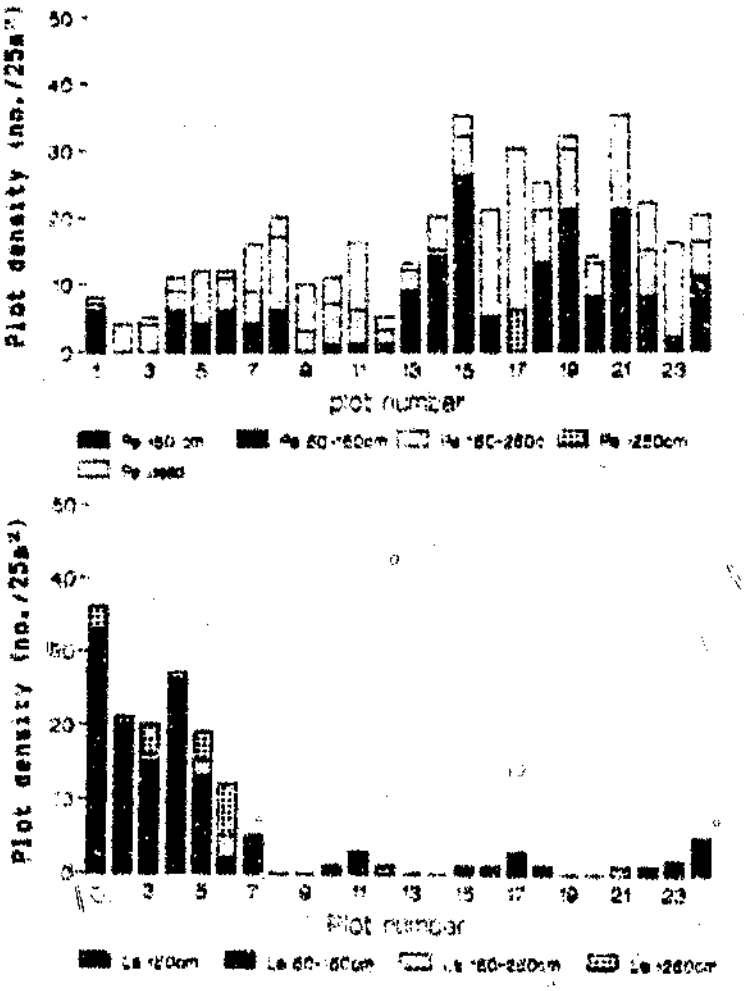


Figure 4.3.X.6. Height class stucture of *P.evansii* (Pe) and *L.sericea* (Ls) in the transect 2 woody plots in 1986.

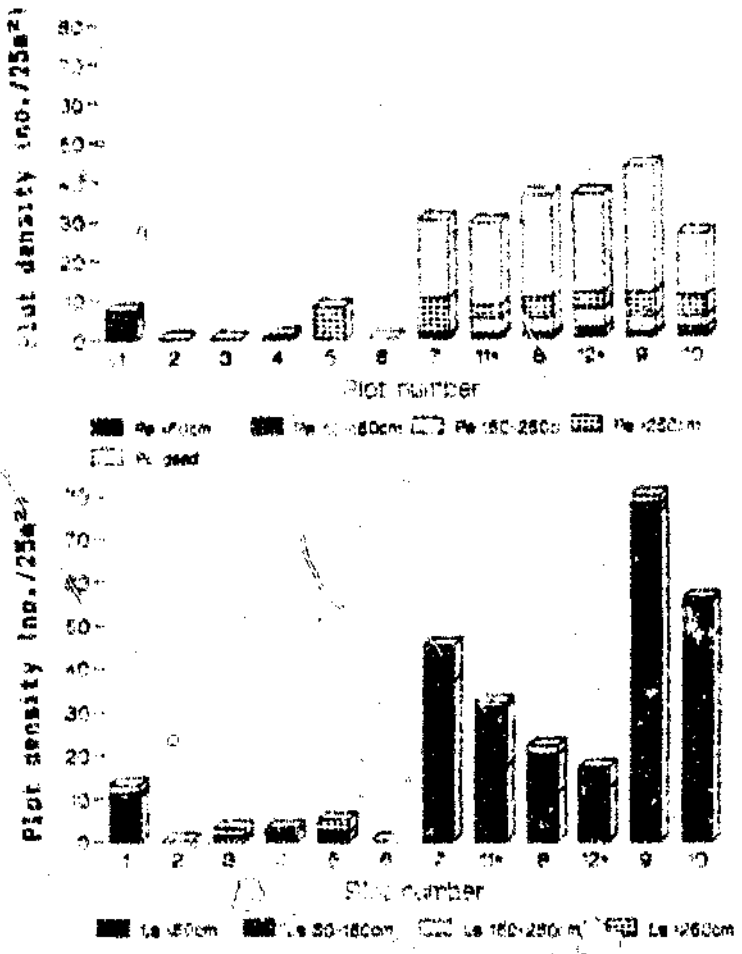


Figure 4.3.3.7. Height class structure of *P.evansii* (Pe) and *L.sericea* (Le) in the transect 6 woody plots in 1986.

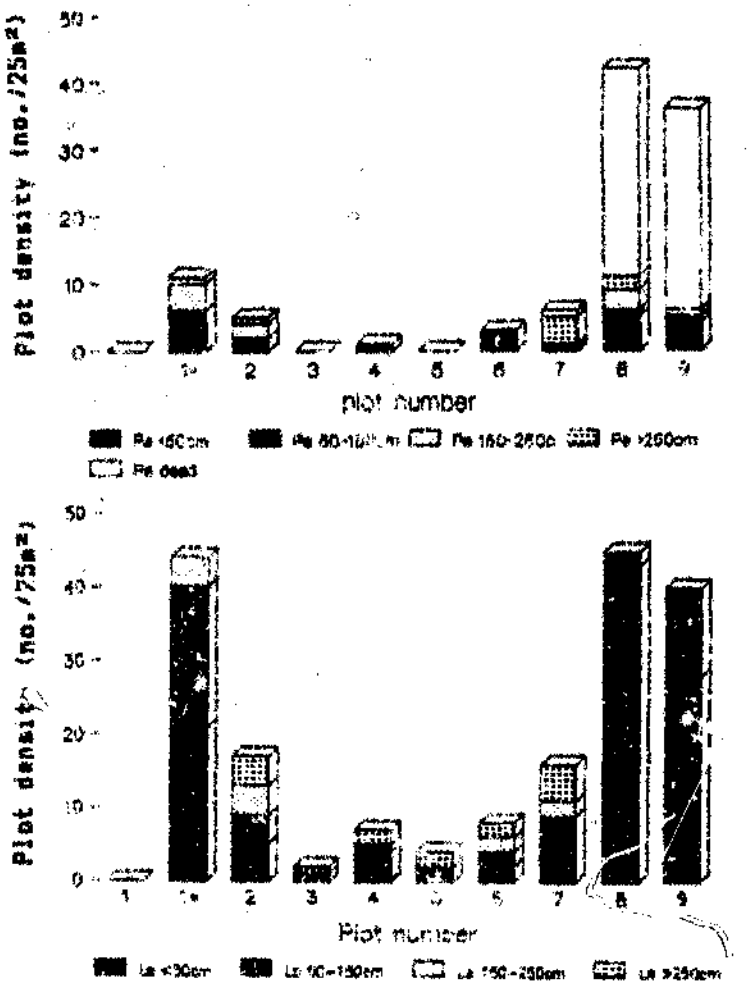


Figure 4.3.3.8. Height class stucture of *P.sylvestris* (Pe) and *L.sericea* (Ls) in the transect 7, bottom section, woody plots in 1986.

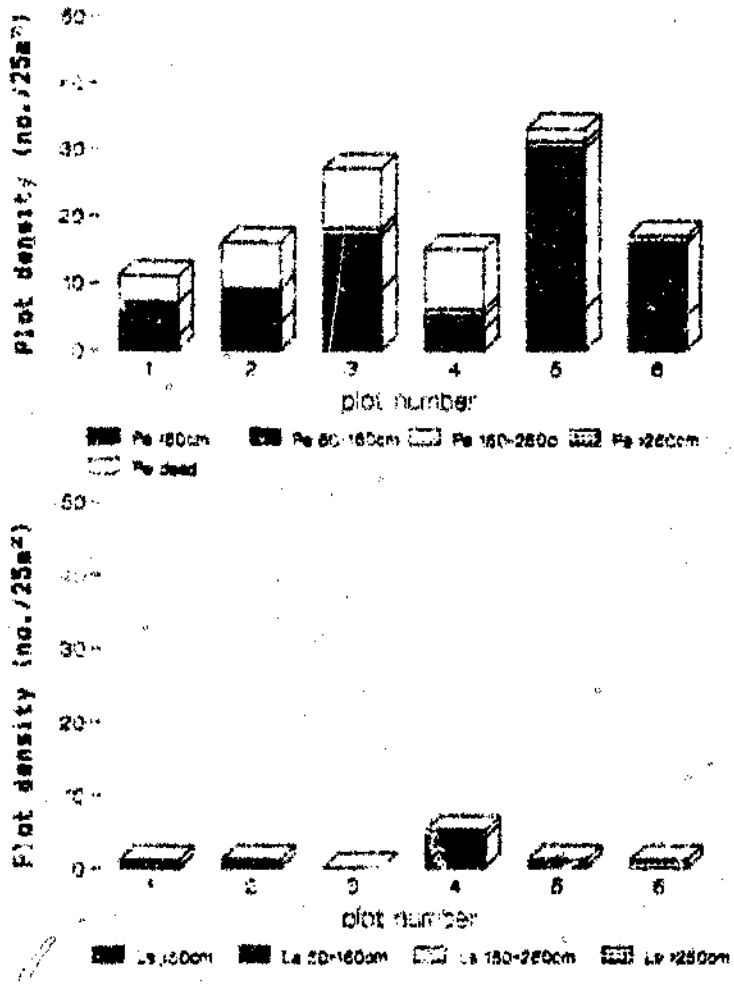


Figure 4.3.3.9. Height class stucture of *P.evansii* and *L.sericea* in the transect 7 top woody plots in 1988.

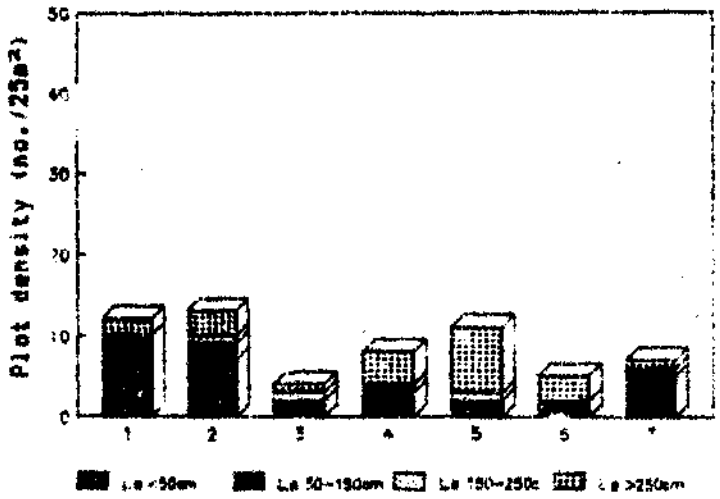


Figure 4.3.3.10 a) Height class stucture of *L.sericea* in the North Western woody plots in 1986.

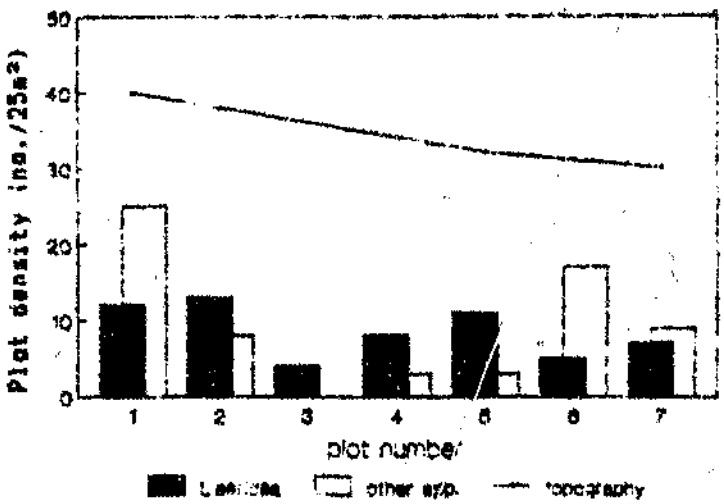


Figure 4.3.3.10 b) Densities of *L.sericea* and later successional species in the North Western woody plots in 1986.

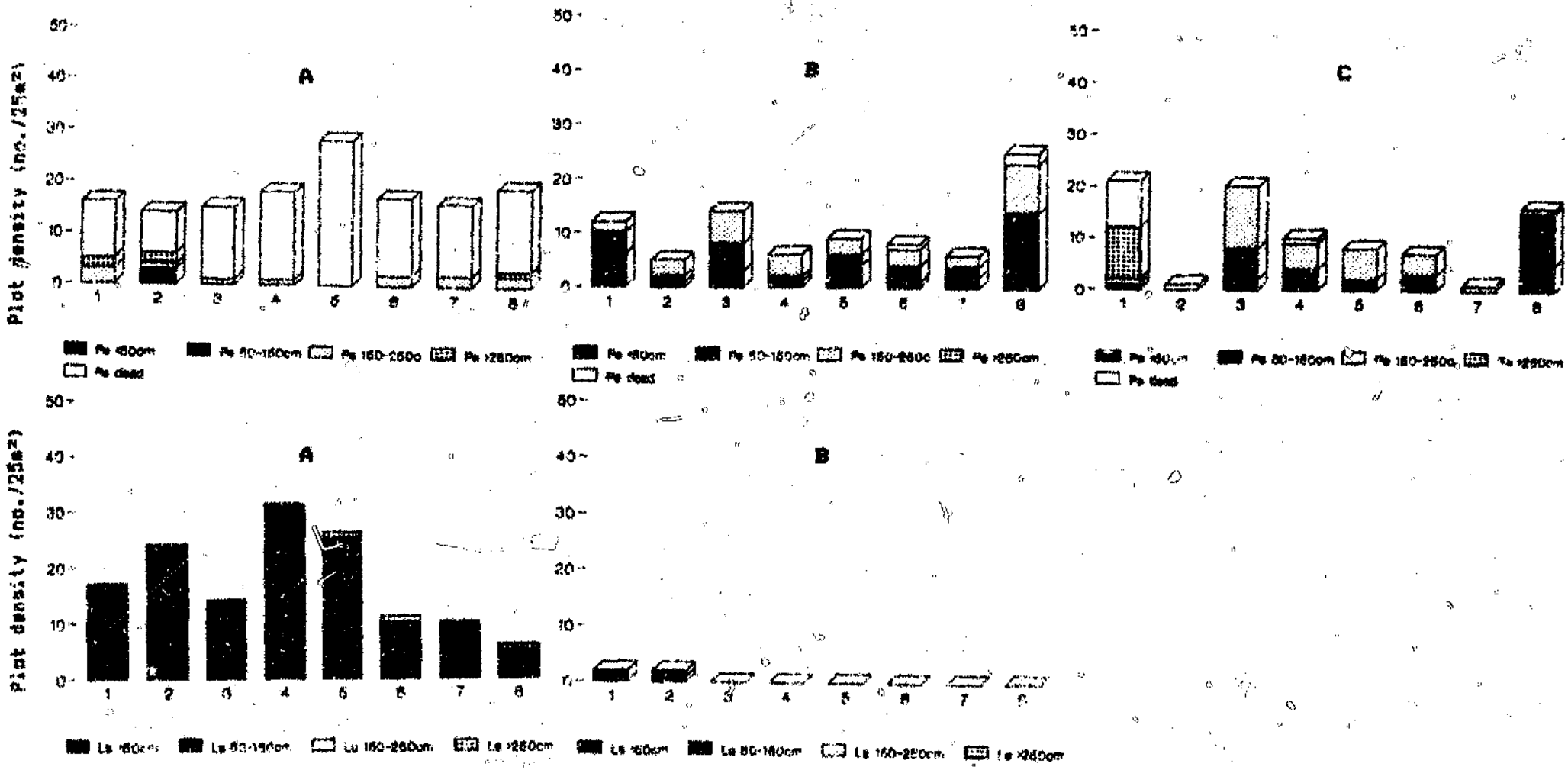


Figure 4. 3.1. Height class stucture of *P.evansii* (Pe) and *L.sericea* (Ls) in A, B and C plots in 1986 (*L.sericea* was absent in the C plots).

4.3.2 OVERALL TRENDS OF DENSITY AND MEAN HEIGHT CHANGE SINCE 1973

4.3.2.1 Changes in overall densities

L.sericea increased significantly in overall density in T 1, T 2 bottom and top area, and T 6 top area (P>= Z are 0.029, 0.005, 0.013 respectively). *P.evansii* showed no significant overall changes in density in any of the areas. Results of Mann-Whitney U tests are given in appendix 4.3.2 a) and 4.3.2 b).

4.3.2.2. Changes in overall mean heights of species in woody stands

In T 1, and the T 2 bottom area, the *L.sericea* stands decreased in overall mean height (P>= Z are 0.019 and 0.018 respectively). In other areas, there were no significant changes. *P.evansii* showed no significant changes in overall stand height, except for a marginal increase in the T 6 top area (P>= Z, 0.051). Results of Mann-Whitney U tests are given in appendix 4.3.2 c) and 4.3.2 d).

4.3.3 LOCAL CHANGES IN WOODY SPECIES DENSITIES; AND THE PRESENT (1986) HEIGHT CLASS STRUCTURE OF WOODY PLOTS

Fig 4.3.3.1 to fig 4.3.3.4 show the densities of woody plants in 1973 and 1986 in the resurveyed woody plots; fig 4.3.3.5 to fig 4.3.3.11 show the height-class structures of the resurveyed and additional plots. Descriptions of height and density changes, and of 1986 plot height-class structures are given in appendix 4.3.3.

Changes in the densities of species other than the two pioneer woody ones are given in table 4.3.3. *Rhamnus prunoides* has increased the most, with *Rhus dentata* and *Diospyros austro-africana* next. Counts of *Buddleia salviifolia* may be inaccurate: In transect 1 this species produced new sprouts vegetatively, and individuals could not be separated. 1986 counts in plots 13 and 14 involved plants taller than 1m only. Nevertheless *B.salviifolia* did not appear to decrease in overall density in transect 1, but rather spread to plot 12 and plot 7 (see fig 4.3.2.1).

Table 4.3.3 Densities (no. per transect) in 1973 and 1986 of later successional species in resurveyed plots in C IX.

SPECIES	YEAR	T1	T2	T7
Rhamnus prunoides	'73	1	0	0
	'86	20	0	24
D.austro-africana	'73	6	0	0
	'86	24	6	11
Rhus dentata	'73	0	2	0
	'86	19	1	4
Euclea natalense	'73	0	0	0
	'86	7	0	1
Calpurnia spp.	'73	11	0	0
	'86	20	0	0
Hallaria lucida	'73	0	0	0
	'86	8	0	0
Heteromorpha trifoliata	'73	0	0	0
	'86	2	0	0
Scolopia mundtii	'73	0	0	0
	'86	1	0	0
D.whytsana	'73	0	0	0
	'86	1	0	0

4.3.4 PATTERNS OF RECRUITMENT, GROWTH AND MORTALITY OF L.SERICEA, P.EVANSII AND LATER SUCCESSIONAL SPECIES IN WOODY PLOTS

The results of correlation analysis of the log10 height-class densities of all the plots is presented in appendix 4.3.4.1., and for the A, B, and C areas in appendix 4.3.4.2.

4.3.4.1 *L.sericea* seedling recruitment

4.3.4.1.1 All plots

From all the woody plot data, it was found that *L.sericea* seedling density was positively correlated with the density of dead *P.evansii* and senescing plants (Pe>250cm), and negatively correlated with small *P.evansii* (Pe<150cm). It was also positively correlated with the density of *L.sericea* plants of <150cm and <250cm (appendix 4.3.4.1)

Altogether these five variables accounted for 61.88% of the variation in *L.sericea* seedling density. Additive elements analysis however, indicated that none of them had any great unique explanatory power (table 4.3.4.1.1.). In fact, the sum of variation uniquely accounted for was just 23.396%, therefore most of the model's variation (38.491%) was shared in some way between the five. Nevertheless, using a ridge trace it was shown that with the exception of L1250, the variables held their explanatory power through changes in theta, confirming the above relationships and identifying them as suitable for inclusion in the model explaining *L.sericea* seedling density.

Table 4.3.4.1.1. Percentage of the total variation in *L.sericea* seedling density (Lss) accounted for uniquely by each of five explanatory variables.

EXPLANATORY VARIABLE	PRIMARY ELEMENTS:% of variation in Ls<50 uniquely explained
Dead *P.evansii*	5.153
Senescing *P.evansii*	2.456
Small *P.evansii*	5.236
Middle sized *L.sericea*	1.594(N.S)
Small *L.sericea*	8.955
MODEL:	61.887% of total variation

There is no evidence here that, in general, seedling densities are lower in areas with tall *L.sericea*'s (closed canopy shrubland). Nevertheless, *L.sericea* seedling recruitment beneath its own canopy is investigated in 4.3.5.

4.3.4.1.2. A, B and C plots

The correlation matrix of data from areas A, B, and C indicated that *L.sericea* seedling density was correlated positively with that of dead *P.evansii* and negatively with that of small ones (Pe<150cm). However, because *P.evansii* canopy cover and the densities of small and middle sized *P.evansii* were all inter-correlated, partial correlation analysis was used to determine which of the three to include in the model explaining *L.sericea* seedling density. Small *P.evansii* (P1150) was the most highly correlated with *L.sericea* seedling density and with stand canopy cover, so it was chosen to include in the regression

model. P1150 could be substituted by either of the other two variables, with only a small loss in explanatory power.

The contribution of dead and small *P.evansii* to the variation in *L.sericea* seedling density is given in table 4.3.4.1.2. The amount of variation in *L.sericea* seedling density (73.24%) accounted for was large. The lack of either variable having a large unique explanatory power indicated that there was collinearity between them, ie they had the same relationship to *L.sericea* seedling density - they could be substituted for each other. Dead *P.evansii* however, had the largest unique contribution, and could more reasonably be used in "explaining" *L.sericea* seedling density.

Table 4.3.4.1.2. Additive elements obtained when regressing dead *P.evansii*, small *P.evansii* and grass biomass on *L.sericea* seedling density.

Source of variation	SS	% of variation
Residual	33.73	26.76%
MODEL	92.31	73.24%
Primary elements (UNIQUE):		
Dead *P.evansii*	19.17	15.20%
Small *P.evansii*	4.62	3.66%
Secondary elements (SHARED):		
Dead/small *P.evansii*	63.20	49.58%
TOTAL	126.04	100%

From this analysis, it is evident that *L.sericea* seedling density increases as the density of dead *P.evansii* increases.

4.3.4.2. *P.evansii* seedling recruitment

4.3.4.2.1. All plots

The correlation matrix shows that *P.evansii* seedling densities were positively correlated with small and middle sized *P.evansii*. However, only 31.12% of the variation in *P.evansii* seedling density in all the plots was accounted for by these two variables - 15.68% by small Pe, 1.66% by middle-sized P.e - and 13.77% is shared. Of the variables examined, small *P.evansii* density, or a combination of the two size classes (plants of 50 to 250cm tall), would provide the best

"explanation" of *P.evansii* seedling density, but clearly other factors not studied here were also determining seedling densities.

4.3.4.2.2. A, B and C plots

P.evansii seedling density in the A, B and C plots was correlated positively with grass biomass and the density of small *P.evansii*, and negatively with the density of dead ones (appendix 4.3.4.2). Elements of the sums of squares of the regression of these to variables on *P.evansii* seedling density are in table 4.3.4.2.2. Grass biomass had the greatest primary element and the smallest secondary element, identifying it as a variable with the most explanatory power. Colinearity between dead and small *P.evansii* was shown by their large secondary element, and only one could be used in the regression model. The best choice was small P.evansii which had a small secondary element with grass biomass, and therefore had some additional effect (i.e. explanatory power) on *P.evansii* seedling density.

Table 4.3.4.2.2. Results of additive elements analysis of the regression of logged dead, and small, *P.evansii* on *P.evansii* seedling density.

