THE STRUCTURE AND DYNAMICS OF RIVERINE VEGETATION IN THE UMFOLOZI GAME RESERVE

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by
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DECLARATION

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

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12 day of February 1991.

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ABSTRACT

The cyclone Domoina floods of 1984 were responsible for the large scale destruction and devastation of riverine vegetation in the Umfolozi Game Reserve. This event highlighted the need to gain an understanding of the structure and dynamics of riverine vegetation and to use this knowledge to develop a management strategy directed at the future recovery and maintenance of riverine vegetation in the Umfolozi Game Reserve.

The explanation of the structure and dynamics of vegetation has been a central theme to several theoretical tenets in ecological literature, each having been developed under its own range of conditions and circumstances, and therefore offering different strengths, weaknesses and applicabilities under a variety of different conditions.

The objectives of the study were to 1. obtain a testable knowledge of the structuring and dynamics of riverine vegetation in the Umfolozi Game Reserve, 2. obtain a testable knowledge the relative merits of employing three alternative approaches in the understanding of riverine systems, and 3. utilise this knowledge to assist with the development of a management strategy for riverine areas.

The three approaches which were adopted in determining vegetation structure and dynamics were based on different underlying tenets, namely, succession theory, disturbance theory and community organisation theory.

The succession theory approach provided useful information regarding possible successional pathways in riverine areas. However, as these did not correspond with those explicitly defined by the classical view of succession, it was concluded that this approach and its findings were un-testable.

The disturbance theory approach provided valuable information regarding the importance of flooding regime on the structuring and dynamics of riverine vegetation. Test of the intermediate disturbance hypothesis were confounded by the presence of the riverine environmental gradient, and because species richness data was in short supply, it was not possible to compare the findings with current disturbance models which predict species diversity in response to flooding frequency. A conceptual model was presented based on a three dimensional modification of the intermediate disturbance model in order to predict the effects of recurrent floods on riverine species diversity. The life history characteristics of riverine species were investigated to determine which species are best suited to different flooding frequencies. Only those species which respond quickly in the interval between flood events are able to persist in areas subjected to frequent flooding (ruderal species), while (competitor) species persist under conditions of infrequent flooding.

The response of the riverine system to recurrent flooding over the last century was revealed using correspondence analysis and a Markov modeling procedure. The dynamics of the system within its domain of attraction was demonstrated using the classical ball-in-cup analogy. The system displayed a high degree of resilience to floods and was found to have remained within its domain of attraction during this time despite the effects of large floods. The riverine system rarely, or never attains its equilibrium state.

Five relevant community hypotheses were tested in the riverine situation with the community organisation theory. All were found to apply simultaneously. These findings were then interpreted in the light of a current resource based community organisation approach which predicts the application of different community organisation hypotheses as well as the importance of interspecific competition under various combinations of resource supply and distribution and the responses of exploiters. This allowed for the construction of a conceptual map which predicts the application of five community organisation hypotheses both spatially and temporally in riverine areas.

It was concluded that island size, resource/habitat heterogeneity, the effects of ecological time, the individualistic responses of species and the impact of enemies are primary structuring factors in different areas of the riverine environment at different times of the year. However, the effects of disturbance, particularly flooding, have a more important effect on this structure. A combined disturbance and community organisations approach is therefore best suited to the determination of riverine structure and dynamics.

Management recommendations were proposed which aim at maintaining the effects of flooding and to maximise species diversity by applying the intermediate disturbance model in riverine areas. The lower and upper thresholds which define the desired diversity of the system are needed to identify when the system is in a state of low diversity. The monitoring of future floods, the supply of water and determining the impact of these on the structuring and dynamics of riverine vegetation was suggested. Research recommendations were aimed at addressing the apparent increase in flood frequency and intensity and the use of fire and alien/exotic species control measures to aid the recovery of riverine vegetation.

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CHAPTER 1 INTRODUCTION

1.1 Introduction to study

In January 1984 cyclone Domoina was responsible for the torrential rain that fell in the catchment areas of the Black and White Umfolozi rivers. The unusually high rainfall caused both rivers to flood extensively. Apart from causing substantial damage to roads, road and railway bridges, houses, and other structures in Zululand and Natal, the flood waters were responsible for the destruction and removal of large stands of riverine vegetation in the Umfolozi Game Reserve. This damage was the cause of great concern to the Natal Parks Board which initiated a study aimed at determining the ecological effects and management implications of the floods within the Reserve. This study (Wills, 1984) identified the need for a second and more substantial study aimed at gaining a comprehensive knowledge base on the structure, functioning and dynamics of the Umfolozi riverine communities. In addition, it was hoped that the study would address the formulation of practical and effective techniques which could assist with the recovery of these communities and thereafter to maintain them in a state which is consistent with the management plan for the reserve (Anon, 1985).

1.2 Objectives of the study

The prime objectives of this study were as follows.

1. Obtain a testable knowledge that reflects the structuring and dynamics of riverine communities on the Black Umfolozi river within the Umfolozi Game Reserve.

2. Obtain a testable knowledge about the relative merits of employing three alternative theoretical approaches, to determine the structuring of riverine communities. These approaches were based on succession theory, disturbance theory and a resource based community organisation theory as proposed by Price (1984), as well as its five relevant sub-hypotheses.

3. Utilise information on riverine community structuring in order to provide input towards a management strategy directed at the recovery and maintenance of riverine areas.

1.3 The cyclone Domoina flood and its effects

The tropical cyclone Domoina made its appearance over the Mozambique channel on 28 January 1984, and later moved over the land mass of southern Africa. During its six day visit, torrential rains fell over this region. The isohyetal map, constructed by the Department of Water Affairs, identified the Umfolozi catchment as being one of the six areas where most of the rainfall occurred. Rainfall figures, recorded in this region during the course of these few days, exceeded their three day, 200-year value, which constituted its highest rainfall ever recorded (Kovacks et al, 1985). The water levels in the Black and White Umfolozi rivers rose rapidly, attaining estimated above normal vertical displacements in the region of 18 to 22 metres. These high water levels, with considerable force, were responsible for the devastation of riverine vegetation on the banks of these two rivers.

The large stands of sycamore figs (Ficus sycomorus) which characterised these river banks were almost completely annihilated. Wills (1984) determined that 96 percent of the riverine vegetation on the banks of the Black Umfolozi river suffered damage to an extent of between 75 and 100 percent. In addition, certain plant species which were characteristic of these areas (e.g. Trichilia emetica, Rhus chirindensis and Acacia schweinfurthii) were no longer recorded in this post Domoina survey. This riverine vegetation, apart from having aesthetic value, served as the prime habitat and breeding area for many bird and mammal species (Whateley, 1986; Hitchins, 1980; MacDonald and Birkenstock, 1980; Bourquin et al, 1971; Wills, 1984; Melton, 1978). River bends, low lying alluvial flats and other areas which displayed relatively low water velocities collected large quantities of fine sand and silt due to deposition.

After the flood, conservationists feared that the riverine communities, which were characteristic of these rivers (Whateley and Porter, 1983; Anon, 1985), might not recover from this devastation or that, with the large scale removal of the dominant species, they might be completely replaced by other less desirable species. Since certain alien species have become increasingly significant over the last decade (Macdonald, 1983; Wills, 1985), it was feared that these species might become more dominant as a result of the flood, thereby constituting a major management problem.

It is currently believed that flood events in the Umfolozi rivers may well be increasing in size with time (Anon, 1986) and that this is a consequence of the gradual increase in water run-off throughout the Umfolozi catchment areas because of overgrazing (Kovacks et al, 1985) and the poor management of arable land. In addition it is possible that the natural attenuation of flood waters, which is normally brought about by dense vegetation on river banks, has been considerably reduced upstream by the extensive utilisation of these riverine areas for agricultural and domestic purposes.

1.4 Rationale

The massive devastation of riparian vegetation caused by the cyclone Domoina floods and subsequent speculation regarding its recovery highlighted the general lack of knowledge about the dynamics and functioning of riverine systems. The numerous fears expressed concerning the possible future and recovery of the riverine vegetation in the Umfolozi Game Reserve have spelled out the need to develop a successful riverine management strategy. However, in order to manage riverine areas successfully, it is essential to identify the underlying factors which are responsible for their structure and functioning. Furthermore, by identifying the relationships which exist between the fundamental factors of the system, it may be possible to investigate the dynamics of the system simultaneously.

The factors responsible for community structure have been a major issue in ecological literature for decades. During this time numerous alternative theories have been proposed and debated. It is important to identify which of these theories have applicability in the riverine situation. For the sake of this study, three of these major theoretical tenets were investigated separately as three broad approaches. These approaches were based on succession theory, disturbance theory and community organisation theory. The latter approach embraced a number of opposing hypotheses which could be addressed simultaneously by considering the availability and distribution of basic resources and the responses of exploiter species to them.

Since its inception by Clements in 1916, succession has become a fundamental tenet in attempting to explain sequential vegetational changes and has since occupied a central and significant place in ecological literature. It has generated much philosophical controversy by both its supporters and critics alike such as Tansley (1947), Gleason (1927; 1939), Odum (1959), Whittaker (1970; 1975), Drury and Nisbet (1973), Connell and Slatyer (1977), Noble and Slatyer (1980), Grime (1979), Horn (1976), and Finegan (1984).

Disturbance theory, as it is known, became commonplace in ecological literature soon after Drury and Nisbet (1973) suggested a gradient of disturbance intensity as a practicable alternative explanation to successional change. Subsequent documentation has highlighted the importance of disturbance in many communities (Connell, 1978; White, 1979; Pickett, 1980). The various regimes of disturbance (Sousa, 1984) and the responses of certain species types to these regimes have often been investigated (Denslow, 1980; Osman, 1977; Connell, 1978).

A large number of hypotheses are extant in ecological literature which pertain to community organisation and those environmental factors which are responsible for structuring communities. Competition theory has consumed much time and energy over the last decade (Pianka, 1974; Ricklefs, 1979; Odum, 1971). Gleason (1926) and Whittaker (1952; 1956) emphasised the importance of the individualistic responses of species to specific environmental factors. Andrewartha and Birch (1954), Southwood (1961) and Whittaker (1975) identified time as a major organising force in ecological communities. MacArthur and Wilson (1963; 1967) and Connor and McCoy (1979) have highlighted the importance of island or area size. Brower (1958), Park (1948), Paine (1969) and McNaughton (1979) identified the impact of natural enemies on the structure of certain communities. In an attempt to construct a global picture of community organisation theory, Price (1984) proposed a resource based approach which requires the simultaneous testing of five hypotheses under different conditions of resource availability and exploiter responses to these resources.

1.5 Project approach

The project was approached by separately applying and addressing the three ecological tenets to the riverine situation. These three theoretical approaches were considered to be particularly applicable given the characteristics of the study site, the riverine vegetation and the stochastic and devastating nature of the cyclone Domoina floods.

1.5.1 Approach based on succession theory

The cyclone Domoina flood represented the perfect disturbance on which to base a successional study. It was clearly responsible for largely resetting the successional state of riverine communities which, it is believed, were in or near a state of climax before the floods. Other large floods have been recorded, particularly the 1925 and 1963 floods, which also caused large damages and re-initiated the successional sequence. The fact that riverine communities had re-attained a climax state before the Domoina floods is proof that succession may play a leading role in the structuring of riverine communities, and for this reason it was worthwhile investigating. The approach promised to specifically shed light on the various components, the mechanisms responsible and the structure and dynamics of riverine vegetation.

1.5.2 Approach based on disturbance theory

The cyclone Domoina floods and previous floods are examples of disturbance as an inherent part of the Umfolozi riverine system. The characteristics of the recurrent disturbances and their effects have not been satisfactorily investigated and identified. The community dynamics of the system seem to have changed as a consequence of these events. The apparently dominant species _Ficus sycomorus_ appears to have been displaced in favour of other species which are not particularly characteristic of these riverine areas. On this basis, these areas are ideal to study in terms of disturbance theory.

This approach differed from that of the succession based approach in that it concentrated on the incidences of disturbance, the regimes, the organising role, the predictions of disturbances and the system dynamics as a consequence of repeated disturbance and thereby offered to supply information which the successional approach was not capable of supplying.

1.5.3 Approach based on community organisation theory

Riverine areas provide an ideal testing ground for hypotheses pertaining to community organisation. These areas display a vast range of different resources, resource distributions and plant exploiters by virtue of their characteristically heterogeneous topography, geology and soils and climate. The effects of large and small scale flooding also provides for wide ranges in the spatial distribution of resources. These factors undoubtedly have a bearing on the structure of riverine communities. It is likely that certain factors have a major influence while others are less important. With this range of environmental factors available, it is possible to test several theories concerned with community organisation and determine which have particular relevance in the riverine situation.

In addition, the various combinations of these factors provides for a wide range of resources that adequately represent the range provided for in the Price (1984) approach. The variables associated with the various resource types and distributions as well as exploiters present are easily measurable, identifiable and amenable to extensive experimental manipulation and can therefore be employed adequately to test for the simultaneous application of numerous community organisation hypotheses. This approach therefore offered to focus specifically on every major aspect of community structure in riverine areas

1.6 Literature review

In order to allow for comparisons between the three approaches and to streamline the body of each in their respective chapters, a single, combined literature review is presented below.

In order to avoid discussing numerous alternative hypotheses which have already been reviewed repeatedly in current ecological sources, only an overview of the most relevant hypotheses, which sheds sufficient light on the specific problems associated with this study has been presented. Clear distinction was drawn between the three tenets on the basis of disparities which exist between the primary basis, support for and regime of each in ecological literature. In addition to this, each approach offers to address the problem from a different angle, thereby offering the chance to gain a thorough understanding of the system.

1.6.1 Succession theory

1.6.1.1 Introduction

From the work of numerous early botanists, most notably that of Cowles (1899), Clements (1916) and Watt (1947) it became accepted that changes in vegetation occur both spatially and temporally. Two types of vegetation changes were noted.

First, fluctuation occurs where vegetational changes do not tend to alter the overall appearance of the area. Second, succession occurs where vegetational changes clearly alter the appearance of the area.

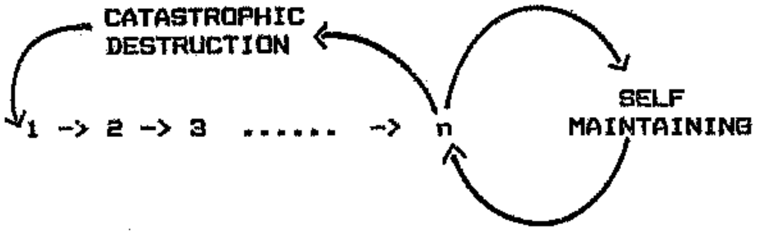
Awareness of vegetation succession became widespread in the last century with the work of Cowles (1899). However, Clements (1916) is generally considered to be the father of succession theory.

1.6.1.2 Clementsian succession

Clements saw succession as a directional change of vegetation types, each successive type establishing itself because the preceding type had modified the site in a way favourable to its successor. Site modification or reaction, as he termed it, was seen as the driving force of successional change. This succession of species continued until the species combination best suited to the regional climate and the site was established, finally ending in a "climax" type that was stable (persistent in time) and self maintaining under the current conditions of site and climate. The gradual attainment of this climax was accompanied by a convergence in species and therefore displayed a trend towards increased uniformity in species composition. This process was envisaged as being purely deterministic in that the final vegetational composition of a site could be predicted, when one was aware of the specific site and climatic conditions of the area in question. The characteristics of those species, which replace others, could be predicted and certain unstable and successional species recognised. Similarly, species and associations of organisms could be assigned to places in a successional order. A multitude of seres were of this description identified and defined, each occupying a different place in the successional series and each sporting a unique and predictable series of species assemblages - eusere, hydrosere, mesosere, psamosere, pyrosere, xerosere, etc.

If the climax or any other stage of the sequence was destroyed by some catastrophic event, it was believed that its preceding stages would be repeated and the same climax would be re-established, provided the climatic conditions of the site were unchanged. Disturbance was therefore considered responsible for arresting or reversing the course of succession and, depending on its size, responsible for re-initiating succession from a point lower down the sequence.

The basis of Clements' ideas can be symbolically represented by the following figure (Miles, 1979).



Where 1 represents the pioneer stage of the sere
2,3 etc represent intermediate stages
n represents the climax stage

Clements drew a further distinction between the changes which occur during the colonization of a new and skeletal habitat initially lacking in soil and vegetation (primary succession) and those which characterise the much more common circumstance in which succession is a feature of the process of recolonisation of a disturbed habitat (secondary succession).

1.6.1.3 Alternative models of succession

Since its inception, Clements's model of succession has been the target of much critique due to its inability to adequately explain observed trends in vegetational succession. Numerous alternative models of succession have been drawn from various quarters, these have been reviewed in detail in Drury and Nisbet (1973), Van Hulst (1979) and Peet and Christensen (1980).

Recent workers have attempted to elucidate further successional mechanisms which could explain differences in observed successional characteristics. Connell and Slatyer (1979) proposed three models responsible for successional change. All three models agree on the initial stages that certain species will usually appear first at a site after perturbation because they have evolved colonizing characteristics. The three models differ in terms of the mechanisms that determine how other species appear later in the sequence.

1. Facilitation mechanism

This mechanism is essentially identical to that initially proposed by Clements (1916). Once established at a disturbed site, early succession species modify the environment so that it is more suitable for later-succession species to invade and grow to maturity. As a result of this phenomenon usually designated as "reaction", successional species replace one another until, finally, the site is occupied by species which do not appreciably alter site conditions and are therefore able to maintain themselves perpetually. These species represent the climax community.

2. Tolerance mechanism

Modifications to the environment and the effects of "reaction" brought on by the earlier species neither increase nor reduce the rates of recruitment and growth to maturity of later colonists. Species that appear later are simply those that arrived either at the very beginning or later and then grew slowly, displaying complete tolerance for all other species present. Therefore the sequence of species at the site is determined solely by their life history characteristics. The climax is reached when the most tolerant species available occupies the site and occupies/removes essential resource(s) to such an extent that no other species can survive.

3. Inhibition mechanism

Once early colonists secure the space and/or resources, they inhibit the invasion of subsequent colonists or suppress the growth of those already present. Any disturbance which removes these species will therefore facilitate the colonization of other species. These new species gradually accumulate over time and eventually replace the initial inhibitor species.

Independent support has been shown for the three mechanisms from various sources. Drury and Nisbet (1973) believed that, according to natural selection, it makes more sense for plants to release products, which facilitate the growth of their own species, than to alter their habitat in such a way as to facilitate the growth of other competing species. Niering and Egler (1955) supported the tolerance model by proposing that much of secondary succession is simply a consequence of differential longevity and that most of the eventual dominants enter a community in the earliest developmental stages when competitive pressures are low.

The three mechanisms have subsequently become embroiled in numerous controversial discussions of holistic and reductionistic theories. The facilitation mechanism represents Clements' supposed "holistic" outlook while the tolerance and inhibition mechanisms represent the reductionistic approach to succession. The development and interrelationship of holistic and reductionistic theories have been reviews by McIntosh (1980) and briefly by Finegan (1984). It appears however, that the exact distinction between "holism" and "organicism" (the essence of Clements' ideology) has been neglected by such reviews.

Finegan (1984) proposed a synthetic (Darwinian) approach to succession where facilitation, tolerance, inhibition and allogenic change are accepted as interdependent mechanisms in succession, which may affect the same individual successively or simultaneously during its life cycle. The relative importance of the various mechanisms is likely to vary widely between environments and are not mutually exclusive.

The meaning of Clements' term "reaction" has never been clearly defined. Since it is supposedly the driving force behind succession, it is important that its exact nature be elucidated. It has already been stated that, initially, successional change was thought to be caused by cumulative changes in environmental conditions (autogenic change), which, in turn, are thought to be at least partially determined by the vegetation present. However, there has been a corresponding shift in emphasis from habitat factors - supposedly changed by early successional species as they prepare the path for later successional species - to community processes such as competition (allogenic change). Since the early workers were only concerned, at that stage, with the replacement of communities and not of populations, they consequently did not place much importance on competition and the need to distinguish between competition and reaction in their explanations of succession.

Daubenmire (1968) believed that autogenic change as well as allogenic influences are responsible for succession. Both groups of forces work simultaneously but, under different circumstances, one or the other usually seems to exert the stronger influence. Along similar lines, Drury and Nisbet (1973) suggested that most of the phenomena of succession can be understood as consequences of differential growth, and differential survival (differential colonising ability) of species adapted to growth at different points on environmental gradients. Successional sequence is therefore simply a type of stress gradient to which plants are adapted.

Picket (1976) proposed that succession is a form of gradient along which species are competitively displaced. Identification of vital attributes and combination of these attributes of plant species present at a site could be used to predict successional change. This view was subsequently supported and backed up by Van Hulst (1978). Noble and Slatyer (1980) attempted to make a detailed breakdown of the minimum number of vital attributes and the combinations thereof displayed by different species types during the course of a successional sequence. Grime (1979) applied a similar approach to succession with particular emphasis on the combination of basic strategies used by plants in overcoming the three major forces which determine the composition of vegetation at a site i.e. competition, stress and disturbance.

1.6.1.4 Problems with studying succession

The mechanisms producing the sequences of species and the true nature of the driving force behind succession have not been elucidated for several reasons.

First, direct evidence is available only for the earlier stages when many species are short lived and amenable to experimentation. The sequence later in succession has not been directly observed for the obvious reason that these later-appearing species persist for much longer than the usual ecological study or even the investigator. Therefore the latter sequence has to be reconstructed from indirect evidence of various sorts (Connell and Slatyer, 1979).

Second, the slow and complex processes involved with successional change supposedly require long-term studies for elucidation and testing. Strayer et al (1986) identified the numerous problems associated with such studies. The typical research funding cycle of 1 to 3 years does not satisfy the demand of long-term studies for a sustained commitment of money, facilities, manpower and time. In addition, if funding and job security are guaranteed over the long term, such studies tend to fall into an unproductive complacency which threatens its continued existence. The future is uncertain and even scientific paradigms might change so much over decades as to render some research questions and the data collected, in relation to them, obsolete (Mentis, 1988).

Third, some possible mechanisms have been ignored, particularly the effects of disturbances such as herbivory (Connell and Slatyer, 1979), the intensity and frequency of fire, floods, landslides etc. (Sousa, 1984).

Fourth, the mechanisms that determine succession have not been defined clearly or stated in the form of acceptable testable hypotheses (Connell and Slatyer, 1979). Mentis (1988), described succession as a non-scientific issue because of its inability to conceivably demonstrate inconsistencies between observation and expectation, prediction or explanation.

Due to the complexity of succession theory, it is exceptionally difficult to test it. Any vegetation change which does not comply with the proposed description of succession as stated by Clements (1916) is not succession and therefore cannot be used to test succession theory and can therefore be described to be a "non-scientific" (non-falsifiable or metaphysical) issue (Mentis, 1988).

1.6.1.5 Methods of studying succession

The definitive approach to studying succession is to employ a dynamic method, which is based on repeated observations of the same site through time. However, due to their long term nature, it is difficult to adopt such studies because of the numerous obstacles already mentioned, which present themselves during the process. In attempting to elucidate long time scale issues such as succession, Strayer et al (1986) has called for the use of approaches other than direct long-term studies. Several short-term approaches might be adopted. Such "snap-shot" approaches being the only real alternative for short-term researchers.

These two main approaches have been employed in many different ways in the study of succession.

1. Studies of the same area

These can be based on the following.

A. Permanent plots

Peet and Christensen (1980) advocated the use of a population dynamics approach to the study of succession through the long-term observations of marked individuals under carefully designed experimental conditions.

In forested stands, trees can be labeled and periodically re-measured for diameter, height changes, and mortality. New seedlings can be marked. Herbaceous vegetation may be assessed and periodically re-evaluated in permanently fixed sub-quadrats, as individual counts, cover measurements or frequency measurements.

By these means, a general pattern of vegetation development can be carefully monitored in terms of the establishment and mortality of individuals and the development of a balance between the two.

B. Studies of exclosures

This type of study relates to the course of community or population development in a similar way except under the exclusion of browsers and grazers. An exclosure often allows for an experimental comparison of arrested succession or even regressive succession outside with progressive succession as occurring in the exclosure.

C. Evidence of change found in the present community

A structural analysis of the woody plant species of a community by size and/or age classes may reveal important trends of succession. A species with a large number of individuals in the small size classes and fewer in the large size classes shows, active reproduction and persistence on the site. Species displaying no small size classes and, therefore, showing no reproduction at all, may be interpreted as disappearing from the community. Such analyses are the most important tool for gathering information on succession (Braun, 1950), because permanent plot data are not always available.

D. Retrospective studies

These are carried out in different ways.

i. Aerial photographs taken at different times

Aerial photographs of the same area, taken at different times, can be an excellent tool for studying succession. However, the detail obtained is limited by scale and usually only the more general structural changes such as the development of grass cover to woody plant cover or a change in dominance of certain tree species, may be evaluated by this technique. The varying proportions of different vegetation states, over time, can be arranged relative to the extremes and presented as a time sequence.

ii. Historical and file records

Written descriptions of the vegetation cover of an area at earlier dates may reveal useful information about succession. Exact successional trends are not inferred by these means and it is open to bias.

The analysis of retrospective data collected by these means can be aided by means of Markov models. Recently Markov models have been used to describe long term vegetation change in forest ecosystems (Horn, 1975). In this context they are commonly used to determine the probabilities of transition from one vegetation state to another, as well as the final equilibrium proportions of the various states involved. A comprehensive description of the uses of Markov models and the procedures involved is given by Jeffers (1978).

2. **Substitution of space for time**

   With this approach, succession trends are usually judged from a study of contemporary communities in geographically separate places. These communities are chosen on the basis that they represent different stages of the same successional sequence, and are accordingly arranged into a time sequence. The separate descriptions of each community, once pieced together in the correct order, supposedly describes the entire successional sequence. The substitution of communities which are situated in different climatic areas, which display markedly different soil or geological characteristics or where the dates of the last major disturbance are unknown, can reduce the value of the technique and its predictive ability. The validity of such treatments depends on a thorough knowledge of the ecology of the entire area studied. The better studies of this sort are supplemented with data about current population structures.

1.6.1.6 Predictability of succession

Succession has been viewed as a purely deterministic process which, after each successive disturbance at a particular site, is believed to occur by means of the same basic pathways and mechanisms to eventually attain the same predictable outcome. In recent years there have been increasing attempts to predict the various pathways and products of succession using mathematical models. A number of probabilistic and deterministic models have been employed in an effort to describe succession and predict the outcome of succession. Jeffers (1978) and Horn (1975) propound the use of Markov models. Unfortunately, in order to avoid large, slow and unwieldy mathematical structures, it is only possible to consider the most important aspects of any particular successional sequence in such models. Consequently, current models reflect few of the complexities of succession, and are unable to make predictions which encompass them.

1.6.1.7 Failures of succession theory

Miles (1979) stated that successional sequences show an endless variety of patterns and that no two sequences have yet been recorded with identical mixtures and proportions of species. Many workers have stressed the role of chance in causing this variety (Webb et al, 1972). Chance factors include the occurrence of good seed years for particular species, favourable weather conditions for establishment and numerous others. A large number of studies have highlighted the effect of variations in the occurrence, severity and nature of disturbance. The effects of multiple and reacting chance events clearly play a major role in determining the final outcome of succession. This clearly shows that succession is not as predictable and deterministic as initially proposed. This has important implications concerning the use of the theory in predicting and understanding the dynamics and structure of different systems.

Mentis (1986) discussed one of the frequently described weaknesses of succession theory, namely that of the possible non-existence of the climax state. In essence, from successional theory, the climax state is supposedly utopian and stable and therefore the ideal state. However, if this is so, why would a system shift from this state and why does it not persist? If the classical concept of succession did apply, all systems would be in this stable and utopian state. However, this is clearly not the case. Rangelands are a good example of this.

Walker et al (1986) identified the importance of periodic 'events' such as the effects of total rainfall on grassland dynamics and concluded that this 'event' has the single major influence on the sward dynamics. Other factors such as inter-tuft competition, the differential growth of grasses and the interactions between grass and grazing patterns were identified as playing only a small role. It is commonly believed however, that these factors represent 'reaction' as Clements described it, which supposedly acts as the driving force of succession. These findings contradict the essence of classical succession theory, since it appears that this system is 'event driven' (Walker et al, 1986) rather than 'reaction driven'. Mentis (1988) stated that any form of vegetational change which does not comply with the classical definition of Clementsian succession is not succession and therefore cannot be used to test succession theory. Due to the fact that succession is not amenable to proper hypothesis testing, he described succession as a 'non-scientific issue'.

These arguments have been used on numerous occasions to undermine succession theory in favour of disturbance theory which identifies disturbance and its regime as being of major importance in the structuring of ecological systems.

1.6.2 Disturbance theory

1.6.2.1 Introduction

Disturbance is a major source of both temporal and spatial heterogeneity in the structure and dynamics of natural communities. For this reason it is vital that any study pertaining to community structure should include the effects of disturbance (Sousa, 1984 a). According to Denslow (1980), natural disturbances to plant communities are simultaneously a source of mortality for some individuals and a source of establishment sites for others. The frequency, extent and nature of disturbances are therefore likely to be important selective factors on their life history strategies.

Drury and Nisbet (1973) proposed that communities are structured in response to a gradient of disturbances. This implies that disturbance events are essentially responsible for driving the system rather than 'reaction'. It is this basis that clearly separates succession and disturbance theory. Disturbance theory therefore concentrates on a. the different types of disturbance and their effects b. disturbance regime which is responsible for determining the structure and composition of a system.

Subsequent to the suggestions by Drury and Nisbet, the impact and effects of disturbances on community structure have been highlighted in many studies (Connell, 1978; White, 1979; Pickett, 1980; Denslow, 1980).

1.6.2.2 Definition

Disturbances have been traditionally defined as uncommon and irregular events that cause unusually abrupt changes to communities, moving them away from their normally static equilibrium conditions.

This traditional definition is misleading for two reasons (Sousa, 1984 a).

1. A gradient of changes can be experienced by a community depending on the intensity of the disturbance and the vulnerability of the species present. It is not possible to define on this continuum of change the exact point at which the change constitutes a disturbance.

2. There is no clear demarcation between communities that are in the equilibrium state and those which are not.

The problem of defining the "normal" for the environmental settings of natural systems inevitably leads to semantic debate regarding the true definition of the word. Evidence suggests however (Connell and Sousa, 1983) that due to the frequency of disturbances, few natural populations or communities persist at or near an equilibrium condition on a local scale.

Further definitions of disturbance have been proposed which have particular application to the system in question.

> A discrete, punctuated killing, displacement, or damaging of one or more individuals that directly or indirectly creates an opportunity for new individuals to become established (Karr and Freemark, 1983)
>
> Any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment (White and Pickett, 1985).

> A change in the structure of a system which usually affects its functioning. Disturbances are often caused by aperiodic events, such as floods, particularly severe storms, prolonged droughts, excessive herbivory, or activities such as bush clearing and cultivation. Disturbance may result from one, but more often a combination or sequence of extreme values of environmental variables. These may or may not cause mortality of individuals. Opportunities are created for new individuals of the same or different species to become established. Increasingly, disturbances are the result of human activities (Frost et al, 1986).

The characteristics of disturbances are highly variable, even within one type of disturbance which arises from a similar source (e.g. flood, fire). In defining disturbance it is important to allow for the fact that disturbance is relative to the spatial (e.g. organism size) and temporal (e.g. organism lifespan) dimensions of the system at hand (White and Pickett, 1985). It follows then that in order to investigate the effects of the different characteristics of disturbance and to understand the dynamics of the communities which are affected by the disturbance, it is necessary to define each regime. In addition, the subsequent management of disturbed areas can be greatly assisted with this knowledge.

1.6.2.3 Disturbance regime

Sousa (1984 a) lists five descriptors or factors which are commonly used to describe the disturbance regime of an area.

1. Areal extent - the size of the disturbed area.

2. Magnitude - consists of two components.

    a. Intensity - a measure of the strength of the disturbing force.
    b. Severity - a measure of the damage caused by the disturbing force.

3. Frequency - the total number of disturbances that occur in a geographical area per unit time.

4. Predictability - a measure of the probability of the disturbance recurring at any time.

5. Turnover rate - the mean time required to disturb the entire area.

Within any particular habitat, a variety of agents operate independently or in concert to generate the overall regime of physical disturbance to which the organisms respond. The heterogeneity of natural disturbance regimes is due, in part, to local variation in the intensity, timing and spatial distribution of potentially disturbing forces.

1.6.2.4 Types of disturbance

The kinds of natural disturbance vary regionally and also within one landscape as a function of topography, substrate, and the vegetation present. It is mainly the physical agents of disturbance such as floods, fires, drought and winds which are most often associated with the term disturbance, but biological processes can also act as agents of disturbance (White, 1979). Numerous forms of disturbance have been identified in the literature.

For the sake of this study, only the three most common forms of disturbance to the riverine system will be discussed. Namely, flood and fire as physical disturbance and herbivory as a biological disturbance.

1. Floods

The disturbance created by floods is primarily achieved by means of the sheer force and velocity of the flood waters. Depending of the force of the water and the susceptibility of the trees, they can be completely uprooted, broken off at ground level, or stripped of their foliage, leading to the reduction of biomass and mortality. In terms of the destruction of the larger woody components, floods can be selective to the degree that those species which offer the greatest resistance to river flow, due to their stem or canopy size or their rigidity, will be removed most effectively. Trees with smaller canopies and which have more flexible characteristics are often able to survive floods more effectively (Wills, 1984). Herbaceous species are readily removed along with underlying soils and substrata.

The ability of flood waters to erode existing sediments as well as various layers of underlying rock is related to its sediment load which it carries as a suspended load (small particles - silt and fine sand) and as a bed load (larger particles - sand, gravel as well as stones and small rocks). The suspended particles are carried within the internal eddies of the flood waters, while the bed load is simply moved along the river bed by the force of the water. The velocity of the water determines the size of the particle which can be carried by the suspended mode. As water velocity drops, so does the ability of the water to carry the larger particles and these particles are dropped by the water and deposited. Areas where channel velocity are reduced are therefore characterised by large quantities of sand and silt depositions. The deposition of large quantities of silt and sand constitutes a further form of disturbance to riverine vegetation. Point bars (inner bends) and river flats are major areas of such deposition.

Floods are responsible for the continuous removal of old substrates and the creation of new ones (by means of the erosion and deposition of sediments) and the displacement and migration of river channels. These changes, along with the varying abilities of plants to tolerate flooding and to survive and colonise after flooding, leads to the continuous shifting of vegetation along these disturbance created gradients (Franz and Bazzaz, 1977). The presence or absence of certain plant species along rivers is related to flood frequency and intensity. In addition, the variable probabilities of floods of different sizes occurring, means that the gradient from river's edge to upland is a spatial gradient reflecting flood frequency (Bell, 1974). However, this gradient is complicated by the presence of numerous bends in the river, where the flow on the inner and outer bends are exaggerated by the force of the flow.

Floods are also responsible for seed bank dynamics. The seed bank of a riverine area is partially or completely removed along with the soils they are associated with by the erosive force of the flood waters. Towards the end of the flood, when water velocity slows down, the deposition of sediments occurs. Seeds from riverine areas are simultaneously deposited with these sediments, bringing about a turnover in the seed bank. By these means, plant species from areas higher up the river as well as in the catchment areas are able to appear and establish themselves in lower lying areas. It is by these means that alien plant species are able to spread so successfully in riverine conditions.

The potential for flooding on a riverine system depends on four main physical parameters of the catchment area (Looser, 1985),

a. intensity and duration of rainfall in the area,
b. topography of the area,
c. soil permeability, and
d. vegetation cover.

Roberts (1985) highlighted the effects of land use in catchment areas and how different land usages bring about changes to the soil permeability and vegetation cover, thereby affecting the potential for flooding.

The land usages he identified were,

a. afforestation,
b. soil conservation practices,
c. river abstractions and damming,
d. urbanisation, and
e. cultivation.

2. Fire

The disturbance resulting from a fire is primarily brought about by the destruction of plant matter and associated organisms by the intense heat of the fire. Secondary effects concern the reduction in organic matter and total nitrogen as well as carbon and sulphur through volatilisation and removal in smoke and ash (Frost et al, 1985).

Fire is a periodic event, often occurring over a wide area and affecting both living and dead plant material irrespective of their nutritional quality. It can be selective to the degree that there are considerable differences between species in their susceptibilities and responses to fire (Frost, 1984). The incidence of fire is largely a function of the dry-season standing crop of grass, itself a product of both the amount of rainfall and plant production during the previous wet season and the extent of herbivory (Frost et al, 1985).

In high rainfall areas and areas of high water availability, where grass production is substantial, the dry-season fires are very intense. In these areas, fire effectively kills seedlings and small trees .., consequently, woody plant recruitment is generally episodic (Frost et al, 1985). Fire also damages above-ground parts of plants and retards the growth of shrubs and seedlings, thereby lowering the biomass of woody plants (Rutherford, 1981).

The local intensity, frequency and areal extent of fire in terrestrial plant communities is controlled by complex interrelations between six factors (Vogl, 1977; Sousa, 1984 a).

a. frequency and seasonality of ignition sources,
b. moisture content of fuel,
c. rate of fuel accumulation,
d. structural and chemical characteristics of fuel,
e. mosaic nature of the landscape, and
f. local weather conditions at the time of fire.

Since all of these factors vary over space and time, there is considerable heterogeneity in local fire regimes. In addition, there are widely varied responses and susceptibilities of different plant species to fire as a consequence of their varied life history strategies to disturbances of different kinds. In certain areas, plants have evolved with fire and have subsequently adapted to its effects. In these areas, the proportion of species which are easily killed is very low. They nevertheless exist and there is a continuum from those which are highly susceptible to those which are extremely resistant. The relative abundance of the two extremes on any site is a fair reflection of the fire history of the site (Walker, 1981 a). Most species are easily killed as seedlings and their resistance increases with age and size, up to a point where they become senescent and again susceptible.

Plants have evolved different ways to avoid damage by fire. Among the woody plants, some species are adapted to withstand fire by such characteristics as a thick, corky bark and others die back to ground level but regrow vigorously by coppicing. These strategies are often related to the type of substrate the plants occupy (Walker, 1981 a).

As a consequence of these variable fire regimes and the susceptibilities of plants to fire, the effects of fire on vegetation are highly variable.

There is ample evidence to show that fire retards the development of vegetation towards the climax state (West, 1971). Phillips (1930) identified that vast areas of Africa remain in a non-climax state as a result of fire.

Fire and other forms of disturbance frequently interact. For example, frequent fires keep woody plants at a certain height and in an acceptable state for browsers. The effect of the browsers is to reduce woody plant growth and keep plants within the size range most affected by fire (Trollope, 1974). In a similar way, the effects of flooding can interact with those of fire as well as those of herbivory to generate an overall fire, flood, herbivory regime.

3. Herbivory

Herbivory refers to the removal, for purpose of ingestion, of plant matter by both vertebrates and invertebrates. Herbivores consume and damage plant matter and are able to kill individual plants, particularly seedlings. At what point the removal of plant matter constitutes a disturbance is unclear but commonly is considered to be when such removal leads to the complete removal of a plant, its death, or when it seriously affects or retards the further growth of that plant.

The effects of large wild ungulates have been highlighted in most studies on herbivory, particularly when such studies are conducted in wildlife reserves where different types of domestic livestock are excluded. However, it must be emphasised that these are not the only nor necessarily the most important herbivores. Invertebrates such as grasshoppers and locusts, leaf cutting ants and harvester termites can also exert major effects in certain systems under specific conditions.

Herbivory is usually limited to particular plant species and plant parts, especially those of above ground nutritional quality. There is considerable variation between herbivores in the degree of selectivity in their diets, reflecting a complex interplay between the kind of animal, its body size and associated energy and nutrient requirements and the growth form, structure, chemistry and phenology of potential food plants (Frost et al, 1985). This selection for certain species of plant can have a significant bearing on the abundance and possibly even the presence or absence of certain species in a community.

Invertebrate herbivores tend to be more specialised feeders than vertebrate herbivores, and while they can have profound effects on the population dynamics of individual species, they do not seem able to control the physiognomy and life form of vegetation in the way that many vertebrate herbivores can (McNaughton, 1979).

Grasslands are prime examples of vegetation often controlled, manipulated and altered by grazing. Over the past decade it has become evident in South Africa that the heavy grazing of certain grasslands has led to the marked increase in the relative abundance of undesirable (unpalatable) grasses (Acocks, 1953). In an attempt to overcome this problem, much empirical work has been done on grazing management systems. Various systems have been recommended, in which the frequency, intensity and seasonal timing of grazing are altered in different ways by the application of different management activities such as differential stocking rates, use of fire and bush clearing.

Similarly, woody vegetation is also affected to a large extent by browsing. The effects of elephants on the woody vegetation : grass ratio have been recorded in many areas (Anderson and Walker, 1974; Thompson, 1975), while Anderson and Walker (1974) have described how the species composition of the woody vegetation has been changed by elephant. Taylor and Walker (1978), demonstrated that the density of small woody plants can be significantly reduced by browsers and this effect can result in a reduced density of all age classes present.

The effects of herbivory depend on six factors (Frost et al, 1985),

a. growth form of the plant,
b. specific plant parts removed,
c. intensity, frequency and season of use,
d. growth stage of the plant,
e. soil type and soil moisture conditions, which affect water and nutrient availability and thereby the plants capacity to grow, and
f. history of the plant, particularly the time since a previous occurrence of defoliation by other herbivores or other disturbances.

Since recovery from defoliation is not instantaneous, future events such as heavy rainfall, drought, or further defoliation by herbivores and fire can also influence the eventual outcome. Walker et al (1986) found that although the responses of grass growth to grazing, and other biological and environmental factors do affect the dynamics of mixed swards in grasslands, they are relatively insignificant compared to the effects of rainfall.

1.6.2.5 Repopulation of communities after a disturbance

Plant propagules are rarely able to invade and become established in areas densely occupied by other plants (Connell and Slatyer, 1977). Resident plants inhibit recruitment from propagules by simply engaging the space, by reducing the available supply of essential resources or by modifying site conditions in ways that inhibit the germination of these propagules.

One of the major principal effects of natural disturbance is to alter the availability of resources for plant growth. There are at least two mechanisms by which disturbance can temporarily increase the availability of light, water, and soil nutrients (Pickett and White, 1985). The first is simply the reduction in rates of uptake or use of resources due to the loss of biomass. The second mechanism is the decomposition and mineralisation of nutrients held in organic matter. In general there is a positive relationship between disturbance size or intensity and the availability of resources for plant growth. An important feature of any increase in resource availability produced by a disturbance is its transient nature. As biomass is re-established at the site, the relative availability of resources for future colonists will decline (Pickett and White, 1985).

According to Sousa (1984 a), the rate and pattern of re-establishment following a disturbance depends on a number of factors.

1. The morphological and reproductive traits of species present during disturbance. Such traits will determine the likelihood that these species will survive the disturbance and rapidly re-occupy the site.

2. The reproductive biology of species that occupy the site after the disturbance.

3. The characteristics of the disturbed patch which include,

    a. magnitude of the disturbance that created it,
    b. size and shape of patch,
    c. location and distance of patch from source of colonists,
    d. heterogeneity of its internal environment, and
    e. time it was created.

The resources made available by a disturbance are soon exploited by colonists and regenerating survivors, and a successional sequence of species replacements usually ensues (Noble and Slatyer, 1980). One or a few competitively dominant and/or long lived species come to monopolise the resources and hierarchical competitive interactions or differential longevities will eventually lead to the monopolisation of patch resources.

In attempting to explain patterns of species diversity Connell (1978) and Huston (1979) postulated a competitive equilibrium that occurs in the absence of repeated disturbance. However, both argue that due to the frequency of disturbance events in nature, such a competitive equilibrium is probably not a common occurrence and therefore the variation in species diversities that we observe among communities are the result of variation in the rate of disturbance (Connell, 1978) or of variations in the "dynamic equilibrium" between disturbance rates and the rates of competitive displacement among species (Huston, 1979).

1.6.2.6 The effects of disturbance on community dynamics

Two characteristics of communities are affected by disturbance.

1. Demography

The communities and sub-communities inhabiting different regions after a disturbance may differ in age or size structure. This may be due to the differential vulnerabilities of the particular components of the patch to the disturbance. This has the effect of over representing the size class which is less affected by the disturbance and under representing those classes which are particularly affected. An uneven demographic structure has important implications to the recovery and further development of a community and the rate at which this takes place. Should the occurrence of floods favour the large or mature size class at the expense of the juvenile class, recovery may be substantially shorter since the mature age class would be able to rapidly ensure a copious supply of seeds and offspring to reinstate a healthy age structure within a short time. However, should a flood event favour the juvenile size class at the expense of the mature size class, recovery is likely to be substantially longer with the eventual attainment of a competitive equilibrium and the growth and development of juveniles to mature trees.

2. Species diversity

Disturbance acts from this point to maintain within patch diversity by one of two mechanisms. (Connell, 1978; Huston, 1979; Abugov, 1982).

a. Compensatory mortality

According to the compensatory mortality hypothesis, compensatory mortality refers to the situation where the potential late successional dominant or species with the highest competitive ranking, suffers a disproportionately higher rate of disturbance related mortality compared to other species present. By this mechanism, competitive elimination of the less competitive species can be eliminated if not prevented indefinitely. This prevents the progression towards a low diversity forest which is dominated by highly competitive species, thereby maintaining a high level of diversity.

b. Intermediate disturbance

Connell (1978), Huston (1979) and Grime (1973) postulated an "intermediate" disturbance level at which most species could coexist and where diversity is highest. Intermediate disturbance refers to the situation where disturbance renews resources at a rate or intensity sufficient to allow for continued recruitment and persistence of species that would otherwise be excluded. The disturbance must occur with some intermediate frequency or intensity but it can be anywhere in the entire range of frequencies or intensities depending on the rate of competitive displacement. It is stated that periodic or recurrent disturbance at this intermediate level perpetuate pioneer and mid-seral species. Under these conditions, species with different life history strategies are able to coexist and consequently high levels of species richness are maintained. If the frequency/intensity of disturbance increases beyond this, only species (colonising species) with high growth and/or dispersal rates, the pioneer and mid-seral species, are able to exist. This represents an extreme represented by a low species richness. The other extreme would apply if the frequency/intensity of disturbance had to decrease. Here, only the highly competitive climax species which are better at maintaining resources would exist and equilibrium would eventually be attained. Other less competitive species would be excluded and consequently the species richness would be maintained at a low level.

Based on the intermediate disturbance hypothesis, Miller (1982) separately considered the intensity and frequency of disturbance events in the determination of species richness. Malanson (1984) modified this hypothesis to produce a three dimensional model of species richness in response to different degrees of both intensity and frequency of disturbances.

1.6.2.7 Disturbance and the stability and resilience of ecological systems

Ecological systems respond differently to the impact of disturbance or the combination of numerous disturbance events. Two types of ecological systems have been identified on the basis of their response to disturbance (Holling, 1973; Walker, 1980).

1. A stable system is one which is able to return to its equilibrium state after a disturbance. Stability therefore represents the ability of that system to reach this state. The more rapidly it returns and the less it fluctuates, the more stable it would be. Such a system shows little variability through time in the amounts of its state variables. This stability view of ecological system behaviour emphasises the equilibrium, the maintenance of the predictable world and the harvesting of nature's excess production with as little fluctuation as possible (Holling, 1973).

2. A resilient system is one which is able to absorb change and disturbance and still maintain the same relationship between populations or state variables Resilience is therefore a measure of the persistence of systems and their ability to absorb disturbance.

   A resilient system is usually not stable and the values of its state variables often change considerably when subjected to disturbance (Walker, 1980). More importantly, the parameters of the system which influence its dynamics also change, thereby redefining the boundaries within which the system remains attracted to its equilibrium point. The interaction of random events, along with other deterministic forces act to define the shape, size, and characteristics of the domain of attraction (Holling, 1973). According to Walker et al (1981), redefinition of the boundaries of the domain of attraction by disturbances allow for the easy accommodation of future disturbances of the same type.

1.6.2.8 Predictability of disturbance theory

General predictions concerning the diversity and composition of natural systems are made possible by applying the intermediate disturbance hypothesis and, if information is available concerning the growth rates of species present, by application of the dynamic equilibrium model. Both approaches clearly rely on predictions regarding either the frequency or intensity of disturbance events. The accuracy of such predictions are therefore dependent on the ability of scientists to predict the occurrence of disturbance events which are likely to have an impact on the system. The complexity of the disturbance regimes of different systems in turn determines the level of confidence which can be placed on these predictions.

Kovacks et al (1985) employed different prediction models in an attempt to determine the probability of different sized flood events in the Pongola river system. Essentially, such predictions are for the planning and construction of large bridges over the various rivers but this type of information can be used adequately, along with other information about the disturbance regime, to predict the structure and dynamics of riverine vegetation.

1.6.2.9 Failures of disturbance theory

The major failing of disturbance theory is the inability of scientists to predict 'catastrophic' or 'stochastic' events. Since these cannot be predicted, it is not possible to include such events in disturbance models. Events of this magnitude have a major effect on the structure and dynamics of ecological systems and consequently can substantially restrict the accuracy of predictions relating to vegetation structure and composition.

Another problem associated with the disturbance theory predictions is the need for long term data on the particular disturbance being investigated. Data of this nature is very seldom available. This is particularly true for the investigation of flood events. While flood gauging stations are strategically placed on the larger rivers of most catchments in the country, they have only been placed relatively recently and even then, large magnitude flood events tend to recurrently remove them. These factors reduce the accuracy of flood prediction models considerably.

1.6.3 Community organisation theory

A large number of different theories have been proposed regarding community structure and organisation and those factors responsible for structuring communities. The complexity of existing theories and their relationships under different resource and environmental conditions has plared community organisation theory into a state of confusion. In addition, it has been traditional to test existing theories independently instead of together or simultaneously, thereby further confusing the importance of these theories relative to each other. This largely explains the existence of different schools which support contrasting mechanisms in the organisation of natural communities.

Five community organisation hypotheses, which are central to the project and the approach adopted, are discussed below. These selected hypotheses, while they reflect an important component of the total number of existing theories pertaining to community organisation, do not cover the entire range extant in the literature.

1.6.3.1 Island size hypothesis

Documentation pertaining to the positive correlation between the species richness of an area and its size has been commonplace in ecological literature for the last fifty years (Preston, 1960, 1962 a; MacArthur and

Wilson, 1963, 1967; Williams, 1964; Simberloff, 1972; Schoener, 1976; Connor and McCoy, 1979; Gould, 1979; Strong, 1979; Schoener and Schoener, 1981; Martin, 1981).

The relationship between island size and the number of species occupying the islands has been most frequently investigated. MacArthur and Wilson (1963) proposed the equilibrium theory which considers species number to be the result of a dynamic balance between the independently or simultaneously varying immigration and extinction rates of species. This research led to the development of the area per se hypothesis by Preston (1962 a,b) and MacArthur and Wilson (1963, 1967) and the habitat-diversity hypothesis by Williams (1964).

The area per se mechanism posits that larger homogeneous areas support larger populations of each species causing lower extinction rates relative to immigration.

Due to the large quantities of data contained in the species lists from islands of varying size, use of the species-area relation assisted in simplifying these analyses by minimising the contributions of individual species. This approach was particularly justified by the taxonomically oriented researchers in the interests of documenting underlying general patterns.

The species-area relation is by no means confined to truly insular situations. Cairns and Ruthven (1970) applied the species-area approach to the relationship between volume of substrate corresponding to area and the number of freshwater protozoan species present. Similarly, the species-area concept has been used for numerous other reasons such as the investigation of arthropod species dynamics on Juniper plants (Ward, 1977) and the justification of conservation practices in large areas (Diamond, 1975).

Species-area curves have also been employed to determine optimal sample sizes for particular areas (Cain, 1938; McIntosh, 1967). The techniques involved are described in Mueller-Dombois and Ellenberg (1974).

In order to facilitate the prediction of species in larger areas and the comparison of different areas in terms of the species area relation, work has focused on the mechanistic descriptions of the relationship and on the biological explanations of variation in species area parameters. The comparison of numerous early species area curves revealed an asymptotic trend particularly for large areas (Fig. 1.1). Plant ecologists first attempted to elucidate the exact form of this curvilinear relationship by attempting to fit numerous mathematical models to this relationship. Preston (1962 a,b) emphasised firstly, the need for large samples (>100) in order to avoid the effects of contagion and secondly, that samples should be taken from areas as homogeneous as possible.

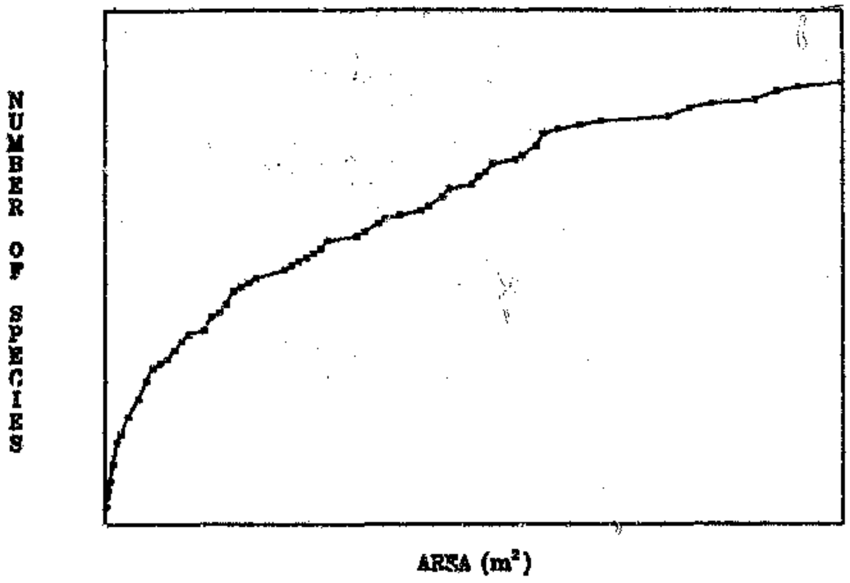


Figure 1.1 A typical asymptotic species area curve

In order to determine the best-fit model it has been common to transform either the independent and/or the dependent variable(s) in a regression analysis in order to transform a curvilinear relationship into a linear one and in so doing, allowing for an increase in the proportion of variance explained. The model displaying the highest r-squared value is then taken as the best-fit model (Connor and McCoy, 1979). By these means, the species-area relation is generally described as either an exponential one (Gleason, 1922),

$$S = \log k + z \log A$$

or a power function (Arrhenius, 1921),

$S = k A^z$ which is approximated by a double logarithmic transformation

$$\log S = \log k + z \log A.$$

Connor and McCoy (1979), analysed 100 species-area curves available from the literature, and concluded that the best-fit model for a particular species-area curve can only be determined empirically and that there is no conclusive best-fit model which fits all situations.

Due to its relative ease of interpretation and manipulation, however, the power function has naturally been preferred and since the work of Preston (1962 a), it appears to be the most uniformly accepted mathematical model giving the best statistical fit in most cases. The power function exponent (slope) describes the rate of increase in species numbers with area and often is the subject of comparative studies of different areas. The slope has been derived from species abundance models (May, 1975) and from MacArthur - Wilson equilibrium models (Schoener, 1976) and has been found to be relatively constant. For truly isolated areas involving large total species numbers, Preston (1962 a) predicted a value of 0,262 and considered values within the range of 0,17 and 0,33 to be within canonical range. MacArthur and Wilson (1967) defined the possible range to exist between 0.20 and 0.25. Schoener (1976) has extended the range acceptable for such areas to fall between 0 and 0,5. Gould (1971) hypothesised that it may be that only slope values deviating from this range possess biological significance and that slopes falling within this range indicate the lack of a functional relationship. On the basis of the equilibrium hypothesis, MacArthur and Wilson (1963) and Diamond (1973) interpreted that an adequate fit of the power function to observed species numbers implies the existence of a dynamic equilibrium between the immigration and extinction of species.

Numerous explanations have been proposed to explain the variations in slope values.

- Steeper slopes are more commonly found with the combination of random samples than with the continuous expansion in size of a single sample (Greig-Smith, 1964).

- Slope is negatively correlated with the degree of isolation (Connor and McCoy, 1979).

- The steepness of the slope is dependent on the size of the source pool of species (Schoener, 1976).

- The steepness of the slope is dependent on the size of the area (Martin, 1981).

Despite these numerous factors which can affect the degree of correlation between species number and area, the species-area relation has value. By removing and considering as many of these factors as possible, by standardisation of techniques and by recognising the basic assumptions, it may serve as a valuable analytical tool.

Connor and McCoy (1979), have reviewed the published usages and mis-usages of the species-area curves in the literature and detailed the ultimate value of the method for biological research. They believe such curves will be most useful in comparing diversities between geographical regions, habitats, or taxa over a range of sample sizes or between different sized samples. They can also be used to "factor out" the effect of area on diversity, so that the effects of other variables on species numbers can be determined.

1.6.3.2 Resource heterogeneity hypothesis

The resource/habitat heterogeneity hypothesis was developed by Williams (1964) as an alternative to the area per se (island size) hypothesis. Williams agreed that species numbers indeed increase with increasing area, that this increase is not a consequence of the increasing area per se, but as a consequence of the increasing abundances of habitats which become available for colonization as area increases. Therefore as the amount of area sampled increases, new habitats with their associated species are encountered and thus, species number increases with area. Since the inception of this hypothesis, Abele (1974), Harman (1972) and Dexter (1972) have all demonstrated a positive correlation between species number and number of habitats. Price (1984), focused on the simultaneous increase in resources with increasing habitat availability, and thereby renamed this hypothesis the resource heterogeneity hypothesis.

The relationship between the range of resources on a quality gradient, their quantity and the population responses to these resources can be graphically represented (Fig. 1.2).

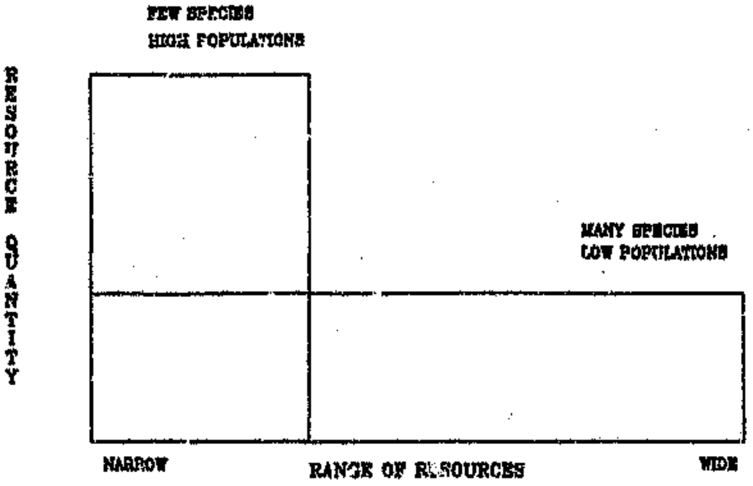


Figure 1.2 The relationship between range of resources on a quality gradient and quantity of resources, comparing two communities with the same amount of resources but distributed in different ways

Root (1973) proposed the resource concentration hypothesis which states that large bodies of a resource provides a concentrated resource for specialists which increases the attraction and accumulation of specialist species, the time they spend on the resource and their reproductive success. This hypothesis was developed mainly to explain the differences between the herbivorous insect populations which exist on pure grown and mixed grown crops but it serves as a converse to the resource heterogeneity hypothesis. Its essence is clearly explained by Figure 1.2.

1.6.3.3 Individualistic response hypothesis

The individualistic hypothesis was proposed independently by Ramensky (1924) and Gleason (1926). Prior to this, the Clementsian interpretation (Clements, 1916) also termed the 'community-unit' hypothesis (Whittaker, 1975) enjoyed wide support. This hypothesis asserted that vegetation is structured into well-defined natural units and that sharp boundaries (ecotones) exist between these community types as a result of competition between dominant species present.

The individualistic hypothesis therefore served as an alternative, asserting instead, the principle of species individuality. Namely, that the distribution of any plant species is a product of its own physiological requirements, genetic structure and tolerances, modified by the availability of resources that are subjected to competitive utilisation by associated species. Along the gradient, different communities integrate continuously as a consequence of the gradual changes in population levels of species along continuous environmental gradients (ecocline), thereby forming a complex continuum of populations (coenocline)

According to Gauch (1985) and Gauch and Whittaker (1972), the individualistic responses of species along an environmental gradient are explained by the Gaussian model of community structure, which is characterised by 12 proposed elements.

1. The abundance of each species along an environmental gradient generally form a bell-shaped, unimodal curve approximating the Gaussian (normal) curve. This curve has three parameters, a. the mode, b. the maximum value, and c. the dispersion in units of standard deviation. Given two environmental gradients, a species' distribution generally approximates a Gaussian curve along each gradient, together constituting a Gaussian response surface over the plane defined by the two gradients. This response can be extended to three or more dimensions.

2. The modes of species distributions are scattered individualistically along an environmental gradient and do not tend to be concentrated into groups of highly associated species with little overlap. Minor species are scattered at random but major species show regular spacing.

3. The maximum abundances of each species may form lognormal or lograndom distributions. Species maxima may be grouped into octaves, where each octave is a doubling of the maximum value. The two different

distributions may be considered as alternatives for different circumstances. A lograndom distribution is characterised by octaves on a logarithmic scale and therefore random allocation leads to approximately equal octave counts. A lognormal distribution involves a normal curve with logarithmic scaling of maximum abundances. This distribution is common, especially for communities with a large number of species.

4. Species dispersions vary, with some species restricted to narrow ranges along an environmental gradient and others occurring more broadly. Coenoclines involving numerous species have been found to have a set of species dispersions tending to form a normal distribution, with a standard deviation of about 0.3 times the average value.

5. Environmental gradients used as separate axes in direct gradient analysis may, in fact, not be entirely independent in their effects on the communities. Instead, there may be a partial correlation between gradients. There are three possibilities for the angle of rotation between gradients, which imply unique interactions between environmental gradients and species distributions. a. uniform orientation, with no interactions b. random distribution, with inconsistent interactions and c. normal distribution, with consistent interactions.

6. Correlations between the three parameters of Gaussian curves and the six parameters of the bivariate Gaussian surface do not appear to characterise field data along an environmental gradient.

7. A gradient of community composition (coenocline) can be characterised by the amount of species turnover from one end to the other. This property is termed 'beta diversity' and is expressed as the number of average standard deviations of species turnover along the gradient (SD). An alternative measure is the half-change (HC) which is equivalent to 1.34 SD ideally and approximately 1 with typical field data.

8. Community studies vary in the number of species which are encountered in a sample (alpha diversity) and in the total number of species encountered in the study (gamma diversity).

9. Gaussian species response surfaces can be modified by competition with other species. This may lead to the shouldering and skewing or flattening of the bell shaped curve (Fig. 1.3). Bimodal distribution curves may be evident within some taxa consisting of several ecotypic classes, as a consequence of biotic effects or in areas where recurring environmental features occur.

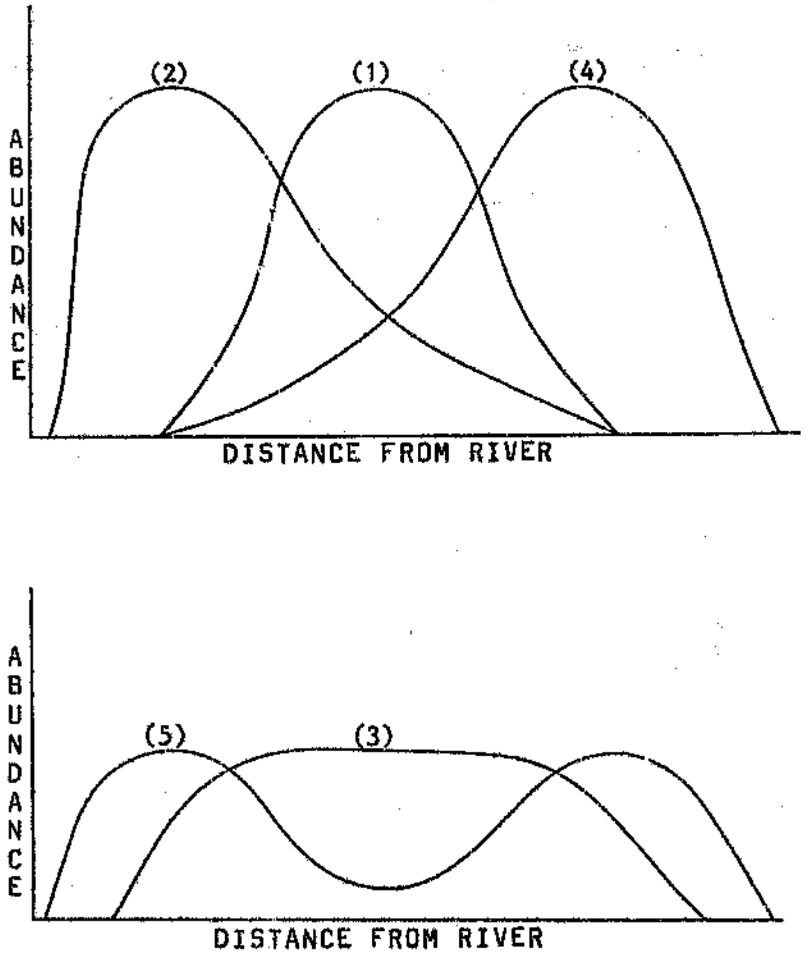


Figure 1.3 Diagrammatic representation of species distribution types

(1) Normal or Gaussian
(2) & (4) Skewed
(3) Platykurtic
(5) Bimodal

10. The flanks of Gaussian surfaces extend indefinitely and the point at which a species is absent (or very rare)in real field data is analogous to mathematically truncating the flank of a Gaussian surface at some small value.

11. Field data are noisy. Noise is seen when variations in one species abundance is not correlated with variations in the abundances of other species present. Field data vary in noise levels between replicate samples taken at the same position on the environmental gradient. A similarity measure between samples reflect low noise at 80 to 90 percent, medium noise at 70 to 80 percent and high noise at 50 to 70 percent similarity.

12. Patterns of sample placement within the community gradients present may vary. Various sample placement procedures can be modeled as a. random placement, b. placement in regular transects and grids, and c. deliberate placement in order to produce sample clusters or any desired pattern.

The central assumption of the 12 elements concerns the shape of the curve relating species' abundance to an environmental gradient, i.e. whether it is a bell-shaped Gaussian curve or is perhaps bimodal. If the majority of the curves are not Gaussian then many of the elements become inapplicable (Austin, 1985).

Austin (1976) determined the proportions of the different plant distribution types along an environmental gradient. He classified the distribution of species according to a. linear distributions, and b. non-linear distributions as either Gaussian, skewed, platykurtic or bimodal. He found that 95 percent were non-linear. Of this, only 26 percent displayed Gaussian distributions. The rest displayed platykurtic, and bimodal distributions.

The concerted work of Whittaker (1967, 1975), McIntosh (1967), Dansereau (1968), Gauch and Whittaker (1972) and Ellenberg (1954) led to the development of 'gradient analysis' as a method which deals with this apparent vegetation continuum and the various gradient relationships associated with it. The distributions of many species along gradients of important environmental factors are commonly displayed by means of 'direct gradient analyses' (DGA). Direct gradient analyses are essentially the study of transects, since these relate community gradients with environmental gradients (Whittaker 1966). It is accepted with this approach that a complex-gradient (Gauch, 1985) of many environmental characteristics exists and population distributions are observed in relation to one another along this complex-gradient.

Direct gradient analyses are often employed to investigate which environmental factor(s) in a range of factors principally affect the distribution of species. This is usually very difficult to assess at this level because many factors vary together and one cannot differentiate between the species and the positions they occupy on more than basic criteria. In addition, the primary factor itself is often a complex one and the exact contribution of each aspect is difficult to assess. Secondary environmental factors which do have some bearing on the distributions of species are difficult to identify because they are usually overshadowed by the primary gradient or gradients and they often involve relatively few species and samples of the data set (Gauch, 1982). Direct gradient analyses are useful when important environmental factors are readily appreciated and measured and when research purposes call for direct, integrated use of environmental data. It must be remembered that such analyses are only applicable with clearly evident environmental gradients and therefore has limited applicability in certain circumstances.