Source of variation	SS	% of variation
MODEL	28.08	44.5%
Residual	35.02	55.5%
PRIMARY ELEMENTS (unique)		
Dead *P.evansii*	1.74	2.76%
Small *P.evansii*	2.58	4.16%
grass biomass	4.82	7.64%
SECONDARY ELEMENT (shared)		
Dead/small *P.evansii*	9.71	15.42%
Dead *P.e.*/grass	5.14	8.15%
small *P.e.*/grass	-1.25	-1.98%
TERTIARY ELEMENT (shared)		
dead/small *P.e.*/ grass biomass	5.44	8.62%
TOTAL	63.103	100%

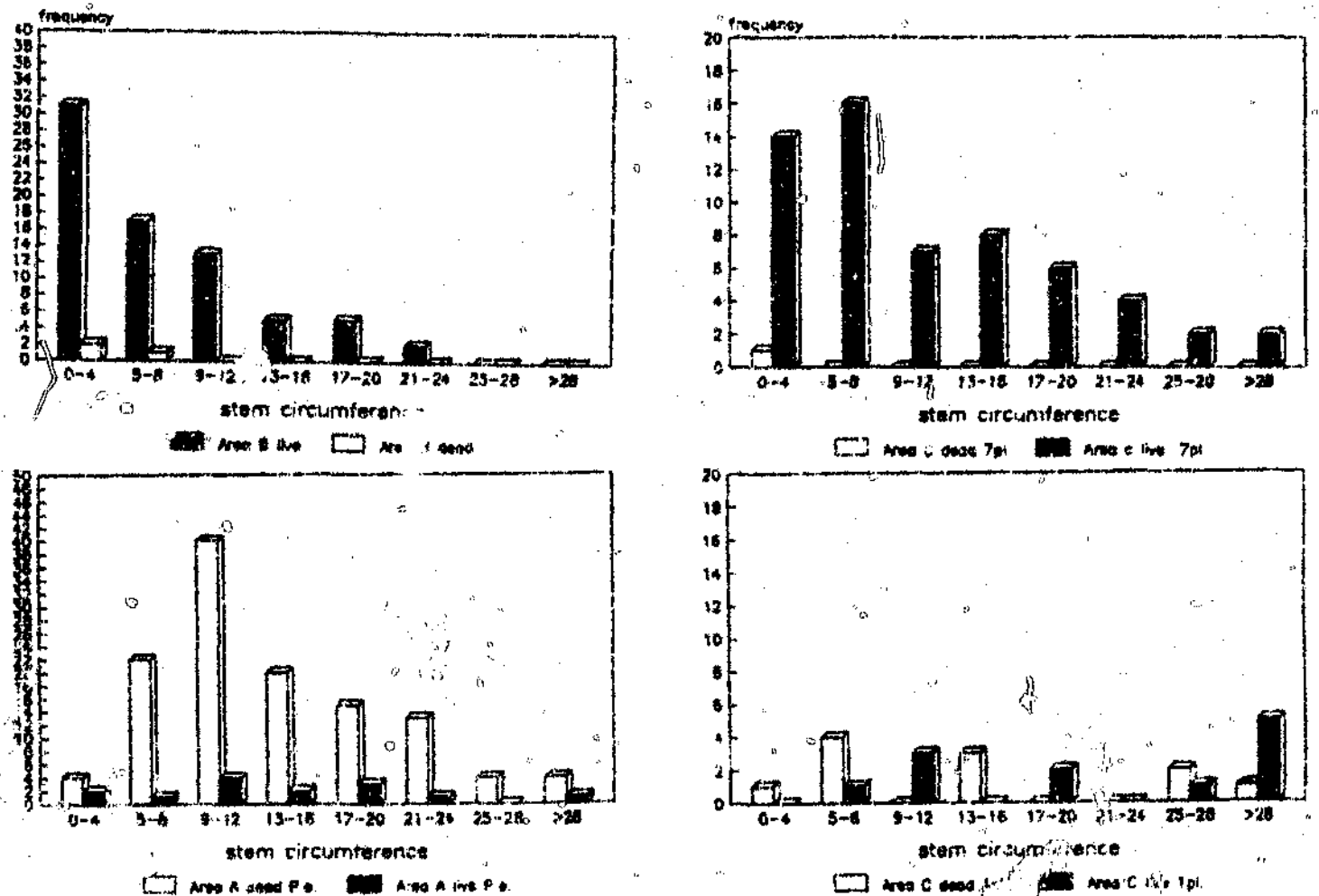


Figure 4.3.4. Stem circumference class frequency of live and dead *P.eraesii* in areas B, C and A, showing phases of stand development. The trend is for an increasing frequency of larger stems in plots (from the younger area B to older area C - excluding one plot); and then mortality occurring in all size classes (in senescing area A and the first plot of area C).

4.3.4.3. Forest precursor and forest species seedling recruitment

The density of "other" (forest and precursor) species seedlings was positively correlated with that of tall *L.sericea* (ls>250). It was also positively correlated with middle-sized *L.sericea* density, and negatively correlated with total *P.evansii* density (appendix 4.3.4.1). These three variables accounted for 57.7% of variation in the density of "other" species: Uniquely, tall *L.sericea* accounted for 19.18%, middle-sized ones 4.76%, and total *P.evansii* density accounted for 4.24%. Tall *L.sericea* shared just over 11% of the variation with both total *P.evansii* density and with middle sized *L.sericea* density, while only a very small amount was shared between these last two variables (0.002%). This implies that tall *L.sericea* on its own could be used to explain most of the model's variation (47.9%).

4.3.4.4. Growth and mortality of *P.evansii* during stand development

The correlation matrices (appendix 4.3.4.1, 4.3.4.2) showed that the densities of *P.evansii* seedlings, small and middle-sized plants are correlated, whereas these height-classes are un-correlated with the densities of senescing and dead *P.evansii*. From this it was hypothesized that in C IX, *P.evansii* stand development proceeded in "phases" of stand initiation, growth and then stand mortality. In some areas a new cohort may have been initiated among the remaining live (senescing) plants and dead wood of a former stand, resulting in a plot height-class structure where intermediate height classes are missing, and where the densities of older plants are un-correlated with those of the new recruits (eg T2 top area, fig 4.3.3.6). In other areas of old stands, a new "wave of recruitment" would have not yet occurred (see fig 4.3.2.11, Area A).

Evidence of this phasic stand development comes from mortality data of the A, B and C plots. Fig 4.3.4 shows how young stands (Area B) have high densities of smaller plants, lower densities of larger plants and a virtual absence of mortalities, which are confined to smaller plants. Stands at a later phase of development (Area C, excluding the first plot) have higher densities of larger plants, but still have many small plants. Mortality is still restricted. The last

phase (Area A, first plot of Area C) is characterized by massive stand mortalities in all size-classes.

This type of stand development seemed to occur in areas invaded for the first time by pure *P.evansii*. In mixed *L.sericea-P.evansii* scrubland where *P.evansii* populations are older, they appeared to be self-replacing at low densities, or dwindling at a slow rate (eg T1, T2 bottom area).

The relationship between *P.evansii* height and basal circumference

The relationship between *P.evansii* height and basal circumference fitted a multiplicative model, circumference = a x height x b. The correlation coefficient was 0.

HEIGHT	CIRCUMFERENCE
50cm	est.1.81cm
100cm	5.01cm
150cm	9.08cm
200cm	13.85cm
250cm	19.21cm
300cm	25.1cm

4.3.4.5. Growth and mortality of *L.sericea* during stand development

In contrast to *P.evansii*, *L.sericea* stands did not show sudden mortality at later stages of stand development, but rather a steady decrease in the mortality rate as plants grew taller and the stand thinned out. During the surveying of the plots, only four dead plants (two <150cm, two >250cm) were found, all in transect 1. The vast majority of deaths in *L.sericea* occurred during the establishment phase of the plants' life-cycles. (Counts of seedlings <50cm tall, including those less than 6cm tall, were made under the canopies of 5 *L.sericea* bushes. Seedlings <6cm occurred at an average density of 17.6/m², about 30 times denser than seedlings above this size). Deaths continued to occur among smaller plants as the stand ages, resulting in a *L.sericea* shrubland with a relatively low density of tall plants which can be quite long lived (a *L.sericea* grove in C IX contains plants older than 40 years).

4.3.4.6. Growth and mortality of later successional species

Except for *B.salvifolia*, few canopy plants of later successional species were found in the woody plots. Either sufficient time has not elapsed for them to grow, or their growth has been slowed by under-canopy conditions. Low light would probably be one reason. In a study of the light requirements of neotropical tree seedlings (Augspurger 1984), it was found that of fifteen species, none survived better in the shade than in the sun, although shade-tolerance varied. During these surveys, no mortalities were recorded among smaller later successional species, but in closed canopy areas about T6 and T1, some dead or 'dying' *Diospyros austro-africana* were found.

4.3.5. RECRUITMENT PATTERNS OF L.SERICEA, FOREST PRECURSOR AND FOREST SPECIES SEEDLINGS BENEATH CANOPY PLANTS

4.3.5.1 The probabilities of forest precursor or forest species replacing canopy *L.sericea*

The ratios of later successional species seedlings to *L.sericea* seedlings in different aged stands were used to indicate the probabilities of a *L.sericea* being replaced by a later successional species on its death. The ratios are presented at the end of table 4.3.5.1. Most stands had a ratio above or near one, indicating it is likely that a species other than *L.sericea* will replace a canopy *L.sericea*. Scattered *L.sericea* and the semi-closed vegetation of transect 2, bottom section, showed the reverse trend: *L.sericea* is more likely to replace itself in these sites.

Table 4.3.5.1. Densities of seedlings beneath *L.sericea* canopy trees in vegetations of different physiognomy:
T1 = transect 1, plots 4 to 8 - closed canopy mature *Leucosidea* scrubland;
LT = *Leucosidea* thicket, 10 individual trees in closed canopy mature *Leucosidea* scrubland;
NWC = North-western bush clump, plots 1 to 7 - closed canopy mature *Leucosidea* clump;
T7 = transect 7, plots 2 to 7 - almost closed canopy mature *Leucosidea* scrubland;
ILP = 10 individual trees in, open *Leucosidea-Pteridium* veld;
SL = Scattered *Leucosidea* individuals, 7 trees on NW of C IX and on NE ridge below the we[illegible];
T2b = transect 2 bottom section, 6 plots - almost closed canopy *Leucosidea-Phillipcia* scrubland;
RT = *Rhamnus prunoides* thicket, 2 plots in closed canopy *Rhamnus-Leucosidea* shrubland.

	T1	LT	NWC	T7	ILP	SL	T2b	RT
AREA SAMPLED m2:	125	106	175	150	95	64	150	50
PHYSIOGNOMY:	C	C	C	1/2C	O	O	1/2C	C
Seedling species (<50cm)	Seedling density (No./m2)							
Diospyros austro-africana	.032	.028	.171	.03	.39	.264	.026	.02
Rhus dentata	.104	.009		.007		.077	.007	.06
Rhamnus prunoides	.032	.047	.114	.127	.074			4.46
Euclea natalensis	.008	.037		.02				.36
Maytenus spp.			.023					.34
Calpurnia sericea	.064	.009			.01			
Halleria lucida	.064	.028	.006					
Heteromorpha trifoliata	.016							
Olinia emarginata								.02
Scolopia mundtii	.008							
Diospyros whyteana	.008							
Celtis africana			.006					
Sum of densities:	.272	.158	.32	.134	.474	.341	.033	5.24
Proportion of other spp. to *L.sericea* seedlings:	1.25	1.01	1.89	1.63	1.04	0.41	0.05	6.09

4.3.5.2. Differences in *L.sericea* recruitment rate during stand development

The densities of *L.sericea* seedlings beneath closed canopy *L.sericea* vegetation were significantly less than those beneath open *L.sericea* vegetation (df = 3; H = -81.209; p < .0001), from the Kruskal-Wallis one-way ANOVA of four areas of *L.sericea* vegetation (two representing later successional closed canopy scrubland and two

representing earlier successional, open vegetation with scattered trees).

Mean *L.sericea* seedling densities for each sample area were as follows:

CLOSED CANOPY AREAS	SEEDLING DENSITY
Transect 1, 5 plots:	0.218/m²
L.sericea trees in thicket:	0.157/m²
OPEN CANOPY AREAS	
Isolated *L.sericea* among *Pteridium*:	0.45/m²
Scattered *L.sericea* in grass:	0.83/m²

Mean *L.sericea* seedling densities for other *L.sericea* areas were:

CLOSED CANOPY AREAS	SEEDLING DENSITY
NW *L.sericea* clump:	0.171/m²
Transect 7, 6 plots:	0.113/m²
Rhamnus thicket:	0.06/m²
SEMI-CLOSED CANOPY AREAS	
Transect 2, bottom section:	0.63/m²

4.3.5.3. Densities of forest and forest precursor species seedlings in different areas of C IX

Table 4.3.5.1 shows the seedling densities of forest and forest precursor species beneath *L.sericea* canopies, in areas at different stages of succession and with different vegetation physiognomies. *L.sericea* areas with a closed canopy had higher diversities of forest and precursor species seedlings, but lower total seedling densities for these species (no test made). The area with the highest density of forest and precursor species was the *Rhamnus prunoides* thicket, which had a mixed canopy of this species and *L.sericea*. A seedling of the forest species *Podocarpus latifolius* was found near this site.

In other areas where *L.sericea* was infrequent and not a canopy dominant, later successional species also occurred. Roadside verges in the catchment, originally supporting *B.salvifolia*, showed the abundant presence of other species (no records taken), mainly *Rhamnus*

prunoides, but including *Euclea natalensis*, *Maytenus species*, *Olinia emarginata*, *Halleria lucida* and *D.austro-africana*. The mean seedling densities of forest and forest precursor seedlings around *Protea* trees, and under a *Buddleia salvifolia* dominated closed canopy area of transect 1, were higher than any of the previous areas (except for the *Rhamnus prunoides* thicket - see table 4.3.5.2).

Table 4.3.5.2. Mean seedling densities (plants <50cm tall) of forest and forest precursor species under 12 *Protea* trees on the East ridge of C IX, and in three closed canopy *Buddleia salvifolia* dominated plots of transect 1. The mean density of all later successional species in these sites are given (total mean density)

canopy species:	*Protea spp.*	*Buddleia salvifolia*
Seedling species	mean seedling density (No./m2)	
Diospyros austro africana	.813	.227
Rhus dentata	.141	.04
Rhamnus prunoides	047	.028
Euclea natalensis	047	.09
Maytenus spp.		
Calpurnia sericea		.587
Halleria lucida	.04	
Heteromorpha trifoliata		
Olinia emarginata		
Scolopia mundtii	.012	
Diospyros whyteana		
Celtis africana		
Rhus tomentosa	.012	
Rhus lucida	.047	
Rhus spp.	.012	
Total Mean Density	1.284	1.341

The trends in precursor and forest species seedling recruitment beneath canopies hypothesized from these observations, were that

1), areas of vegetations having the highest seedling densities and diversities of forest and forest precursor species, are those where *L.sericea* is either not dominant or absent,

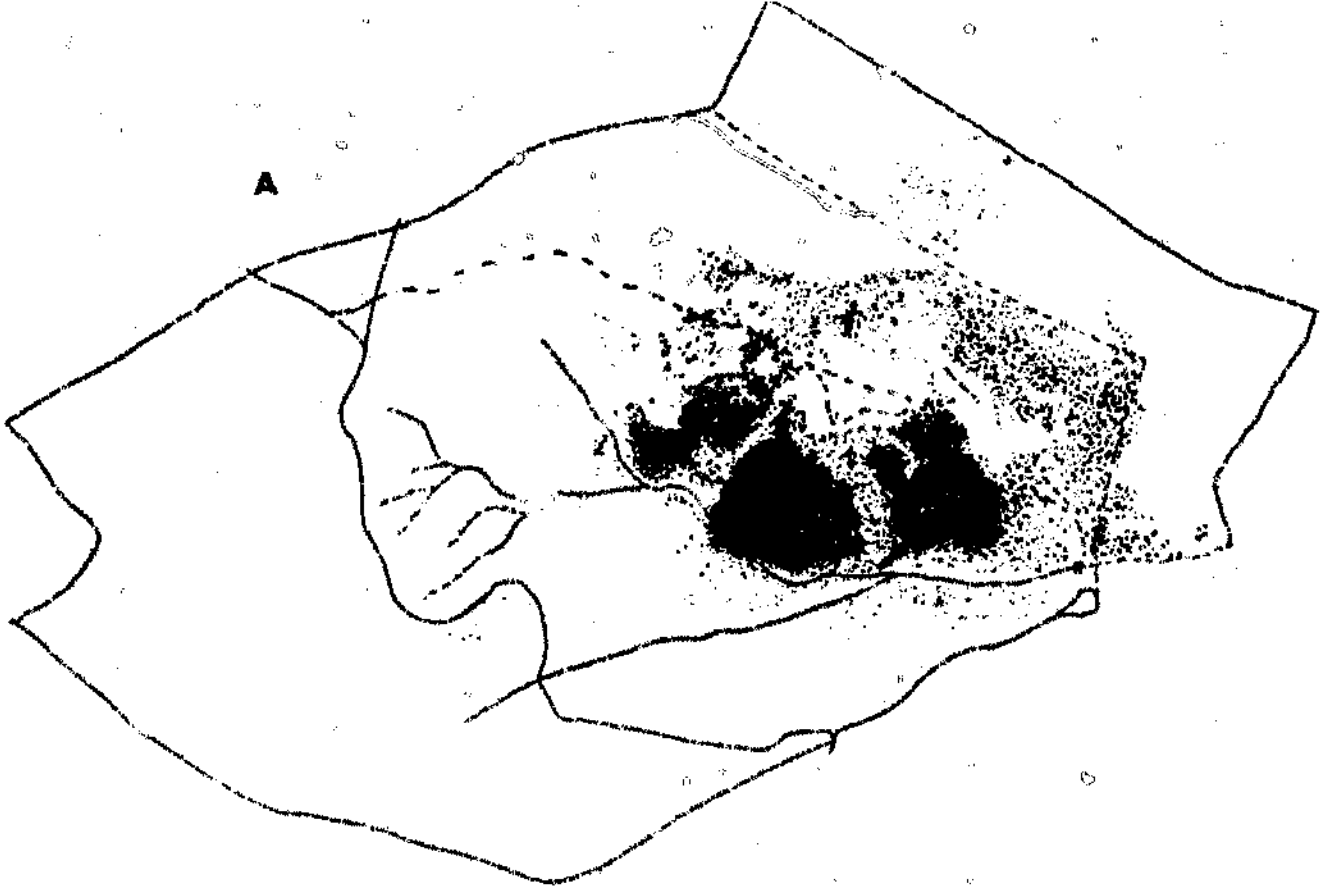


Figure 4.4.1. Maps of C IX showing the distribution of *P.evansii* (A) and *L.sericea* (B) in 1986, 21 years after total fire protection (and 42 years after partial withdrawal of fire).



2) sites with more available space and less competition for light (eg road verges and beneath *Protea Spp*) provide adequate conditions for precursor and forest species; the presence of a closed canopy *per se* (see *Protea Spp*) does not facilitate higher densities of later successional species.

4.4 DISCUSSION

The sequence of woody vegetation change in C IX varied with different initial dominant vegetation. *L.sericea* was slower to invade *Themeda triandra* grassland areas, but quicker to invade *Miscanthus capensis* grassland areas. As observed by Killick and Granger, both *P.evansii* and *L.sericea* favoured moister sites and invaded them first, but clearly the species differed in their requirements for seedling establishment and growth.

Since 1973, *P.evansii* has continued to invade the moister south slope of C IX. Stands in the re-surveyed plots which established before 1973 have shown no overall decrease in density, but within individual plots there were changes in density resulting in local spatial shifts in the population (eg. Transects 1 and 2, figs 4.3.3.1 and 2). *P.evansii* dominance also appeared to be shifting, away from older stands where *L.sericea* has increased to become dominant or co-dominant, to new sites higher up on the south slope, a feature visible in fig 4.4.1.

P.evansii's decline in dominance in initially pure *P.evansii* stands was partly due to the patterns of stand development exhibited by this species, and partly due to the "facilitation" of *L.sericea* in declining older stands characterized by stand mortality. A mono-specific stand where *P.evansii* is apparently maintaining its dominance is in the T2 top area. Here the stand development is patchy, with mixed older and younger stands.

The details of how *L.sericea* is facilitated in grassland areas during *P.evansii* stand decline were not resolved. Although no evidence for a relationship was found in this study, there is still the possibility that the litter of senescing *P.evansii* causes a decline in the grass biomass, which increases the survival of *L.sericea* seedlings:

the densities of dead *P.evansii* were negatively correlated with grass biomass, and positively correlated with *L.sericea* seedling densities. Other possible reasons may exist: A study involving *Baccharis pilularis* (Hobbs & Mooney, 1985), a species which showed a similar growth-form and life history to *P.evansii* (though maybe not as long lived), found that the abundances of all herbaceous species declined greatly after the plants formed a closed canopy. This was due in part to shading, but also increased herbivory by small mammals on herbaceous species seeds. Further fieldwork on *P.evansii* stands is required to resolve this issue.

L.sericea has invaded other areas of C IX, as predicted by Granger. Invasion has been faster in the mixed *Miscanthus capense-Pteridium* [illegible]*inum* area in the flatter, lower-lying area of C IX, and much slower in grassland areas away from streams. Whether it is the lack of moisture in these grassland sites, or the grass sward itself which inhibits this invasion, is not known.

There is little question that *L.sericea* will dominate most of C IX, but its continued dominance as the last, self-replacing vegetation is not certain. *L.sericea* seedling recruitment is much lower in closed canopy *L.sericea*-shrub communities than in less developed stands, implying that in the long term, *L.sericea* may not be able to replace itself in C IX. Seedlings of forest and other forest precursor species were growing in the *L.sericea*-shrub communities, and probabilities are that when a canopy *L.sericea* dies, one of these species will fill the resultant gap. However, there are also indications that the *L.sericea*-shrub vegetation does not provide the ideal environment for the growth of later successional species: The diversity and density of later species is greater in areas where *L.sericea* is not dominant, e.g. under *Protea* species, *B.salvifolia* trees and in the *Rhamnus prunoides* thicket.

There are two possible reasons for this. Firstly, it may be that *L.sericea* shrubs make comparatively poor perch sites (though better than *P.evansii*) for frugivorous birds bringing seed of forest precursor and forest species. The *Protea* trees, prominently situated on the ridge of the catchment, may provide good perch-sites for birds

who have come from a meal of fruits in the forest patches below the weir, or in the forests of N'dedema gorge below C IX. *L.sericea* communities were less prominently situated for visiting birds. Also, established later successional plants such as *Rhamnus prunoides* are themselves seed sources, and provide food for frugivores, who also deposit the seed of other species at that site. *L.sericea* provides no food for the carriers of bird-dispersed seed.

Secondly the *L.sericea* environment may have some inhibitory physiological effect on seedlings. Circumstantial evidence of this comes from comparing L.sericea scrubland with adjacent *B.salvifolia* canopy plants. The *B.salvifolia* supported more later successional seedlings, even though sites were close together and the same in overall environmental features.

The ameliorated moisture climates of closed canopy situations *per se* did not result in higher densities and diversities of forest and forest precursor seedlings, but canopy plants may have reduced herbaceous competition beneath them, enabling seedling recruitment. Sites relatively free of competition such as the road verges proved suitable for establishment of some forest precursor species, even without the canopy influence of a nearby *B.salvifolia*. Special local environmental conditions (besides a certain freedom from competition) may therefore not be required for the establishment of such species. The reason for later successional species being late may be mostly because of their method of seed dispersal.

Whatever the effects of site conditions on later successional species seedling establishment, the availability of suitable perch-sites for frugivorous birds was the most important factor in determining the presence of these species in C IX. They were virtually confined to under- or near-canopy situations (excluding those of *P.evansii*, which make insubstantial perches). Their future role in the catchment depends on their ability to replace the canopy dominants.

The patterns of woody vegetation change appear to be proceeding largely as Granger predicted, except with regard to later successional species. The populations of these species should increase faster in non-*L.sericea* 'woodlands', including the road verges. These sites of nucleation (Yarranton and Morrison 1974) for later successional species should expand into adjacent vegetations, coalescing with the smaller populations already occurring there. Although the distinction between forest and forest precursor species has not been clarified previously, it may be predicted that precursor species such as *Rhamnus prunoides* or *Rhus dentata* which produce copious fruit will attract frugivores and may accelerate the development of populations of forest species such as *Podocarpus latifolius* and *Scolopia mundtii*.

This study of woody plants depended partially on a sample design initiated by Granger, and highlighted the uses and deficiencies of such an approach. Besides the lack of plot boundary markers, a major limitation was that the plots were positioned to merely document the changes at a site, and did not represent all situations in the catchment. Nor were they replicated in one area, resulting in problems of pseudo-replication, so that they did not provide data on woody plant changes which would enable the testing of hypotheses.

This study has expanded the design somewhat to include other areas. Their positioning provided a contrast to existing plots and allowed the preliminary testing of certain hypotheses, but was again not designed to provide a full record of woody changes. Despite limitations in sample design in both years and in the data record from 1973, a number of woody plant population characteristics were identified which gave insight into the patterns of woody change, and prompted hypotheses regarding their processes.