Many descriptive models of the individualistic hypothesis based on direct gradient analyses have been published but very few have ever been mechanistic. They do not provide clear statements about the shape of species response curves or indicate whether the curves might show continuum or community type patterns along environmental gradients. Shipley and Keddy (1987) suggested that direct gradient analysis suffers from the problem of using subjective methods of analysing the observed patterns by failing to use inferential statistics to compare empirical data to the proposed model. Austin et al (1984) stated that to date, direct gradient analyses have a. lacked an explicit sampling strategy, b. displayed a high rejection rate of samples, and c. lacked rigorous statistical analyses. They were among the first to apply a statistical approach with the application of generalised linear modeling (GLM) to investigate the relative importance of four environmental variables in predicting the presence of eucalypt species in an area. Shipley and Keddy (1987) pointed out that the use of this GLM technique can only be used to test between competing hypotheses concerning species ecological response curves but that this method cannot be used directly to test between the community-unit and individualistic concepts. After stating falsifiable hypotheses based on the predicted patterns of the individualistic and community-unit concepts, the observed patterns of boundaries along the gradient were compared to these hypotheses using an analysis of deviance (McCullagh and Nelder, 1983). Austin (1987) also quantitatively tested the distribution of the modes using a Chi-square test.

Whittaker (1966) proposed that plant species are so individualistic in their requirements that samples can usually be arranged according to their own floristic characteristics. The complex-gradient and the coenocline are coupled together in many ways, which allows for the contribution of each to the determination of the other. This process of arranging samples in relation to one or more gradients or axes of variation is termed ordination (Goodall, 1954) and forms the basis of 'indirect gradient analysis'. Here species and samples are arranged in a low dimensional space in such a way that similar entities are close by and dissimilar entities are far apart. Vegetation samples (or species) are arranged in relation to one or more ecological gradients and allow for the abstraction of axes that may represent environmental gradients. Loucks (1961) and Persson (1981), investigating moisture gradients, found that vegetation characteristics gave more effective ordinations than such factor gradient magnitudes as light intensity, soil water-retaining capacity and drainage. Needless to say, the ordination of samples on this basis is more cost-, time- and labour-effective.

Numerous authors have supported the use of a phytosociological weighted averages technique for basic ordination by means of vegetational characteristics (Dix and Smeins 1967, Whittaker 1951). This technique employs a phytosociological scale which is developed from using plants themselves as indicators of particular environmental characteristics such as drainage and temperature. Another method of basic ordination is achieved by means of end point sample comparisons (Whittaker, 1966) or polar ordination (Bray and Curtis, 1957). Here all samples are compared by means of an index of similarity (Sorensen, 1948) or dissimilarity (Bray and Curtis, 1957) with the end point samples. These two samples are considered as the two extremes of the gradient in question and therefore allow the other samples to be ordinated relative to these poles.

These basic ordinations and their algorithms serve as the basis for a large number of modifications such as that of Goff and Cottam (1967), who adapted the weighted averages method to develop an index iteration technique, which forms the basis of reciprocal averaging (Hill, 1973). Polar ordination has partial similarities, mathematically and functionally, to eigenvector ordinations such as principal component analysis (PCA) (Goodall, 1954), detrended correspondence analysis (DECORANA) (Hill, 1979) and other multivariate ordination techniques. These techniques, despite their basic similarities, are functionally very different and the differences in the quality of ordination results may be great for particularly difficult data sets and complex gradients. Very detailed reviews of these techniques can be found in Gauch (1985) and Greenacre (1984). Of particular importance, are the differences between these techniques in terms of the way they handle the so called 'non-linearity' problem (Swan, 1970). This effect is due to the fact that the different measures of similarity between samples which are employed by the different techniques are nonlinear functions of gradient separation. This leads to the distortion in the ordinations themselves thereby graphically displaying the gradient in different nonlinear ways.

To this point, acceptance of the individualistic hypothesis appears to have been based on accumulating circumstantial evidence provided by ordination methods. Few ecologists, applying an ordination approach to the individualistic and continuum concepts, proceed to an hypothesis testing phase (Austin, 1985). While doubt remains about the ecological meaning of the mathematical models used in ordination, exploratory ordination methods cannot provide unequivocal evidence for the continuum and individualistic concepts. Inappropriate ecological assumptions implicit in the mathematics of the method may produce an apparent continuum as an artifact of the method (Austin, 1980).

Consequently, ordination should be seen as an exploratory data-analysis technique that seeks pattern (trends, clusters or outliers) in a multivariate data set. The power of ordination techniques lies in their ability to generate hypotheses and/or summarise complex data in fewer dimensions.

1.6.3.4 Enemy impact hypothesis

Park (1948) displayed one of the earliest examples of enemy effects while studying the role of a parasitic protozoan species on the outcome of competition between two other protozoan species. Since then, Brower (1958) hypothesised that predators can effect the structure of prey species by limiting the similarity between them. These observations plus the supportive findings of Ricklefs and O'Rourke (1975) and Otte and Joern (1977), appear to form the framework of the enemy impact hypothesis.

Numerous biologists and ecologists have since published details about the effects of enemies and their organising and optimising roles in different communities. Paine (1969) described the organising role of predators in the marine intertidal community and Risch and Carroll (1982) described the effects of a predaceous ant on insect communities. McNaughton (1979) provided a substantial literature review pertaining to the compensatory growth upon plant tissue damage by herbivory and the subsequent adaptation of these plants to herbivores. Kemper (1984) found the hypothesis applicable while studying the effects of waterfowl on wetland vegetation.

In essence, the enemy impact hypothesis states that enemies have a significant impact on the structure of the particular population or community being investigated. The enemy may be defined as a predator, herbivore, parasite or any other organism which exerts an influence on the way the population or community is structured by utilising or feeding on it or its components. The exact structural changes which are experienced can be vast and depend on numerous factors,

- quantity and/or size of the enemy,
- extent of the community,
- number of individuals in the community,
- palatability or desirability of the individuals,
- accessibility of the community for the enemy,
- relationship between individuals of the community,
- life history strategies of the individuals,
- time of year, and
- equilibrium status of the community.

Lawton and Strong (1981) described the organising role of enemies on folivorous insects. This role was achieved by keeping the populations below those levels at which resources become limiting. The species richness in a community was limited to those that could be distinct enough not to be exploited by a common enemy and by selecting for the divergence of sympatric species in such a way that enemies were not shared.

By definition, this hypothesis does not include the effects of competition between two or more species for resources where the end result is the exclusion or displacement of the inferior species.

This hypothesis has received considerable attention and support recently (Lawton, 1978; Lawton and Strong, 1981) but its importance relative to other structuring forces in communities has not been adequately assessed.

1.6.3.5 Time hypothesis

The time hypothesis was initially pioneered by Southwood's (1961) study which displayed that species of trees in Britain with a more extensive fossil record, support more species of insects than those with a lesser record. Wilson (1969) supported these findings but included the role of interspecific competition in defining the final limit to this accumulation of species in an area.

These studies form the basis of the theory that species numbers in communities accumulate with time and consequently long established sites are characterised by more species than young sites. The hypothesis has been applied most frequently to evolutionary time as it ensures that species co-evolve and develop a more efficient means of coexistence, thereby allowing for more species to occupy an area (Lawton and Price, 1979).

Time, however, is also important in the ecological sense, as it takes time for species to accumulate after a disturbance or perturbation. Species accumulation studies such as those carried out by Simberloff and Wilson (1969), Davies (1973) and Price (1980) have identified an initial period of accumulation (non-interactive phase) which proceeds unhampered by interactions from resident species.

Monitoring and comparing the actual quantities of species which accumulate over a defined period of time assists to define the time hypothesis in its strict definition. The passing of time can be seen as a organising force in itself which is responsible for determining the structure of communities, regardless of the trends in species numbers.

Since the work of Southwood (1961), the time hypothesis has been considered in three different ways, each representing separate sub-hypotheses.

- Evolutionary time (non-competitive approach)

  Here time, in the evolutionary sense, considers the increase in species which accumulate at a site with the coevolution of species and the improved abilities of species to coexist in this time. No limit to the accumulation of species on an area or resource has been acknowledged.

  Evolutionary time (competitive approach)

  Once again evolutionary time is considered important, with interspecific competition determining the ceiling number of species which are able to accumulate at the site.

- Ecological time

  With this approach, because the time scales are far less, time since disruption or disturbance is of extreme importance. Continued disturbance or perturbation may maintain a community in a non-equilibrium state where the non-interactive phase is continually evoked and the limit to species accumulation is never reached.

It is important at this point to identify the differences which exist between the time hypothesis and succession theory. The process of succession, as envisaged by Clements (1916), is a detailed description of the recovery processes which occur after a disturbance. The time hypothesis is essentially much simpler in that it only proposes the accumulation of species numbers after a disturbance. No alternative mechanisms were proposed for the accumulation of species and no predictions were made regarding the resulting community, apart from the fact that it would be more species diverse than the starting point. This relative simplicity has major implications in terms of the ability to adequately test the theory.

1.6.3.6 Resource based community organisation approach

Price (1984) identified that there is a clear problem with the global application of existing theories on community organisation. Each theory has been developed under a very narrow range of resource conditions, where they have been found to have significant influence. In reality, however, there exists a large array of different resources and a vast diversity of organisms which exploit them. When considered in this light, the importance of these theories are placed into true perspective and the importance of certain theories are possibly de-emphasised. On this basis, there exists a clear need to devise studies to test among alternative hypotheses, so that we can determine the relative merits of each and their relative importance in communities of differing resource types.

In an attempt to overcome this problem, Price (1984) introduced an approach which concentrates on resources and the response of individuals and populations to these resources. The approach consists of three steps.

1. Price broadly categorised the resource types available into five temporal patterns. This was done as an effort to categorise a continuum of resource types. These temporal resource patterns are summarised in Figure 1.4.

   a. Rapidly increasing resources

      Resources which increase over much of the active season of the exploiting populations and then decline rapidly at the end of this season.

   b. Pulsing or ephemeral resources

      Resources which increase rapidly, then decline rapidly. Here only a short pulse of resources is displayed in a relatively long period of otherwise favourable conditions.

   c. Steadily renewed resources

      Resources that are produced for prolonged periods of time and are not readily overexploited.

   d. Constant resources

      Resources which are physical in nature and which are not influenced by seasonal change, exploitation or other factors.

   e. Rapidly decreasing resources

      Resources which are produced in a short period of time each season and subsequently decline through the remainder of the season.

2. The response of exploiters were categorised according to their responses to the five kinds of resources (while they persist). In order to depict the extremes in the range possibilities, they were regarded as either rapid or slow.

3. The spatial distribution of resources available were similarly categorised as either uniform or patchy in order to depict the extremes in the range of possibilities.

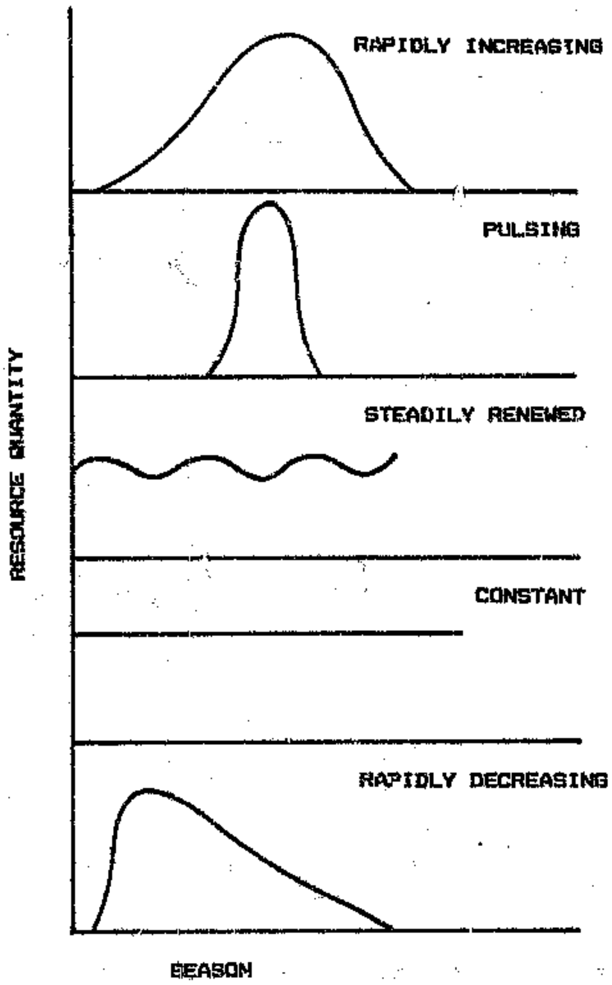


Figure 1.4 Five temporal resource patterns (Price, 1984)

Considering these categories of resource types, exploiter responses and the distributions of these resources, Price (1984) predicted the conditions under which each of five alternative hypothesis would apply and constructed a hypothesis summary table (Table 1.1). From this it can be seen that different hypotheses predictably have application under different sets of resource conditions and exploiter responses and that under a defined set of resource conditions, several hypotheses could display importance simultaneously.

The five hypotheses which Price (1984), considered were,

a. Island size hypothesis - ISLAND

This incorporates three sub-hypotheses, namely, the area per se, habitat diversity and the passive sampling hypotheses (ISLAND).

b. Resource heterogeneity hypothesis - RES HET.

c. Individualistic response hypothesis - INDIV.

d. Enemy impact hypothesis - ENEMY.

e. Time hypothesis - TIME.

This incorporates the ecological time scale, which has particular relevance and the evolutionary time scale (TIME). The effects of competition were also considered TIME (*).

Table 1.1 Hypothesis summary table showing predicted population responses of rapid and slow on a matrix of six different rates of resource change and spatial distribution of resources from uniform to patchy (from Price, 1984)

SPATIAL DISTRIBUTION	UNIFORM		PATCHY	
POPULATION RESPONSE	RAPID	SLOW	RAPID	SLOW
RATE OF RESOURCE CHANGE				
(A) RAPIDLY INCREASING	(ISLAND) TIME (*) ENEMY	INDIV (ISLAND) TIME	INDIV (ISLAND) TIME	INDIV (ISLAND) TIME
(B) PULSING (EPHEMERAL)	(TIME)	INDIV (TIME)	INDIV (TIME)	INDIV (TIME)
(C) STEADILY RENEWED	RES HET ISLAND TIME (*) ENEMY	RES HET ISLAND TIME (*) ENEMY	(ISLAND) TIME	(ISLAND) TIME
(D) CONSTANT	RES HET ISLAND TIME (*) ENEMY	RES HET ISLAND TIME (*) ENEMY	RES HET ISLAND TIME (*) ENEMY	(ISLAND) TIME
(E) RAPIDLY DECREASING	RES HET ISLAND TIME (*) ENEMY	RES HET ISLAND TIME (*) ENEMY	RES HET ISLAND TIME (*) ENEMY	(ISLAND) TIME

For further explanations of hypotheses, see relevant chapters.

This approach is unique in that it not only allows for the evaluation of the relative merits of each hypothesis but it also identifies the fact that more than one hypothesis can be applicable at any one time or on any one kind of resource, thereby permitting for a breakaway from the traditional trend for single hypothesis support in community ecology. This approach has value under conditions where numerous resource types and exploiter responses to these resources exists and allows for the determination of which hypotheses play the most important role under a defined set of resource conditions.

The approach has immediate appeal for application in particular areas as it offers to provide a firm understanding of the resources, exploiters and their responses, as well as the mechanisms responsible for structuring these communities.

Guidelines for application of the approach

Firstly, Price (1984) listed certain community qualities which are necessary in order to apply the approach successfully to a particular area in question.

1. Members of the community must be easily defined and recognised.

2. Resources must be easily measured at a level of detail relevant to the exploiting organisms.

3. The pool of potential colonists must be clearly defined.

4. The community and resources must be amenable to extensive experimental manipulation.

Secondly, Price (1984) described two methods by which communities should be selected for the approach.

1. At random, without any knowledge of the specific organisms present or how the resources are arrayed, so that no preconceived ideas hamper the objective testing among hypotheses.

2. By the use of coexisting phylogenetically related species in a community which allows for a particularly valid test of such hypotheses.

1.6 Study area

1.6.1 Brief description

The Natal Parks Board is responsible for administering the Umfolozi Game Reserve which lies between 28° 00' and 28° 26' S and 31° 43' and 32° 09' E in central Zululand, South Africa (Fig. 1.5). The reserve is 47 753 hectares in extent, and forms the southern part of the Hluhluwe - Corridor (State land) - Umfolozi Game Reserve Complex which has a total area of 96 453 hectares. The reserve is essentially located between the Black and White Umfolozi rivers, which enter the reserve from the west and flow eastwards, converging at the eastern boundary of the reserve (Fig. 1.6). All streams within the reserve form tributaries to the Black or White Umfolozi rivers.

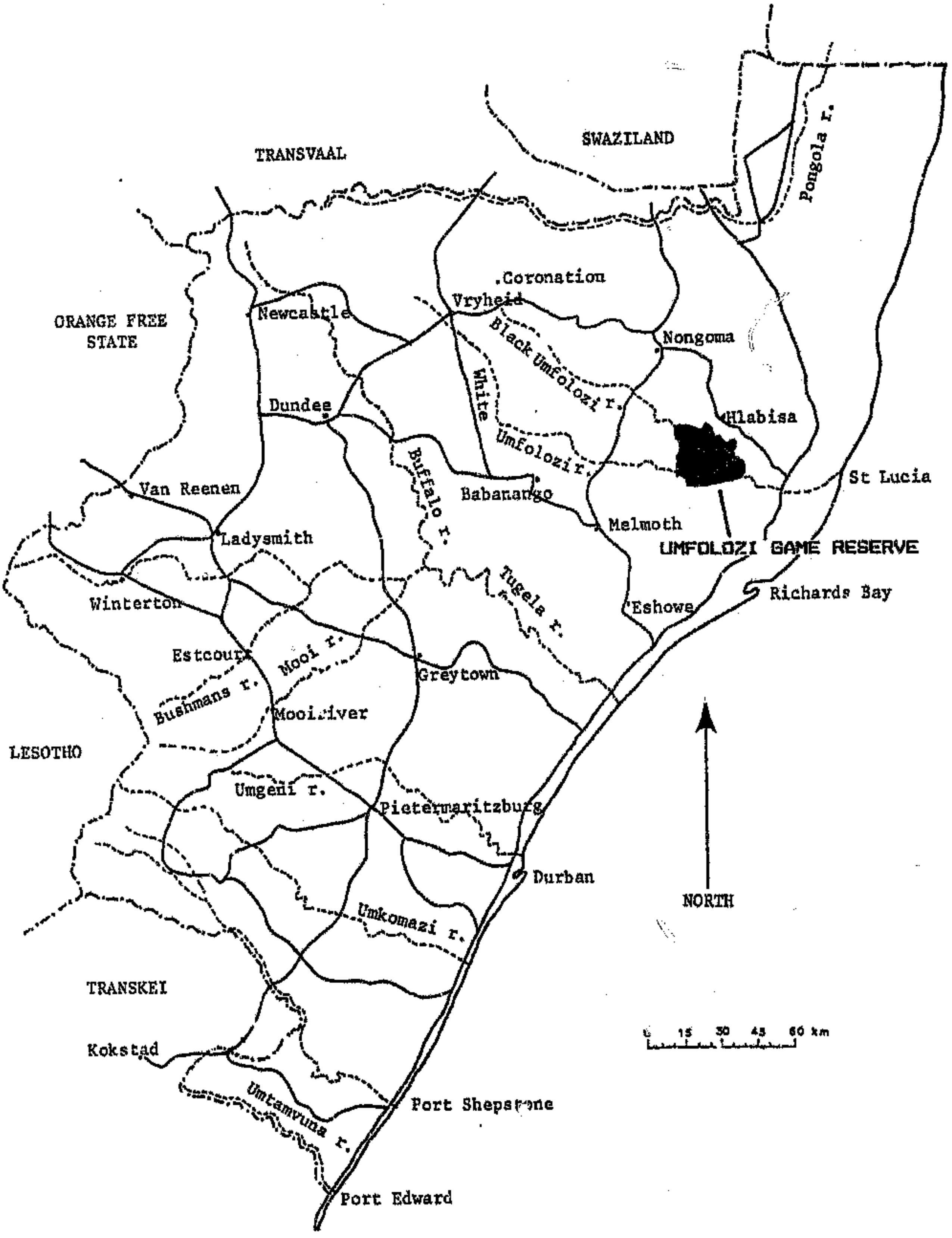


Figure 1.5 Map of Natal showing the location of the Umfolozi Game Reserve, the Black and White Umfolozi rivers and their catchment areas relative to major towns and rivers

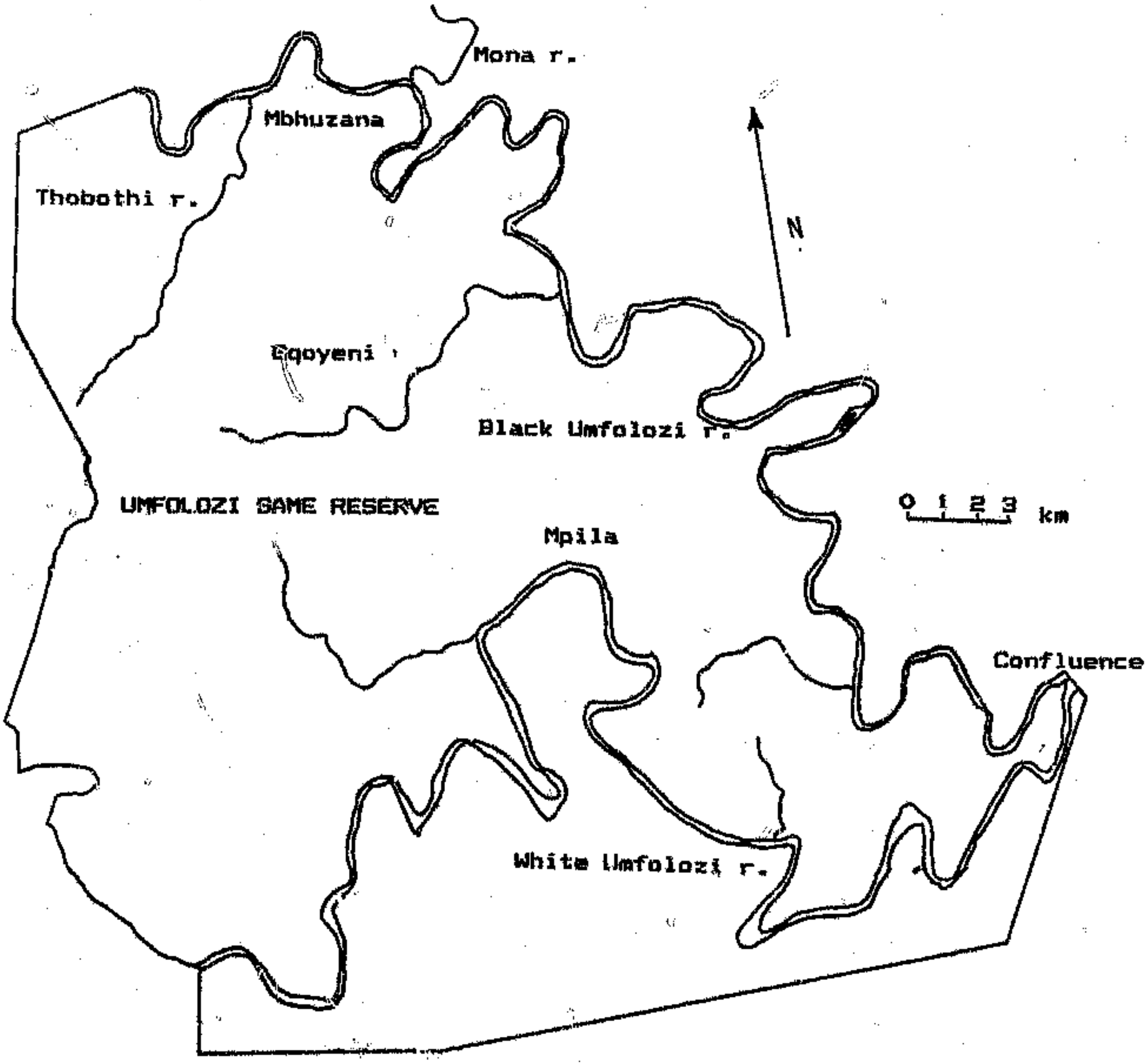


Figure 1.6 Map of Umfolozi Game Reserve showing the position of the reserve relative to the Black and White Umfolozi rivers and their major tributaries

The Black Umfolozi river has its major catchment in the area east of Vryheid and south of Coronation in northern Natal (Fig 1.5). It covers approximately 200 kilometers from its origin to its entry point in the Umfolozi Game Reserve. Within the Umfolozi Game Reserve, the Black Umfolozi river covers an approximate distance of 61 kilometers, which constitutes 122 kilometers of riverine habitat. It displays a meandering pattern at bankfull stages and floods and a braided channel pattern at low stages. The width of the river itself ranges from approximately 50 to 200 metres while the riverine habitat on its banks ranges from 20 to 500 metres. These widths depend on the topography and geology of the areas through which the river passes. The relatively steep banks and undulating topography of the riverine areas reflects a youthful river setting (van Heerden, 1984).

1.6.2 Topography, geology and soils

Two large valleys formed by the Umfolozi rivers have helped in creating a very diverse topography throughout the reserve. The riverine areas on the Black Umfolozi reflect this diversity. The riverine slopes vary from 2 to 35 degrees and display vertical displacements of between 8 and 32 metres (Appendix 1). The Black Umfolozi river has an eastward gradient of 0.6 m/km, while the flood plain areas of the river are generally flat.

The geology and soils of the reserve are variable and described in detail by Downing (1972). In brief, (Whateley and Porter, 1983), the largest area is covered by shales and sandstones of the Volksrust, Vryheid and Pietermaritzburg formations (Ecca series). Dolerite sills have intruded and are extensive in the reserve.

Swartland and Sterkspruit are the main soil forms associated with the Ecca series, whereas extensive areas of Shortlands as well as Milkwood and Bonheim series are found on doleritic areas. Shallow Mispah soils also occur extensively.

The riverine soils are largely characterised by unconsolidated alluvia which vary in depth from 20 cm to 8 metres. These alluvia are unstable and are easily removed and translocated by flood waters. Recent floods have carried larger sediment loads than average and have subsequently deposited large quantities of sediment on flood plain areas and point bars.

The Springfield, Kiaora, Mispah, Arcadia, Uitvlugt, Bonheim and Kentucky soil series characterise the higher lying riverine areas (MacVicar et al, 1977). A varied parent material of Ecca and Beaufort sediments and Basalt and Dolerite outcrops are responsible for the production of these soils.

1.6.3 Vegetation and climate

The Umfolozi Game Reserve lies within two veld types as described by Acocks (1988). Most of the area lies within the Lowveld subcategory of the Tropical Bush and Savanna Types and the remainder is Zululand Thornveld, a subcategory of the Coastal Tropical Forest Types. These areas correspond with bioclimatic subregions 9 and 10 as described by Phillips (1973).

Using the combined physiognomic descriptions of Zululand by Phillips (1973) and Pratt et al (1966), Whateley and Porter (1983) recognised the existence of two forests, two riverine forests, ten woodlands, one thicket, and one induced thicket in the Game Reserve Complex. Only fourteen of these communities are found extensively in the Umfolozi Game Reserve. These are,

a) <u>Celtis africana</u> - <u>Euclea schimperi</u> forest,
b) <u>Ficus sycomorus</u> - <u>Schotia brachypetala</u> riverine forest,
c) <u>Spirostachys africana</u> - <u>Euclea schimperi</u> riverine forest,
d) <u>Spirostachys africana</u> woodland,
e) <u>Combretum apiculatum</u> woodland,
f) <u>Euclea divinorum</u> woodland,
g) <u>Acacia karroo</u> woodland,
h) <u>Acacia nilotica</u> woodland,
i) <u>Acacia burkei</u> woodland,
j) <u>Acacia gerrardii</u> woodland,
k) <u>Acacia nigrescens</u> woodland,
l) <u>Acacia tortilis</u> woodland,
m) <u>Acacia caffra</u> thicket, and
n) <u>Acacia karroo</u> - <u>Dichrostachys cinerea</u> induced thicket.

The <u>Ficus sycomorus</u> - <u>Schotia brachypetala</u> riverine forest is confined to the banks of the large rivers and their major tributaries in the area where extensive but narrow stands are to be found. <u>Ficus sycomorus</u>, due to its size, is the most prominent tree, while <u>Schotia brachypetala</u> has the highest frequency. Three canopy strata are readily distinguishable with ceiling heights of 3-4 metres, 6-10 metres and 15-20 metres for the lower, middle and upper strata respectively. This riverine forest community is well utilized by herbivores and is particularly important as a food source during the dry winter months.

The <u>Spirostachys africana</u> - <u>Euclea schimperi</u> riverine forest occurs throughout the area as a narrow strip along seasonal water courses. Three canopy strata are distinguishable, with the top stratum reaching a height of 8 metres. In this community, 64 tree species were recorded with heights of excess of 2 metres, while 53 species were recorded with heights of below 2 metres.

Rain falls mainly in the summer months from October to March, with January and February being the wettest months. Winter is very dry with June and July generally being the driest months. The Umfolozi Game Reserve has a mean annual rainfall of 720 mm (Whateley and Porter, 1983). A definite precipitation gradient exists from high rainfall in the east of the reserve (705 mm mean annual since 1959 - Mpila camp) to low rainfall in the west (632 mm mean annual since 1982 - Mbhuzana outpost) (Venter, 1988).

Recorded mean maximum air temperatures range from a minimum in June/July of 25 degrees to a maximum of 32.9 degrees in February. The corresponding minimum mean temperatures for these months are 13,2 and 21,6 degrees respectively (Venter, 1988).

being the driest months. The Umfolozi Game Reserve has a mean annual rainfall of 720 mm (Whateley and Porter, 1983). A definite precipitation gradient exists from high rainfall in the east of the reserve (705 mm mean annual since 1959 - Mpila camp) to low rainfall in the west (632 mm mean annual since 1982 - Mbhuzana outpost) (Venter, 1988).

Recorded mean maximum air temperatures range from a minimum in June/July of 25,3 degrees to a maximum of 32.9 degrees in February. The corresponding minimum mean temperatures for these months are 13,2 and 21,6 degrees respectively (Venter, 1988).

CHAPTER 2 APPROACH BASED ON SUCCESSION THEORY

This chapter addresses a currently adopted view of succession theory with the aim of testing it and highlighting its uses and its limitations in elucidating the structure and dynamics of riverine vegetation.

2.1 Introduction

Briefly stated, succession theory postulates that after a disturbance such as the cyclone Domoina floods, riverine vegetation recovers by means of the migration of propagules to the recently denuded site, the colonisation and establishment of species and the sequential replacement of these species by means of reaction and competition. By this process there is a progressive, deterministic and convergent development of the vegetation towards a stable climax state via one of three species replacement mechanisms, namely, facilitation, tolerance and inhibition. The impact of further disturbance during this process brings about the retardation of further development and returns the system to a state which was previously attained. Development proceeds in the same manner, thereafter, unless disturbed still further.

Succession has previously been described in the riverine communities of the Black Umfolozi river (Downing, 1972). However, this study was purely descriptive and almost restricted to succession on completely denuded areas. Secondary succession was described only superficially.

Considering the paucity of successional studies of the Umfolozi riverine vegetation, the possible role of succession in riverine areas is unclear and remains to be elucidated. Particularly in terms of its importance in structuring riverine communities, the various successional pathways associated with recovery after a disturbance, the characteristics of the various vegetation states and the importance of disturbance in re-initiating the entire successional process. The aim of this approach was to address these issues with a view to assessing the merits of applying succession theory to understand the structure and dynamics of riverine vegetation.

Due to the limited availability of data on Umfolozi riverine vegetation and the long time periods associated with collecting such data sets, this study was confined to snap-shot approaches only. Three distinct approaches were possible. a. Substitution of space for time using present day communities in various stages of recovery. b. Comparison of field data collected in the past. c. Comparison of past sets of aerial photographs. The latter two approaches were essentially retrospective in nature.

2.2 Objectives

The objectives of this approach were as follows.

1. Test succession theory in riverine areas by means of several distinct successional approaches.
2. Determine the characteristics of the major vegetation states, pathways and components which are evident during succession in riverine areas.
3. Determine whether adopting a successional approach is practicable for determining and predicting the structure and dynamics of riverine areas.

2.3 Methods

2.3.1 Substitution of space for time

This study was based on the assumption that present day riverine communities (1986) are represented by spatially separated communities which display a range of seres and ages since their last major disturbance. These differently aged communities exist as a consequence of the differential protection afforded to them, due to their unique locations relative to different past flood events and the variable characteristics of these floods. Since the Umfolozi river follows a distinct meandering course and the topography of the area it passes through is extremely variable, a large number of highly protected refugia exist. These refugia undoubtedly support communities which reflect different disturbance histories. It was anticipated that it would be possible to analyse the vegetational composition of these communities, identify their characteristics as they exist in the present day and relate these to their estimated successional ages. Thereafter it would then be possible to order the various seres present on the basis of their successional ages and eventually reconstruct a complete successional sequence.

Location of sites and community age determinations

Five separate sets of aerial photographs have been taken of the Black Umfolozi river. These were taken in 1937, 1954, 1960, 1973 and 1983. These photographs were sorted according to their year of origin and river positions. Densely forested areas were located on the photographs. These areas were considered to be communities in an advanced stage of recovery and their positions and relative sizes were separately mapped for each set of photographs. The mouths of tributaries which open into the Black Umfolozi river were excluded because, although these areas also have the ability to support climax communities, they are disturbed recurrently by relatively small flood events experienced within the tributaries. This recurrent disturbance, of unknown frequency, made it difficult to determine the approximate age and successional status scores of these areas. Finally, all five maps were overlaid to identify those riverine areas where climax stands display the potential of development due to their specific substratum and resource characteristics. Fifty eight areas were identified and numbered sequentially. The locations of these climax potential sites were mapped for all the sampling dates available and transcribed onto a single 1:50 000 map of the reserve.

For all sets of photographs the communities which occupied these areas were carefully examined visually to determine their successional status score on a five-point scale. This was done on the basis of the relative proportions of three discernible vegetation states according to the status score table (Table 2.1).

Table 2.1 Status scoring table. Approximate successional status of potential climax riverine areas on the basis of the relative proportions of three vegetation classes

PROPORTION STATE 1	PROPORTION STATE 2	PROPORTION STATE 3	SUCCESSIONAL STATUS	
(GRASS/HERB)	(SMALL TREES)	(LARGE TREES)	SCORE	STATUS
LOW	LOW	HIGH	5	CLIMAX
LOW	MEDIUM	MEDIUM	4	MIDDLE/CLIMAX
LOW	HIGH	LOW	3	MIDDLE
MEDIUM	MEDIUM	LOW	2	EARLY/MIDDLE
HIGH	LOW	LOW	1	EARLY

The latest (1986) photographs were then scrutinised to determine whether any of these sites still supported mature forested stands after the Domoina floods. In order to determine the approximate dates when each existing community was last disturbed and, therefore, its successional age, the status scores for each community were related with available flood history records. The successional age of each community was taken to be the number of years that elapsed since each community was last disturbed extensively. Whether a community was disturbed or not was identified subjectively by changes seen in the vegetational cover, density of trees and size of the community as seen from the aerial photographs available. This value should not be considered as accurate but should be used as an indication of successional age.

All communities were then ordered by their estimated successional ages. They were then visited and assessed as follows. Woody individuals present were identified, counted, and placed into one of three height categories a. less than 2m, b. 2m to 7m and c. greater than 7m. The height of the trees was assumed to adequately reflect the age structure of the trees present. The age structure and species compositions of these stands were then analysed in terms of the species present, the contribution of each species to each of three size classes and the percentage contribution of each size class. The community age structure was then related to its estimated successional age as determined earlier. On this basis an attempt was made to construct a whole successional sequence which revealed the participating species and their dynamics over time.

2.3.2 Retrospective approach using PCQ data of a single site collected on different occasions

This approach was based on the comparison of detailed vegetation data collected at one riverine site on three separate occasions. It was anticipated that since a large flood separated the first two occasions(1979 and 1984), and a reasonable time span separated the last two (February 1984 and September 1986), this would allow for the identification of the species associated with a reasonably mature sere as well as two separate early seres. In addition, it was hoped that information may be gathered concerning the mechanisms responsible for the succession of species.

Quantitative data was available from a description of the woody communities of the Umfolozi Game Reserve which was carried out by Whateley and Porter (1983). Their description of the riverine community was obtained from a point centered quarter (PCQ) transect placed in a community (Thumbu river mouth) which to their mind, best represented a mature riverine community at the time. In 1984, immediately after the cyclone Domoina floods, another PCQ was carried out at the exact position using the same technique. These two data sets served as a reasonable comparison of riverine community composition from before and after the floods. The further collection of data from 1986 (two years after Domoina floods) was necessary to allow for a comparison between three different stages of succession in the same area. Firstly, immediately after disturbance (1984), secondly, in the early stages of recovery (1986), and thirdly in a relatively advanced stage of recovery towards the climax state (1979).

a. PCQ technique and data collection

The point centered quarter (PCQ) transect was conducted in the area west of the Gqoyeni mouth where similar transects had been conducted on two previous occasions by Natal Parks Board personnel (1979 and

1984). In order to facilitate accurate comparisons between the results of the three transects, it was ensured that the exact transect placements and techniques employed were identical to those used previously (Whateley, A.M., pers. comm.[1]).

The technique employed was adapted from that described in Mueller-Dombois and Ellenberg (1974). Fifty PCQ sampling points were spaced at 50 m intervals at a distance of fifty metres from the river's edge. In each quarter, at each sampling point, the nearest woody individuals were identified and recorded. In this approach it was not necessary to distinguish between individuals of different size classes.

The frequency of occurrence of each species was then determined according to the method outlined in Mueller-Dombois and Ellenberg (1974). As the number of sampling points used for the PCQ differed slightly for the three monitoring sessions, accurate comparisons between the three sessions called for standardisation of the data with a correction factor based on the minimum species frequencies obtained for each sampling date.

b. Data analysis

PCQ results were analysed and compared using correspondence analysis. Here, through necessity, the species frequency data from all three monitoring sessions were treated as active and no supplementary data sets were employed. Both the year of data collection and the species present were presented graphically on the same set of axes to represent a successional sequence of riverine species over time. The interpretation of this data rested on the assumption that, given a chance to recover, the succession of riverine vegetation would proceed along the same deterministic species pathways each time and terminate in the same climax state.

2.3.3 Retrospective approach using aerial photographs

This approach relied on the use of aerial photographs, from as many different occasions as possible, in order to compare the proportions of the different riverine vegetation states on each occasion in response to different disturbance events.

Five separate sets of aerial photographs have been taken of the Black Umfolozi River. These were taken in 1937, 1954, 1960, 1973 and 1983. Despite the fact that these sets of photographs have different scales and qualities, they did offer sufficient detail which could be used to

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[1] A.M. Whateley, Yew Tree cottage, Skinners Lane, Chiddingfold, Surrey GU8 4XT

compare basic vegetation states from year to year and to locate and identify communities with different proportions of vegetation classes. In order to construct a successional gradient, represented by different stages of recovery after disturbance, a further set of photographs was required of the same areas post Domoina. These photographs were taken using the technique described below. Correspondence analysis was then used to order the different years according to the proportions of the various vegetation states they displayed.

A Markov model was then used to determine the probabilities of transition from one state to the next, the final equilibrium proportions of these states and the length of undisturbed time required to attain these proportions.

a. Post Domoina aerial photographs

De la Harpe (1983) perfected a mounting bracket suitable for a 50mm camera which is suitable for the collection of aerial photographs from a Cessna 150, 172, 182 or 210 aircraft. A Cannon A1, 35mm camera was found to fit this bracket with minor modifications. The approximate height of the aircraft was determined using the following basic formula (Lo, 1976).

$$\text{Height of aircraft (m)} = \frac{A \times B}{C}$$

where: A = maximum linear dimensions of site (m)
B = the focal length of the lense (mm)
C = the size of the film (e.g. 35mm)

Only a 35mm camera was available at the time of the flight. This posed a problem, as the smaller the film size, the larger the size of the grain on the final product, particularly when enlarged to a manageable size. It was therefore necessary to keep the site dimensions as small as possible, but with due consideration of the negative effects of grain size on community detail. This required the very careful and efficient determination of flight paths for the aeroplane to follow in order to capture the entire length of the river as well as the riverine strip on both sides of the river. The camera lense was taped securely in the infinity position and the camera shutter speed set at 500th of a second for all photographs. The films were processed and final prints were made as large as possible without introducing unnecessary grain. These were finally produced to a size of 30x15 cm. Photograph scales were then determined by comparison with true ground distances between various points.

b. Location and sampling of aerial photographic sites

Using a zoom transfer scope, seventy two quadrats (100x150 m) were randomly located in the riverine areas of the Black Umfolozi river on a set of aerial photographs of the Umfolozi Game Reserve. The same quadrats were located on five other sets of photographs which were all taken on separate occasions since 1937. Within each quadrat the abundances of four discernible vegetation states were visually determined according to a five-point scale. These vegetation states were

a. grass/sand (GRASS),
b. reeds (REEDS),
c. Acacia spp. and other small trees (ACACIA),
d. Ficus sycomorus and other large trees (FIGS).

The mean abundances of each vegetation state were then determined for each year represented.

c. Data analysis

These proportions of the four vegetation states were then compared from year to year using correspondence analysis. All data were treated as active and no supplementary rows were used. The correspondence analysis results were presented graphically with both the years and the vegetation states investigated being placed on the same set of axes to represent the successional replacement of vegetation over time. The numerical output of the analysis was prepared as an appendix.

d. Markov model

The Markov model was constructed according to the procedure described by Jeffers (1978). These are briefly described. Using the quadrats previously laid out on the six sets of available aerial photographs, the estimated probabilities for the transition between the four vegetation states were determined for the five time steps investigated. These probabilities (which add up to 1) were then placed into the required matrix form.

Using a computerised spreadsheet, the matrix was then repeatedly multiplied by itself until a state was reached at which each row of the matrix appeared the same as every other row, constituting a fixed probability vector. The fixed probability vector gives the limit at which the probabilities of passing from one state to another are independent of the starting state and expresses the final equilibrium proportions of the various states which will eventually be attained after an undisturbed period. Important to this hypothesis is the time which is required for equilibrium to be reached. This was determined from the number of times the matrix was multiplied by itself to arrive at the fixed probability vector, multiplied by the time step between the two years investigated.

The final equilibrium proportions and the times necessary to reach them were determined for the five time periods available for study. The predicted equilibrium proportions were then applied to the above correspondence analysis as supplementary rows.

2.4 Results

2.4.1 Substitution of space for time

Figure 2.1 (A+B) displays the locations of the 58 potential climax community areas on the Black Umfolozi river and their approximate sizes as identified from the six available sets of aerial photographs. The length and width of these areas vary considerably. Ground truthing revealed that these areas are often located on alluvial flats composed of deep sand. They rarely occur on rocky slopes or areas with a shallow substratum.

Table 2.2 displays the successional status scores for each of these communities for each sampling date as identified using the status scoring table (Table 2.1). The individual scores for the different areas vary according to the effects of flood events and the susceptibility of each area to floods. Areas which are sheltered from particular flood events show little change in their scores, while susceptible areas display a reduction in score. The absence of floods for a lengthy period would lead to a gradual increase in these scores. The mean score is therefore a reflection of the successional status of all of these communities at the time of sampling. An extensive or disruptive flood may therefore have the effect of reducing this score and, consequently, the successional status of the communities. The Domoina flood was responsible for the complete destruction of 65 percent of these potential climax communities. In 1983 these communities reflected a mean successional status score of 3.9 (mid/late status) while, after the flood, this figure was reduced to 1.3, thereby placing it into the early successional status.

Figure 2.2 displays the relative percentage contributions of the 5 status scores for each of the sampling dates. The approximate positions of particularly disruptive flood events are arrowed, relative to the 6 sampling dates examined, to assess their effects on the successional status of the communities. The years 1954 and 1960 displayed large proportions of mid/late and late status communities with very small proportions of

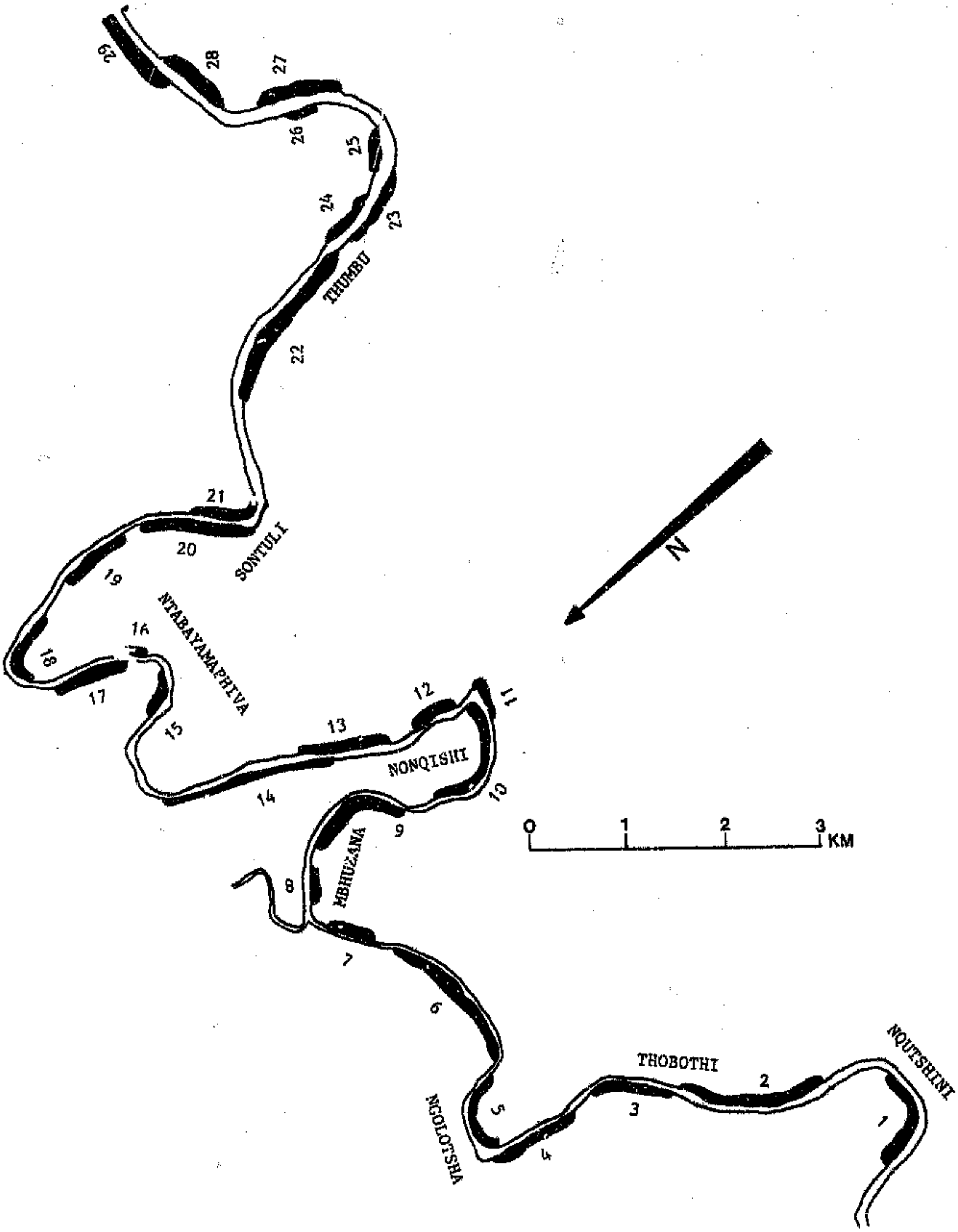


Figure 2.1 Map of the entire Black Umfolozi riverine area within the Umfolozi Game Reserve showing the locations and approximate sizes of the 58 climax potential stands as identified from aerial photographs

(A) Climax Potential Stands 1 to 29

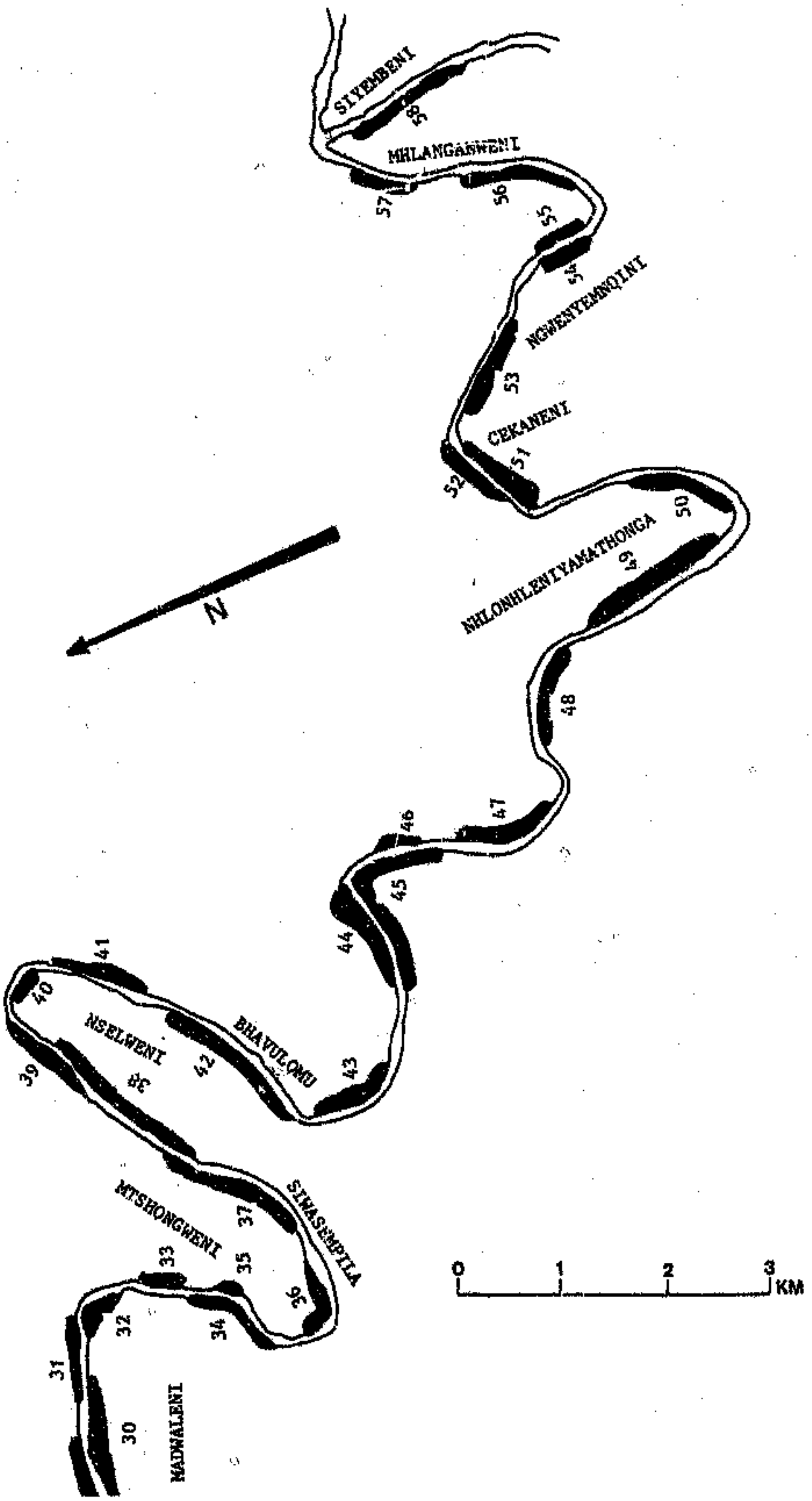


Figure 2.1 continued

(B) Climax Potential Stands 30 to 58

Table 2.2 Successional status scores for each of the 58 potential climax communities as obtained from six sets of aerial photographs

	COMMUNITY NUMBER																												
YEAR	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
1937	1	1	2	2	2	4	3	3	5	3	2	3	5	4	2	1	4	3	4	4	3	3	3	3	3	1	2	3	3
1954	5	5	4	4	4	4	4	4	–	–	–	–	–	4	–	–	–	–	–	–	–	5	4	5	5	3	4	4	5
1960	–	–	5	5	4	5	4	5	5	5	3	5	5	5	4	3	3	4	5	5	4	5	4	5	4	4	4	5	5
1973	–	–	4	5	5	4	4	4	5	4	4	4	5	5	3	3	3	–	4	5	4	5	4	4	4	4	3	4	4
1983	5	4	5	5	4	5	4	4	5	4	5	4	4	5	4	3	3	4	5	5	2	5	4	4	3	3	2	3	4
1986	1	1	1	3	1	1	1	2	1	2	1	1	2	1	1	1	2	1	1	2	1	2	1	1	1	2	1	1	2

	COMMUNITY NUMBER																													
YEAR	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	MEAN
1937	4	2	1	1	5	2	2	4	3	4	2	3	4	3	3	3	3	4	3	3	3	3	4	5	4	4	4	2	5	3.02
1954	3	4	4	4	5	5	4	5	5	5	4	5	5	5	5	4	5	–	–	–	–	–	–	–	–	–	–	–	5	4.31
1960	4	4	4	4	5	4	5	5	5	5	5	5	5	5	5	5	5	5	4	4	5	4	5	4	4	4	5	[illegible]	[illegible]	4.54
1973	4	3	2	3	5	4	3	5	5	5	2	3	4	4	4	4	3	4	3	4	4	4	4	4	[illegible]					
1983	3	3	3	3	4	4	4	5	5	5	4	4	4	4	5	4	2	3	3	4	4	4								
1986	1	1	1	1	2	2	1	2	1	2	1	1	1	1	2	1	2	1	1	[illegible]										

mid-successional communities. The years 1973 and 1983 displayed the appearance of early/mid and larger proportions of mid and mid/late status communities at the expense of late status communities. This reduction in the successional status was a consequence of the effects of 2 floods before 1973 and a further 2 before 1983. After the 1984 and the 1985 floods only early and early/mid status communities were represented. This reduction in successional status of the communities from 1954 to 1986, as seen by the reduction in mean status scores, reflects the general degradation of climax status communities to early status communities, due to the effects of a number of extensive flood events.

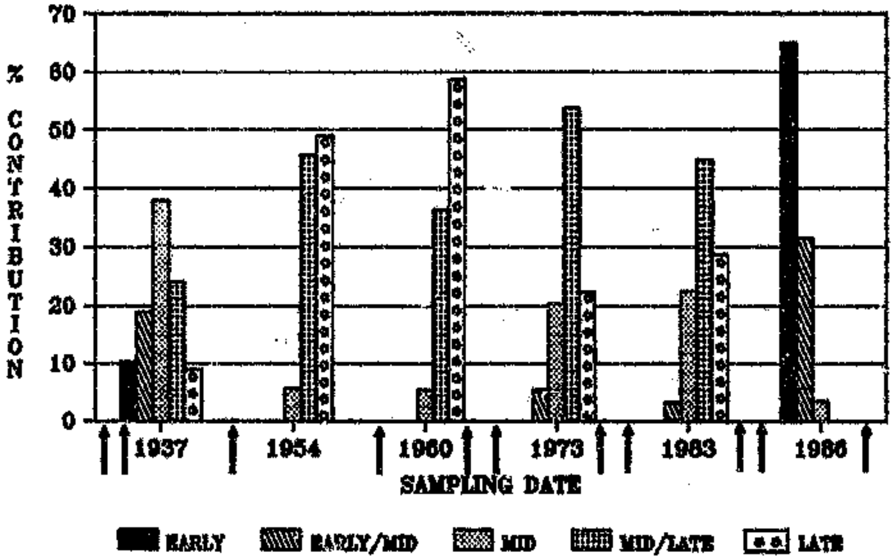


Figure 2.2 The percentage contributions of each of five status scores for six sampling dates investigated. The positions of particularly destructive flood events are arrowed relative to the years examined

According to Table 2.3, in 1986 a total of 38 communities (65%) exhibited early successional status while 18 communities (31%) exhibited early/middle successional status. The mean successional ages for these 2 communities were determined to be 4.3 and 16.5 years respectively. The disruptive force of the Domoina flood left only 2 communities (3.4%) which exhibited status ratings above middle successional with status scores above 3, community 4 - score 3 and community 58 - score 4. These were visited and their age structures were determined.

Table 2.3 The abundance and percentages of the 58 communities which exhibited each of the 5 successional status scores as well as the mean estimated successional ages of these communities

STATUS SCORE	NUMBER OF COMMUNITIES	PERCENTAGE	MEAN ESTIMATED AGES (YEARS)
1	38	65.5	4.3
2	18	31.1	16.5
3	1	1.7	50–60
4	1	1.7	> 60
5	0	0	–

Attaching reasonably accurate successional ages to middle and middle/climax communities was difficult due to the absence of aerial photographs from before 1937. Community 4 was considerably disturbed by the 1924/5 floods and was still in an early/mid stage of succession in 1937 and it was estimated that the large trees remaining from the Domoina flood were in the region of 55–60 years old.

Community 58 was estimated to be even older than this due to the fact that it was not considerably damaged by the 1924/5 floods and was still in a late successional state in 1937. When sampled in 1986, some of the _Ficus sycomorus_ individuals were as much as 1.5 to 2 metres in diameter with heights in excess of 20 metres.

Figure 2.3 displays the age structure for community 4 for three size classes. This community was given a status value of 3 (mid-successional). However, the major proportion of woody species present are from the juvenile size class with the second size class only contributing 19 percent to the total. The third size class is barely evident. The size class contributions of each species (Fig. 2.4) show that five species contribute to the second size class, while only one species, _Ficus sycomorus_, contributes to the third size class. Apart from this, the community is clearly in an early successional state due to its large proportion of seedlings of different species and individuals under 2 metres in height.

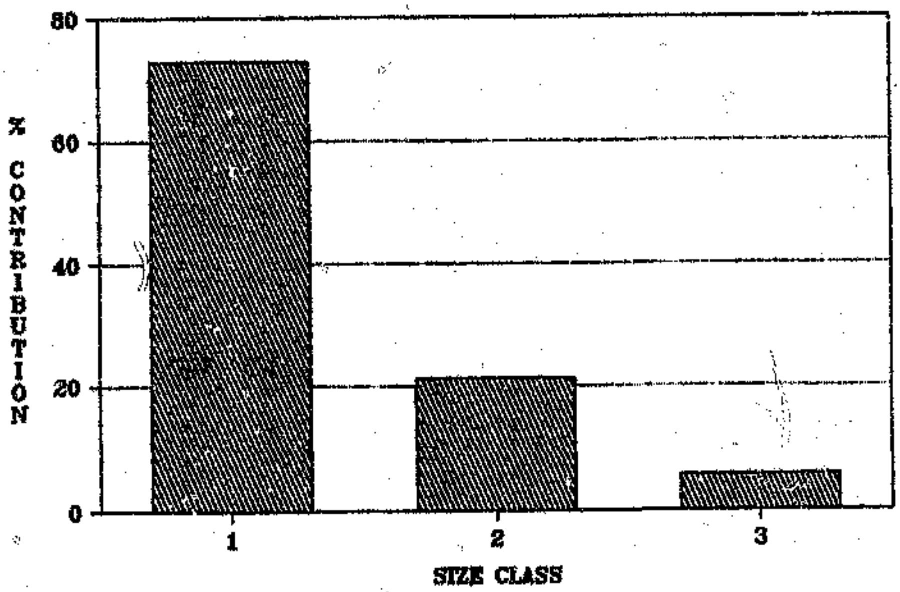
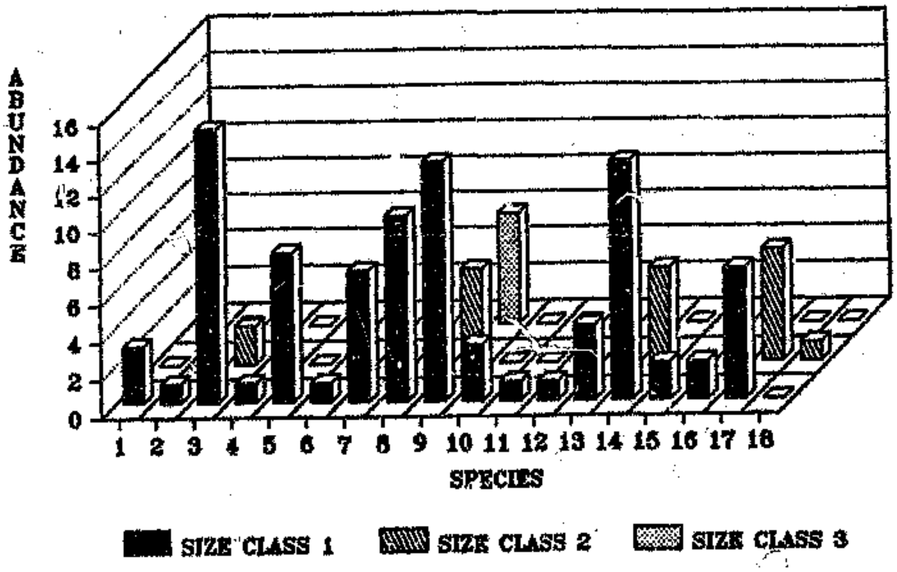


Figure 2.3 The age structure of community 4 on the basis of three size classes

The corresponding age structure for community 58 (Fig. 2.5) reflects that both the first and the third size classes are strongly represented while contributions to the second size class are poor. The size class contributions of the component species to the general age structure of this community (Fig. 2.6) shows that only two species, Ficus sycomorus and Rauvolfia caffra, contribute significantly towards the second and third size classes. The majority of species present represented the juvenile size class.

The comparison of age class distributions for three apparently different stages of riverine succession are displayed in Figure 2.7. The initial scrutiny of the aerial photographs succeeded in separating the different areas according to the different abundances of the three size classes as envisaged in the status scoring table (Table 2.1). However, from the species compositions of the supposed mid-successional and climax communities identified, it is evident that the conceptual basis of the approach is incorrect.



SPECIES KEY

No	SPECIES	No	SPECIES
1	Acacia robusta	2	Acacia schweinfurthii
3	Azima tetracantha	4	Boscia albitrunca
5	Croton menyhartii	6	Cussonia sp.
7	Dovyalis caffra	8	Ehretia rigida
9	Ficus sycomorus	10	Maerua rosmarinoides
11	Pappea capensis	12	Plectroniella armata
13	Rhus pentheri	14	Salix woodii
15	Sclerocarya birrea	16	Sesbania sesban
17	Spirostachys africana	18	Ziziphus mucronata

Figure 2.4 The contribution of each component species to the overall age structure of community 4

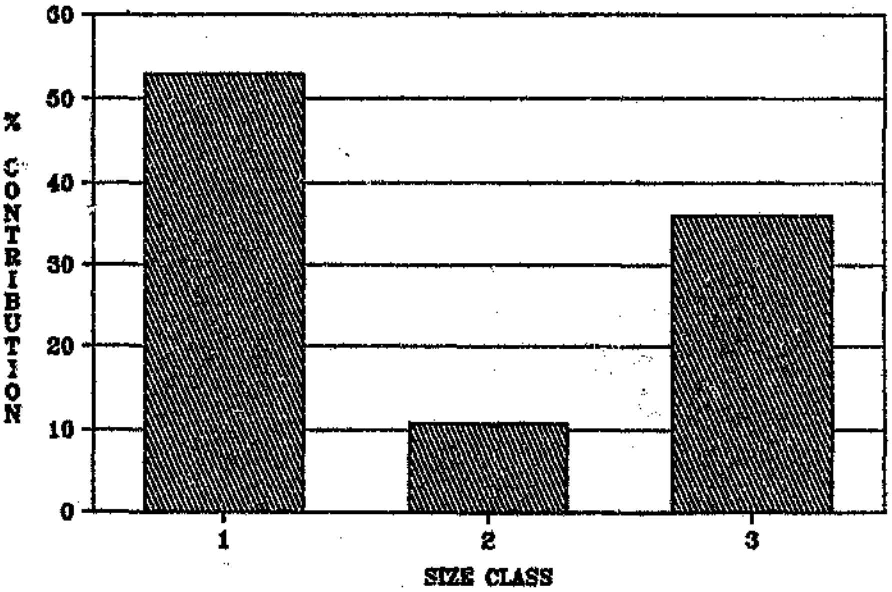
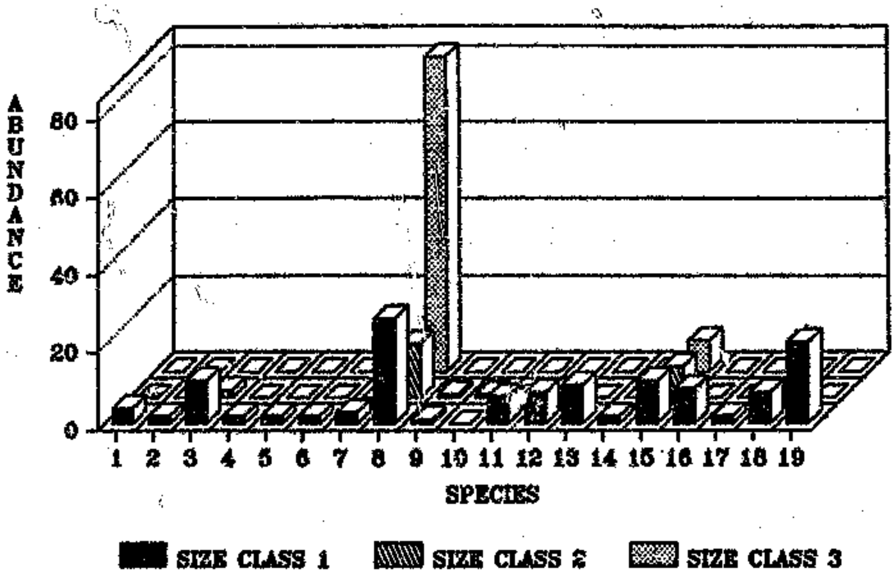


Figure 2.5 The age structure of community 5B on the basis of three size classes



SPECIES KEY

No	SPECIES	No	SPECIES
1	Acacia robusta	2	Azima tetracantha
3	Capparis tomentosa	4	Combretum erythrophyllum
5	Dombeya rotundifolia	6	Dovyalis caffra
7	Euclea schimperi	8	Ficus sycomorus
9	Gardenia volkensii	10	Maytenus senegalensis
11	Melia azedarach	12	Nuxia oppositifolia
13	Phyllanthus reticulatus	14	Plectroniella armata
15	Rauvolfia caffra	16	Rhus chirindensis
17	Sesbania sesban	18	Sideroxylon inerme
19	Ziziphus mucronata		

Figure 2.6 The contribution of each component species to the overall age structure of community 58

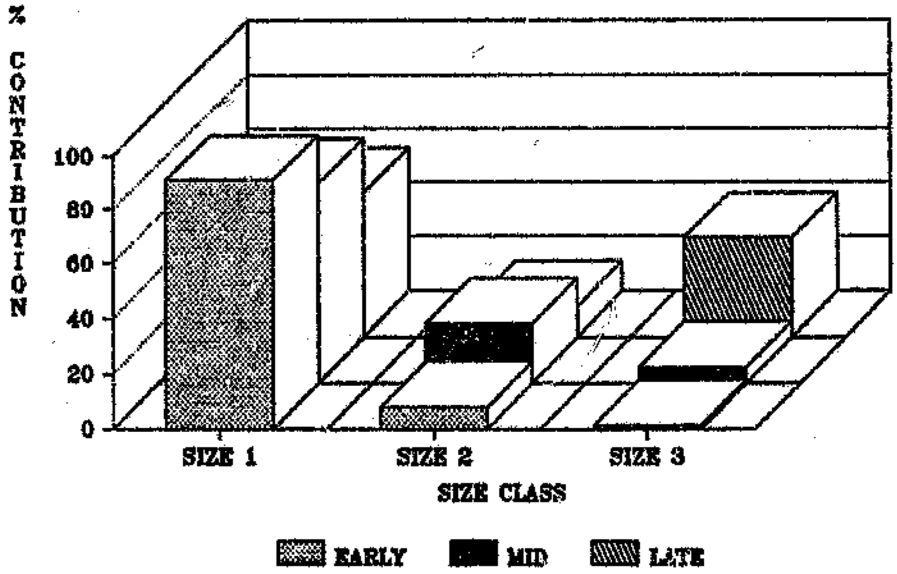


Figure 2.7 The comparison of the three size classes investigated for three apparently different stages of riverine succession

2.4.2 Retrospective study using PCQ data of a single site collected on different occasions

The correspondence analysis display (Fig 2.8) and its associated numerical output (Appendix 2.1) reveals that the three sampling dates examined were separated on the basis of species present and their frequencies of occurrence. 99.9% Of the variation in the data was accounted for by the first two axes. Although data from the later stages of succession are not represented, due to absence of data from a mature sere, this still gives an indication of the species which are important in the more frequent stages of a successional sequence and allows for these species to be roughly classified accordingly (Table 2.4).