Conclusions

1) In the surveyed woody plots up to 1987, there were four different pathways of woody plant succession in C IX. These occurred at different sites. Three of these involved *L.sericea* in areas of vegetation without the influence of *P.evansii*; and one, occurring on the south slope of C IX, involved *P.evansii* being the initial invader of *Themeda triandra* grassland. Forest precursor and forest species

were just starting to become abundant in *L.sericea* and selected other areas, but not in *P.evansii* stands.

2) *P.evansii* populations are still largely restricted to the south-facing slope of C IX, but were expanding to new areas of the slope and onto the East ridge.

3) *P.evansii* populations were decreasing in their dominance of existing areas, although maintaining their overall densities. The rate of recruitment in already-colonized areas, and in new areas of C IX, appears slower than the initial invasion of the south slope.

4) *L.sericea* populations are maintaining their dominance in existing stands, and increasing it in other areas - (in order of rate of invasion), mainly *Miscanthus* or *Pteridium* areas, the *P.evansii* stands on the south slope, and the grassland adjacent to moist sites

5) *L.sericea* invasion of grassland areas on the south slope is facilitated in the declining phases of *P.evansii* stand development.

6) *L.sericea* seedling recruitment decreases in situations of closed canopy *L.sericea*, while the diversity of forest and forest precursor seedlings increases. If seedling survival rates are equal, these plants have a greater chance of replacing a canopy *L.sericea* than one its own seedlings does.

7) Higher densities and diversities of forest and forest precursor seedlings occur in areas where *L.sericea* is not dominant. *L.sericea* may have some inhibitory effect on later successional species.

8) The behavior of frugivorous birds has the greatest influence on the distribution of later successional species in C IX. Subsequent effects patterning these species may involve inhibition by *L.sericea* and competition for resources (especially light).

CHAPTER 5

FEATURES OF VEGETATION CHANGE IN C IX

5.1. INTRODUCTION

This chapter examines the population patterns that occurred during post-fire vegetation change in C IX. It compares them to those patterns suggested by the successional theories discussed in chapter 1. The aim is to reveal some general features of vegetation change after withdrawal of fire in the Little Berg.

To aid this discussion, theories relating to various aspects of vegetation change were translated into a number of questions:

* Were seral stages (Clements 1916) evident in C IX, with whole species assemblages replacing others, or did species change independently of others in time and space (Gleason 1936)?

* What were the roles of the initial floristic composition, and relay floristics (Egler 1954) in C IX?

* Was succession uni- (Clements 1916) or multi-directional?

* What was the role of autogenic change (Clements 1916) in C IX?

* How did the rates of floristic change (species turnover) vary in C IX (Bornkamm 1981)?

* What population interactions (facilitation, tolerance or inhibition, Connell and Slatyer 1977) occurred?

* What population patterns were found to reflect species life-history characteristics (Pickett 1982, Noble and Slatyer 1980, Drury and Nisbet 1973)?

5.2. DISCUSSION

5.2.1. WERE SERAL STAGES EVIDENT IN C IX VEGETATION CHANGE?

In succession, a seral stage (Clements 1916) would theoretically be characterized by a group of species whose relative abundances in space and time varied in similar ways. As one species in the sere increased, so should the others, and so on. A sere is thus comparable to Clements' "community unit" (Whittaker 1975), and depends on the existence of discrete plant communities rather than an "individualistic" plant response, or gradient in species composition (Gleason 1939, McIntosh 1967). As discussed in chapter 2 (p 29), but not explicitly tested, many species showed gradual abundance changes along the catchment gradients, while a few had particular site preferences and more discrete distributions. Shipley and Keddy (1987) propose that neither the individualistic nor the community unit concept alone, reflect actual plant distribution patterns, and that other descriptions of community structure should be sought. Future studies of succession should address this aspect.

Of the species groups examined in this study, few clear seral stages were identified. Rather, each species had its own distribution pattern in the catchment, and its localized increases and decreases did not track those of any other species (see figs 3.3.2.2 a)-e). For example, the 1973 distribution of *Acalypha punctata* was quite similar to that of *Pteridium aquilinum*, but it did not consistently decrease when *P.aquilinum* decreased. Nor was its increase in some areas paralleled by an increase in *P.aquilinum* (this is clearly seen in fig. 3.3.2.2 b) and c)).

However, when viewed with less attention to details, there were broad "physiognomic groups" which formed crude "seres" or replacement sequences in some areas. These were from grassland to a) bracken veld then *L.sericea*-shrubland and scrub forest, or b) to *P.evansii* shrubland then *L.sericea/P.evansii* shrubland, then scrub forest.

5.2.2. WHAT WERE THE ROLES OF RELAY FLORISTICS AND INITIAL FLORISTIC COMPOSITION?

In relay floristics, facilitation of new arrivals (invaders) by the initial site occupants is implied (Egler 1954). The influences of the initial floristic composition includes species characteristics interacting with each other and environment in many ways. The appearance of either pattern depended on the spatial scale at which the vegetation was viewed. At the broad scale of the entire catchment, and among most species, the initial floristic composition of the vegetation (itself influenced by initial site conditions), determined the observed patterns of vegetation change.

Only among the woody species was there the possibility of relay floristics at this broad scale. Yet although forest precursor species had "invaded" *L.sericea*, *B.salviifolia* and other areas (see section 4.3.5.3), they had not yet replaced the original plants present there (as would occur in relay floristics). Also, initial occupants may have *facilitated* their arrival (as discussed in 4.4) by providing perch sites for seed-dispersers; but in some areas they have *suppressed* (see 4.3.5.2) the growth of such species.

At a finer scale, particular sites displayed possible signs of relay floristics. They were invaded and later dominated by species initially present elsewhere. The most obvious examples of this are *P.evansii*, *L.sericea* (see maps in fig 4.1.1, 4.1.2 and 4.4.1), and *P.aquilinum*, which invaded areas away from streams (see fig 3.3.2.2 b)). Also, the grasses *D.amplectens*, *H.turgidulum* and *P.natalense* (section 3.3.2.1, fig 3.3.2.2 a) and Fig 3.3.2.2 e) (respectively) had invaded and become co-dominants in some sites. However, barring *L.sericea*'s facilitation in declining *P.evansii* stands (shown in section 4.3.4.1), the role of facilitation in these changes is unknown.

Many other widespread species did not shown signs of replacing, or being replaced by, other species. They merely altered their relative frequencies in different areas (eg *A.punctata*, *R.ludwigii*, *T.triandra*, *H.Falx*, *T.leucothrix*, *A.appendiculatus* and *H.umbraculigerum*, see figs 3.3.2.2 a)-e)).

The greater effect of the initial floristic composition during the first few decades of vegetation change is not unexpected (Noble and Slatyer 1981). The majority of available flora in the Little Berg (excluding forest precursor and forest species) have evolved under the influence of recurrent fire regimes. They persist (even at low frequencies) in the vicinity after a burn. Non- or poorly fire adapted species include those associated with forests, which only "invade" areas later on in the absence of fire. Yet to show the pattern of relay floristics, facilitation of the growth of these invaders must still be demonstrated.

5.2.3. DID UNIDIRECTIONAL OR MULTIDIRECTIONAL SUCCESSION OCCUR?

Succession in C IX up to 1986 was largely multidirectional, without following predictable sequences as suggested by Clements (1916). Over the time period examined in this study, most sites of similar species composition diverged (see section 3.3.1.2 and figs 3.3.1.2 a)-e)).

This may be the result of many species with roughly equal competitive abilities being present from the start. Small local differences in environmental conditions and competitive balances could have resulted in different directions of change.

However, a few species imposed a slight degree of unidirectionality on the overall pattern of change (eg *Helichrysum aureo-nitens*, *Panicum natalense*, *Helictotrichon turgidulum* and *Pellaea quadripinnata* increasing in most places; *Elionurus muticus*, *Themeda triandra*, *Pheteropogon filifolius*, and *Buchenroedera lotononoides* decreasing - see section 3.3.1.2). Also, the invasion of *L.sericea* plus associated species (ground forbs and creepers), and the appearance of forest precursor/forest species, will lead to convergence toward forest *later* in succession, even in initially quite different communities.

5.2.4. THE ROLE OF AUTOGENIC CHANGE

Facilitation through enhanced invasion, or increasing resource availability (Pickett et al. 1987), are signs of autogenic change, and are discussed later. Many workers (eg Horn 1971, Peckham and Harding 1981, Pickett et al. 1987; but see Huston and Smith 1987) think that

during succession soil moisture conditions ameliorate at a site as light conditions worsen. This is because the developing vegetation canopy intercepts light and reduces heat build up near the soil, and along with stem-flow and litter, improves rain's infiltration. This amelioration supposedly directs succession.

Species distributions along gradients from dry to moist (excluding aquatic or marsh species) and high to low radiation levels, may therefore broadly reflect their position in a successional sequence (eg Tilman 1985, Drury and Nisbet 1973). Species distributions in C IX from the stream to the ridge tops, from steep south-facing to flat areas or north-facing slopes, and from Katspruit to Misbah soils represented their moisture and radiation preferences (see section 2.3). Evidence of amelioration of site conditions in the catchment would theoretically come from observing successional shifts of species along these gradients. Mesic, low light species should increase, while "dry", high light ones should decrease in most areas. Intermediate species should decrease in low-lying, moist soil and shaded areas, and increase in medium altitude (not dry) and high (drier) altitude soils.

Species frequency changes (determined in section 3.3.2.2) which reflected this pattern, were *L.sericea*, (to some extent *C.africana*) and *P.evansii* (mesic); *T.triandra* and *D.filifolius* (dry); and *P.quadripinnata*, *H.felix*, *P.aquilinum*, *R.ludwigii*, *S.alopecuroides*, and *H.turgidulum* (intermediate).

Other species showed patterns of change at odds with those expected from their positions along the gradients, indicating that site amelioration was not necessarily a dominant influence. The mesic species *C.natalensis* and *H.umbraculigerum* decreased in many areas. *A.sumialata*, *R.alters*, *P.natalense* and *H.aureo-nitens*, which occurred more frequently in drier sites in 1973, often increased in both moist, and dry areas. The intermediate species *A.appendiculatus*, *F.caprina*, *E.muticus*, *S.isatideus* and *A.punctata* had varying responses (for example, *A.appendiculatus* and *F.caprina* decreased in dry areas and increased in the moist vegetation group 20; while *E.muticus* declined in many places). The mesic species *H.capense*'s varied response was perhaps due to its particular preference for higher radiation levels,

causing its decline in shaded sites. The "drier" *S.bupleuroides* decreased in dry sites and increased in less dry sites, including vegetation group 10.

Later successional forest precursor and forest species occurred in moist, lower light sites, but were also prolific in exposed ridge top areas, with lower moisture and higher radiation levels. This showed that amelioration of site conditions was not essential for their establishment. Rather, their population pattern was highly reliant on the vagaries of their bird dispersers.

A reason for the unpredictable response along the light and moisture gradient of many grassland species, may be that they have evolved under the major selective force imposed by fire. Other factors like shade tolerance, may not be as important in determining grassland species composition when fire is frequent (Vogl 1974). Rather, changes in the grass layer may result from differential tillering levels and storage (Everson 1985) in species with growth optima at different fire frequencies.

Current knowledge is also biased toward grass behavior under a regime of fire. Less is known about grass reactions in its total absence. Many aspects of hypothesised amelioration during succession are based on observations of woodland communities, where the species have very different life-history strategies to grasses. One may expect grass species responses to withdrawal of fire to be less predictable using criteria usually applied to woodland species. Indeed many grassland changes in C IX were not predicted by previous researchers.

Changes (including autogenic ones) in the post-fire environment have played a greater role in the evolution of woodland species life-history properties (eg the development of shade tolerance, or the ability to maximize light capture in canopy situations). Such species persist only when long fire-free periods occur. Yet even among poorly fire-adapted woody species, the influences of site amelioration in the early stages of woody stand development are doubtful. The (autogenic) role of perch sites in determining their distribution is predominant.

5.2.5. RATES OF SPECIES TURNOVER

The rate of species turnover in the 13 years from 1973 to 1986 (section 3.3.3) was slowest in communities representing later successional (woody) stages (ie the mature *L.sericea* areas). It was fastest in areas with communities not yet dominated by *sericea* (eg ridge top, and open *P.aquilinum* areas). The slow change in wooded areas could be because woody species are slower growing than herbaceous ones, promoting the prolonged coexistence of associated species (Huston 1979). It may also indicate the tenacity of *L.sericea* in these sites.

5.2.6. POPULATION INTERACTIONS (FACILITATION, TOLERANCE AND INHIBITION)

Facilitation of later species by the initial site occupants was found. Senescing stands of *P.evansii* facilitate *L.sericea* recruitment (section 4.3.4.1). *L.sericea* stands facilitate (by providing perch-sites) the arrival of forest and forest precursor species (4.3.4.3). *Protea* species and *B.salvifolia* facilitate forest precursor and forest species' arrival and perhaps their establishment (4.3.5.3). Forest precursor and forest types also facilitate the arrival of other such species.

Some evidence of inhibition was also found. *L.sericea* seems to inhibit the establishment of forest precursor and forest species (4.3.5.3). *L.sericea* (and perhaps senescing *P.evansii* ?) inhibit grass (this is obviously visible beneath *L.sericea* shrubs). *P.aquilinum* inhibits *P.evansii* (Everson and Breen 1983). Although there is no direct evidence, the sparsity of *L.sericea*, forest and forest precursor seedlings in pure grassland sites may mean that grasses suppress these species' establishment (through root competition ?).

Evidence of tolerance, where later species are successful whether or not earlier species have preceded them, was circumstantial. *P.evansii* was able to establish and grow to maturity in grassland (section 4.3.4.2.2), while *L.sericea* rarely did so. *P.natalense*, *P.quadripinnata* *H.aureo-nitens*, *A.implexens* and *H.turgidulum* may have exhibited tolerance in that they increased in many areas, irrespective of the other species occurring there (sections 3.3.2.1 and 3.3.2.2).

Their increase may also be explained by a form of competitive release after withdrawal of fire.

The dominant effects of the initial floristic composition in C IX also suggests the "Tolerance mechanism" (Humphrey 1984). Most species (especially herbaceous ones) were present since withdrawal of fire in C IX, and change was largely characterized by local shifts in their dominance (perhaps reflecting Horn (1976)'s "competitive hierarchy", specific to local site conditions).

5.2.7. POPULATION PATTERNS AND SPECIES LIFE-HISTORY CHARACTERISTICS

The life history characteristics of a few species seemed to be reflected in their changing population patterns in C IX. Only some of these are discussed here.

One obvious pattern was a result of the clonal growth of *P.aquilinum*, as clarified by Watt (1947). The current survey showed that bracken stem frequencies were decreasing in the low-lying, moist areas in C IX where it existed before withdrawal of fire (ie in the older parts of the colony). In newer parts of the colony at higher-lying, less moist sites, bracken was increasing (section 3.3.2.2).

Another species showing clonal growth patterns which have allowed its spread in the catchment was *Helichrysum aureo-nitens*. Its colonies have extended, but become more diffuse at their original centers.

P.evansii's population pattern revealed the establishment, growth, and relatively sudden mass mortality of its stands during invasion of new grassland areas (fig 4.3.4, section 4.3.4.4). Also evident was its relatively low competitive ability in established stands of other woody species (eg. *L.sericea*). This may be due to its needle leaf characteristics and many-layered branching geometry, which does not suit very low light levels (Horn 1971).

L.sericea's pattern of invasion of C IX reflected (besides the spatial pattern of wind dispersal which was not investigated) its response to a), the moisture distribution, and b) to levels of shading and competition during its establishment. This is shown by its

presence in moist, old *P.aquilinum* areas with an open frond structure; in senescing *P.evansii* areas, possibly where the sward has become less vigorous; and in its relative slowness to establish in closed-sward grassland areas and beneath its own closed canopies.

The application of the vital attributes scheme (Noble and Slatyer, 1980) in this study is limited by inadequate knowledge of the species. Also, the scheme is unable to account for situations where the attributes and their relative strengths differ, depending on the community or site context. Some examples of the few generalities were as follows.

Most perennial grasses and forbs have the V attribute of being largely unaffected by fire: they sprout [illegible] roots and re grow very rapidly. This allows them to exist [illegible] plant types when fire is relatively frequent, and [illegible] after a burn. The extent of seed dispersal in many grasses is limited to a few meters from the parent (O'Conner pers com). Seed [illegible] such species is unlikely to arrive from outside the area, and is not always freely available as required in vital attribute's D attribute of long distance dispersal. The existence of long-lived seed stores (and therefore an S attribute) in perennial grasses and forbs is unknown, but rodent seed predators must severely limit seed stores in grassland areas (Adams pers com).

L.sericea exhibits the V vegetative attribute of sprouting after fire (Smith 1982), but requiring time to grow to their pre-fire form. Seeds may disperse quite large distances (D), but seem unable to establish in grassland areas. In these circumstances, two different actions can promote its spread. One is the facilitating action (section 4.3.4.1) of senescing *P.evansii* stands (resulting in an R attribute); the other is the slower spread of this species by establishing in sites at the edge of its canopy influence, where herbaceous species are less vigorous, but where the influence of the parent plant is weak enough not to inhibit the seedlings. The possibility that *L.sericea* is unable to replace itself under closed canopy situations

(see section 4.3.5.2) gives it some I attribute characteristics as well. It has a life-span between that of woody forest species and the short-lived shrub *P.evansii*.

P.evansii cannot re-sprout, but its seed is stimulated to germinate after fire (G attribute) (Smith 1982). Further recruitment is delayed until mature plants produce seed (possibly at 1-2 years old); and seeds may disperse over long distances (D). The continued spread of this species in C IX since fire protection shows that germination still occurs in the absence of fire. Its establishment in grassland areas suggests it is tolerant (T attribute) of competition from herbaceous species initially present at the site. However, seedling recruitment drops off in mature and senescing stands of *P.evansii*, as shown in 4.3.4.2. This feature results in an I attribute, where *P.evansii* is unable to continue recruitment under the increased influence of woody plants. *P.evansii* is short-lived relative to other woody species.

Woody species with bird-dispersed seed (ie mainly forest and forest precursor species) do not persist at a site through coppicing when fire is frequent. In a fire-free period, though, their seed may arrive through frugivory, given them the "D" attribute of long-distance dispersal. The availability of perch-sites appears to act as a "qualifier" to this attribute. These species seem to establish anytime near perch trees. They are tolerant (T-attribute) of competition from some species (eg *B.salviifolia*); but may be inhibited (I-attribute) by others (eg *L.sericea*, see section 4.3.5.3). (These attributes are surprising - the original vital attributes scheme never encompassed the influence of bird-dispersal on the population patterns of these species, nor the influence of different canopy species). Other attributes of forest and forest precursor species, are a relatively long life-span; and some degree of tolerance of (shade?) competition from adults of their own or similar kind, but perhaps not of (root?) competition from grassland species.

Further speculations can not be made in applying the vital attributes scheme. The attributes described above do predict some overall succession patterns in C IX; from grassland, to *P.evansii* shrubland, then *L.sericea* shrubland and finally some form of forest. However, a better knowledge of species' life-history characteristics would be required, to explain in detail the observed patterns of vegetation change at a mechanistic level, where strategies of resource use and plant-plant interactions are considered.

5.3. FINAL CONCLUSIONS

This study has been mainly at a descriptive level. It allowed hypotheses to be developed about the nature of some of the main patterns of vegetation change in C IX, but did not provide strong evidence of the underlying processes involved. Some inadequacies of the study were a result of the relatively broad scale at which the changes were viewed; but it seemed clear that answers to many questions posed by successional theories did vary with scale. The finer details of species responses and interactions would better be studied with a Harperian population biology approach (Harper 1977).

In summary, the main features of vegetation change found in this study were as follows.

* Species changes were individualistic. Only in broad physiognomic groups could seral stages be observed.

* The initial floristic composition governed the dominant patterns of change. Clear relay floristics, involving grasses, *P.evansii* and *L.sericea*, was only found in some sites.

* Most sites similar in 1973 diverged in species composition.

* A few species with consistent, widespread changes, caused a small degree of unidirectionality of change. The future spread of *L.sericea* and forest and forest precursor species will, however, lead to convergence, even in initially different sites.

* Site amelioration may have influenced some species changes, but most were influenced by other factors.

* Change was fastest in areas free of *L.sericea*, and slowest where this species was dominant.

* Evidence of facilitation, tolerance and inhibition was found. Each mechanism was important in determining some patterns of change, but the possible simultaneous operation of all three complicated other patterns.

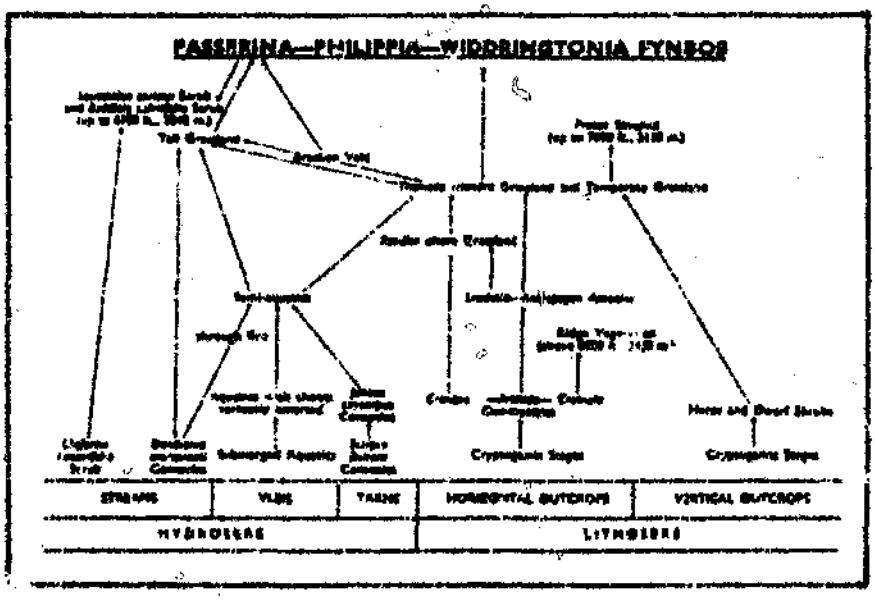
* Changing population patterns in C IX reflected known species life-history characteristics.

* Species interactions at particular sites resulted in small-scale variation in the patterns of change. These interactions need to be understood to fully describe succession.

APPENDIX 1.1. Sampling intensities of 1m wide transects in 1973 and 1986. Transect lengths were estimated from maps or from measuring along 1986 transect routes. Only part of transect 1 was re-located in 1986.

TRANSECT	estimated length(m)	SAMPLING INTENSITY 1973	1986	Proportion of '73 intensity
A	137	48	49	1.1
1	40	40	19	.48
2	751	724	201	.28
3	801	758	253	.33
4	423	403	237	.59
5	215	195	90	.45
6	115	75	58	.77
7	470	332	155	.47

APPENDIX 1.2. Pathways of community change proposed by Killick (1963) for Sub-alpine areas like C IX.



APPENDIX 1.2. Species identified in plant communities along transects in C IX in 1986.

TRANSECT A

TA.1

Acalypha punctata
Ajuga ophrydis
Andropogon appendiculatus
Aster spp.
Athanasia punctata
Buchenroedera cf lotononoides
Bulbostilis cf oritrephes
Clutia natalensis
Commelina africana
Diheteropogon amplectens
Elionurus muticus
Festuca caprina
Harpochloa falx
Helichrysum emboraculigerum
Helichrysum herbaceum
Helichrysum platypterum
Helictotrichon turgidulum
Heteropogon contortus
Koeleria cristata
Leucosidea sericea
Micrachaetus capensis
Oxalis obliquifolia
Pellaea quadripinnata
Philippia evansii
Polygala ohlendorfiana
Pteridium aquilinum
Rabdosia calycina
Rhus discolor
Rumex woodii
Scilla spp.1
cf Schoenoxiphium lehmanii
Senecio spp.(creeper)
Themeda triandra
Trachypogon spicatus
Tristachya leucothrix
Vernonia hirsutata
Wahlenbergia zeyheri

TA.2

Acalypha punctata
Andropogon appendiculatus
Aster spp.
Buchenroedera lotononoides
cf Bulbostilis oritrephes
Commelina africana
Diheteropogon amplectens
Elionurus muticus
Epilobium capense
Harpochloa falx
Helichrysum platypterum
Helictotrichon turgidulum
H. emboraculigerum
Heteropogon contortus
Hypericum aethiopicum
Koeleria cristata
Oxalis obliquifolia
Pteridium aquilinum
Rabdosia calycina
Rhus ludvigii
Rumex woodii
Senecio spp.
Schistostephium crataegifolium
cf schoenoxiphium lehmanii
Scilla spp. 1
Scilla spp. 2
Senecio spp. (creeper)
Tristachya leucothrix
Vernonia hirsutata

TA.3

Acalypha punctata
Aloteropsis semialata
Andropogon appendiculatus
Athanasia punctata
Buchenroedera lotononoides
Diheteropogon amplectens
Elionurus muticus
Epilobium capensis
Festuca caprina
Harpochloa falx
Helichrysum platypterum
Helichrysum emboraculigerum
Helictotrichon turgidulum
Hypericum aethiopicum
Lessertia perennans
Leucosidea sericea
Micrachaeta capra
Oxalis obliquifolia
Oxalis smithiana
Panicum natalense
Pteridium aquilinum
Rabdosia calycina
Rhus discolor
Rubus ludvigii
Rumex woodii
Schistostephium crataegifolium
Scilla spp. 1
Scilla spp. 2
Themeda triandra
Tristachya leucothrix
Vernonia hirstuta

TA.4

Acalypha punctata
Ajuga ophrydis
Andropogon appendiculatus

Aster spp.
Athanasia punctata
Commelina africana
Dimeteropogon amplectans
Diospyros austro-africana
Elionurus muticus
Festuca caprina
Harpochloa falx
Helichrysum platypterum
Helichrysum umbraculigerum
Helictotrichon turgidulum
Hermannia woodii
Hypericum aethiopicum
Indigofera longibarbata
Lessertia perennans
Leucosidea sericea
Miscanthus capensis
Oxalis obliquifolia
Pellaea quadripinnata
Philippia evansii
Pteridium aquilinum
Rhus discolor
Schizostachyum crataegifolium
cf. Scaenoxiphium rufum
Senecio isatideus
Themeda triandra
Tristachya leucothrix
Vernonia hirsuta

TA.5

Acalypha punctata
Asparagus asparagoides
Asparagus microraphus
Carex sp.
Celtis africana
Cineraria sp.
Clematis brachiata
Clutia natalensis
Commelina africana
Diospyros austro-africana
Dicospyros whyteana
Disperis fanniniae
Elionurus muticus
Euclea crispa
fern spp
Gunnera perpensa
Harpochloa falx
Helichrysum odoratissimum
Helichrysum umbraculigerum
cf. Hermannia woodii
Hypericum aethiopicum
Indigofera longibarbata
Indigofera spp.
Koeleria cristata
Leucosidea sericea
Meliianthus villosa
Miscanthus capensis
Myosotis sylvatica
Myrsine serrata
Oxalis obliquifolia
Pellaea quadripinnata
Philippia evansii
Plectranthus grallatus
Podocarpus latifolius
Polygala confusa
Polygala ohlendorfiana
poplar sp.
Pteridium aquilinum
Rhamnus prinoides
Rhus dentata
Rhus discolor
Rhynchosia caribaea
Riocreuxia torulosa
Rubus ludwigii
Schizostachyum crataegifolium
cf. Scaenoxiphium rufum

TRANSECT 1

T1.1

Acalypha punctata
Aster spp.
Carex spp.
Cephalaria spp.
cf Chenopodium spp.
Cineraria deltoidea
Clematis brachiata
Clutia natalensis
Commelina africana
Crassula pellucida
Diospyros austro-africana
Festuca caprina
Gallium rotundifolium
Galopina crocylloides
Geranium ornithopodum
Hallaria lucida
Helichrysum umbraculigerum
Helichrysum platypterum
Helictotrichon turgidulum
Hypericum aethiopicum
Indigofera longibarbata
Leonotis spp.
Leucosidea sericea
Miscanthus capensis
Myrsine serrata
Oenothera rosea
Oxalis obliquifolia;
Pellaea quadripinnata
Philippia evansii
Polygala ohlendorfiana

Pteridium aquilinum
Rabdosia calycina
Rhamnus prunoides
Rhus dicolor
Rhus dentata
Rhynchosia caribaea
Riocreuxia tomentosa
cf Schoenoxiphium rufum
Shoenoxiphium lehmannii
Tysonia africana
Vernonia hirsuta
Zehneria scabra

T1.2

Berkheya montana
Carex spp.
Cephalaria spp.
Cleonia brachiata
Clutia natalensis
Commelina africana
Crassula pellucida
Diospyros austro-africana
Geranium dourianum
Geranium ornithopodum
Helictotrichon hirtulum
Hypericum aethiopicum
Indigifera longibarbata
Kniphofia ritualis
Leonotis spp.
Lunconidea sericea
Miscanthus capense
Myrsine serrata
Myosotis sylvatica
Oxalis obliquifolia
Pellaea quadripinnata
Plectranthus grallatus
Polygala ohlendorfiana
Rhus dentata
Rhus discolor
Riocreuxia tomentosa
Saturea reptans
Schoenoxiphium rufum
Sebaea macrophylla
Senecio erubescens
Tysonia africana
Vernonia hirsuta
Zehneria scabra

TRANSECT 2

T2.1

Acalypha schintzii
Andropogon appendiculatus
Dihoteropogon filifolius
Erica woodii
Festuca costata
Harpechlos falx
Helichrysum aureo-nitens
Helichrysum herbaceum
Helichrysum miconifolium
Helichrysum pallidum
Hermannia woodii
Heteropogon contortus
Hypoxis spp. (acuminata?)
Kohautia amatymbica
Panicum natalense
Pteridium aquilinum
Rendlia altera
Senecio hyoseroides
Themeda triandra
Trachypogon spicatus
Tristachya leucothrix

T2.2

Acalypha punctata
Acalypha schintzii
Alloteropsis semialata
Asclepias stellifera
Aster platycephalus
Cephalaria spp.
Clutia monticola
Digera muricata
Dihteropogon amplectans
Dihteropogon filifolius
Erica woodii
Festuca costata
Harpechlos falx
Helichrysum glomeratum
Helichrysum herbaceum
Helichrysum miconifolium
Helichrysum umbraculigerum
Helichrysum pallidum
Helichrysum undata
Hermannia woodii
Heteropogon con
Hypoxis spp. (a
Kohautia amatymbica
Monsonia attenuata
Oxalis smithiana
Pachycarpus spp.
Panicum ecklonii
Panicum natalense
Pellaea quadripinnata
Polygala rehmannii
Pteridium aquilinum
Rendlia altera
Rhus discolor
Rubus ludwigii
Schizoglossum flavum

Senecio arenosens
Stiburus alopecuroides
Themeda triandra
Trachypogon spicatus
Tristachya leucothrix

T2.3

Acalypha punctata
Alloteropsis semialata
Aster pleiocephalus
Buchnerodera lotononoides
Diheteropogon amplectens
Diheteropogon filifolius
Helichrysum umbraculigerum
Hermannia woodii
Kohautia amatymbica
Leucosidea sericea
Panicum natalense
Pellaea quadripinnata
Pteridium aquilinum
Rendlia altera
Rubus ludwigii
Stiburus alopecuroides
Themeda triandra
Tristachya leucothrix

T2.4

Acalypha punctata
Alloteropsis semialata
Anthospermum herbaceum
Aster pleiocephalus
Clutia natalensis
Commelina africana
Diospyros austro-africana
Festuca caprina
Ficinia spp.
cf Galtonia viridiflora
Harpochloa falx
Helichrysum oleratissimum
Helichrysum platypterum
Monalaria cristata
Leucosidea sericea
Oxalis obliquifolia
Panicum acklonii
Pteridium aquilinum
Rabdosia calycina
Rubus ludwigii
Rumex woodii
Schoenoxiphium lehmannii
Solanum rodiflorum
Stiburus alopecuroides
Themeda triandra
Tristachya leucothrix
Vernonia hirstuta

T2.5

Acalypha punctata
Andropogon appendiculatus
Clutia natalensis
Commelina africana
Diheteropogon amplectens
Diheteropogon filifolius
Gaigeria spp.
Geranium ornithopodum
Gunnera perpensa
Harpochloa falx
Helichrysum umbraculigerum
Hermannia woodii
Hypericum aethiopicum
Kniphofia ritualis
Koelaria cristata
Leucosidea sericea
Melianthus villosus
Miscanthus capensis
Myosotis sylvatica
Oxalis obliquifolia
Panicum natalense
Pelargonium luridum
Plectranthus grallatus
Polygala ohlendorfiana
Pteridium aquilinum
Rabdosia calycina
Rhus discolor
Rubus ludwigii
Saturea reptans
Schistostephium crataegifolium
Schizoglossum flavum
Themeda triandra
Tristachya leucothrix
Tysonia africana
Vernonia hirstuta

T2.6

Acalypha punctata
Acalypha schinzii
Agapanthus campanulatus
Aristoma peduncalata
Asparagus asparagoides
Berkheya cf speciosa
Berkheya cf speciosa
Carex spp.
Clutia natalensis
Commelina africana
Crassula vaginata
Galium mittenbergense
Gunnera perpensa
Gathria pelchra
Helichrysum umbraculigerum

Helichrysum platypterum
Hypericum aethiopicum
Leucosidea sericea
Miscanthus capense
Myosotis sylvatica
Oxalis obliquifolia
Panicum natalense
Philippia evansii
Polygala ohlendorfiana
Rhus discolor
Saturea reptans
Schistostephium crataegifolium
Schizoglossum spp.
Senecio gerrardii
Stachys spp.

T2.7

Acalypha punctata
Ajuga ophrydis
Berkheya rhapontica
Carex zuluense
Cephalaria spp.
Clutia natalensis
Commelina africana
Festuca costata
Calium wittebergense
Harpechloa falx
Helichrysum umbraculigerum
Helictotrichon turgidulum
Leucosidea sericea
Melianthus villosus
Miscanthus capense
Mohria caffrorum
Myosotis sylvatica
Myrsine africana
Oxalis obliquifolia
Oxalis smithiana
Panicum natalense
Pelargonium alchemilloides
Pelargonium luridum
Pellaea quadripinnata
Philippia evansii
Polygala ohlendorfiana
Rhus discolor
Saturea reptans
Senecio erubescens
Vernonia hirsuta

T2.8

Acalypha punctata
Andropogon appendiculatus
Aristida monticola
Berkheya rhapontica
Carex spp.
Clutia natalensis
Commelina africana
Crassula pellucida subsp. brachypetala
Festuca caprina
Ficinia spp.
Harpechloa falx
Helichrysum umbraculigerum
Helichrysum pilosellum
Helictotrichon turgidulum
Heteropogon contortus
Xeiphoria ritualis
Leucosidea sericea
Miscanthus capense
Mohria caffrorum
Oxalis obliquifolia
Oxalis smithiana
Panicum natalense
Pellaea quadripinnata
Polygala ohlendorfiana
Rubus ludwigii
Schoenoxiphium lehmannii
Themeda triandra
Trachypogon spicatus
Tristachya leucothrix
Wahlenbergia fasciculata

T2.9

Andropogon appendiculatus
Berkheya rhapontica
Carex zuluense
Diheteropogon amplectens
Diheteropogon filifolius
Diospyros austro-africana
Elionurus muticus
Geranium ornithopodium
Harpechloa falx
Helichrysum aureo-nitens
Helichrysum cymosum
Helichrysum herbaceum
Helichrysum herbaceum
Helichrysum miconiifolium
Helichrysum umbraculigerum
Helichrysum squamosum
Helictotrichon turgidulum
Koeleria cristata
Leonotis spp.
Leucosidea sericea
Oxalis obliquifolia
Panicum natalense
Pellaea quadripinnata
Philippia evansii
Pteridium aquilinum
Rubus ludwigii
Schistostephium crataegifolium

Senecio dregeanus
Senecio erubescens
Solanum nodiflorum
Stiburus alopecuroides
Themeda triandra
Trachypogon spicatus
Tristachya leucothrix
Wahlenbergia fascicularis
Wahlenbergia zeyheri
Zehneria scabra

T3.4

Acalypha punctata
Andropogon appendiculatus
Commelina africana
Diheteropogon amplectens
Festuca caprina
Geranium ornithopodum
Harpechloa falx
Helichrysum umbraculigerum
Helichrysum pallidum
Helictotrichon turgidulum
Koeleria cristata
Leggeria perennans
Leucosidea sericea
Oxalis obliquifolia
Pteridium aquilinum
Rubus ludwigii
Senecio bupleuroides
Senecio erubescens
Senecio isatideus
Solanum nodiflorum
Themeda triandra
Tristachya leucothrix
Zehneria scabra

T3.5

Acalypha punctata
Ajuga ophrydis
Andropogon appendiculatus
Commelina africana
Diheteropogon amplectens
Epilobium capense
Festuca caprina
Geranium ornithopodum
Harpechloa falx
Helichrysum aureo-nitens
Helichrysum glomeratum
Helichrysum herbaceum
Helichrysum pallidum
Helictotrichon turgidulum
Kniphofia laxiflora
Kniphofia ritualis
Koeleria cristata(?)
Leggeria perennans
Leucosidea sericea
Monsonia attenuata
Oxalis obliquifolia
Pelargonium luridum
Pteridium aquilinum
Senecio bupleuroides
Senecio dregeanus
Senecio erubescens
Senecio inornatus
Senecio isatideus
Stiburus alopecuroides
Themeda triandra
Trachypogon spicatus
Tristachya leucothrix
Wahlenbergia zeyheri

T3.6

Acalypha punctata
Ajuga ophrydis
Andropogon appendiculatus
Diheteropogon amplectens
Festuca caprina
Harpechloa falx
Helichrysum cooperi
Helichrysum glomeratum
Helichrysum herbaceum
Helichrysum nicoritifolium
Helichrysum umbraculigerum
Helichrysum pallidum
Helichrysum platypterum
Helictotrichon turgidulum
Koeleria cristata(?)
Leucosidea sericea
Pentarrhinum natalense
Pteridium aquilinum
Rubus ludwigii
Rumex woodii
Senecio bupleuroides
Senecio dregeanus
Senecio erubescens
Senecio inornatus
Stiburus alopecuroides
Themeda triandra
Trachypogon spicatus
Tristachya leucothrix
Wahlenbergia squamifolia
Wahlenbergia zeyheri

T3.7

Acalypha punctata
Commelina africana
Diheteropogon amplectens
Diheteropogon filifolius

Schoenoxiphium lehmannii
Sebaea macrophylla
Senecio bupleuroides
Senecio sp.x (creeper)
Themeda triandra
Trachypogon spicatus
Tristachya leucothrix
Wahlenbergia fasciculata
Wahlenbergia zayheri

T2.10

Allotaropsis semialata
Aristoma pedunculata
Aster perfoliatus
Dicoma anomala
Diheteropogon amplectens
Diheteropogon filifolius
Festuca costata
Fisinia spp.
Haplocarpa scaposa
Harpechloa falx
Helichrysum aureo-nitens
Helichrysum herbaceum
Helichrysum miconiifolium
Helichrysum umbraculigerum
Helichrysum pallidum
Helichrysum pilosellum
Hypoxis spp. (acuminata?)
Lotonotis corymbosa
Monsonia attenuata
Oxalis obliquifolia
Panicum natalense
Pellaea quadripinnata
Pendlia altera
Rubus ludwigii
Senecio dregeanus
Senecio erubescens
Senecio inaequidens
Senecio spp. (creeper)
Themeda triandra
Trachypogon spicatus
Tristachya leucothrix
Wahlenbergia montana
Wahlenbergia sdazzifolia

T2.11

Acalypha punctata
Andropogon appendiculatus
Cephalaria spp.
Commelina africana
Diheteropogon amplectens
Diheteropogon filifolius
Elionurus muticus
Erica woodii
Festuca costata
Harpechloa falx
Helichrysum aureo-nitens
Helichrysum herbaceum
Helichrysum miconiifolium
Helichrysum umbraculigerum
Helichrysum pallidum
Helictotrichon turgidulum
Heteropogon contortus
Hypericum lalandii
Kniphofia laxiflora
Oxalis obliquifolia
Oxalis smithiana
Panicum natalense
Philippia evansii
Pteridium aquilinum
Rabdosia calysina
Pendlia altera
Rubus ludwigii
s423 ? (Granger)
Schoenoxiphium rufum
Senecio bupleuroides
Senecio erubescens Ait. var
dichotomus DC.
Senecio spp. (creeper)
Stiburus alopecuroides
Themeda triandra
Trachypogon spicatus
Tristachya leucothrix
Vernonia hirstuta

T2.12

Andropogon appendiculatus
Anthericum longistylum
Aster perfoliatus
Berkheya rhapontica
Bulbostilis (cf) critrephes
Cephalaria spp.
Cephalaria spp.
Cineraria doltoidea
Diheteropogon amplectens
Diheteropogon filifolius
Elionurus muticus
Epilobium capense
Festuca costata
Haplocarpa scaposa
Harpechloa falx
Helichrysum herbaceum
Helichrysum miconiifolium
Helichrysum monticola
Helichrysum umbraculigerum
Helichrysum sp.
Helictotrichon turgidulum
Kniphofia laxiflora

Kohautia amatymbica
Lotonotis corymbosa
Oxalis obliquifolia
Oxalis smithiana
Pellaea quadripinnata
Phyllopsis avanaii
Pteridium aquilinum
Rendlia altera
Rubus ludwigii
Scabiosa columbaria
Schoenoxiphium rufum
Senecio bupleuroides
Senecio spp. (creeper)
Themeda triandra
Trachypogon spicatus
Tristachya leucothrix
Vernonia hirstuta
Wahlenbergia zeyheri

TRANSECT 3

T3.1

Alloteropsis semialata
Aster perfoliatus;
Berkheya rhapontica
Clutia monticola
Crassula setulosa
Diheteropogon amplectens
Diheteropogon filifolius
Haplocarpa scaposa
Harpechloa falx
Helichrysum aureo-nitens
Hypericum lalandii
Kniphofia laxiflora
Koeleria cristata
Lotonotis corymbosa
Myrsine africana
Oxalis smithiana
Panicum natalense
Pellaea quadripinnata
Rabdosia calycina
Ranunculus cooperi
Rendlia altera
Rubus ludwigii
Schizoglossum flavum
Senecio bupleuroides
Stiburus alopecuroides
Themeda triandra
Trachypogon spicatus
Tristachya leucothrix
Wahlenbergia squamifolia
Wahlenbergia zeyheri

T3.2

Alloteropsis semialata
Andropogon appendiculatus
Aster perfoliatus
Berkheya rhapontica
Clutia monticola
Crassula setulosa
Diheteropogon amplectens
Epilobium capense
Harpechloa falx
Helichrysum aureo-nitens
Helichrysum gloneratum
Helichrysum miconifolium
Helichrysum umbraculigerum
Helichrysum pallidum
Hemizygia transvalica
Kohautia amatymbica
Monsonia attenuata
Oxalis obliquifolia
Panicum natalense
Pellaea quadripinnata
Pteridium aquilinum
Rendlia altera
Rubus ludwigii
Schoenoxiphium lehmannii (?)
Senecio bupleuroides

T3.3

Acalypha punctata
Andropogon appendiculatus
Buchnerodera lotonoides
Diheteropogon amplectens
Diheteropogon filifolius
Epilobium capense
Harpechloa falx
Helichrysum aureo-nitens
Helichrysum gloneratum
Helichrysum miconifolium
Helichrysum umbraculigerum
Helichrysum pallidum
Hemizygia transvalica
Kohautia amatymbica
Monsonia attenuata
Oxalis obliquifolia
Panicum natalense
Pellaea quadripinnata
Pteridium aquilinum
Rendlia altera
Rubus ludwigii
Schoenoxiphium lehmannii (?)
Senecio bupleuroides

Erica woodii
Festuca caprina
Harpechloa falx
Helichrysum pureo-nitens
Helichrysum cooperi
Helichrysum glomeratum
Helichrysum herbaceum
Helichrysum miconiifolium
Helichrysum umbraculigerum
Helichrysum pallidum
Helichrysum pilosellum
Hermannia woodii
Heteropogon contortus
Hypericum lalandii
Koeleria cristata
Kohautia amatymbica
Leucosidea sericea
Panicum natalense
Pellaea quadripinnata
Pteridium aquilinum
Rubus ludwigii
Rumex woodii
Senecio oregeanus
Senecio arubescens
Stiburus alopecuroides
Theneda triandra
Trachypogon spicatus
Tristachya leucothrix
Wahlenbergia fasciculata

T3.8

Acalypha punctata
Ajuga ophrydis
Andropogon appendiculatus
Buchenrodera lotonoides
Commelina africana
Diheteropogon amplectens
Festuca caprina
Gunnera perpensa
Harpechloa falx
Helichrysum cooperi
Helichrysum umbraculigerum
Helictotrichon turgidulum
Hypericum aethiopicum
Kniphofia ritualis
Koeleria cristata
Kohautia amatymbica
Leucosidea sericea
Monsonia attenuata
Oxalis obliquifolia
Panicum natalense
Pelargonium luridum
Polygala chlendorfiana
Pteridium aquilinum
Rabdosia calycina
Rubus ludwigii
Rumex woodii
Schistostephium crataegifolium
Senecio hupleuroides
Senecio erubescens
Senecio isatideus
Stiburus alopecuroides
Theneda triandra
Trachypogon spicatus
Tristachya leucothrix

T3.9

Acalypha punctata
Andropogon appendiculatus
Carex spp.
Clutia natalensis
Commelina africana
Epilobium capense
Festuca caprina
Festuca costata
Galium rotundifolium
Geranium ornithopodum
Gunnera perpensa
Harpechloa falx
Helichrysum adoratissimum
Helichrysum platypterum
Helictotrichon turgidulum
Kniphofia ritualis
cf. Lessertia spp.
Leucosidea sericea
Myrsine africana
Oxalis obliquifolia
Oxalis smithiana
Panicum natalense
Rabdosia calycina
Rhus discolor
Rubus ludwigii
Rumex woodii
Schistostephium crataegifolium
Schoenoxiphium lehmannii
Senecio hupleuroides
Senecio erubescens
Senecio inornatus
Senecio isatideus
Tristachya leucothrix
Vernonia hirstuta
Zehneria scabra

T3.10

Clutia natalensis
Epilobium capense
Geranium ornithopodum
Helichrysum umbraculigerum
cf. Lessertia spp.