The proximity of the 1979 and 1984 points on Figure 2.8 indicates that a reasonable degree of similarity appears to exist between the species present before the Domoina flood (1979) and after (1984). The 1984 PCQ was carried out immediately after the flood before early successional species had begun to appear. The only individuals and species present at this time were those which were capable of withstanding the force of the flood. Species such as <u>Maytenus heterophylla</u> and <u>Plectroniella armata</u> are both shrubs or small trees and are capable of displaying reasonable flexibility to flood waters. It is suggested that this explains their importance immediately after the floods. Consequently, the 1984 PCQ data cannot be used to reflect an early stage of succession as initially anticipated. The 1986 vegetation had sufficient time (approximately two and a half years) to establish itself after the Domoina flood and was clearly different from the 1979 vegetation. For this reason it is interpreted as being a more accurate reflection of an early sere.

A whole spectrum of species exist which display their optimal frequencies or dominance at different points between the early and late seral stages of succession. Three broad species components are identified from the display and are highlighted accordingly. The species which correspond to the numbers on the display are listed in Table 2.4. Those which become dominant in the early stages of succession (EARLY), and those which appear to display dominance in a late stage of succession (LATE). The third cloud of species (MIDDLE) are clearly those species which were capable of surviving the force of the flood. However, it is suggested that these species also represent the middle seral stages of succession.

2.4.3 Retrospective study using aerial photographs

The graphical output of the correspondence analysis between the six sampling dates and their corresponding vegetation states is displayed by Figure. 2.9. The corresponding numerical output is displayed in by Appendix 2.2.

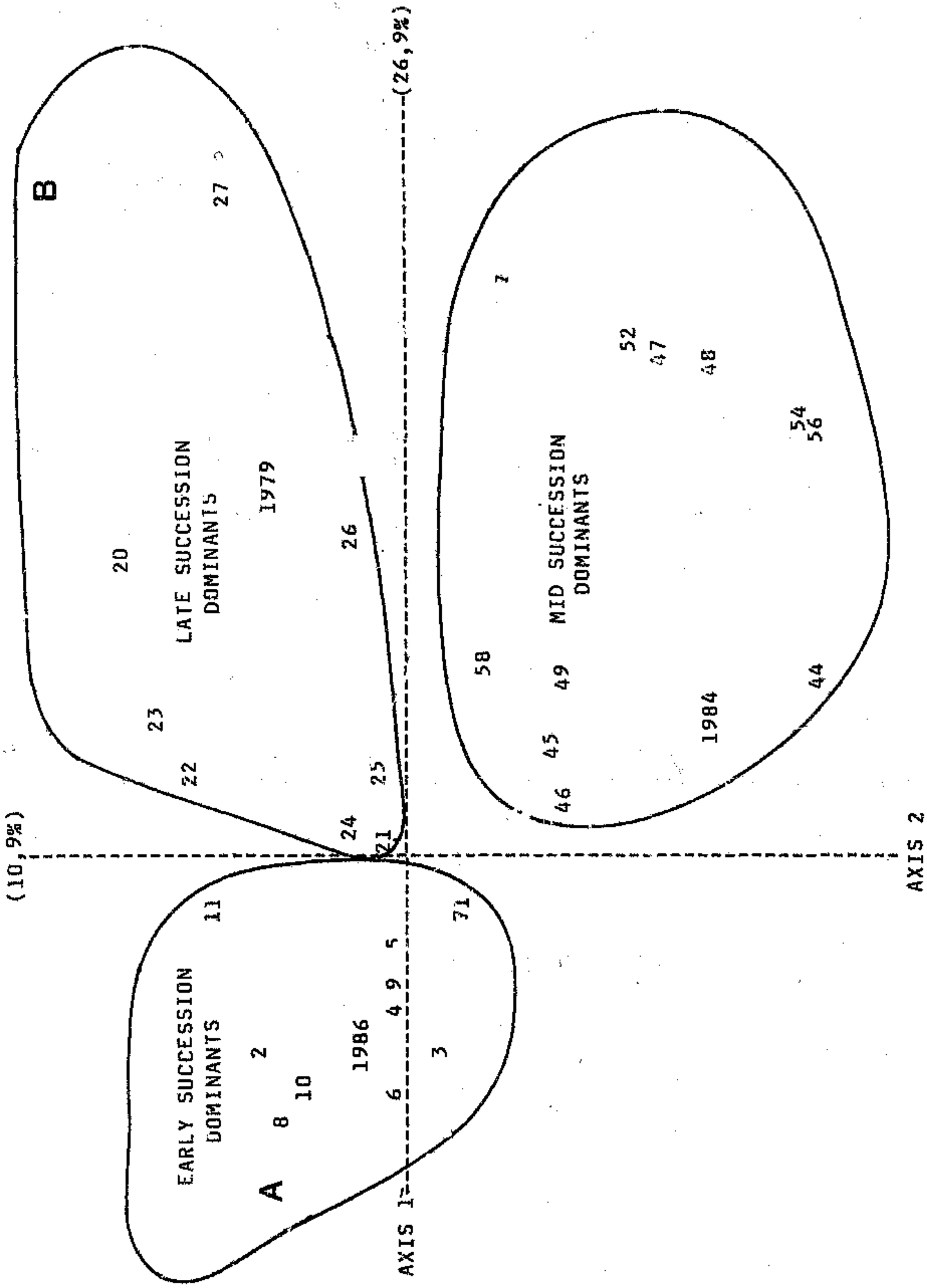


Figure 2.8 Two Dimensional correspondence analysis display of species frequencies at the Thumbu river mouth for three separate occasions - 1979 (before flooding), 1984 (immediately after) and 1986 (two and a half years after flooding) - see Table 2.4 for species names

Point A represents species 12 - 19
B represents species 28 - 43

Table 2.4 The classification of species at the Thumbu river mouth as early, middle or late succession dominants on the basis of their abundances in three different seres

1986 - Early sere
1984 - Middle sere
1979 - Late sere

(A) EARLY SUCCESSION DOMINANTS - 1986

1) Acacia robusta
2) Strychnos decussata
3) Dovyalis caffra
4) Ficus sycomorus
5) Maytenus senegalensis
6) Phyllanthus reticulatus
7) Sclerocarya birrea
8) Tarchonanthus camphoratus
9) Spirostachys africana
10) Ziziphus mucronata
11) Acacia schweinfurthii
12) Acacia tortilis
13) Capparis tomentosa
14) Dichrostachys cinerea
15) Grewia flavescens
16) Grewia sp.
17) Melia azedarach
18) Sesbania sesban
19) Cussonia paniculata

(B) MIDDLE SUCCESSION DOMINANTS - 1984

20) Ehretia rigida
21) Euclea schimperi
22) Euclea undulata
23) Hippobromus pauciflorus
24) Pappea capensis
25) Azima tetracantha
26) Schotia capitata
27) Acalypha glabrata
28) Croton menyhartii
29) Diospyros glandulifera
30) Diospyros lycioides
31) Diospyros simii
32) Euclea divinorum
33) Euclea natalensis
34) Galpinia transvaalica
35) Manlikara concolor
36) Mimusops obovata
37) Ochna arborea
38) Olea africana
39) Phoenix reclinata
40) Rhus chirindensis
41) Thespesia acutiloba
42) Trichelia emetica
43) Turraea obtusifolia
44) Maytenus heterophylla

(C) LATE SUCCESSION DOMINANTS - 1979

45) Plectroniella armata
46) Schotia brachypetala
47) Mimusops caffra
48) Cassine aethiopica
49) Sideroxylon inerme
50) Erythroxylon emarginatum
51) Euphorbia tirucalli
52) Dombeya cymosa
53) Albizia sp.
54) Acacia grandicornuta
55) Trema orientalis
56) Acokanthera sp.
57) Nuxia oppositifolia
58) Rhus natalensis

Interpretation of the graphical display should be done with care. Since the year and the vegetation states investigated are represented by objects and variables respectively, comparisons between them should therefore be confined to comparisons between the angles of the two points relative to the centroid (0.0). Interpretation of the numerical output is preferable as it makes the evaluation of between time differences more rigorous. The interpretation of both the graphical and numerical outputs of correspondence analysis is described in Greenacre (1984).

Large proportions of grass and open sand (GRASS) were particularly characteristic of the years 1937 and 1986. Similarly, large proportions of reed beds (REED) were associated with the years 1973 and 1983, and large proportions of large trees (FIG) and smaller trees (ACACIA) were associated with the years 1954 and 1960. It appears that a gradient in vegetation states existed from the period 1937 to 1986 and that these states fluctuated noticeably over time. If one compares this with the occurrences of major floods in the system over the same period (Fig. 3.1), it is clear that these fluctuations were a consequence of the effects of flooding and the subsequent recovery and succession of vegetation. This gradient reflects the succession of vegetation states which occur in riverine areas in response to major flood events, given enough time for succession to proceed.

Two separate successional pathways which possibly occur in two different parts of the riverine areas after a severe disturbance were discernible from Figure 2.9. It is envisaged that these start at approximately the same point and display separate successional pathways towards a common climax (Fig. 2.10).

Firstly, in high lying riverine areas, the denuded site are colonised by grasses which are able to respond quickly due to their fast growth rates and extensive seed banks. The record of previous large flood events (Fig. 3.1) revealed that large flood events were experienced before 1937 (1924/25) and 1986 (Domoina - 1984) therefore returning the vegetation of these years to early seres. Due to aerial photographic limitations, it was not possible to distinguish the finer details of this early sere in terms of the various herbaceous and woody components which established themselves. However, it is postulated, based on ground truthing, that this stage is initially characterised by species such as _Panicum maximum_, _Urochloa mosambicensis_ and _Cenchrus ciliaris_ and that, towards the late grass stages, large quantities of forbs and woody plants do appear. This sere only becomes significant after very large scale floods, such as that of Domoina, when the high water mark far exceeds that of the lower lying areas. The successional pathway then leads to the appearance of small trees which are, to a large extent _Acacia_ spp. and numerous other species.

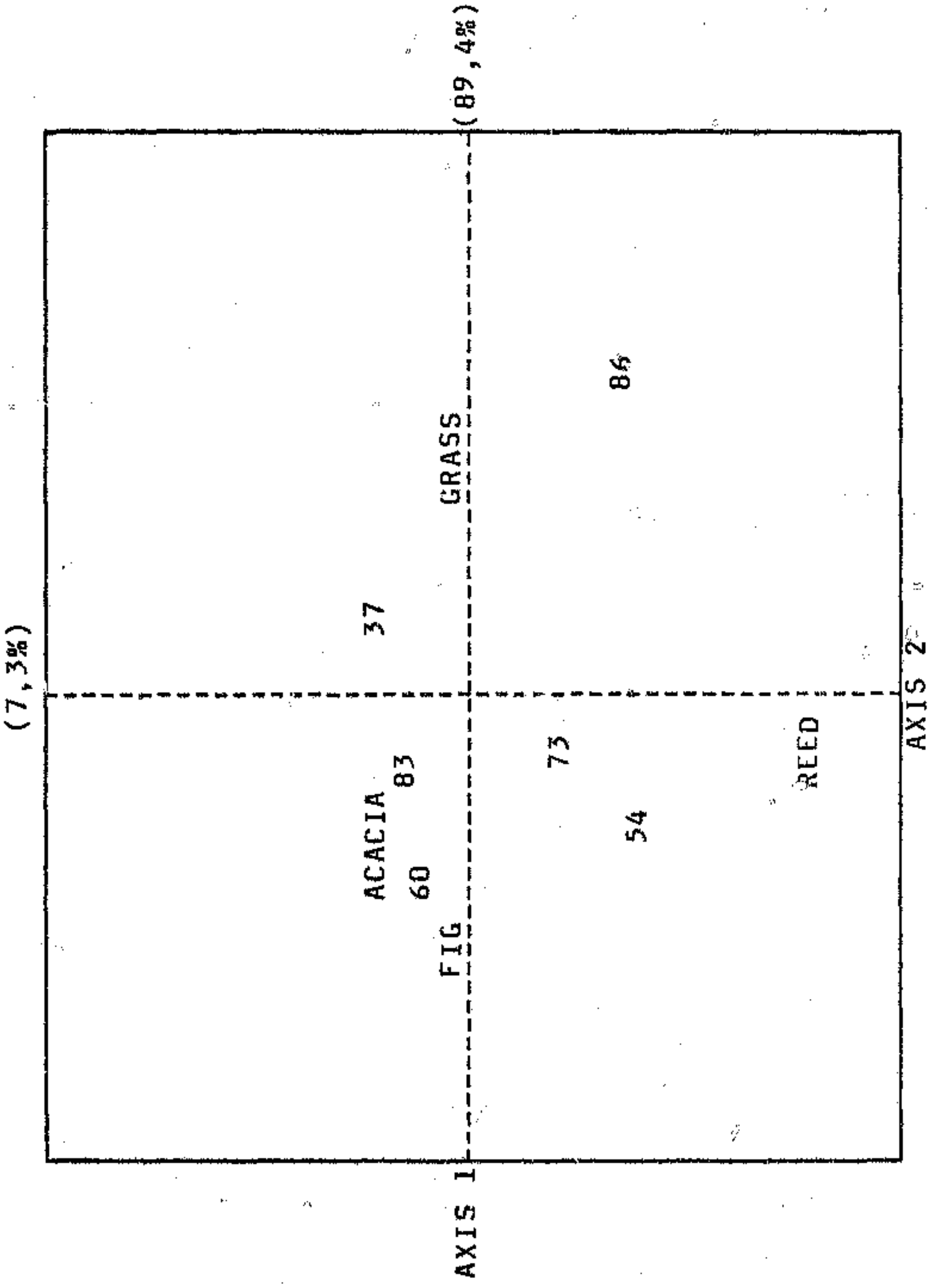


Figure 2.9 Two dimensional correspondence analysis graphical display of 4 vegetation states for 5 time periods since 1937

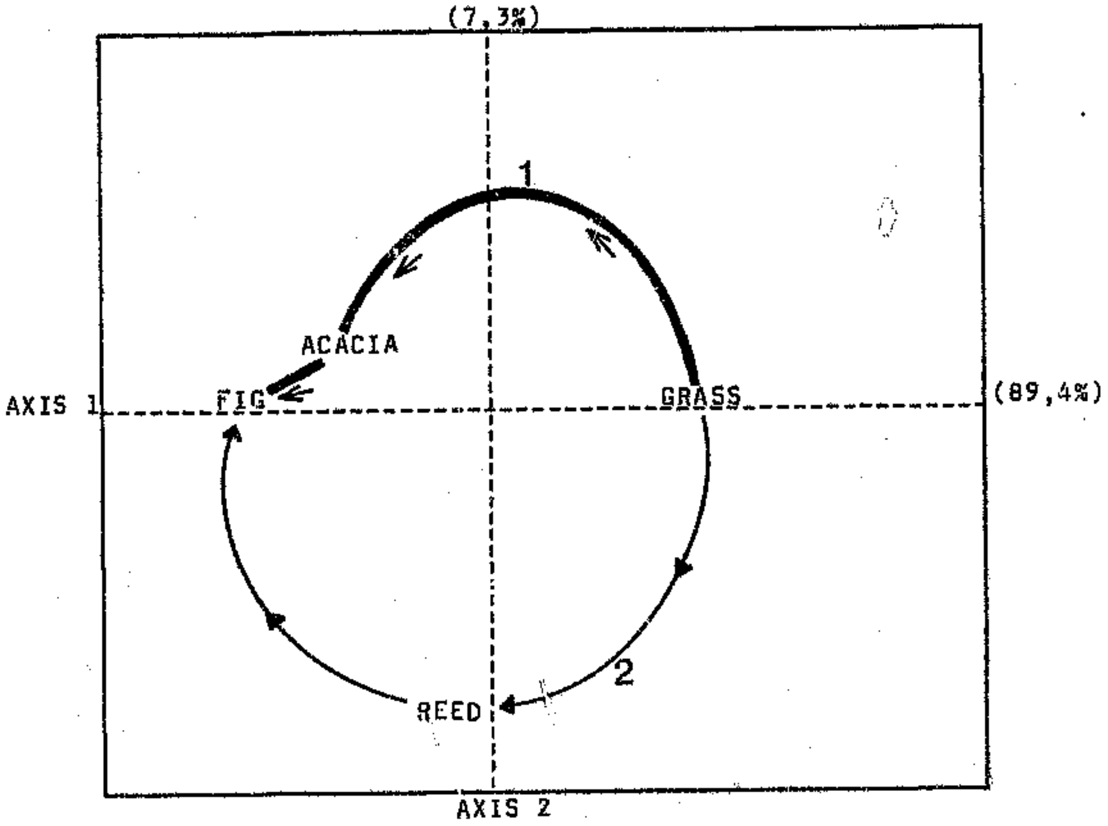


Figure 2.10 Two dimensional correspondence analysis graphical display of 4 vegetation states for 5 time periods showing two possible successional pathways which occur in different parts of riverine areas after a severe disturbance

(1) in higher lying areas, away from the river
(2) in lower lying areas, close to the river

The succession of vegetation appears to terminate at a point which is characterised by large proportions of these small trees as well as larger canopy trees such as Ficus sycomorus and Schotia brachypetala.

Secondly, in lower lying areas and at the river's edge, the denuded site is first occupied by hydromorphic grass species such as Imperata cylindrica and Paspalum distichum and small sedges. With time these are replaced by larger sedges and large quantities of reeds. Once again photographic detail restricted the detection of finer details of this early sere. However, it is postulated that this stage is characterised by sedges such as Cyperus immensus and Cyperus sexangularis. Towards the end of this stage, Typha capensis and Phragmites spp. then appear and dominate the area. The successional pathway then eventually leads to the appearance of the same sub-climax and climax communities as described for the higher lying riverine areas.

Further development of the ideas of Figure 2.9 was possible by examining each time period separately by means of a Markov model (Fig. 2.11 A - E). It is possible to see which periods were characterised by recovery and succession and, therefore, displayed a progressive development and which periods were characterised by major disturbances and, therefore, displayed a retrogressive development. In this figure the 2 years used to derive the predicted equilibrium proportion were joined by a solid line. This line was then extended to the projected/predicted equilibrium proportions by means of a broken line. In order to facilitate interpretation, for each period, these projected equilibrium proportions lines have been superimposed over Figure 2.9 as a supplementary matrix (see Greenacre, 1984).

The projected/predicted equilibrium states as well as the times required to attain these states, for the five different time periods, are evidently very variable (Fig 4.14). Only the periods 1937 to 1954 (Fig. 2.11 A) and 1973 to 1983 (Fig. 2.11 D) displayed progressive developments (from right to left). The predicted equilibrium proportion for the period 1937 to 1954 was composed almost entirely of the climax component, while for the period 1973 to 1983, it was clearly characterised by a large sub-climax element. The rest of the periods investigated are clearly characterised by retrogressive developments (from left to right). This is a clear indication that significant flood events or other large scale disturbances were responsible for retarding succession and development during these periods.

Further consultation of the record of previous floods (Fig. 3.1) reveals that the only time period which was relatively free from large disruptive floods was that of 1937 to 1954. It was this disturbance free period which made it possible for succession to proceed unhampered for approximately 17 years and represent this progressive development. The projected proportions of the five vegetation states obtained from this period are therefore likely to be the most accurate. It appears that a large proportion of Ficus sycomorus and other large trees (63%) would characterise this community - this could be considered as a possible climax state for these riverine areas. The model predicts that a further 629 flood free years are required in order to achieve this true equilibrium state.

2.5 Discussion

2.5.1 Substitution of space for time

Extensive floods since 1954 had the effect of reducing the successional status of riverine communities by reducing the abundance of large trees from forested riverine communities.

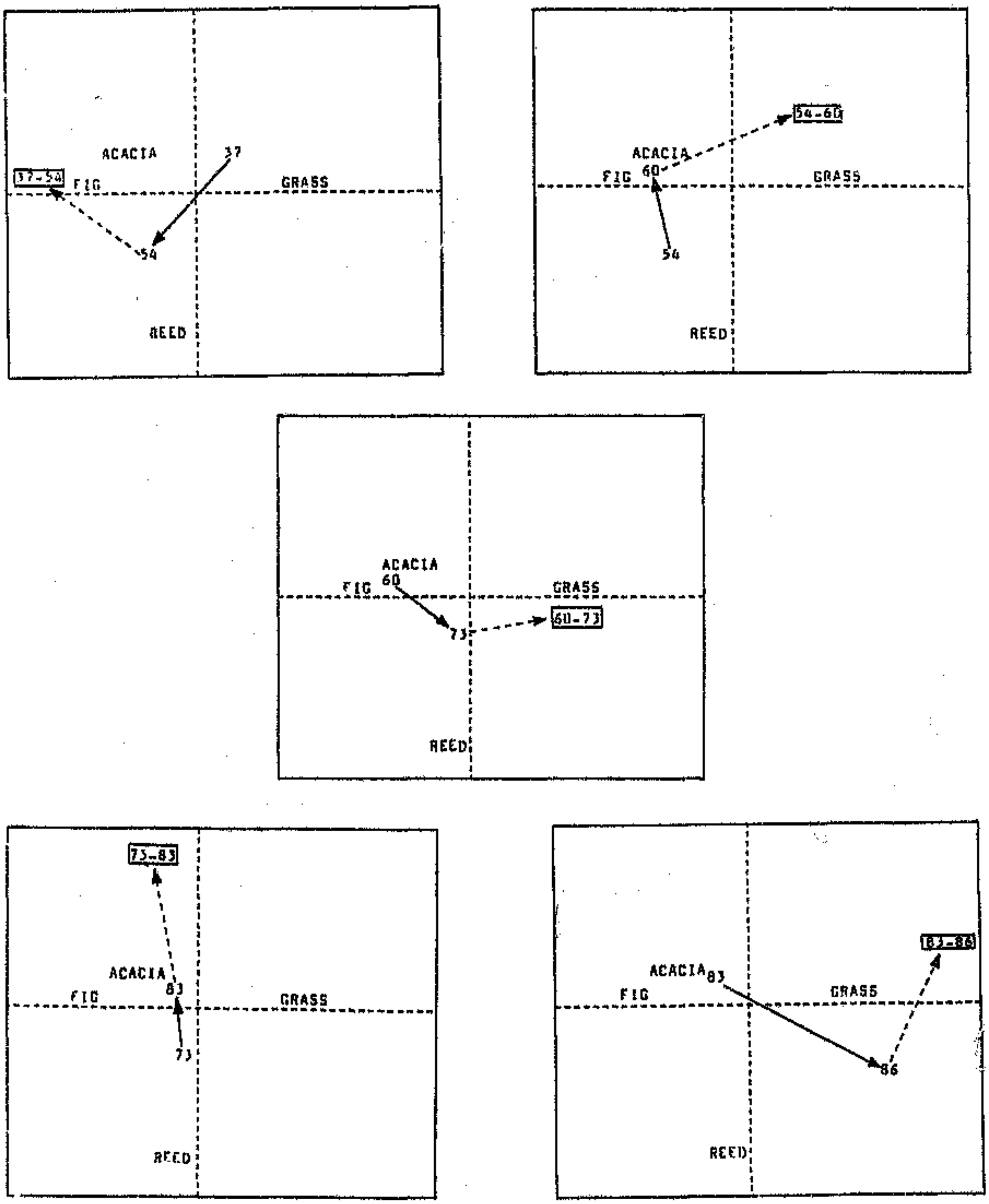


Figure 2.11 The recovery/development status of riverine vegetation for 5 time periods extended to their predicted equilibrium proportions - each superimposed over Fig. 2.9

Positive development - from right to left
Retrogression - from left to right

(A) 1937 - 1954
(B) 1954 - 1960
(C) 1954 - 1960
(D) 1973 - 1983
(E) 1983 - 1986

The relative proportions of the three size classes employed by the successional status score system were also changed. This system was therefore useful in identifying general dynamics of the successional status of vegetation. With this approach, communities were classified according to their successional status on the proportions of different tree size classes remaining after different flood events. However, after carrying out an analysis of the species composition of these different communities, it is clear that this classification is conceptually incorrect.

Certain riverine areas, due to the locations, shapes and sizes relative to the river and therefore to large floods, clearly do act as refuges which offer certain communities a degree of protection from floods. Even the Domoina flood did not succeed in removing large trees in certain areas of the Black Umfolozi. However, those trees remaining after the flood are not the only components of the climax state community but are only those individuals which were capable of surviving the force of the flood. These remaining species, instead of indicating communities which were untouched by flood waters, as envisaged at the outset of the project, are in reality, only indicators of a partially disturbed community. Certain species are particularly capable of withstanding the force of large floods by virtue of their firm rooting or flexible canopy characteristics and are therefore likely to be well represented in such refuges. Other species are not as capable of resisting such forces and consequently are likely to be poorly represented or not represented at all. While certain large individuals still remained in these areas after the flood, large quantities of other species from the large and smaller size classes had been completely removed.

On this basis, this approach has shed insufficient light on the true characteristics of the middle and late successional stages of riverine communities. In this respect, by adopting such an approach, no further knowledge can be gained over that possibly gained by a basic community analysis approach.

The determination of status scores by means of the status score table (Table 2.2) was evidently inaccurate. The status scores in this table were based purely on the proportions of the different vegetation states which were visibly discernible from the aerial photographs. A number of shortcomings were evident which rendered the technique inadequate for the investigation of succession.

1. It was clearly not possible to assess from aerial photographs that the major contribution to the large size class was made by only a few species rather than by a community of several species, as had been assumed. It is obviously not possible to clearly discern between different tree species using aerial photographs.

2. The actual size class distributions of the communities investigated revealed a distinct absence of individuals from the second size class. This is confusing because, in order for a community to have attained a status score of 3 or 4 using the status score table, a high proportion of small/medium sized trees should have been evident from the photographs. Ground truthing of the areas in 1987 revealed that large herbaceous plants such as <u>Ricinus communis</u> and <u>Solanum mauritianum</u> were confused for small/medium sized trees. These fast growing herbaceous species were probably in the region of 3 to 4 years old and could not be substituted for small/medium sized trees which would be significantly older.

3. The status score table did not cater for the absence of small/medium sized trees and therefore was not able to attach a status score to this condition. This raised an important point. In what successional state are such communities? Are they in an early successional state due to the abundance of juveniles or are they in an advanced state, due to the contribution of large individuals of an apparently climax species?

The Clementsian description of succession is also misleading. It proposes that succession proceeds at a site, after a disturbance via a series of distinct and definable states, to eventually attain the final climax state. However, in reality, it is not possible to identify distinct and definable seres in the succession of vegetation. Due to the erratic and non uniform way in which any community is disturbed and the differential way in which each of the component species and individuals are affected b the disturbance, it is always likely that a wide variation in the species present and their abundances and age distributions would be found. This circumstance applied here, so much so that it was not easy to assess at what point along the successional pathway certain communities should be placed.

The ability of certain large tree species to survive the force of destructive flood waters is of significant importance to the recovery and further succession of riverine vegetation. The presence of aged individuals of any one species at a site will afford that species added advantage in the community. Certain species, (e.g. <u>Ficus sycomorus</u>) due to their proximity to the water, are able to fruit at any time of the year, thereby ensuring a continuous source of seedlings and, in a short space of time, these individuals will then represent all three size classes. By these means, the lengthy process of interspecific competition is effectively bypassed as other species are obviously out-represented and possibly out-competed from the early stages of recovery. This is likely to speed up the successional process considerably.

2.5.2 Retrospective study using PCQ data of a single site collected on different occasions

The correspondence analysis display related Ficus sycomorus with the early successional dominant class. This is confusing since it is well known that it is a dominant component of climax riverine communities. In this regard it is important to consider the following.

a. The species were ordinated according to their species frequencies and Ficus sycomorus displayed its highest frequency in the early stages of succession.

b. While a species may display its optimum frequency in an early sere, the same species is still capable of being an important component of a late sere by virtue of its size and reproductive potential. Good examples of this are Ficus sycomorus and Spirostachys africana which were both very well represented in the early sere and yet are generally considered to be climax species, due to the substantial sizes they are capable of attaining in sub-climax and apparently climax riverine areas as well as their ability to exclude other species. This strategy affords these species the chance of adequate representation in any seral stage.

In the 2 years that elapsed after the 1984 PCQ, those species which survived the flood, as described above, disappeared to a large degree. This was not only due to the fact that their relative contribution was small in the early stages of succession compared to large frequencies of pioneer species. These individuals also died rapidly in the first few months after the flood possibly as a consequence of damages which they sustained from the flood or they were simply not able to compete with the pioneer and early dominant species and were excluded.

In order to construct a complete successional series for these riverine areas, according to the Clementsian approach, it would be necessary to identify different seral stages with distinctly different participating species for each. This would involve understanding the contribution of each riverine species and where it makes its major contribution. To achieve this, it would be imperative to make use of as many monitoring events and different riverine sites as possible, preferably at different intervals after significant disturbance events. Depending on the frequency and intensity of such events, this may require an exceptionally long term and complex study in order to record sufficient replicates of each stage of the series. In addition, due to frequent disturbance, there is no guarantee that any medium to late seral stages will be experienced and be adequately monitored during the period of the study. It is highly unlikely that distinct seres with unique participant species do actually occur during a successional series and, therefore, in order to identify these distinct species clouds it would be necessary to make use of a classification technique which would be able to separate or synthesise them from the complex cloud of all participating species. It is suggested that any classification of this sort would be completely artificial, compounded still further by the effects of recurrent disturbances.

While this approach apparently identified the various species associated with the early and late seral stages, it did not allow for the identification of the mechanisms responsible for species change from stage to stage. This shortcoming is due to the fact that data was, through necessity, collected from discrete points in time along the successional gradient. In order to detect the subtle dynamics of a system such as this, it would again be necessary to monitor the various components on a continuous basis or to make use of more frequent monitoring sessions.

A further shortcoming lies in the fact that the ordering of seres to construct a complete successional series does not necessarily correspond with their actual chronological order. This is likely to shuffle the subtle interactions which exist between the component species, thereby further complicating the interpretation of the mechanisms responsible for the succession of species. In addition, as seen from the substitution of space for time approach employed above, it is possible that the construction of the complete series may not be possible due to the complications introduced by communities which are only partially disturbed. It may not be possible to determine at what point on the series these communities belong, due to the combined representation of species and individuals from an early sere as well as a mature sere.

2.5.3 Retrospective study using aerial photographs

While the interpretation of the correspondence analysis output allowed for the identification of two possible successional pathways in lower and higher lying riverine areas, it did not allow for the accurate determination of the time periods associated with these pathways. In order to derive this type of information, it would be necessary to ensure that photographs are taken at more regular and frequent intervals. It would then be possible to calibrate the axes in time units and could thereby allow for year by year comparisons to be made in terms of the rates of succession of the vegetation. The same scale could also be used to compare the impacts of different flood and other disturbance events. To relate these accurately, it would be necessary to gather more detailed information concerning both minor and major disturbance events, during the period of study, so that successional setbacks can be monitored adequately and then related to the general successional process.

Limited information is available on time intervals between the various vegetation states. This is based on the relative positions of objects and variables relative to the centroid on the correspondence analysis display.

This was confirmed with simultaneous reference to the numerical output of the analysis. This suggests that the initial stages of succession from the grass to small tree state and reed to small tree state are slower than from the small tree state to the climax state. This is not consistent with the fact that the growth and development of trees from the seedling stage to the mature individual is a very slow process. The visual identification of different tree sizes from aerial photographs, used previously, has shown that large and fast growing herbaceous species may be confused for small and medium sized trees. It is very likely that this has occurred and would lead to the described effect. However, it is difficult to assess whether this is an adequate reflection of an actual time interval or merely an artifact which is associated with either the non-linearity characteristics of the technique or the limitations which are imposed on the study, due to the use of aerial photographs.

The Markov model findings also give an indication of the time required for succession from one state to another, along with the projected equilibrium proportions which are determined for the different time periods investigated (Table 4.14). However, unless they are related to the vegetation states and the years investigated, the interpretation of these results is very difficult. For this reason, the projected equilibrium proportions of the four vegetation states were superimposed over the previous correspondence analysis display by including them as a supplementary matrix. By carefully considering the predicted equilibrium proportions obtained by this technique and the time intervals required to attain these proportions, it is possible to make basic predictions about the different vegetation states and the time required to attain these states. It is evident from the Markov model that, in order to attain the climax vegetation state in riverine areas from a state characterised by large quantities of pioneer species, as in 1937, in the region of 629 disturbance free years would be required.

It is apparent that the succession of riverine vegetation towards the climax state is a very slow process but can be attained given sufficient disturbance free time. This process is persistent and important in shaping riverine communities despite the effects of disturbance. However, the impact of disturbance in reducing these areas to the open sand/grass state is far more effective and frequent and is generally achieved a lot faster.

Consultation of the flood record and consideration of the recent frequency and intensity of disturbance in riverine areas reveals that a flood free period of the required length is very unlikely to occur, therefore, clearly preventing the attainment of a true climax condition and highlighting the impact of disturbance on the structure of riverine communities. Disturbance therefore is clearly the more important and persistent process in determining the state and condition of the vegetation present.

For this reason it appears that this riverine system, as it exists today, is primarily structured by disturbance and is said to be "event driven" as opposed to "succession or reaction driven". In essence, when one aims to understand the structure and dynamics of the riverine system, this highlights the need to investigate, in considerable detail, the characteristics of the different forms of riverine disturbance and the impact they have on the structure and dynamics of riverine vegetation. This simultaneously highlights the inadequacies of succession theory as a possible tool for understanding riverine structure and dynamics.

2.6 Conclusions

The above findings suggest the need for the monitoring of component species and their interactions by means of a long term programme on a continuous basis. The advantages and disadvantages of such programmes have been discussed earlier. The 'event driven' nature of the Umfolozi riverine system further discounts the value of a continuous programme. It is highly improbable, considering the frequency and characteristics of large floods, that sufficient recovery time will be afforded to riverine areas in order to allow for sufficient information to be gathered concerning the characteristics of the mid, late and climax seres of succession. A long term approach which relies on the retrospective construction of a complete successional series by the ordering of separate successional events of different durations, might be the most effective way of addressing the problem, but is likely to be of exceptionally long duration. Furthermore, such an approach is not able to guarantee a successful construction of the successional series due to the absence of visibly distinct seral stages. In addition, it is unlikely to shed further light on the mechanisms responsible for succession.

Due to the complexities introduced by the frequency, intensity and heterogeneous nature of riverine disturbances and the heterogeneous response of species to these disturbances, the three approaches employed could not be used to construct an adequate picture of succession in riverine areas. It would be impossible to successfully test succession theory under such circumstances. The 'event driven' nature of the Umfolozi riverine system makes it practically impossible to adequately determine the structure and dynamics of riverine vegetation by means of either long or short term successional approaches.

While it was possible to identify the species associated with possible stages of succession in a single area and to identify two successional pathways which may exist in riverine areas, it was not possible to identify the mechanisms responsible for the succession of species. It appears that riverine succession does not proceed in the ordered and logical way as is commonly described by supporters of Clementsian succession. Instead, it appears that the succession of riverine species is likely to proceed by means of a complicated and disordered interaction of species and individuals in response to a complicated and heterogeneous disturbance regime. Since these findings did not correspond well with the characteristics of succession, it was not possible to apply them as a test of the theory.

CHAPTER 3 APPROACH BASED ON DISTURBANCE THEORY

This chapter addresses the characteristics of recurrent flood events in the Umfolozi riverine system and attempts to place their importance and their effects on riverine communities into perspective, in the light of current disturbance theory. In addition, the effects of fire as a second form of disturbance is also briefly investigated and discussed.

3.1 Introduction

The cyclone Domoina flood and the damage it caused to riverine vegetation in the reserve highlighted the importance of floods as a disruptive and possibly as an organising force in riverine areas. Large floods, which cause major destruction to riverine vegetation, are commonly viewed as unusual and rare. However, during the author's two year study in the reserve, floods exceeded flow rates of 3000 cubic metres per second on two separate occasions, each causing considerable damage to riverine vegetation. The impact of floods on retarding the successional process of riverine vegetation was demonstrated in the previous chapter.

Other disturbances such as fire and herbivory are also responsible for structuring riverine communities in the periods between large flood events. However, due to the complexity of these disturbances, data regarding the regimes and impacts of these disturbances are not usually readily available. The application of fire is commonly controlled by means of the timing, intensity and location of burns in order to address specific management objectives at different times such as the removal of excess moribund material, the stimulation of grass growth and the prevention of woody plant enchroachments. For information regarding the use of fire in the Umfolozi Game Reserve see Wills (1987). The diverse applications of fire in the past and the specific characteristics of the different burns over time have complicated the interpretation of the fire regimes. Herbivory is also an important organising force and its effects are often felt hand in hand with those of fire. Due to the large and diverse number of participants, each with their own specific resource, habitat and feeding requirements, the effects of herbivory are more subtle and difficult to define. The continuous interaction of these requirements with heterogeneous and erratic vegetational dynamics ensures that the effects of herbivory are relatively unpredictable.

Due to the limited scope of the project and the complexity of fire and herbivory as disturbances, it was not possible to adequately investigate their regimes. The effects of fire on riverine vegetation was attempted but, due to a run away fire which swept through the control plots, this study was confined to a brief investigation only. The effects of browsing and grazing were investigated in the light of the enemy impact hypothesis (see community organisation approach - chapter 4).

Since floods are such major and apparently overriding disturbances and since relatively long term data regarding their regimes and effects are obtainable, it was possible to clarify their incidences and characteristics and understand their organisational role in riverine communities. Furthermore, it was also possible to place the impact of floods into perspective in terms of current disturbance theory in order to determine and predict the structure and dynamics of riverine vegetation.

3.2 Objectives

The objectives of this approach were as follows.

1. Investigate the disturbance regime of floods in the Umfolozi riverine system.
2. Investigate the effect of the flood regime on the species diversity and demography of riverine vegetation by testing relevant hypotheses.
3. Model the effects of past flood events on the proportions of various vegetation states.
4. Place the flood regime and relevant findings into perspective in the light of current disturbance theory in order to make broad predictions regarding the structure and dynamics of riverine vegetation.
5. Investigate briefly the effects of fire on riverine vegetation.

3.3 Approach and methods

The approach adopted investigated the characteristics of floods and their impact on species diversity and demography of riverine communities by the analysis and presentation of available data and the testing of relevant hypotheses. Available data was then used to model the effects of floods on the dynamics of riverine vegetation.

3.3.1 Disturbance regime

The regimes (characteristics) of the floods were defined according to Sousa's (1984 a) five descriptors of disturbance regime namely,

1. magnitude as a. intensity and b. severity,
2. frequency,

3. duration,
4. areal extent, and
5. predictability.

3.3.1.1 Intensity and frequency

Two relevant hypotheses were tested with regard to the intensity and frequency of floods and the reasons for possible trends.

1. Large flood events are increasing in intensity and frequency with time.

   Since river flow data for the nearest recording station on the Black Umfolozi river were generally sparse and unreliable, the maximum flood peaks at the recording station at the main railway bridge on the Umfolozi river were used instead. These figures were available from 1890, and were collected with the assistance of the Department of Water Affairs and personal communications with Lund, B.G.A[1] and Bale-Smith, I[2]. These data (floods in excess of 1500 m^3/s), which included the 1987 flood peak value, were then plotted against time of occurrence to display the intensity and frequency of large flood events.

   The total time period of 97 years from 1980 to 1987 was divided into two 48 year periods. The null hypothesis employed stated that no differences existed in intensity and frequency between these two periods.

   The distribution of flood data for the entire 70 year period was compared with that of a normal distribution. Since the data conformed adequately to that of a normal distribution, a students t-test was used to compare flood intensities between the two periods. The flood frequencies for the two 48 year periods were compared for significance using a Chi-square test.

   However, since available flood data was sparse, a significant difference was not expected to be detected at the p=0.05 level. It was decided that any p value less than 0.2 would be considered as significant instead.

2. Large rainfall events in the catchment area of the Umfolozi river are increasing in intensity and frequency with time.

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[1] B.G.A. Lund, P.O. Box 7744, Halfway House, 1685

[2] I. Bale-Smith, Umfolozi Sugar Mill, P.O. Riverview, 3930

Rainfall data was obtained from Nongoma which is the longest standing rainfall station in the Umfolozi catchment area. Data was available for a 70 year period from 1916 to 1986. Both the annual as well as the January figures from this station were plotted together on a horizontal time sequence.

Annual values in excess of 950 mm (mean= ±910 mm) were used to represent large rainfall events. The period was sub-divided into two 35 year periods. These were then compared for differences in rainfall intensities with a student's t-test and for differences in frequencies using a Chi-square test. These results were tabulated for comparison. The null hypothesis, employed for this test, stated that no significant differences exist between large rainfall intensities and frequencies between the two periods investigated. The null hypothesis would be rejected if the differences between the rainfall intensities and frequencies were found to be different at $p< 0.2$. This high probability value was considered as significant, since adequate rainfall data is relatively scarce and also because this level was used for the test for flooding intensity and frequency.

3.3.1.2 Severity

It was envisaged that since the force of the flood varies considerably from point to point along the length of the river, a comparison of extreme river positions would reveal differences in flood severity. With these extremes in mind, it would therefore be possible to piece together an understanding of flood severity for other areas of the river. Comparisons were therefore made between the flood severities experienced on a. the inside of river bends, b. the outside of river bends, and c. on straight river stretches.

The null hypothesis for the test stated that all three river positions are subjected to the same flood severity and therefore display similar tree losses, as a consequence of the flood.

Flood severity measurements were determined from aerial photographs of these three areas, by comparing the percentage proportions of large trees from before and after the Domoina floods. Tree losses were used as a measure of flood severity.

Transects with ground dimensions of approximately 100x300m where located on the aerial photographs in areas which could be classified as belonging to either of the three river positions. Twenty transects were located for the inner river bends, twenty one for the outer bends and only seven were located as straight stretches. The data were compared using a one-way analysis of variance.

Comparisons were graphically compared using 95 percent least significant difference (LSD) intervals (Parker, 1973), to display differences in flood severity between the three river positions.

3.3.1.3 Duration

The flood hydrographs were collected for past flood events on the Umfolozi river system. Unfortunately, the complete hydrographs for the full duration of these floods were largely unavailable, which made it impossible to make detailed duration comparisons between them. Such comparisons were therefore restricted to simple descriptive trends only.

3.3.1.4 Aerial extent and dynamics of floods

A 1:22 000 map of a 6.5 kilometre stretch of the Black Umfolozi river was constructed directly from aerial photographs taken in 1986. This map extensively detailed the riverine area from the Thobothi river mouth to the mouth of the Mona river and included erosion and deposition points as well as the high flood mark which were caused by the Domoina flood. Using arrows to depict the points of maximum force of the flood waters, the same base map was then used to describe three hypothetical phases of the Domoina flood. The first phase described an early phase in which the water level was still largely contained by the river banks. The second phase described the point at which the water levels exceeded the river bank and began to remove riverine vegetation. The final phase described the flood peak when the water levels reached their maximum and began to cause the extensive erosion of the river bank and by-pass the lower-lying river bends. The exercise was used to gain a conceptual understanding of the areal extent and dynamics of large floods and the corresponding erosion of river banks, deposition of sediments and the removal of riverine vegetation.

3.3.1.5 Predictability

The predictability of floods with flow rates in excess of 2000 cubic metres per second were determined by applying the flood peak data to the Weibull equation, as described by Fleming (1975). The objective of the analysis was to determine the number of years within which an event, of chosen size, is likely to occur at least once. This time period is referred to as the 'return period' and was determined by abstracting the annual instantaneous maximum from the records and by ranking them in order of magnitude with the largest value first. The plotting positions of these annual maxima were then estimated from the Weibull equation below. The calculated return period was then plotted against the magnitude of the respective floods.

The formula for the Weibull equation is as follows,

$$Tp = \frac{n + 1}{m}$$

Where, Tp = return period (in years),
n = length of flood record (in years),
m = rank in descending order.

Using regression analysis, a best-fit straight line was then drawn through the points which defines the general relationship between them. The resulting straight line was based on the assumptions inherent in the particular probability distribution which was chosen. The choice of scale on the abscissa determined the probability distribution to which the points were fitted. Fleming (1975) emphasised that no universal distribution exists that defines the distribution of floods for all rivers and that the selection of the distribution should be made purely on the basis of obtaining the best-fit for all existing data. Normal, log normal and log log distributions were applied to the regression analyses and plotted and predictions pertaining to the probable return periods of floods were determined.

3.3.2 The effects of floods on species diversity of riverine communities

The effects of floods on the community species diversity of riverine vegetation were investigated by testing the intermediate disturbance hypothesis.

3.3.2.1 Intermediate disturbance hypothesis

The intermediate disturbance hypothesis was tested by two distinct approaches.

According to the first approach, it was assumed that a range of flooding frequencies exists and that the frequency of flooding is greatest at or near the river's edge. The larger a flood, the further its effects are felt up the riverine slope and, due to the relatively infrequent occurrences of large floods, areas lower down on the river bank experience more frequent flooding than areas situated further up. With regard to this application, the hypothesis predicts that species richness is relatively low at the river's edge as well as towards the higher reaches of the riverine slope and that an area exists between these two points where species richness is greater. The hypothesis states that only certain "fugitive species " are able to exist in areas of high or frequent disturbance, while only highly competitive species would be found in areas of low or infrequent disturbance. The areas subjected to intermediate frequencies and magnitude of disturbance should be able to support species from both groups and therefore display a larger species richness.

According to the second approach, the species richnesses of three different river positions were compared in the light of the flood severity findings for these three positions. In this regard the hypothesis predicts that these three areas (inner bends, outer bends and straights) would display different species richnesses and specifically that the areas, subjected to the extremes of disturbance, would display low species richnesses while areas, exposed to intermediate levels of disturbances, would display higher species richnesses.

The null hypotheses, employed with both approaches, was that all riverine areas display the same species richness, regardless of their disturbance characteristics. Any discrepancies in species richness are due to other factors which exert an influence.

Transect approach

Twenty six transects were situated by means of a stratified random technique in riverine areas. For transect details and the location procedure adopted, see the island size hypothesis - chapter 4. A dumpy level was used to determine the elevation above river level of each component quadrat of each of 27 transects. The herbaceous and woody species occurring in these quadrats were recorded for each quadrat by the methods described in the island size hypothesis. The total number of herbaceous and woody species present in these quadrats were totaled as species richness totals for each quadrat. A regression analysis was conducted to investigate the relationship which exists between species richness and height above river level as an ampliative technique (Mentis, 1988), in order to identify patterns in the data and possibly formulate alternative hypotheses.

River position approach

With this approach, the spectrum of flood severities for investigation was restricted to only three river positions, namely, inner bends, outer bends and straight river stretches. These positions were previously chosen (see 3.3.1.2) to represent the extremes of the entire flood severity spectrum. Consequently, with this test of the hypothesis, the application of an inductive approach, using ampliative techniques, was not possible. Instead, it was necessary to apply a method to arbitrarily separate the species richness data into three distinct classes to correspond with these three river positions.

A one-way analysis of variance was conducted using the species richness data for the first six quadrats of each transect (some transects only had 6 quadrats). A least significant difference test (LSD) was used to display significant differences between transects. The transects were then placed in ascending order of their means and divided into three arbitrary classes based on their means and LSD values. These were a. from 10 to 16, b. from 17 to 20, c. from 21 to 28. In order to relate species richness to flood severity at different river positions, it was necessary to classify the transects according to the three river positions employed with the flood severity investigation, as stated above. These were a. inside bends, b. outside bends or c. straights. The classification of transects, according to these three classes, is displayed in Appendix 1.

A contingency table was then constructed to facilitate comparison between the proportions of the three river position classes and the three species richness classes investigated. Comparisons were then determined using a Chi-square test.

3.3.2.2 The effects of floods on the demography of riverine communities

Due to the shortage of sufficient species data from before the Domoina flood, it was not possible to adequately test the compensatory mortality hypothesis. The effects of floods on the demography of riverine vegetation was therefore confined to a brief investigative PCQ study instead.

Details of the PCQ technique employed and the location of transects and other information are detailed in the successional approach - chapter 2. In addition to this, three tree size classes were investigated, a. below one metre, b. between one and seven metres and c. above seven metres in height.

In order to determine whether any particular size/age class of riverine vegetation was disproportionately affected by the Domoina flood, correspondence analysis was used to compare the PCQ species frequency data for 57 species from three different sampling dates, 1979, 1984 and 1986. The three sizes classes were investigated for each year as separate columns, while the species were treated as rows of the input matrix. All data were treated as active and no supplementary data were used.

Since the variation accounted for by the first two axes was relatively low (43.3%), it was necessary to consider a third axis, thereby increasing the total variation described to 62%. A three dimensional display and its associated numerical output were produced to aid with the interpretation of the results. Only the three size classes for the three years investigated were plotted as the graphical output, as it was only this relationship which was important for the investigation. The numerical output for only the columns was produced to aid interpretation. The lengths of the lines, which connect the years and size classes investigated, were used as a measure of the flood damages sustained as a consequence of the flood and the degree of dis-similarity between the size classes.

According to Greenacre (1984), variable-variable distances are an approximation of the Chi-square differences between variables and therefore it is acceptable to use these distances as an index of similarity between them. One must take care, however, not to attempt comparison between the positions of variable and objects as no such distances are defined. To simplify the interpretation, it was necessary to convert the dis-similarity measure between size classes to a similarity measure instead. This was done by way of the following formula.

Similarity measure (%) = [1 / line length (mm)] x 100 (dis-similarity)

3.3.3 Modeling the effect of floods on the proportions of various vegetation states

Seventy two random quadrats were selected on six different sets of aerial photographs of the Black Umfolozi river. Within each, the proportions of four discernible vegetation states were determined, using a zoom transfer scope. (For additional information, regarding the aerial photographs used, see successional approach - chapter 2.) These data were then analysed, using correspondence analysis, to reveal the changes in these vegetation states as a consequence of the effects of major floods and the recovery of these areas over time.

The relative proportions of four vegetation states were determined from aerial photographs on six different sampling dates. The relationships between the four vegetation states were determined, using correspondence analysis and the output was plotted graphically. This final correspondence display was used to construct a conceptual model, based on the dynamics of the relative proportions of the different riverine vegetation states in response to the occurrence of flood events. This model was then used as a basis for predicting the effects of future flood events on riverine vegetation. The construction of this model was approached as follows. The five time intervals between the sampling dates were considered separately and plotted on separate axis. The vegetation states, at the begining and end of each time interval as well as the length of each time interval, were used as variables for a Markov Model. Assuming that future conditions would be similar to those experienced during each time interval, the Markov model predicted the likely equilibrium condition of the vegetation in terms of the four vegetation states plotted on the correspondence analysis output.

3.3.4 The effects of fire on riverine vegetation

Six 10x30 m transects were laid out in the riverine area according to the procedure described in the island size hypothesis (see community organisation approach - chapter

4). The density of woody and large herbaceous species were monitored within these transects in August-September 1986. It was initially intended that three transects would be used as experimental blocks and the remaining three as control blocks. Fire was introduced into the three experimental blocks but, in the process, control of the fire was lost and the control blocks were subsequently burned as well. Despite this, all six transects were again monitored in the same way as in early December. Changes in the densities of woody and large herbaceous species were then used to detect the effects of fire on these species. Control blocks were required with which to compare these experimental blocks in terms of changes which occurred in the area in the absence of fire. However, since these were burned as well, it was necessary to make conclusions without this evidence.

3.4 Results

3.4.1 Disturbance regime

3.4.1.1 Flood intensity and frequency

Figure 3.1 displays flood sizes in excess of 1500 cubic metres per second for a period of 97 years from 1890 to 1987 as measured at the railway bridge on the Umfolozi river.

The Umfolozi river is fed by both the Black and White Umfolozi rivers, and the catchments of these rivers are situated in two different areas of Natal (Fig. 1.3). It must be noted therefore that the flood values obtained from this station situated on the Umfolozi river, exceed those which were experienced on the Black Umfolozi river alone.

From visual scrutiny of Figure 3.1, it appears that large flood events are increasing in both size and frequency with time. According to Table 3.1, the frequency of floods was found to be approximately one flood every six years. This frequency displayed an significant increase (p=0.16) from one flood every 8 years for the period from 1890 to 1939 to one flood every 4.9 years for the period from 1940 to 1987. The mean flood peak size of large floods was found to be 4856 cubic metres per second, which displays a significant increase (p=0.15) from 3640 for the period from 1890 to 1939 to 5615 cubic metres per second for the period from 1940 - 1987. These differences were only displayed with reasonably high probability values (p=0.15 and 0.16), which, it is suggested, was largely a consequence of the paucity of suitable data. Considering this, the observed differences were considered to be significant and the null hypothesis was rejected.

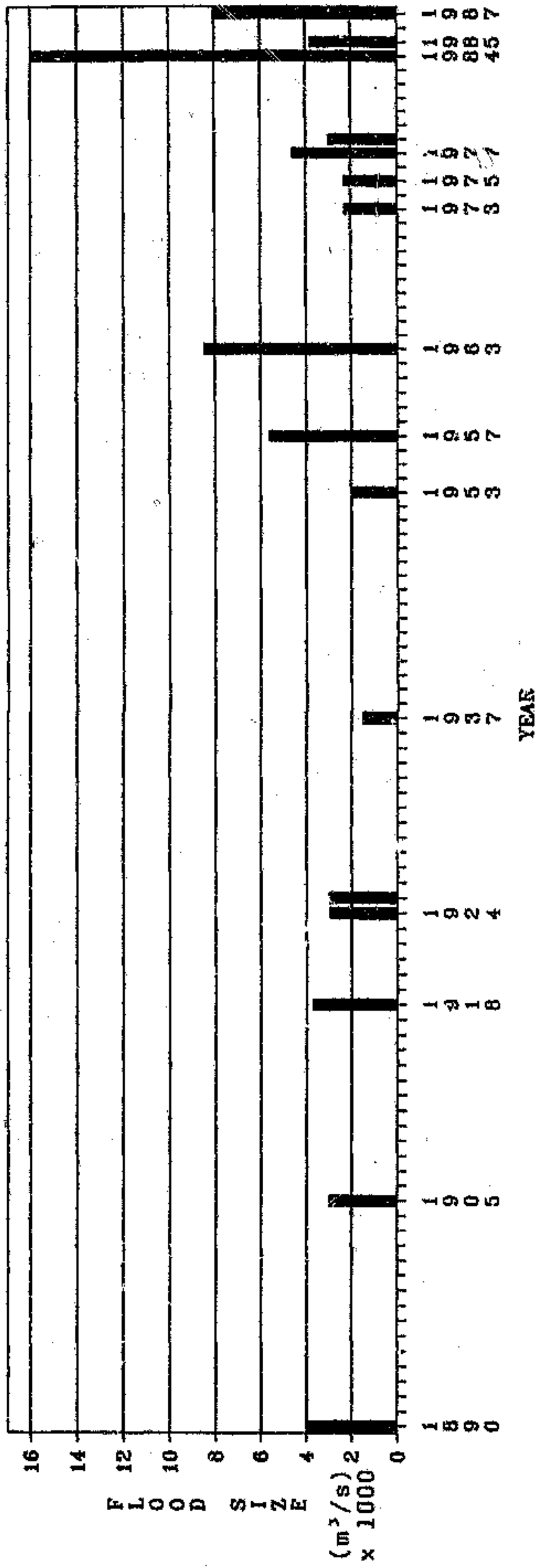


Figure 3.1 The incidences and magnitudes of floods of the Umfolozi river system in excess of 1500 cubic metres per second from 1890 to 1987

Table 3.1 Flood intensity and frequency statistics for three time periods a. 1890–1987, b. 1890-1939, c. 1940–1987 for floods in excess of 1500 m³/s

	PERIOD 1890 - 1987	PERIOD 1890 - 1938	PERIOD 1938 - 1987	SIGNIFICANCE
MEAN FLOOD SIZE (m^3/s) (>1500)	4856	3640 (n=6) (SE=28)	5615 (n=10) (SE=125.8)	student's t-test p ≤5
MEAN FLOOD FREQUENCY (>1500m^3/s)	0.17 (1/6)	0.13 (1/8)	0.20 (1/4.9)	Chi-square test p=0.16

Figure 3.2 displays the annual and January rainfall figures from Nongoma for the 70 year period from 1916 to 1986. Two distinct rainfall peaks are evident from this figure. Firstly, the annual total for 1925 was clearly the largest rainfall event ever recorded from this station, and was due to a 1519 mm event during March of 1925. Secondly, the monthly total for January 1984, was due to the 496 mm event associated with cyclone Domoina. Both events were responsible for large destructive floods within the Umfolozi river system.

Table 3.2 reveals that the mean annual rainfall (in excess of 950 mm/yr) increased from 1237 mm for 1916-1951 to 1247 mm for 1952-1956. However this increase was not significant, even at $p \leq 0.15$. The frequency of large rainfall events has evidently increased from 0.37 (1 every 2.7 years) to 0.42 (1 every 2.4 years), however, this difference is also not significant, even at $p < 0.16$. The null hypothesis was accepted.

3.4.1.2 Flood severity

Flood severity differences between the inside and outside river bends and on straight river stretches are displayed in Figure 3.3. Severity was found to be highest on the inside bends and straight stretches and least severe on the outside bends. The LSD bars show that significant differences ($p=0.05$) in flood severity existed between the inside and outside bends. Only 16.2 percent of large trees remained on the inside bends after the floods, while 24.3 percent remained on the outside bends. No significant differences were found between the inside bends and straight river stretches. A large variation was found in the abundances of trees removed from the

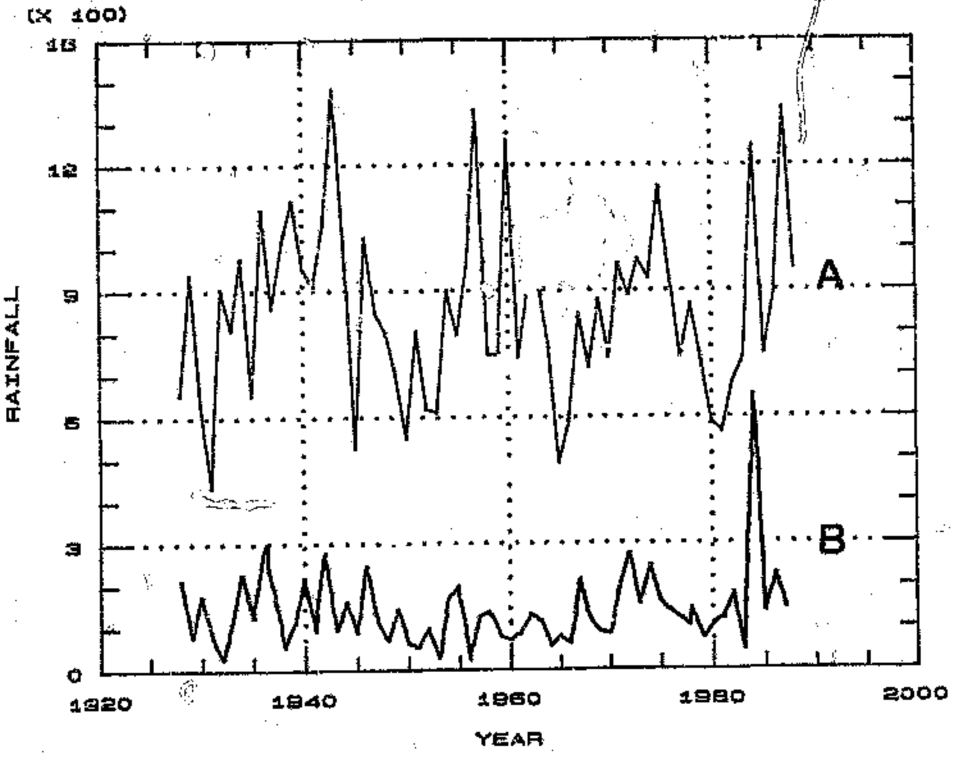


Figure 3.2 Horizontal time sequence plot for annual rainfall and January rainfall for Nongoma for the period 1916 to 1986

A - Annual rainfall
B - January rainfall

Table 3.2 Summary statistics of the intensities and frequencies of large rainfall events (events greater than 950 mm per year) for Nongoma for two periods, 1916-1931 and 1932-1986

	PERIOD 1916 - 1951	PERIOD 1952 - 1986	SIGNIFICANCE
MEAN ANNUAL RAINFALL (mm/yr) (>950)	1239.9 (n=13) (SE=107.6)	1247.6 (n=15) (SE=199)	ns (p=0.9) Student's t-test
RAINFALL FREQUENCY (>950 mm/yr)	0.37 (1/2.7)	0.42 (1/2.4)	ns (p=0.4) Chi-square test

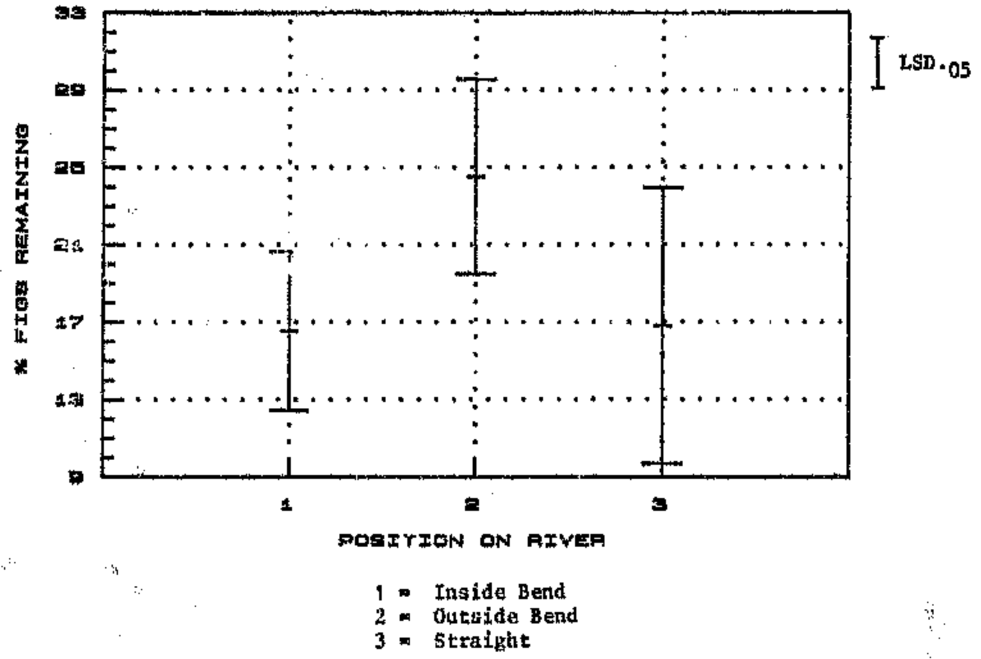


Figure 3.3 Flood severity differences between the inside and outside river bends and on straight riverine stretches

straight stretches which consequently increased the width of the LSD interval considerably. This was due to the difficulty involved with clearly defining a straight. In most cases a straight river stretch which followed immediately after a bend could not be used as it was subjected to overwash from the bend. The characteristically winding nature of the Black Umfolozi river therefore made this task exceptionally difficult.

3.4.1.3 Duration

The duration of past floods (in excess of 1500 m^3/sec) in the Umfolozi system has been highly variable, ranging from three to thirty days.

1952 - 3 days
1957 - 9 days
1963 - 11 days
1977 - 30 days
1984 - 5 day
1987 - 10 days

Figure 3.4 displays the flood hydrographs for the (A) 1957, (B) 19[illegible] and (C) 1977 floods. Individual flood events are clearly idiosyncratic, often displaying numerous peaks of variable duration.

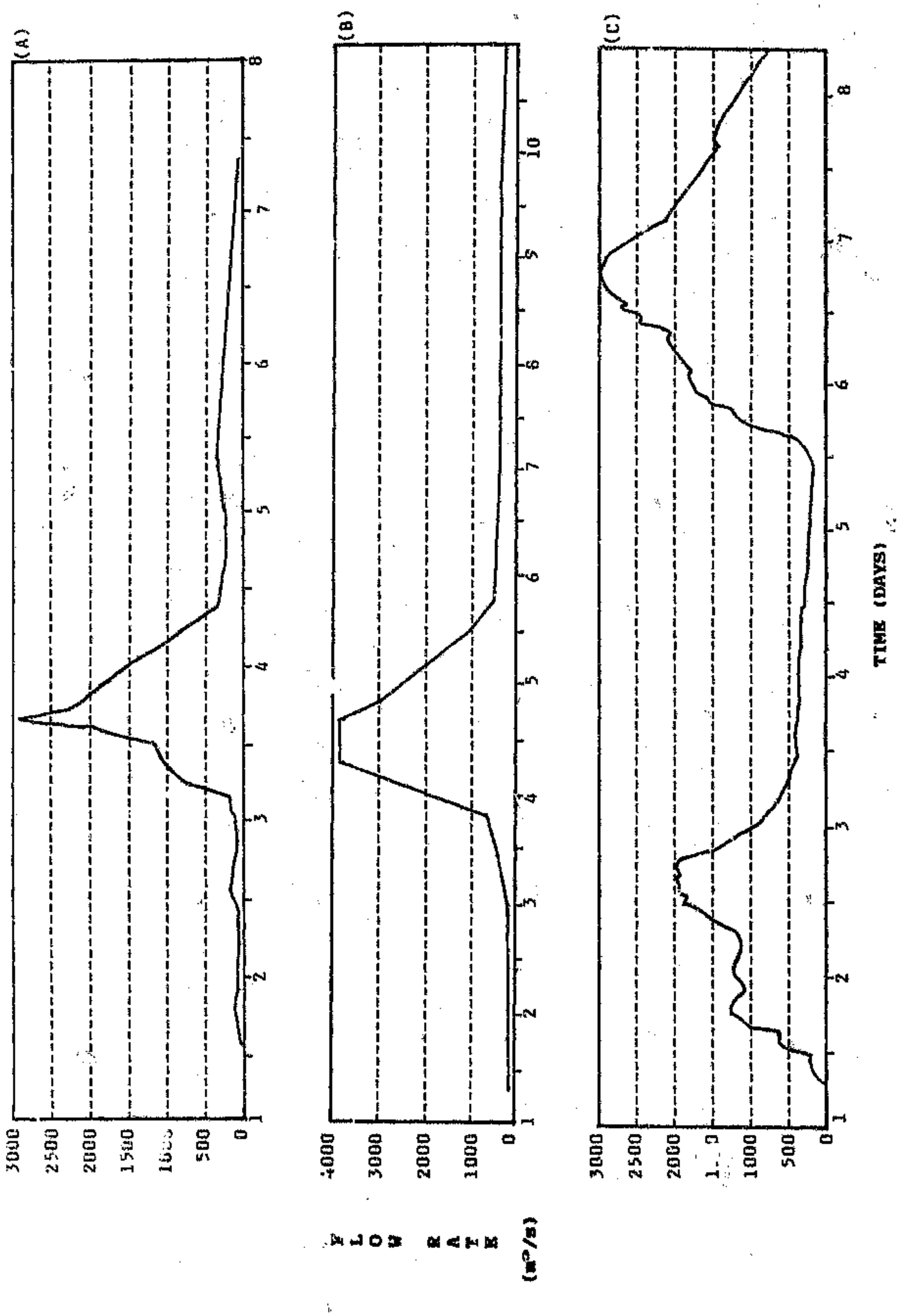


Figure 3.4 Flood hydrographs for the 1957 (A), 1963 (B) and 1977 (C) floods as obtained from the Department of Water Affairs

The 1957 flood displayed a single peak with short duration, while the 1977 floods displayed a double peak over a relatively long period. A complete hydrograph was not available for the Domoina flood.