Myrsine africana
Phytolacca spp.
Pteridium aquilinum
Rabdosia calycina
Rubus ludwigii
Senecio bupleuroides
Senecio arubescens
Themeda triandra

T3.11

Andropogon appendiculatus
Clutia natalensis
Eriosema capense
Harpechloa falx
Helichrysum umbraculigerum
Pteridium aquilinum
Rubus ludwigii
Senecio bupleuroides
Senecio arubescens
Themeda triandra

T3.12

Acalypha punctata
Alloteropsis semialata
Clutia natalensis
Commelina africana
Diheteropogon amplectens
Diospyros austro-africana
Elionurus muticus
Festuca caprina
Harpechloa falx
Helichrysum umbraculigerum
Koeleria cristata
Leucosidea sericea
Monsonia attenuata
Myrsine africana
Oxalis smithiana
Panicum natalense
Pteridium aquilinum
Rabdosia calycina
Rhus discolor
Rubus ludwigii
Schoenoxiphium lehmannii
Senecio bupleuroides
Senecio arubescens
Senecio spp. (sticky, tall)
Themeda triandra
Trachypogon spicatus
Tristachya leucothrix
Vernonia hirstuta
Wahlenbergia squamifolia
Zehneria scabra

T3.13

Acalypha punctata
Alloteropsis semialata
Andropogon appendiculatus
Berkheya rhapontica
Cyphia alata
Diheteropogon amplectens
Elionurus muticus
Harpechloa falx
Helichrysum aureo-nitens
Helichrysum glomeratum
Helichrysum umbraculigerum
Koeleria cristata
Oxalis obliquifolia
Panicum ecklonii
Panicum natalense
Pellaea quadripinnata
Pteridium aquilinum
Rubus ludwigii
Senecio arubescens
Senecio spp. (sticky, tall)
Themeda triandra
Trachypogon spicatus
Tristachya leucothrix

T3.14

Acalypha punctata
Alloteropsis semialata
Aster pleurocephalus
Diheteropogon amplectens
Harpechloa falx
Helichrysum glomeratum
Helichrysum herbaceum
Helichrysum umbraculigerum
Heteropogon contortus
Hypericum aethiopicum
Koeleria cristata
Oxalis obliquifolia
Panicum natalense
Pellaea quadripinnata
Pteridium aquilinum
Rubus ludwigii
Senecio bupleuroides
Senecio arubescens
Senecio sp. (creeper)
Stiburus alopecuroides
Themeda triandra
Trachypogon spicatus
Tristachya leucothrix
Wahlenbergia squamifolia

T3.15

Acalypha schinzii
Alloteropsis semialata

Myrsine africana
Phytolacca spp.
Pteridium aquilinum
Rabdosia calycina
Rubus ludwigii
Senecio bupleuroides
Senecio erubescens
Theneda triandra

T3.11

Andropogon appendiculatus
Clutia natalensis
Eriosemum capense
Harpochloa falx
Helichrysum umbraculigerum
Pteridium aquilinum
Rubus ludwigii
Senecio bupleuroides
Senecio erubescens
Theneda triandra

T3.12

Acalypha punctata
Alloteropsis semialata
Clutia natalensis
Commelina africana
Diheteropogon amplectens
Diospyros-austro-africana
Elionurus muticus
Festuca caprina
Harpochloa falx
Helichrysum umbraculigerum
Koelaria cristata
Leucosidea sericea
Monsonia attenuata
Myrsine africana
Oxalis smithiana
Panicum natalense
Pteridium aquilinum
Rabdosia calycina
Rhus discolor
Rubus ludwigii
Schoenoxiphium lehmannii
Senecio bupleuroides
Senecio erubescens
Senecio spp. (sticky, tall)
Theneda triandra
Trachypogon spicatus
Tristachya leucothrix
Vernonia hirstuta
Wahlenbergia squamifolia
Zahneria scabra

T3.13

Acalypha punctata
Alloteropsis semialata
Andropogon appendiculatus
Berkheya rhapontica
Cyphia alata
Diheteropogon amplectens
Elionurus muticus
Harpochloa falx
Helichrysum aureo-nitens
Helichrysum glomeratum
Helichrysum umbraculigerum
Koelaria cristata
Oxalis obliquifolia
Panicum schinzii
Panicum natalense
Pellaea quadripinnata
Pteridium aquilinum
Rubus ludwigii
Senecio erubescens
Senecio spp. (sticky, tall)
Theneda triandra
Trachypogon spicatus
Tristachya leucothrix

T3.14

Acalypha punctata
Alloteropsis semialata
Aster pleiocephalus
Diheteropogon amplectens
Harpochloa falx
Helichrysum glomeratum
Helichrysum herbaceum
Helichrysum umbraculigerum
Heteropogon contortus
Hypericum aethiopicum
Koelaria cristata
Oxalis obliquifolia
Panicum natalense
Pellaea quadripinnata
Pteridium aquilinum
Rubus ludwigii
Senecio bupleuroides
Senecio erubescens
Senecio sp. (creeper)
Stiburus alopecuroides
Theneda triandra
Trachypogon spicatus
Tristachya leucothrix
Wahlenbergia squamifolia

T3.15

Acalypha schintzii
Alloteropsis semialata

Diheteropogon amplectens
Helichrysum glomeratum
Helichrysum herbaceum
Helichrysum umbraculigerum
Heteropogon contortus
Oxalis obliquifolia
Panicum natalense
Pellaea quadripinnata
Senecio erubescens
Themeda triandra
Trachypogon spicatus
Tristachya leucothrix

T3.16

Acalypha schintzii
Alloteropsis semialata
Digitaria flaccida (?)
Diheteropogon filifolius
Eragrostis capensis
Erica woodii
Haplocarpa scaposa
Hebenstretia dentata
Helichrysum adenocarpum
Helichrysum aureo-nitens
Helichrysum herbaceum
Helichrysum miconiifolium
Helichrysum umbraculigerum
Helichrysum pallidum
Helichrysum pilosellum
Helio spiralepsis
Hermannia woodii
Heteropogon contortus
Hypoxis spp. (acuminata?)
Leonotis spp.
Loudetia simplex
Maxulua thudeana
Nemesia denticulata
Oxalis obliquifolia
Panicum ecklonii
Pellaea quadripinnata
Polygala rehmanii
Rendlia altera
Senecio bravidentatus
Senecio bupleuroides
Senecio erubescens
Themeda triandra
Trachypogon spicatus
Tristachya leucothrix
Wahlenbergia montana
Wahlenbergia squamifolia

TRANSECT 4

T4.1

Alepidea amatymbica
Alloteropsis semialata
Andropogon appendiculatus
Anthericum longistylum
Anthospermum herbaceum
Aristoma pedunculata
Aster perfoliatus
Berkheya rhapontica
Cephalaria s.
Cliffortia linearifolia
Clutia monticola
Crassula setulosa
Diheteropogon amplectens
Diheteropogon filifolius
Elionurus muticus
Epilobium capense
Eragrostis capensis
Erica woodii
Haplocarpa scaposa
Harpechloa falx
Helichrysum herbaceum
Helichrysum miconiifolium
Helichrysum monticola
Helichrysum umbraculigerum
Helichrysum pallidum
Helichrysum pilosellum
Heliotetrichon turgidulum
Heliophila rigidiuscula
Hermannia woodii
Heteropogon contortus
Hypericum lalandii
Kniphofia laxiflora
Kniphofia rufa Bak. (= K. laxiflora)
Koeleria cristata
Kohautia amatymbica
Ledebouria cooperii
Lotonotis corymbosa
Microchloa cafra
Monria caffrorum
Monsonia attenuata
Oxalis obliquifolia
Panicum natalense
Pellaea quadripinnata
Philippia evansii
Pleuropsis sericeus
Psammotropha myriantha
Rendlia altera
Rhamnus prunoides
Rubus ludwigii
Scabiosa columbaria
Schizoglossum flavum
Schoenixiphium lehmannii
Sebaea macrophylla
Senecio bupleuroides
Senecio drageanus

Senecio erubescens
Senecio sp. (creeper)
Senecio spp. 674(s187) (Granger)
Stiburus alopecuroides
Themeda triandra
Trachypogon spicatus
Tristachya leucothrix
Wahlenbergia fasciculata
Wahlenbergia squamifolia
Wahlenbergia zeyheri

T4.2

Andropogon appendiculatus
cf. Argyrolobium spp.
Cephalaria sp
Commelina africana
Cyprus rupestris Crassula spp.
Epilobium capense
Harpechloa falx
Helichrysum aureo-nitens
Helichrysum miconiifolium
Helichrysum umbraculigerum
Helichrysum pallidum
Hypericum lalandii
Monsonia attenuata
Oxalis obliquifolia
Panicum natalense
Pellaea quadripinnata
Rendlia altera
Rubus ludwigii
Schoenixiphium lehmannii
Senecio bupleuroides
Senecio erubescens
Senecio sp. (creeper)
Stiburus alopecuroides
Themeda triandra
Tristachya leucothrix

T4.3

Andropogon appendiculatus
Bulbostylis oritrephes
Diheteropogon amplectens
Erica woodii
cf.Fimbriostilis spp.
Harpechloa falx
Helichrysum aureo-nitens
Helichrysum cooperi
Helichrysum miconiifolium
Helichrysum umbraculigerum
Helichrysum pallidum
Helictotrichon turgidulum
Heteropogon contortus
Hypericum lalandii
Leucosidea sericea
Monsonia attenuata
Oxalis obliquifolia
Panicum natalense
Pellaea quadripinnata
Pteridium aquilinum
Rendlia altera
Rubus ludwigii
Schoenixiphium lehmannii
Senecio bupleuroides
Senecio erubescens
Senecio sp. (creeper)
Silene undulata
Stiburus alopecuroides
Themeda triandra
Trachypogon spicatus
Tristachya leucothrix
Wahlenbergia fasciculata
Wahlenbergia zeyheri

T4.4

Acalypha punctata
Andropogon appendiculatus
Bulbostylis oritrephes
Commelina africana
Festuca caprina
Harpechloa falx
Helichrysum umbraculigerum
Helictotrichon turgidulum
Koelaria cristata
Lessertia perennans
Leucosidea sericea
Nemesia denticulata
Oxalis obliquifolia
Panicum natalense
Pelargonium luridum
Pellaea quadripinnata
Pteridium aquilinum
Rhus discolor
Rubus ludwigii
Senecio erubescens
Senecio sp. (creeper)
Silene undulata
Stiburus alopecuroides
Themeda triandra
Tristachya leucothrix
Vernonia hirsuta

T4.5

Acalypha punctata
Andropogon appendiculatus
Anthericum longistylum
Buchenroedera lotononoides
Bulbostylis oritrephes
Clutia natalensis

Ajuga ophrydis
Andropogon appendiculatus
Berkheya montana
Buchnerodendra lotononoides
Clutia natalensis
Commelina africana
Diheteropogon amplectens
Diheteropogon filifolius
Diospyros austro-africana
Festuca caprina
Festuca costata
Gunnera perpensa
Harpochloa falx
Helichrysum aliconifolium
Helichrysum umbraculigerum
Helictotrichon turgidulum
Hypericum aethiopicum
Hypericum lalandii
Kniphofia ritualis
Kohautia amatymbica
Leonotis spp.
Leucosidea sericea
Merxmuellera stricta
Oxalis obliquifolia
Oxalis smithiana
Pellaea quadripinnata
Philippia evansii
Pteridium aquilinum
Rabdosia calycina
Rhus discolor
Rubus ludwigii
Rumex woodii
Saturea rupestris
Schistostephium crataegifolium
Senecio hupleuroides
Senecio erubescens
Thamnea triandra
Tristachya leucothrix
Tulbaghia spp.
Tysonia africana
Vernonia hirsuta
Zehneria scabra

14.8

Acalypha punctata
Alepidea amatymbica
Andropogon appendiculatus
Berkheya montana
Berkheya rhapontica
Buchnerodendra lotononoides
Carex cernua
Carex zuluensis
Clutia montícola
Clutia natalensis
Commelina africana
Crassula pellucida
Diospyros austro-africana
Euphorbia epicyparissias
Festuca caprina
Festuca costata
Galium rotundifolium
Galium wittebergense
Geranium buchananii
Geranium ornithopodum
Gunnera perpensa
Haplocarpa scaposa
Harpochloa falx
Helichrysum umbraculigerum
Helichrysum platypterum
Helictotrichon turgidulum
Hypericum aethiopicum
Kniphofia ritualis
Leonotis spp.
Lobostemon paniculatus
Leucosidea sericea
Merxmuellera stricta
Nemesia denticulata
Oxalis obliquifolia
Oxalis smithiana
Pellaea quadripinnata
Plectranthus grallatus
Polygala ohlendorfiana
Pteridium aquilinum
Rabdosia calycina
Rhus discolor
Rhoicrauxis tomentosa
Rubus ludwigii
Rumex woodii
Saturea rupestris
Schistostephium crataegifolium
Senecio erubescens
Tysonia africana
Zehneria scabra

14.9

Berkheya montana
Carex zuluensis
Clutia natalensis
Commelina africana
Crassula pellucida
Diospyros austro-africana
Epilobium spp.
Helichrysum umbraculigerum
Helictotrichon turgidulum
Kniphofia ritualis
Leucosidea sericea
Merxmuellera stricta
Oxalis obliquifolia
Pellaea quadripinnata
Polygala ohlendorfiana

Commelina africana
Diheteropogon filifolius
Festuca caprina
Harpochloa falx
Helichrysum herbaceum
Helichrysum miconiifolium
Helichrysum umbraculigerum
Helichrysum pallidum
Helichrysum glacyphyrum
Helictotrichon turgidulum
Heteropogon contortus
Kohautia amatymbica
Leucosidea sericea
Monsonia attenuata
Nemesia denticulata
Oxalis obliquifolia
Panicum aclenis
Panicum natalensis
Pelargonium luridum
Pellaea quadripinnata
Polygala ohlendorfiana
Pteridium aquilinum
Rendlia altera
Rhus dregeana
Rubus ludwigii
Rumex woodii
Saturea reptans
Schoenoxiphium rufum
Scilla nervosa
Senecio bupleuroides
Senecio arubescens
Senecio inornatus
Senecio sp. (creeper)
St beres alopecuroides
Themeda triandra
Trachypogon spicatus
Tristachya leucothrix
Vernonia hirsuta
Wahlenbergia fasciculata

T4.6

Acalypha punctata
Ajuga ophrydis
Andropogon appendiculatus
Antheticum longistylum
cf. Arevraiophyma spp.
Asclepias montic.
Asparagus asparagoides
Asparagus macrorapnus
Berkheya montana
Buchnerodendra lotononoides
Bulbostylis oritrephes
Carex cernua
Cephalaria spp.
Clutia natalensis
Commelina africana
Crassula pellucida
Cyphia corymbosa
Diheteropogon amplectans
Diheteropogon filifolius
Disperis fanniniae
Festuca caprina
Galium rotundifolium
Galium wittebergense
Harpochloa falx
Helichrysum miconiifolium
Helichrysum umbraculigerum
Helictotrichon turgidulum
Heteropogon contortus
Hypericum aethiopicum
Hypericum lalandii
Kniphofia rufa
Kohautia amatymbica
Leonotis sp.
Leonotis sp.
Leucosidea sericea
Lithospermum officinale
Monsonia denticulata
Oxalis obliquifolia
Oxalis smithiana
Panicum natalense
Pelargonium luridum
Pellaea quadripinnata
Philippia evansii
Polygala ohlendorfiana
Pteridium aquilinum
Sebaea calysina
Rhus cf. panthera
Rhus dentata
Rhus discolor
Rhynchosia totulosa
Rubus ludwigii
Rumex woodii
Saturea reptans
Schistostephium crataegifolium
Schizoglossum flavum
cf. Schoenoxiphium lehmannii
Senecio bupleuroides
Senecio arubescens
Senecio inornatus
Senecio isatidens
Senecio sp. (creeper)
Themeda triandra
Themeda triandra
Tristachya leucothrix
Tulbaghia spp.
Vernonia hirsuta

T4.7

Acalypha punctata

Saturea rupicola
Senecio arabescens

T4.10

Acalypha punctata
Alloteropsis semialata
Andropogon appendiculatus
Aster pleistocephalus
Dechenreuddera lotononoides
Dolbostilis oritrephes
Carex cernua
Carex zuluensis
Commelina africana
Crassula peli[illegible]
Dimeteropogon amplectens
Diospyros austro-africana
Epilobium spp.
Harpochloa falx
Helichrysum cooperi
Helichrysum umbraculigerum
Helichrysum platypterum
Helictotrichon turgidulum
Hermannia woodii
Kniphofia laxiflora
Kniphofia ritualis
Koeleria cristata
Kohautia amatymbica
Lessertia perennans
Leucosidea sericea
Merxmuellera stricta
Microchloa caffra
Monsonia attenuata
Oxalis obliquifolia
Pellaea quadripinnata
Polygala ohlendorfiana
Pteridium aquilinum
Pygmaeo[illegible]hamaedendrum
Rhus discolor
Rubus ludwigii
Saturea rupicola
Senecio spp. (creeper)
Themeda triandra
Trachypogon spicatus
Tristachya leucothrix

T4.11

Alloteropsis semialata
Anthospermum herbaceum
Aster perfoliatus
Dimeteropogon filifolius
Harpochloa falx
Helichrysum aureo-nitens
Helichrysum glomeratum
Helichrysum miconiifolium
Helichrysum monticola
Heliophila rigidiuscula
Hermannia woodii
Heteropogon contortus
Lotononis corymbosa
Monsonia attenuata
Panicum natalense
Plectrosis sericea
Rendlia altera
cf. Schoenoxiphium lehmannii
Senecio erosulus
Themeda triandra
Trachypogon spicatus
Tristachya leucothrix

TRANSECT 5

T5.1

Acalypha punctata
Alloteropsis semialata
Andropogon appendiculatus
Aster pleistocephalus
Buchenroedera lotonoides
Carex zuluensis
Cliffia natalensis
Commelina africana
Dimeteropogon amplectens
Epilobium capense
Eriosema spp.
Festuca caprina
Fimbristylis spp.
Geranium ornithopodum
Gerbera serpensa
Harpochloa falx
Helichrysum umbraculigerum
Helictotrichon turgidulum
Hypericum aethiopicum
Kniphofia ritualis
Leucosidea sericea
Monsonia denticulata
Oxalis obliquifolia
Oxalis smithiana
Pteridium aquilinum
Rabdosia calycina
Rubus ludwigii
Saturea rupicola
Schistostephium crataegifolium
Senecio bupleuroides
Senecio isatideus
Senecio spp. (creeper)
Themeda triandra
Tristachya leucothrix
Vernonia hirsuta
Wahlenbergia squamifolia
Wahlenbergia zeyheri

cf Zehneria scabra

T5.2

Acalypha punctata
Alepidea amatymbica
Alloteropsis semialata
Andropogon appendiculatus
Aster pleiocephalus
Carex carnua
Carex zuluense
Clutia natalensis
Commelina africana
Dihoteropogon amplectens
Epilobium capense
Eragrostis curvula
Festuca caprina
Geranium ornithopodum
Gunnera perpensa
Harpechloa falx
Helichrysum cooperi
Helichrysum umbraculigerum
Helictotrichon turgidulum
Kniphofia ritualis
Lessertia perennans
Leucosidea sericea
Nemesia denticulata
Oenothera rosea
Ophioglossum reticulatum
Oxalis obliquifolia
Oxalis smithiana
Pellaea quadripinnata
Pteridium aquilinum
Rabdosia calysina
Rubus ludwigii
Senecio bupleuroides
Senecio inornatus
Senecio isatideus
Themeda triandra;
Tysonia africana
Wahlenbergia squamifolia
Zehneria scabra

T5.3

Acalypha punctata
Agrostis barbuligera
Anagillis huttonii
Andropogon appendiculatus
Carex carnua
Carex zuluense
Clutia natalensis
Commelina africana
Crassula pellucida
Epilobium capense
Eragrostis capensis
Geranium ornithopodum
Gunnera perpensa
Hebenstreidtia cotherlandii
Helichrysum aureo-nitens
Helichrysum mundii
Helichrysum umbraculigerum
Helictotrichon turgidulum
Heteropogon contortus
Hibiscus trionum
Kniphofia ritualis
Lessertia perennans
Leucosidea sericea;
Melasma scabrum
Monsonia attenuata
Nemesia denticulata
Nidorella auriculata subsp. polycephala
Oenothera rosea
Ophioglossum reticulatum
Oxalis obliquifolia
Pellaea quadripinnata
Polygala ohlendorfiana
Pteridium aquilinum
Rabdosia calysina
Rabdosia calysina
Rubus ludwigii
Senecio bupleuroides
Senecio erubescens
Senecio inornatus
Senecio isatideus
Themeda triandra
Wahlenbergia zeyheri

T5.4

Acalypha punctata
Andropogon appendiculatus
Argyrolobium tuberosum
Carex zuluense
Clutia natalensis
Commelina africana
Dihoteropogon amplectens
Epilobium capense
Eragrostis capensis
Eragrostis curvula
Festuca caprina
Geranium ornithopodum
Harpechloa falx
Hebenstreidtia sutherlandii
Helichrysum aureo-nitens
Helichrysum mundii
Helichrysum umbraculigerum
Helictotrichon turgidulum
Kniphofia ritualis
Lessertia perennans
Leucosidea sericea

Oenothera rosea
Oxalis obliquifolia
Pellaea quadripinnata
Polygala ohlendorfiana
Pteridium aquilinum
Rabdosia calysina
Rubus ludwigii
Schistostephium crataegifolium
Schoenoxiphium lehmann
Senecio bupleuroides
Senecio erubescens
Senecio isatideus
Themeda triandra
Tristachya leucothrix
Vernonia hirstuta
Wahlenbergia zeyheri

T5.5

Acalypha punctata
Andropogon appendiculatus
Argyrolobium tuberosum
Carex zuluensis
Commelina africana
Diheteropogon amplectens
Eragrostis curvula
Festuca caprina
Geranium pulchrum
Gunnera perpensa
Harpochloa falx
Hebenstaidtia rutherlandii
Helichrysum aureo-nitens
Helichrysum herbaceum
Helichrysum umbraculigerum
Helictotrichon turgidulum
Leucosidea sericea
Mohria caffrorum
Oenothera rosea
Oxalis obliquifolia
Pellaea quadripinnata
Polygala rehmanii
Pteridium aquilinum
Pychnostachys reticulata
Rabdosia calysina
Rhus discolor
Rubus ludwigii
Senecio bupleuroides
Themeda triandra
Trachypogon apicatus
Tristachya leucothrix
Vernonia hirstuta
Wahlenbergia zeyheri

T5.6

Acalypha punctata
Ajuga ophrydis
Alloteropsis semialata
Andropogon appendiculatus
Anthosperum herbaceum
Aster pleiocephalus
Clutia natalensis
Commelina africana
Diheteropogon amplectens
Festuca caprina
Gunnera perpensa
Harpochloa falx
Helichrysum aureo-nitens
Helichrysum herbaceum
Helichrysum umbraculigerum
Helictotrichon turgidulum
Hermannia woodii
Heteropogon contortus
Hypoxis spp. (acuminata?)
Leucosidea sericea
Monsonia attenuata
Oenothera rosea
Oxalis obliquifolia
Pellaea quadripinnata
Polygala ohlendorfiana
Pteridium aquilinum
Rhus discolor
Rubus ludwigii
Sebaea macrophylla
Senecio bupleuroides
Senecio erubescens
Senecio spp. (creeper)
Themeda triandra
Tristachya leucothrix
Tysonia africana
Vernonia hirstuta

T5.7

Alloteropsis semialata
Andropogon appendiculatus
Aster pleiocephalus
Carex cernua
Chironia krebsii
Clutia natalensis
Commelina africana
Diheteropogon amplectens
Festuca caprina
Gunnera perpensa
Harpochloa falx
Helichrysum aureo-nitens
Helichrysum herbaceum
Helichrysum umbraculigerum
Helichrysum pallidum
Hermannia woodii
Heteropogon contortus
Koeleria cristata

Leucosidea sericea
Merxmuellera stricta
Microchloa cafra
Mohria caffrorum
Monsonia attenuata
Nidorella auriculata subsp. polycephala
Ophioglossum reticulatum
Pelargonium Zonal
Polygala ohlendorfiana
Pteridium aquilinum
Pycnostachys reticulata
Schoenoxiphium lehmanii
Sebaea macrophylla
Sebaea repens
Senecio bupleurifolius
Senecio drubescens
Senecio spp. (creeper)
Themeda triandra
Trachypogon spicatus
Tristachya leucothrix
Wahlenbergia fasciculata
Xyris gerrardii

TRANSECT 8

T6.1

Acalypha punctata
Alepidea amatymbica
Asclepias stellifera
Asparagus asparagoides
Asparagus microraphis
Athanasia calva
Berkheya montana
Berkheya rhapontica
Carex spp.
Cephalaria natalensis
Cephalaria spp.
Cineraria deltoidea
Clematis brachiata
Clutia natalensis
Commelina africana
Crassula pellucida
Cyphia rogersii
Diheteropogon amplectens
Diospyros austro-africana
Epilobium capense
Euphorbia epicyparissias
Galium rotundifolium
Galium wittebergense
Geranium baurianum
Geranium ornithopodum
Geranium pulchrum
Harpechloa falx
Helichrysum umbraculigarum
Hibiscus trionum
Hypericum asthiopicum
Kniphofia ritualis
Leucosidea sericea
Lithospermum officinale
Melianthus villosus
Merxmuellera stricta
Mimanthus capense
Mohria caffrorum
Myosotis sylvatica
Myrsine africana
Oxalis ohlendorfiana
Pellaea dolomitica
Philippia [illegible]
Plectranthus grallatus
Polygala ohlendorfiana
Polytrichum spp.
Poplar
Pteridium aquilinum
Pteris cretica
Ranunculus baurii
Rhus dentata
Riocreuxia tenuiloba
Saturea reptans
Sebaea macrophylla
Senecio inornatus
Sopubia cana
Syncolostemon macranthus
Themeda triandra
Tristachya leucothrix

T6.2

Acalypha punctata
Alepidea baurii
Andropogon appendiculatus
Asparagus asparagoides
Athanasia calva
Berkheya rhapontica
Clematis brachiata
Clutia natalensis
Commelina africana
Crassula pellucida
Cyphia coryifolia
Diospyros austro-africana
Epilobium capense
Euphorbia epicyparissias
Festuca caprina
Galium rotundifolium
Geranium ornithopodum
Harpechloa falx
Helichrysum umbraculigarum
Helictotrichon turgidulum
Hypericum lalandii
Koeleria cristata
Leonotis spp.

3) The frequency of presence and absence of each key species in each section of transect was determined. The frequencies from different sections which fell in the same environmental group were summed. This resulted in a contingency table for each species, containing the frequency of presence and absence of the species in each environmental group.

4) Each cell of the contingency tables was then converted from a frequency count into a standardized residual, SR, so that each species could be compared on an equal footing. The SR of a cell expressed the number of standard deviations by which the count departs from a count expected if the species showed no preference for any group of an environmental parameter. It thus quantified the presence-absence response of a species to a particular environmental group (Strahler 1978).

Standardized residuals were calculated as follows:

The uncorrected standardized residual, SR_{ij}, is

$$SR_{ij} = (o_{ij} - e_{ij}) / \text{sqroot}\ e_{ij}$$

where o_{ij} is the observed frequency in the ith row and jth column of the table and e_{ij} is the expected frequency of this cell (calculated as in Chi-squared tests).

The corrected standardized residual, SR, adjusted for sample size is

$$SR_{ij} = SR_{ij} / \text{sqroot}\ [(1-(r_i/n))(1-(c_j/n))]$$

where r_i is the row total for the ith row, c_j the column total for the jth column, and n is the total frequency of all cells.