3.4.1.4 Areal extent of flooding and flood dynamics

Figure 3.5 is a map of a 6.5 km stretch of the Black Umfolozi river from the Thobothi river mouth to the mouth of the Mona river. The high water mark of the flood is indicated by a solid line running parallel to the river's edge. The zone between the river's edge and the high water mark, the flood zone, is an indication of the relative steepness of the riverine slope. The inner river bends are flat (wide flood zones), while the outer bends are steep (narrow flood zones).

Zones of heavy erosion within the flood zones are shaded, these indicate areas where the force of the flood was particularly high, exposing underlying layers of rock or hard basal soils. One could expect that erosion would be highest in areas where changes to the direction of the river are enforced (i.e. at outer areas of river bends). Both the inner and outer bends display areas of severe erosion, but large areas are also evident between bends at distinct heights above the river level. Figures 3.6 (A) to (C) represent three different stages of the Domoina flood. The arrowed lines represent points where maximum flood force was experienced during each particular stage of the flood.

During the early stages of the flood (A), the water level increased from a relatively low level (for the month of February) to the maximum level contained by the river banks. The normal river course was followed by the flood waters and as the levels increased further, river bend exaggeration occurred placing maximum force on the outer bends where its velocity was the highest, leading to bank erosion. Eventually, as the water levels rose further, the flood waters were no longer contained by the river banks and began to wash over the banks (B).

This allowed for the water to take the shortest route over the inner bends. Since these inner bends are most severely affected by floods, the plants and alluvia on these bends were readily removed as the force of the flood was partially shifted onto them from the outer bends. Force was also exerted further and further along the outer bends, leading to the initiation of further eroded areas. Eventually, inner bends were cut short by as much as 300 metres by the flood waters to attain vertical displacements of 40 metres above normal river level. A second phase of inner bank exclusion occurred in the region of the flood peak (C), where water levels were so high that they began to wash over the lower lying areas at the bases of inner bends but since the river was essentially flowing on a relatively straight path at this stage, erosion to these areas was minimal.

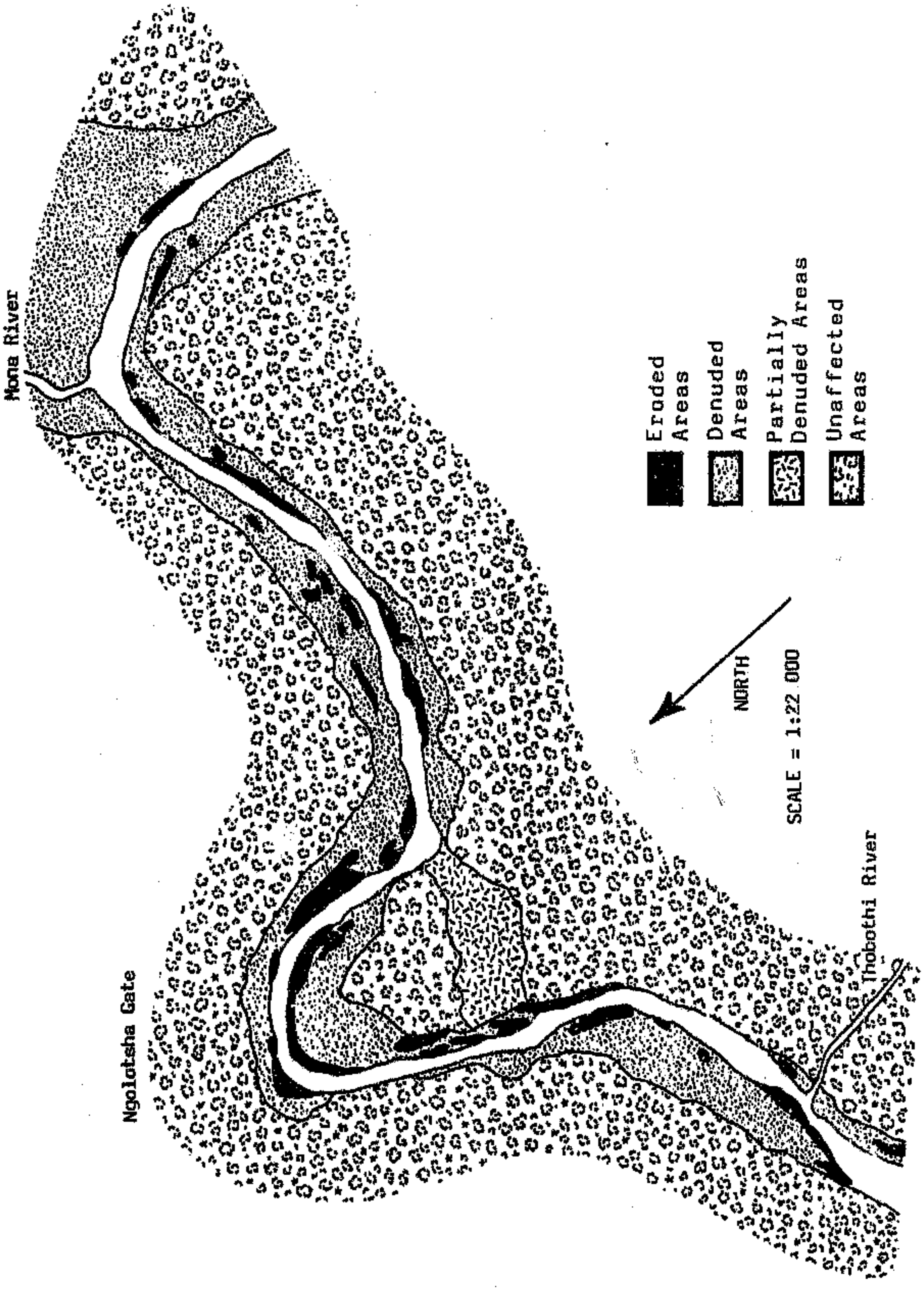


Figure 3.5 A 1:22 000 map of a stretch of the Black Umfolozi river from the Thobothi river mouth to the mouth of the Mona river displaying the high water mark of the Domoina flood and the zones of erosion and soil deposition created by this flood

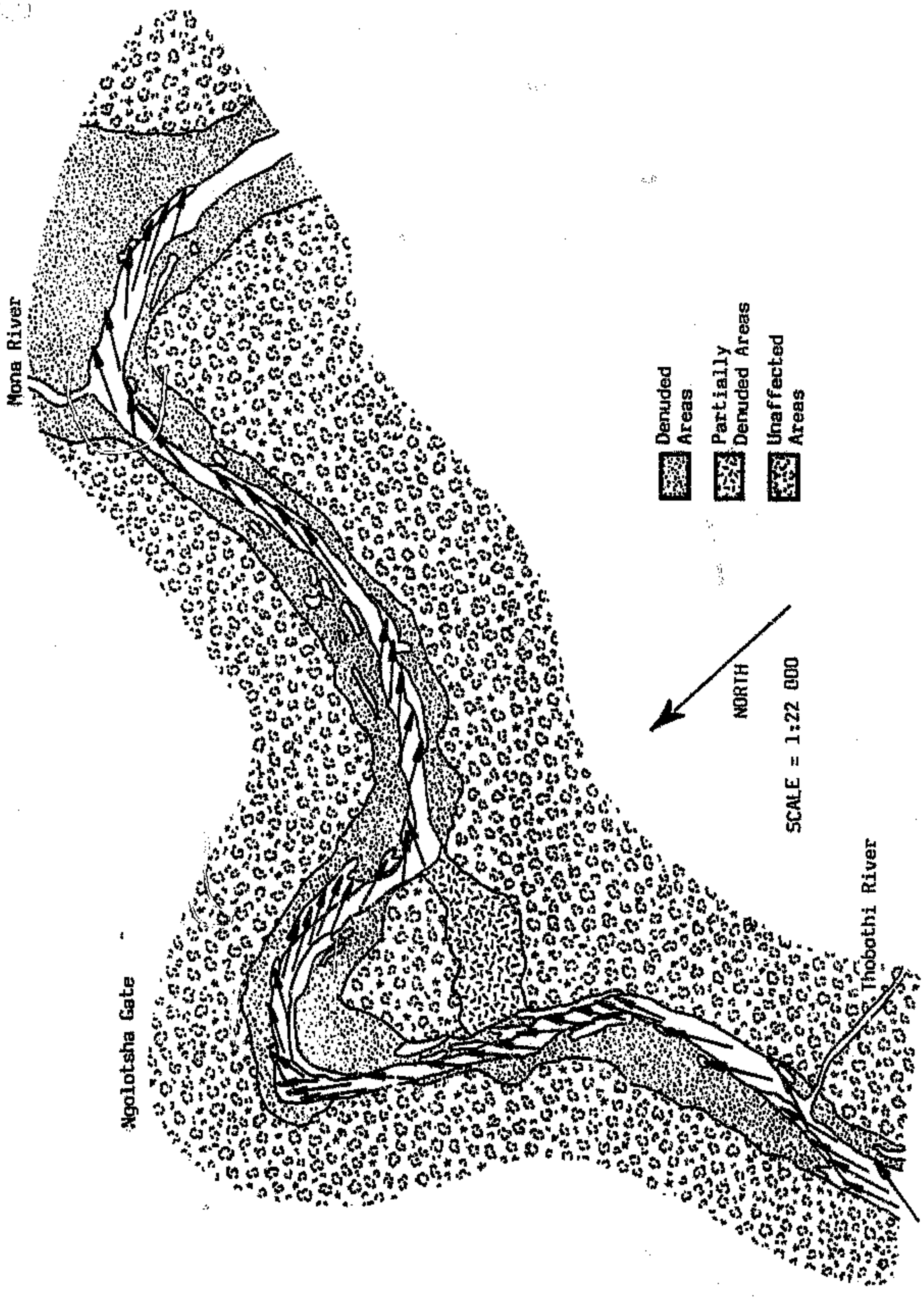


Figure 3.6 Map of a stretch of the Black Umfolozi river showing points of maximum erosion at various stages of the Domoina flood

(A) Early stage of flooding

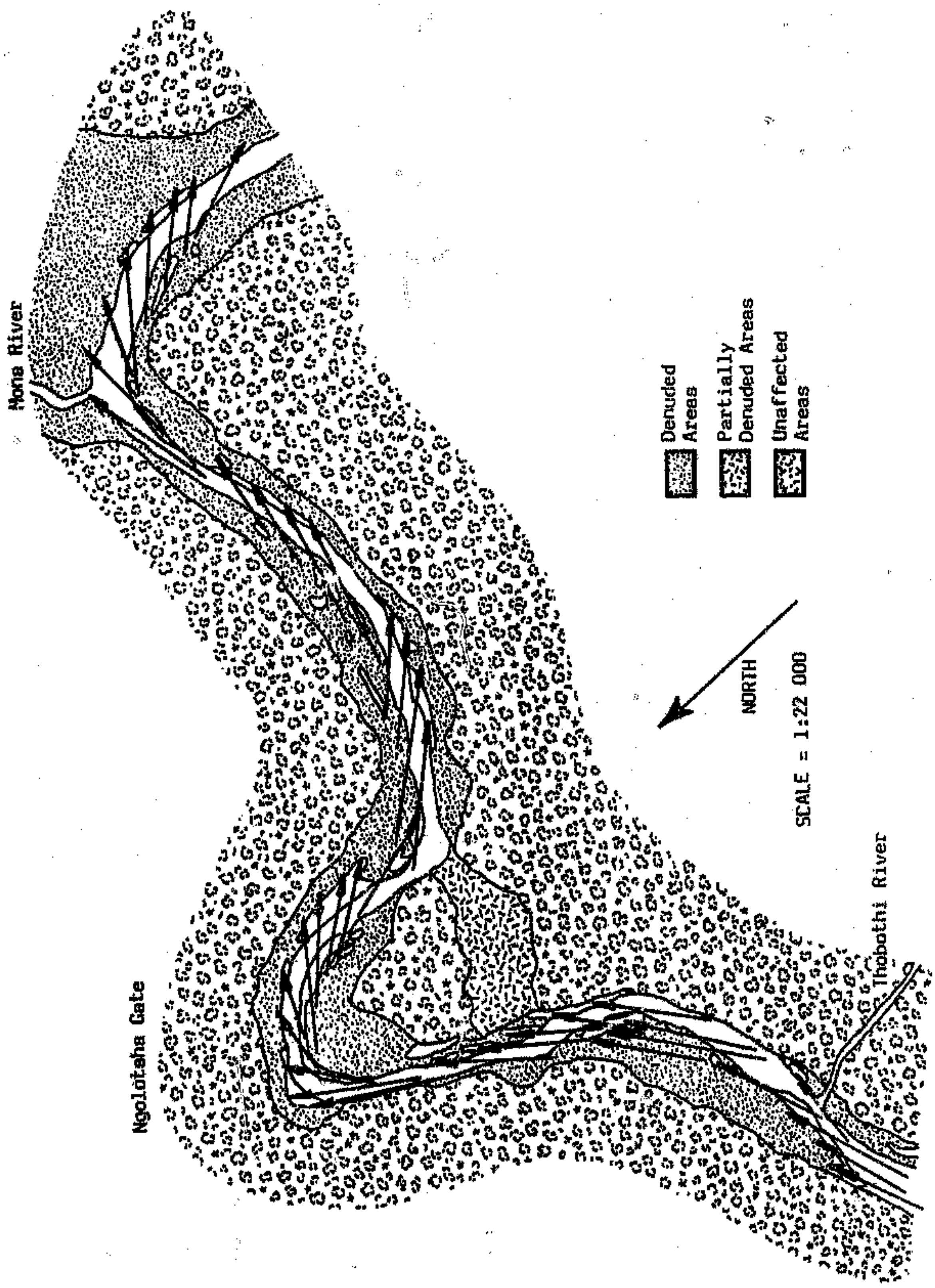


Figure 3.6 continued

(B) Middle stage of flooding

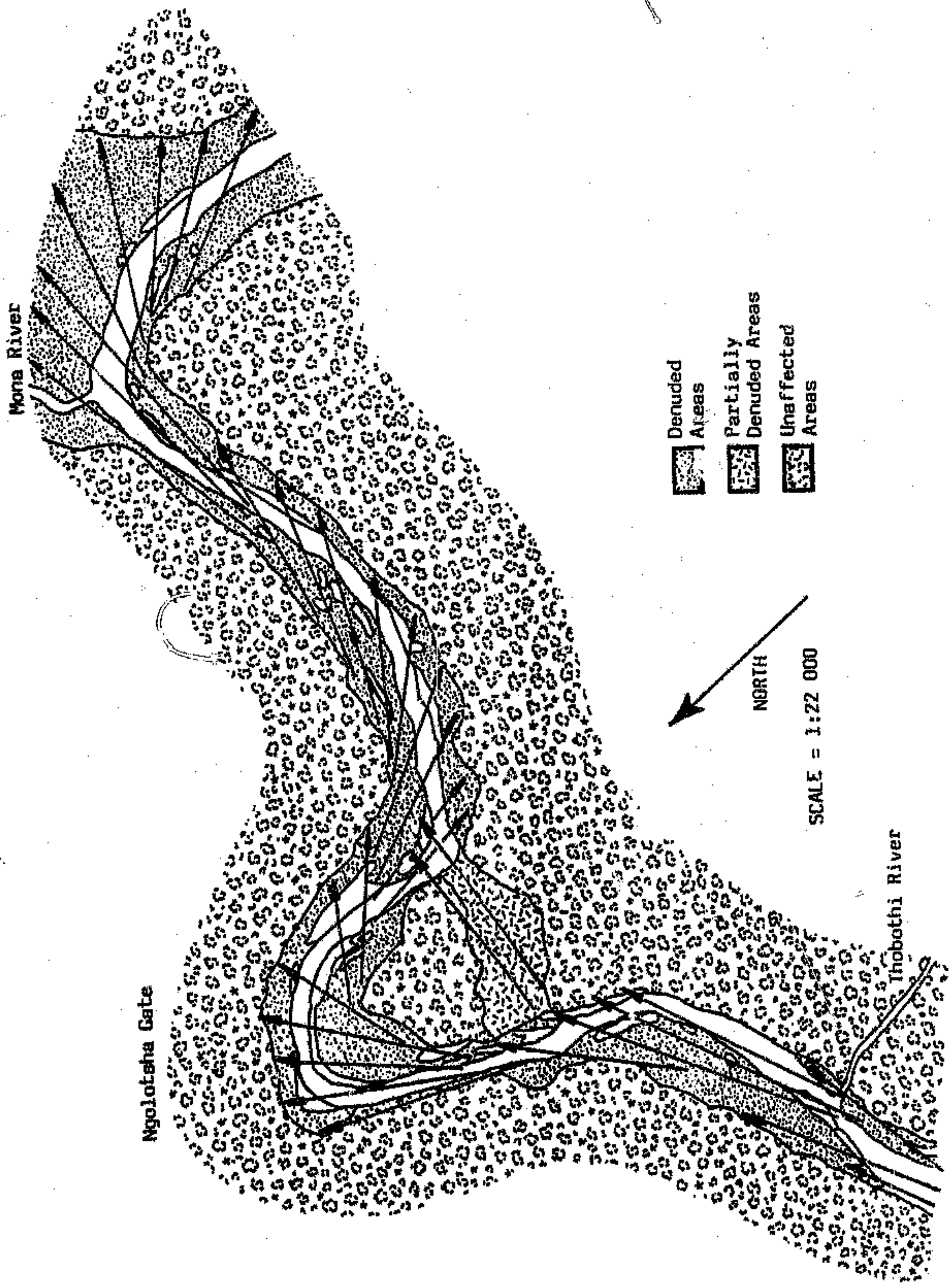


Figure 3.6 continued

(C) Late stage of flooding

Flood waters are characterised by large sediment loads which are carried in the internal eddies of the turbulent waters. These sediments largely arise from exposed and eroded areas of the catchment which are removed by the impact of rain drops and subsequently carried into the river. Additional particles are also collected along the way from river banks and other areas which are eroded by the force of the flood.

The smallest particles are collected most readily and are carried for greater distances. These particles are referred to as the suspended load. Larger particles, the bed load, are carried less readily and are the first to be deposited as the water velocity decreases (Morgan, 1979).

As the river level begins to decline after the flood peak is reached, the water velocity begins to decrease. It is at this stage that silt deposition occurs. Areas where water velocity is particularly reduced, due to obstruction or redirection of the main path of the river, are particularly prone to heavy depositions. This is particularly true on the inner bends of rivers, where silt depths after the Domoina flood were measured in excess of six metres. The suspended load carried by floods within the Umfolozi river system has gradually increased over the last few years (Looser, 1985) leading to the deposition of increasing quantities of silt and fine sand on the river bends within the reserve.

3.4.1.5 Flood predictability

Figures 3.7 and 3.8 display the log-normal and log-log models respectively as applied to flood peak data in excess of 2000 cubic metres per second at the Umfolozi river recording station. These data also include the 1985 and 1987 flood statistics. Both the fitted distributions displayed high R-squared values (0.93 and 0.95) which indicates the high degree to which they fit the data. The return period values for floods of various sizes have been extrapolated on these figures. These return period predictions for floods of different sizes are presented for both models in Table 3.3. This enables the effective comparison of the two models and their return period predictions.

The models predict the probable return period of a flood the size of the 1957 flood (5650 m^3/sec) to be 15 to 22 years, a flood the same size of the 1963 flood (8500 m^3/sec) to be 30 to 38 years and a flood the same size as the Domoina flood (16000 m^3/sec) to be 91 to 108 years.

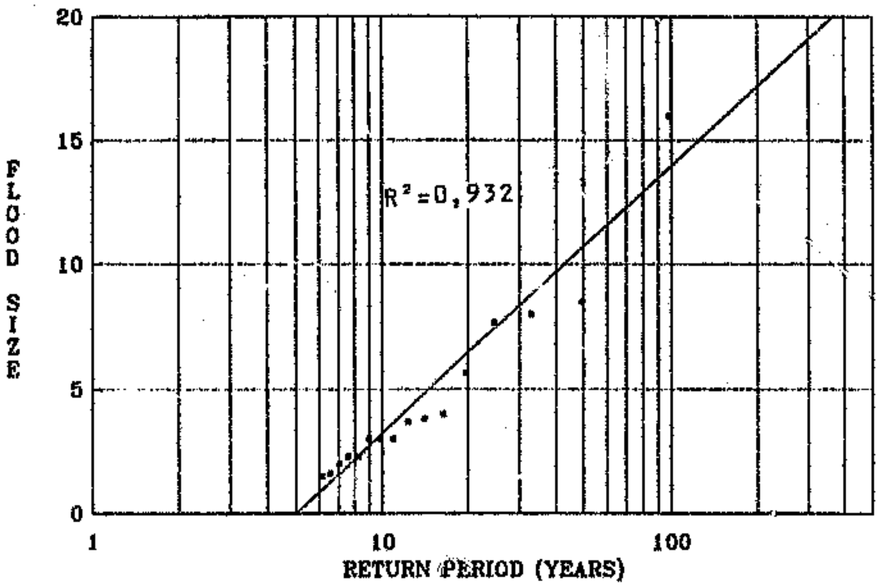


Figure 3.7 Log normal flood prediction model as applied to flood peak data in excess of 2000 cubic metres per second for the period from 1890 to 1987

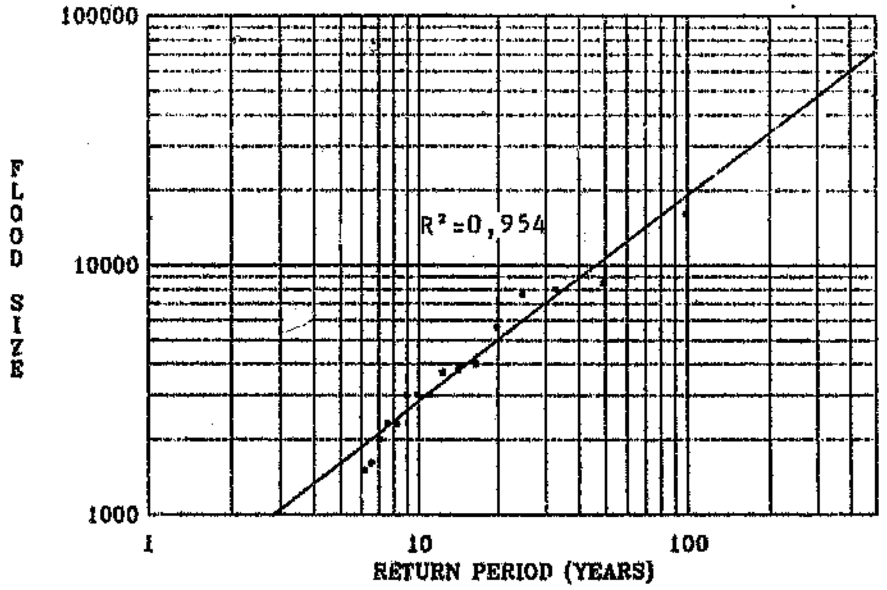


Figure 3.8 Log log flood prediction model as applied to flood peak data in excess of 2000 cubic metres per second for the period from 1890 to 1987

Table 3.3 Probable return period predictions for floods of different sizes as determined by log normal and log log models

	APPROXIMATE RETURN PERIOD PREDICTION (YEARS)	
FLOOD SIZE (m^3/SECOND)	LOG-NORMAL MODEL	LOG-LOG MODEL
2000	6.2	5.8
4000	10.1	13.0
6000	18.0	23.0
8000	28.0	33.0
10000	42.0	43.0
12000	68.0	62.0
14000	100.0	81.0
16000	103.0	91.0

3.4.2 Effects of floods on the species diversity

3.4.2.1 Intermediate disturbance hypothesis – transect approach

Figure 3.9 displays the regression for species richness for increasing height above river level. Of the six different models investigated, the linear model was found to fit the data best (R-squared = 0.125). The correlation coefficient of 0.354 indicates a positive relationship between species richness and quadrat height above river level. The R-squared value however indicates that the regression only accounts for 12.54 percent of the variation in species richness along the height gradient investigated.

Three transects were left out of the analysis.

a. Two entire transects were situated on completely flat riverine areas. Once the river bank level is breached by a flood at these sites, small increases in river level would lead to the complete submergence of the entire transect, thereby revoking the basic assumption that increases in flood size would have an effect further up the riverine slope. Vegetation transects were not carried out far enough up the slope to enable comparisons of these transects.

b. The remaining site had a large tributary running behind it, which may have complicated the species richness values at the upper end of the gradient.

No curvilinear trends, which describe a higher species richness in the intermediate zone of this height gradient, appear to exist.

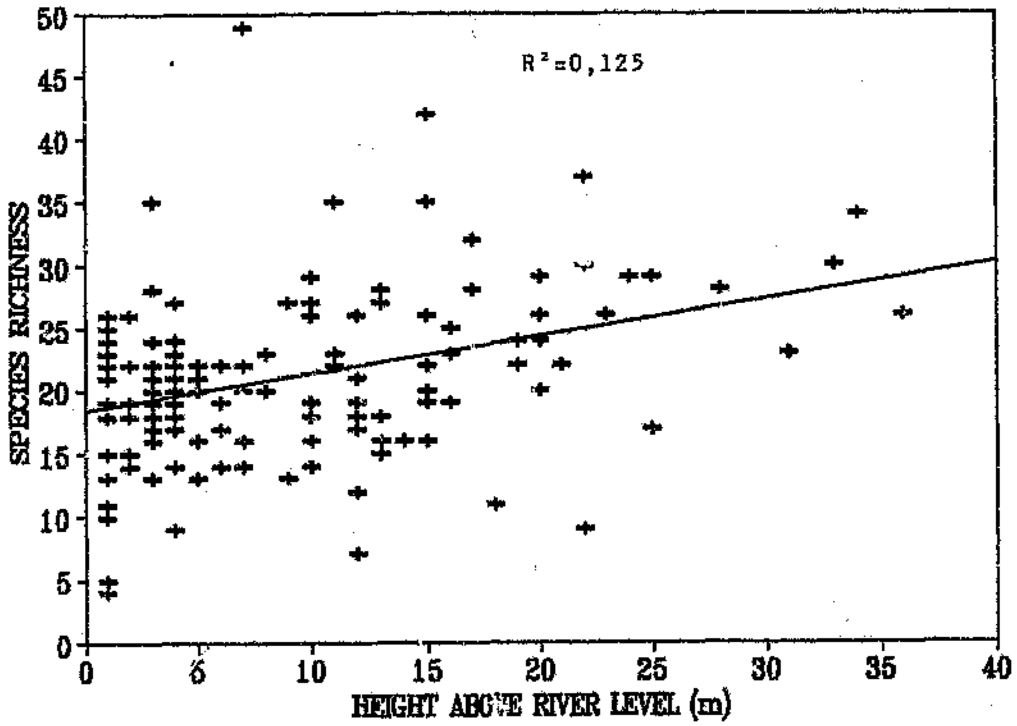


Figure 3.9 The regression of total species richness for increasing height above river level

3.4.2.2 Intermediate disturbance hypothesis - river position approach

The species richness, in ascending order of their means, for the 26 transects employed are displayed in Figure 3.10. The three species richness classes are labeled as A, B, and C to represent the low richness, medium richness and high richness classes respectively. The delineation of these classes was based arbitrarily on the presence of three visually discernible classes. However, significant differences in species richness between the first and last classes do exist.

The contingency table of species richness versus river position classes (Table 3.4) reveals a significant association between the three river positions and their corresponding species richnesses. Inner bends are associated with middle class species richnesses, outside bends are associated with high species richnesses and straight river stretches are associated with low to middle species richnesses.

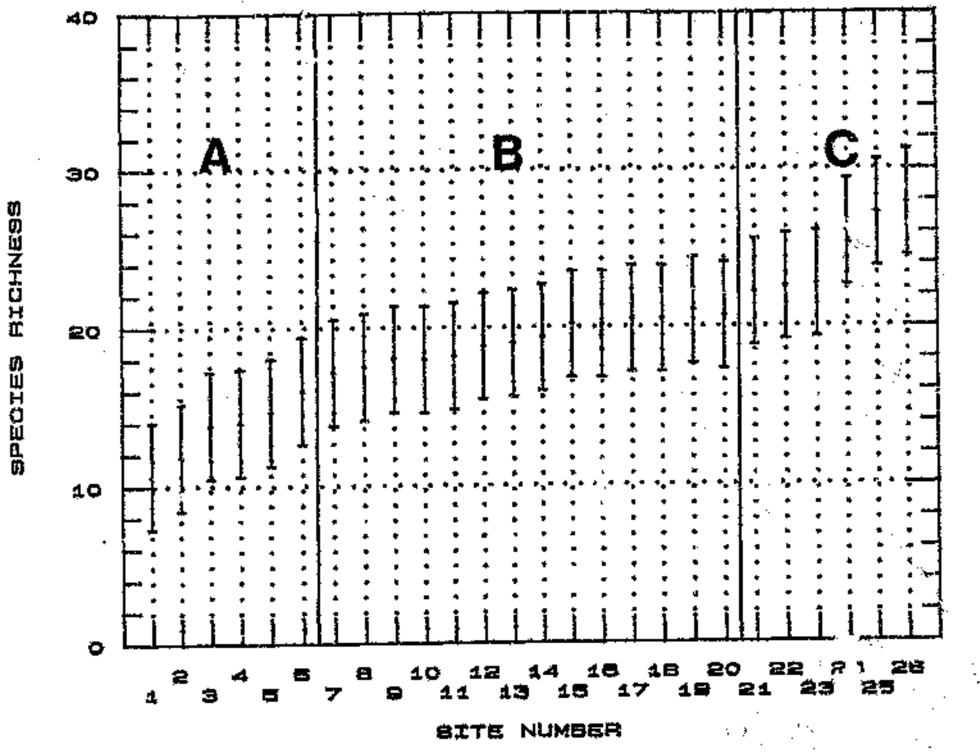


Figure 3.10 Species richness means with LSD (p=0.05) intervals for 26 transects in ascending order of means, displaying three arbitrary species richness classes

A - low richness class
B - medium richness class
C - high richness class

Table 3.4 Contingency table of species richness versus river position classes

	SPECIES RICHNESS		
RIVER POSITION	LOW	MEDIUM	HIGH
INSIDE BENDS	0	1	0
OUTSIDE BENDS	0.14	0.28	0.58
STRAIGHTS	0.39	0.46	0.15

Chi-square - 11.53
D.F. - 4
Significance - 0.02

The relationship between flood severity and species richness at the three river positions is achieved with reference to Figure 3.3. This relationship is summarised in Table 3.5.

Table 3.5 Summary table of the relationship between river position, flood severity and species richness

RIVER POSITION	FLOOD SEVERITY	SPECIES RICHNESS
Inside bend	High	Intermediate
Outside bend	Low	High
Straights	Intermediate	Low to Intermediate

3.4.3 The effects of floods on the demography of riverine communities

Figure 3.11 displays the 3 dimensional correspondence analysis displays for three separate PCQ transects conducted near the Gqoyeni mouth. The associated numerical output of the analysis is presented in Appendix 2.3.

(A) displays the results with the three years connected by lines, in chronological order, for the three tree size classes investigated. The variations in species frequencies, as a consequence of the flood and the period thereafter, are represented by the total length of the lines joining the years.

Losses sustained due to the floods alone (first period), are represented by the line lengths joining 1979 to 1984. Subsequent losses, due to damages sustained (second period), are then represented by the line lengths between 1984 and 1986. Table 3.6 (1) compares these losses using an arbitrary measure of line lengths.

For the first period, the largest losses were sustained by the small trees and large trees while the medium sized trees were affected to a lesser degree. For the second period, however, medium sized trees and small trees were most severely affected and large trees were least affected. The total flood losses sustained for the total period investigated, therefore, were sustained by the small trees and medium sized trees while the large trees were far less susceptible.

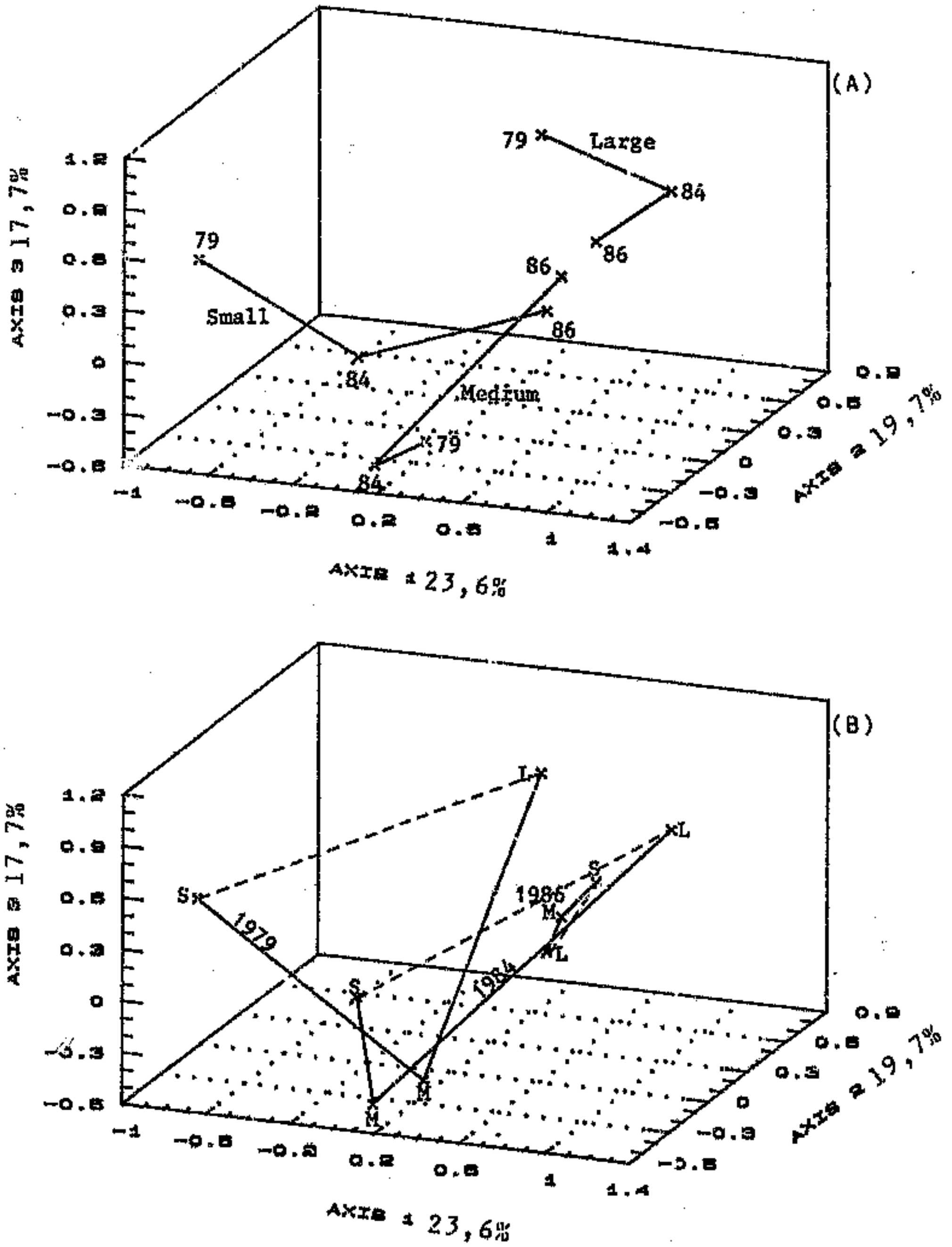


Figure 3.11 Three dimensional correspondence analysis display for PCQ transect results obtained from three separate sampling dates - 1979, 1983, 1986 for three tree height classes, SMALL - less than 1m in height,
MEDIUM - between 1 to 7m in height,
LARGE - greater than 7m in height.

(A) Displays the results with the three sampling dates connected by lines in chronological order. The arrows reveal the direction of the order, 1979 (before Domoina floods), 1984 (immediately after) and 1984 (2 years after)

(B) Displays the same set of results with the three different size classes connected by lines - small, medium and large

Table 3.6 Relative measurements of losses sustained and species frequency similarities for three tree size classes between three sampling dates from a PCQ study conducted near the Gqoyeni river mouth, showing

(1) losses sustained by three size classes of tree species in terms of initial losses (due to flood), subsequent losses (due to subsequent die-off after flood) and total losses

(2) species similarity measurements for the three sampling years between three different size classes of trees

(1) SIZE CLASS	INITIAL FLOOD LOSSES (PERIOD 1) (mm)	SUBSEQUENT FLOOD LOSSES (PERIOD 2) (mm)	FINAL FLOOD LOSSES (TOTAL) (mm)
Small	28	29	57
Medium	8	40	48
Large	21	8	29

(2) YEAR	SIMILARITY MEASURE (SMALL-MEDIUM) (%)	SIMILARITY MEASURE (MEDIUM-LARGE) (%)	SIMILARITY MEASURE (SMALL-LARGE) (%)
1979	2.3	2.0	1.8
1984	6.2	1.6	1.9
1986	12.5	16.6	7.6

(B) displays the results with size classes connected by lines for each of the three years investigated. The length of the lines represents the dis-similarity between the three size classes in terms of species present and their frequencies. Table 3.6 (2) compares the similarities between size classes using the percentage inverses of the line lengths.

Similarities between the size classes in 1979 were small between all three size classes investigated. This was due to the large diversity of species and their frequencies. All three size classes was represented by species which were not represented by the other classes. The similarities between the size classes are represented, on the display, by an almost equilateral triangle of similarities between classes. It is suggested that this represents a healthy balance between the three size classes and defines a stable age/size structure of the species present and their frequencies.

After the 1984 flood, similarity between the size classes generally increased due to the loss of species and the decrease of overall species frequencies. The similarity between size classes is represented, in the display, by a triangle with unequal sides. This is particularly true for between the small and medium sized classes which were disproportionately affected by the flood, which had the effect of decreasing their similarity with the large tree class.

In 1986 subsequent tree deaths due to flood sustained damages lead to a further increase in the similarity between size classes. Once again the similarity between the size classes, in the display, is represented by a an unequal triangle. The similarity between small and large trees is the smallest.

3.4.4 Modeling the effect of floods on the proportions of various vegetation states

Figure 3.12 displays the 2 dimensional graphical output of correspondence analysis for the correspondence between four different vegetation states and six sampling dates. The interpretation of these results is assisted with reference to the associated numerical output of the analysis (Appendix 2.2), Figure 3.1 which display the dates and sizes of previous flood events, and Figure 4.35 which reveals the exact proportions of each vegetation class at each sampling date. Figure 3.12 appears to define the disturbance gradient of the system which evidently takes the form of an arch, with low disturbance on one end and high disturbance on the other. A corresponding trend in the proportions of the four vegetation states is evident as a consequence of this disturbance. Equilibrium at one end with large proportions of tall trees and dis-equilibrium at the other end characterised by large proportions of the grass/sand state.

The 1954 sampling date displays a high correspondence with large proportions of reeds (REEDS), tall trees (FIGS) and smaller trees (ACACIA) and a small proportion of grass (GRASS). The time period from 1925 to 1957 was relatively free from floods with flow rates larger than 1500 cubic metres per second. This thirty year period provided sufficient time for the system to reach an equilibrium. The point representing 1954 in Figure 3.11 is therefore considered to represent a riverine community close to equilibrium. The early spring floods of 1957 disturbed this condition (by the removal of herbaceous cover and woody seedlings), with both large trees and medium sized trees remaining in 1960 at the expense of small trees, reeds and grass. The winter floods of 1963 were severe and removed significant quantities of large and small trees. However, despite this major disturbance, by 1973 the system had recovered to a large degree, and the proportions of the four vegetation states had almost returned to their 1954 state.

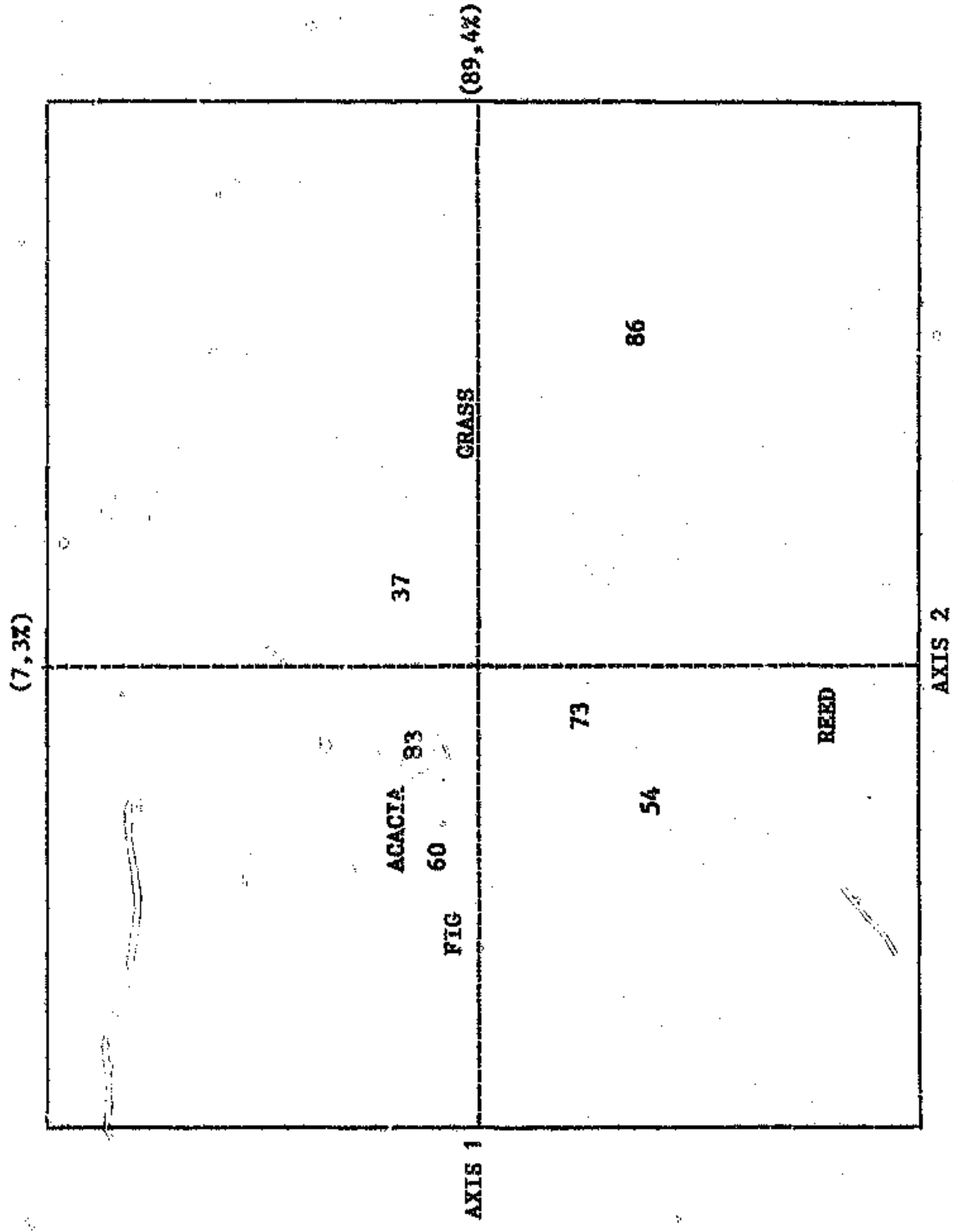


Figure 3.12 Two dimensional correspondence analysis display for aerial photographic data collected from six sets of photographs - 1937, 1954, 1960, 1973, 1983 and 1986

The 1973, 1975 and 1977 floods initiated the start of a significant decline in large tree proportions, with the simultaneous increase in small trees and grass/sand proportions. The point representing 1983 reflects this move away from large tree proportions, with increasing proportions of *Acacia* and grass. The Domoina floods in 1984 then brought about a further shift in this direction. The position of the 1986 point relative to the 1983 point reflects the severity of the Domoina floods, which removed the majority of large and small trees, placing it into close association with the grass state.

The end-point proportions as predicted by the transition matrix models (Table 4.14), serve to support these findings. The predictions for periods of time, which were plagued by large or recurrent flooding, display possible equilibrium proportions which are characterised by large proportions of grass and small trees. (i.e. 1954-1960, 1960-1973, 1973-1983, and 1984-1986). The period 1937-1954 predicted large proportions of tall and small trees, which serves as a valuable indicator of the direction of recovery of the system.

3.4.5 The effects of fire on riverine vegetation

Differences in the density of woody and large herbaceous species, as a consequence of the impact of fire in riverine areas, are presented in Table 3.7. Negative values indicate a net loss of individuals, while positive values indicate a net gain of individuals as a consequence of the burning. Zero values therefore indicate no changes.

Despite the shortage of adequate control data, some important findings are still evident. Species marked with an "*" in Table 3.7 either displayed reasonable consistency in their responses to burning in at least 50 percent of the transects investigated, or an extreme response. They were then classified according to such a response in Table 3.8 as either fire sensitive or fire insensitive. The data for species not marked with an "*" is clearly of little value due to shortage of replicates.

Three species which are particularly characteristic of riverine areas, *Ficus sycomorus*, *Sesbania sesban* and *Phyllanthus reticulatus*, displayed strong sensitivity to fire, while a further three species, *Trema orientalis*, *Schotia brachypetala* and *Nuxia oppositifolia*, displayed weak sensitivity. *Acacia robusta*, another riverine species, showed no sensitivity to fire. Since the majority of plants were under two metres in height, this is an indication that fire generally serves to retard the re-colonisation of riverine areas by characteristically riverine species.

Table 3.7 Differences in woody species densities from before and after the 1986 burns for six transects

SPECIES	SITE NUMBER 1	2	3	4	5	6	TOTAL
Acacia gerrardii	0	1	0	2	0	-4	-1
Acalypha glabrata	15	1	1	0	2	0	19*
Acacia karroo	0	0	-	-	-	-	0
A. nigrescens	0	-	1	-	-	-	1
A. robusta	3	-2	2	2	3	0	8*
A. schweinfurthii	-	-	-	0	0	-2	-2
Azima tetracantha	-	-	-	0	-1	245	244*
Acacia tortilis	-	-	-	0	0	4	4
Berchemia zeyheri	1	-	0	-	-	-	1
Cassia didymobotrya	-	1	-	-	0	-1	0
Dovyalis caffra	0	-2	-	-	-	-	-2
Dichrostachys cinerea	0	-1	0	-	-	3	2
Ehretia rigida	2	-	-	-	-	-	2
Euclea schimperi	0	-1	-2	-	-	-	-3
Ficus sycomorus	-13	-7	-2	-1	-1	0	-24*
Grewia occidentalis	-	-2	-	-	-	-	-2
Lippia javanica	-	2	3	2	-	-	7*
Melia azedarach	-2	-1	0	-	-	-	-3
Maytenus heterophylla	0	-2	-1	2	15	26	40*
Maytenus senegalensis	2	1	0	-2	-15	-24	-38
Nuxia oppositifolia	-1	-	-	-	-	-	-1
Plectroniella armata	4	1	0	-	-	-	5
Pluchea dioscoridis	4	-7	-2	-	-	-	-5*
Phyllanthus reticulatus	-	-18	-2	-	1	-2	-21*
Ricinus communis (juv)	150	335	905	190	296	95	1971*
Ricinus communis (mat)	-84	-28	-35	-62	-49	-23	-281*
Rhus gueinzii	-	-1	-	-	-	-	-1
Rhus pentheri	3	-	1	-	-	-	4
Spirostachys africana	-5	-3	7	-6	0	0	-7
Sclerocarya birrea	-	-	-	-1	-	-	-1
Schotia brachypetala	-1	0	-1	-	-	-	-2
Sideroxylon inerme	2	0	2	-	-	-	4
Sesbania sesban	-2	-9	-7	0	-	-	-18*
Thespesia acutiloba	-	1	-	-	-	-	1
Trema orientalis	-	-	-1	0	0	-3	-4
Ziziphus mucronata	-	0	2	-	-	-	2

Table 3.8 Sensitivity / insensitivity groups of woody and large herbaceous species to fire based on responses in Table 3.7

GROUP	SPECIES
SENSITIVE	*Ficus sycomorus* *Maytenus senegalensis* *Phyllanthus reticulatus* *Ricinus communis* (mature) *Sesbania sesban* *Spirostachys africana*
INSENSITIVE	*Acalypha glabrata* *Acacia robusta* *Azima tetracantha* *Lippia javanica* *Maytenus heterophylla* *Ricinus communis* (juvenile)

Three exotic species were also present, two of which displayed sensitivity to fire, which has management implications. Mature *Ricinus communis* plants, which accumulate in large numbers on sandy slopes and which are capable of reaching four metres in height, are removed very effectively by fire. However, it does appear that the seedlings of this species are fire induced, and germinate in exceptionally large numbers after a fire. This poses a major management problem. *Melia azedarach* displayed an inconclusive sensitivity to fire.

Also with management implications, *Spirostachys africana* and *Maytenus senegalensis*, which both form dense, impenetrable thickets in certain riverine areas, displayed conclusive sensitivity to fire. Unfortunately *Dichrostachys cinerea*, which also form such thickets, was not present in large enough quantities to be assessed adequately.

3.5 Discussion

3.5.1 Disturbance regime

3.5.1.1 Flood magnitude and frequency

The reasons for the increasing frequency and intensity of large flood events are unclear. There are two main theories which could be applicable.

1. **Condition of catchment areas**

   Comparisons between the intensities of the 1925 and 1984 floods relative to the sizes of the rainfall events which were responsible for them, reveals differences between the two occasions in terms of the relative condition of the system and its ability to resist flooding. From the markedly larger 1925 annual rainfall compared with that of 1984 and the smaller resulting flood compared with that of 1984, it appears that the system was in a better state to resist flooding in 1925 than it was in 1984.

No information is available regarding the condition of the catchment area prior to the 1925 flood, but a study was carried out by Looser (1985), which described the pre-Domoina condition of the Black Umfolozi catchment area using infra-red LANDSAT images. In this study, 36 percent of the 1648 km^2 catchment was described as "badly damaged" and composed of only bare soil. This study compared the relative condition of a number of areas using the same technique and it was stated that this condition was a consequence of overgrazing. It is currently held that stocking rates of cattle and other livestock in the traditional subsistence areas of South Africa are generally higher than in those areas where Western standards are applied. Consequently, traditional areas, particularly those in semi-arid regions, are in a different state characterised by a heavily grazed and greatly reduced vegetal and litter cover and a high incidence of soil capping. Water run-off is positively correlated with soil capping and negatively correlated with mean grass and litter cover (Venter, 1988) and consequently, accelerated levels of water run-off are expected under these conditions. This increased run-off of water in the catchment areas of the Black Umfolozi is channeled via streams and tributaries and eventually contributes to the flow rate of the Umfolozi river.

The implications of this increased run-off of water are as follows.

a. Rainfall events which, in the past, would have contributed negligibly to the flow rate of the river, would now, due to the addition of further run-off, have the effect of causing major floods. This explanation could explain the increasing size of flood events in the system.

b. Flood events which would have been below 1500 m^3/s in the past, would now, with the additional water run-off, exceed that value and would develop into large flood events. This explanation could explain the increased frequency of large floods in the system.

2. Phase of greater extreme in global climatic conditions

It has been suggested (Bryson, 1974) that the earth's climate has entered a new phase which is generally characterised by greater extremes and variability. No climatic data has been presented to corroborate this claim in the area under investigation, however, if one considers the historical variability of the earth's climate (Lamb, [illegible]1) using a suitable time scale, it is apparent that this is a likely scenario.

From the relatively inadequate data set available and on the time scale investigated, it is evident that the intensity and frequency of large rainfall events are not increasing with time. Consequently, it appears that both the 1925 and 1984 rainfall events were only chance events. While it may appear that the intensity of such chance rainfall events is actually increasing with time, there is insufficient data to test this theory. Only a period of 70 years was investigated in the study, which was as far back as available data would allow. It is possible that a similar investigation, conducted over a longer time period would display trends of this sort.

An arbitrary figure of 1500 m^3/s was used to classify floods as 'large'. It therefore appears that the problem of flood sizes and frequencies is a man-made problem based on this definition. However, a critical flow rate does in fact exist in the riverine situation. This is the point at which bank overflow takes place and water is no longer contained by the banks of the river. Water flowing with high velocities above this level brings about considerable damage to riverine vegetation. This critical level varies from point to point along the length of the river and is dictated to a large degree by the topography of the areas through which the river flows. In mountainous areas this level is high, and it is rare that bank overflow occurs in such places. However, in relatively flat areas such as on river bends and flood plains this level is attained relatively easily and considerable damage can occur. The frequent flooding of such areas would bring about major changes to the structure of the communities which occupy them.

Vegetation on the edges of a river is responsible for consolidating the river banks and thereby serves to check the velocity of floodwaters, prevent river banks erosion and reduce the sediment flow of the river during floods (Alexander, 1978). It can therefore be expected, that along with an increase in flood intensity and frequency, large quantities of sediment would become associated with these floods, and that river bank erosion would become increasingly serious. Sedimentation and the deposition of large quantities of sand and gravel have already become a problem in the slower flowing areas of the Umfolozi river system (Anon, 1986).

A number of characteristics of both events are not evident from the horizontal time plot of rainfall from the Nongoma weather station. These factors had a bearing on the intensity of the resulting floods.

a. The 1925 rainfall event was distributed over the entire month of March, with large events being well separated by smaller events. The total downpour was distributed heterogeneously over a wide area, with the largest value on a single day being 203 mm. The implications of this type of rainfall distribution is that the water is given sufficient time to saturate the soil and, thereafter, to run off at a rate which is not destructive to vegetation.

b. Ninety percent of the 1984 rainfall event fell over a period of three days and exceeded the 3 day 200 year record for the area (Kovacks et al, 1985). The total area covered to this degree was estimated to be approximately 32000 km^2, which included the entire catchment area of the Umfolozi river. Evidently, although the total size of the event was smaller than that for in 1925, it was more intense and homogeneously distributed over a very wide area. This type of rainfall distribution is particularly conducive to the production of large and destructive floods.

The increasing tendency of large flood events in the Umfolozi system was evidently due to a combination of the condition of the catchment area prior to cyclone Domoina, the chance appearance of the Domoina rainfall event and the characteristics of this event.

It is difficult to ascribe the condition of the catchment area purely to past and existing management practices. These areas, while they are largely subjected to a third world approach to pastoralism, were subjected to a long period of drought just prior to 1984. This drought, along with associated ecological effects, was responsible for substantially reducing grass production and ground cover. In addition, previous to this (1973, 1975, 1978 and 1978), a series of four large floods had been experienced in these areas which also affected the condition of the area. The combination of the condition of the catchment areas and the characteristics and timing of the rainfall in 1984 possibly represented the worst extreme which is possible in these areas. It is therefore no surprise that the resulting floods were the largest ever recorded within the Umfolozi system.

3.5.1.2 Flood severity

Before the exercise it was envisaged that, since the force of a flood is usually greatest on the outer edges of a river bend, the severity would also be greatest there. However, it is clear that the force of a flood is not the only factor which determines flood severity.

The inside bends of rivers are typically composed largely of alluvium which is deposited from previous flood events. This acts as a poor anchoring substrate for vegetation, which then facilitates the easy removal of these plants by a flood which is large enough to exceed the banks of the river. In contrast to this, outside bends are often steep scarps composed of hard consolidated soils. These offer vegetation an excellent anchorage, limiting erosion as well as their removal by floods with low erosivity characteristics. This explains why a larger proportion of large trees were left remaining on the outside bends as opposed to the inside bends where they were readily removed. Flood severity is therefore greatest on the inside bends while remaining relatively lower on the outside bends.

3.5.1.3 Duration

The peaks, observed on the available flood hydrographs, correspond to the unphased timing of the numerous tributaries which feed into the river being investigated. This unphased timing is largely a consequence of the following factors.

a. Variation in the distances from the catchment area to the river.
b. The catchment slopes and the resulting variations in water velocities.
c. The distribution and patchiness of rainfall events.

Floods of long duration, like those of 1957, 1963 and 1984 can be unusually destructive, particularly when followed by a second or third major peak as in 1957. This is because the longer water is able to soak into soil the softer and looser it becomes and can then be removed very easily by a second and third peak. The critical duration however is not reflected by the entire hydrograph. The major disturbance is caused to riverine vegetation when the water flow rate reaches the point where overbank flow occurs. As a consequence of the highly unique nature of different flood events and the relative shortage of data of this type, it was not possible to even broadly classify the different types of floods and determine their comparative frequencies of occurrence. It was only possible to consider separate flood events and their magnitudes with regard to the disturbance to riverine vegetation.

3.5.1.4 Areal extent of flooding and flood dynamics

Various stages of the Domoina flood were responsible for the erosion and destruction of different riverine areas. The general patchiness of the area after the flood was a consequence of a variety of factors.

a. The patchiness of different substrates and their relative positions and erodibilities.
b. The degrees of exposure of different areas to flood waters.
c. the degree to which different areas were afforded protection by grass and vegetation cover.
d. The force of the flood at different stages.

The implications of this resulting mosaic of eroded, partially eroded and un-eroded patches in riverine areas is that all patches have been disturbed to different extents and are consequently in different stages of recovery. This reflects the complexity of riverine vegetation as a consequence of the impact of floods.

3.5.1.5 Flood predictability

Lund (pers. comm.) previously predicted the return period of the 1957 and 1963 floods to be in the region of 50 and 100 years respectively, while Kovacks et al (1985) had predicted the Domoina return period to be approximately 300 years. However, these predictions had been constructed using different models and data from only up to 1985.

From Figures 3.7 and 3.8 it appears that the 1985 and 1987 flood data, by contributing as large floods, evidently had a significant bearing on predictions, bringing about a general reduction in return period forecasts for the larger flood events. This finding highlights the increasing probability of experiencing more frequent large and destructive floods in the future.

3.5.2 Effects of floods on species diversity

3.5.2.1 Intermediate disturbance hypothesis - transect approach

The regression results are not consistent with the intermediate disturbance hypothesis because no trends were found to exist which describe or even partially describe a higher species richness in the intermediate zone of the height gradient investigated. Since a positive and linear relationship was found to exist between species richness and increasing height above river level, the findings are not consistent with the null hypothesis either.

It is not clear, however, whether this observed relationship is a consequence of the effects of differential disturbance frequency or intensity with increasing height above river level alone. Differences which exist in the distribution of resources along the riverine gradient are likely to have an influence which would complicate the effect of disturbances along this gradient considerably.

3.5.2.2 Intermediate disturbance hypothesis - river position approach

These findings largely support those of the previous approach that increased flood frequency or intensity results in a decreased species richness.

Straight river stretches display a wide species richness response. However, instead of displaying a higher species richness, in agreement with the intermediate disturbance hypothesis, they generally display lower species richnesses. It is suggested however, that this is only an anomaly which is explained by the difficulty in clearly defining a straight river stretch (see section 3.4.1.2).

Difference exist between the soil characteristics of the three river positions (see section 3.5.1.2). It is, therefore, very likely that these areas would display different resource characteristics and have the possibility of supporting different species richnesses.

3.5.2.3 Intermediate disturbance hypothesis - general

The findings of both approaches suggest that an inverse linear relationship exists between disturbance frequency or intensity and species richness. However, since it is very likely that other complicating factors may be partially or completely responsible for this effect in both cases, it complicates the possibility of proposing an alternative hypothesis which states that species richness decreases linearly with increasing flood frequency/intensity.

It may be argued that the full spectrum of the flood intensity or frequency was not clearly defined first and that the areas identified as being least severely or least frequently flooded, could well represent areas receiving an intermediate intensity instead, which accounts for their higher species richness. This criticism may be well founded, however, for in both tests of the hypothesis there were complications with the identification of the entire flood spectrum.

In the first test, the floods regularly exceeded the bounds of the riparian zone and cause considerable disturbance to the zone above it as well. The two zones have distinctly different characteristics and are likely to display distinct differences in species richness under different disturbance pressures. It is clearly necessary to investigate the hypothesis for each zone independently, and this was not possible.

In the second test, three broad river positions were identified to represent the diversity of river positions along the whole river. These were, in turn, used to describe the full flood severity spectrum. However, in reality each of these three positions display a vast array of characteristics during a flood which are dictated by the topography of the area, the shape of the river immediately before the position the angle of the bend and a variety of other factors. Consequently it was not possible to describe the entire spectrum of the disturbance by these means.

It is suggested that due to differences which exist between the resource conditions down the riverine gradient in the first test and between the three river positions in the second test and due to the difficulties experienced with attempting to define the full spectrum of the disturbance with both tests, it is not possible to refute the intermediate disturbance hypothesis by these approaches. From the outset of the study, no substantial species richness data was available to conduct the definitive approach which would investigate and compare the species richnesses between different sampling dates in relation to a number of flood events.

3.5.3 The effects of floods on the demography of riverine communities

It appears that there are two stages of tree loss as a consequence of flooding. Firstly, the deaths and losses of trees which are a direct result of the force of the flood and the removal of individuals. Secondly, the subsequent deaths which are the result of damages sustained to trees during flooding. Both stages lead to similar losses, depending on the particular size class (Table 3.6).

Large trees experienced the smallest total losses and small trees experience the largest total losses as a consequence of the flood and subsequent die-off after the flood. Both periods contribute equally to the final losses. Medium sized individuals suffered only slight damages during the first period, with their second period losses being much higher. This effect resulted in a final community in 1986 which was very dissimilar in small and large sized trees on the basis of species frequency.

These findings reveals two possible characteristics of riverine communities.

1. The differential susceptibilities of the three tree size classes to flood damage.

   Medium sized trees are relatively unsusceptible to removal by floods, possibly as a consequence of their flexibility and low resistance to water flow - this supports an observation made by Wills (1984).

   Large trees, because of the large resistance of their canopies to flood waters and their relative inflexibility are easily damaged and removed. Small size class individuals have shallow rooting depths and are readily removed by superficial erosion of the substratum by flood waters.

2. The abilities of different size classes to survive the damages sustained by flooding.

   It is proposed that medium sized trees, once damaged by floods, are prone to die from their damages. In contrast, large and small trees are far less prone to death from damages sustained during flooding. It is suggested that this differential ability to survive is related to the size of nutrient reserves available to different sized trees. These reserves would be used to see the individuals through their recovery.

These characteristics describe the effect of an intense flood and help to understand the structure of communities which remain after such a disturbance. This knowledge can be used to explain the structure of existing riverine areas and understand and predict their recovery and the likely effects of future floods of increasing intensity and frequency on this recovery.

A large flood initially removes large quantities of trees below 1 metre in height and above 7 metres in height, leaving a disproportionate quantity of medium sized trees remaining on the site. However, with time these display a disproportionate die off due to their flood damages. Since large trees experience the smallest total losses, it can be expected that the final remaining riverine communities would be represented by unequal proportions of the three size classes. Remaining stands would be characterised mainly by large trees, fewer medium sized trees, and a small proportion of small trees.

It is suggested that these remaining large trees serve a number of important functions with regard to the recovery of these areas.

a. They serve as an important source of seeds and coppice and thereby ensure that future communities are comprised to a large degree of individuals of the same species.

b. Seeds and coppice are provided as soon after the flood as possible to encourage a fast recovery.

c. Large quantities of seeds are provided to augment the greatly depleted seed bank which was removed by the flood along with the superficial soil layers.

d. They serve to outcompete other species which display a faster growth rate than the seedlings of the large tree species. It is envisaged that this mechanism applies particularly well with the exclusion of alien tree species.

3.5.4 Modeling the effect of floods on the proportions of various vegetation states

From the manner in which the riverine system has behaved in response to recurrent large flood events over the last century, it appears that this is a resilient system. A conceptual model is presented (Fig 3.13), based on the classical "ball-in-cup" analogy. This model describes the behaviour of the system to recurrent floods, and strongly

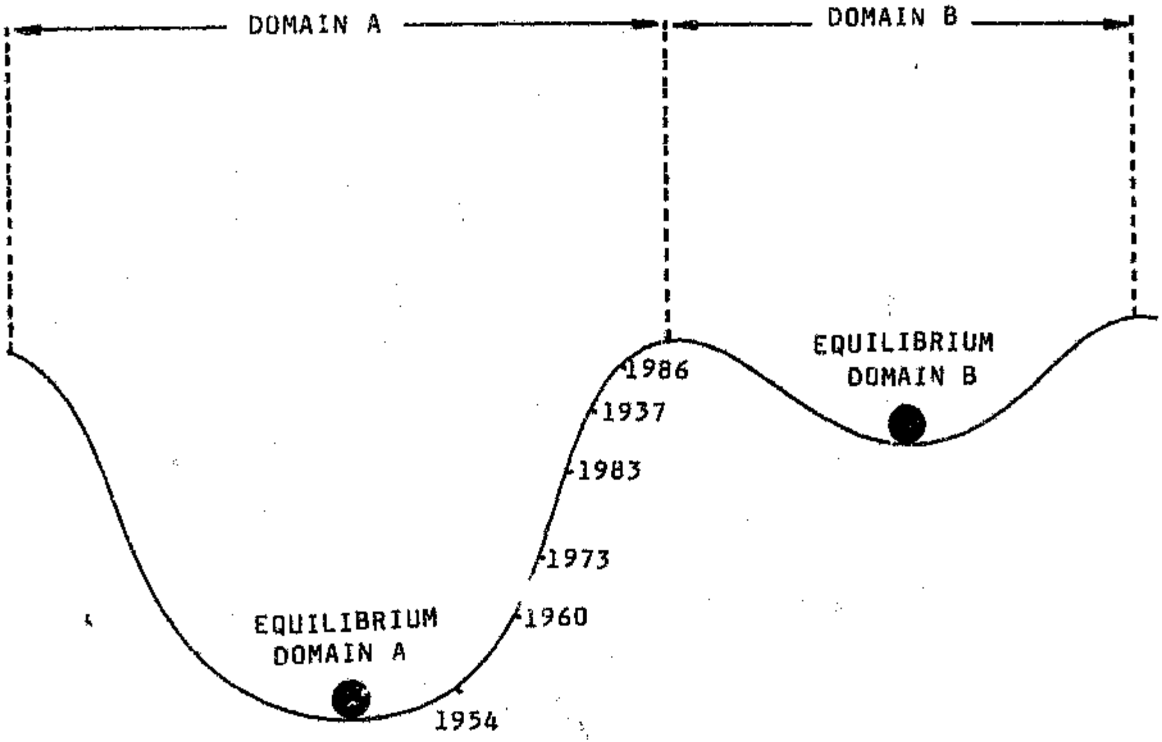


Figure 3.13 Conceptual "ball-in-cup" model for riverine areas

Domain A represents the domain of attraction in which the Umfolozi system currently exists. The years displayed indicate the relative state of the system at each date in response to large flood events over the last 98 years.

Domain B represents a possible alternative domain of attraction which would become applicable should domain A be exceeded.

The circle in each domain indicates its equilibrium condition which would be attained in the absence of further disturbances.

supports current equilibrium theory. During the full period covered by the study, from 1890 to 1986, the system displayed its resilience by repeatedly recovering after each successive flood event and moving back towards the equilibrium state.

During this period, the system has evidently remained within a single domain of attraction. The impact of the 1924/1925 floods served as a good indication of this. These floods were devastating and shifted the system far from the equilibrium state as indicated by the 1937 point. Despite this, by 1954, the system had re-attained a state which is considered to be close to the equilibrium state. Similar recovery was evidently displayed after the 1957 and 1963 floods as well as the combined floods of 1973, 1975 and 1977.

According to available records, the 1986 state (after the Domoina floods) is the furthest that the system has been moved from its equilibrium yet. Since no aerial photographs are available from after 1986 and the direction of recovery after 1986 has not been determined, it is not clear whether the same behaviour has applied after the Domoina flood and whether the system has remained within the same domain of attraction. Further monitoring would be necessary in order to confirm this but there is no evidence which suggests that this event has caused the system to exceeded this domain.

3.5.5 The effects of fire on riverine vegetation

Due to the uneven distribution of species present, the patchiness of the burns and the loss of the control plots, it was not possible to carry out rigorous statistical comparisons between the before and after density figures. Consequently, no confidence limits could be attached to the findings.