Positive SR's for the presence rows indicate preference for an environmental group, and negative SR's indicate avoidance.

5) The SR's from each environmental parameter were assembled into matrices of species (rows) by environmental group (columns), and the matrices - for Q-mode FA - were each separately entered into a FA program for analysis. The factors obtained are left un-rotated, because in that mode the factor loadings reveal the nature of the orthogonal trends in the vegetation which best separate the environmental groups (Strahler 1978). Scatter plots of the factor scores show how each species responds to the FA factors.

6) The SR's from each environmental parameter were re-assembled into matrices of environmental group (rows) by species (columns) and each separately entered into a FA program. This R-mode FA used varimax rotation (Strahler 1978) - the object being to identify and maximize the distinctness of groups of species with similar response patterns to the environmental factors.

Appendix 2.2.1.2. Standardized residuals for species on altitude groups.

Species	ALT 1	ALT 2	ALT 3	ALT 4	ALT 5	ALT 6	ALT 7	ALT 8	ALT 9	ALT 10	ALT 11	ALT 12	ALT 13	ALT 14	ALT 15
H.rapae	8.34	22.51	12.99	-2.79	-3.35	-4.71	-5.75	-6.33	-5.45	-2.68	-3.30	-1.75	-1.07	-1.65	-2.04
P.oleracea	-2.43	21.89	-1.31	-1.15	1.21	6.35	7.44	11.68	5.65	-2.84	-1.18	-1.15	-1.13	-1.26	-1.15
L.sarcitoxa	1.22	4.60	-1.79	6.24	4.72	3.12	1.34	-3.41	-4.42	-3.63	-3.14	-2.53	-1.44	-2.26	-2.78
P.aequilineum	6.27	22.76	6.45	4.39	-1.99	-1.18	-0.47	2.67	-1.89	-3.17	-3.42	-2.15	-0.12	-0.45	-0.89
E.officinale	2.70	12.92	2.67	0.59	-0.37	-0.31	2.04	0.42	-2.75	-4.85	-4.96	-3.75	-2.25	-3.47	-1.76
C.substriatus	1.39	9.52	7.01	...	-1.99	1.63	1.91	-3.59	-4.50	-4.14	-3.97	-3.60	-1.79	-2.85	3.12
P.vulgaris	-0.19	16.25	2.64	5.24	4.92	0.09	2.16	-4.11	-5.38	-1.97	-1.19	-2.12	-1.31	-2.01	-2.42
H.fabis	-3.53	-6.46	-5.45	-6.28	-1.22	-1.14	0.03	3.47	3.22	0.18	2.27	1.13	-0.11	-4.87	-4.70
S.lupulorum	2.10	-1.84	-1.35	1.97	-2.53	4.58	8.47	-5.91	-1.13	-0.66	0.21	-1.37	-1.14	-1.72	-2.16
S.appendiculatus	-1.70	-6.62	-3.51	-1.01	4.97	7.06	10.54	1.14	1.33	0.79	-2.22	-2.55	-3.19	-5.61	-3.59
S.rapalanicus	-1.69	-1.63	-2.56	0.76	-2.49	-1.13	2.19	1.75	2.14	-2.11	-1.17	-0.53	-1.01	-1.56	-1.93
S.ludwigii	-3.47	-0.72	3.16	2.71	-0.56	1.61	-1.16	4.16	2.16	-2.56	0.37	-3.16	-3.17	-4.34	3.62
S.scabriculmis	-2.42	-4.38	-5.79	-1.43	-2.66	-2.19	5.03	10.73	-3.49	-1.67	-3.17	-2.41	-1.47	-2.30	-2.82
S.subrepandus	-4.05	-3.02	-1.22	-3.79	-4.11	-2.35	4.19	11.94	14.78	-0.75	-1.23	-3.64	-3.36	-2.72	-1.78
S.circumjulum	-1.76	-1.67	-2.65	-1.09	-2.67	-1.29	-2.47	11.65	1.11	-2.11	-2.24	-1.59	-1.03	1.60	-1.66
S.aurosericeum	-1.26	-1.49	-3.62	2.38	-1.79	-3.47	-1.46	4.38	-3.65	-2.27	-1....	-1.49	-0.91	-1.42	4.32
S.alpestre ssp.tatricum	-2.37	-2.17	-3.46	-3.11	-3.71	-3.64	-1.34	-.02	9.45	-3.37	-3.76	-3.31	-1.24	2.11	1.68
S.frigidianum	-3.27	-3.36	-3.47	-1.02	2.14	0.35	2.17	-2.41	-2.27	-1.41	3.59	0.68	-1.55	3.42	1.33
P.auratiacum	-0.36	0.53	-1.03	-0.16	2.36	0.56	0.25	0.51	-1.05	-0.17	2.27	-0.54	-0.53	1.51	-0.63
S.semialatum	-0.62	3.53	1.25	-.. 72	-0.52	-1.42	-0.45	1.01	-3.12	0.14	-...	0.30	11.0.	2.31	-0.11
T.brevicolle	-6.42	0.16	-0.11	-6.24	0.09	-0.25	4.01	4.13	-.41	5.11	-0.02	-0.12	-0.63	2.35	5.03
T.levigatellum	-3.01	-10.32	-6.63	5.52	-1.45	-1.51	4.72	-1.27	1.7.	5....	4.35	5.06	4....	5.14	4.02
R.albescens	-5.95	-5.10	-3.13	2.74	4.19	-0.21	5.16	-5.27	-1.01	-3.12	3.43	3.94	2....	2.32	7.05
T.spicatum	-3.39	-5.21	-2.67	-3.61	-1.51	-3.42	-3.55	-0.41	1.42	2.85	6.61	1....	0.94	0.99	2.10

APPENDIX 2.2.2. The sequence of quadrat numbers from 1973 found in sections of transect divided according to soil type, altitude and radiation level. These divisions were used in Binary Discriminant Function Analysis (soil, altitude and radiation codes are as in appendix 2.2.1). Counting in the direction of the transect numbering, the number of the last quadrat in each community is given.

SOIL	MAP DISTANCE	1973 quad. no.
TRANSECT 2	(m)	
M	25	25
GS	10	35
GD	31	56
M	80	136
road		
M	81	211
MM	30	239
GD	40	276
MM	44	317
K (stream)	11	327
GD	5	332
M	181	509
M	5	513
plateau edge		
M	52	565
M	80	[illegible]
GS	57	702
M	35	726
end used in 1986		
TRANSECT 3		
M	36	36
M	45	81
M	5	86
CD	31	116
M	5	121
M	3	123
pole		
M	12	135
M	30	163
GD	9	171
GS	64	231
GD	125	348
road		
GD	36	382
M	211	570
CS	23	590
M	63	643
CS	88	711
M	16	743
end 1986		

Leucosidea sericea
[illegible] preslii
[illegible] africana
Oxalis obliquifolia
Pellaea quadripinnata
Philippia evansii
Plectranthus grallatus
Polygala ohlendorfiana
Polygala rehmanii
Pteridium aquilinum
Rhus dentata
Plectranthus tomentosa
Rubus ludwigii
Rumex woodii
Sebaea macrophylla
Senecio bupleuroides
Senecio arabescens
Syncolostemon macranthus
Themeda triandra
Tristachya leucothrix
Vernonia hirsuta
Wahlenbergia zeyheri

T6.3

Alloteropsis semialata
Andropogon appendiculatus
Diheteropogon amplectens
Festuca caprina
Harpochloa falx
Helichrysum odoratissimum
Helictotrichon turgidulum
Hypericum lalandii
Kniphofia laxiflora
Koelakia cristata
Leucosidea sericea
Myrsine africana
Nemesia denticulata
Oxalis obliquifolia
Pellaea quadripinnata
Philippia evansii
Pteridium aquilinum
Rhus dentata
Rubus ludwigii
Senecio bupleuroides
Senecio arabescens
Senecio spp. (creeper)
Stipurus alopecuroides
Themeda triandra
Tristachya leucothrix
Ver[illegible] hirsuta
Z[illegible]ria scabra

T6.4

Andropogon appendiculatus
Diheteropogon amplectens
Harpochloa falx
Helichrysum miconiifolium
Helichrysum umbraculigerum
Helictotrichon turgidulum
Heteropogon contortus
Leucosidea sericea
Oxalis obliquifolia
Pellaea quadripinnata
Philippia evansii
Pteridium aquilinum
Rhus dentata
Senecio bupleuroides
Senecio spp. (creeper)
Themeda triandra
Trachypogon spicatus
Tristachya leucothrix

TRANSECT 7

T7.1

Carex spp.
Clutia natalensis
Diospyros austro-africana
Helichrysum
Zedigerura dimidiata
Leucosidea sericea
cf. Microchloa caffra
Pteridium aquilinum
Rhynchosia caribaea
Rubus ludwigii
Schmaeuxiphium rufum

T7.2

Acalypha punctata
Ajuga ophrydis
Alloteropsis semialata
Andropogon appendiculatus
Asparagus asparagoides
Carex spp.
Clutia natalensis
Commelina africana
Diospyros austro-africana
Eliomurus muticus
Festuca caprina
Harpochloa falx
Hebenstretia dentata
Helichrysum odoratissimum
Helictotrichon turgidulum
Hypericum aethiopicum
Hypericum lalandii
Ko[illegible] cristata
Leucosidea sericea
Miscanthus capense

Myrsine africana
Mamesia denticulata
Oxalis obliquifolia
Oxalis smithiana
Panicum natalense
Philippia evansii
Pteridium aquilinum
Pygmaeothamnus chamaedendrum
Rhus dentata
Rhus discolor
Rubus ludwigii
Rumex woodii
Schoenoxiphium lehmanii
Schoenoxiphium rufum
Senecio bupleuroides
Senecio erubescens
Senecio isatideus
Senecio sp. (creeper)
Tristachya leucothrix
Vernonia hirsuta

IV.3

Acalypha punctata
Agapanthus campanulatus
Alchemilla natalensis
Alepidea amatymbica
Alloteropsis semialata
Andropogon appendiculatus
Athanasia calva
Berkheya montana
Berkheya rhapontica
Carex zuluensa
Cineraria deltoidea
Clematis brachiata
Clutia natalensis
Commelina africana
Crassula pellucida subsp. brachypetala
Curtonis paniculatus
Cyphia coryifolia
Drimia ceriniformis
Elionurus muticus
Euphorbia epicyparissias
Galium mittebergense
Geranium baurianum
Geranium ornithopodum
Gunnera perpensa
Helichrysum umbraculigerum
Helictotrichon turgidulum
Heteromma simplicifolium (?)
Hypericum aethiopicum
Indigofera dimidiata
Kniphofia rufa
Leucosidea sericea
Loenotis spp.
Miscanthus capense
Mohria caffrorum
Myosotis sylvatica
Myrsine africana
Oxalis obliquifolia
Oxalis smithiana
Panicum ecklonii
Panicum natalense
Pelargonium alchemilloides
Pellaea quadripinnata
Philippia evansii
Plectranthus grailatus
Polygala ohlendorfiana
Pteridium aquilinum
Rhamnus prunoides
Rhus discolor
Riocreuxia tosulosa
Rubus ludwigii
Rumex woodii
Schistostephium crataegifolium
Senecio erubescens
Senecio sp. (creeper)
Syncolostemon macranthus
Thamnia trinadra
Tristachya leucothrix
Tysonia africana
Vernonia hirsuta
Wahlenbergia zeyheri

IV.4

Acalypha punctata
Ajuga ophrydis
Alloteropsis semialata
Andropogon appendiculatus
Aristida monticola
Asparagus asparagoides
Aster perfoliatus
Berkheya rhapontica
Carex zuluensa
cf. Lobelia pleoliis
Clutia natalensis
Commelina africana
Cyphia coryifolia
Diheteropogon amplectens
Diheteropogon filifolius
Elionurus muticus
Festuca caprina
Geranium ornithopodum
Gunnera perpensa
Helichrysum odoratissimum
Helichrysum umbraculigerum
Harpechloa falx
Helichrysum aureo-nitens
Helichrysum miconiifolium
Helichrysum odoratissimum

Helictotrichon turgidulum
Heteropogon contortus
Hypericum aethiopicum
Koeleria cristata
Leonotis spp.
Leucosidea sericea
Meltanthus villosus
Myrsine africana
Nemesia denticulata
Oxalis obliquifolia
Oxalis smithiana
Panicum natalense
Pelargonium luridum
Pellaea quadripinnata
Philippia evansii
Plectranthus grallatus
Pteridium aquilinum
Rhadsia calycina
Rhus discolor
Rubus ludwigii
Satureja reptans
Schizostephium crataegifolium
Schoenoxiphium lehmannii
Schoenoxiphium rufum
Scoenoxiphium filiforemes (?)
Senecio sp. (creeper)
Thesoda triandra
Trachypogon spicatus
Tristachya leucothrix
Vermonia hirstuta
Wahlenbergia zeyheri
Zennaria scabra

11.3

Acalypha punctata
Agapanthus campanulatus
Ajuga ophrydis
Anadropogon appendiculatus
Aristida monticola
Asparagus asparagoides
Berkheya rhapontica
Clutia natalensis
Commelina africana
Crassula setulosa
Diheteropogon amplectens
Epilobium capense
Festuca caprina
Festuca costata
Geranium oraithopodum
Gunnera perpensa
Harpachloa falx
Helichrysum aureo-nitens
Helichrysum umbraculigerum
Helictotrichon turgidulum
Heteropogon contortus
Hypoxis spp. (acuminata?)
Koeleria cristata
Leucosidea sericea
Myrsine africana
Nemesia denticulata
Oxalis obliquifolia
Oxalis smithiana
Panicum natalense
Pellaea quadripinnata
Pteridium aquilinum
Rabdosia calycina
Rhus dentata
Rubus ludwigii
Rumex woodii
Schizostephium crataegifolium
Schoenoxiphium lehmannii
Schoenoxiphium rufum
Senecio bupleuroides
Senecio erubescens
Senecio serratuloides
Senecio spp. (creeper)
Thesoda triandra
Trachypogon spicatus
Tristachya leucothrix
Valeriana capensis
Vernonia hirstuta
Wahlenbergia zeyheri

11.4

Acalypha punctata
Andropogon appendiculatus
Aristida monticola
Arthraxia angustissima
Asparagus asparagoides
Berkheya rhapontica
Helichrysum herbaceum
Carex spp.
cf. Richrochloa caffra
cf. Tulbachia leucantha
Crassula setulosa
Crassula pellucida subsp.
brachipetala
Dicoma anomala
Diheteropogon amplectens
Diheteropogon filifolius
Epilobium capense
Festuca caprina
Festuca costata
Harpachloa falx
Helichrysum adenocarpum
Helichrysum aureo-nitens
Helichrysum herbaceum
Helichrysum miconiifolium
Helichrysum umbraculigerum
Helictotrichon turgidulum

Heteropogon contortus
Hypericum aethiopicum
Hypericum lalandii
Leucosidea sericea
Mohria caffrorum
Nemesia denticulata
Oxalis obliquifolia
Oxalis smithiana
Panicum natalense
Pellaea quadripinnata
Philippia evansii
Pteridium aquilinum
Rabdosia calysina
Rendlia altera
Rhus discolor
Rubus ludwigii
cf Schoenoxiphium lehmannii
Carex zuluensis
Senecio bupleuroides
Senecio dregeanus
Senecio isatidous
Themeda triandra
Trachypogon spicatus
Tristachya leucothrix
Vernonia hirsuta

TT.7

Arthrixia angustissima
Berkhuya rhapontica
Bromus speciosa
Carex spp.
Crassula setulosa
Dicoma anomala
Diheteropogon amplectens
Erica woodii
Festuca costata
Harpechloa falx
Helichrysum aureo-nitens
Helichrysum herbaceum
Helichrysum micromifolium
Helichrysum monticola
Helichrysum umbraculigerum
Helichrysum sutherlandii
Heliophila rigidiuscula
Xanthia anatymbica
Nemesia denticulata
Oxalis obliquifolia
Pellaea quadripinnata
Rendlia altera
Themeda triandra
Trachypogon spicatus

Appendix 2.2.1. Binary Discriminant Analysis procedure used on the data from 1973.

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1) The environmental parameters soil type, altitude and average annual solar radiation levels (radiation: Granger 1976) were coded into variables, called environmental groups. The environmental groups were as follows:

SOIL TYPES

CD = Clovelly form & series, deep phase
CS = Clovelly form & series, shallow phase
GD = Griffin form & series, deep phase
GS = Griffin form & series, shallow phase
H = Hutton form, Faringham series
HH = Hutton form, Faringham series, wet phase
K = Katsaruit form & series
M = Muspah form & series

RADIATION

0 = 6 to 8.9 x 10^4 J/m^2
1 = 9 to 11.9 x 10^4 J/m^2
2 = 12 to 14.9 x 10^4 J/m^2
3 = 15 to 17.9 x 10^4 J/m^2
4 = 18 to 20.9 x 10^4 J/m^2
5 = 21 to 23.9 x 10^4 J/m^2
6 = 24 to 26.9 x 10^4 J/m^2
7 = 27 to 29.9 x 10^4 J/m^2
8 = 30 to 32.9 x 10^4 J/m^2

ALTITUDE
(a.m.s.l.)

1 = 1840m-1850m
2 = 1851-1860m
3 = 1861m-1870m
4 = 1871m-1880m
5 = 1881m-1890m
6 = 1891m-1900m
7 = 1901m-1910m
8 = 1911m-1920m
9 = 1921m-1930m
10 = 1931m-1940m
11 = 1941m-1950m
12 = 1951m-1960m
13 = 1961m-1970m
14 = 1971m-1980m
15 = 1981m-1990m

2) The transects 2 to 7 were divided up into sections which fell on different environmental groups, ie on different soil types, at different altitudes and at different radiation levels (unfortunately the species codes for the 1973 data in transects 1 and 8 were missing at the time of this analysis, so these areas were not included in this section). The divisions were made separately for each environmental parameter, so that three sets of sections were obtained for each transect. This was done using maps (Granger 1976). The transect positions were superimposed over soils, contours and radiation levels. The effect of relief on the positioning of the transect sections was accounted for, and adjustments were made to accommodate the error in the location of Granger's quadrats, ie where the distance between points in the 1973 transects (as determined from Granger's diagrams) did not coincide with the distance on the map (appendix 2.2.2.).

APPENDIX 2.2.1.1. Standardized residuals for species in soil groups
(See Appendix 2.2.1 for names of soils)

SPECIES	L	HH	HD	CD	CS	H	HS	M
M.capense	9.37	14.99	0.59	-1.43	-3.58	-5.64	-2.14	-3.51
P.oblendorfiana	6.31	18.28	-2.61	2.15	-1.33	-6.76	-2.48	-3.54
C.natalensis	5.81	14.69	1.75	3.19	-1.65	-6.14	-4.14	-5.39
C.africana	2.25	12.04	5.[illegible]	0.21	-0.79	-5.[illegible]	-4.77	-6.98
L.sericea	7.65	1.87	-0.01	2.76	-1.75	-7.[illegible]	-3.28	-5
B.raphontica	1.39	-1.12	0.9	1.78	1.41	-0.69	0.63	-2.51
P.aquilinum	5.66	-0.81	11.85	0.09	-4.73	3.73	5.01	-13.4
H.falx	-1.42	-6.91	5.43	-2.87	2.63	.94	6.25	-2.05
R.ludwigii	-4.39	-3.65	5.31	-2.23	3.85	-3.65	0.15	-6.48
S.isatadeus	1.41	0.97	7.04	-7.75	-0.74	-0.57	3.32	-4.39
H.turgidurum	1.29	-2.02	2.34	-1.57	3.29	-0.26	0.47	5.9
S.bupleuroides	0.16	-1.52	4.23	-1.78	0.44	-2.03	-2.63	1.69
P.evensii	0.95	2.14	-0.11	1.89	6.23	-3.64	-1.76	-3.09
S.dregeanus	-1.86	-4.72	3.61	-2.01	10.7	1.63	0.38	-3.92
A.appendiculatus	-1.55	-3.07	-2.47	-0.09	3.79	6.39	-2.52	-5.5
H.aureo-nitens	-1.35	-2.74	-2.79	-1.79	-1.8	3.65	-2.36	-1.37
S.alopecuroides	-1.98	-4.03	-3.43	4.58	0.46	6.32	-3.03	-2.35
A.memialata	2.82	-4.57	2.12	2.63	-5.4	0.83	7.45	3.48
T.triandra	-10.85	-18.72	0.42	0.45	5.81	5.55	4.33	3.05
T.leucothrix	-8.56	-15.59	-3.89	-1.96	3.95	5.26	6.22	6.32
R.altera	-2.56	-4.3	-2.61	8.08	-4.28	0.16	1.25	8.11
P.natalense	-0.48	-0.38	-0.47	-0.58	-1.21	1.26	2.13	3.47
D.ilifolius	-3.42	-5.67	-4.38	-2.02	-2.51	-6.34	4.34	14.04
T.spicatus	-2.97	-5.41	5.17	0.78	0.52	-2.38	1.08	14.19

APPENDIX 2.5.1.5. Standardized residuals for species in radiation groups

SPECIES	RAD 1	RAD 2	RAD 3	RAD 4	RAD 5	RAD 6
P.evansii	10.11	5.19	6.84	-3.73	-7.35	-2.65
S.lugubris/cuneifer	12.31	-1.91	-3.37	-2.06	5.99	-2.47
H.fala	7.04	-3.67	0.48	-0.31	-2.12	-7.54
T.briandra	6.31	4.70	8.56	-19.6	7.03	-1.15
A.appendiculatus	-0.4	4.93	6.62	0.53	8.93	0.27
P.indutus	-2.58	5.06	6.46	0.83	-4.05	-4.66
P.rabalensis	-3.32	2.56	-3.11	0.48	1.4	-2.29
L.sericea	-3.14	3.16	1.06	0.75	-1.16	-5.11
S.dreyeranus	1.73	-1.89	3.57	11.94	-11.13	-4.83
S.rosalindae	1.48	-1.89	3.57	11.94	-11.13	-4.83
R.rophuntica	-1.13	-2.52	2.75	2.32	-1.26	-1.64
H.turquidulum	-1.34	-1.46	-2.52	6.66	-1.48	-2.22
S.alopecuroides	-3.38	-6.76	-5.01	8.33	1.27	-2.84
H.cucumiformis	-1.62	0.	1.33	4.42	-5.76	-1.76
P.aquilinum	-4.73	-0.91	-3.06	-1.14	7.68	-4.97
H.reponse	-1.09	-3.82	-3.33	-3.04	7.07	-2.28
C.africana	-3.95	-4.82	-2.21	11.62	6.91	-4.51
P.dilendorfiana	-2.91	-0.04	9.13	-2.38	2.73	-1.97
R.semialata	-4.27	-3.31	-5.04	-2.34	9.14	9.49
R.altera	-1.4	0.26	-0.3	-4.02	5.86	1.28
T.leucotricha	0.12	-1.11	-1.23	-0.63	0.64	2.53
T.spicatus	1.03	-2.44	-5.05	0.17	1.93	6.16
P.rabalense	-9.38	-0.5	0.82	-1.31	-1.05	5.16
D.filifolius	-3.78	-1.64	0.78	-0.38	-3.51	13.84

TRANSECT 4		
M	19	15
pole		
M	28	43
CS	30	73
GD	31	105
old track		
CS	35	137
H	93	222
CS	12	233
M	8	240
CS	10	249
stream		
CS	21	261
M	31	286
CS	67	344
HH	13	355
K	3	357
K	9	369
HH	8	378
H	10	389
M	13	403
TRANSECT 5		
gauge		
M	8	8
H	8	13
HH	5	18
K (stream)	8	25
HH	3	27
H	37	58
HH	5	62
H	10	70
HH (stream)	8	78
K	13	90
HH	53	141
H	28	168
GD	20	195
TRANSECT 6		
K	5	11-15
stream		
k	3	18
HH	25	39
CD	25	52
CS	71	85
TRANSECT 7		
road		
H	75	35
HH	47	59
K	5	62
stream		
K	3	64
Hf	25	76
GD	103	138

CD	17	155
GD	12	167
stream		
GD	22	190
M	38	229
CS	54	286
M	46	332
end		

ALTITUDE	MAP DISTANCE	1973 quad. no.
TRANSECT_2		
8	33	33
7	31	64
6	28	92
5	31	123
4 (road)	44	165
3	408	267
2 (stream)	62	329
3	24	350
4	42	390
5	51	446
6	29	475
7	27	502
8 (plateau edge)	5	507
8	128	629
9	40	667
10	25	691
11	22	713
12	+-10	726
end		
TRANSECT_3		
pole		
15	94	93
14	31	123
pole		
14	34	155
13	28	181
12	25	204
11	40	242
10	52	291
9	54	341
8 (road)	7	348
8 (stream)	2o8	582
8	35	617
9	68	685
10	34	719
11	16	735
12	8	743
end? used in 1986		

APPENDIX 3.3.2.3 a) Species frequencies in plant communities (derived from NAA, Granger 1976) in 1973 and 1986, and the results of tests for changes in species frequency between years significant at p< 0.05. The G-statistic, or Fisher's exact probability test for small samples, were used. The direction of change is given: i = increase, d = decrease.