It is evident that numerous transects incorporating as many common species as possible would have been required to achieve conclusive results. This would not have been possible for a number of practical and financial reasons. It would also have been necessary, with this required scale, to incorporate this study into the annual burning plans for the reserve. It is essential with such a study to ensure that all fires are kept under control at all times and that suitable contingency plans are formulated in advance. This is to cater for the possibility that the fires may not respond according to plan because of variable fuel loads and changes in wind direction. Important areas must be identified and marked to ensure that they are not accidentally burned in the process. It is also essential to discuss the objectives of the study with the managers beforehand so that such plans could be adopted should any problems arise.

3.5.6 General

3.5.6.1 Recovery of the system post Domoina

After the Domoina flood, the Natal Parks Board expressed concern about the prospects of recovery of the system, and whether it would ever return to a similar state which existed in the 1960s and 1970s. Suggestion were even proposed which included the planting of truncheons of certain species to accelerate the recovery of the system to this climax state. It is assumed therefore that the climax state is highly desired, even if management intervention is required to achieve this.

On the basis of the above discussion, the outlook is good, that given sufficient time, the system would return to this equilibrium state. However, if one considers the increasing frequency and intensity of flood events, the prospects of such a recovery are bleak. By considering the state of the system in 1986 on the conceptual model (Fig 3.13) relative to its state as it was in 1937, one can make rough estimates regarding the recovery time required to attain equilibrium in these areas. The condition of riverine communities in 1986 were represented by a state situated at a conceptual point still further away from the equilibrium state than in 1937. Since this 1937 state required in the region of 30 years to recover adequately, one can estimate that approximately 35 to 40 large flood-free years would be necessary to allow for the 1986 state to recover to the equilibrium. However, the system currently experiences a large flood every 4.9 years, and would be likely to experience 7 or 8 large floods during this period of recovery. It is highly likely that these floods would retard the recovery process and maintain the system in a state of dis-equilibrium.

The maintenance of species diversity by means of the frequency/intensity of floods is clearly an essential process and is a major determinant of the structure and functioning of riverine areas. It is suggested therefore that this process should be maintained to ensure that the species diversity of these areas is kept as high as possible.

3.5.6.2 Plant strategies in riverine areas

Grime (1979), classified plant strategies according to two external factors, namely, stress and disturbance. Three of the four permutations of high and low levels of both stress and disturbance are viable as plant habitats. During the evolution of the plants found in these areas, the established phase of the life-cycle has experienced three fundamentally different forms of natural selection, which have selected for distinct plant characteristics under each condition.

All three permutations are important in the riverine situation under different conditions of flood frequency and intensity, and exposure to floods. These areas are as follows.

a. Those exposed to low levels of stress and low levels of disturbance. These areas are found where the frequency and intensity of floods is low, and the equilibrium or climax state is attained. The species selected for under these conditions are termed 'competitors'.

b. Those exposed to low levels of disturbance and high levels of stress. These areas are found under conditions of high flood intensity in isolated riverine areas which are not removed or destroyed by large floods. Here floods do not act as disturbances, but instead act as a form of stress by removing branches, stripping the tree of its leaves, removing the litter cover and primary soil layers. The species selected for are termed 'stress-tolerators'.

c. Those exposed to high levels of disturbance and low levels of stress. These areas are common under conditions of dis-equilibrium when frequent and large floods are responsible for completely removing and inflicting damage to plants. The species selected for are termed 'ruderals'.

By describing relevant characteristics of these three species classes (cf Grime, 1979) and by classifying riverine species according to them (from personal observation), it is possible to predict which species are likely to be found in these areas under different flooding conditions.

1. Competitors

These species are characterised by high competitive ability, facilitated by maximising the capture of resources in productive areas.

Life forms - Shrubs and trees
Morphology - High, dense canopy of leaves
Longevity - Long
Flowering - Flowers produced after periods of maximum potential. Established plants produce flowers each year
Leaf phenology - Well defined peaks of production
Seeds - Small proportion of annual production devoted to the production of seeds
Regenerative strategies - Vegetative expansion, numerous large seeds or wind dispersed seeds
Growth rate - High
Litter - Copious, often persistent
Palatability - Various

Possible species

Acacia nigrescens
Acacia schweinfurthii
Pappea capensis
Rhus chirindensis
Schotia capitata
Sideroxylon inerme
Trichilia emetica
Acacia robusta
Ficus sycomorus
Plectroniella armata
Schotia brachypetala
Sclerocarya birrea
Spirostachys africana

2. Stress tolerators

These species are generally characterised by reduced vegetative and reproductive vigour which allows for endurance and persistence in unproductive environments.

Life forms	-	Herbs, shrubs and trees
Morphology	-	Very wide range of forms
Longevity	-	Long to very long lived
Flowering	-	No general relationship between time of flowering and season. Flowering is intermittent over a long life-history
Leaf phenology	-	Evergreens, with various patterns of production
Seeds	-	Small proportion of annual production devoted to the production of seeds
Regenerative strategies	-	Vegetative expansion, persistent seedling bank, large fleshy seeds
Growth rate	-	Slow
Litter	-	Sparse
Palatability	-	Low

Possible species

Ficus sur
Melia azedarach
Sclerocarya birrea
Ziziphus mucronata
Ficus sycomorus
Pappea capensis
Trichilia emetica

3. Ruderals

These species are characterised by short life spans and the production of large quantities of seeds. High rates of mortality are inevitable under these conditions, and the cost of a marginally-increased rate of parental fatality is outweighed by the benefits of high fecundity at an early stage after establishment. Grime (1979) considered that only herbaceous species would be able to persist under these conditions. However, from personal observations, it was noted that woody species can also be successful. This success is achieved by the means of highly effective vegetative expansion (suckering and coppicing) and the production of large quantities of seeds and fruit at an early age.

Life forms - Herbs (and fast growing trees and shrubs)
Morphology - Small stature
Longevity - Short lived
Flowering - Flowers produced early in life history in very high frequency and quantities
Leaf phenology - Short phase of leaf production in period of high potential production
Seeds - Large proportion of annual production devoted to the production of seeds
Regenerative strategies - Persistent seed bank, large quantities of wind dispersed seeds, Fast vegetative expansion (suckering and coppicing)
Growth rate - Very fast
Litter - Sparse
Palatability - High

Possible species

Acacia gerrardii
Acacia robusta
Chromalaena odorata
Ficus sycomorus
Lippia javanica
Ricinus communis
Sesbania sesban
Ziziphus mucronata
Acacia karroo
Cassia didymobotrya
Dichrostachys cinerea
Lantana camara
Melia azedarach
Sesbania punicea
Spirostachys africana

It is important to note that certain species are able to persist in all three types of environments, subjected to different selection pressures. This suggests that individuals were subjected to different types of selection early on in their evolution and have consequently developed different genetic characteristics in the different areas. These species are highly successful and it is unlikely that they would be excluded from the system under any conditions.

3.5.6.3 Species richness modeling

Insufficient species richness information was available to attach to the six sampling dates and consequently it was not possible to associate species richness with the proportions of the four vegetation states for each sampling date. In addition, the two tests of the intermediate disturbance hypothesis failed to refute the hypothesis or produce an alternative hypothesis of species richness in response to different levels of disturbance frequency and/or intensity. It does appear however, that the disturbance gradient, identified in the correspondence analysis study, supports current disturbance theory based on the intermediate disturbance hypothesis. In order to maximise predictions pertaining to the recovery and dynamics of riverine areas in response to floods, this explanation was therefore adopted. A model based on this hypothesis (Connell, 1978) was applied in order to model the response of riverine communities to different levels of flooding frequency and intensity.

According to this model (Fig. 3.14), it is stated that periodic or recurrent floods, at an intermediate level, perpetuate pioneer and mid-seral species. Under these conditions, species with different life history strategies are able to coexist and consequently high levels of species richness are maintained. If the frequency/intensity of flooding increases beyond this, only species (colonising species) with high growth and/or dispersal rates, the pioneer and mid-seral species, are able to exist. This represents an extreme represented by a low species richness. The other extreme would apply if the frequency/intensity of flooding had to decrease. Here, only the highly competitive climax species which are better at maintaining resources would exist and equilibrium would eventually be attained. Other less competitive species would be excluded and, consequently, the species richness would be maintained at a low level.

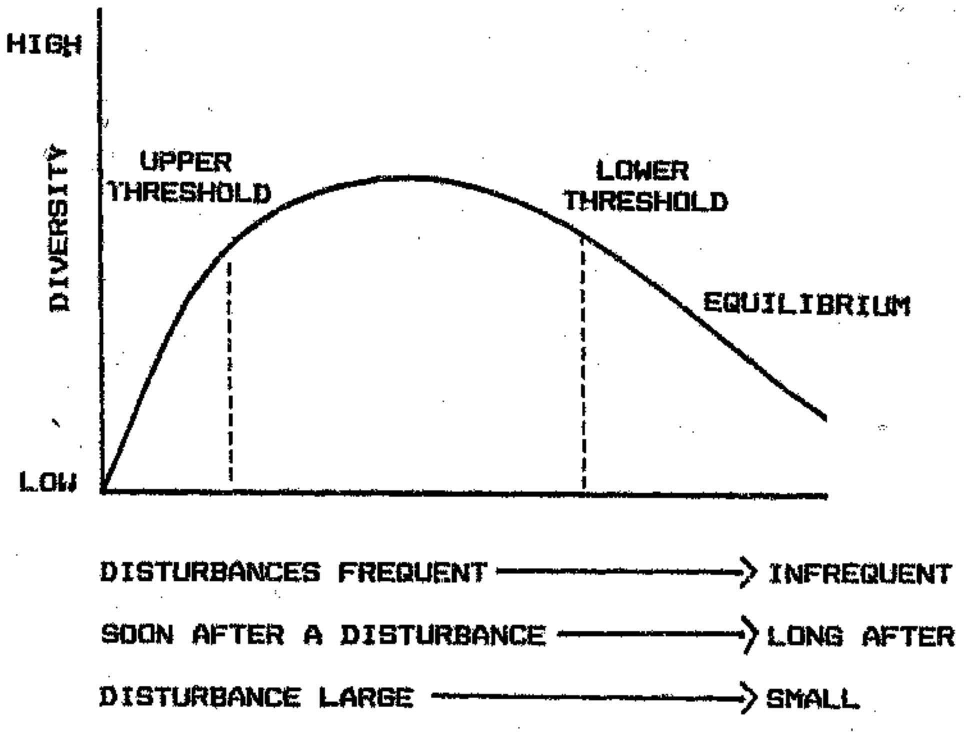


Figure 3.14 The intermediate disturbance hypothesis. Levels of species diversity in response to a range of frequencies/intensities of disturbance

Both extremes could realistically be encountered within the riverine system. The presently increasing frequency and intensity of floods is a firm indication that the high extreme is most likely to apply in the future. However, should flooding frequency decrease, possibly due to future management intervention, the lower extreme may become important. Ideally, in order to maintain riverine communities in a state characterised by high species richness, it would be necessary to determine both the upper and lower thresholds of flooding frequency/intensity which would maintain this condition.

Since both the intensity and frequency of floods appears to be changing simultaneously, it would be important to consider this effect and how it influences species diversity in riverine areas. Miller (1982) separated the effects of the intensity and frequency of disturbance events towards the determination of species richness. Malanson (1984), modified this hypothesis to produce a three dimensional model of species richness in response to different degrees of both intensity and frequency of disturbances (Fig. 3.15).

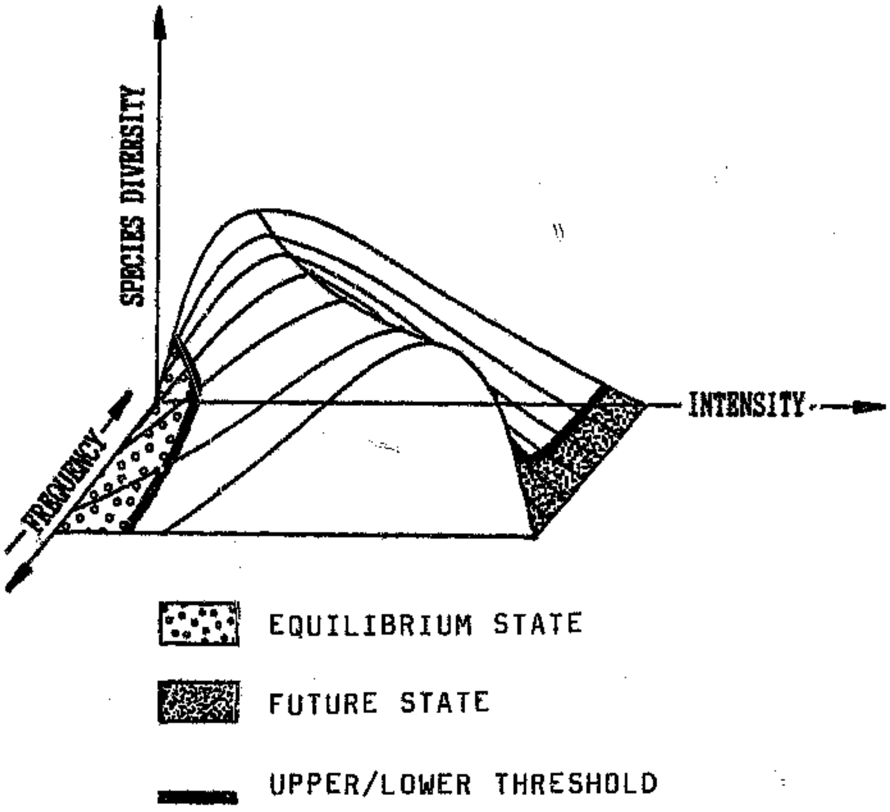


Figure 3.15 Projections of species diversity over a surface defined by an axis of flood intensity and an axis defined by flood frequency (modified from Malanson, 1984). The relative positions of the equilibrium state, a future vegetation state and the lower and upper thresholds of flooding frequency/intensity are indicated

The relative locations of the equilibrium or climax state, the likely position of the system as it would exist in the future (given increasing intensities and frequencies of flooding) and the lower and upper thresholds of frequency and intensity have been marked. Peak species diversities are projected for high intensity, infrequent disturbances, and low intensity, frequent disturbances. The increasing tendency in both flood intensity and flood frequency gives rise to the situation where low species diversity would result. In order to attain a state of high diversity from this point, it would require either a reduction in flood intensity and/or a reduction in flood frequency. A reduction in both factors simultaneously would initially lead to an increased diversity, followed by a reduction in diversity to the point where the equilibrium state would be attained. The determination of the lower and upper thresholds which define the desired levels of species diversity in riverine areas are complicated considerably by this model. This highlights the need to clearly define the relationship between the intensity and frequency of floods first before one attempts to determine these parameters. Until this relationship is clearly defined, it may be convenient to consider the two factors together as a first measure.

3.5.6.4 Upper and lower flood thresholds

The upper threshold would be characterised by a time interval between successive flood events of a length which is insufficient to allow for the majority of woody species to respond, grow and reproduce successfully. Only species which display fast growth rates and highly effective reproductive characteristics (ruderals) would stand any chance of existing under these conditions.

The lower threshold would be characterised by a time interval which is long enough to allow competitive woody species to establish themselves and eventually exclude the less competitive species. In order to remain under these conditions they would have to be able to display a fast growth rate over the entire period and compete strongly for resources by means of dense canopies and effective above- and below-ground rooting systems (competitors).

The determination of the lower and upper thresholds of flood frequency/intensity should be approached separately. Two approaches could be employed to achieve this.

Firstly, by applying a modeling approach as in section 3.5.4, and determining the broad response of different vegetation states to different frequencies of flooding. This approach would allow for the identification of rough threshold frequencies but no knowledge would be gleaned concerning the major species components associated with different flooding frequencies.

Secondly, the definitive approach would be to consider the main species components of the system and to classify them into Grime's (1979) ruderal and competitor classes. All major species should then be considered in terms of their characteristics in both areas as follows,

a. growth rates,
b. reproductive and vegetative strategies observed in
   response to floods,
c. earliest and optimum reproductive and vegetative ages,
d. canopy and rooting characteristics, and
e. seed bank characteristics.

Species would then be classified according to different time intervals to determine at which point they would be most successful and when they would be excluded due to insufficient available time. The application of this knowledge would then be used to predict those ruderal species which could persist in response to a range of flooding frequencies.

The competitor species would be determined by comparing those species with the longest optimal reproductive and vegetative ages and the most effective competitive characteristics as seen by their canopy and rooting characteristics. Predictions would then be made regarding the persistence of these species in response to a range of flooding frequencies.

This approach would lead to a thorough understanding of the species associated with each interval of flooding frequency and would allow for reasonably accurate predictions in this regard. However, it is clearly a detailed and complex study and would require considerable time and effort.

3.6 Conclusions

The flood regime on the Umfolozi river system appears to be changing to one which is characterised by large variations in magnitude, frequency and duration. In addition, it appears that the frequency and intensity of large floods is increasing. The reasons for this shift in flooding regime are unclear, but it appears that it could be due to the present condition of the catchment areas.

The recurrent removal of vegetation and the differential responses of various size classes of trees to floods and their subsequent effects, is having an impact on the structure of riverine communities within the Umfolozi Game Reserve. This process appears to maintain them in a dynamic state of dis-equilibrium, largely characterised by ruderal species which are able to persist under extreme conditions of flood frequency/intensity.

Recurrent flooding is evidently an essential process which maintains the species diversity of riverine areas and is therefore a major determinant of the structure and functioning of these areas. The maintenance of this process should be encouraged, and in order to achieve this, the upper and lower thresholds of flooding frequency/intensity should be identified which define the conditions under which the process applies.

The system appears to display a high degree of resilience to such flood events, but it is not clear whether it might go beyond its domain of attraction, and under what conditions this would occur.

The generally disruptive influence of fire on the recovery of riverine areas by affecting the seedlings and juvenile size classes of characteristically riverine species as well as its effect on the induction of certain exotic species shows that fire should be applied carefully and judiciously in riverine areas.

CHAPTER 4 APPROACH BASED ON COMMUNITY ORGANISATION THEORY

This chapter deals with the application of a resource based community organisation approach to understand the structuring and dynamics of riverine vegetation. The different hypotheses which make up the approach are presented in five separate sub-chapters. A conceptual map summarising the conditions under which each hypothesis applies in the riverine situation, is included. The value of the approach in understanding the structure and dynamics of riverine vegetation is also discussed.

4.1 Introduction

The heterogeneous nature of available resources in the study site and the wide variety of species which respond to these resources made the riverine conditions ideal to apply and test the resource based community organisation concept proposed by Price (1984) (see literature review - section 1.6.3).

The complexity in topographical, geological, pedological and other environmental conditions present ensures that a wide range of resource types are available for exploitation by plants. The intensity and frequency of various disturbances, which are recurrently responsible for altering the distributions and availabilities of the numerous resources present, ensure that this heterogeneity is maintained. Consequently, it is very likely that the entire range of resource spatial distributions and rates of change, as detailed in the resource distributions map of Price (1984), are available for exploitation. In addition, a large number of plant species were recorded during the course of the study. These represent a wide range of different life history strategies which would lead to broad exploitation of the available resources.

4.2 Approach

In order to test the entire scope of the Price (1984) approach, it would be necessary to comprehensively test all five hypotheses under each of the predicted conditions according to the hypothesis summary table (Table 1.1). Depending on which hypothesis to be tested, this could range from 6 to 9 tests. A total of 47 tests would then be required to test all five hypotheses. Due to the limited scope of the project, this was considered to be impracticable.

Instead, the five pertinent hypotheses were tested separately for a single practical and most likely combination of resource and exploiter conditions. Tests were conducted using suitable null hypotheses in areas within the study site, with the closest adherence to the community selection criteria and community quality requirements as specified by Price (1984). Time, financial and practical constraints were an important consideration in the execution of the project and, in many instances it was not possible to meet with the strictest conditions and requirements specified. Where practically and financially possible, more than one test was applied simultaneously for most hypotheses tested, in order to aid in drawing strong inferences.

As all hypothesis were tested independently in the riverine situation, each has been appended below as a separate sub-chapter. In order to avoid confusion, each sub-chapter covers the objectives, null hypotheses, methods used, results, discussion and conclusions associated with the particular test and hypothesis under consideration. The findings of each test were then discussed together in the light of the approach proposed by Price (1984). The applicability of the approach to explaining the structuring of communities under different conditions of resource availability and exploiter responses was determined.

SUB-CHAPTER 1 ISLAND SIZE HYPOTHESIS

This sub-chapter aims to apply the island size hypothesis in the riverine situation and to test, by means of a suitable null hypothesis, its ability to describe and predict the species richness of riverine vegetation.

1.1 Introduction

The island size hypothesis, as is commonly applied, states that the species richness of an area is directly related to its size. Since its introduction, numerous researchers have extensively used the island size hypothesis to describe the species composition of different areas and to predict the species richness of these areas by their size alone (see literature review - section 1.6.3.1). This hypothesis has been found to apply under numerous conditions and circumstances and promises to hold true for riverine areas as well.

Riverine areas appear to consist of different disturbance zones which display different size and shape characteristics. These zones represent a large proportion of riverine areas and, due to their variability in size, could be of assistance in testing the island size hypothesis. Should a positive correlation exist between the size of these zones and species richness, a large proportion of the variability in species richnesses in riverine areas would be accounted for.

1.2 Objectives

The objectives of this chapter were as follows.

1. Test the island size hypothesis as described above, and using a suitable null hypothesis, determine its applicability in riverine areas.

2. Determine the ability of the island size hypothesis to predict the species richness in other riverine areas.

3. Apply the different species-area curves obtained from this approach to understand the equilibrium state of riverine areas.

1.3 Null hypothesis

The null hypothesis employed was that no relationship exists between the size of riverine areas and their species richness. At the outset of the test it was expected that the null hypothesis would be rejected if significant species-area curves were found to exist and if the characteristics of these curves could be applied to adequately reflect the characteristics of riverine areas. In addition, it was considered important that the characteristics of these curves were comparable or explainable with similar characteristics published in ecological literature.

Should the species-area curves for riverine patches be found to adequately describe the relationship between species and area, the best-fit models for these curves, by means of regression analysis, would be determined. The unequivocal definition of this relationship, should this be statistically significant, would then serve to allow for the rejection of the null hypothesis.

It was envisaged that such models would then facilitate the accurate prediction of species richness in other areas of known size. It was further envisaged that the slope parameter of these best-fit models could then be compared with published values to determine the equilibrium states of the areas investigated.

1.4 Methods

1.4.1 Hypothesis test

The definitive sampling strategy for this test would have required adequately replicated plots of different sizes located randomly within the riverine area. However, due to the rough and inaccessible terrain, this sampling strategy would not have been practically possible. Instead, nine sites, each 1500 meters in length, were located in the riverine strip at different points on the Black Umfolozi river by means of a stratified random procedure based on accessibility and convenience (for the exact locations see Appendix 3). It was essential that a road or vehicle track passed within close proximity and that the transects were easily accessible. Three transects were located randomly within each site and numbered 1 to 3. These transects were divided into a number of contiguously arranged 30x10 metre quadrats originating at the rivers edge, running up the riverine slope and terminating within the first few metres of the adjacent community which was situated just above the riverine slope (Fig. 4.1). This situation was easily recognised by a noticeable change in the species composition as one passed into the adjacent community. Transects varied in total length from site to site but ranged between 60 and 120 metres.

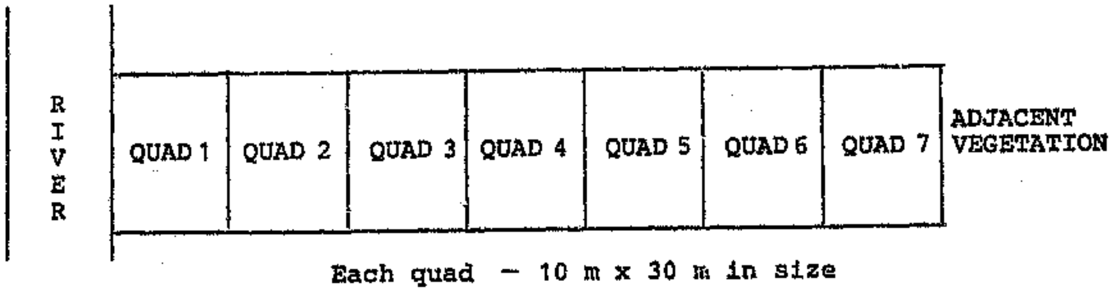


Figure 4.1 Diagrammatic representation of transect and quadrat layout

Within each quadrat, all woody species were identified and recorded. Unknown species were collected in a plant press and identified later. The herbaceous species present were sampled by randomly placing 20, 1 x 1 metre sub-quadrats in each quadrat. The species occurring in these sub-quadrats were identified and recorded.

For each transect, the number of species occurring in the first quadrat were counted and only the additionally occurring species in the subsequent quadrats were added to this count. These counts were then plotted against increasing area to produce separate species-area curves for each transect. The data for the first twenty transects were combined in order to construct a single species-area curve which would represent the entire riverine area.

A least squares regression technique was employed (Sokal and Rohlf, 1969) to assist with fitting three different models to all species-area curves. As described by Connor and McCoy (1979) an untransformed model, the log normal model and the log log (power function) models were fitted to these curves. The best-fit model was then considered to be that curve which displayed the largest R-squared value.

Findings from the above species-area curves necessitated the examination of a lower riverine patch, which displayed a different species-area relationship to that of the main curve already investigated. The characteristics of both this lower riverine patch and the upper riverine patch were investigated at a site (Ngolotsha east), where their presence was particularly noticeable because of their clearly defined widths.

At this site, a series of nested plots were laid out in these areas in a similar procedure to that described in Mueller-Dombois and Ellenberg (1974). Since this area was situated close to the river on flat ground, which was reasonably accessible,it was possible to apply this technique. Due to the irregular shape of the areas being investigated, instead of doubling the size of the plot each time, the plot was increased in size by an amount which could be accommodated by the patch. All woody and herbaceous species were recorded as they occurred within these plots. The repetition of this procedure continued until such time as no further species were recorded for a further five iterations.

The number of additional species present for each plot was determined and the species-area curves were then constructed for both patches. The species overlap between the two patches was determined by identifying which species were recorded in both areas.

1.4.2 The prediction of species richness in other riverine areas

As a positive correlation was found to exist between species richness and area size, it was possible to make predictions of species richness in other areas. With the formulation of species richness predictions in these areas, it was necessary to have a knowledge of their size and the extent to which they incorporated the lower riverine patch. In areas where this lower riverine patch was not present or its contribution to the species-area relationship in the area was negligible, total species richness were predicted using the species-area curve for the upper riverine patch. However, where this lower riverine patch was present, the prediction of total species richness was complicated. In order to make such predictions, it was necessary to consider the species-area curves of both patches separately.

Total species richness were then determined using the following formula.

$$T = (A + B) - C$$

Where, T = total species richness
A = species richness of patch A
B = species richness of patch B
C = number of species shared by both patches

A mean species overlap of 61.3% was observed to exist between the lower and the upper riverine patches. It was assumed that the comparative characteristics of the two patches remained constant and consequently this overlap figure was used in the above equation as C.

Having accounted for the presence of different sub-areas of the riverine strip, it was essential to determine a best-fit model for both species area curves in order to facilitate the accurate prediction of total species richness for larger riverine patches. The curve fitting procedure used with the hypothesis test was also applied here.

The prediction of species richness in other riverine areas was achieved by comparing the expected species richness for the following six transects with those actually present by means of a linear regression technique (Parker, 1973).

1.4.3 Application of species area curves to determine the equilibrium state of riverine areas

The slope values of the best-fit models obtained for of the 27 transects were compared with currently accepted slope values published by Preston (1962 a) and MacArthur and Wilson (1967). The slope characteristics of these sites were then used to determine their state of equilibrium after the 1984 flood.

1.5 Results

1.5.1 Hypothesis test

The combined species-area curve for the first 20 transects investigated is shown in Figure 4.2. As the progressive increase in area corresponded with increasing distance from the river, area on the X-Axis were equated with distance from river. A very clear asymptotic species-area curve is displayed, consistent with that described by Connor and McCoy (1979). This is particularly true for the first 90 metres (i.e. 90x30 metres) from the river's edge where a plateau in species number is reached at approximately 62-68 species. Any further increase in area reveals a clear departure from this trend, displaying significant increases in species number for the next thirty metres.

Confusion regarding the demarcation of the boundary between the riverine communities and those of the adjacent communities, as a consequence of the removal of vegetation by the Domoina floods from both areas, resulted in the unnecessary inclusion of parts of these adjacent communities in several of the transects. This departure was therefore due to the contributions of additional species from these adjacent communities to the riverine species-area curve and allowed for the mean width of the riverine community to be determined. This was determined to be approximately 90 metres wide.

Scrutiny of the separate species-area curves for each of the 26 transects highlighted the existence of yet another area which displays different species-area characteristics. This area, because of its infrequent occurrence, did not make its impression on the main species-area curve of Figure 4.2. This lower riverine patch is represented by an "X" on the species-area curve for site 2 2 (Fig. 4.3). It was identified by its comparatively low slope and its close proximity to the river. It appeared in only 7 of the 26 transects (freq - 0.27) and only attained widths of up to 20 metres. The visual examination of these areas revealed that they were characterised by permanently high soil moisture levels and subjected to regular inundation attributable to slight variations in the level of the river. These patches were only found in areas where the riverine profile was relatively flat. They were colonised largely by sedges and other species capable of tolerating conditions of high anoxia.

Table 4.1 shows the regression statistics for the fit of an untransformed model, the exponential model and a power function (or log log) model for the main species-area curve and for the lower and upper riverine patches at Ngolotsha. The best-fit model for the main curve is clearly an exponential one because of its high R-squared value of 98.73 as opposed to 92.68 for the untransformed model and 98.44 for the power function model. The lower and upper riverine patches are best described by the power function model. The final best-fit models for the lower riverine patch, represented by the lower patch at Ngolotsha and upper riverine patch, represented by the main species-area curve, are shown in Figure 4.4.

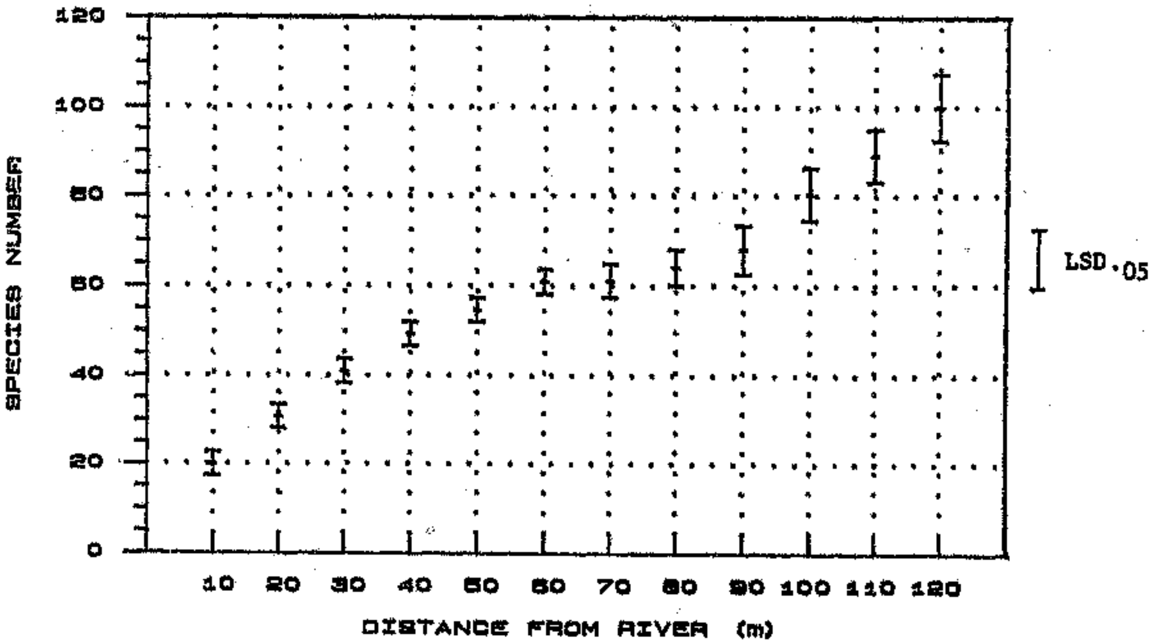


Figure 4.2 Combined species-area curve for the first twenty transects - area is equated with distance from river

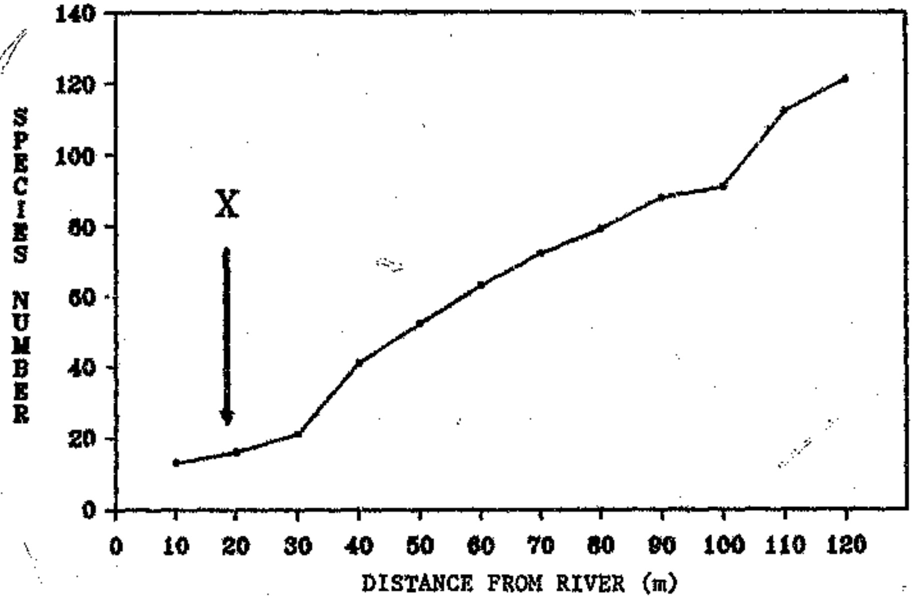
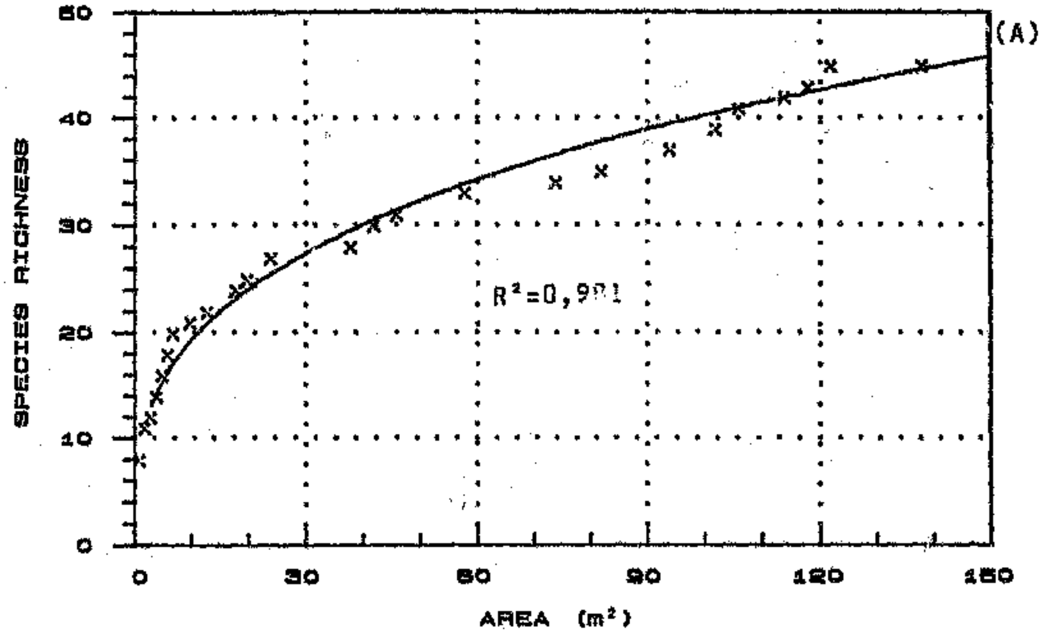


Figure 4.3 Species-area curve for site 2 R showing position of lower riverine patch (marked with an X)

Table 4.1 Regression statistics of three models for the main species-area curve and those of the lower and upper riverine patches

MODEL	EQUATION	MAIN	LOWER	UPPER
A) UNTRANSFORMED	$S = z A + k$			
SLOPE		0.02	0.23	0.06
INTERCEPT		19.55	16.49	28.17
R-SQUARED		0.92	0.90	0.88
B) EXPONENTIAL	$S = \log k + z \log A$			
SLOPE		0.04	0.13	0.06
INTERCEPT		4.93	-0.42	2.17
R-SQUARED		0.98	0.96	0.87
C) POWER FUNCTION	$\log S = \log k + z \log A$			
SLOPE		0.37	0.32	0.44
INTERCEPT		-0.25	2.22	1.42
R-SQUARED		0.98	0.98	0.99



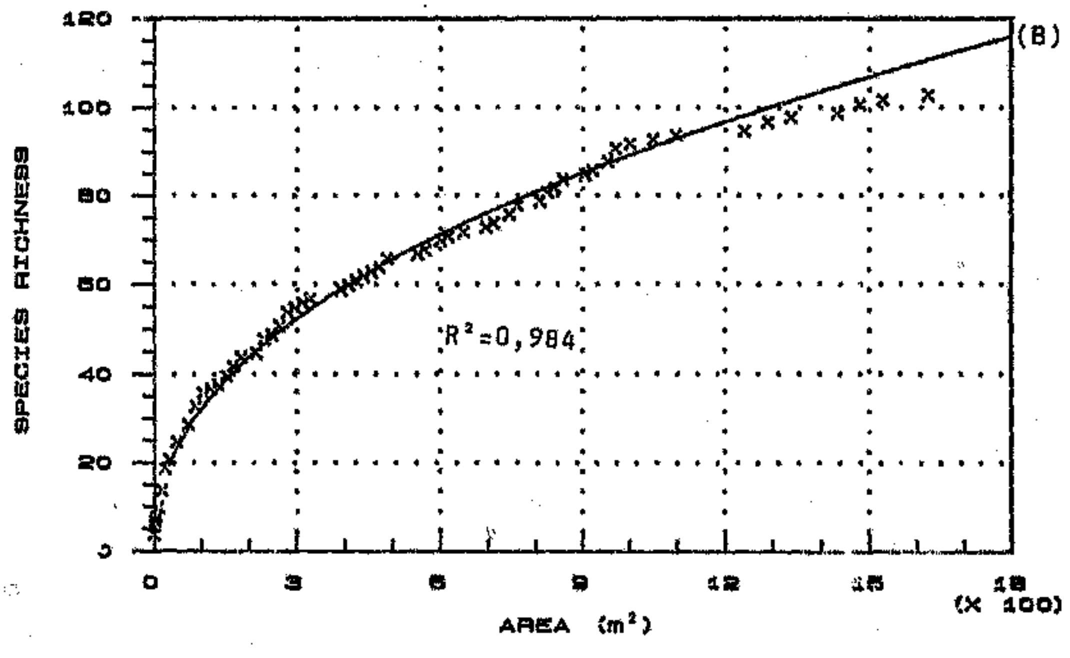


Figure 4.4 Final best-fit curves for two areas

(A) lower riverine patch - Ngolotsha (power function)
(B) upper riverine patch - combined curve (exponential model)

1.5.2 The prediction of species richness in other riverine areas

Figure 4.5 displays the results of the regression of observed species richness of the last six transects and expected species richness. Expected species richness values were derived from the main species-area curve constructed with the first twenty transects. Only one transect required the use of the lower species-area curve to make adequate predictions.

The R-squared value obtained from this regression reveals that approximately 75 percent of the variation in total species richness was accounted for by the size of the patches.

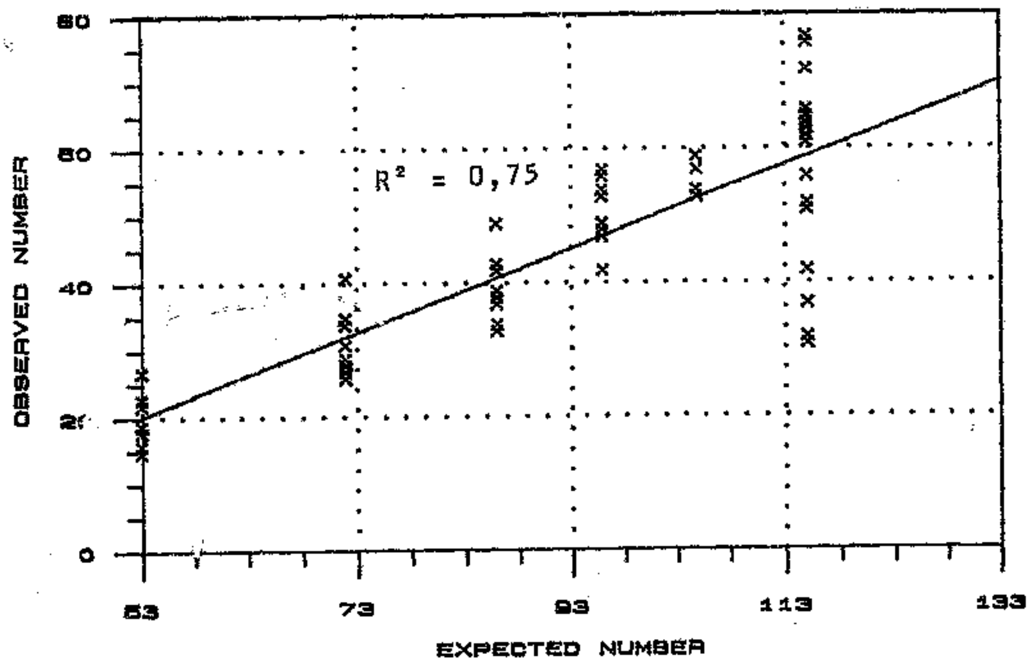


Figure 4.5 The relationship between the observed and expected species richness for riverine patches of different sizes

1.5.3 Application of species area curves to determine the equilibrium state of riverine areas

The slope values for the best-fit models as shown in Table 4.1 and for each of the 27 transects (Table 4.2) can be compared with currently accepted slope values in current literature (see literature review - 1.6.3.9). In terms of the estimations made by Preston (1962 a) and MacArthur and Wilson (1967), only the lower riverine patch (0.32) and two of the transects (site 6 2 - 0.288 and site 6 3 - 0.331) fall within their predicted ranges of 0.17 to 0.33 and 0.20 to 0.35. The remainder of the values generally deviate from those expected by the equilibrium model.

Table 4.2 Slope and R-squared values, in order of increasing slope, of best-fit species-area models

SITE	R-SQUARED	SLOPE	SITE	R-SQUARED	SLOPE
6 2 NSELWENI	0.988	0.288	5 2 THUMBU	0.979	0.636
6 3 NSELWENI	0.991	0.331	8 1 THOBOTHI WEST	0.982	0.657
6 1 NSELWENI	0.980	0.367	8 2 THOBOTHI WEST	0.966	0.665
3 1 MBHUZANA	0.979	0.432	7 2 SIYEMBENI	0.991	0.681
8 3 THOBOTHI WEST	0.979	0.460	9 1 NGOLOTSHA WEST	0.957	0.715
4 2 SONTULI	0.980	0.467	1 3 THOBOTHI	0.970	0.764
7 1 SIYEMBENI	0.997	0.470	1 2 THOBOTHI	0.943	0.825
4 1 SONTULI	0.993	0.482	5 3 THUMBU	0.995	0.839
3 2 MBHUZANA	0.994	0.498	9 3 NGOLOTSHA WEST	0.987	0.857
9 2 NGOLOTSHA WEST	0.961	0.535	2 2 NGOLOTSHA	0.974	0.9[illegible]
2 1 NGOLOTSHA	0.974	0.548	1 1 THOBOTHI	0.993	0.961
5 1 THUMBU	0.976	0.570	2 3 NGOLOTSHA	0.963	1.180
3 3 MBHUZANA	0.992	0.622	4 3 SONTULI	0.877	1.373

1.6 Discussion

1.6.1 Hypothesis test

The species-area curves obtained from the transects appear to have succeeded in identifying the relationship which exists between species richness and the size of the riverine areas investigated. However, it appears that the sampling strategy employed lead to a confusion of the species-area relationship with differences which exist along the riverine environmental gradient. This effect occurred because the transects employed were run from the edge of the river and up the riverine gradient. The accumulation of species along this gradient were then used to construct the species-area curves. The fact that this confusion did actually occur was seen by the identification of the lower riverine area which displayed different species-area characteristics. Had a large number of replicated plots of different size been randomly scattered within the riverine strip and species-area curves been constructed from these, this anomaly might not have been detected.

For the sake of applying the approach, Price (1984) prescribed that "communities should be chosen at random, without any knowledge of the specific organisms present or how the resources are arrayed, so that no preconceived ideas hamper the objective testing among hypotheses". Difficulty was experienced with this prescription.

At the outset of the study it was necessary to consider a sampling strategy which would be useful for the collection of data for as many of the tests as possible and it was not possible to apply specific sampling strategies for each test. In addition, due to time constraints, it was very important to consider sampling strategies which were practical and which could be executed as cost- and time-effectively as possible. For the sake of the test of the individualistic hypothesis, it was necessary, with this specific test, to use the same transects and in so doing sacrifice the random component of the prescription. The application of random plots would also have been placed at different intervals relative to the environmental gradient. However, the effect of this would not have been identified but rather described as 'noise' on the resulting species-area curves. This noise would have accounted for a larger degree of the total variation in the data and the best-fit curves would have displayed generally lower R-squared values. Despite this, it is suggested that a positive relationship would still have been displayed between the size of these areas and their species richnesses.

1.6.2 The prediction of species richness in other riverine areas

It appears that a significant proportion of the variation in total species richness in riverine areas can be accounted for by the size of these areas alone. It would have been preferable to have conducted the test against a larger number of transects. However, this was a further practical limitation to the study.

1.6.3 Application of species area curves to determine the equilibrium state of riverine areas

In support of the equilibrium theory (MacArthur and Wilson, 1963) and the findings of Diamond (1973), this departure implies the general absence of a dynamic equilibrium between the immigration and extinction of species in these riverine areas. Since these areas had recently been disturbed during the Domoina and subsequent floods, they had not yet been able to attain a state of equilibrium. This dis-equilibrium was assumed to be due to the excessive weighting of either those species which were removed by the floods or those which arrived subsequently. A balance between the newly immigrated species and the extinct species therefore determined the relative position these areas occupy on the equilibrium/dis-equilibrium continuum.

The slope values therefore reflect the relative positions of the areas on the continuum from near-equilibrium (low slope) to far-equilibrium (high slope). Site 6 2 is therefore in equilibrium, while site 4 3 is in a state of maximum dis-equilibrium. The position a site occupies on the continuum is dependent on numerous factors such as the extent of the last disturbance, the time since it was last disturbed, the magnitude of the disturbance, the site characteristics and many others.

The equilibrium theory was initially conceived on islands where the immigration and extinction of species were easilv envisaged. It is in this context that the theory is most readily applied. Riverine areas can be perceived as insular in the sense that they are able to receive new colonists from either the river, as wash-up during flood, or from the adjacent areas by means of seed fall, wind, bird and animal dispersals and water run-off. The theory is particularly applicable after a major disturbance when the areas have been considerably denuded and the subsequent immigration and extinction of species and resulting equilibrium states can be envisaged. Figure 4.6 (A) demonstrates the equilibrium theory and the concept of equilibrium as adapted for riverine areas from MacArthur and Wilson (1963).

The descending curve (immigration curve) is the rate at which new species enter a denuded riverine area from the river or the adjacent areas after a major flood. The curve falls more steeply at first, which is a consequence of the fact that some species are commoner immigrants than others after a disturbance and that these rapid immigrants are likely to be the first species present. The intercept, I, represents the rate of immigration of species, new or already present into the area. The curve falls to zero at the point N = P where all the immigrating species are already present and no new species are arriving. P therefore represents the size of the total pool of species which are able to colonize riverine areas from the river and adjacent communities.

Similarly, the rising curve (extinction curve) represents the rate at which species are lost or removed from riverine areas by flooding. The two curves intersect at a point (*), the value of N for which the rate of immigration of new species is balanced by the rate of species loss. This characterises the equilibrium point for the particular area.

Each riverine area and patch displays its own characteristics in terms of distance from river and size. As displayed by the species-area curves, the basic area of the various patches will affect the rate at which propagules reach the area. This will be reflected by a change in the slope of the immigration curve. Larger areas will exhibit steeper slopes than smaller areas (Fig. 4.6 (B))

Disturbance frequency is highest at the river's edge and tends to decrease with distance from the river. In this way, the rate of species removal from a patch is related to the distance of the patch from the river. Patches situated near the river are therefore likely to display a steeper extinction curve than areas situated further away. On this basis one can envisage the final equilibrium proportions which should be attained at any particular riverine area given time for species to accumulate after the last major flood.

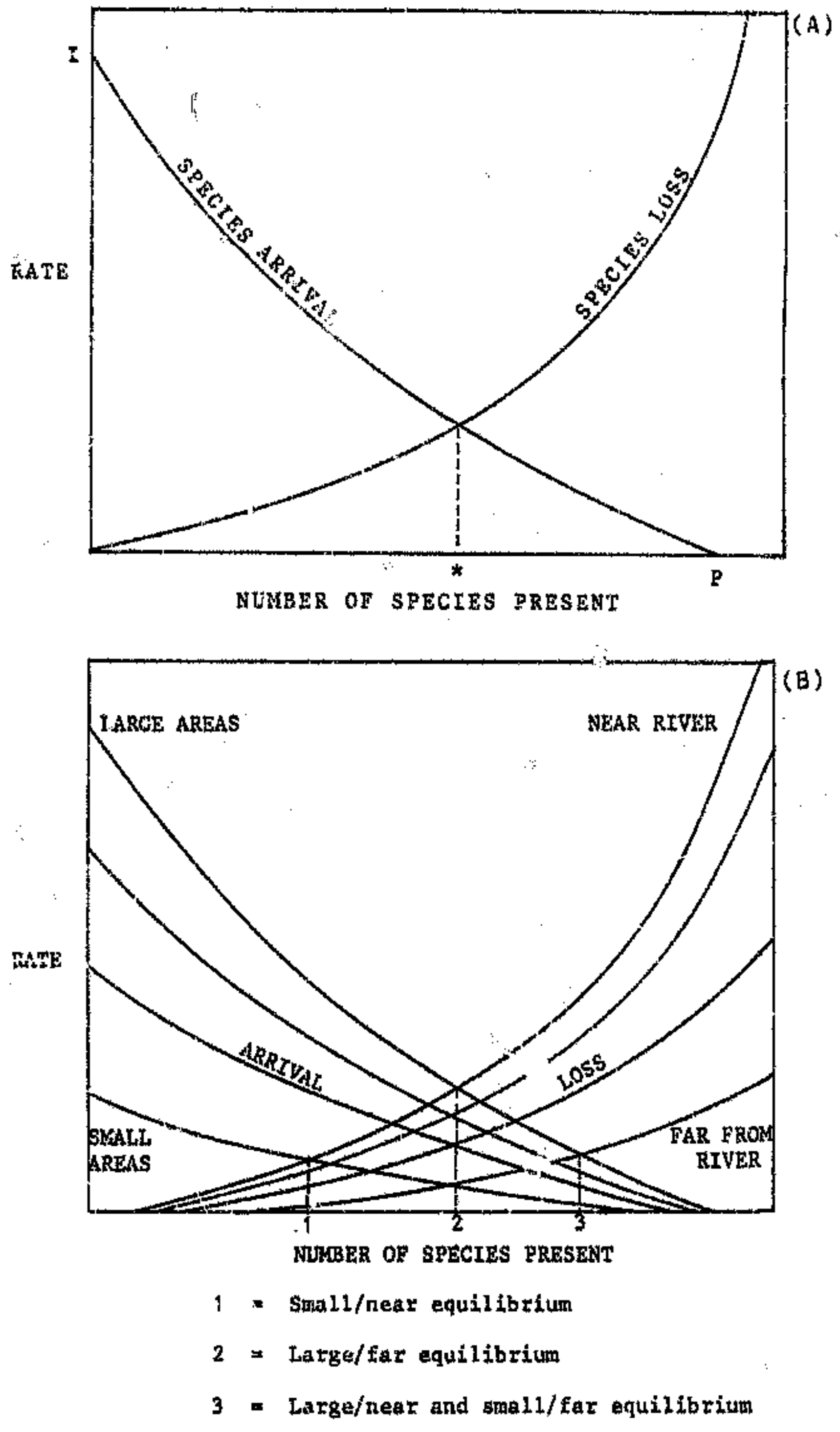


Figure 4.6 Equilibrium models for riverine areas – adapted from MacArthur and Wilson (1963)

(A) Theoretical model displaying position of equilibrium relative to the arrival and loss of species

(B) Model for riverine areas of variable sizes and distances from river

The apparent equilibrium of the lower riverine area, as seen by its low slope value, is not surprising. The equilibrium theory predicts that, due to its small area and proximity to the river, its final equilibrium proportion would be low relative to larger areas situated further from the river. Adequate time has passed to allow for this relatively small quantity of species to accumulate and therefore reach equilibrium proportions.

The anoxic conditions characteristic of these areas would ensure still smaller quantities of species necessary for equilibrium by discouraging unsuitable species from growing and establishing. In addition, due to their proximity to the river, the species found in this patch have adapted to regular disturbance by developing the ability to establish and grow as quickly as possible thereby speeding up the equilibrium. Larger numbers of species are necessary to accumulate in areas which are larger and which are situated further from the river. In addition, the conditions characteristic of these areas are more suitable for colonization by most species.

It is expected therefore, that if adequate time is able to pass after a major disturbance, an adequate number of species will accumulate and the slope values of these areas will gradually decline simultaneously, until such time as they reach equilibrium, and fall within the range predicted by MacArthur and Wilson (1963). Since these areas would then be in equilibrium, the equilibrium theory could be used to predict species richness in areas of different size and at different proximities to the river.

1.7 Conclusions

A significant positive relationship exists between the species richness in the riverine strip and the size of the areas. The island size hypothesis is therefore seen to play an important part in the structuring of vegetation in riverine areas and allows for a firm rejection of the null hypothesis.

The prediction test involving other areas revealed that approximately 75 percent of the variation in total species richness was accounted for by the size of the patches. The island size hypothesis alone can therefore be used to adequately predict a large proportion of the total species richness in riverine areas of measurable size.

Species-area curves and their slope characteristics can be used effectively to determine the equilibrium status of riverine areas and identify different riverine zones and their characteristics.

SUB-CHAPTER 2 RESOURCE HETEROGENEITY HYPOTHESIS

In this sub-chapter, the resource heterogeneity hypothesis was applied and tested in the riverine situation using a suitable null hypothesis. Species-area curves were related to visibly discernible habitat types to explain the type of habitats present and their effects on the species richness of these areas.

2.1 Introduction

The resource heterogeneity hypothesis attempts to explain the species richness of different areas as a consequence of the quantity of suitable habitats/resources present (for further details of the hypothesis - see the literature review, section 1.6.3.2).

The highly variable geology and topography of riverine areas, the variability of flood sizes and the effects of other disturbances on these make them very habitat diverse. Large abundances of spatially patchy areas are present where erosion and silt depositions have occurred to different extents. The digging and burrowing activities of various animals and the patchy nature of fires and other disturbances have contributed their share to this patchiness. These areas are all formed under different sets of conditions and have unique characteristics. Consequently, each patch offers different combinations of resource and habitat prospects for colonizers. The resources which differ most markedly from patch to patch are the soil bulk densities and particle size distributions, which in turn have a bearing on the soil moisture availabilities and rooting capabilities for colonizers. In some areas erosion has uncovered underlying patches of rock which offer restricted water availabilities and poor rooting prospects, while other areas have been formed by the erosion of high clay sub-soils which then accumulate water and form small pans.

2.2 Objectives

The objectives of this chapter were as follows.

1. Test the resource heterogeneity hypothesis in riverine areas using a suitable null hypothesis.

2. Investigate the major forms of resource and habitat diversity and their effects on the species richness of riverine areas.

2.3 Null hypothesis

The null hypothesis applied stated that the structure and species diversity of vegetation in riverine areas is not determined by the availability of resources / habitats but by other factors instead. Therefore, no defineable or clear relationship exists between species richness and the number of resources / habitats present.

2.4 Approach and methods

Two distinct sampling strategies were employed with this test.

2.4.1 Transect technique

Twenty six transects were located in the riverine strip using a stratified random technique (for a description of transect specifications and sampling procedure - see island size hypothesis). In addition to this, the species present in each transect were counted and recorded. The environmental characteristics of all transects were noted and recorded in terms of their slopes, substratum types and depths, particle size distributions, the presence or absence of rock outcrops, minor tributaries, game paths and other features which could be exploited and therefore serve as separate habitats or resources for colonizers. A list of all possible visible physical habitats was constructed and each transect was given a habitat score according to which habitats were present. A presence/absence matrix was constructed with sites as rows and the habitat types as columns. The presence of a habitat type at a site was recorded in the matrix as a '1' and the its was recorded as a '0'.

In order to investigate the relationship between the species richness at each site and the quantity of the various habitat types present, it was necessary to determine a habitat score for each site. This was done by summing up the quantity of different habitats which were observed at each site. However, the problem with this approach is that certain habitat types may be strongly related and, consequently, this would lead to the over-weighting of these habitats in the final habitat score. This would be particularly true for certain sites. In order to identify the correspondence between habitat types present the 20 variables were tested for independence using a Cochran's Q-test (Sokal and Rohlf, 1981). Here, the null hypothesis employed stated that the 20 variables were mutually dependent at the 26 sites investigated.

If habitat scores were found to be dependent ($p>0.05$), the scores which gave rise to this high measure of dependence were identified and removed from the matrix to prevent the over-weighting of related habitat types. Once the independence of the habitat scores was achieved, a linear regression analysis (Sokal and Rohlf, 1981) was then carried out between the species richness and habitat

scores for each transect. The relationship between visibly discernible habitats at each site and their species richnesses were then determined on the basis of the R-squared value, the correlation coefficient and its level of significance obtained from the regression.
Should the regression indicate a significant ($p<0.05$) relationship between species richness and habitat score, the null hypothesis would be rejected.

2.4.2 Nested plot technique

It was envisaged that a nested plot sampling technique would include numerous heterogeneous patches, particularly if they existed in large quantities. The species-area curves obtained would then reveal the presence of these areas by displaying minor and major changes in species abundances as dips, bumps, plateaus and other abnormalities which correspond with these patches. The size and extent of any abnormalities would reflect the extent of the patch and its bearing on plant distributions and abundances. The characteristics of these patches should support these findings by displaying discrepancies in either particle size distribution, soil profile depth, slope, and aspect.

Should the species-area curves in the first test not display these abnormalities in shape, it would imply that communities are structured by the more precise factor of increasing area alone. In addition, should abnormalities in the species-area curves not be explained by the characteristics of the patch in question, despite differences in the availability of resources, other factors aside from area would be considered responsible for these discrepancies.

With the interpretation of species-area curves, certain minor slope abnormalities, which are a reflection of the basic size of the nested plot used for sampling the area in question can always be expected to occur. These will be displayed as serrations which appear along the entire length of the curve. Every effort should be made to prevent confusing these serrations with the abnormalities caused by the presence of zones displaying heterogeneities in resource and habitat characteristics.

Three riverine areas were sampled with the use of a 1x1 metre quadrat. The quadrat was initially laid out at a arbitrary starting point in each study area. The total numbers of species present in the first quadrat were recorded. The quadrat was then shifted to the area directly adjacent to it and only additional species were recorded. Recording in subsequent quadrats was continued in this way until such time as no further species were recorded for a further five iterations. A species list was run concurrently to ensure that species present were not recorded more than once.

While quadrats were located, attempts were made to keep the area which was being sampled clearly defined to facilitate easy mapping of the area. The approximate dimensions of the areas sampled were determined with the assistance of previous sampling runs which were carried out in all three areas a few months previously. Species-area curves were constructed for each area sampled. The areas investigated were mapped briefly in terms of slope and aspect variations, proximity to river, particle size distributions and the presence or absence of small pans, tributaries, rock outcrops and undulations.

The species-area curves were checked for minor and major physical abnormalities. The locations and sizes of all abnormalities were recorded and their positions and sizes were compared with those of the environmental characteristics to assess the role these areas play in distributing the species present.

2.5 Results

2.5.1 Transect technique

Table 4.3 displays the habitat score matrix of 20 riverine habitats at each site by the presence (1) or absence (0) of these habitats at each. For habitat types corresponding to the numbers in this table see the corresponding habitat list (Table 4.4). All sites display combinations of the various habitat types with certain transects displaying higher habitat scores than others - these range from 7 to 15. The modified scores range from 6 to 12. The results of the Cochran's Q-test revealed that $Q = 128.3 > X^2_{.001(19)} = 43.8$. This states that the variables were found to be independent at the p=0.001 level. The null hypothesis was therefore rejected which stated that the 20 variables displayed dependence at the 26 sites investigated. Consequently, it was not necessary to remove any of the variables and the regression was performed.

The correlation coefficient (+0.56) for the regression of species richness and habitat scores (Fig. 4.7) for each transect reveals that there is a positive correlation between these two variables. The R-squared value of 31.2 shows that approximately 30 percent of the variability in species richness is explained by the presence of these visibly discernible habitats at the different sites, this being significant at the 95 percent confidence level.

Table 4.3 Habitat types and habitat scores for individual sites based on presence or absence within transect

	HABITAT NUMBER																				HABITAT SCORE
SITE No	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	
1 1	X	X	X	X			X	X	X	X		X	X	X		X		X			13
1 2	X	X	X		X	X	X	X	X	X	X		X	X		X	X		X		15
1 3	X	X	X	X	X		X	X	X	X		X	X	X						X	13
2 1	X					X	X			X	X	X	X	X		X		X			10
2 2	X			X		X	X			X	X		X	X		X	X	X			11
2 3	X			X	X					X	X		X	X		X	X	X			11
3 1	X			X		X	X	X		X	X		X	X						X	10
3 2	X	X		X				X		X	X		X	X							7
3 3		X	X	X		X		X	X	X			X	X		X	X				11
4 1	X		X	X	X		X		X	X			X	X		X				X	11
4 2		X	X			X	X		X	X			X	X		X				X	10
4 3		X	X		X	X	X		X	X			X	X		X			X	X	12
5 1	X	X	X		X	X	X			X	X	X	X	X	X	X	X	X			15
5 2	X	X	X		X	X	X			X	X	X	X	X		X	X	X			14
5 3	X	X	X	X		X	X		X	X	X	X	X	X	X						13
6 1	X	X				X	X			X			X	X		X	X		X		10
6 2	X	X		X		X	X		X	X			X	X		X	X		X		12
6 3	X	X		X		X	X			X			X	X		X	X		X		11
7 1	X			X	X		X		X				X				X		X		8
7 2	X				X		X		X				X				X		X		7
8 1	X	X		X	X	X	X		X	X	X			X		X	X	X		X	14
8 2	X	X		X	X		X			X	X			X		X	X			X	11
8 3	X	X		X		X	X			X	X			X		X	X			X	11
9 1	X	X	X	X	X		X	X	X	X				X		X	X	X			13
9 2	X	X	X		X	X	X	X	X	X			X	X		X	X		X	X	15
9 3	X	X	X		X	X	X	X	X	X			X	X		X	X			X	14

Table 4.4 Habitat list corresponding to Table 4.3

HABITAT NUMBER	HABITAT DESCRIPTION	
1	FLAT PROFILE	SLOPE ANGLE
2	MEDIUM PROFILE STEEPNESS	
3	STEEP PROFILE	
4	SHALLOW	SURFACE SOIL DEPTH
5	MEDIUM DEPTH	
6	DEEP	
7	LOOSE	SUBSTRATUM COMPACTNESS
8	TIGHT	
9	FINE	SURFACE PARTICLE SIZE
10	MEDIUM	
11	COURSE	
12	ROCKS	OTHER FEATURES
13	GAME PATHS	
14	BARE GROUND	
15	SMALL PANS	
16	SAND BANKS	
17	DEPRESSIONS	
18	INUNDATED PATCHES	
19	TRIBUTARIES	
20	EXPOSED FACE	

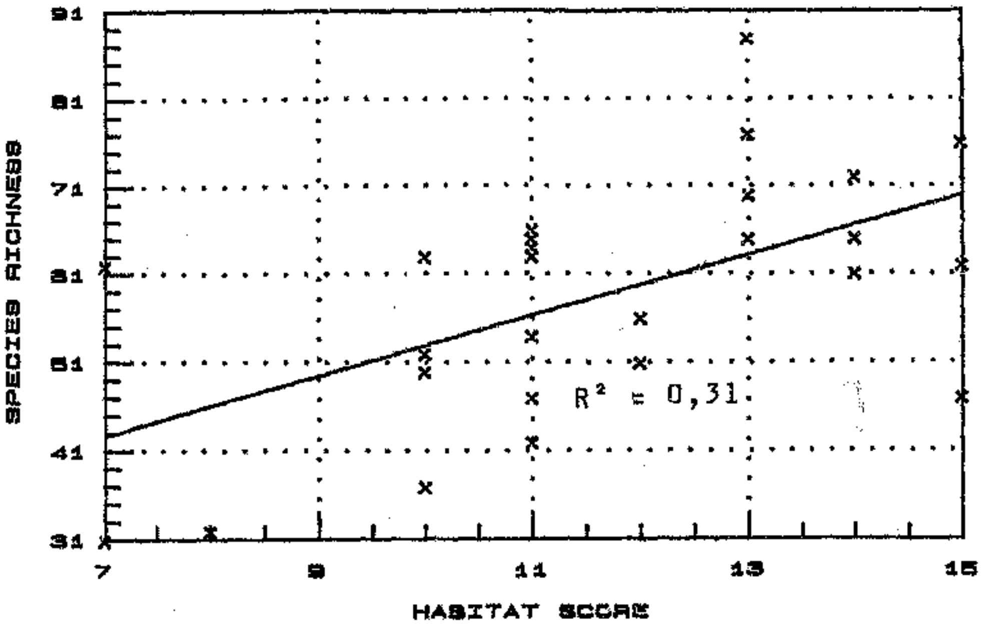


Figure 4.7 The relationship between species richness at a site and its corresponding habitat score

2.5.2 Nested plot technique

Figures 4.8 to 4.10 (A) display the species-area curves for the three riverine areas investigated. The areas are mapped in Figures 4.8 to 4.10 (B). The quadrat numbers and positions have been included to facilitate the easy identification of areas and their sizes. The first area (Fig. 4.8 A) displays a species-area curve which is extensively disfigured due to slope abnormalities (arrowed). The map which corresponds to that area (Fig. 4.8 B) displays the presence of four physical discrepancies to the otherwise homogeneous area. The first is a large undulation situated at the river's edge, the second another large undulation at the river's edge, the third is a deep patch of gravel and the fourth is another small pan of water. The positions and sizes of these discrepancies correspond well with the positions and sizes of the slope abnormalities on the species-area curve.

The second area sampled (Fig. 4.9 A) displays a relatively well formed species-area curve. Close scrutiny of the curve however reveals that this shape is largely due to the scale and the size of the area involved, which tends to reduce the significance of any aberrations. The top part of the curve (from 1000 m^2 upwards - arrowed), does reveal an area of lower slope. The position of this abnormality is adequately explained (Fig. 4.8 B) once again by the presence of a large depression at the base of a slope. This depression is characterised by an unusually high clay content. It appears that water run-off from the slope firstly led to the creation of the depression and secondly transported with it the clay which is characteristic of the substratum above the slope.

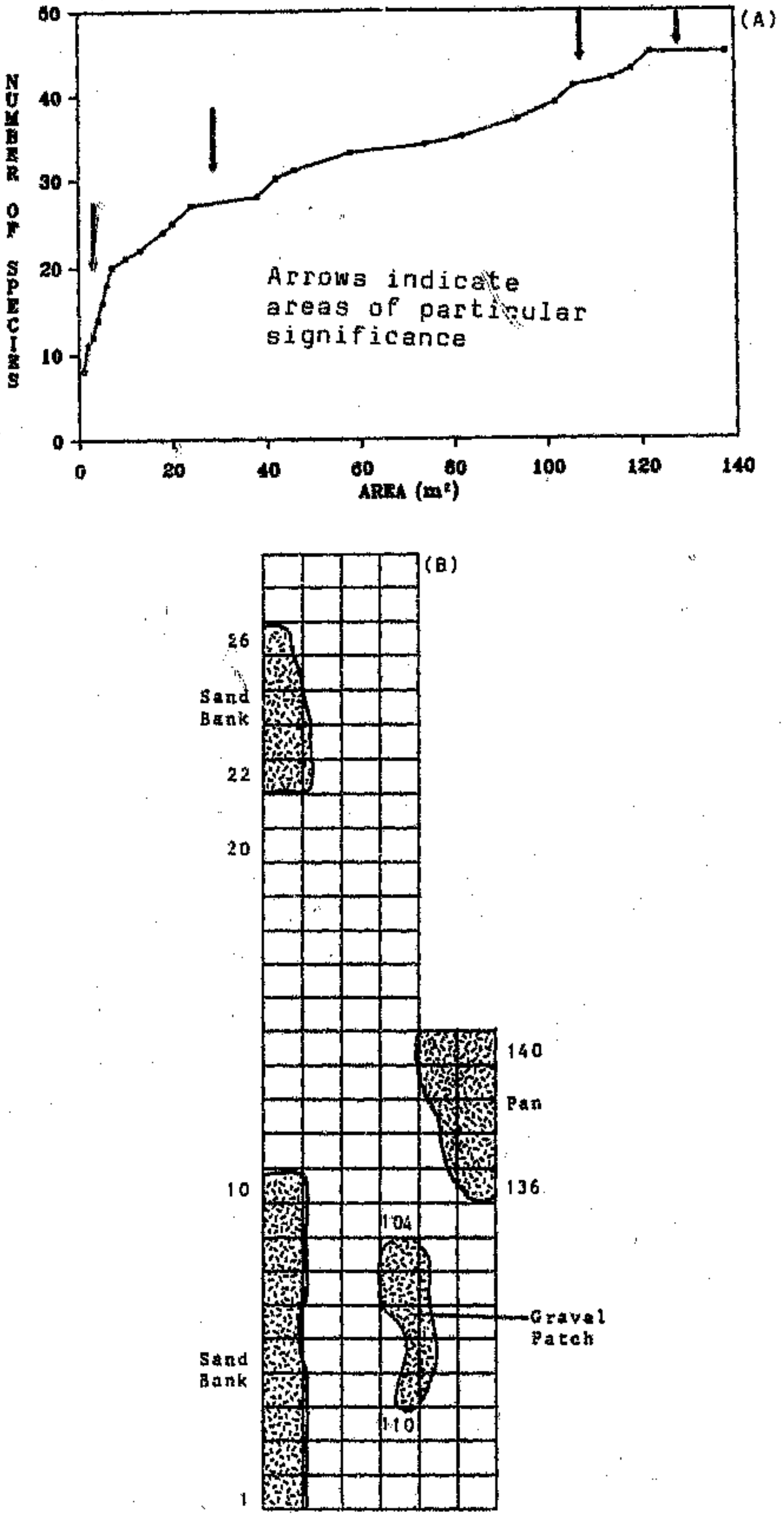


Figure 4.8 First area sampled

(A) species-area curve
(B) corresponding map of area

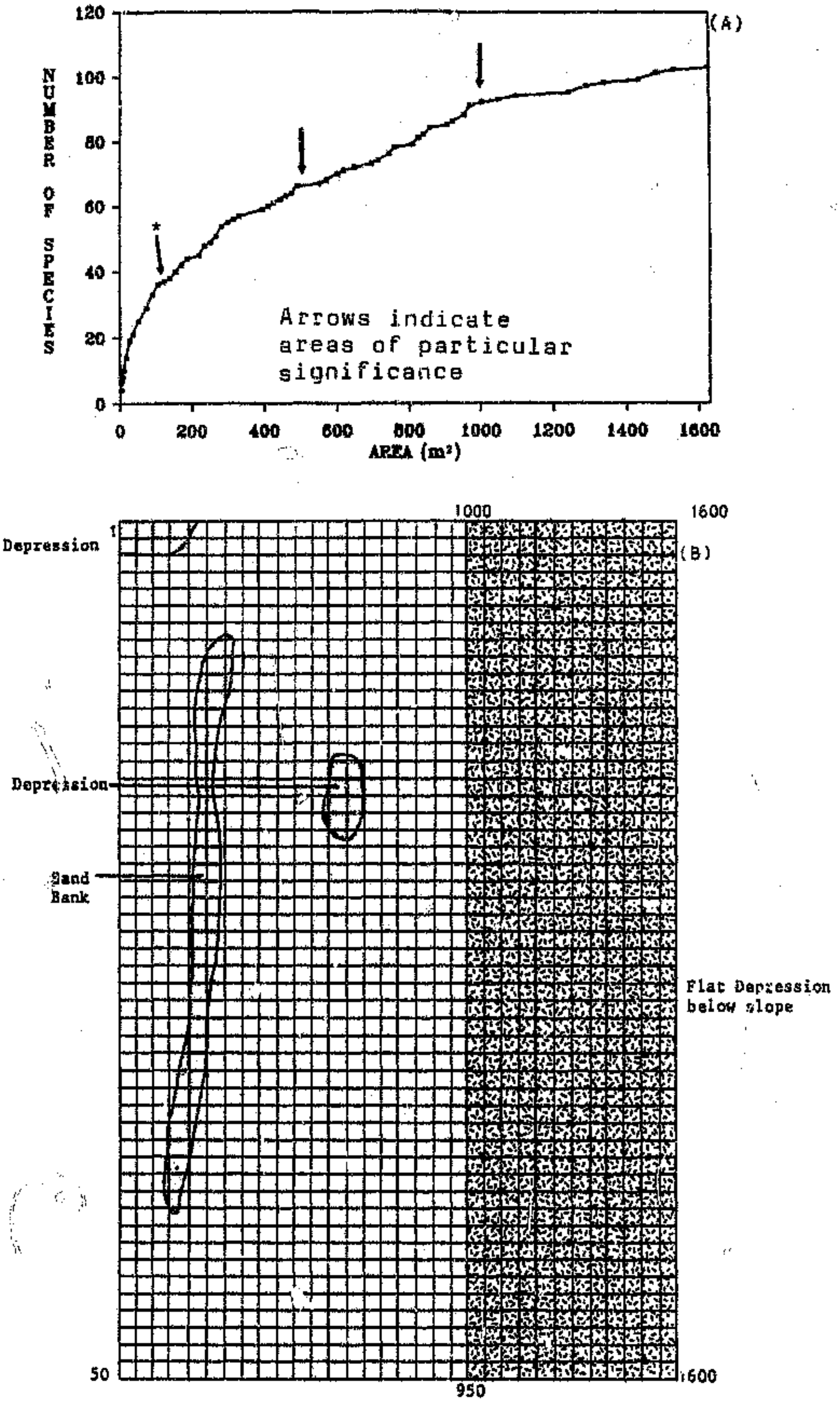


Figure 4.9 Second area sampled

(A) species-area curve
(B) corresponding map of area

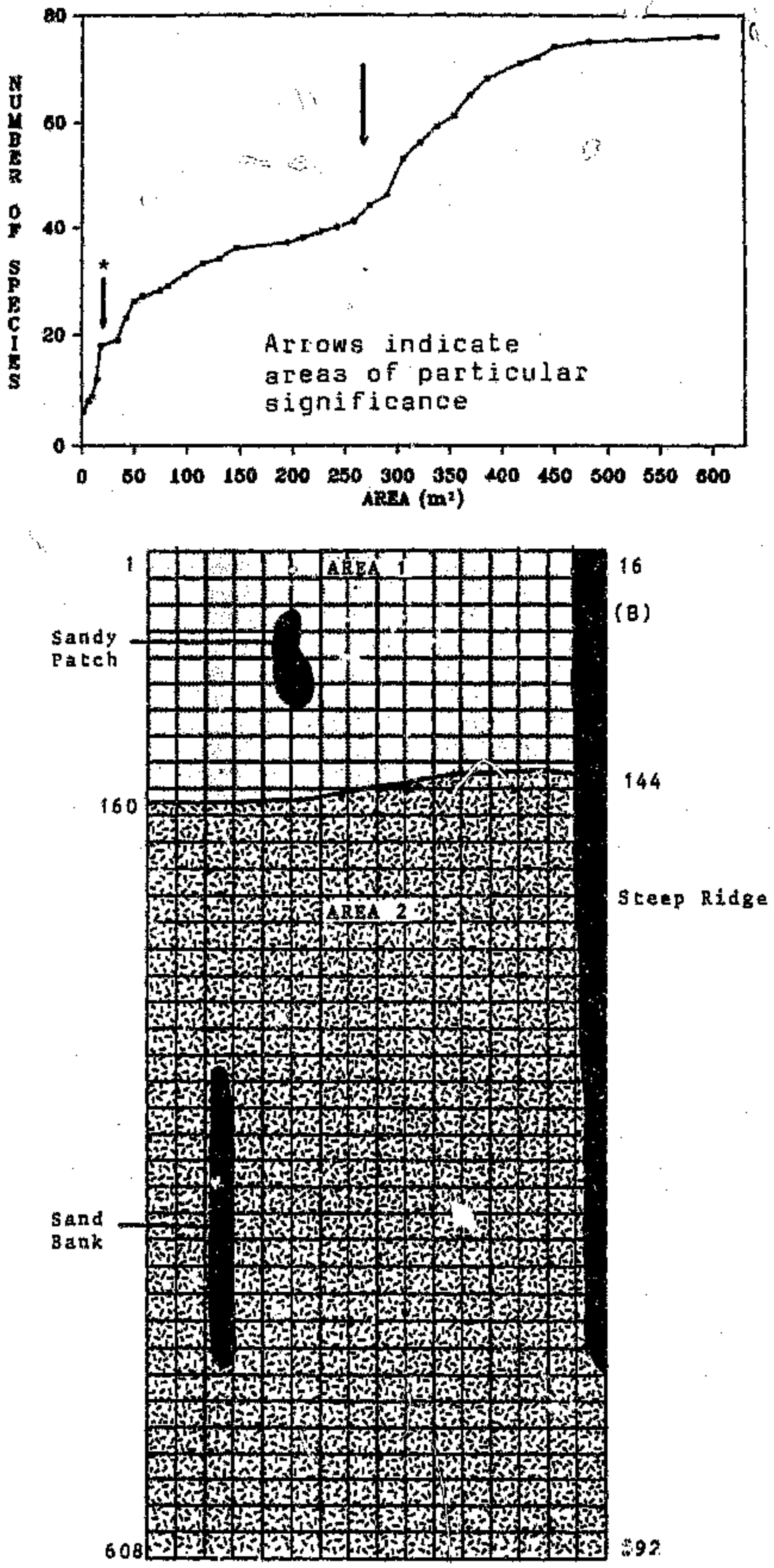


Figure 4.10 Third area sampled

(A) species-area curve
(B) corresponding map of area

Physical features such as two other depressions and a sand ridge are also evident on Figure 4.8 B. These features, due to the scale of the curve and their relatively small sizes, have been reduced to the small unidentifiable bumps on the curve and consequently it is hard to distinguish these bumps from those caused by the size of the quadrat mentioned previously. In addition, the curve identifies a small bump marked with a "*" which is not present on the map of the area. This is probably due to the presence of an invisible zone of high nutrient status.

The third area sampled (Fig. 4.10 A) displays two abnormalities (border arrowed) which are once again adequately explained by the environmental characteristics of the area (Fig. 4.10 B). The whole area is effectively divided into two large sub-areas. The first is an erosion exposed rock outcrop which has become covered by a patchy layer of fine sand and well colonized by grass, while the second is the area adjacent to it which was not subjected to flood erosion. This area is characterised by a deep soil layer and a wide variety of plants. Once again the scale of this curve prevents it from adequately reflecting small aberrations which are evident on the map. Again evident with this curve is a bump (marked with a "*") which does not make itself clear on the map of the area studied.

2.5 Discussion

2.5.1 Transect technique

It appears that only 31.2 percent of the variation in species richness was accounted for by the presence of visibly discernible habitats in the areas investigated. While this is not particularly high, it is a significant and positive relationship. It must be noted that this value did not include the variation accounted for by other habitats which were not visibly discernible, such as nutrient and resource hotspots formed by fires, animal burrows and other localised processes. Had it been possible to identify such areas, their inclusion in the regression would possibly have increased this figure.

As with the island size hypothesis (sub-chapter 1), it is pointed out that the sampling strategy employed was not entirely independent. While the location of the transects was determined by means of a stratified random procedure, the quadrats used were contiguously located in these transects, which were run up the riverine gradient. In other words, the samples required for the test per se were not independent. According to Green (1979), the assumption of 'independence of errors' is the only one in most statistical methods for which violation is both serious and impossible to cure after the data have been collected. In their review of 'consequences of failure to meet assumptions', Glass et al (1972) concluded that correlated errors can have more serious consequences on the validity of tests of significance than all other violations. If the errors are positively correlated, the test will tend to be more liberal than the the nominal level (e.g. p=0.05). However, if negatively correlated, the tests would tend to be more conservative. In this particular case, since the likely errors are positively correlated, it can be expected that the test results would appear more significant than they actually are. Green (1979) stated that the truly random allocation of samples is the necessary and sufficient safeguard against this violation. The problems associated with the truly random placement of samples in recently disturbed riverine areas and the necessary trade-offs which had to be made at the outset of the study have been discussed in sub-chapter 1.

2.5.2 Nested plot technique

The construction of species-area curves with the data obtained from the nested plots assisted with understanding the relationship between visibly discernible habitats and species richness. It is clear that as sampling area increases, so new habitats are encountered which are suitable for colonization by plants. The majority of these habitats appear to take the form of a clear physical feature such as mounds of sand, small pans or rocky outcrops but a small quantity of these habitats are "hotspots" which display high nutrient status and which are not clearly evident. These patches appear to be small, localised areas which were probably formed by concentrated burns on old tree stumps and roots, old rhino middens, animal diggings and a wide variety of other localised processes.

2.6 Conclusions

Approximately 30 percent of the variation in species richnesses of riverine areas was accounted for by the presence of visible patches/habitats present. Consequently, the null hypothesis was firmly rejected. While this figure is not particularly high, the presence of other invisible patches is likely to assist in raising the accountable percentage of species richnesses still further.

Riverine communities are clearly heterogeneous and composed of numerous patches of different sizes and shapes. These patches are a consequence of the patchy nature of the erosions and silt depositions which occur during flooding and heterogeneous geology and topography. This results in the formation of sand banks, steps, depressions, undulations, open rocky patches and a wide range of physical aberrations which are available for colonization when the floods recede. In addition, further patches are created by the activities of animals and localised fires, which also present themselves as possible habitats for colonization by plants. The presence of these habitats can be reflected on the species-area curves for these areas as localised abnormalities to their general shape.

SUB-CHAPTER 3 INDIVIDUALISTIC RESPONSE HYPOTHESIS

Gauch (1985) proposed twelve distinct elements of the individualistic response hypothesis. This chapter deals with testing three of these elements to reach conclusions regarding the applicability of the individualistic response hypothesis and its alternative, the community-unit hypothesis. In addition, using an ordination technique, riverine data were explored with the aim of elucidating the major determinants to which riverine species individualistically respond.

3.1 Introduction

The individualistic response hypothesis attempts to explain the distribution and diversity of vegetation in an area on the basis of the individualistic responses of plants to specific resource and/or habitat requirements. For further details of the hypothesis and the 12 proposed elements of hypothesis, see the literature review, section 1.6.3.3.

The major elements proposed by Gauch (1985) are as follows.

A. Element 1. Species response curves approximate normal (Gaussian) curves i.e. the curves are symmetric and bell-shaped in relation to an environmental gradient.

B. Element 2. The modes of major species tend to have a uniform distribution along the environmental gradient, while the minor species modes are randomly distributed.

C. Element 7. A gradient of community composition (coenocline) can be characterised by by the amount of species turnover (beta diversity) from one end to the other.

The community-unit hypothesis represents the alternative or null-hypothesis to the individualistic hypothesis. It states that vegetation is structured into well-defined natural units and that sharp boundaries (ecotones) exist between these community types as a result of competition between dominant species present.

Interpretation of the Price (1984) hypothesis summary table (Table 1.1) reveals that the individualistic response hypothesis is expected to apply in the study area in early spring and summer when the rates of resource change are steadily increasing or in early winter when resources begin to pulse. The hypothesis is expected to apply largely in areas with patchy resource distributions where various species could respond in any way or in areas of uniform distribution with only slow responding species. Resource and environmental characteristics vary considerably down the length of the riverine profile as well as between different riverine areas. For this reason, both situations are ideal for investigating the applicability of the hypothesis. Conditions which vary along the riverine profile are particularly noticeable in terms of soil and slope conditions, availability of water and utilisation by ungulates. Different riverine areas differ considerably in terms of their positions relative to the river, prevailing winds and exposure to the sun, their aspect relations, degrees of disturbance, rainfall and soil conditions.

On this basis, it was envisaged that data collected from transects run down the length of the riverine profile, from numerous randomly selected areas, would serve adequately to test the hypothesis. In addition, that by conducting an ordination of this data, knowledge could be gleaned concerning the major resources and/or environmental characteristics responsible for the distribution of species in riverine areas.

3.2 Objectives

The objectives of this chapter were as follows.

1. Test element one of the individualistic response hypothesis by determining the relative proportions of observed plant distribution types in riverine areas and making comparisons with those reported by Austin (1985) and Whittaker (1956).

2. Test element two of the individualistic response hypothesis in riverine areas by analysing the distribution of species modes between the ends of the gradient.

3. Test element seven of the individualistic response hypothesis by analysing the species turnover (beta diversity) along the length of the riverine gradient.

4. Employ direct/indirect gradient analysis techniques to a. display the response of species down the riverine gradient, and b. to investigate those key factors to which plant species respond and which largely determine their distribution and diversity in riverine areas.

5. On the basis of the above findings, reject or accept the community-unit hypothesis which stands as a null-hypothesis to the individualistic response hypothesis.

3.3 Methods

3.3.1 Data collection

Twenty six transects were laid out in the riverine area (see island size hypothesis). Data collection involved the identification (or later identification with the assistance of Palgrave (1983) or the Botanical Research Institute) and stem counts of all woody species present within each quadrat. Twenty 1x1 metre sub-quadrats were laid out randomly within each quadrat. Within each sub-quadrat, all herbaceous species were identified or collected for later identification (as with trees) and recorded. For each quadrat, species frequencies of herbaceous species were determined from the counts made in each sub-quadrat and the densities of woody species were determined from total stem counts.

Each transect was described in terms of the following environmental characteristics.

- position on river
- distance from river to adjacent community
- aspect
- profile of slope
- presence/absence of environmental discontinuities
- approximate extent of erosion or siltation

A dumpy level was used to determine the height above river at the centre of each quadrat. This facilitated the separate construction of the riverine slope profiles for each site.

Soil samples were taken from each distinct layer in the first 100 cm below the surface from soil pits located within each quadrat. All samples were sieved with a set of sieves ranging in diameter size from 0.0625 mm to 4 mm. The various particle sizes and their distributions were then used to determine the proportions of three textural classes namely mud (clay and silt), sand and gravel. These proportions were compared in the different transects and their respective quadrats.

3.3.2 Data analysis

3.3.2.1 Test of element one of hypothesis

In order to determine the response of each species to specific environmental conditions down the riverine gradient, the abundances of five observed distribution types were determined.

Linear distributions were considered to be those present in all or a few quadrats of the transect in approximately the same abundances.

Non-linear distributions were considered to be those present in all or a few quadrats, but displayed uneven abundances within their distribution range. These distributions were then classified into four groups as follows.

A. Gaussian, if their maxima were found to exist at a single quadrat located approximately in the centre of their distribution range.

B. Skewed, if their maxima were found to exist at either end of their distribution range.

C. Platykurtic, if both flanks tapered off but their maxima were found to exist in the centre and in more than one quadrat simultaneously.

D. Bimodal, if both flanks tapered off but their maxima were found to exist in two different quadrats separated by one displaying a lower abundance.

The relative proportions of four distribution types were determined for 26 transects at 9 sites for both the herbaceous and woody components. Using a Chi-square test, these observed distributions were then compared with those published by Whittaker (1956) and Austin (1976) to determine the extent of the individualistic responses of species.

The null hypothesis employed was that species distributions would approximate those published by Austin (1976).

Should the Gaussian distribution be found to represent the majority of the distribution types present, the null hypothesis would be rejected and this would imply the validity of the 12 elements of the Gaussian model of community structure (Gauch, 1985). However, should it be found that the Gaussian distribution is rare, then it would imply that many of the elements of this model are inapplicable and would remove the need to proceed with testing them.

The proportions of the five distributions were then graphically compared in the 9 sites investigated to infer the effect of environmental and biotic factors.

3.3.2.2 Test of element two of hypothesis

This test of the second element of the individualistic hypothesis was taken directly from Austin (1987) and applied to riverine transect data. It involved testing the modal distributions of major and minor species for a possible departure from a random modal distribution in the two species classes.

The modal positions (1 6 quadrats) and maximum modal frequencies of each species were determined down the length of the riverine gradient. Species were classified as major species if they displayed maximum modal frequencies greater than 0.5 and as minor species if they displayed maximum modal frequencies less than or equal to 0.5. Austin (1978) used a modal frequency of 0.3 to distinguish between major and minor species. However, in this case, the figure was found to include too large a proportion of species in major species category. A table was then constructed of the modal abundances in each quadrat for both species classes.

The distribution of modes along the gradient was then compared with a randomly selected distribution of the same sized modes using a Chi-square test. According to Austin (1978), a one-tailed test for Chi-square is necessary to test for a regular departure from randomness (a uniform distribution). This can be accepted when the observed value exceeds the $p<0.05$ value for the random expectation minus the one-tailed value at $P<0.05$. With 5 degrees of freedom, this would be 11.07 - 5.35 = 5 53.

The null hypothesis employed was that no differences existed between the modal distributions of major and minor species from that of a random distribution of modes. This finding would then disprove the second element of the hypothesis. Should the null hypothesis be rejected, this would imply that the modes of species conform to an even or uniform distribution down the length of the gradient in support of the second element of the hypothesis.

3.3.2.3 Test of element seven of hypothesis

This test involved the determination of the turnover of species from one end of the riverine gradient to the other. The following formula was employed to determine beta diversity (Magurran, 1988),

$$\text{beta diversity} = [A + B] \times [1 - S]$$

where, A = number of species in quadrat 1,
B = number of species in quadrat 2, and
S = the similarity index between the 2 quadrats.

The similarity index employed was that of Sorensen (1948),

$$S = \frac{2 \times C}{A + B}$$

where, C = the number of species common to both quadrats.

The beta diversity was determined in both the herbaceous and woody species down the length of the gradient. These values were then tabulated.

The null hypothesis employed was that no turnover of species exists between the ends of the riverine gradient. The null hypothesis would be rejected should a species turnover be identified between the ends of the gradient.

3.4.2.4 Gradient analysis

3.4.2.4.1 Direct gradient analysis

A gradient commonly exists in riverine areas. Due to the proximity of the river, a high soil moisture exists at the river's edge and an increasingly lower soil moisture is evident with increasing distance from the river. This decline in soil moisture reflects the natural attenuation of lateral water movement through the pore spaces in soils as distance from the river increases. Water moves readily from a standing water table (with high free energy) to a dry soil (with low free energy) (Brady, 1974). As the matrix force offered by the soil gets larger and larger, relative to the free energy of the soil water, so the lateral movement of the water into the adjacent soil will attenuate and eventually cease. In addition to this soil moisture gradient, substratum textural and nutrient characteristics also change noticeably down the length of the riverine profile. This is therefore an ideal gradient on which to investigate the response of plants to specific requirements. An ordination of species data along it should then directly display the nature and extent of the gradient itself. Due to the complexity of the gradient and the various responses of species to it, the total variation which is accounted for by the first few principle axes of the ordination is expected to be low.

Species present were ordered, for each transect, according to their abundances (densities or species frequencies) and distributions on the riverine gradient. These distributions were then combined for all transects. Correspondence analysis was then employed, as a direct gradient analysis technique, to ordinate the quadrats on the riverine gradient and to produce a graphical display of the response of species to the gradient. The vegetation present at different positions on the gradient were therefore used to ordinate the quadrats and place them relative to each other on the gradient. Assistance with the concepts and technical details of the correspondence analysis technique and its interpretation were obtained from Greenacre (1984; 1986).

3.4.2.4.2 Indirect gradient analysis

Correspondence analysis was also employed to determine indirectly the major factors responsible for determining the relative distributions of species between the sites investigated. This was achieved by ordinating all sites on the basis of herbaceous and tree species present. Woody species were compared on the basis of their densities, while herbaceous species were compared on their species frequencies. A supplementary row of environmental characteristics at the sites was overlaid on the data set as described in Greenacre (1986). The graphical and numerical outputs of correspondence analysis were then used to determine the correspondence between major environmental factors and the species present at each site.

It was envisaged that this ordination should reveal factors, apart from distance from river, which play a role in the structuring of riverine areas. Due to the extensive and complex nature of the riverine environment and the large number of species which respond to it, it was expected that this gradient would be very complex. Consequently, the variation accounted for by the first few axes of the ordination was expected to be low.

3.4 Results

3.4.1 Test of element one of hypothesis

The comparison of a total of 1371 herbaceous and 382 woody distributions from 26 transects (Table 4.5) revealed that 73.9 percent of herbaceous and 67.9 percent of woody distributions were true Gaussian in form. Slight differences existed between the herbaceous and the woody species in terms of the proportions of the 5 distribution types. The woody species displayed fewer true Gaussian and larger quantities of platykurtic distributions. Bimodal distributions were equally common for both herbaceous and woody species.

Table 4.5 Comparison of herbaceous and woody species distributions in response to the riverine gradient

DISTRIBUTION TYPE	PROPORTION (%)			
		Herbs	Trees	
- Linear		0.7	0	
- Non-linear				
Gaussian		73.9	67.9	
Skewed or	80.7			82.2
Platykurtic		6.8	14.3	
Bimodal		18.6	17.8	

According to Table 4.6 the proportions of the various distribution types in these areas were not consistent with those published by Austin (1976) but similar to those published by Whittaker (1956). Austin reported generally larger proportions of distorted distributions and considerably fewer true Gaussian distributions, while Whittaker reported larger proportions of true Gaussian distributions with the complete absence of skewed and platykurtic forms.

Table 4.6 Species distribution proportions as published by Austin (1976) and Whittaker (1956)

Differences (p<0.05) between the observed values and those reported are indicated by (*)

Distribution type	Proportion (%)	
	Austin	Whittaker
- Linear	5(*)	0
- Non-linear		
Gaussian	26(*)	86.4
Skewed/platykurtic	45(*)	0(*)
bimodal	29(*)	13.6

Figure 4.11 compares the mean proportions of the various species distributions in the 9 sites investigated. Scrutiny of the distorted distributions (linear, skewed, platykurtic and bimodal) reveals that there are differences between the sites. The abundances of linear, skewed and platykurtic do not appear to display any trends. However, a trend is evident with the abundances of bimodal distributions. The sites have been arranged from left to right in the order of increasing bimodality. Sites 2,3,7 and 6 display particularly large proportions of bimodal distributions, while sites 1,8,5 and 4 displayed low abundances of bimodal distributions. The environmental characteristics of the sites investigated are presented in Appendix 1. Here the angle of the riverine slope at sites 2,3,6 and 7 indicate that they have flat profiles. Sites 1,8,4 and 9 display steep profiles.

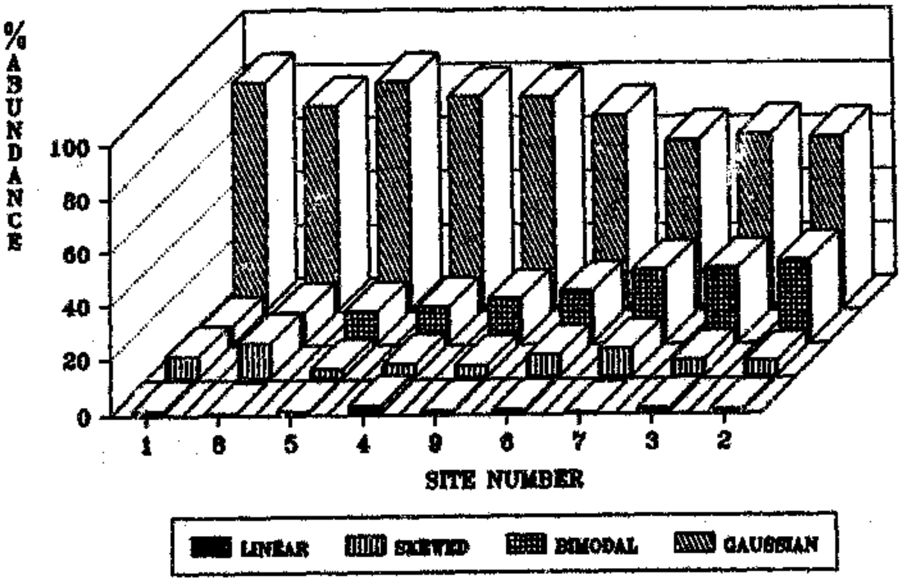


Figure 4.11 Mean proportions of four species distribution types for the 26 transects investigated

3.4.2 Test of element two of hypothesis

Table 4.7 reveals that, in both species classes, there is a significant departure from the random distribution. In addition, both values exceed that $p<0.05$ value (5.35) which is indicative of a uniform distribution of the modes. The null hypothesis was therefore rejected, which implies that both species classes are uniformly distributed along the riverine gradient.

Table 4.7 The modal abundances in each quadrat and a randomly selected distribution of the same sized modes for major and minor species

POSITION ON RIVERINE GRADIENT (QUADRAT NUMBER)	MAXIMAL MODAL FREQUENCY			
	MAJOR SPECIES	RANDOM	MINOR SPECIES	RANDOM
1	34	14	38	12
2	7	34	12	13
3	14	8	13	9
4	18	7	15	26
5	8	11	9	15
6	11	18	26	38

Major species Chi-square 75.3 D.F. 5 - p=0.001
Minor species Chi-square 69.0 D.F. 5 - p=0.001

3.4.3 Test of element seven of hypothesis

Table 4.8 reveals that the length of the riverine gradient is characterised by a continuous turnover of both herbaceous and woody species and, consequently, the null hypothesis was rejected. The number of herbaceous species which are associated with this turnover are generally higher than for woody species.

Table 4.8 Species turnover (beta diversity) values along the riverine gradient from quadrat 1 at the river's edge to quadrat 6

	BETA DIVERSITY (species abundance)	
BETWEEN QUADRATS	HERBACEOUS SPECIES	WOODY SPECIES
1 - 2	63	20
2 - 3	68	14
3 - 4	75	17
4 - 5	72	15
5 - 6	59	20

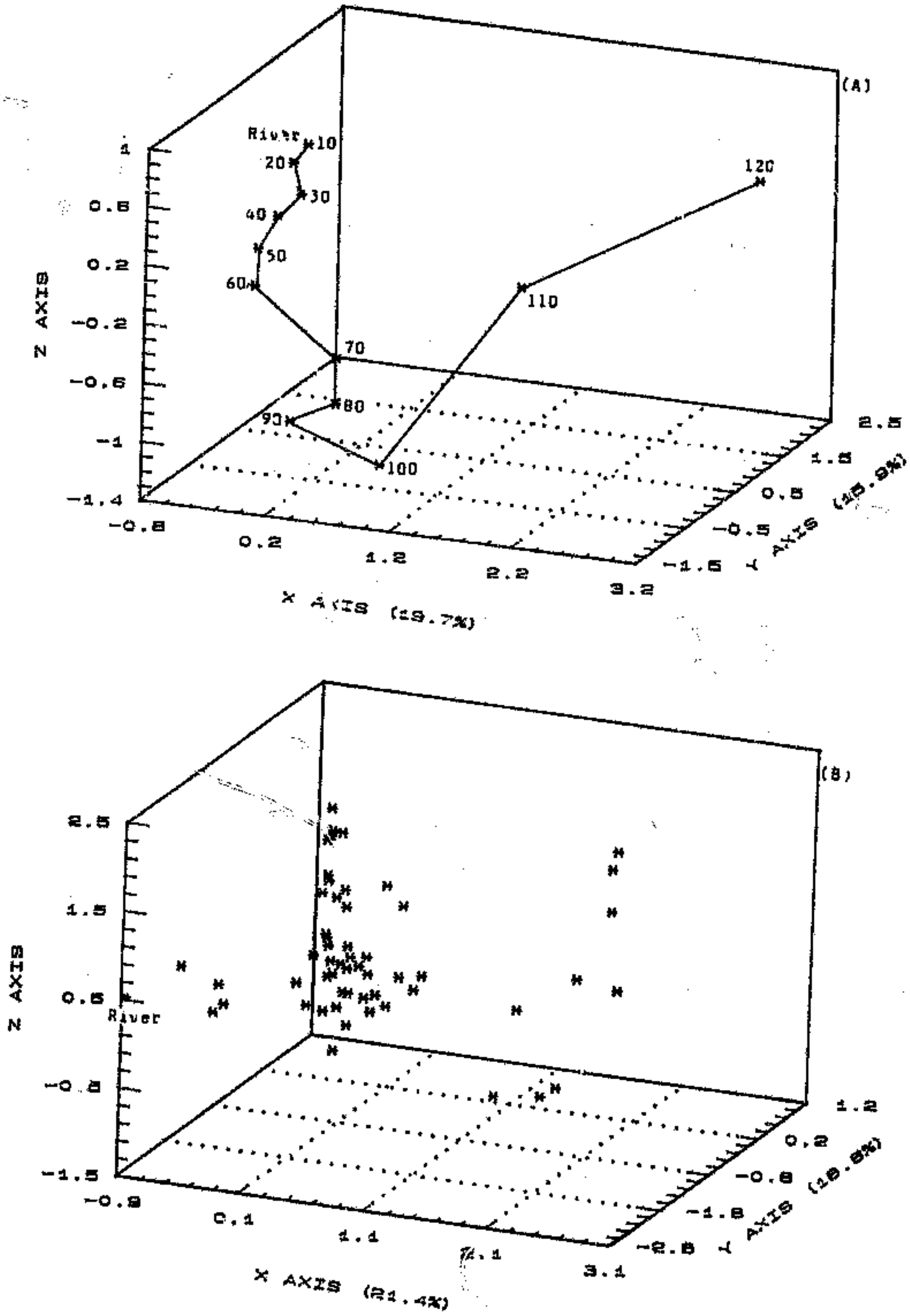
3.4.4 Gradient analysis

3.4.4.1 Direct gradient analysis

The direct gradient analyses of woody and herbaceous vegetation along the gradient obtained from correspondence analysis are displayed by Figures 4.12 A and 4.13 A. Their corresponding species coenoclines are displayed by Figures 4.12 B and 4.13 B. Since the variation accounted for by the first two axes in each case were relatively low (35.6 to 40.2 percent), the results are presented in three dimensions in an attempt to account for a larger percentage of the total variation. To clearly display the coenocline as well as the gradient, they have been plotted separately.

C

C



C

Figure 4.12 Correspondence analysis plot of woody species distributions along the riverine gradient for all transects combined

C

(A) gradient from river's edge to top end of profile, where figures represent distance from the river's edge in metres

(B) corresponding coenocline of species

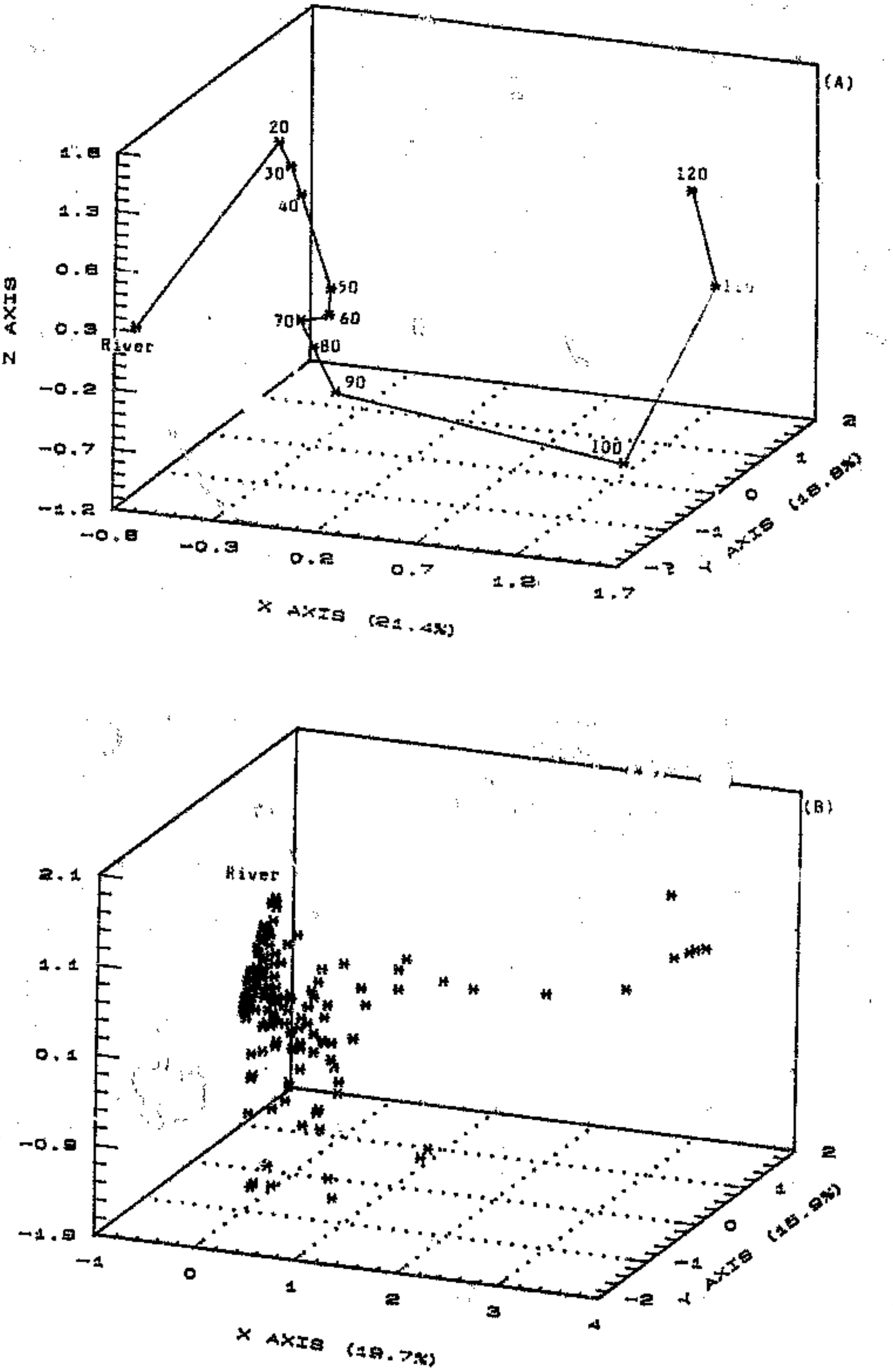


Figure 4.13 Correspondence analysis plot of herbaceous species distributions along the riverine gradient for all transects combined

(A) gradient from river's edge to top end of profile, where figures represent distance from the river's edge in metres

(B) corresponding coenocline of species down the gradient

Mesic species are found near the river's edge and the more xeric species towards the top of the riverine slope. Apart from these two distinct groups of species in the lower and upper reaches of the gradient, different species are found almost continuously between the two extremes. This indicates that a continuum of species exists over the length of the gradient with a distinct overlap of species distributions. Since the correspondence analysis technique only displays the mode of each species along the gradient, it is not easy to envisage the overlap of species distributions along the profile.

The distributions of species present at a single transect (Fig. 4.14) clearly reveals this overlap of distributions. The presence of bimodal species is indicated where species have deviated from the gradient arch and exist in the space between two particular points on the gradient where they exhibit their distribution peaks. The position of these points relative to the gradient supports the view that bimodality is largely explained by environmental characteristics rather than the effects of competition.

The distributions of both woody and herbaceous species (Appendix 4 A and 4 B), used as the input file in the correspondence analysis technique, display the distributions of species for all the transects combined.

The woody species were placed in order of their optimal distributions along the soil moisture gradient. This serves as a simple classification of species according to their moisture requirements. Since the abundances of herbaceous species fluctuate considerably in response to local and global changes in the water regime, a similar exercise for these species would be of little management value and consequently these species were simply placed in alphabetic order.

Appendix 5.1 A to 5.27 A displays the responses of sedges, grasses, forbs and trees to the moisture gradient. This crude breakdown reveals the unique requirements of each group but since each group is represented by generalist and specialist as well as mesic and xeric species, this response appears broad and unresponsive.

Generally, sedges were associated with the lower reaches of the slopes, while trees were largely associated with the top ends of the profiles. Grasses and forbs generally displayed a homogeneous distributions along the profiles. It is important to compare these distributions with their positions on the riverine slope (Appendix 5.1 B to 5.27 B) and the soil characteristics of the areas they occupy (Appendix 5.1 C to 5.27 C).

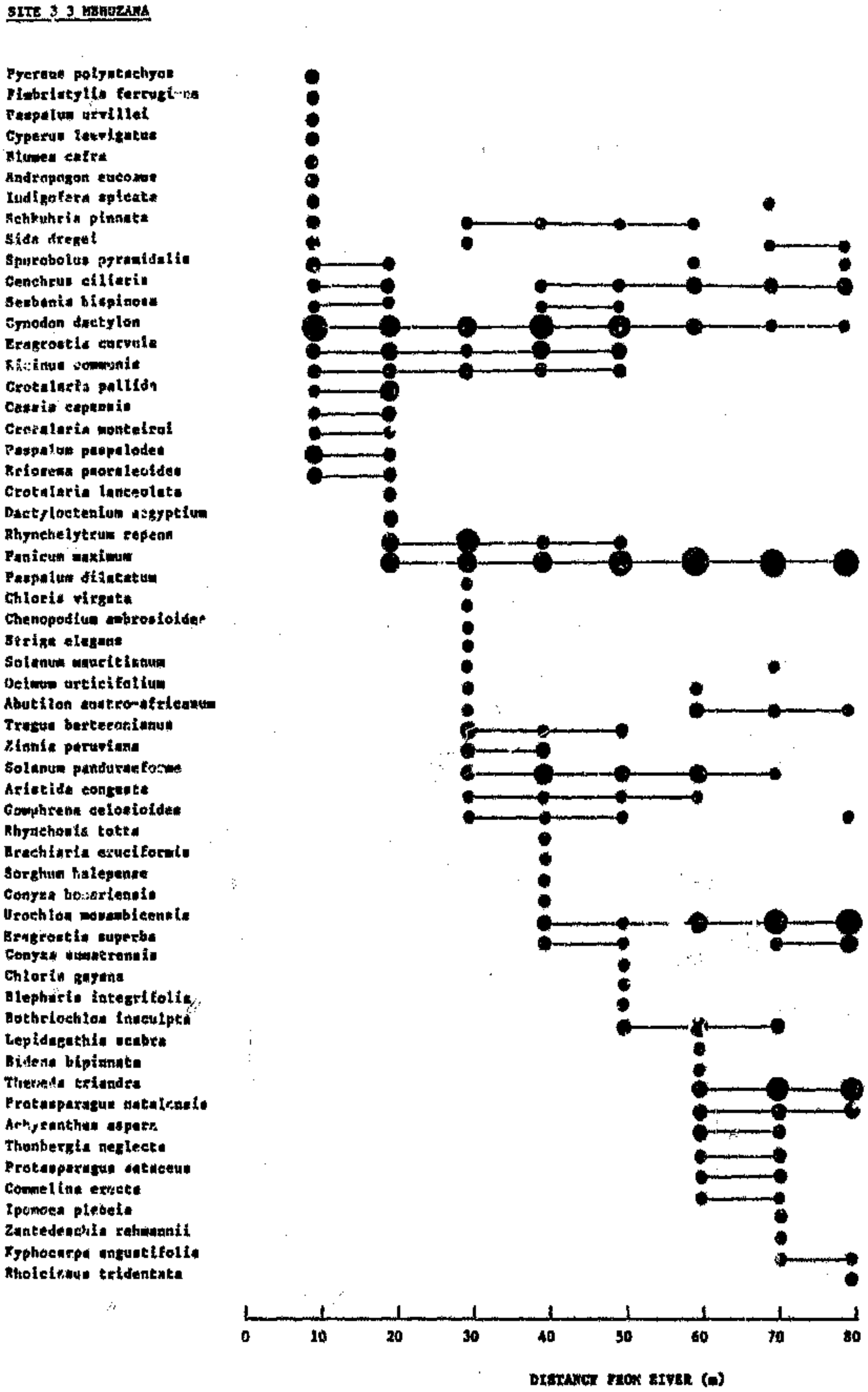


Figure 4.14 The distribution of herbaceous species along a single riverine transect. The circle diameters for each species indicate their relative abundances in each quadrat

3.4.4.2 Indirect gradient analysis

Figure 4.15 (A & B) displays the results of the ordination of herbaceous species between sites using correspondence analysis. (For numerical output see Appendix 2.4). In order to display the complexity of the coenocline, which in turn reflects the complexity of the gradient itself, the ordination of species is presented as a three dimensional display (Fig. 4.15 A). Four corners of the coenocline are evident. These represent four zones of species which have different moisture requirements and tolerances.

Comparison with the two dimensional display of the sites (Fig 4.15 B) reveals that these zones correspond well with the aspect and slopes of the sites they colonize. The first principle axis (represented by axis 1) represents the aspect factor of the gradient and accounts for 38.9 percent of the moisture gradient. The second principle axis (represented by axis 2) represents the riverine slope factor and accounts for 19.1 percent of the gradient. The aspect and slope factors of the riverine environment occupy a further seven percent due to their partial representation by axis 3. Therefore, in total, these factors account for only 65 percent of the total soil moisture gradient in riverine areas. This fact indicates the complexity of the gradient and the response of herbaceous species to it. A further 35 percent of the total variation has not been accounted for by the analysis which extends into a further three dimensions. This variation is possibly partially accounted for by other factors, such as the precipitation gradient, which extends from east to west along the reserve and the overall soil differences between the sites.

Xeric species are associated with areas which are north facing and particularly if these sites have steep slopes (Appendix 1 lists the characteristics of all sites). At the other end of the moisture continuum, mesic species are found on south facing areas. Flat south facing areas are situated at the extreme of the continuum. The intermediate moisture populations (sub-xeric and sub-mesic) are arranged by means of a delicate balance between the aspect and the slope of the areas they colonise. Sub-xeric species are found on two areas with similar moisture conditions but subtly different slope and aspect characteristics. Sites 5 and 6 display this clearly.

Site 6 is north facing, but is a comparatively flat area. This keeps it from being grouped with the other north facing sites (due to its low water run-off characteristics). Site 5 displays a medium slope but is east facing and, therefore, not exposed to extremes in temperature and sunlight conditions as are north and south facing areas. Sites which sport sub-mesic species are characterised by south facing slopes but exhibit high water run-off conditions due to their steep slopes.

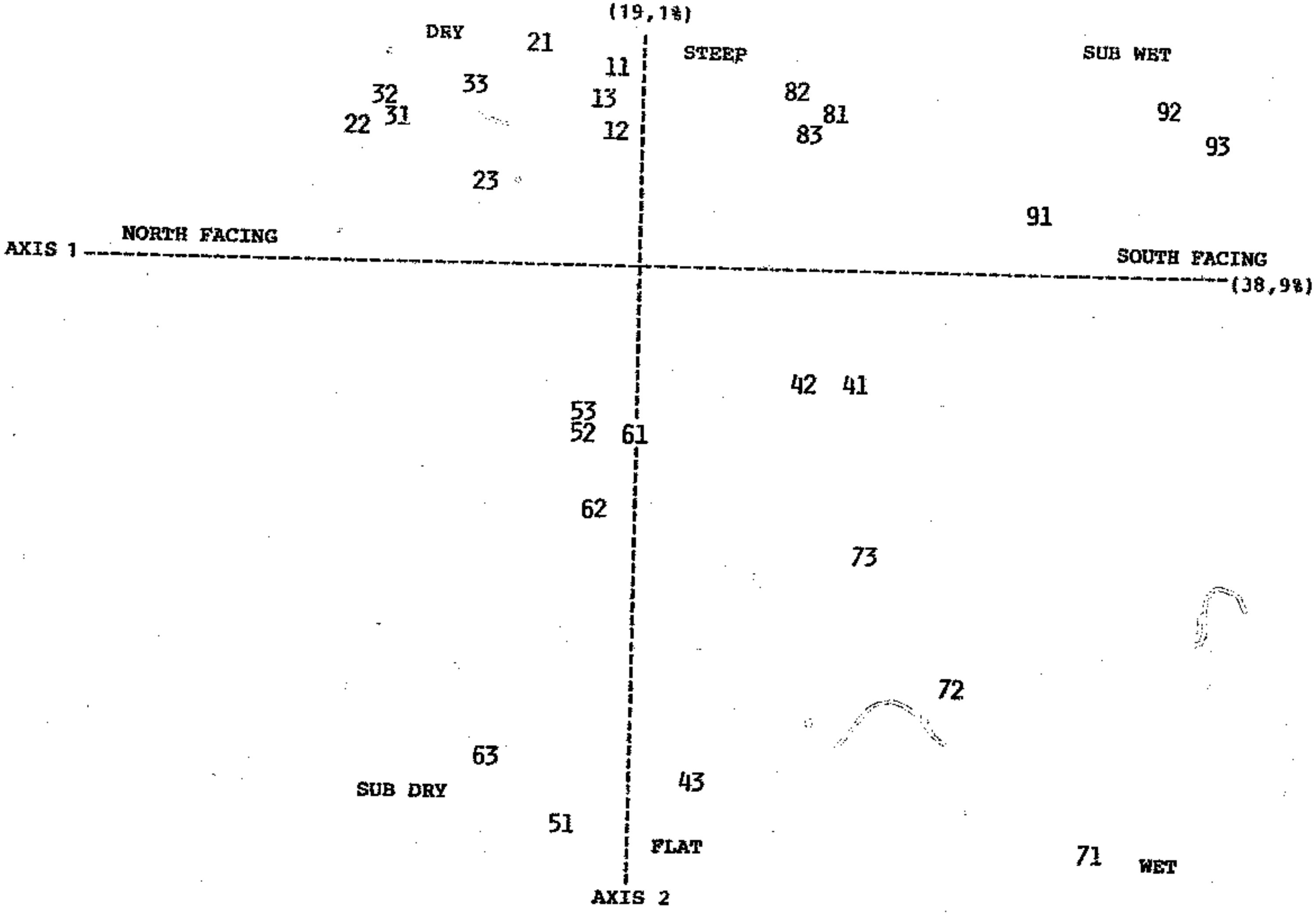


Figure 4.15 (A) Two dimensional correspondence analysis display of sites based on herbaceous species present

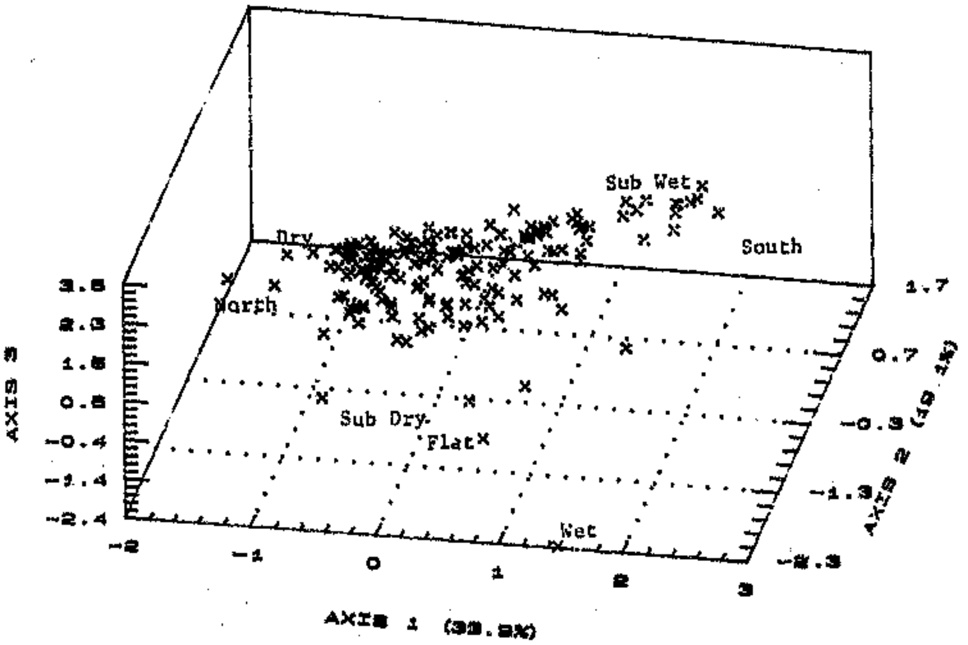


Figure 4.15 (B) Three dimensional correspondence analysis display showing the coenocline of herbaceous species

The interpretation of these findings is assisted by Table 4.9. Here the intensity of noon isolation is expressed as a percentage of the maximum possible isolation at noon on the following four days. It displays that north aspects generally receive a higher insolation intensity than do south facing slopes. This is the case both in summer as well as in winter and is particularly true for steeper slopes.

The dry extreme of the soil moisture gradient is represented by steep north facing slopes. As a consequence of high mean insolation, high evaporation, high mean temperatures and high water run-off, the species in these areas face conditions of high water stress. The next point on the continuum is represented by sub-dry areas. Here moisture conditions are less harsh. Either the slopes are east facing or, if north facing, the slopes are not so steep. In both cases, this tends to reduce the mean insolation (and therefore evaporation) and run-off. The next point on the gradient is represented by steep south facing slopes. As these areas are south facing, they are subjected to milder insolation and temperature conditions but still face high run-off.

Table 4.9 Comparative noon insolation intensities for north and south facing sites of varying slopes at different times of the year. Adapted from Downing (1972)

SITE		PERCENT MAXIMUM POSSIBLE NOON ISOLATION			
SLOPE	ASPECT	OCTOBER	DECEMBER	APRIL	JUNE
0	-	89.4	99.8	97.3	62.2
10	N	96.0	99.8	94.7	75.0
	S	82.0	97.0	78.0	49.0
20	N	99.6	96.6	98.8	85.2
	S	68.0	90.7	65.5	34.0
30	N	99.8	90.7	100.0	93.0
	S	57.0	83.0	52.3	21.0
40	N	95.0	82.0	98.7	98.1
	S	44.0	71.4	38.0	10.0

The wet extremes are characterised by lower mean temperature, mean insolation, evaporation, exposure and run-off. Species occupying these areas face little stress due to water shortages but may at times be subjected to high anoxia.

The indirect gradient analysis of woody species at the same site is displayed by Figure 4.16 A & B. (For numerical output - see Appendix 2.5). Here one must consider the differences between trees and herbs with regard to their rooting depths (their water reach ability) and how they are affected by evaporation and drainage. In this case, the three corners of the triangle in Figure. 4.16 A represent the coenocline/moisture gradient (in 2 dimensions). The dry/xeric extreme is once again represented by steep north facing areas. To deep rooting woody species these areas are dry due to high evaporation and run-off and because increasing distance to the water table is associated with increasing slope, they have trouble reaching water. These species are consequently subjected to moisture stress, particularly on hot summer days.

The moisture gradient proceeds to the opposite extreme on the basis of the differential ability of trees to reach water. The concomitant effects of evaporation and exposure of species to extremes in temperature and exposure are superimposed on this. Species occupying this extreme (flat or south facing slopes) are unlikely to experience stress due to significantly lower evaporation rates, lower mean temperatures and close proximity to the water table.

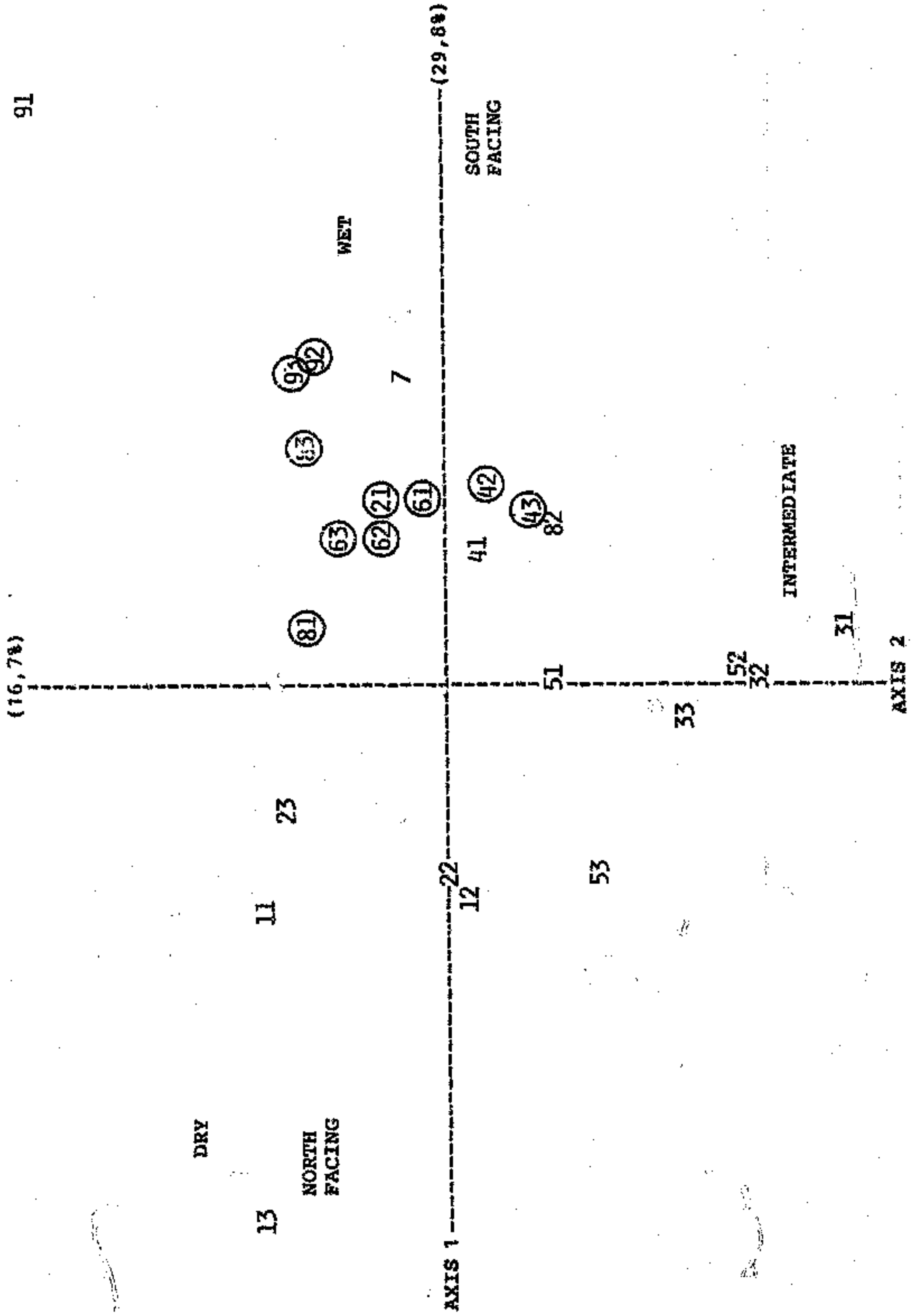


Figure 4.16 (A) Two dimensional correspondence analysis display of transects based on woody species present. Circled sites extend into the third dimension

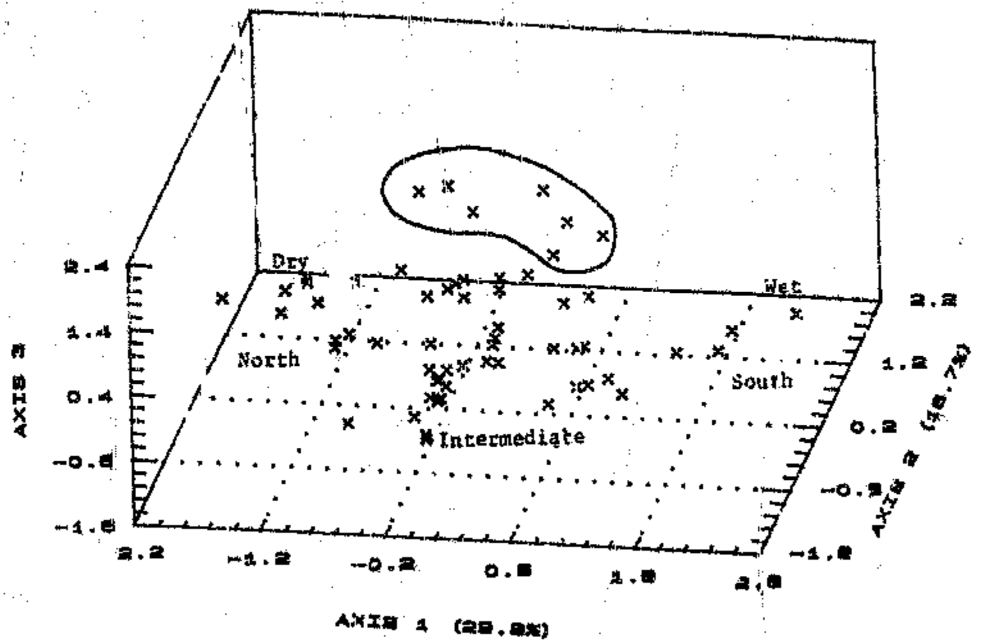


Figure 4.16 (B) Three dimensional correspondence analysis display showing coenocline of woody species

Due to the relatively low representation of the first two axes in terms of the total variation (46.5%), the interpretation of these results is best achieved with the assistance of the third axis. Figure 4.16 B reveals a clump of points (circled) which extends upwards and which is best represented by axis 3. In Figure 4.16 A, sites which extend upwards are circled. The aspect (and subsequent insolation) characteristics of the sites still accounts for the largest part of the moisture gradient (29.8%) as it still represents axis 1. Axis 2 (16.7%) represents the slope (or mean height above river) factor, and axis 3 (14%) partially represents (with axis 4 not shown) the rooting depth of the trees.

3.5 Discussion

3.5.1 Test of element one of hypothesis

Since the true Gaussian distribution was found to be most common in the transects investigated in both herbaceous and woody species, this implied that the majority of the elements of the Gaussian model were applicable in riverine areas and it would be worthwhile to proceed with testing these where possible.

Comparisons of the proportions of the 5 different distribution types revealed that the riverine areas were comparable with those areas studied by Whittaker (1956) and very different from those studied by Austin (1976). However, it is conceded that the distributions obtained can be affected considerably by the sampling procedure employed. It is possible that by decreasing the size of the quadrats and by sampling at smaller intervals, the sensitivity of the technique could have increased markedly and distributions which were classified as Gaussian, may well have displayed platykurtic or skewed characteristics. Austin et al (1984) state that the careful stratification of sample sizes and placements within the study site can lead to this effect.

According to element nine of the hypothesis (Gauch, 1985), the distribution curves can be distorted by environmental or biotic factors. Competition has been reported to be a frequent cause of bimodal species responses (Cormack, 1979; Westman, 1980). It is possible therefore to infer characteristics of the biotic and environmental conditions of areas on the relative abundances of the distorted distributions observed.

The difference between the bimodal distributions observed in the transects can be explained largely on the basis of the environmental characteristics as follows. Sites 2 and 3, with the exception of 1 transect, are characterised by long undulating lower slopes with slight gradient as well as areas (of similar characteristics) which are disrupted spatially by uneven and rocky patches. This encourages the formation of numerous areas displaying similar features and also supports the appearance of similar species. Sites 6 and 7 also encourage bimodality due to their generally flat profiles and the existence of a second mesic zone behind them. The areas displaying low bimodality were characterised by either steep slopes or slopes displaying few irregularities.

Since the environmental characteristics do appear to explain the existence of bimodal distributions to a large degree this implies that competition between species is less important. Since the areas were recently disturbed, it is very possible that the competition for resources has not started to develop yet.

It is suggested that differences between the proportions of the different distribution types, which have been reported by numerous authors in the literature, could possibly all be explained by the particular environmental and biotic conditions at the various study sites.

3.5.2 Test of element two of hypothesis

With the rejection of the null hypothesis, the distribution of the species modes of both major and minor species were found to be uniformly distributed along the riverine gradient. This is not entirely consistent with the second element of the hypothesis which states that the modes of minor species are randomly distributed. The modes of both major and minor species were both found to depart to a highly significant degree ($p<0.001$) from a random distribution. However, the minor species were marginally less significant, which implies that they are possibly better described by a random distribution than the major species are. It is suggested that the maximum modal frequency which is used to distinguish between major and minor species might have an effect on the significance of this departure. Austin used a value of 0.3 to distinguish between the two groups, but this value was found to be inappropriate for this study.

Shipley and Keddy (1987) applied a technique which investigates the distribution of species boundaries along a gradient. However, in order to meet the requirements of this approach, it would have been necessary to discard all species which displayed boundaries which coincided with the top and bottom borders of the gradient. It would therefore have been necessary to have discarded 43 of 62 (69%) woody species and approximately 155 of 240 (64%) of the herbaceous species present for the sake of the test. This proportion of the total species present was considered to be too high. The major reason for this problem was that the riverine gradient only spanned a distance of 60 to 70 metres and a large oroportion of the species covered this distance. It is suggested that this technique is better suited to a substantially longer gradient, while the technique proposed and applied by Austin (1987) is better suited to shorter gradients.

3.5.3 Test of element seven of hypothesis

The constant turnover of species between the ends of the riverine gradient and from quadrat to quadrat along its length implies that it is characterised by a continuum of uniformly distributed species.

3.5.4 Gradient analysis

3.5.4.1 Direct gradient analysis

The graphical and numerical outputs of the correspondence analysis reveals that the optimal distribution (modes) of each species corresponded with their individualistic soil moisture requirements and/or tolerances along the gradient. Different species were found almost continuously between the two extremes of the gradient, which indicates that a continuum of species exists over the length of the gradient with a distinct overlap of species distributions.

These analyses clearly display the non-linearity problem, which is characteristic of the correspondence analysis technique. This is displayed as an arch with the extremes of the gradient being found at either end. This appears to be particularly noticeable when there are a number of underlying gradients which results in the further twisting in site and species positions relative to each other. Under these circumstances, it appears that the best way to understand the display is to interpret the positions of points along an approximate gradient curve rather than on a gradient represented by a straight line. As Greenacre points out, the curved pattern of the points can enrich the interpretation when there are some points on the concave and/or convex sides of the curve.

In addition to defining the coenocline of species in response to decreasing soil moisture along the profile, the distribution of species also reveals the presence of two distinct zones of plant distributions. Namely, a lower zone and an upper zone which corresponds with the two similar zones identified on the basis of their soil textural characteristics as described above. The species associated with this upper riverine zone are particularly common to the <u>Spirostachys africana</u> and <u>Acacia nigrescens</u> communities which are located immediately adjacent to the riverine community. Due to the distinct differences between these zones, the presence of these two zones does not undermine the basis of the individualistic response hypothesis. This reveals the essential differences between these communities which are evidently based on distinct soil characteristics. Such differences are expected to support different species with different habitat requirements. Certain species clearly exist in areas between these two zones. This discounts the presence of a distinct ecotone between the two areas and further supports the fact that each species exhibits individualistic requirements.

3.5.4.2 Indirect gradient analysis

In total, the three axes investigated only accounted for 65 percent of the total soil moisture gradient in riverine areas. This fact indicates the complexity of the gradient and the response of herbaceous species to it. A further 35 percent of the total variation has not been accounted for by the analysis which extend into a further three dimensions. This variation is possibly partially accounted for by other factors such as the precipitation gradient which extends from east to west along the reserve and the overall soil differences between the sites.