TRANSECT/ COMMUNITY	SAMPLE SIZE 1973	1986	A.punctata Ap73	Ap86	A.semialata As73	As86	A.appendiculatus Aa73	Aa86	B.raphontica Br73	Br86	B.lotononoides Bl73	Bl86	C.natalensis Cn73	Cn86	C.africana Ca73	Ca86	D.filifolius Df73	Df86	E.muticus Em73	Em86	F.caprina Fcp73	Fcp86	F.costata Fcs73	Fcs86	H.falx Hf73	Hf86	H.aureo-nitens Han73	Han86	H.umbraculigerum Hu73	Hu86	H.turgidulum Ht73	Ht86	L.sericea Ls73	Ls86	M.capense Mc73	Mc86	P.natalense Pn73	Pn86	P.quadripinnata Pq73	Pq86	P.evansii Pe73	Pe86	P.ohlendorfiana Po73	Po86	P.aquilinum Pa73	Pa86	R.altera Re73	Re86	R.ludwigii Rl73	Rl86	S.bupleuroides Sb73	Sb86	S.isatideus Si73	Si86	S.rigidecurvoides Sa73	Sa86	T.triandra TT73	TT86	T.leucothrix Tl73	Tl86
TA.1	14	14	12	8	0	0	14	7.84 d	r	0	0	5	2	1	0	0	0.005 i	7	0	0	14	7.84 d	7	0	1	0	0	10	10	0	0	0	5	0	0.05 i	4	4	0.05 i	10	6	8	0	0	0	1	0	2	0	2	14	6.02 d	8	0	0	0	0	9	1	0	0	0	0	14	6.02 d	8	8	11
TA.2	6	6	4	4	3	0	5	6	0	0	1	1	0	3	3	0	0	6	5	5	0	1	0	0	0	0.05 i	4	0	0	0	1	0	3	0	1	0	0	0	0	1	0	0	0	0	4	5	0	0	0	3	3	2	0	0	0	0	6	0.00 d	0	1	3
TA.3	9	9	7	8	2	2	7	6	1	0	4	1	0	0	6	4	0	0	8	8	2	2	0	0	2	6	0	0	5	5	0	0	i	8	0	2	1	0	0	1	0	0	0	0	8	6	0	0	5	5	0	0	0	0	0	9	0.00 d	5	3	6
TA.4	10	10	7	5	5	0.05 d	0	7	5.52 d	1	0	0	1	0	0	0	3	0	0	8	16	0	1	0	0	4	0.025 i	10	0	0	0	0.05 i	4	0	0.05 i	4	0	4	0	2	0	0	1	1	0	1	0	0	7	10	0	0	0	1	6	0.02 d	0	0	2	0	0	10	8	0	2
TA.5	9	10	0	2	0		0	0		0	0	0	0	0	3	0	2	0	0	0	0	0	0	0	0	1	0	0	0	6	4	0		0	7	6	1	3	0	0	0	1	0	1	3	3	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
TOTAL	48	49	30	27	10	5.09 d	2	33	6.63 d	20	1	0	11	4	1	3	9	3.86 i	19	0	0	35	30	2	5	0	0	16	7.64 i	31	0	0	11	19	0	25.4 i	19	11	5.21 i	23	8	13	0	1	2	5	0	4	0	3	36	32	0	0	5	10	18	13.2 d	3	0	2	0	0	39	14.0 d	21	12	22
T1.1	29	14	11	2	0		2	0		0	0	0	0	6	6	20		6	0	0	3		0	0	1	0	0	0		0	0	0	2	16.3 i	10	0		0	17	4.22 i	13	29	5.82 d	10	0	0	4	4.53 i	7	10		1	9	7	20		5	0	0	0	0	0	0		0	0	0	0	0
T1.2	11	5	2	0	0		0	0		0	0	0	3		1	8		1	0	0	0		0	0	0	0	0	0		0	0	0	5		3	0		0	9		5	11		4	0	0	5		1	3	0	6	3	6	0	0	0	0	0	0		0	0	0	0	0
TOTAL	40	19	13	2	0		2	0		0	0	0	9		7	28	4.55 d	7	0	0	3		0	0	1	0	0	0		0	0	0	7	12.5 i	13	0		0	26	5.26 i	18	40		14	0	0	9		8	13	4.47 d	1	15		10	26	6.39 d	5	0	0	0	0		0	0	0	0	0
T2.1	27	8	3	0	13	5.16 d	0	2		1	0	0	0		0			0	0	4	16.9 i	8	25	21.48 d	0	0		0	0	0		0	1		2	0		1	6		0	0		0	0		0	0		0	1		1	0		0	0		0	0	0.047 i	2	3	13.3 i	7	1		0	23	7.69 d	1	0		0	0		0	26		6	22		8
T2.2	88	30	55	13	38		19	42	26.8 d	0	0	0	0		0			0	87	14.7 d	22	21	9.88 d	0	0		0	0	0	5	9.04 i	9	0		0	3	7.7 i	7	0		0	0		0	0		0	4	10.6 i	9	0	15.6 i	7	0		0	0		0	0	0	0		0	1	64		18	71	3.95 i	29
T2.3	21	8	19	5	18		8	6		0	0	1		1	4			0	0	0	10		1	10	0.05 d	0	0		0	0	0	2		1	0		0	11		2	0		0	0	0.015 i	3	0		0	0.005 i	4	0		1	3		0	0	0	0	0	16		7	0	0.00 i	4	2	0.01 i	5	6		0	0		0	0		1	7		2	8	7.81 i	8
T2.4	78	21	56	17	42	9.7 d	3	23	38.86 d	0	0	0	6		0	15		4	10		3	6		0	65	56.7 d	0	0	5.51 i	3	0		0	8	8.7 i	9	0		0	34	7.9 d	2	0		0	0	52 i	15	1		0	0		0	0		0	0		0	0		0	71		18	0		0	42		16	8		0	0		0	0		0	23		3	31		4
T2.5	76	19	36	13	9		1	13		3	0	0	2		0	41		12	38		9	11		1	9		0	0		1	0		0	9		6	0		0	35		6	0		0	5	28 i	13	43		7	0	12.4 i	5	0		0	1		0	15		2	57		12	0		0	31		12	0		0	0		0	0		0	15		2	7		3
T2.6	23	6	6	3	0		0	0		0	0	0	0		0	10		2	23		5	0		0	0		0	0		0	0		0	16		5	0		0	21		6	19		5	0	6.3 i	3	0		0	5		2	19		3	12	4.61 d	0	0		0	1		0	0		0	0		0	0		0	0		0	0
T2.7	23	6	7	1	0		0	4		0	6		1	11	3	0		0	0		0	8		0	12		3	1		1	0		0	10		5	0		1	3	4.3 i	4	16		6	0		1	3		3	7		1	2		2	9		0	0		0	0		0	1		0	0		0	0		0	1		0	0	
T2.8	14	4	3	1	0		0	13	0.02 d	1	5		3	7		0	0	0.005 i	3	4		3	2		0	0	0.00 i	4	0		0	6		1	0		0	7		1	0	0.002 i	4	0		2	0		2	0	0.039 i	2	0	0.005 i	3	2		0	0		2	12	0.005 d	0	2		0	11		4	5		0	0		0	0		0	13	0.02 d	1	9	2
T2.9	163	44	8	0	18	5.69 d	0	94	30.9 d	5	0		2	0	0	0		0	0	70	6.93 d	9	28		3	1		0	0		0	38	119 i	35	21		9	61	13.5 d	4	0		2	11	10.7 i	12	0		0	1		2	38	6.92 i	20	32	6.9 i	18	1		0	2	14.1 i	8	37	5.4 d	3	15	15.3 i	16	104	25.4 d	9	0		0	0		0	157		41	143		29
T2.10	52	13	0	0	27		9	7		0	5		0	0	1	0		0	15		6	45		11	0		0	1		0	1	2	14.2 i	7	4		1	3		1	0		0	0		0	0		0	0		0	1		2	1		1	0		0	0		0	0		0	0		0	45		12	39		12
T2.11	111	29	51	14	2		0	72		17	7		0	8	0	0		0	0	0	14		2	2		1	1		0	0		1	68		17	17		6	48	10.5 d	3	4	22.9 i	12	0		0	0		0	8.6 i	4	2		0	0		1	0		0	103		23	10		5	81	12.8 i	10	5	38.3 i	17	3		0	0		1	98		26	66		18
T2.12	50	13	1	0	4		0	13		6	25		10	0	0	0		0	0	0	11		0	0		1	6		0	6		1	48		13	0		0	6	7.5	7	0	0.039 i	2	0		0	0		0	0		0	11		4	7		2	0		0	0	9.05 i	4	18		5	11	5.5 i	8	13	4.16 i	8	0		0	0		0	47		12	47		10
TOTAL	726	201	248	67	171		40	289	40.5 d	33	52		16	26	8.45 d	2	76		22	101		29	264	6.06 d	54	160	53.4 d	5	17	5.79 i	8	18		6	168	40.2	101	42	11.6 i	17	240		43	4	42.8	21	40	65.3 i	55	81		20	7	109.9 i	33	55	19.9 i	39	54		24	38		9	264		76	90	21.7 i	54	200	6.5 i	75	242		35	3		0	0	7.99 i	3	496		123	445		133
T3.1	18	8	0	1	0	17.9 i	7	2		0	0	9.9 i	5	0	0	0		0	0	0	18	9.9 d	3	0		0	9	4.9 d	0	0		0	0	17.9 i	7	0		2	0		0	0		0	0		0	0		0	2		2	0	6.79 i	4	0		0	0		0	0		0	0		0	0		0	10		7	16		7
T3.2	36	13	0	0	19		4	9		5	22	8.4 d	2	0	0	0		0	0	0	15	7.6 d	0	0		0	17	9.3 d	0	0		0	0	13	10.98 i	12	0		1	6		1	0		0	0		0	0		0	0		1	11	6.69 i	10	0		0	0		0	0		0	0		0	0		0	0		7.3 i	4	6		6	12		8	0		0	0		1	38		13	26	3.8 i	13
T3.3	64	22	5	1	4		0	35	10.4 d	3	0		0	1	2	0		0	9	0	17	4.2 d	1	0		0	40	28.8 d	0	0		0	0	12	8.17	12	9	22.4 i	9	30		7	0		0	1		0	0		0	10	i	5	3	5.77 i	6	0		0	0		0	0		0	1	12.3 i	7	8	15.4 i	13	2		3	36		8	1		0	15		9	64		21	44		16
T3.4	32	11	20	4	7		0	13		8	0		0	3	0	0		0	1	3	7		0	0		0	16		3	0		0	1		1	0		0	18		5	7		3	0		2	0		0	0		0	0		0	0		0	30		11	0		0	32	10.8 d	6	2	19.6 i	9	2	3.95 i	4	4		1	30		9	8		7
T3.5	26	9	20	5	0		0	10	5.3 i	8	0		0	0	0	3		0	2	1	0		0	0		0	19.5 i	7	1		0	0		0	6		0	2		1	0		0	18		0	0		0	0		0	0		0	0		0	15		4	0		0	10		0	7		5	26	11.3 d	4	6		4	25		9	20		5
T3.6	42	14	32	6	1		0	19	5.8 d	1	0		0	1	0	0		0	1	1	3		0	0		0	3		1	0		0	30		7	0		0	27		6	4		3	0	1.03 i	3	0		0	0		0	0		0	40		13	0		0	16		5	7		4	7		0	11	7.2 i	10	42		14	31		12
T3.7	86	31	19	10	6		0	37	18.2 d	1	0		0	1	0	0		0	2	10		1	0		0	1	4.3 i	4	0		0	66	4.47 d	20	2	22.2 i	12	23		5	0		2	0	4.38 i	3	0		0	0	23.8 i	8	0	4.38 i	3	0		0	0		0	0		0	9		7	1		0	1	6.5 i	5	18		3	2		0	25		6	86		30	84		28
T3.8	54	19	27	6	0		0	34	6.4 i	18	0		0	9	1	2		0	17	11	5		0	0		0	0	16 i	7	0		0	50	4.47 d	13	0		0	22		5	10		6	0	4.55 i	3	0		0	0	7.18 i	4	0		0	0		0	0		0	53		16	2		0	3	22.7 i	12	13	12.6 i	14	24		12	4		2	52		15	31		9
T3.9	32	18	21	7.3 d	4	0		0	6	14.7 i	14	0		0	2	0	15	12.4 d	0	24	11.3 d	4	0		0	0		0	0	29.9 i	13	0		1	12	6.17 i	14	0		0	8		7	13	7.3 i	15	1		3	0		0	14.4 i	8	0		0	0		0	0		0	19		11	0		0	20		7	1	10.7 i	5	30		13	0		0	26	11.3 d	2	6		2
T3.10	20	6	17	0.005 d	0	7		0	4		1	0		0	0	1	0		0	13		2	1		0	0		0	0		0	2	0.002 i	5	0		0	0		0	0		0	0		0	0		0	0		0	0		0	0		0	17		4	0		0	2*		6	1		1	6		0	0		0	9		2	3		0
T3.11	8	4	6	1	3		0	2		0	0		0	1	0	5		0	0	0	0		0	0		0	0		0	0		0	2	0.02 i	4	0		0	0		0	0		0	0		0	0		0	0		0	0		0	2		3	0		0	3		4	1		0	4		0	0		0	6		0	1		0
T3.12	83	30	59	43.5 d	1	20		2	31	18.5 d	0	0		0	2	0	15		2	15	6.5 d	0	0		0	0	6.8 i	4	0		0	69	28.7 d	8	0		0	61	9.1 d	12	0		1	0	4.37 i	3	0		0	0	6.9 i	4	2		0	0		0	0		0	78		27	7		0	6	13.6 i	12	22	7.32 d	1	2		0	0		0	83		30	63		28
T3.13	41	14	20	3	17		2	15		3	0		1	1	0	3		3	5	3.87 d	0	0		0	0		2	0		0	26	5.06 d	3	0		1	29		8	0		0	0		0	0		0	0		1	1		1	0		0	0		0	41		12	6		0	21		11	5		0	0		0	0		0	39		13	31		14
T3.14	66	24	51	10.4 d	9	63		22	14	6.06 d	0	0		0	0	0	0		0	12	4.7 d	0	0		0	1	1	0		0	33		9	0		0	40	4.2 d	8	0		0	0		0	0		0	0		0	28 i	11	0		2	0		0	0		0	53		22	13	5.4 i	0	4	21.1 i	13	10		1	0		0	0	4.7 i	3	64		21	64		23
T3.15	13	5	6	2	12		5	2		0	0		0	0	0	3		0	0	5		0	0		0	0		0	0		0	0		0	1		2	0		0	0		0	0		0	0		0	0		0	0		0	0		0	0		0	0		0	13		3	0		0	7		1	0		0	0		0	12		5	13		3
T3.16	137	25	17	0	18		1	30	7.61 d	0	0		0	0	0	8		0	46	4.17 d	3	0		0	0	1	0		0	23		0	10	6.83 i	7	1		0	1		0	0		0	0		0	1		0	3		3	0		0	1		0	0		0	72		18	2		0	110		20	0		0	53	7.5 d	0	134		23	120		25
TOTAL	758	253	320	38.2 d	53	177		43	263	8.85 d	62	22		8	23		3	19		2	90		30	160	55.3 d	8	0		0	83	5.49 i	43	1		1	339		114	12	48.9 i	34	971		75	53	8.47 i	34	2	25.7 i	18	0		0	3	112.1 i	47	20	27.2 i	30	0		0	1		0	358		137	122		41	151	23.4 i	90	269		83	103		33	118		36	704	13.3 d	214	561		192

| TRANSECT/ COMMUNETY | SAMPLE SIZE 1973 | 1986 | A.punctata Ap73 | Ap86 | A.semilata As73 | As86 | A.appendiculatus Aa73 | Aa86 | B.raphonotica Br73 | Br86 | B.lotononoides Bl73 | Bl86 | C.natalensis Cn73 | Cn86 | C africana Ca73 | Ca86 | D.filifolius Df73 | Df86 | E.muticus Em73 | Em86 | F.caprina Fcp73 | Fcp86 | F.costata Fcs73 | Fcs86 | H.falx Hf73 | Hf86 | H.aureo-nitens Han73 | Han86 | H.umbraculigerum Hu73 | Hu86 | H.turgidulum Ht73 | Ht86 | L.sericea Ls73 | Ls86 | M.capense Mc73 | Mc86 | P.natalense Pn73 | Pn86 | P.quadripinnata Pq73 | Pq86 | P.evansii Pe73 | Pe86 | P.ohlendorffiana Po73 | Po86 | P.aquilinum Pa73 | Pa86 | R.altera Re73 | Re86 | R.ludvigii Rl73 | Rl86 | S.bupleuroides Sb73 | Sb86 | S.isatadeus Si73 | Si86 | S.elopecuroides Se73 | Se86 | T.triandra TT73 | TT86 | T.leucothrix Tl73 | Tl86 |
|---|---|---

TRANSECT 4		
rain gauge		
7	13	403
6	25	359
stream		
6	60	358
7	75	309
stream		
7	30	249
8	70	222
9	58	158
road		
9	15	105
10	30	90
11	26	59
12	19	10-33
end pole, 1986		
TRANSECT 5		
7	115	104
8	100	195
rain gauge		
TRANSECT 6		
3	5	11-15
stream		
3	8	22
4	16	36
5	42	59
6	33	74
7	25	85
TRANSECT 7		
pole		
1	127	61
stream		
1	26	73
2	20	82
3	43	101
4	93	168
stream		
4	5	173
5	31	205
6	28	235
7	24	259
8	20	279
9	21	300
10	16	316
11	16	332

RADIATION	MAP DISTANCE	1973 quad. no.
TRANSECT 2		
5	30	30
6	106	136
road		
6	10	145
5	181	315
4	10	325
stream		
4	11	336
3	136	471
2	32	502
3	11	513
plateau edge		
3	5	518
4	85	598
3	43	638
2	70	705
3	9	714
4	17	726
TRANSECT 3		
5	365	348
road		
5	53	397
4	106	494
5	57	545
4	42	582
stream		
4	137	715
5	29	745
TRANSECT 4		
rain gauge		
5(stream)	41	403
4	38	357
3	23	325
4	48	307
3	25	269
stream		
2	14	250
2	27	234
3	32	209
4	70	180
3	25	112
2	49	88
3	7	43
4	21	16-36
pole		

TRANSECT_5
rain gauge
5 25 22
stream
5 61 71
stream
5 14 84
4 83 144
5 32 145
pole

TRANSECT_6
pole
2 5 11-15
stream
2 44 52
3 30 65
2 45 85

TRANSECT_7
5 110 51
4 7 56
3 10 61
stream
3 7 62
2 33 78
3 21 83
4 121 168
stream
3 5 173
2 65 239
1 78 319
2 7 326
3 6 332
end

APPENDIX 2.2.3. Quadrat numbering for 1973 and 1986 in modified NAA communities as used in this study. (Counting in the direction of the transect numbering, the number of the last quadrat in each community is given).

COMMUNITY (NAA, modified)	1973 quad.no.	1986 quad.no.
TRANSECT 0		
pole		
TA.1	10-24	1-14
TA.2	30	20
TA.3	39	29
TA.4	49	39
TA.5	58	49
pole		
TRANSECT 1		
pole		
T1.1	1-29	1-14
T1.2	40	19
pole		
TRANSECT 2		
pole		
T2.1	1-27	1-8'
T2.2	115	38'
T2.3	136	46'
road		
T2.4	214	1-21
T2.5 (stream)	290	40
T2.6	313	45
T2.7 (stream)	336	52
T2.8	350	56
T2.9	513	100
T2.10	585	113
T2.11	676	142
T2.12	724	155
TRANSECT 3		
T3.1	750	1-0
T3.2	732	21
T3.3	696	43
T3.4	632	54
T3.5 (stream)	600	63
T3.6	574	77
T3.7	532	108
T3.8	446	127
T3.9	392	130,-110-10
T3.9 cont.		300-304
T3.10	360	308
road		
T3.11	348	310
T3.12	340	349
T3.13	257	334
T3.14	216	378

T3.15	150	380,27',26'
T3.16 (pole)	1-137	25'to1'
pole		

IRANBECI_4

T4.11	1-15	1'-19'
T4.1	16-106	1-47
(old track)		
T4.2	135	61
T4.3	183	89
T4.4	217	108
T4.5	250	126
stream		
T4.6	284	149
T4.7	323	171
T4.8 (stream)	341	194
T4.9	373	200
T4.10	403	218
rain gauge		

IRANBECI_5

pole		
T5.1	195-159	1-11;100-107
T5.2	145	15,110
T5.3	115	24,115
T5.4 (stream)	84	32,121
T5.5 (stream)	67	37,123
T5.6	66	48,127
T5.7 (stream)	1-26	56,131
rain gauge		

IRANBECI_6

pole		
T6.1 (stream)	11-43	1-17
T6.2	61	34
T6.3	77	50
T6.4	85	58
pole		

IRANBECI_7

road		
T7.1	1-10	1-4,a-c
T7.2	48	23,k
T7.3 (stream)	83	41,m,a1-a2
T7.4 (stream)	173	70,a21
T7.5	258	87,a32
T7.6	311	98,a39
T7.7	332	101,a40
(dying tree)		

APPENDIX 3.2.3. Pathways of succession in C IX proposed by Granger 1976.

The hydrosere

a) [illegible] channels

Such sites are usually occupied by almost pure communities of *Merxmuellera macowanii* which in the absence of fire gradually becomes invaded by species such as *Ranunculus baurii* and *Cliffortia linearifolia* followed by *Leucosidea sericea*. However, fire served to maintain the grassland character of the *M.macowanii* so that succession was held in check. Established areas of *L.sericea* appeared to act as foci from which various associated woody species such as *Philippia evansii* spread into surrounding herb and grass dominated communities provided fire was excluded. Where fire penetrated stands of mature riparian *L.sericea* a much more open character was imparted to this vegetation and *Berkheya montana* plus species evident in the earlier stages of succession became abundant.

b) Vleis

The single vlei in C IX occurred as an almost level area immediately west of rain-gauge IX BR. The first communities which invaded the very wet soils were those in which species such as *Oenothera rosea*, *Gunnera perpensa*, *Eleocharis dregeana*, *Pycreus oakfortensis*, *Scirpus costatus*, *S.macer* and *Thelypteris confluens* were dominant. where soils were slightly drier, *Eragrostis curvula* appeared to have been the dominant species in early succession. With the exclusion of fire, many of these communities disappeared. On the wettest sites this was often found to be due to the invasion of *Festuca costata*, while on the drier areas *Andropogon appendiculatus* appeared to have invaded extensively. At this stage, *F.costata* was generally invaded by species such as *Pteridium aquilinum* and *Clutia natalensis*. Such *Festuca-Pteridium-Clutia* and *A.appendiculatus* dominated communities were then invaded by *L.sericea* to form what is at present (1975-4) an open immature community. This might well become a mature *L.sericea* dominated community.

The lithosphere

a) Moist soils

Oenothera rosea might well have been an early dominant. In the wettest areas *E.curvula* was the next species most likely to invade, in turn invaded by *Miscanthus capense*. Where soils were slightly drier, it seems that various *Senecio* species such as *S.isatideus* and

S.inermatus might invade the *E.curvula* community and in turn be replaced by *P.aquilinum*. Both alternatives appeared to lead to the *Miscanthus-Pteridium-Clutia* community.

On the wetter sites there appeared to have been direct invasion of *L.sericea* which ultimately developed into a mature *L.sericea* community. In this sequence, *P.evansii*, although present, did not appear to as important in the establishment of *L.sericea* as on the less wet sites. In these last-mentioned areas the *Miscanthus-Pteridium-Clutia* community appeared to become more floristically diverse as species such as *Rubus ludwigii*, *Helianthus villosus*, *Athanasia punctata* and *Calpurnia obovata* invaded. This gradually led to the development of the immature *Philippia-Pteridium-Rhus discolor-Rubus* communities as woody species invaded. This was gradually invaded by *L.sericea*, ultimately leading to a mature *Philippia-Myrsine-Leucosidea* community. Where *Myrsine africana* was found to be locally abundant this generally appeared to be due to the effects of fires that had penetrated the woody vegetation. Gradually mature *L.sericea* communities were invaded by species such as *Widdringtonia cupressoides*, *Rhamnus prunoides*, *Euclea crispa*, *Rhus dentata* and *Olinia emarginata* until *Podocarpus latifolius* dominated forest became established. The abundance of *P.evansii* and *M.africana* in the margins of this forest patch occasional fires and to local site conditions which have not yet become suitable for the establishment of more serally advanced species. On some deep areas in the vacinity of this forest patch it also seemed that *Cymbopogon validus* and subsequently *H.contortus* dominated communities have given rise to woody forest precursor communities.

b) Soils of varying characteristics

On exposed rock... the primary mat-builders which were most noticeable in crevices and small overhangs were mosses. These appeared to be invaded by firstly *Selaginella* spp.and then by ferns such as *Mohria caffrorum* and by *Streptocarpus dunnii* and *Crassula setulosa*. On more exposed sites *Aristida junciformis* and *Crassula setulosa* were among the earliest invaders. *Eragrostis racemosa* *Heteropogon contortus* and *Loudetia simplex* appeared to be the next most important species to invade and dominate on these very shallow soils. With an increase in soil depth a *Diheteropogon filifolius-Rendlia altera* community was the next stage to develop. These were invaded by *Themeda triandra* to form the large *T.triandra* dominated C IX (in the early 1950's). With the exclusion of fire these communities developed in different directions.

On steep sites and on cool southerly and easterly aspects where soils were fairly deep there was invasion by species such as *Elionurus muticus* and *Alloteropsis semialata*. As soil moisture conditions improved a *Themeda-Andropogon appendiculatus* community developed. This was invaded by species such as *Pellaea quadripinnata*, *Acalypha punctata*, *Hypoxis acuminata*, *Senecio burchellii* and *Helichrysum aureo-nitens*. Later as soil depth and moisture improved species such as *R.ludwigii*, *Pteridium aquilinum*, *Rubioxiella calycina*

and *H.umbraculigerum* appeared leading to a *P.aquilinum* dominated community then invaded by woody species such as *L.sericea* and *P.evansii* until a mature *L.sericea* community developed.

When fire had been a frequent factor influencing C IX there were extensive communities in which *Buchenroedera lotononoides* predominated. With fire exclusion this species had all but disappeared largely due to the invasion of *P.aquilinum* and the few examples that remained were subject to high radiation levels.

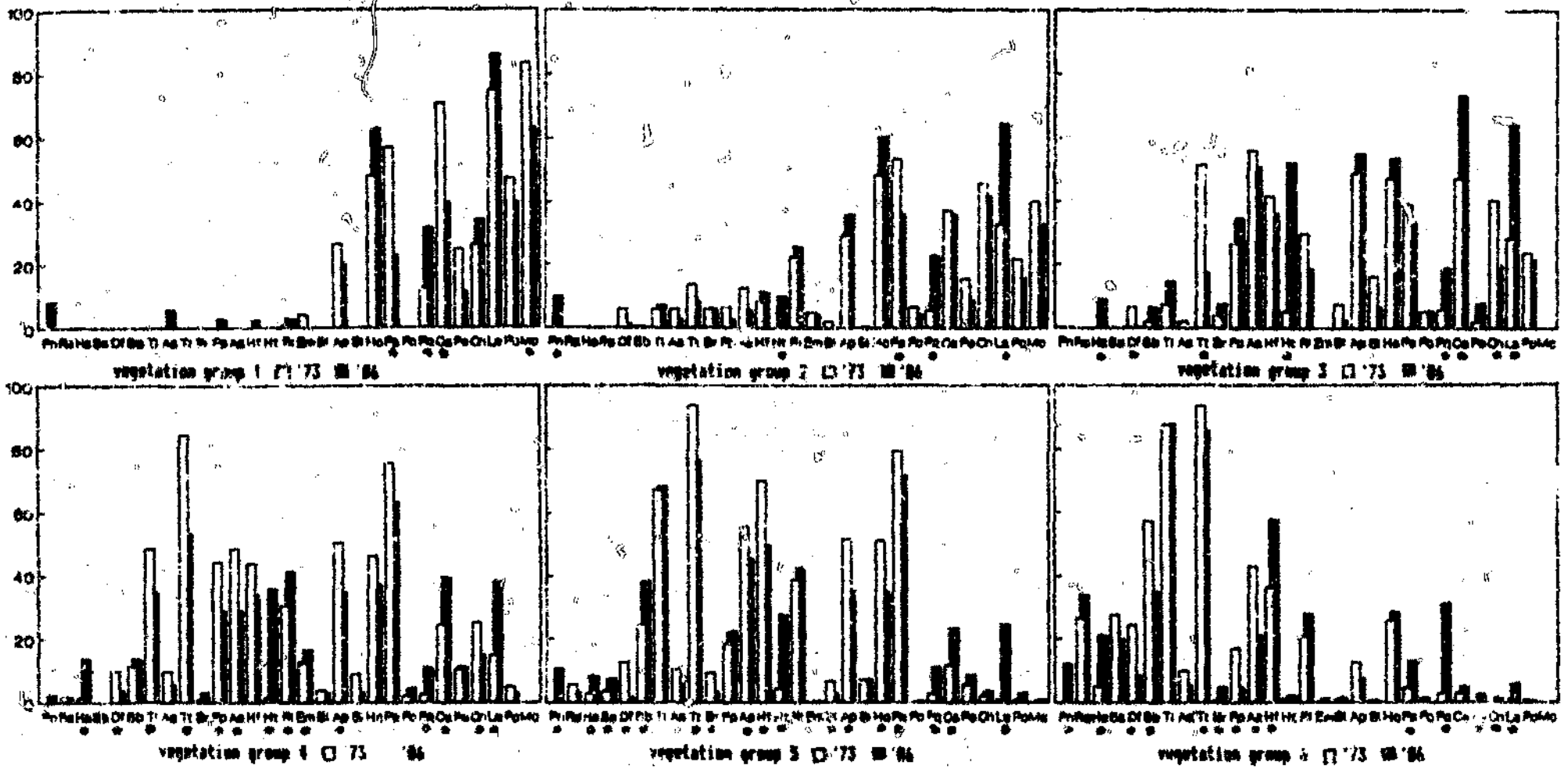
On sites subject to high radiation levels but underlain by shallow soils (eg ridge tops) the *Heteropogon-Eragrostis-loudetia* and *Diheteropogon-Rendlia* grassland communities were invaded by *T.triandra* and *Protea caffra* and *P.roupelliae*. The presence of the occasional plant of *Asparagus microraphis*, *Dovyalis rhamnoides*, *Rhus tormentosa* and *Diospyros austro-africana* under a number of *Protea* trees suggests that where adequate protection from fire and wind might occur then some sort of *L.sericea* dominated scrub or scrub forest might develop.

On very steep and rocky south-facing slopes the *Heteropogon-Eragrostis-loudetia* and *Diheteropogon-Rendlia* grassland communities were invaded by *T.triandra* and *Berkheya raphontica*, *Moraea pubiflora* and *Helichrysum sutherlandii*. In the more exposed and shallow soiled areas species such as *Cliffortia repens* and *Erica straussiana* appeared and evidence suggested this might lead to *Protea* dominated communities.

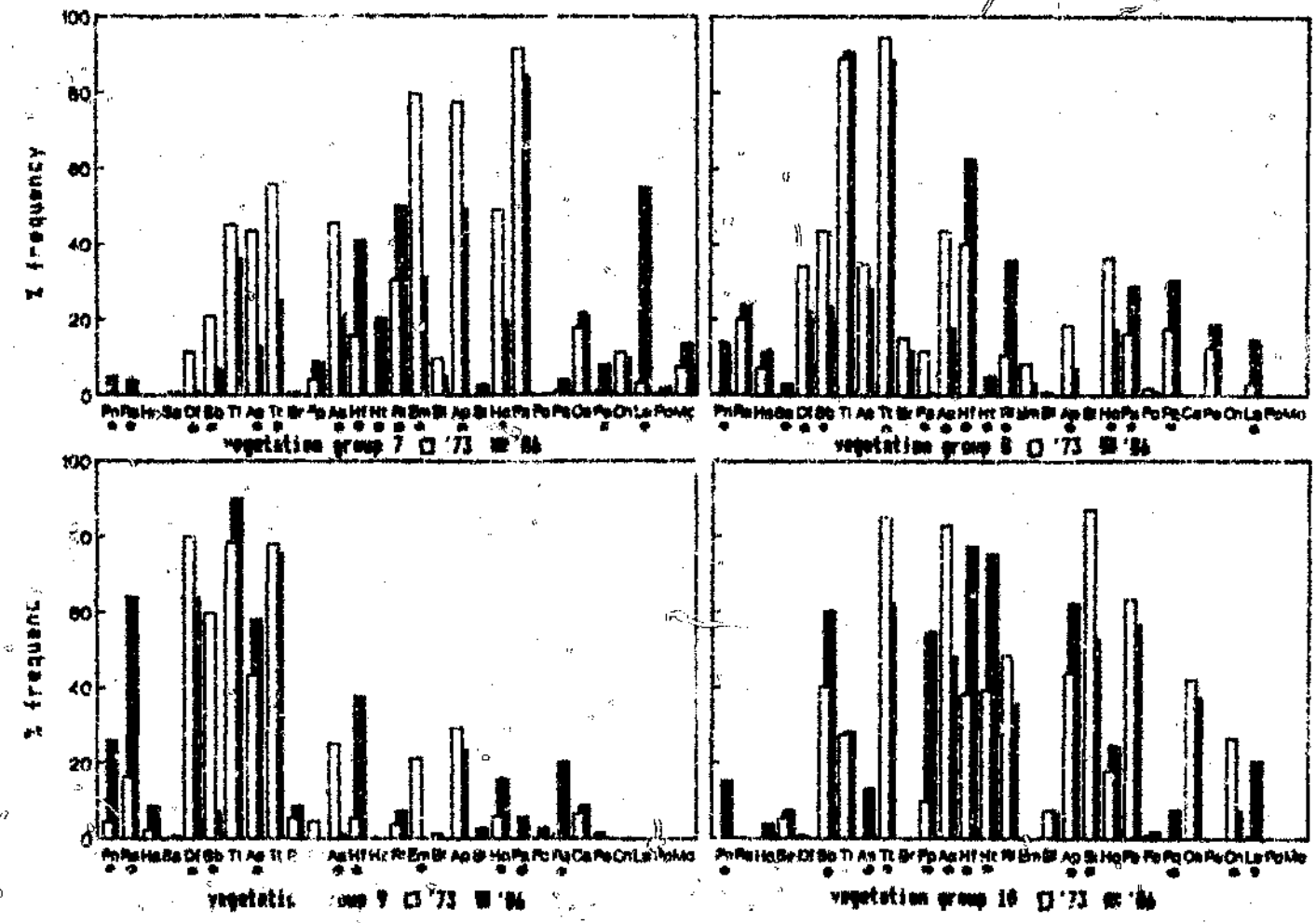
Elsewhere on steep southerly slopes *T.triandra* grassland appeared to become invaded directly by *P.evansii* communities in turn invaded by *H.africana* and *L.sericea*. These eventually developed into mature *L.sericea*.

c) Disturbed soils

The successional trend at these sites passes from *E.curvula* dominated communities directly or via *stiburus alopecuroides* to *Rubus-Pteridium-Eragrostis curvula* communities which become invaded by *Buddleia salviifolia*. As soil moisture improves a *Buddleia-Diospyros austro-africana-Leucosidea* community develops which may lead to mature *L.sericea* communities.



Appendix 3.3.2.2. Average percentage frequencies of species in vegetation groups, with species ordered as they occur along the joint 1973-1986 DCA axis 1. Changes in frequency significant at the 95% level (G-statistic) are given (*). Species abbreviations are given in fig 3.3.1.1.



Appendix 3 2.2. (continued)

APPENDIX [illegible] Estimates of the least % change detected significant at p [illegible] in communities and transects, given the sample sizes available in this study. The power of tests to detect change as significant at this level are given for some transects (Year 1982).

TRANSECT		% CHANGE	POWER	TRANSECT		% CHANGE	TRANSECT		% CHANGE
1A	1	28.6%	0.82	T3	1	50.0%	T4	10	24.4%
1A	2	66.7%	0.98	T3	2	27.8%	T4	11	41.4%
1A	3	44.4%	0.99	T3	3	22.0%	T4	TOTAL	6.6%
1A	4	40.0%	0.98	T3	4	30.1%			
1A	5	50.0%	0.97	T3	5	50.0%	T5	1	28.6%
1A	TOTAL	20.0%	0.91	T3	6	21.4%	T5	2	50.0%
				T3	7	11.7%	T5	3	41.9%
T1	1	34.2%	0.96	T3	8	24.2%	T5	4	33.9%
T1	2	52.7%	0.89	T3	9	34.7%	T5	5	53.7%
T1	TOTAL	27.2%	0.73	T3	10	68.4%	T5	6	50.0%
				T3	11	75.0%	T5	7	75.0%
T2	1	25.0%	0.87	T3	12	10.0%	T5	TOTAL	13.6%
T2	2	15.9%	0.95	T3	13	12.2%			
T2	3	47.6%	0.99	T3	14	27.2%	T6	1	17.6%
T2	4	14.3%	0.92	T3	15	64.6%	T6	2	31.4%
T2	5	15.8%	0.92	T3	16	71.6%	T6	3	31.2%
T2	6	32.7%	0.99	T3	TOTAL	5.2%	T6	4	75.0%
T2	7	53.6%	0.96				T6	TOTAL	12.7%
T2	8	67.9%	0.71	T4	1	19.4%			
T2	9	11.0%	0.92	T4	2	36.9%	T7	1	50.1%
T2	10	26.9%	0.92	T4	3	16.6%	T7	2	14.9%
T2	11	10.3%	0.91	T4	4	32.0%	T7	3	18.3%
T2	12	35.5%	0.96	T4	5	27.7%	T7	4	19.6%
T2	TOTAL	1.6%	0.63	T4	6	24.6%	T7	5	39.9%
				T4	7	16.4%	T7	6	31.1%
				T4	8	29.2%	T7	7	50.5%
				T4	9	66.6%	T7	TOTAL	[illegible]

APPENDIX 4.2.4. Plot canopy cover of *P.evansii*, and estimated grass biomass in plots from areas A, B and C.

AREA	Plot no.	CANOPY COVER (m2/plot)	GRASS BIOMASS (EST.) (g/m2)
A	1	0.25	44.9
	2	0.75	51.3
	3	0.25	77.1
	4	0.25	45.0
	5	0.0	52.8
	6	0.5	91.1
	7	0.[illegible]	93.1
	8	0.5	66.7
B	1	5.1	113.4
	2	2.3	77.8
	3	5.3	112.8
	4	6.4	109.5
	5	10.0	87.4
	6	7.2	79.2
	7	3.9	90.6
	8	19.0	67.9
C	1	3.0	11.1
	2	0.0	60.2
	3	18.0	46.2
	4	14.0	50.0
	5	15.0	48.2
	6	10.0	8.1
	7	1.5	62.5
	8	3.0	103.6

APPENDIX 4.3.1. Estimates of woody stand age in resurveyed and additional woody plots. Plots are sequenced as in fig. 4.3.1.

PLOT POSITION	STAND AGE (years)								
	T1	T2	T5	T7 bot	A	B	C	T7 top	NW
1st	15	15	13	20	20	15	20	13	20
2nd	15	15	42	20	20	15	17	13	20
3rd	20	15	42	20	20	15	17	13	20
4th	20	20	42	42	20	15	17	20	20
5th	20	20	42	42	20	15	17	20	20
6th	20	20	42	42	20	15	17	20	20
7th	20	20	20	42	20	15	17		20
8th	33	20	20	15	20	15	17		
9th	42	20	20	13					
10th	42	20	20						
11th	>42	20	20						
12th	42	20	20						
13th	42	20							
14th	42	20							
15th		20							
16th		20							
17th		20							
18th		20							
19th		20							
20th		20							
21st		20							
22nd		20							
23rd		20							
24th		20							

APPENDIX 4.3.2.a) Mann-Whitney U tests for changes in *L.sericea* density from 1973 to 1986.

AREA	AVERAGE RANK 1973	1986	SAMPLE SIZE 1973	1986	Z-VALUE	P>=Z
T 1	11.07	17.93	14	14	2.186	0.029
T 2 bottom	3.5	9.5	6	6	2.812	0.005
T 2 top	13.9	23.06	18	18	2.882	0.004
T 6 bottom	7.17	4.6	6	5	-1.203	0.229
T 6 top	2.5	7.5	4	6	2.482	0.013
T 7	7.27	11.72	9	9	1.726	0.084

APPENDIX 4.3.2.b) Mann-Whitney U tests for changes in *P.evansii* density from 1973 to 1986.

AREA	AVERAGE RANK 1973	1986	SAMPLE SIZE 1973	1986	Z-VALUE	P>=Z
T 1	13.54	15.46	14	14	0.610	0.541
T 2 bottom	5.25	7.75	6	6	1.131	0.258
T 2 top	16.28	20.72	18	18	1.252	0.210
T 6 bottom	7.08	4.70	6	5	-1.100	0.271
T 6 top	7.0	4.5	4	6	-1.191	0.234
T 7	10.94	8.05	9	9	-1.112	0.266

APPENDIX 4.3.2.c). Mann-Whitney U tests for changes in mean height of *L.sericea* stands from 1973 to 1986.

AREA	AVERAGE RANK 1973	1986	SAMPLE SIZE 1973	1986	Z-VALUE	P>= Z
T 1	18.18	10.82	14	14	-2.349	0.019
T 2 bottom	9.08	3.92	6	6	-2.415	0.016
T 2 top	15.61	21.39	18	18	1.793	0.073
T 6 bottom	7.17	4.6	6	5	-1.187	0.235
T 6 top	4.0	6.5	4	6	1.206	0.228
T 7	10.5	8.5	9	9	-0.752	0.458

APPENDIX 4.3.2.d). Mann-Whitney U tests for changes in the mean heights of *P.evansii* stands from 1973 to 1986.

AREA	AVERAGE RANK 1973	1986	SAMPLE SIZE 1973	1986	Z-VALUE	P>=Z
T 1	14.78	14.21	14	14	-0.163	0.870
T 2 bottom	5.25	7.75	6	6	1.131	0.258
T 2 top	16.22	20.78	18	18	1.296	0.195
T 6 bottom	6.83	5.0	6	5	-0.827	0.408
T 6 top	3.13	7.98	4	6	1.954	0.051
T 7	11.0	8.0	9	9	-1.156	0.248

APPENDIX 4.3.4. Descriptions of the density and height changes in re-surveyed woody plots, and of the 1986 height-class structure of additional and re-surveyed woody plots.

TRANSECT 1

Density changes

P.evansii declined at either end of the transect but increased in density toward to center before the stream. *L.sericea* density remained low around the stream, but increased through the rest of T1, especially in the first three plots. Forest precursor species increased markedly in density everywhere except around the stream. This increase was especially marked in the last three plots (fig. 4.3.3.1).

Height class structure

A breakdown of the 1986 height-class structure of the plots show that more dead *P.evansii* occurred in the initial plots; the inner plots contained more taller (>250) plants; and that *P.evansii* seedling recruitment was patchy and not prolific. On the other hand, *L.sericea* showed heavy seedling recruitment in the first three plots, and less in other plots where taller, mature shrubs occurred (fig. 4.3.3.5)

TRANSECT 2

Density changes

In the bottom area of T 2, *P.evansii* density increased in the 6 plots. Further along the transect, increases in density were patchy. *L.sericea* increased in density in the bottom 6 plots of T 2. In the top area, where *L.sericea* had been largely absent in 1973, densities were still very low although more plots were found to contain the species (fig. 4.3.3.2)

Height class structure

From the height class data it was seen that the *P.evansii* stands often contained many dead plants, but few senescing ones (>250cm). The density of middle and smaller sized *P.evansii* was higher in plots 13 to 24. Seedlings were present in almost all plots, excluding those on the steep slope above the stream. The bottom plots of T 2 contained many tall (>250cm) *L.sericea*, beneath which seedling recruitment was prolific. Elsewhere, the spread of this species was limited to a few seedling in 7 plots in the top area (fig 4.3.3.6)

TRANSECT 6

Density changes

P.evansii density declined throughout transect 6, except in the first and last plots. *L.sericea* showed a large increase in density in the top area, and a small decline in the area after the stream (fig 4.3.3.3)

Height class structure

Dead *P.evansii* abounded at the top of T 6, and seedlings were virtually absent from the transect plots. Plants taller than 150cm (ie. middle sized and senescing ones) dominated the top area and plot 5. In contrast, *L.sericea* showed massive seedling recruitment in the top area, some recruitment in the first plot, and little in the plots on the steep slope above the stream, where tall plants occurred (fig. 4.3.3.7).

TRANSECT 7

Density changes

P.evansii density increased in the plots on flat ground before the stream, but decreased greatly in the other plots. *L.sericea* density increased before the stream, and in the last three plots on less steep parts of the slope, where it had been all but absent in 1973. *L.sericea* density declined slightly on the steep parts of the slope after the stream (fig 4.3.3.4).

Height class structure

High densities of dead *P.evansii* occurred in the last two plots of T7, but seedlings were still being recruited there and in the flat area before the stream. Elsewhere the stands were of low density and without seedlings. In the last two plots and plot 1*, *L.sericea* seedlings were very abundant, but at the stream and on the steep slopes above it, where taller plants were common, recruitment was lower. Tall plants were absent from areas of high seedling density (fig. 4.3.3.8).

HEIGHT CLASS STRUCTURE OF ADDITIONAL PLOTS

The height class structure of plots in areas A,B and C are presented in fig 4.3.3.11, a) to e).

Area A

Area A was dominated by dead *P.evansii*, with some senescing and middle sized plants present in most plots. Seedlings occurred in plot 2 only. In contrast, *L.sericea* seedlings abounded in the overall younger stands of this species.

Area B

Area B contained stands of *P.evansii* below 250cm tall. Only one stand, which contained some dead plants, lacked seedlings. *L.sericea* plants, all <150cm, occurred only in the first two plots.

Area C

Area C had a disjunct distribution of size classes: The first two plots had dead plants, plot 1 being dominated by senescing *P.evansii* individuals and skeletons. Plots 3 to 8 contained no senescing plants, only ones <250cm, and a few seedlings. *L.sericea* was absent from all plots.

Transect 7 top area

The height-class structure of these plots are shown in fig 4.3.3.9. Dead *P.evansii* occurred in most plots, but no senescent and few middle sized plants occurred. Seedlings and smaller plants dominated the plots. Plot 6 contained one tall *L.sericea* and a few smaller sized plants and seedlings were present in the other plots.

North-Western Bush Clump plots

The north-western bush clump was dominated by tall (>250cm) individuals of *L.sericea* (*P.evansii* was totally absent). Plant of 50-250cm were infrequent, and seedling densities were generally low. Many plants of other woody species were present in this area, except in plot 3 (fig 4.3.3.10).

APPENDIX 4.3.4.1. Pearson's product moment correlation matrix of the densities of *Philippia evansii* (Pe) and *Leucosidea sericea* (Ls) height classes, *P.evansii* canopy cover and grass biomass in woody plots', for areas A, B and C.(<50 refers to size class 5cm to 49cm. <150 is size class 50-149cm, etc).

	Pe<50	Pe<150	Pe<250	Pe>250	Pedead
Pe<50	1				
Pe<150	.51	1			
Pe<250	.31	.65	1		
Pe>250	-.25	-.43	-.31	1	
Pedead	-.59	-.68	-.51	.60	1
Ls<50	-.33	-.77	-.52	.48	.79
Ls<150	-.22	-.48	-.38	.04	.49
Ls<250	-.25	-.34	-.27	-.17	.41
Ls>250	-.17	-.23	-.04	.26	.26
grass	.47	.18	.20	-.55	-.44
canopy	.12	.77	.60	-.39	-.48

	Ls<50	Ls<150	Ls<250	Ls>250	grass
Ls<50	1				
Ls<150	.61	1			
Ls<250	.43	.39	1		
Ls>250	-.16	.32	-.06	1	
grass	-.21	-.12	-.02	-.06	1
canopy	-.61	-.48	-.26	-.17	-.15

APPENDIX 4.3.4.2. Pearson's product moment correlation matrix of logged plot size class densities and total plot densities of species, of all woody plots.

	Pe<50	Pe<150	Pe<250	Pe>250	PeDead
Pe<50	1				
Pe<150	.54	1			
Pe<250	.39	.52	1		
Pe>250	-.16	-.18	.04	1	
PeDead	.04	.09	.23	.37	1
Ls<50	-.18	-.36	-.13	.48	.41
Ls<150	-.04	-.22	.08	.35	.29
Ls<250	-.13	-.27	-.11	.18	-.12
Ls>250	-.21	-.32	-.32	-.01	-.42
Ls Total	-.19	-.41	-.2	.44	.27
other	-.31	-.32	-.45	.003	-.37

	Ls<50	Ls<150	Ls<250	Ls>250	Pe Total
Ls<50	1				-.14
Ls<150	.67	1			0.02
Ls<250	.42	.55	1		-.17
Ls>250	.26	.11	.38	.1	-.40
other	.29	.12	.47	.69	-.47

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