Certain discrepancies were evident when comparing the correspondence analysis results for herbaceous and woody species.

Firstly, sites (6 and 2 1) which were described by the herbaceous ordination as dry, were described differently by the tree ordination. This is explainable due to the differential abilities of herbs and trees to extract water from the substratum. As herbs only have superficial rooting they are subjected to the water moisture fluctuations which are characteristic of soil surfaces. High insolation can therefore lead to rapid moisture deficiencies and their ability to survive is dependent on the replacement of water by the water table or by lateral soil movement. Tree species, due to their deep rooting systems, are far less susceptible to these fluctuations. Trees can tap water from the ground table and remain unstressed at times when superficial herbaceous species are under considerable stress. Both sites 6 and 2 1 are north facing and represent very dry areas for herbaceous species. Due to their relative flatness, these sites serve as wet areas for trees which are simply able to draw water from the water table not far below.

Secondly, the woody ordination appears to be far more complex than the herbaceous ordination, particularly when viewed in three dimensions. Since herbs are subjected to the continually fluctuating soil moisture conditions of the soil surface, they are only found in areas where these conditions are ideal. Tree species, however, can survive in a large variety of areas avoiding stress and death by means of their extensive rooting characteristics.

Since only two factors account for major variations in the soil moisture gradient for herbaceous species, this allows for the easier delimitation and definition of the gradient, even in three dimensions. Clearly then, the distribution of herbs in an area is a far more sensitive indicator of superficial soil moisture conditions than that of the distribution of trees.

The determination of a moisture gradient by the ordination of the woody species is complicated by the addition of a third major factor, namely rooting depth. This factor is highly variable and could be used in isolation to explain the complex nature of the three dimensional representation of woody species.

3.6 Conclusions

The test of three of the twelve elements of the individualistic response hypothesis managed to reject the null hypothesis in each case.

The test of the first element indicated that true Gaussian species responses were found to be common and more abundant than any other type of species response down the length of the riverine gradient. The test of the second element revealed that the modes of species down the gradient are uniformly distributed rather than randomly or contiguously distributed as proposed by the community unit hypothesis. The test of the seventh element of the hypothesis revealed that species turnover is continuous between the ends of the gradient. In addition, the application of direct gradient analysis techniques displayed the existence of a riverine gradient, covered by a continuum of species responding individualistically to their specific requirements down its length. Both herbaceous and woody species were shown to display unique distributions along the gradient and form a coenocline over the length of the gradient.

This evidence was considered to be sufficient to allow for the rejection of the community-unit hypothesis.

The gradient analysis revealed that the factor accounting for the major proportion of the soil moisture gradient is distance from river, which corresponds with the attenuation of soil water free energy due to the matrix force offered by the complex soil matrix. A large diversity of other factors account for the rest of the total moisture gradient. From area to area, however, the major factors contributing to the moisture gradient, as revealed by a between site indirect gradient analysis, are aspect and riverine slope. These factors account for 58 percent of the gradient, the rest being accounted for by factors such as precipitation gradients and soil characteristics.

Due to their superficial rooting systems, herbaceous species are more sensitive and accurate indicators of soil moisture conditions and reflect a clear picture of the soil moisture gradient. The ability of woody species to draw water from greater depths and the variability in their root lengths, complicates their use as reliable indicators of the soil moisture gradient.

SUB-CHAPTER 4 ENEMY IMPACT HYPOTHESIS

This sub-chapter tests the enemy impact hypothesis using a suitable null hypothesis. In addition, it investigates the role of grazers and browsers on riverine vegetation and the corresponding responses of these species to utilisation.

4.1 Introduction

The enemy impact hypothesis attempts to explain the structure of communities as a consequence of the impact of their enemies. The applicability of the hypothesis has been demonstrated by several authors in a diverse range of systems (see the literature review - section 1.6.3.4).

Numerous ungulate species are present in the Umfolozi Game Reserve with each species exhibiting different feeding requirements and preferences. The diversity in both browser and grazer species and numbers reveals their potential impact on vegetation in the Reserve. At the time of the study, riverine communities were particularly susceptible to the impact of ungulates since large proportions of tree species were in the juvenile recovery stage after the Domoina flood and a wide diversity of grass species were present.

The riverine community has been identified as an important winter feeding area for ungulates and as a prime habitat for the black rhinoceros and bushbuck (Porter, 1981; Wills, 1984). The vertebrates of the reserve have been identified and discussed by Bourquin et al. (1971). The estimated abundances of the major species present during the study period were recorded by Knott (1985; 1986). Hitchins (1968) recorded the plant species utilised by herbivores within the reserve. Opinions have been expressed concerning the removal of Ficus sycomorus seedlings in riverine areas by ungulates (Zaloumis G., pers.comm.[1]) and the clear absence of these seedlings in particular riverine areas (MacDonald I.A.W., pers.comm. [2]). However, the impact of the browsers and grazers on the vegetation of the riverine community itself has not been clearly established.

The true test of the enemy impact hypothesis should include the investigation of the impact of all enemies including invertebrates, birds, rodents, primates as well as large and small ungulates. However, in terms of the structures needed to exclude all these enemies, as well as the maintenance of these structures, it would be impracticable to investigate the effects of all the enemies of the riverine vegetation. In order to aid the management of these areas, it would have been futile to include details of the unmanageable fraction of this component. Consequently, the test of this hypothesis only addressed the impact of small, medium and large ungulates.

4.2 Objectives

The objectives of this chapter were as follows.

1. Test the enemy impact hypothesis in riverine areas using a suitable null hypothesis.
2. If the hypothesis was found applicable, to determine the probable impact of browsers and grazers on the structure of riverine communities in other areas which are naturally accessible to ungulates.
3. Apply (2) to determine the likely structural differences between affected areas and other areas which are naturally inaccessible to ungulates.

---

[1] G. Zaloumis, Natal Parks Board, Pietermaritzburg

[2] I.A.W. MacDonald, c/o Percy Fitzpatrick Institute, University of Cape Town.

4.3 Null hypothesis

The null hypothesis employed was that the presence or absence of ungulates in an area have no effect on the structure and composition of riverine areas, and that areas exposed to ungulates and other areas completely protected from ungulates would reflect the same same structure and composition after a suitable period of time. The null hypothesis would be rejected if clear differences in the structure and species composition were found to exist between protected areas and their controls by the end of the study. Acceptance of the null hypothesis would be justified if the proportions of the various components in control and exclosure plots differ during the period of study. A simple removal of herbage or foliage, measured by tree height and percentage cover, would be considered as evidence of browsing/grazing but in isolation would not warrant acceptance of the hypothesis. In addition to this, clear differences in the abundances of trees or herbs, measured by the number of individuals of each species and percentage frequencies, should be evident by the end of the period, as it is this which largely indicates structural change. The consideration of both factors, however, could assist in understanding the exact nature of the pressure borne by browsers and grazers.

4.4 Methods

4.4.1 Site location and exclosure construction

Due to financial constraints the total number of exclosures was limited to three, each with their respective control sites. Three riverine areas were identified which allowed for the free access of ungulates and which simultaneously offered a reasonable measure of protection from small to medium flood events. In these areas two 30x30 metre plots were judgementally located adjacent to each other so that both plots would receive similar exposure to large floods and browsing pressure.

The first plot was protected from ungulate entry by an electrified fence. The details of the fence construction and the energizer connections are shown in Figure 4.17. At the corners of the plot, large (4 m x 22 cm) wooden poles were cemented into the ground to a depth of two metres. Along the perimeter of the plots smaller wooden poles (3 m x 10 cm) were buried to a depth of one metre at 10 metre intervals. Six rows of fencing wire were then tightly strung between the poles at 30 cm height intervals using a wire tensioner. In order to prevent these wires from leaking current to the poles, and therefore running the batteries down at a faster rate than necessary, insulators were included in the wires between the poles.

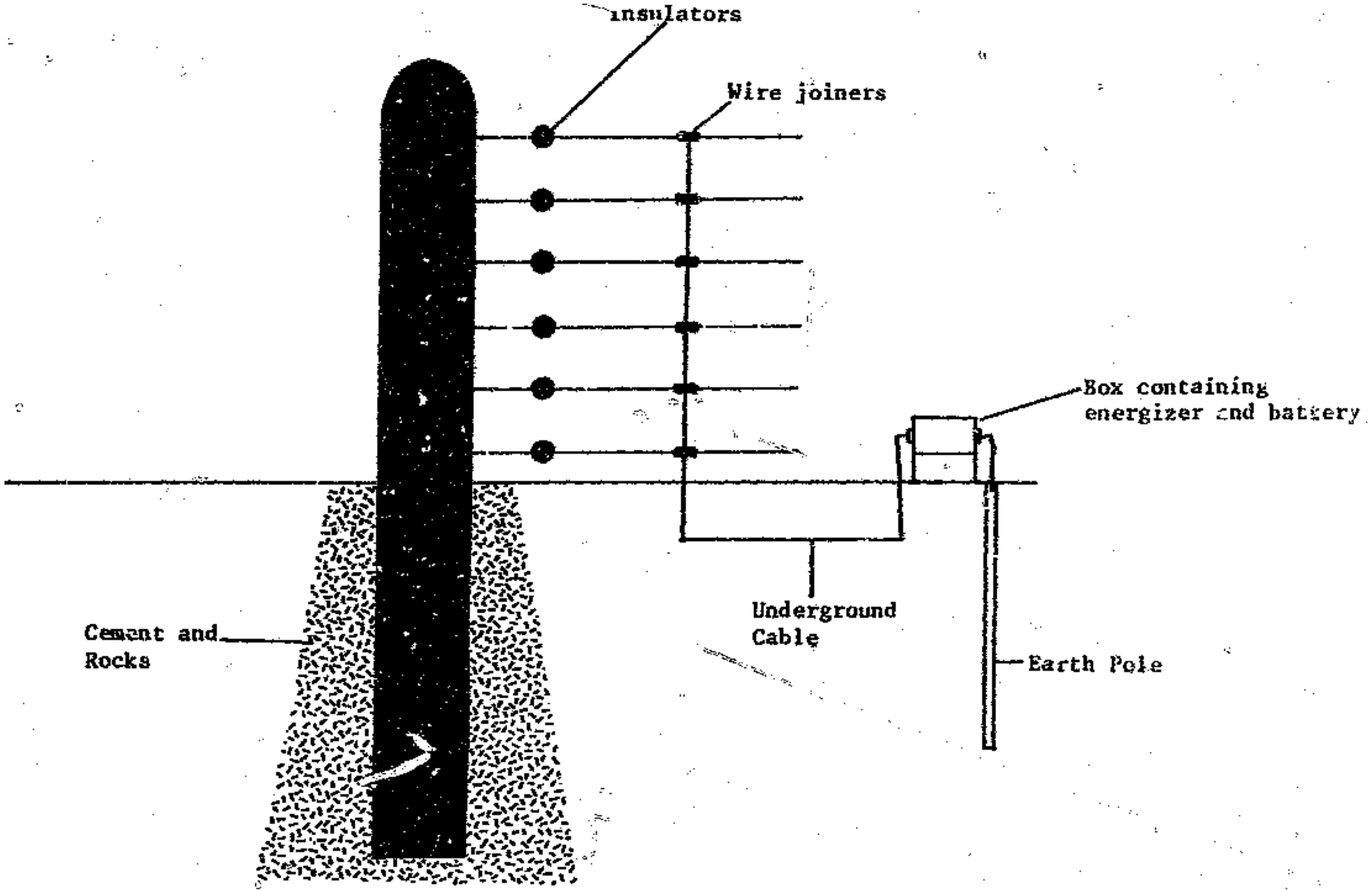


Figure 4.17 Diagram of exclosure construction showing details of energizer connection to fence and earth

A fence energizer was situated close to the fence within a strong steel box. Connection between the box and the fence was achieved by means of a buried cable. The energizer was adequately earthed using a two metre steel pole buried deep into the sand. A 12 volt car battery was used to power the unit and was recharged at three weekly intervals. The corners of the second plot were adequately marked using rock piles and served as the experimental control for comparison with the exclosure findings. The control and experimental plots were located approximately 15 metres apart to ensure that ungulates did not avoid the control plots due to the proximity of the fence surrounding the experimental plot.

One of the three sites was located in an area where the riverine zone was relatively narrow and due to the steep riverine slope this zone was used extensively as a pathway by game. This placed undue stress on the exclosure fence and it regularly suffered extensive damage by passing rhinoceros and buffalo. At an early stage of the study the fence was irreparably damaged by these means and consequently data collected from this site was not included in the results. Despite the careful location of exclosures in areas where they were unlikely to be affected by floods, the study was prematurely terminated after seven months due to the complete destruction or removal of all exclosure fences by a medium sized flood.

4.4.2 Data collection

Within each exclosure and associated control plot the herbaceous and woody components were sampled on three different occasions. On each occasion 70, 1x1 metre quadrats were systematically placed within the plots using a standardised procedure. The herbs present in each quadrat were identified and recorded. In addition, the percentage cover contribution of each species was judged using a five point scale and recorded. The woody species present within the plot were identified and counted and the height and stem diameters were measured.

4.4.3 Data analysis

Comparisons were made between the data of each exclosure and control plot for the three sampling dates. Due to the large variation in species and their distributions in riverine areas, adequate statistical comparisons between species were largely impossible. The density and species frequencies of those species which were adequately represented were compared by means of one-way analysis of variance tests (with LSD intervals) and Chi-square tests (Parker, 1973). Those inadequately represented were presented without statistics. Due to the heterogeneous nature of the vegetation and obvious financial constraints, it was not possible to avoid pseudoreplication as described by Hurlbert (1984). In such cases, where further independent sites were not possible, Hurlbert advised that the further replication within sites and the application of inferential statistics would not make the results any clearer or the conclusions any firmer. Here simple tabular or graphical interpretation is adequate.

To simplify the interpretation, data from both exclosures were lumped together. The same was done for control plots. Tree species were compared on the basis of their abundances and heights, while herbaceous species were compared on the basis of their percentage cover and percentage frequencies. Due to their large numbers, both woody and herbaceous species were grouped into one of six categories on the basis of the trends they displayed during the period of study in both the exclosure and control plots.

These groups were as follows.

1. Increasing species, which describes those species which increased continually in abundance or height from the beginning until the end of the study.

2. Emerging species, which describes those species absent at the beginning, but which appeared during the course of the study. These species then remained until the end of the study.

3. Constant species, which describes those species which displayed a constant abundance or height throughout the study.

4. Decreasing species, which describes those species which decreased in abundance or height continually from the beginning until the end of the study.

5. Fading species, which describes those species which were present at the beginning but disappeared during the course of the study.

6. Transient species, which describes those species which were absent at the beginning and the end but which appeared for a brief period during the study.

In the case where samples sizes were large enough to enable true statistical comparisons between abundance and height and cover values, these were carried out using a one-way analysis of variance with LSD intervals. Species frequencies were compared using a Chi-square test. After the abundance values of particular species were compared between the exclosure and control plots, they were then assigned to secondary groupings on the basis of their response to browsing or grazing. Utilisation response groups were as follows.

A. Increaser species, which describes those species which increased in abundance despite the pressure of browsing or grazing.

B. Decreaser species, which describes those species which decreased in abundance under the pressure of browsing or grazing.

C. Constant species, which describes those species which remained in constant abundance under the pressure of browsing or grazing.

In addition, an index of similarity (Si) (Sorensen, 1948) was used to compare the similarity of herbaceous species composition between the exclosure/exclosure, control/control and exclosure/control plots from sampling date to sampling date.

The formula for this index is,

$$Si = \frac{2\,C}{A + B}$$

where A = number of species in sample A,
B = number of species in sample B, and
C = number of species common to both samples.

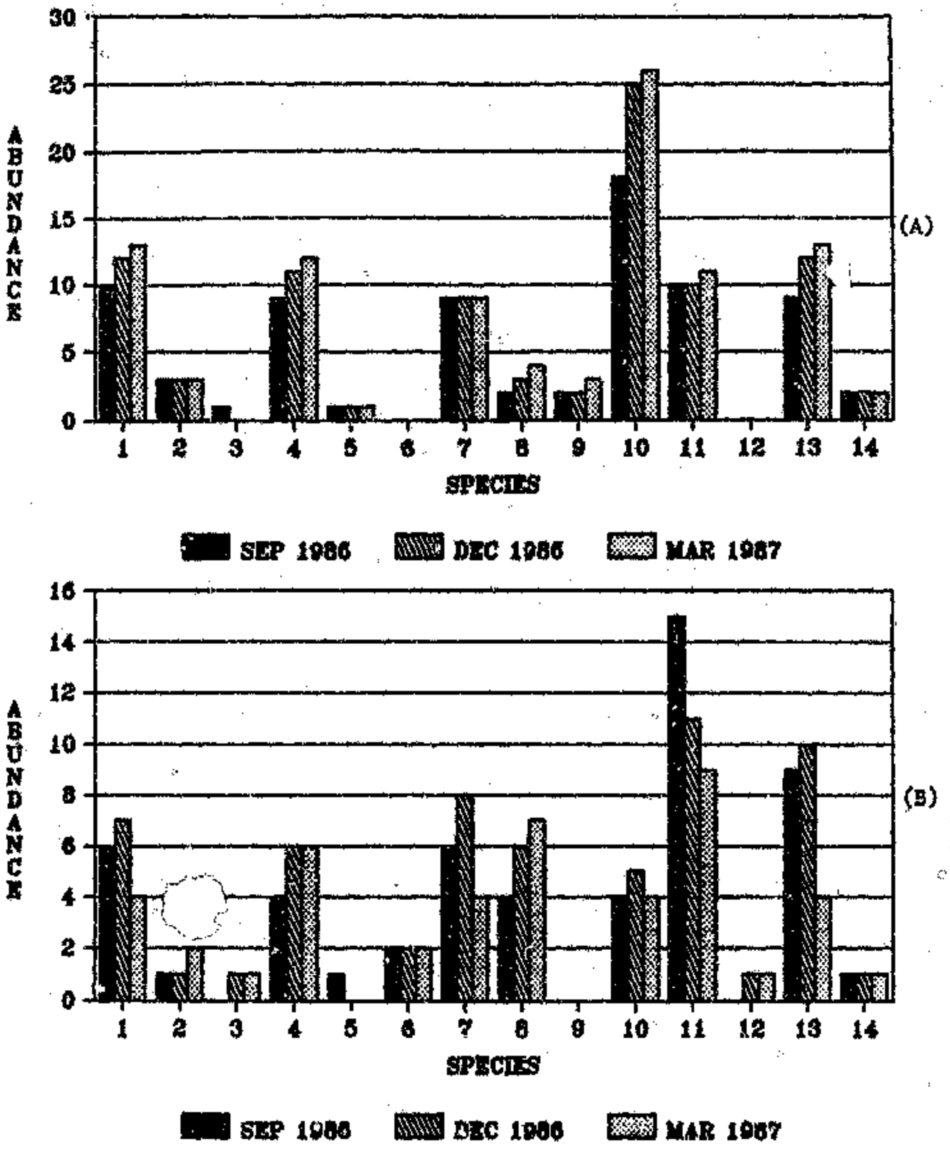
The higher the value of Si, the greater the similarity which exists between the two samples.

4.5 Results

4.5.1 Woody species

Comparisons of the two plots in Figure 4.19 in exclosure and control plots for the individual species reveals the impact of browsing and the effect of excluding browsers on the abundances of species. The response of different species to the experimental treatments (Fig. 4.19) reveals that the majority (33%) of the control plot species suffered a reduction in abundance with browsing (decreasing species). This reflects their apparent palatability and the preference of the browsers for these species. Three species (constant species) - (25%) managed to maintain their abundances despite browsing (F. sycomorus, A. sieberana and T. orientalis). This ability to hold their own under the pressure of browsing implies the comparative unpalatability of these species and/or their ability to avoid browsing. The three most unpalatable species within the control plot (increasing species) managed to increase despite browsing pressure (A. robusta, A. karroo and D. cinerea). Two new species emerged in the control plots during the course of the study (A. nigrescens and S. birrea) and managed to remain constant.

The mean number of individuals per species in the exclosure and control plots changed continually from the outset of the study (Fig. 4.20). This was due to a continuous increase in the number of individuals per



SPECIES KEY

No.	Species	No.	Species
1	*Acacia gerrardii*	8	*Dichrostachys cinerea*
2	*Acacia karroo*	9	*Ficus sur*
3	*Acacia nigrescens*	10	*Ficus sycomorus*
4	*Acacia robusta*	11	*Phyllanthus reticulatus*
5	*Acacia schweinfurthii*	12	*Sclerocarya birrea*
6	*Acacia sieberana*	13	*Sesbania sesban*
7	*Acacia tortilis*	14	*Trema orientalis*

Figure 4.18 The abundances of woody species for the un-browsed (exclosure) (A) and the browsed (control) (B) plots for September 1986, December 1986 and March 1987. See species key for species names

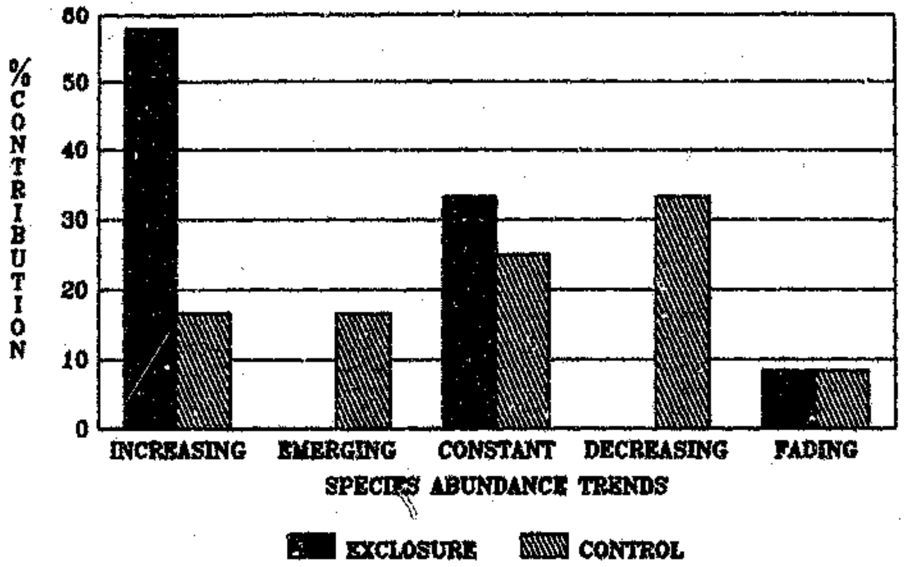


Figure 4.19 Proportion of different species types in response to browsing (control) and in the absence of browsing (exclosure)

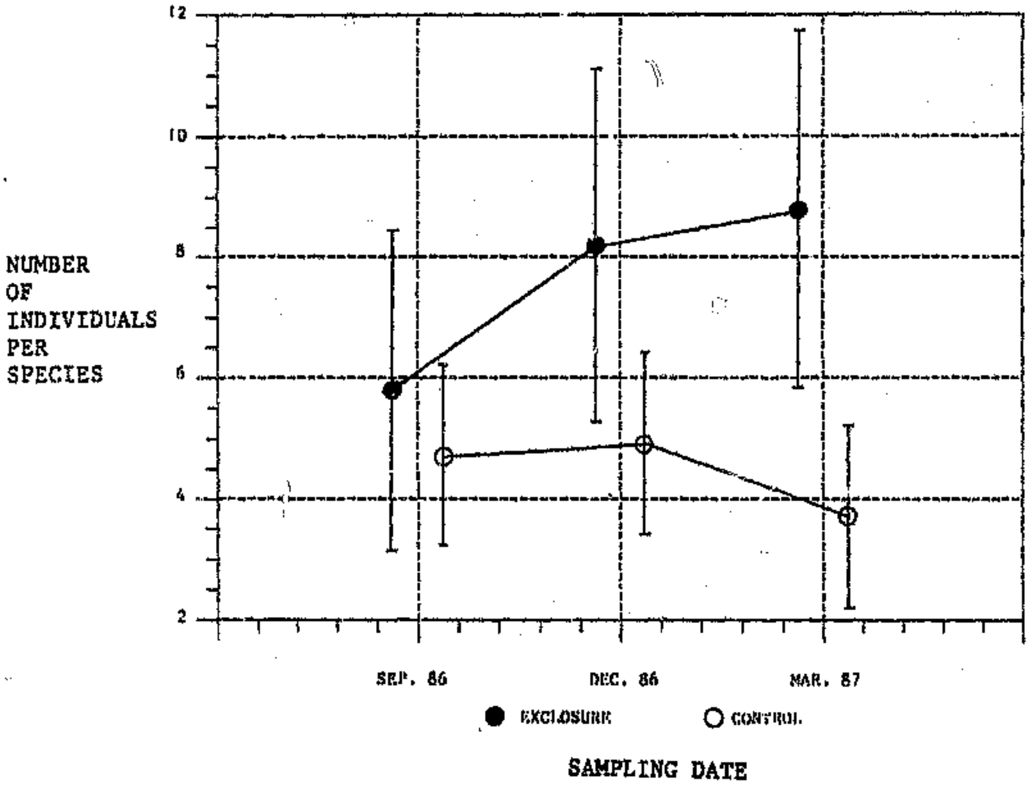


Figure 4.20 Change in number of individuals per species with time for three sampling dates after onset of study

species in the absence of browsing and a continuous decrease in the number of individuals per species in the control plots. By the end of the study the difference between exclosure and control plots in this regard was significant.

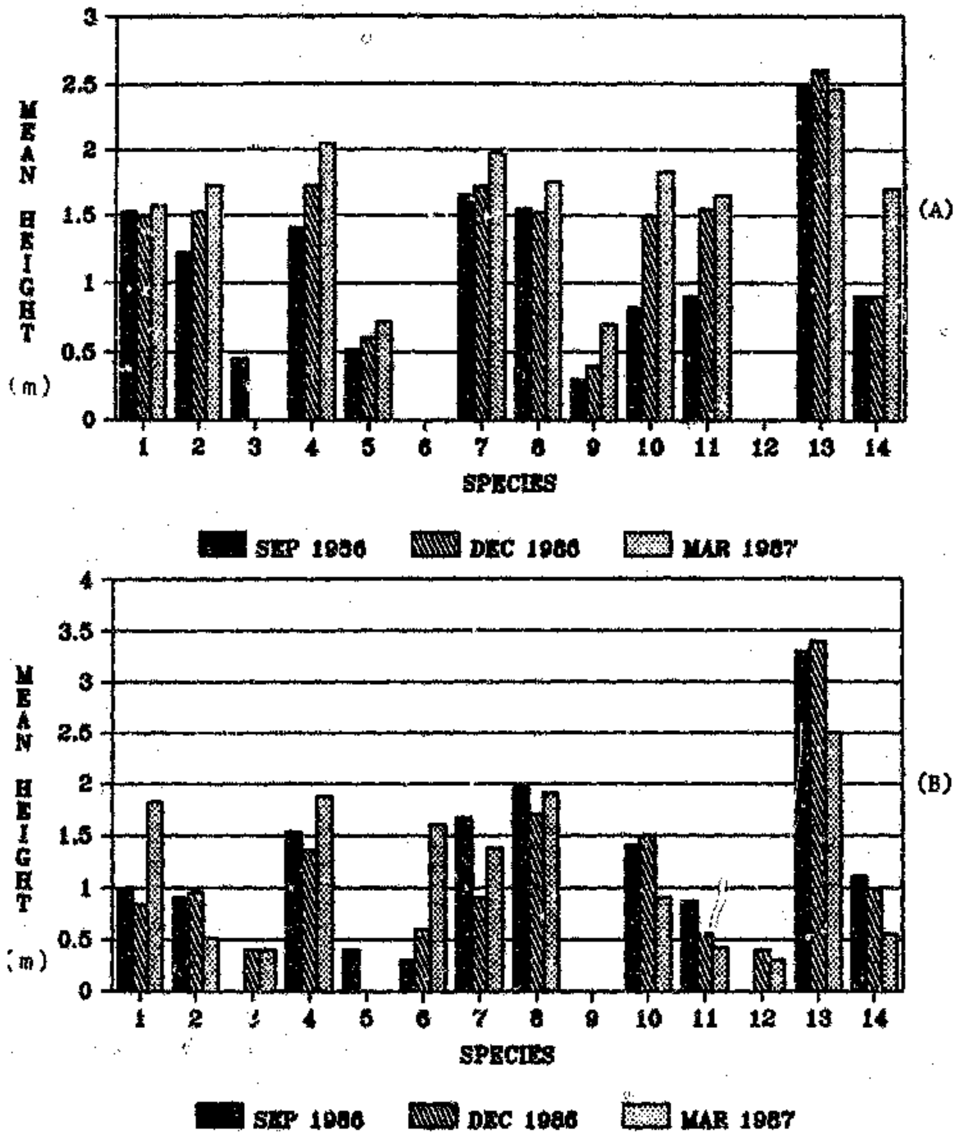
The mean height of individuals of different species within the exclosure noticeably increased continually due to the absence of browsing, while the mean height in the control plot declined due to the effect of browsing (Fig. 4.21). By the end of the study the difference in mean heights of individuals between the exclosure and control plots was significant (Fig. 4.22).

The scrutiny of Figs. 4.21 to 4.23 reveals the impact of browsing pressure on woody species. The mean heights of woody species were affected differently by the impact of browsing. Three major effects of browsing were evident in Figure 4.21 and were used to classify the woody species into three basic groups (Table 4.10). The relative proportions of these three trends in mean height as a response to browsing are displayed by Figure 4.22.

Browsing brought about a decrease in the mean heights of 50 percent of the species in the control plots. As a comparison, 82 percent of the exclosure species were able to show increases in mean height in the absence of grazing (Fig. 4.23). Certain control plot species either displayed constant heights or height increases despite browsing (Fig. 4.21). This implies their relative unpalatability, but is misleading because the removal of seedlings of some of these species led to an accompanying increase (height switch) in mean height due to the height gap between the seedlings and the parent plants (e.g. *A. gerrardii* and *A. tortilis*). This height switching effect, for individuals in the region of 1.5 to 2 metres in height, also implies that plants of a critical height are no longer stunted by browsing - this height approximately corresponding to that height where the browsers can no longer reach the sensitive parts of these individuals.

Comparisons of the exclosure and control plots also revealed that browsed areas encouraged the appearance of species (emerging species) which were not present at the outset of the study. Since the frequency of this observation was low, it is not possible to draw any concrete conclusions. It does appear however, that the removal of individuals by browsing leaves patches open which can then be colonised by other species.

The white rhinoceros, *Ceratotherium simum*, displayed an affinity to trampling and damaging large individuals of *S. sesban*, which largely explains their decrease in mean height and abundances in unprotected areas. *A. nigrescens* disappeared from the exclosure plot and showed poor performance in the control plot - which implies their unsuitability to these lower riverine areas.



SPECIES KEY

No.	Species	No.	Species
1	<u>Acacia gerrardii</u>	8	<u>Dichrostachys cinerea</u>
2	<u>Acacia karroo</u>	9	<u>Ficus sur</u>
3	<u>Acacia nigrescens</u>	10	<u>Ficus sycomorus</u>
4	<u>Acacia robusta</u>	11	<u>Phyllanthus reticulatus</u>
5	<u>Acacia schweinfurthii</u>	12	<u>Sclerocarya birrea</u>
6	<u>Acacia sieberana</u>	13	<u>Sesbania sesban</u>
7	<u>Acacia tortilis</u>	14	<u>Trema orientalis</u>

Figure 4.21 Mean heights of species for exclosure and control plots

(A) Exclosure (un-browsed)
(B) Control (browsed)

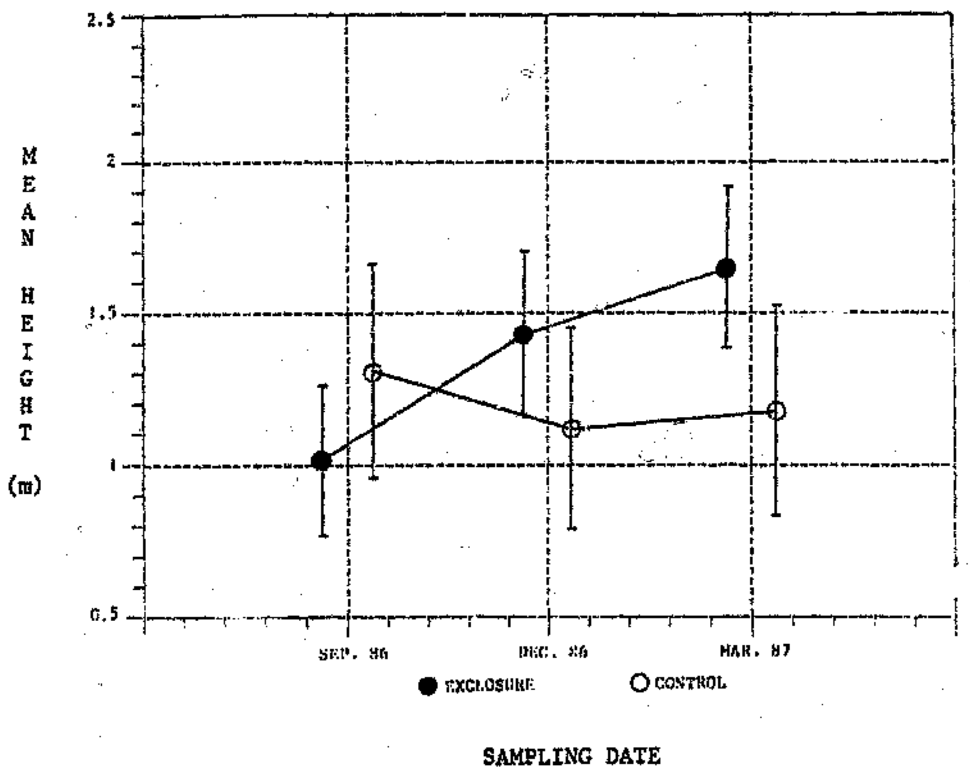


Figure 4.22 Mean height differences of woody species between exclosure and control plots for three sampling dates

Table 4.10 Classification of riverine woody species on the basis of responses to browsing and trampling by large ungulates

RESPONSE GROUP	SPECIES
DECREASER SPECIES	*Acacia gerrardii* *Acacia tortilis* *Acacia schweinfurthii* *Phyllanthus reticulatus* *Sesbania sesban*
CONSTANT SPECIES	*Ficus sycomorus* *Sclerocarya birrea* *Trema orientalis*
INCREASER SPECIES	*Acacia karroo* *Acacia robusta* *Acacia sieberana* *Dichrostachys cinerea*

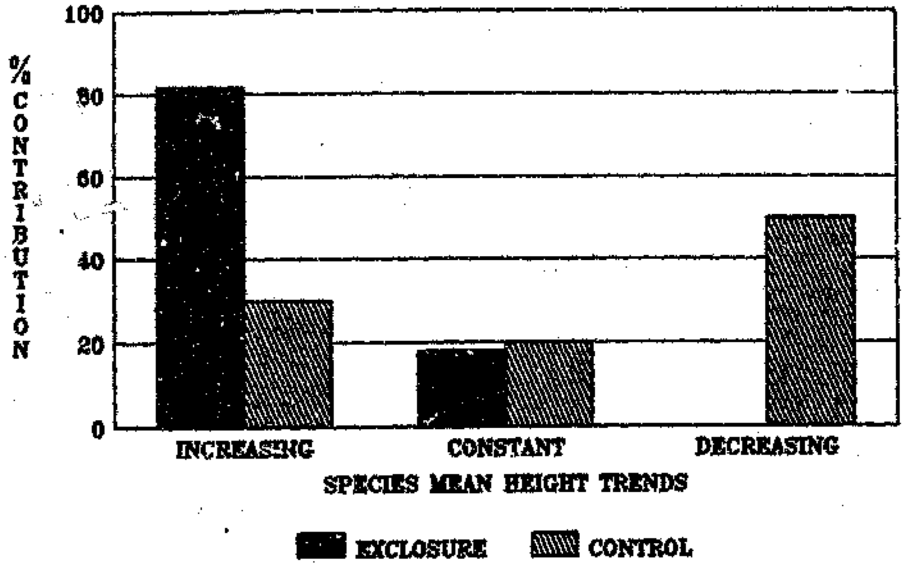


Figure 4.23 Woody plant mean height trends in response to browsing and trampling by ungulates

4.5.2 Herbaceous species

Herbaceous percentage cover changed differently in the exclosure and control plots during the study (Fig. 4.24). Within the exclosure plot, percentage cover increased steadily from 71 to 92 percent over the eight month of monitoring and instead of being reduced by grazing, were able to increase in cover and reduce the percentage of bare ground. The control plots initially displayed an increase in cover, with a decrease again between December and March as a consequence of grazing pressure. The cover difference between the two plots was visually evident by the end of the study period.

Herbaceous species also displayed different abundance trends in the exclosure and control plots (Fig. 4.25). The trends evident in the two plots are clearly different. The proportion of increasing and emerging species was higher for the unprotected plots, while the protected plots displayed a larger proportion of decreasing and fading species.

Figure 4.26 supports these observations. The species richness of the control plots steadily increased during the study while the exclosure plot displayed an overall decrease in species richness, until, by the end of the study, the control plots sported a larger species richness than the exclosure plots did. This implies that the removal of herbage by grazers opens up areas suitable for colonizers and simultaneously reduces those competitive interactions which encourage the increase of some species at the expense of others.

In addition to this apparent increase in percentage cover (Fig. 4.24), the ungrazed areas showed a decline in species richness as well (Fig. 4.26). It is speculated that the competition between species in these plots led to the decrease or complete loss of competitively inferior species.

Due to the assumed high levels of competition between herbaceous species, it is difficult to determine the response of individual species to grazing in isolation. However, certain species showed clear responses to grazing which were overriding compared to the effects of competition between species (Table 4.11).

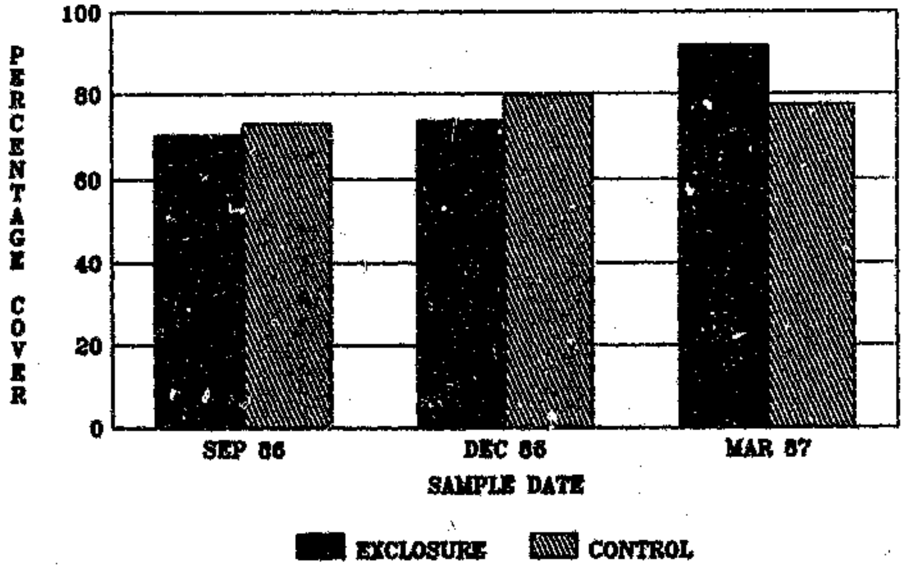


Figure 4.24 Changes in percentage cover of herbaceous species for exclosure and control plots for three sampling dates

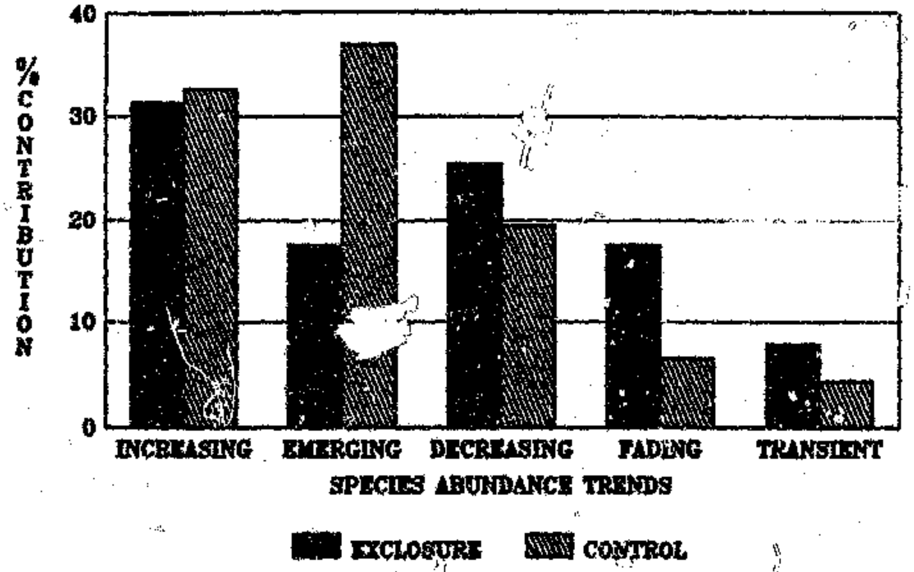


Figure 4.25 Five classes of species abundance trends for exclosure and control plots

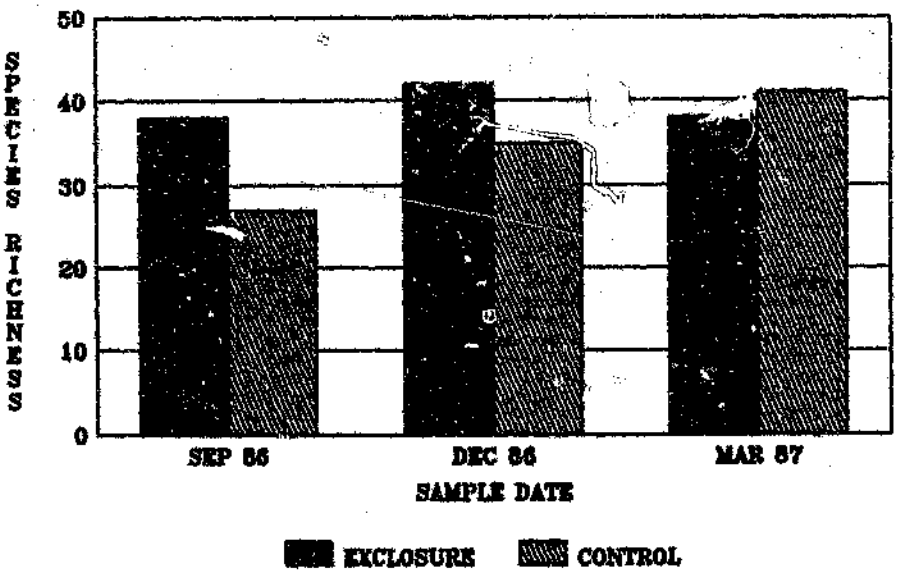


Figure 4.26 Changes in species richness for exclosure and control plots on three sampling dates

Table 4.11 Response groups of herbaceous species to grazing pressure

RESPONSE GROUP	SPECIES
DECREASERS	*Cassia floribunda* *Cryptolepis obtusa* *Cynodon dactylon* *Eragrostis curvula* *Heteropogon contortus* *Paspalum distichum*
INCREASERS	*Asclepias fruticosa* *Cenchrus ciliaris* *Chloris gayana* *Eragrostis superba* *Eriosema psoraleoides* *Panicum maximum* *Sporobolus pyramidalis* *Tridax procumbens* *Urochloa mosambicensis* *Paspalum paspalodes* *Phragmites australis*

From the similarity index findings (Table 4.12), it is evident that the effects of grazing assisted the control plots to maintain the majority of species which characterised them at the outset, except those that were completely unsuited to the growth conditions present and in addition permitted further species to colonize these areas. So much so that any differences which existed between exclosure and control plots, as a consequence of initial placements of the plots, were almost entirely removed during the course of the study.

Table 4.12 Similarity index (Si) comparisons for herbaceous species between exclosure / exclosure, control / control and exclosure / control plots

	Sep 86 - Dec 86	Dec 86 - Mar 87	Sep 86 - Mar 87
EXCLOSURE / EXCLOSURE	0.83	0.85	0.73
CONTROL / CONTROL	0.80	0.82	0.67
EXCLOSURE / CONTROL	0.67	0.70	0.73

4.6 Discussion

4.6.1 Woody species

It appears that the major impact of browsing on **decreaser species** is firstly effected by means of the removal of the seedlings of these species and secondly by means of the constant removal of the foliage of larger individuals. The further decrease in abundances of individuals, to lower levels than before the study commenced, shows that this continual browsing can lead to the demise of even larger individuals. However, beyond a certain height, the individuals are released from the inhibiting effect of browsing and can continue to gain height. It appears that this height is possibly related to the reach capabilities of the average browser.

Browsers affected the **constant species** mainly by removing the newly emerging seedlings and small individuals which are soft and palatable compared to the larger individuals. It is well known that forage quality diminishes with plant tissue age (Braun, 1973). Browsing of the foliage evidently occurs but the normal growth rate and coppice growth is sufficient to allow these individuals to maintain their size.

Increaser species were evidently browsed negligibly even at the seedling stage. This permitted them to continue growing uninhibited by browsing pressure and to attain large sizes and densities (provided that other biotic and abiotic factors displayed no other detrimental effects).

The relative proportions of these three groups are important. A large proportion of decreaser species were evident in unprotected areas. This ensured the relatively even distribution of browsing pressure among these species throughout the riverine area. This, in addition to a patchy distribution of browsing intensity and seasonal variation in browsing preferences, should ensure the escape of a certain percentage of individuals from the clutches of browsing, thereby allowing them to bridge the height gap. This effect should also afford the constant species still a higher rate of survival and since these species, along with the increaser species, comprise a large proportion of mature riverine areas, it ensures the speedy recovery of these areas after major disturbance. Personal observations were that individuals of <u>Ficus sycomorus</u>, <u>Trema orientalis</u> and various <u>Acacia</u> species growing on inaccessible mounds and gullies managed to escape browsing pressure and attain heights in excess of 3-4 metres within two years.

This picture is also exemplified with the relatively large abundances of <u>Acacia</u> spp. seedlings as opposed to <u>Ficus sycomorus</u> seedlings and the effects of browsing. Personal observations were that the black rhinoceros (<u>Diceros bicornis</u>), frequently seen in riverine areas, is partial to both <u>Acacia gerrardii</u> and <u>Ficus sycomorus</u>

seedlings and foliage. The abundances of A. gerrardii and other decreaser species affords the F. sycomorus reprieve from this persistent browsing pressure, thereby keeping these seedlings from complete annihilation. In other areas where these decreaser species are absent, such as in relatively mature Ficus sycomorus - Schotia brachypetala stands, the seedlings of this species are absent (G. Zaloumis, pers.comm.) except in locations where they are protected from browsers (e.g. in dense reed beds) - (I.A.W. MacDonald, pers.comm.).

The proportions of constant and increaser species are initially lower than those of the decreaser species, but as time progresses, these proportions should increase under browsing and other selective pressures.

4.6.2 Herbaceous species

It appears that the removal of herbage by grazers is responsible for opening up areas suitable for colonizers and simultaneously reduces competitive interactions. This process ensures that species diversity of herbaceous species is maintained at a high level. These findings are in agreement with those of McNaughton (1979), who proposed that grazing acts as an optimising process and leads to an increase in the diversity of herbaceous species.

In the absence of grazing, it is postulated that competition between herbaceous species leads to a decrease or complete loss of competitively inferior species and, therefore, maintaining species diversity at lower levels.

It is proposed that the assumed high levels of competition between herbaceous species also complicates the determination of the response of individual herbaceous species to grazing. However, due to the heterogeneous distribution of herbaceous species in riverine areas, this problem could only be overcome with the use of sufficient quantities of exclosure/control plots. The effects of destructive flood events and the continuous pressure of large ungulates would require that these structures be maintained regularly. This maintenance can be both costly and time consuming.

4.7 Conclusions

Despite basic differences in the responses of the herbaceous and woody components to the impact of ungulates, the null hypothesis clearly did not apply to both components of the vegetation in riverine areas. Since the impact of enemies was effected by more than purely a removal of foliage and herbage, the null hypothesis did not apply and was rejected.

Grazers and browsers, as enemies, have important effects on the structuring of riverine areas. The direct removal of the foliage of trees and the removal of herbage was clearly evident. However, by displaying their preferences for particular species and by completely removing seedlings and small individuals of these species, as opposed to other species which are browsed to different extents, browsers bring about significant structural changes to the woody component of riverine areas.

The impact on the herbaceous component was effected in a different way. The removal of herbage and the reduction of percentage cover, in general, leads to reduction in competition between the species present, therefore encouraging the colonization of these areas by further species and discouraging the loss of competitively inferior species. On this basis, species richness and therefore species diversity are maintained at higher levels.

Due to the continuous pressure of large ungulates and destructive floods, the construction of exclosures to prevent the access of ungulates to certain riverine areas is unlikely to be a practicable way of managing them. However, should this avenue be explored, for the sake of cost effectiveness it is essential that every effort is made to place such structures in relatively flood safe areas and in areas where the pressure exerted by large ungulates is not pronounced. The use of electric fences for this purpose, while they are relatively cheap and easy to construct, require constant maintenance and attention.

SUB-CHAPTER 5 TIME HYPOTHESIS

This sub-chapter deals with testing the ecological time hypothesis in riverine areas for both woody and herbaceous species separately. Exclosure and control plot, PCQ, and aerial photographic data used in previous hypothesis tests were employed to test the hypothesis.

5.1 Introduction

It was impracticable to consider the time hypothesis in terms of evolutionary time and, therefore, from the outset, the study was confined to testing the ecological time hypothesis in terms only. However, with this limitation removed, extreme difficulty was still experienced in attempting to rigorously test the hypothesis for two reasons.

1. A distinct paucity of riverine data existed from before the Domoina flood. Only data from a descriptive PCQ riverine study, which had been

conducted on two occasions at the same point, was available. Aerial photographs taken on six occasions in the past were also available for comparison.

2. The Domoina flood had been particularly disruptive and had destroyed or removed the majority of the riverine vegetation and associated communities. Since the study was initiated immediately after the flood, very few whole communities were left for comparison.

Due to the recent and effective disturbance of the riverine areas by the Domoina flood, the unique opportunity of monitoring its complete recovery from its early stages of regrowth after disturbance existed. This offered the ideal opportunity to test the time hypothesis. However, in order to test the effects of time alone most effectively it was necessary to consider the following steps.

a. Exclude, as adequately as possible, the effects of other factors which were likely to complicate the findings, such as the impact of enemies. For this reason it was convenient to re-employ data collected from within the exclosure plots used for testing the enemy impact hypothesis.

b. Allow for the passage of sufficient time which would ensure that clear changes were seen to take place during the period of study. This was difficult to achieve since the physical collection of data took place during a period of less than two years. In addition, the period of data collection was disturbed by various large flood events which recurrently reinitiated the recovery cycle.

5.2 Objectives

The objectives of this chapter were as follows.

1. Test the time hypothesis in riverine areas using a suitable null hypothesis.
2. Investigate the effects of time on the dynamics and recovery of riverine vegetation and identify other factors which have important effects on these processes.

5.3 Null hypothesis

The null hypothesis applied stated that the characteristics of riverine vegetation are not determined by the passage of time and that riverine communities of different ecological ages display no differences in species composition and richness.

Should changes in species richness or composition in the exclosure plots be evident by the end of the study, the null hypothesis would be rejected. This would apply to differences in either herbaceous or woody species or both. In this case, since ungulates would be excluded during this period, any differences which exist would be attributed to the effects of interspecific interactions.

Similarly, should similar effects in the control plots be observed by the end of the study, the null hypothesis would be rejected. In this case, any changes which exist would be attributed to the combined effect of herbivory and other interspecific interactions.

5.4 Methods

5.4.1 Exclosure/control comparisons

On three occasions after the Domoina floods, the species compositions and richnesses of woody and herbaceous species were monitored within the two exclosure plots previously described in the enemy impact hypothesis. The test was conducted in two different ways as follows.

a. To separate the effects of time and the impact of herbivores, only exclosure plots were used. The species compositions and richnesses of these plots were compared on the three sampling dates.

b. In order to consider the impact of herbivores over time, the control plots were used. Only the species richnesses of these plots were compared on the three sampling dates.

5.4.2 PCQ comparisons

A point centered quarter (PCQ) transect was conducted in the area west of the Gqoyeni mouth where similar transects were conducted on two previous occasions (1979 and 1984). In order to facilitate accurate comparisons between the results of the three transects, it was ensured that the exact transect placements and techniques employed were identical to those used previously. The technique employed is similar to that described in Mueller-Dombois and Ellenberg (1974). Fifty PCQ sampling points were spaced at 50 metre intervals at a distance of fifty metres from the river's edge. In each quarter, at each sampling point, the nearest woody individuals of three different size classes (viz. shrubs <2 metres high, trees 2 to 7 metres high and large trees >7 metres high) were identified and recorded. The frequencies, percentage compositions and densities of each species were then determined according to the procedures outlined in Mueller-Dombois and Ellenberg (1974). As the total number of sampling points used for the PCG differed slightly in the three monitoring sessions, accurate comparisons between the three sessions called for standardisation of the data, with a correction factor based on the size of the minimum species frequencies obtained for each session. These values were then compared between the three sampling dates. Since the PCQ is only a descriptive technique, it was not possible to provide confidence limits for the data to allow for rigorous statistical comparisons between sampling dates. An index of similarity (SI) based on species richness (Sorensen, 1948) (see enemy impact hypothesis) was, therefore, applied to the data to confirm differences which exist between the three sampling years.

5.4.3 Aerial photograph comparisons

Seventy two transects were randomly located on six sets of aerial photographs which were taken in 1937, 1954, 1960, 1973, 1983 and 1986. The relative abundances of four different vegetation states were determined in each transect. The vegetation states investigated were a. grass, b. reeds, c. small trees (ACACIA) and d. large trees (FIGS). The probabilities for transition from each state to every other were determined from one sampling date to the next. Using this procedure, a matrix of transition values was then produced for each of the five time intervals between the six sampling dates. A Markovian approach was then used (see succession approach - chapter 2) to determine the final proportions of the projected equilibrium states for each period as well as the the recovery periods required to attain these proportions.

5.5 Results

5.5.1 Exclosure/control comparisons

5.5.1.1 Exclosure plots

The changes in the total species richnesses from within the exclosure plots are displayed in Figure 4.27. The contribution of the two components, trees and herbs, are stacked to indicate their proportions of the total species richness. Initially (from September to December), the total species richness increased from 50 to 53 species largely due to the contribution of the herbaceous species. However, during the second period (December to March), the total species richness showed a decrease to 48 species, once again, largely due to the herbaceous component. This implies, in the absence of grazing and browsing, that competition between the herbaceous species is responsible for this effect.

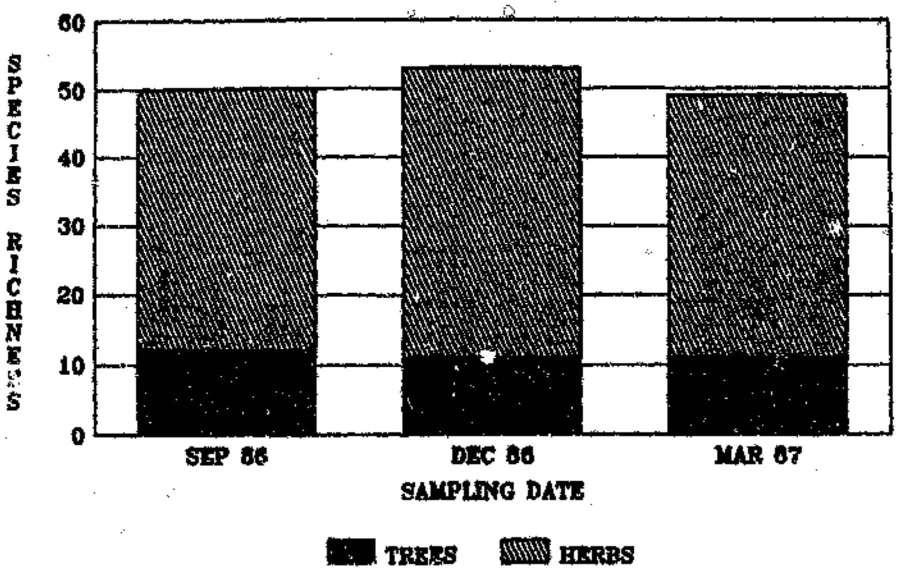


Figure 4.27 Species richness for trees and herbs from within exclosure plots for three sampling dates

Scrutiny of the dynamics of the individual species revealed that five response types were displayed by herbaceous species during the course of the study (Fig. 4.25). The increasing and decreasing responses of species over time are possibly due to competition between the species for waning resources. The simultaneous increase in percentage cover of herbs and the decrease in the percentage of bare ground demonstrates this possibility. Those species, which displayed clear trends from the beginning to the end of the study, were then classified as increaser or decreaser species according to their responses.

Increaser species displayed clear increases in frequency over time. These species and their responses during the time of the study are displayed in Figure 4.28. Decreaser species displayed clear decreases in frequency over time. These species and their responses during the time of the study are displayed in Figure 4.29. For the species names which correspond with a species number in these figures, consult the accompanying table (Table 4.13) which lists the species associated with the two classes.

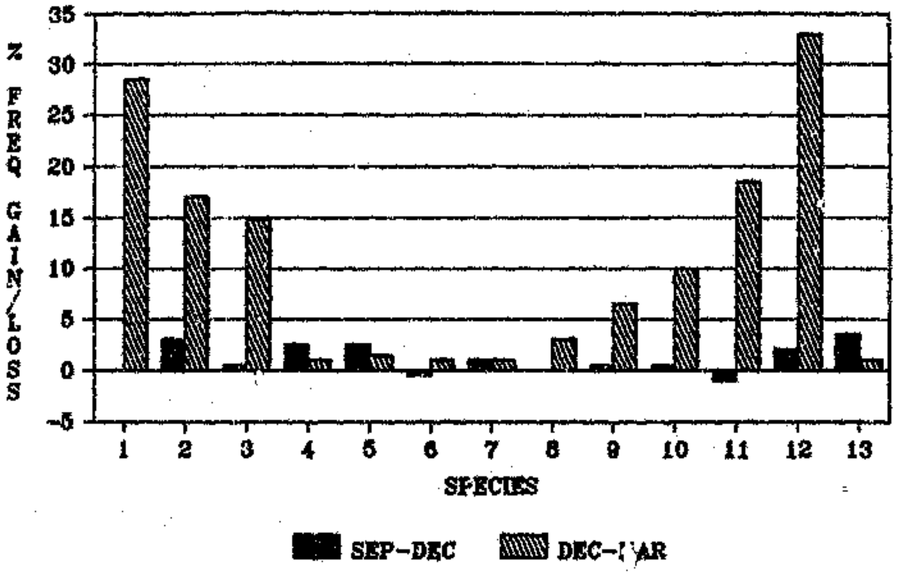


Figure 4.28 Increases in percentage species frequencies over time as displayed by increaser species

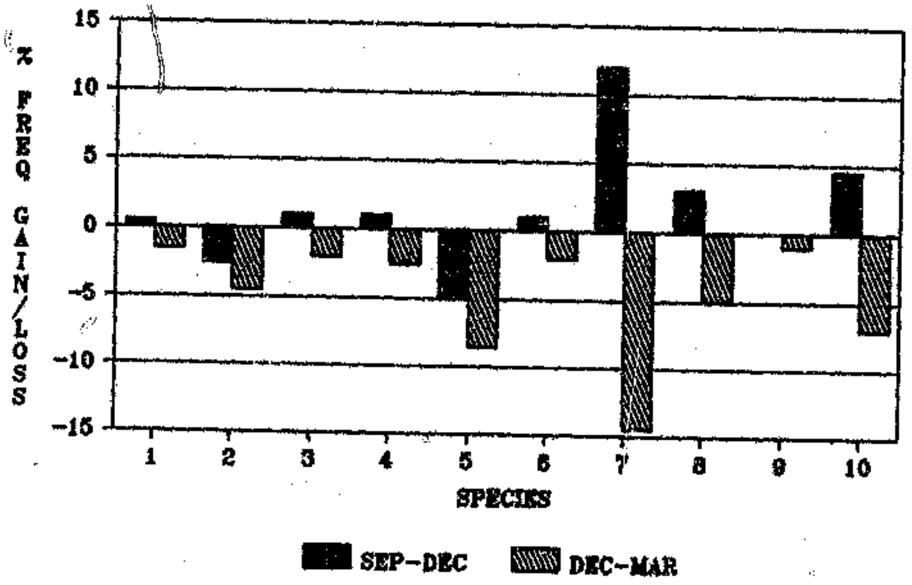


Figure 4.29 Decreases in percentage species frequencies over time as displayed by decreaser species

Table 4.13 The species response classes over time for the major herbaceous species in riverine areas from within exclosure plots

INCREASER SPECIES

No	SPECIES	No	SPECIES
(1)	*Cassia capensis*	(2)	*Chloris gayana*
(3)	*Cryptolepis obtusa*	(4)	*Eragrostis curvula*
(5)	*Eragrostis superba*	(6)	*Cynodon dactylon*
(7)	*Eriosema psoraleoides*	(8)	*Glycine wightii*
(9)	*Lippia javanica*	(10)	*Paspalum urvillei*
(11)	*Pergularia daemia*	(12)	*Tridax procumbens*
(13)	*Urochloa mosambicensis*		

DECREASER SPECIES

No	SPECIES	No	SPECIES
(1)	*Aristida congesta*	(2)	*Cenchrus ciliaris*
(3)	*Cynodon nlemfuensis*	(4)	*Cyperus sexangularis*
(5)	*Indigofera spicata*	(6)	*Phragmites australis*
(7)	*Panicum maximum*	(8)	*Rhynchelytrum repens*
(9)	*Richardia brasiliensis*	(10)	*Solanum panduraeforme*

5.5.1.2 Control plots

Figure 4.30 reveals the changes in herbaceous species richness in control plots only. Woody species displayed very little change in species richness over the study period and, consequently, were not included in the figure. The herbaceous species richness increased steadily from 27 species in the beginning of the study to 41 species at the end.

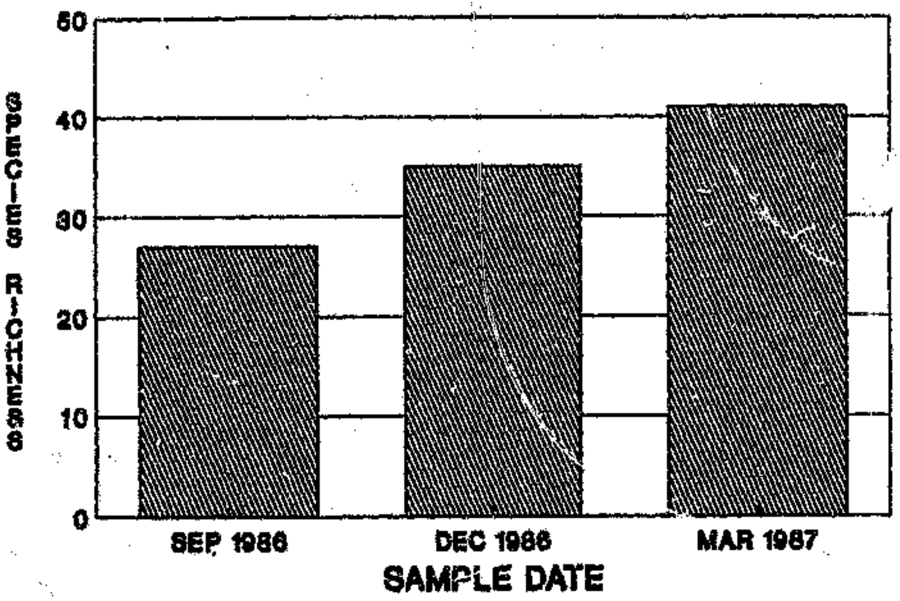


Figure 4.30 Species richness for herbaceous species in control plots for three sampling dates

5.5.2 PCQ comparisons

The standardised PCQ results for 1979, 1984 and 1986 are displayed in Table 4.14. The species richness values are displayed separately in Figure 4.31. The species richnesses of the three size classes investigated are noticeably different in each of the three years. The 1984 values are those taken just after the cyclone Domoina floods and therefore represent the number of species remaining after the floods. The period from 1984 to 1986 displays a clear recovery in terms of the species richness values for the small and medium size classes. This recovery is largely attributed to the colonization of these areas by propagules deposited by floods. The majority of these new species are still in the small and medium size classes and have not yet started to contribute to the large size class.

Table 4.14 Standardised PCQ results for three sampling dates 1979, 1984 and 1986 adapted from Wills (1984)

SMALL - refers to trees less than 2 metres in height
MEDIUM - refers to tress between 2 and 7 metres in height
LARGE - refers to trees greater than 7 metres in height

	DATE			DATE			DATE		
SPECIES	1979	1984	1986	1979	1984	1986	1979	1984	1986
		SMALL			MEDIUM			LARGE	
Acacia grandicornuta	0	0.5	0	0.5	0	0	0	0	0
Acacia robusta	3	3.3	4	6	3	2.5	4	2	1.5
Acacia schweinfurthii	0.5	0	1	4	0	1	0	0	0
Acacia tortilis	0	0	0.5	0	0	1.5	0	0	0
Acalypha glabrata	15.5	0.5	0	3.5	1.5	0	0	0	0
Acokanthera sp.	0	0	1	0	0	0	0	0	0
Azima tetracantha	11.5	3.5	3	1.5	0	0.5	0	0	0
Capparis tomentosa	0	0	0.5	0	0	0.5	0	0	0
Cassine aethiopica	1.5	1	0	1	0.5	0	0	0	0
Croton menyhartii	5	0	0	0	0	0	0	0	0
Cussonia paniculata	0	0	0	0	0	0.5	0	0	0
Dichrostachys cinerea	0	0	4	0	0	1	0	0	0
Diospyros glandulifera	2	0	0	0	0	0	0	0	0
Diospyros lycioides	1	0	0	0	0	0	0	0	0
Diospyros simii	0.5	0	0	0	0	0	0	0	0
Dombeya cymosa	0.5	0	0	0.5	0.5	0	0	0	0
Dovyalis caffra	0.5	0	1	0	1	0.5	0	0	0
Ehretia rigida	2.5	0	0.5	0	0	0	1.9	0	0
Erythroxylum emarginatum	0.5	0	0	0.5	1	0	0	0	0
Euclea divinorum	0	0	0	0.5	0	0	0	0	0
Euclea natalensis	2.5	0	0	0	0	0	1.9	0	0
Euclea schimperi	17.5	4	3.5	4.5	3	5	0	0	0
Euclea undulata	2	0	0	0	0	0.5	0	0	0
Euphorbia tirucalli	0	0	0	0.5	0.5	0	0	0	0
Ficus sycomorus	0	0	2.5	2.5	0	1	0.5	2	0
Galpinia transvaalica	0	0	0	2	0	0	0	0	0
Grewia flavescens	0	0	0.5	0	0	0	0	0	0
Grewia sp.	0	0	0.5	0	0	0	0	0	0
Hippobromus pauciflorus	2	0	0	0.5	0	0.5	0	0	0
Manilkara concolor	0.5	0	0	1	0	0	0	0	0
Maytenus heterophylla	0.5	4	1	3	4	0	0	0	0
Maytenus senegalensis	3.5	1	2	1	1	1	0	0	0
Melia azedarach	0	0	0	0	0	1	0	0	0
Mimusops caffra	1	0	0	1	1	0	0	0	0
Mimusops obovata	0	0	0	1	0	0	0	0	0
Nuxia oppositifolia	0	0	0	1.5	0.5	0	0	0	0
Ochna arborea	0.5	0	0	0	0	0	0	0	0
Olea africana	0	0	0	1	0	0	0.5	0	0
Pappea capensis	0	0	0	6	1.5	0.5	0	0	1.5
Phoenix reclinata	1.5	0	0	0	0	0	0	0	0
Phyllanthus reticulatus	1	1.5	3.5	0.5	0	0.5	0	0	0
Plectroniella armata	7.5	5.5	4	11	8	1.5	0	0	0
Rhus natalensis	0	0	0.5	5.5	2.5	0.5	0	0	0
Rhus chirindensis	1.5	0	0	2.5	0	0	0	0	0
Schotia brachypetala	0	0	0.5	9	1	1.5	3	9.3	3
Schotia capitata	1	1	0	4	0	0.5	0	0	0
Sclerocarya birrea	0	0	0.5	1	0	0	0.5	1	0.5
Sesbania sesban	0	0	1	0	0	0.5	0	0	0
Sideroxylon inerme	0	0	0	2.5	0.5	0.5	0	1	0
Spirostachys africana	11	5	8.5	13.5	5.5	8.5	6	6.5	1.
Strychnos decussata	0	0	0.5	0.5	0	0	0	0	0
Tarchonanthus camphoratus	0	0	0.5	0.5	0	0.5	0	0	0
Thespesia acutiloba	0	0	0	1	0	0	0	0	0
Trema orientalis	0	0	0	0	0	1.5	0	0	0
Trichilia emetica	0	0	0	1.5	0	0	0	0	0
Turraea obtusifolia	0	0	0	0.5	0	0	0	0	0
Ziziphus mucronata	1.5	0	2.5	1.5	0.5	1.5	0	0	1.5

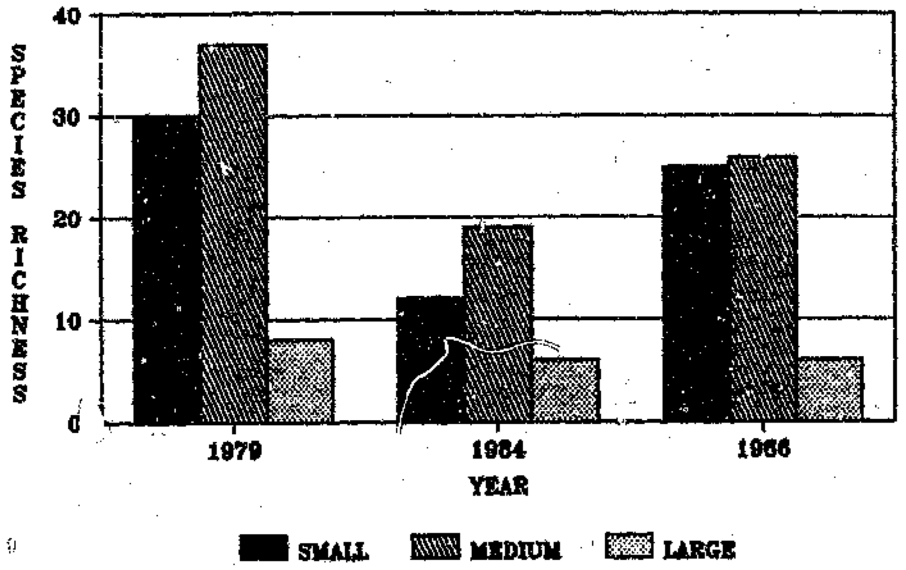


Figure 4.31 Species richness for three size classes investigated by PCQ transects on three separate sampling dates

The similarity index values obtained for the three time periods investigated (Fig. 4.32) also displays that clear differences exist between the different periods in all three size classes of trees. In support of Fig 4.31, the Domoina flood greatly reduced the similarity index of the community (1979-1984) - (low SI values). It is also clear that distinct recovery of the community took place from immediately after the flood (1984) to 1986, to the extent that the similarity value between 1979 and 1986 was relatively high (high SI). The similarity index technique yields a higher degree of sensitivity in the large tree size class than is displayed by comparing species richnesses alone (Fig. 4.31). The recovery of the large class is clearly evident in Figure 4.32 while this difference is not so apparent in Figure 4.31.

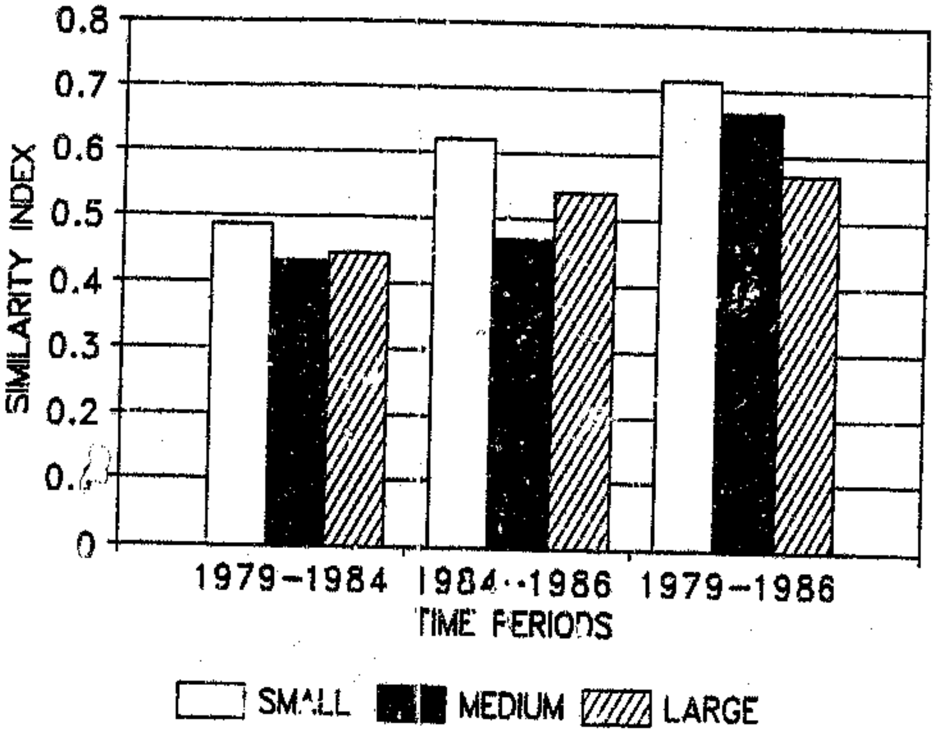


Figure 4.32 Similarity index (SI) values for PCQ results collected at Thumbu for three time periods

5.5.3 Aerial photograph comparisons

The abundances of the four vegetation states obtained from the six sets of aerial photographs are displayed in Figure 4.33. The abundances of the four states are very dynamic and vary considerably. The small tree size class (Acacia) varies between 9 and 22 percent, while the large tree size class (Figs) varies between 1 and 63 percent. The arrows denote flood events in excess of 2000 cubic metres per second. These events appear to have a noticeable influence on the abundances of these two classes.

The transition matrices for the 5 time periods investigated are displayed in Table 4.15. The probabilities of transitions between the four vegetation states are very variable over the five time periods.

The final equilibrium proportions of the four vegetation states and the times required to reach these proportions, as determined by the Markovian model, are presented in Table 4.16.

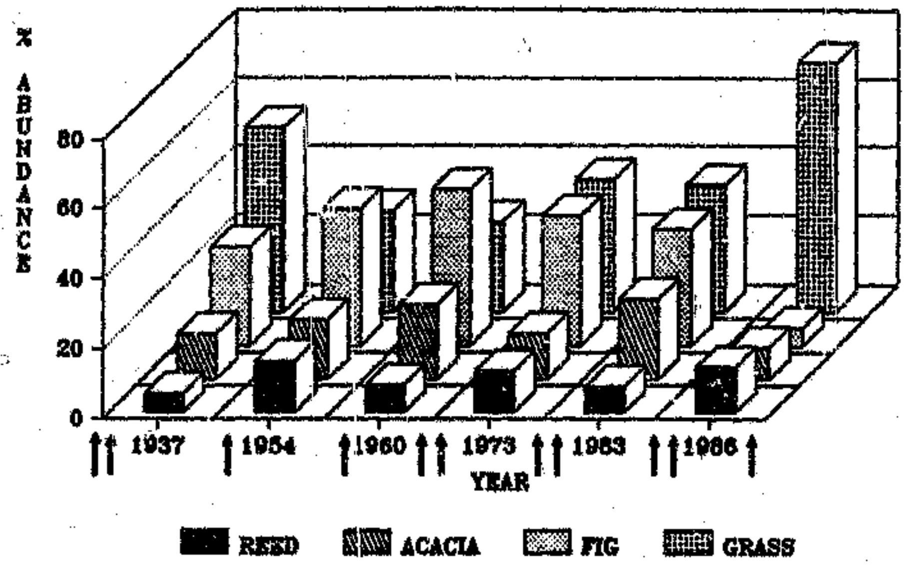


Figure 4.33 Percentage abundances of four vegetation states for six sampling dates as obtained from aerial photographs

Arrows on the X-axis indicate the incidence of large flood events

Table 4.15 The transition matrices for 5 time periods in riverine areas

Matrix values indicate the probabilities of transition between the four vegetation states investigated.

1937 to 1954	SAND	GRASS	REED	ACACIA	FIG
SAND	0.538	0.054	0.027	0.111	0.270
GRASS	0.029	0.523	0.082	0.093	0.273
REED	0.054	0.077	0.687	0.057	0.125
ACACIA	0.009	0.020	0.029	0.829	0.113
FIG	0.003	0.006	0.031	0.040	0.920

1954 to 1960	SAND	GRASS	REED	ACACIA	FIG
SAND	0.956	0.000	0.011	0.022	0.011
GRASS	0.207	0.515	0.037	0.117	0.124
REED	0.276	0.061	0.435	0.092	0.136
ACACIA	0.054	0.006	0.033	0.844	0.063
FIG	0.062	0.019	0.011	0.021	0.887

1960 to 1973	SAND	GRASS	REED	ACACIA	FIG
SAND	0.785	0.078	0.020	0.047	0.070
GRASS	0.020	0.884	0.041	0.000	0.055
REED	0.175	0.190	0.543	0.054	0.038
ACACIA	0.089	0.069	0.061	0.641	0.140
FIG	0.124	0.114	0.033	0.037	0.692

1973 to 1983	SAND	GRASS	REED	ACACIA	FIG
SAND	0.646	0.050	0.015	0.145	0.144
GRASS	0.080	0.810	0.008	0.071	0.031
REED	0.207	0.084	0.488	0.146	0.075
ACACIA	0.029	0.020	0.002	0.907	0.042
FIG	0.101	0.049	0.009	0.103	0.738

1983 to 1986	SAND	GRASS	REED	ACACIA	FIG
SAND	0.695	0.232	0.053	0.007	0.013
GRASS	0.005	0.995	0.009	0.000	0.000
REED	0.023	0.130	0.839	0.003	0.005
ACACIA	0.072	0.355	0.075	0.482	0.016
FIG	0.076	0.519	0.128	0.023	0.254

Table 4.16 **Final equilibrium proportions of riverine vegetation states and time required to attain these proportions**

TIME PERIOD	PREDICTED EQUILIBRIUM PROPORTIONS				TIME REQUIRED
	GRASS	REED	ACACIA	FIG	
1937 - 1954	5.60	9.38	21.21	63.71	629 years
1954 - 1960	65.33	2.50	13.88	18.29	384 years
1960 - 1973	69.85	7.24	5.81	17.10	507 years
1973 - 1983	27.63	1.14	53.33	17.90	380 years
1983 - 1986	99.35	0.59	0.03	0.03	162 years

5.6 Discussion

5.6.1 Exclosure/control comparisons

5.6.1.1 Exclosure plots

It appears that time initially allows for an increase in herbaceous species richness after a major disturbance. This accumulation of species declines after some time and eventually reaches a point where no further species accumulate. This effect is possibly due to the build up of competition between the accumulating species and eventually results in the loss of weaker competitors. This is particularly evident with the fast growing herbaceous species which can employ this strategy to colonize open areas very quickly and establish themselves firmly before resources become limiting. The superficial nature of herbaceous rooting systems ensures that the resources available to them are strictly confined to those occurring on the soil surface or just below. Consequently, competition between herbaceous species is likely to be for resources at these levels only and their depletion is likely to be rapid.

No empirical evidence of interspecific competition was found to exist between the tree species within the exclosure plots. Tree species display much slower growth rates and therefore it is not surprising that the effects of competition had not manifested themselves at this early stage. In addition, due to the different rooting depths of trees, they are able to tap resources from a more extensively distributed resource base which would take much longer to deplete. In order to study the effects of interspecific competition, it would therefore be necessary to monitor these areas for a much longer period than was possible in this study. Large floods were responsible for removing the exclosure structures and thereby prematurely terminated the study.

5.6.1.2 Control plots

The findings reveal that herbaceous species increased in areas where they were exposed to grazing pressure, while the richness of woody species remained relatively static. During the period of the study, personal observations were that ungulates consume large quantities of herbage in riverine areas. It is postulated that this removal of herbage serves to reduce the quantities of the major herbaceous competitor species present. In so doing, competition between these species is maintained at low levels and competitively weaker species are able to colonise and persist in these areas. This effect would adequately explain the increase in species richness in areas exposed to grazing pressure. The fast growth and response rates of herbaceous species in recently disturbed areas ensures that species richness increases steadily under these conditions.

Woody species, due to their comparatively slower growth rates are not able to respond as rapidly to recently disturbed areas and consequently, their species richnesses displayed no significant increases during the period of the study.

5.6.2 PCQ comparisons

These comparisons revealed the remarkable ability of riverine vegetation to recover quickly after a large disturbance. This fast recovery is particularly noticeable in the small and medium size classes and can be attributed to the fast response of woody plant propagules and seedlings after the disturbance. While the larger size class also displayed a substantial recovery after the 1984 flood, it was less noticeable. This is attributed to their slower growth rate compared to the juveniles class.

5.6.3 Aerial photograph comparisons

The highly variable probabilities of transitions for between the four vegetation states reveals the significant effect of floods on woody species. Large floods therefore serve to arrest the accumulation of woody species. Owing to the fact that woody species are relatively slow colonizers, it is unlikely that the frequency of flooding will allow them sufficient time to accumulate to the extent that they will begin to compete for resources.

The Markov model predictions show that in the absence of further disturbance, the proportions of the four vegetation states would eventually reach an equilibrium for all the time periods investigated. This refers to the time required for the gradual accumulation of species with time, the slow depletion of large quantities of resources and the lengthy outcome of competitive interactions between species to eventually arrive at an equilibrium. This factor reflects the time needed for complete recovery under conditions of similar disturbance conditions. As the herbaceous component of riverine areas reach an equilibrium relatively quickly, these long time periods required reflect the lengthy process needed for the accumulation of tree species, their growth and the eventual outcome of the competition between them.

5.7 Conclusions

While it was not possible to carry out rigorous statistical comparisons of vegetation characteristics for the time periods studied, the importance of time in riverine areas was displayed adequately.

Herbaceous species display fast growth and response rates which enables them to respond quickly to newly disturbed areas. This quick response leads to the rapid build-up of species at disturbed sites and, consequently, interspecific interactions occur quickly in response to the rapid depletion of resources and colonisation of further species. During the ecological time span, therefore, there is evidently enough time for interspecific interactions, such as that of herbivory and competition, to have significant effects on community characteristics. The ecological time hypothesis is clearly important and applicable under these conditions. Consequently, the null hypothesis was rejected.

Woody species display a much slower growth and response rate to newly disturbed areas. During the ecological time span it is far less likely that species interactions would have much or any effect on community characteristics. This is particularly true due to the impact of recurrent floods which are continuously responsible for arresting these interactions. Woody species are therefore less subject to the ecological time hypothesis.

It is clearly not possible to study the effects of time in complete isolation of other factors such as interspecific competition, the impact of disturbances and enemies and the effects of stress and environmental change. These are inherent components of the passage of time, in any area, and it would be both impossible and impracticable to eliminate their effects on community recovery.

4.3 Discussion and conclusions - community organisation theory approach

4.3.1 General

The separate tests of five community organisation hypotheses (sub-chapters 1 to 5) managed to refute the null hypotheses associated with each test. Traditionally, a claim of this nature would invoke wild response from the supporters of the various hypotheses with the claim that tests were not conducted rigorously enough and/or that the basic assumptions of each had been violated during the process, thereby removing the ability to provide accurate and adequate comparisons between them. From the individual tests however, it is apparent that all five hypotheses have positive application in the Umfolozi riverine situation. The fact that all five hypotheses were found to be applicable simultaneously in the riverine situation shows that a universal approach such as that proposed by Price (1984) should be considered carefully. The resource/exploiter based theme of the approach is unique and identifies the possibility that several hypotheses could possibly apply in any area, due to differential resource types and their availabilities and the responses of possible exploiters. It must be understood, however, that the approach does not predict that all hypotheses apply in all areas. An area which may only have a few resource types and few exploiter species would obviously not be able to support all of hypotheses simultaneously but only those which are possible under the limited circumstances, while a heterogeneous area, such as the Umfolozi riverine area, does have the potential of supporting all.

It has not been traditional for workers to define the specific range of resource conditions and exploiter responses necessary in order for their hypotheses to have positive application in any specific areas. If this had been achieved from the start, when hypotheses had been initially proposed, it may have been possible to avoid decades of disagreement over the existence and applicability of the numerous community organisation hypotheses. With the problem identified, theory on community organisation should depart from its traditional role of single hypothesis support and instead concentrate on the simultaneous contributions of various hypotheses which have been independently identified and tested. This approach could thereby form an undisputed and stable foundation for the understanding and successful management of areas which display different resource and exploiter characteristics.

The approach clearly has the potential to assist the manager with the treatment of his different areas based on which hypotheses have particular application and his objectives for the areas concerned. For example, in an area where patchy resources are present, the rate of resource change is rapidly decreasing and the exploiter response is slow, it would probably be of little value for the manager to try to increase the species diversity of the area by creating areas of different size, shape and diversity or by introducing different ungulate species. Since neither the resource heterogeneity hypothesis, the island size hypothesis or the enemy impact hypothesis apply under such conditions, it would probably be a futile exercise - his best course of action would be to wait for the passage of time. Whereas in areas of uniform resource distribution, which are rapidly decreasing, this treatment would probably have far reaching success.

Since it was not possible in this study to test each hypotheses under all of the combinations of resource types and availabilities and exploiter responses as proposed by Price (1984), it is necessary that this should be addressed with the aim of confirming and refining the hypotheses summary map of Price (1984). Personal reservation is however expressed over whether all of the relevant resources could be identified to start with, whether it is possible to determine the conditions under which particular resources are available for exploitation and whether it is possible to determine which of the numerous exploiters are making use of the available resources. In other words, is it practically possible to navigate one's self around within the summary table successfully using identifiable land marks as reference points? If difficulty is encountered in this regard, then at best, the approach will either remain very broad and insensitive or purely theoretical and impracticable. If the former is true it would still have some practical appeal, although limited, and if the latter is true, it would remain a purely metaphysical issue.

The approach could become very complex and unweildy if one had to consider all possible combinations of resource types and availabilities and exploiter responses. Under such circumstances, in order to determine which hypotheses have application in an area, it would be necessary to use overlay methods for each of the combinations involved. This necessity may be encountered in areas where no particular resources display overriding importance over others. However, if one had prior knowledge of particular resources which do have overriding importance in an area, for example that of water and soil moisture as in the riverine situation, this task would be simplified considerably. By consideration of the availability of these resources alone, it would be possible to navigate one's self to a point of likely relevance in the table.

4.3.2 Riverine hypothesis applications map

During the testing of hypotheses, it was identified that water and soil moisture have an overriding effect in the Umfolozi riverine situation. Since the supply and distribution of water fluctuates during different times of the year both temporally and spatially, it can be expected that different hypotheses have importance at different times and in different areas during the course of a year. Using the Price (1984) hypothesis applications summary table as a basis, a conceptual map was constructed to predict which hypotheses have particular relevance at different times of the year along the riverine moisture gradient which runs at right angles away from the river (Figure. 4.34). This map refers largely to the dynamics of fast growing and responding herbaceous species and woody seedlings which are able to respond to seasonal fluctuations in water supply. Large trees, themselves, are unlikely to be affected by the differential application of hypotheses according to seasonal and spatial changes in resource supply and distribution. However, the response of seedlings would have an eventual effect in the final structuring of woody communities.

a. Spring/early summer

At this time of the year, soil moisture is rapidly increasing and both uniform and patchy water distributions are present. The summary table indicates that under these conditions, the individualistic response, enemy impact and ecological time hypotheses have particular relevance.

Exploiter species are able to respond to resources according to their specific life history requirements and strategies, as interspecific competition has not yet become evident while the species respond quickly to the newly available and increasing resources. It seems logical, at the same time, that ungulates would then also be able to select their dietary preferences. The application of the time hypothesis means that species richness constantly increases as long as the water supply is on the increase.

Areas within close proximity of the river are guaranteed a uniform distribution of water while the isolated puddles of water, away from the river, which collect after the spring rains, constitute areas with patchy resource distribution.

As species richness increases and time passes, the competition for resources increases. Simultaneously, the distribution of water becomes more constant with regular rainfall, which eventually leads to changes in the resource base and other hypotheses start to feature instead.

	POSITION ON ELEVATIONAL GRADIENT				
	BOTTOM		TOP		
TIME OF YEAR	WATER SUPPLY	APPLICABLE HYPOTHESIS	WATER SUPPLY	APPLICABLE HYPOTHESIS	EXPLOITER RESPONSE
SPRING	RAPIDLY INCREASING (UNIFORM)	INDIVIDUALISTIC TIME	RAPIDLY INCREASING (PATCHY)	INDIVIDUALISTIC TIME	SLOW
		ENEMY IMPACT TIME		INDIVIDUALISTIC TIME	FAST
SUMMER	STEADILY RENEWED (UNIFORM)	RESOURCE HET ISLAND SIZE TIME ENEMY IMPACT	CONSTANT (PATCHY)	RESOURCE HET ISLAND SIZE TIME ENEMY IMPACT	SLOW
		RESOURCE HET ISLAND SIZE TIME ENEMY IMPACT		TIME	FAST
	CONSTANT (UNIFORM)	RESOURCE HET ISLAND SIZE TIME ENEMY IMPACT	PULSING (PATCHY) (UNIFORM)	INDIVIDUALISTIC	SLOW
		RESOURCE HET ISLAND SIZE TIME ENEMY IMPACT		INDIVIDUALISTIC	FAST
AUTUMN	RAPIDLY DECREASING (UNIFORM)	RESOURCE HET ISLAND SIZE TIME ENEMY IMPACT	RAPIDLY DECREASING (PATCHY)	TIME	SLOW
		RESOURCE HET ISLAND SIZE TIME ENEMY IMPACT		RESOURCE HET ISLAND SIZE TIME ENEMY IMPACT	FAST
WINTER	PULSING (CONSTANT) (PATCHY)	INDIVIDUALISTIC			SLOW
		INDIVIDUALISTIC			FAST

Figure 4.34 Riverine hypothesis applications map, adapted from the Price (1984) hypothesis applications table

b. Mid/late summer

The supply of ground water stabilises and soil moisture is relatively constant and uniformly distributed within close proximity to the river. The summary table indicates, under these conditions, that the resource heterogeneity, enemy impact and island size hypothesis have particular relevance.

Flood events are common at this time of the year and are responsible for creating patches of various shapes and sizes which serve as a variety of habitats. Since both hypotheses are applicable, these patches vary in species diversity according to their size and habitat/resource heterogeneity. Further away from the river the supply of water experiences a pulsing effect due to evaporation and transpiration during the day and its re-supply during the night. Here the individualistic response hypothesis remains important. In areas where the supply of water is constant, due to water saturation or the presence of sub-surface clay horizons, the enemy impact, island size and resource heterogeneity hypotheses are important, particularly where exploiter response is rapid. Where exploiter response is slow, only the time hypothesis has application and here species richness is likely to accumulate with time.

c. Autumn/early winter

The supply of water begins to decrease rapidly with diminishing rainfall. This brings about no real change with regard to the application of hypotheses along the entire soil moisture gradient. The enemy impact, resource heterogeneity and island size hypotheses continue to apply. However, at this stage germination and growth rates are declining with the onset of winter.

d. Mid Winter

Water supply is diminished considerably and river flow is reduced at times to sub-surface flow only. Water supply near the river begins to pulse. With uniform distribution, only the time hypothesis has application. At the far end of the gradient it is possible that the supply of water is completely disrupted, in which case no hypotheses really have application.

The testing of relevant hypotheses in the Umfolozi riverine situation took place over the period of more than a year and covered the entire length of the riverine soil moisture gradient at all sites. According to the riverine hypothesis applications map, all five hypothesis are expected to apply over this wide temporal and spatial range and, therefore, it is not surprising that all five were found to be applicable simultaneously.

The riverine hypothesis applications map is based on water as the dominant resource and it does not cover all combinations of resource supply and distribution as well as exploiter responses as proposed in the Price (1984) hypothesis applications table. Being a considerably scaled down version of the hypothesis applications table, it would therefore be easier to test each hypothesis under all combinations of resource and exploiter response variables, at different times of the year and at different points along the soil moisture gradient. This step would be necessary in order to employ the map for the sake of making accurate predictions about the actual spatial and temporal applicability of the hypotheses in riverine areas. Any predictions made about the specific applicability of hypotheses and management oriented decisions, derived from the map, should be seen as tentative and unproven until such tests are conducted.

With this warning in mind, it is possible to make predictions which may assist with the management of riverine areas.

Of the five hypotheses tested, only the enemy impact hypothesis is really amenable to manipulation at a practical level. This is achieved by means of excluding ungulates from certain areas or by managing the quantities of particular problem species. It, therefore, is feasible to consider the importance of this hypothesis, in the light of its applicability in riverine areas, with the aim of assisting the development of techniques for the management of these areas.

According to the map, the enemy impact hypothesis is applicable throughout the year in close proximity to the river. However, in early summer, when water supply is increasing rapidly, only the individualistic hypothesis applies simultaneously. Species with individualistic water and other requirements, most likely true riverine species, will make their appearance. Simultaneously, ungulates with specific feeding requirements will also be abundant and spend long periods selecting and foraging on these species. If grass cover is low at this time of the year, as a consequence of the previous winter burns for example, this would place particular stress on the riverine seedlings which would be easily detected by specialist feeders. It appears that this is a particularly important time of the year for the recruitment and colonisation of riverine plant species. Depending on the abundance of ungulates, their accessibility to riverine areas and the abundance of suitable refuges which afford these species some protection from specialist feeders, ungulates may have a major impact on the recruitment and colonisation of true riverine plant species in riverine areas after a major disturbance.

CHAPTER 5 GENERAL DISCUSSION

Where necessary, this final chapter draws on the findings of the three main approaches employed and discusses these in the light of the prime objectives of the study. The combination of the three different theoretical approaches employed and their findings provided a comprehensive and in-depth insight into the structuring and dynamics of riverine vegetation.

5.1 The structuring and dynamics of riverine communities

The structuring and dynamics of riverine communities is evidently described by a number of theories and processes which apply partially and simultaneously. The long route taken, in building the final picture of riverine structuring and dynamics, reflects the characteristics of scientific revolutions, namely, the destructive-constructive paradigm changes that are brought about by discovery and the invention of new theories (Kuhn, 1962). However, an understanding of the structuring and dynamics of the riverine system can be defined. This is done so with reference to the major processes and characteristics which are evident in riverine areas and which were separately addressed by the three different approaches.

5.1.1 The response of riverine communities to recurrent flood events

Both the succession theory approach (chapter 2) and the disturbance theory approach (chapter 3) identified a persistent response of the riverine system to recurrent flood events. The former approach described this as an 'event driven' response, while the latter approach described this as a 'resilient' one.

The event-driven explanation forms the basis of what is termed 'non-equilibrium' theory. This proposes that the species composition of a community is usually in a state of equilibrium and that after a disturbance it recovers to that state by means of a number of processes. High diversity is then maintained without continuous changes in species composition.

Noble (1986) attributed the ability of the system to remain in a state of equilibrium to the 'inertia' of the system. After a large disturbance the system initially appears to 'stick' in the position to which it was displaced. During this lag period the species present, in their disturbed condition, generate inertia and eventually release it. This then leads to a very fast recovery as the original species appear to 'bounce back' rapidly.

The explanation described by 'resilience' is one which forms an part of 'equilibrium theory'. Equilibrium theory postulates that the ecological systems are seldom in a state of equilibrium due to the effects of recurrent disturbances. Systems are defined in terms of their stability and resilience to these disturbances (see literature review - section 1.6.2.7)

The Umfolozi riverine system displayed a high degree of resilience throughout the study by persistently attempting to return to its equilibrium state after each successive disturbance. The system has evidently remained within a single domain of attraction over the last century, despite the effects of large floods such as those of 1925 and 1963. Data collected during this study was used to determine the position of the system relative to its equilibrium point for a number of sampling dates including 1986. However, since no data has been collected after 1986 its current position relative to the equilibrium state is unknown. Consequently, the direction in which the system is moving after the 1984 floods is also uncertain. This knowledge is necessary to elucidate whether the system is still within the bounds of the same domain of attraction after this particularly destructive event.

The Umfolozi riverine system is evidently maintained in a constant state of dis-equilibrium and rarely, if ever, gets the opportunity to equilibrate.

5.1.2 The effects of floods on species composition in riverine areas

The major regimes of recurrent floods, namely, their intensity, frequency and severity, constitute the major process which controls or maintains the species composition in riverine areas.

The current intensity and frequency of floods appears to maintain riverine communities in a dynamic state of dis-equilibrium, largely characterised by species which are able to persist under extreme conditions of flooding. By selecting for different species which are suited to the flooding conditions, the diversity of species is maintained.

5.1.2.1 The maintenance of species diversity

Recurrent flooding is evidently an essential process which dictates the species diversity of riverine areas. Current understanding of the simultaneous effects of disturbance intensity and frequency on species diversity reveals that species diversity can be explained by a three dimensional surface. This surface is defined by a trough of high species diversity extending between the high frequency and low intensity and the low frequency and high intensity extremes of disturbance. Regions of lower species diversity are found at low frequency and low intensity (the climax or equilibrium state) and high frequency and high intensity.

No work has focused on the separate effects of flooding frequency and intensity on species diversity in these areas. Consequently, the application of theory to address management requirements was restricted to a simple two dimensional model which describes high species diversity at an intermediate level of frequency/intensity of flooding with low levels of diversity existing on either side. According to this model two thresholds of flooding frequency/intensity then exist which define the conditions under which the maintenance of species diversity applies. The importance of determining these threshold values and how these might be achieved were discussed. However, the study did not directly determine realistic values for the areas involved.

The interpretation of findings, from the application of transition matrices and a Markov model in the successional approach (chapter 2), revealed an approximate recovery time requirement of 30 flood-free years in order for the system to reattain its equilibrium state. It is suggested that a value of at least 25 years should then be taken to represent the lower threshold frequency. This is probably a realistic estimate since it could take that length of time for some of the slowest maturing riverine species to reach reproductive and competitive maturity. A rough estimate could also be made of the higher threshold value, which could be derived from the condition of the riverine communities at the time of the study and the length of time that had passed after the Domoina floods. The PCQ findings in 1986 revealed that species richnesses counts of 59 species were well below those of 1979 when 76 species were recorded. This reveals that a flooding frequency of two and a half years coincides with a point on the declining slope of the two dimensional species richness model. In addition, reference to the sampling of control plots (1.5 to 2.5 years after Domoina floods) revealed that tree species displayed mean heights of only 1.3 metres and height ranges of between 0.2 and 5 metres which were considered to be rather small at the time. It is suggested that this state represents one which is close to the higher threshold value.

It is proposed, therefore, that the range of flood frequencies between 2.5 and 25 years defines the maintenance of species richness at levels which are acceptable in the riverine situation. Should these values be exceeded, i.e. below 2.5 and above 25 years, this would then lead to the existence of riverine communities maintained with unacceptably low species diversities.

5.1.2.2 The selection of species in riverine areas

This time period between large flood events is an important determinant of the species which are able to persist and succeed at a site.

Should this length of time be shorter than what is required for the majority of species to reach maturity or an optimum reproductive age, these species are likely to disappear from the site. It is this mechanism which is responsible for the decrease in species richness once the higher threshold is exceeded. Since the ecological time hypothesis was found to apply with herbaceous species, they are unlikely to be limited by the same frequency of floods which limit the woody species.

Should this time period be long enough for the major riverine species to colonise the area and start competing for resources, the less competitive species are likely to be excluded from the site. It is this mechanism which leads to a reduction in species diversity when the lower threshold is exceeded.

Different species have evolved under a variety of different conditions over long periods of time and therefore only certain species which have evolved under similar conditions are then selected for in areas subjected to extremes in flooding frequency. As discussed in the disturbance approach (chapter 3), different types of species have been identified according to their ability to tolerate different conditions of stress and disturbance (Grime, 1979). Of particular interest in this discussion are the ruderal, and competitor species.

A large number of riverine species are characterised as 'ruderals.' Their rapid response to flooding and their presence in riverine areas indicates that they must have evolved under similar conditions. A number of ruderal exotic species are common in the Umfolozi riverine system. Should the frequency of floods continue to increase, only the extreme ruderal species would be selected for, and the slower responding ruderal species would disappear. It is postulated therefore that the exotic ruderals will become more and more important in sympathy with the flooding frequency.

The large and majestic species which are associated with riverine areas represent 'competitor' species. Their large canopies and extensive rooting systems have been evolved to maximise their competitive ability in the less frequently disturbed riverine areas. However, they only attain reproductive maturity after many years, a characteristic which prevents them from persisting in extreme conditions of disturbance. Should the frequency of flooding continue to increase, therefore, it is these species which would be lost from the system first.

It must be noted, however, that a few riverine species exist in the Umfolozi system which have evolved in a wide range of disturbance conditions, including frequently disturbed areas, and it is not uncommon to find them representing a major component of the vegetation in areas of both flooding extremes.

5.1.3 The importance of interspecific competition as a driving force in riverine areas

Interspecific competition has traditionally been assumed to represent the major structuring force in most communities and consequently has become a major paradigm in community ecology.

However, the testing of alternative hypothesis in the riverine situation has revealed that it is not a major structuring factor in these areas. Instead, it appears to apply in only a minority of riverine situations.

The explanation for this is that although a wide range of exploiter species do often exist in similar areas, a natural system is characterised by a large array of resource gradients which are widely distributed. A large number of exploiter species are, in fact specialists, which display very little overlap of their exploitation patterns. Consequently, interspecific competition does not occur, or is relatively unimportant in the majority of real situations.

The majority of the alternative hypotheses tested were found to apply towards the lower part of the riverine gradient where a variety of resource distributions and rates of change do exist under a variety of conditions. However, despite the possibility that water is the major resource in this area, all five alternative hypotheses were found to apply simultaneously.

The test of the ecological time hypothesis revealed that interspecific competition is only important with herbaceous species. Only these species can respond fast enough, in the interval between flood events, to reach the point where competition for resources would occur. Woody species are not able to accumulate fast enough and, consequently, never reach the point where they would compete with each other in the time available.

Ungulate species were found to have an important effect on both woody and herbaceous species. Grazing was found to have an optimising effect on the species diversity of herbaceous species by reducing the degree of competition between major species.

5.2 The applicability of three different approaches in determining the structure and dynamics of riverine vegetation

5.2.1 Approach based on succession theory

The succession approach yielded helpful information regarding the structuring and dynamics of riverine areas. However, because succession theory is very complex and explicit, it was difficult to test. The complexity of events and changes which can take place with time, particularly within a complex system, comprised of a massive array of participants and events which can all interact according to a multitude of combinations. Any approach which attempts to define such changes faces the strong possibility of being declared untenable and non-falsifiable. This is particularly true if it still explicitly details the various pathways by which these changes are likely to occur, despite the fact that the approach may be applied to a wide range of circumstances.

The particular circumstances surrounding the riverine problem made it exceptionally difficult to 'est succession. Due to the length of time required to carry out an ideal successional study, the only true and accurate means of testing succession lies in the comparison of the same areas over time. However, with the present flood regime, the probability of sampling successional events beyond the early stages are very low and, considering the time, funding and effort required to initiate and maintain this type of approach, it would be of very little value. Furthermore, the value of such an approach is greatly reduced due to the constraints imposed by funding agencies, research institutions and human nature, all of which make long-term studies much more difficult to execute than conventional short term studies (Strayer et al, 1986).

The next possible approach to studying succession in riverine areas, that of the substitution of space for time, also failed due to the shortage of data from mid and late successional stages as a consequence of the complexity and effect of the disturbance regime. The approach, therefore, only served to identify the early participants of succession and their relative importances in these early stages. Since little was revealed concerning succession and the mechanisms involved with successional change in riverine areas, it too had very little application. The prospects for its use as a long term study are also rejected for the reasons mentioned above.

Due to its own implicit weaknesses and the complexities posed by the riverine environment, structure and disturbance regime, the succession based approach was clearly not capable of adequately addressing the structure and dynamics of riverine areas.

5.2.2 Approach based on disturbance theory

The application of this approach addressed a range of theories based on disturbance and the impact of disturbances on community structure and dynamics. The flood regime was identified as being a major determinant of the structure and dynamics of riverine communities and succeeded in clarifying the importance of investigating the full diversity of the regimes of a disturbance. Magnitude, frequency, areal extent and predictability (Sousa, 1984) were all found to be of importance when investigating the impact of floods. However, in order to understand the dynamics of riverine communities and to make predictions concerning future community structure in these areas, it is necessary to also consider,

- the available history of as many of these regimes as possible,
- the corresponding vegetation structure in as much detail as possible,
- the responses of component species to the disturbance and their subsequent recovery after disturbance, and
- other factors, apart from disturbance, which are responsible for structuring communities.

Both tests of the intermediate disturbance hypothesis were refuted. However, it is suggested that this was largely due to inconclusive results. These tests were carried out perpendicular to the river and in other distinct riverine areas and, consequently, their findings were compounded by the simultaneous influence of the riverine environmental gradient.

The modeling of disturbance events, relative to different vegetation states, identified that a continuum of vegetation states exist in riverine areas according to their state of equilibrium or dis-equilibrium. It is apparent that these states are related to the intensity/frequency of recurrent floods. Since insufficient data was available regarding the species diversities in each of these states, it was not possible to compare this model with existing disturbance models such as those of Miller (1982) and Malanson (1984). Despite this limitation, it was possible to interpret the available riverine data in the light of these theories and make adequate predictions.

While the disturbance theory based approach contributed considerably to the general understanding of riverine areas and their structure and dynamics, it was inadequate to address the full spectrum of the study. Particularly in terms of other factors responsible for community structuring.

5.2.3 Approach based on community organisation theory

The separate tests of individual hypotheses comprehensively identified the applicability of each in the riverine situation. In addition, various peripheral aspects of each hypothesis and their importance in a diversity of situations, were identified. This information contributed directly and indirectly to gaining an understanding of the structuring and dynamics of riverine areas.

The application of the resource based approach of Price (1984) served to co-ordinate and clarify the conditions under which each hypothesis applies and the reasons for the applicability of each, under a complexity of resource conditions and exploiter responses. By clarifying this point, the approach elucidated three major misconceptions which plague ecological publications.

1. It assisted in understanding the structuring of riverine vegetation comprehensively, by identifying the relevant hypotheses which apply within the range of different resource and environmental conditions present. Using this knowledge it was possible to construct a map, based on the spatial and temporal supply of water in riverine areas, which predicts the application of the five hypotheses under different combinations of resource distribution and exploiter responses.

2. It identified that different hypotheses pertaining to community organisation can apply in the same areas simultaneously and therefore succeeded in integrating a number of hypotheses which have traditionally been viewed as having mutually exclusive application in the same area.

3. It placed the importance of interspecific interactions into perspective in riverine areas by identifying the limited conditions under which interspecific competition and other interspecific interactions actually apply in relation to a suite of alternative hypotheses.

Although the approach does address the effects of disturbances on community structuring and dynamics, it does not directly investigate the specific characteristics (regimes) of the disturbances themselves. It is conceded that a thorough knowledge of these characteristics is not entirely necessary in order to gain an firm understanding of a system and how it is structured. This would be particularly true if the system being investigated is not considerably affected by disturbances. The approach could therefore be used effectively as a stand-alone approach under these conditions. However, for systems which are characterised by disturbances, it is important to understand these characteristics in order to yield more effective interpretations and predictions.

5.2.4 Combined approach

It is proposed that because a large majority of systems are likely to be affected by disturbances to some degree, that a combined approach, towards understanding the structuring and dynamics of the system, should be developed and employed. Since it was found that the investigation of disturbance characteristics cannot be used as a stand-alone approach, this form of approach should only be used to complement and possibly refine the approach proposed by Price (1984).

5.3 Recommendations for the management of riverine areas

It is perceived, by some, that the riverine areas of the Umfolozi system are in bad condition after the 1984 floods. The large, aesthetic climax riverine stands were removed to a large degree by the Domoina flood and replaced by large quantities of pioneer and mid-seral species. The climax stands served as prime habitat for a number of animals and as an aesthetically pleasing site for tourists. In this light, it appears that floods and other forms of disturbance are bad for the system, and that every effort should be made to resist them or prevent them from disrupting this 'utopian' state as much as possible.

However, there is another way to view the incidence of recurrent floods in riverine areas.

Flood records reveal that large floods have been an intrinsic part of the Umfolozi river system for the last century. During this time, they have been responsible for several major fluctuations in the state of riverine communities. The large floods of 1925 and 1963 caused the system to deviate considerably from its equilibrium state. This system has displayed resilience to each successive event by recovering towards its equilibrium state. The Domoina flood was also responsible for a major deviation from its equilibrium. This was clearly the largest flood ever experienced by the system, and yet there is no evidence that the system has been displaced from its domain of attraction. It is also important to note that the during the last century the riverine climax state has rarely, if ever, been attained.

It is believed that large and recurrent floods are responsible for increasing species diversity by removing high levels of competition between major species and thereby allowing other species the chance to colonize the areas. Floods and the subsequent responses of the system to them can therefore be viewed as an important ecological process in riverine areas and a major determinant of the structure and functioning of riverine communities. Since their is no evidence that species diversity has declined as a result of flooding, it is uncertain whether floods are bringing about undesirable changes in riverine areas and whether their effects should be avoided. In this light it is clear that this important process should be maintained.

A discrepancy appears to exists between what is wanted for the system, based on human perceptions and human needs, and what is ecologically correct for the riverine system in terms of the levels of species diversity which are maintained by floods.

It is of prime importance that these issues are elucidated and placed into perspective before any management actions are considered. If necessary the objectives for the reserve should be revised or stated more clearly.

One of the existing management objectives for the Umfolozi Game Reserve (Anon, 1985) reads as follows.

> " To re-instate and/or maintain the ecological processes which are considered to be the main determinants of ecosystem structure and function. Where these are no longer operative and cannot be re-instated, management should attempt to simulate their effects. Apart from this, management input should be minimal."

On this basis, recurrent flood events should be maintained in riverine areas. However, it is uncertain what degree of flooding is required to maintain optimal species diversity. It is suggested, therefore, that the intermediate disturbance model should be applied in order to determine the lower and upper threshold values which define the optimal range of species diversities in response to flooding frequency. With this approach, it would be necessary to identify, initially, the threshold values of flooding frequency which define the optimal species diversity required. This level would be determined according to the specific management objectives set for these areas. The technique could be applied effectively for maintaining areas in either a climax state or in a pre-defined state characterised by specific levels of species diversity.

Should it be detected that the upper threshold value is being exceeded by an undesirable frequency / intensity of flooding, it would be necessary to consider the following aspects in order to maintain or manage (if this is possible) the frequency of floods within the system.

5.3.1 Increase the vegetal cover of catchment areas

The flood data findings revealed that frequency and intensity of large floods are increasing with time. Rainfall data for the same period indicated that this effect is not as direct result of the increased intensity and frequency of large rainfall events. This implies that the condition of the catchment areas is responsible for increases in water run-off and increases in flooding conditions.

Ecological systems in third world areas, such as in the Umfolozi catchment, are in a different state to those found in the first world areas. They are generally characterised by a heavily grazed and greatly reduced vegetal and litter cover and a high incidence of soil capping. This condition is conducive to accelerated levels of water run-off.

This increased run-off of water is channeled via steams and tributaries and is directly responsible for increasing the flow rate of water in the Umfolozi rivers after large rainfall events. Rainfall events which would have contributed negligibly to the flow rate of the rivers in the past, would now have the potential of causing a major floods. Similarly, a higher frequency of rainfall events would now cause floods, thereby accounting for the increased frequency of floods in the Umfolozi rivers.

The answer would be attempt to increase the vegetal cover of these areas to ensure that water run-off is reduced.

5.3.2 Prevent the exploitation of riverine fringes upstream of the Umfolozi Game Reserve

Riverine vegetation is responsible for ameliorating the severity of floods and reducing their sediment loads. The severity of floods is a measure of the force exerted by a flood and is therefore largely responsible for the removal of large trees and scouring out the river profile. This reduction in severity leads to a reduction in sediment load and the deposition of sediments on point bars and other areas of low velocity.

By reducing the exploitation of these riverine areas up-stream of the reserve and by encouraging the recovery of already exploited areas, the severity of floods which reach the reserve would be substantially reduced and the deposition of sediments would be far less significant.

While this approach would be difficult to enforce in homelands once again, a measure of success would be achieved in white farming areas by ensuring, through legislation, that the riverine fringe of a predetermined width should not be cleared for agricultural or other purposes.

In addition to encouraging the recovery of riverine areas, this approach would act to conserve recruitment centres of riverine species above the reserve. These centres would act, in the future, to replenish the seed banks and ensure the recruitment of these species within the riverine fringes of the reserve.

5.3.3 The construction of a large dam up-stream of the Umfolozi Game Reserve

Failure to re-instate the desired or ecologically acceptable flood regime by the above means would surely indicate that it cannot be re-instated, and that management should attempt to simulate its effects instead. The placement of a large dam above the reserve could provide an effective solution to controlling the flood regime, and aiding the recovery and future management of riverine areas within the reserve. This control would be achieved firstly by means of the dam and the dam wall which would act to absorb and attenuate future floods, and secondly by artificially simulating the effects of the desired flood regime by means of the release of water in the desired quantities, in the desired manner at the correct times of the year. The control of the flood regime afforded by the construction of a dam in the Umfolozi system would manifest itself to areas much lower down the system where the effects of floods and silt deposition have caused extensive problems.

While the suggestion of placing a dam site up-stream of the reserve has been a point of contention in the past (Porter, 1981), this study was undertaken before changes in the flood regime of the area had become noticeable, and particularly devastating floods such as that of Domoina had been experienced.

Since there is a definite need for a dam in the area to ensure the future supply of water to the growing human population and industrial concern in the area, the creation of such a dam would be able to address this avenue simultaneously.

However, before such a step should be considered it would be essential to conduct an intensive study which addresses, among a wide range of others, the flood history, regime and requirements, the hydrology, and the full water requirements of the entire Umfolozi system with the aim of conserving and maintaining its current ecosystems and important ecological processes. This study should include intensive planning to eventually incorporate the changing use of land in the area and the corresponding changing demands for water in the future.

5.3.4 Management of riverine areas within the reserve

There are four practical ways in which these areas could be managed to encourage the recovery of riverine vegetation should this be required.

5.3.4.1 Browser management

The study identified that certain riverine species display decreasing tendencies under browsing pressure, and that when protected from browsing they are able to develop into large trees. Little is known about these combinations and the relative palatabilities of the riverine species present. The recovery of these species would be accelerated significantly in the absence of the responsible browsers. It is important that these browsers and their browse preferences are identified first before the management of browsers is considered.

Certain riverine communities have recovered considerably since the Domoina floods. However, a number of areas are still in a poor state of recovery. The sizes and extents of areas which have the potential of recovering have been identified in this study, based on their histories. A number of these areas should be considered for protection from browsing pressure by means of effectively placed fences and brush packing during the spring and summer months when selective browser pressure is particularly high. Areas should be selected according to limited cost required to effectively protect them and their degree of isolation from future flood events which would be responsible for removing these structures.

5.3.4.2 Augmentation of important riverine species

The augmentation of certain riverine species by planting truncheons and vegetative parts in certain areas is theoretically a viable solution to aiding the recovery of these communities. It also has the advantage of allowing for the location of these communities to be carefully selected according to certain aesthetic requirements. In order to obtain the maximum benefit from the technique, truncheons should be as large as possible and planted in the upstream areas of the reserve to ensure that they will be able to supply the reserve with as many seeds as possible once they have reached fruiting age.

The collection, transporting, planting and maintenance of these truncheons would be a costly process however, and would serve as a distinct disadvantage. In addition, truncheons would have to be placed in close proximity to the river to encourage their survival and establishment, which would make them particularly susceptible to removal by even the smallest of floods. It is suggested that the present frequency and intensity of flood events would undoubtedly be responsible for the continual removal and displacement of these truncheons and in the long term would considerably reduce the effectiveness of the technique. This approach is therefore impracticable and should only be considered as a last resort.

5.3.4.3 Alien/exotic species removals

Alien/exotic species appear to be reasonably well contained by the present control system, however, as these species are likely to become more important in the future due to their ability to rapidly and effectively colonize frequently disturbed sites, it will become necessary to coordinate and supervise the scheme more effectively. It is vitally important that the alien species threatening riverine areas are identified and their relative importances, and environmental requirements determined so that these can be incorporated into effective control programmes. This was impossible to assess during this project as most study sites were visited by the control teams on numerous occasions.

5.4 Recommendations for further research

While this study addressed a wide range of aspects regarding the structuring and dynamics of riverine vegetation, it clearly did not adequately cover a number of important aspects pertaining to the management of riverine areas. These aspects need to be addressed as separate studies.

5.4.1 The water and flood regime requirements of riverine vegetation

This study identified that riverine vegetation is structured according to a number of factors, two of these are particularly important.

- Spatial and temporal supply of water

  This is a primary structuring factor which is continually operative, and in order to conserve riverine vegetation and its basic structure therefore, it would be vitally necessary to guarantee the supply of water which corresponds with the quantities required by this vegetation at different times of the year.

- Flood regime of the Umfolozi system

  This is a secondary structuring factor, but has overriding importance when the floods are large and frequent.

The project did not investigate the corresponding changes in the demand for water and the extent to which they are occurring. It is realistic to consider that this demand is growing as the need for water, for both consumptive and agricultural purposes, is increasing accordingly. This is likely to have major implications to the structure of the riverine communities unless the essential water supply to these areas is maintained.

In order to address these problems it is necessary to study the following.

a. The water quantity and quality requirement of riverine vegetation within the reserve

These are key issues which will need adequate understanding in the future when the supply of water begins to diminish. When this drop in water level is finally identified, it will no longer be possible to determine the true requirements of the system and it will be necessary to rely on estimations. It is therefore pertinent to determine such requirements while it is still possible to do so.

As different stages of vegetation development have different water needs, it is essential to develop an understanding of the range of water requirements under normal and sub-normal rainfall conditions for the different stages. Since the water required for riverine vegetation is derived directly from the river, it can be related directly to the availability of water in the river, it would therefore be helpful to relate river water level at different times of the year with its ability to supply the required quantities of water.

b. The flood regime requirements

Due to the fact that flood regime conditions have already started to exceed those which are desired in order to maintain riverine communities in a desired state, it will be necessary to estimate the ideal conditions. These have already been considered in this study to a limited extent based on inadequate flood history records and estimates of riverine structure based on aerial photographs.

5.4.2 The upper and lower thresholds of flooding frequency/intensity

The significance of these threshold values in flooding frequency have been discussed. Once these values have been determined, the monitoring of riverine areas would be confined to recording the size and frequency of large flood events. It is suggested therefore that measuring stations should be placed on both rivers at their points of entry into the reserve. These must be able to monitor flood frequency, magnitude and duration.

5.4.3 Utilization of woody vegetation by browsers

In order to develop procedures to assist the speedy recovery of riverine areas within the scope of their ecological functioning, it is important to understand the nature and extent of woody species utilisation in these areas. A study should therefore be conducted which is designed to investigate the,

- particular species utilised,
- extent to which they are utilised,
- at what time of the year they are utilised most extensively,
- which species are responsible for their utilisation,
- what size classes are most susceptible, and
- the likely impact utilisation is likely to have on the recovery of riverine areas.

5.4.4 The impact of fire on riverine areas

Similarly, an intensive study should be conducted to determine the effects of fire on the ecology and recovery of riverine areas. This study should address the following points,

- species most susceptible to fire damage and/or complete removal by fire,
- most susceptible size classes,
- differential effects of cold and hot fires,
- the possible application of the "behave fire model" to ensure the desired levels of fire intensity,
- development of an effective and practically applicable riverine burning programme.

5.4.5 The importance of alien/exotic species on the Umfolozi rivers

Since these rivers are responsible for bringing in exotic species from their up-stream and catchment areas, they are most prone to alien/exotic infestations. A study should be conducted to address the following points,

- most problematic species in terms of reproductive potential, growth form and accessibility,
- most susceptible areas to infestations and their environmental characteristics,
- extent of alien/exotic seed banks,
- effective and practically applicable control measures for problematic species of different age classes.

Setting specific areas aside within the reserve for the sake of studying these species would be impracticable, as these areas would then act as a source for the further recruitment and augmentation of the seed banks of these species, particularly if situated in the higher reaches of the Umfolozi river. Consequently, the study of alien species should be performed in riverine areas below the reserve as much as possible.

5.4 Conclusions

Due to its own implicit weaknesses and the complexities posed by the riverine environment, structure and disturbance regime, the succession theory based approach was clearly not capable of adequately addressing the structure and dynamics of riverine areas.

Both the disturbance theory approach and the community organisation theory approach contributed considerably to the general understanding of riverine areas and their structure and dynamics. As they are integrally related, it was necessary to consider a combination of the two.

While riverine vegetation is generally structured by a combination of a number of primary determinants such as the spatial and temporal supply of water, the sizes of riverine patches, the number of resources and habitats present, the time since last disturbance (interspecific competition) and the impact of browsers and grazers, the effects of large scale floods act as secondary determinants which overshadow the applicability of these factors.

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APPENDICES 1 - 5

APPENDIX 1 Characteristics for the 9 sites and 26 transects investigated

SITE	LOCATION	ASPECT	LENGTH	ANGLE SLOPE 1	ANGLE SLOPE 2	RIVER POSITION
1 1	THOBOTHI	346 NNW	60 m	20	35	OUTSIDE BEND
1 2	THOBOTHI	349 NNW	60 m	19	29	OUTSIDE BEND
1 3	THOBOTHI	352 NNW	60 m	32	34	OUTSIDE BEND
2 1	NGOLOTSHA	336 NNW	120 m	9	9	INSIDE BEND
2 2	NGOLOTSHA	319 NNW	120 m	3	33	INSIDE BEND
2 3	NGOLOTSHA	318 NNW	120 m	6	31	STRAIGHT
3 1	MBHUZANA	026 NNE	110 m	7	15	INSIDE BEND
3 2	MBHUZANA	015 NNE	110 m	1	17	INSIDE BEND
3 3	MBHUZANA	013 NNE	90 m	20	17	STRAIGHT
4 1	SONTULI	137 SSE	60 m	24	17	STRAIGHT
4 2	SONTULI	137 SSE	60 m	30	23	STRAIGHT
4 3	SONTULI	142 SSE	60 m	30	22	STRAIGHT
5 1	THUMBU	070 ENE	60 m	2	17	OUTSIDE BEND
5 2	THUMBU	063 ENE	60 m	9	15	OUTSIDE BEND
5 3	THUMBU	065 ENE	60 m	6	13	STRAIGHT
6 1	NSELWENI	008 N	60 m	5	17	STRAIGHT
6 2	NSELWENI	009 N	90 m	5	14	STRAIGHT
6 3	NSELWENI	001 N	90 m	1	14	STRAIGHT
7 1	SIYEMBENI	115 ESE	60 m	20	11	STRAIGHT
7 2	SIYEMBENI	116 ESE	60 m	32	17	STRAIGHT
8 1	THOBOTHI WEST	168 SSE	60 m	12	14	STRAIGHT
8 2	THOBOTHI WEST	169 SSE	60 m	11	13	INSIDE BEND
8 3	THOBOTHI WEST	172 SSE	70 m	9	12	INSIDE BEND
9 1	NGOLOTSHA WEST	156 SSE	60 m	33	31	OUTSIDE BEND
9 2	NGOLOTSHA WEST	139 SE	60 m	10	28	OUTSIDE BEND
9 3	NGOLOTSHA WEST	139 SE	60 m	19	28	STRAIGHT

APPENDIX 2 Correspondence analysis numercial outputs

2.1 PCQ transects for three sampling dates

2.2 Four vegetation states for six sampling dates

2.3 PCQ transects for three different size classes

2.4 Herbaceous species abundances in 26 transects

2.5 Woody species abundances in 26 transects

APPENDIX 2.1

CORRESPONDENCE ANALYSIS FOR PCQ DATA ALL CLASSES

INERTIAS AND PERCENTAGES OF INERTIA

```
1 0.269794  71.09%  *************************************************
2 0.109727  28.91%  *****************
  --------
  0.379521
```

ROW CONTRIBUTIONS

```
--+------+-------------+--------------+-------------+
 I! NAME! QLT MAS INR!  k=1 COR CTR!  k=2 COR CTR!
--+------+-------------+--------------+-------------+
 1! 1    !1000  78   4!  -71 274   1! - 115 726   9!
 2! 2    !1000  12  19! -719 884  24!  261 116    8!
 3! 3    !1000  40   7!  236 895   8!   81 105    2!
 4! 4    !1000   6   9! -719 884  12!  261 116    4!
 5! 5    !1000  31  48! -719 884  60!  261 116   19!
 6! 6    !1000  12   6! -413 945   7! -100  55    1!
 7! 7    !1000  28   7! -304 997  10!   16   3    0!
 8! 8    !1000   3   5! -719 884   6!  261 116    2!
 9! 9    !1000   3   5! -719 884   6!  261 116    2!
10! 10   !1000  27   1! -143 963   2!   28  37    0!
11! 11   !1000   6  10! -719 884  12!  261 116    4!
12! 12   !1000  29  17! -465 992  23!   41   8    0!
13! 13   !1000   9   1!  -92 377   0! -118 623    1!
14! 14   !1000   9  14! -719 884  18!  261 116    6!
15! 15   !1000   7   7! -542 756   7!  308 244    6!
16! 16   !1000 234  37! -244 991  51!   24   9    1!
17! 17   !1000  38  32! -504 797  36!  254 203   22!
18! 18   !1000  17   9!  -92  44   1!  428 956   28!
19! 19   !1000   5  24! 1124 700  24! -736 300   25!
20! 20   !1000   7  17!  694 541  13!  638 459   27!
21! 21   !1000  86   2!   67 506   1!   66 494    3!
22! 22   !1000   5   4!  219 155   1!  512 845   12!
23! 23   !1000   5   6!  351 292   3!  547 708   15!
24! 24   !1000   2  11! 1297 962  14! -257  38    1!
25! 25   !1000  21   2!  113 452   1!  124 548    3!
26! 26   !1000  16  11!  459 827  12! -210 173    6!
27! 27   !1000  10  14!  735 974  19!  119  26    1!
28! 28   !1000   8   7!  430 587   6! -361 413   10!
29! 29   !1000   5  48! 1721 780  53!  913 220   37!
30! 30   !1000   2  19! 1721 780  21!  913 220   15!
31! 31   !1000   1  10! 1721 780  11!  913 220    7!
32! 32   !1000   0   5! 1721 780   5!  913 220    4!
33! 33   !1000   0   5! 1721 780   5!  913 220    4!
34! 34   !1000   4  42! 1721 780  46!  913 220   32!
35! 35   !1000   2  19! 1721 780  21!  913 220   15!
--+------+-------------+--------------+-------------+
```

APPENDIX 2.1 continued

```
---+------+--------------+--------------+-------------+
 36| 36   |1000   1   14| 1721 780   16|   913 220   11|
 37| 37   |1000   1   10| 1721 780   11|   913 220    7|
 38| 38   |1000   0    5| 1721 780    5|   913 220    4|
 39| 39   |1000   1   14| 1721 780   16|   913 220   11|
 40| 40   |1000   1   14| 1721 780   16|   913 220   11|
 41| 41   |1000  76   41|  266 347   20|  -365 653   92|
 42| 42   |1000   4   38| 1721 780   42|   913 220   29|
 43| 43   |1000  61   25|  140 125    4|  -371 875   77|
 44| 44   |1000   4    3| -389 555    2|   349 445    4|
 45| 45   |1000   1   10| 1721 780   11|   913 220    7|
 46| 46   |1000   1   14| 1721 780   16|   913 220   11|
 47| 47   |1000   0    5| 1721 780    5|   913 220    4|
 48| 48   |1000   3    5| -719 884    6|   261 116    2|
 49| 49   |1000  24   89|  407 116   15|-1120 884  273|
 50| 50   |1000   4   17| 1170 788   19|  -607 212   13|
 51| 51   |1000   3   16|  980 429   10|-1132 571   33|
 52| 52   |1000   1    8|  994 453    5|-1093 547   15|
 53| 53   |1000   2    8| 1185 815   10|  -565 185    5|
 54| 54   |1000   6   10| -719 884   12|   261 116    4|
 55| 55   |1000  22  145| 1533 938  191|   393  62   31|
 56| 56   |1000   1    8|  994 453    5|-1093 547   15|
 57| 57   |1000   9   14| -719 884   18|   261 116    6|
 58| 58   |1000   0    5| 1721 780    5|   913 220    4|
---+------+--------------+--------------+-------------+
```

COLUMN CONTRIBUTIONS

```
---+------+--------------+--------------+-------------+
  J| NAME| QLT MAS INR|   k=1 COR CTR|   k=2COR CTR |
---+------+--------------+--------------+-------------+
  1|  79  |1000 209 489|   894 897 618|   302 103 174|
  2|  84  |1000 161 266|   306 149  56|  -731 851 783|
  3|  86  |1000 631 244|  -374 949 326|    86  51  43|
---+------+--------------+--------------+-------------+
```

APPENDIX 2.2

ORDINATION OF TRANSITION MATRIX VALUES FOR PERIOD VS STATE

INERTIAS AND PERCENTAGES OF INERTIA

```
1 0.200672  89.47%  *********************************************
2 0.016477   7.35%  ****
3 0.007129   3.18%  **
  --------
  0.224278
```

ROW CONTRIBUTIONS

```
---+-----+-------------+--------------+--------------+
  I¦ NAME¦ QLT MAS INR¦  k=1 COR CTR¦  k=2 COR CTR¦
---+-----+-------------+--------------+--------------+
  1¦ 37  ¦ 937 111  20¦  164 671  15¦  103 267  72¦
  2¦ 54  ¦ 990 111  54¦ -269 662  40¦ -189 328 242¦
  3¦ 60  ¦ 986 111  76¦ -383 961  81¦   62  25  26¦
  4¦ 73  ¦ 858 111  15¦ -113 413   7¦ -118 444  93¦
  5¦ 83  ¦ 526 111  26¦ -146 399  12¦   82 126  46¦
  6¦ 86  ¦ 989 111 226¦  646 917 231¦ -182  72 222¦
---+-----+-------------+--------------+--------------+

---+-----+-------------+--------------+--------------+
 IS¦ NAME¦ QLT MAS INR¦  k=1 COR CTR¦  k=2 COR CTR¦
---+-----+-------------+--------------+--------------+
  7¦ 1   ¦ 991 111 338¦ -822 990 374¦   23   1   4¦
  8¦ 2   ¦ 999 111 105¦  410 792  93¦  209 207 295¦
  9¦ 3   ¦ 939 111 140¦  514 939 147¦   10   0   1¦
 10¦ 4   ¦ 226 111 566¦ -262  60  38¦  436 1661280¦
 11¦ 5   ¦ 970 111 618¦ 1080 938 647¦  202  33 275¦
---+-----+-------------+--------------+--------------+
```

COLUMN CONTRIBUTIONS

```
---+-----+-------------+--------------+--------------+
  J¦ NAME¦ QLT MAS INR¦  k=1 COR CTR¦  k=2 COR CTR¦
---+-----+-------------+--------------+--------------+
  1¦ GR  ¦ 999 440 469¦  488 995 522¦   28   3  22¦
  2¦ RE  ¦ 991  89  69¦  -83  42   3¦ -405 949 887¦
  3¦ AC  ¦ 747 153  89¦ -300 688  68¦   88  59  71¦
  4¦ FI  ¦ 978 318 374¦ -506 974 407¦   32   4  20¦
---+-----+-------------+--------------+--------------+
```

APPENDIX 2.3

CORRESPONDENCE ANALYSIS OF PCQ DATA FOR THREE PERIODS

INERTIAS AND PERCENTAGES OF INERTIA

```
 1 0.376285   23.61%  *************************************************
 2 0.313978   19.70%  *******************************************
 3 0.283458   17.78%  ***************************************
   --------
   0.973721
```

COLUMN CONTRIBUTIONS

```
-+-------------+------------+-------------+-------------+-------------+
J! NAME        ! QLT MAS INR!  k=1 COR CTR!  k=2 COR CTR!  k=3 COR CTR:
-+-------------+------------+-------------+-------------+-------------+
1! 1979 SMALL  ! 798  47 135! -856 161  92! 1329 389 266! 1061 248 188!
2! 1979 MEDIUM ! 563  36  84!-1090 315 112!  922 226  96!  285  22  10!
3! 1979 LARGE  ! 370  36  80! -853 202  69!  766 162  66!  148   6   3!
4! 1984 SMALL  ! 732 219 116!  187  41  20!  357 151  89! -675 540 352!
5! 1984 MEDIUM ! 271 112  86!  198  32  12!  201  33  14! -499 205  99!
6! 1984 LARGE  ! 654 154 124! -448 157  82! -795 493 310!   77   5   3!
7! 1986 SMALL  ! 981 178 169! 1003 663 474!    2   0   0!  695 318 302!
8! 1986 MEDIUM ! 134  77  92!  251  33  13! -319  54  25! -302  48  25!
9! 1986 LARGE  ! 516 142 114! -578 260 126! -543 229 133!  186  27  17!
-+-------------+------------+-------------+-------------+-------------+
```

APPENDIX 2.4

ORDINATION OF HERBACEOUS SPECIES QUANTITY IN 26 TRANSECTS

```
INERTIAS AND PERCENTAGES OF INERTIA
-----------------------------------

 1 0.847194  38.97%  *************************************************
 2 0.416617  19.15%  ******************************
 3 0.169835   7.75%  ****************
   xxxxxxxxxxxxxxxx
   --------
   2.183130

COLUMN CONTRIBUTIONS
--------------------

---+------+-------------+--------------+--------------+--------------+
  J! NAME! QLT MAS INR!  k=1 COR CTR!  k=2 COR CTR!  k=3 COR CTR!
---+------+-------------+--------------+--------------+--------------+
  1!  12  !  26  23  44!  -56   1   0!  291  20   9! -144   5   2!
  2!  21  ! 167  51  43! -218  26   8!  470 121  51! -189  20   9!
  3!  22  ! 236  67  62! -585 171  75!  292  43  26! -211  22  10!
  4!  23  ! 110  57  32! -315  81  18!  177  26   8!  -63   3   1!
  5!  31  ! 338  71  46! -506 178  59!  299  62  28! -373  97  46!
  6!  32  ! 434  74  37! -535 262  69!  358 117  43! -245  55  21!
  7!  33  ! 206  53  33! -346  88  21!  383 107  35! -124  11   4!
  8!  41  !  80  30  33!  374  59  14! -220  21   7!  -37   1   0!
  9!  42  !  77  32  28!  307  49  10! -224  26   7!   60   2   1!
 10!  51  ! 766  40  94!-1103 235 157! -823 131 121! 1442 401 387!
 11!  52  ! 125  29  17! -118  11   1! -359 101  17! -126  12   2!
 12!  53  !  97  27  23! -120   8   1! -304  50  11!  270  39   9!
 13!  61  ! 108  28  19!  -10   0   0! -330  72  14! -231  36   7!
 14!  62  ! 207  50  30! -100   8   2! -507 196  58!  -66   3   1!
 15!  63  ! 326  44  70! -306  27  13! -989 281 193!  249  18  13!
 16!  71  ! 667  25  62!  905 149  66!-1187 257 158!-1195 261 167!
 17!  72  ! 645  22  27!  646 154  30! -837 258  69! -795 233  65!
 18!  73  ! 523  24  19!  447 114  15! -577 190  36! -620 219  43!
 19!  81  ! 187  43  34!  388  88  21!  328  62  21!  252  37  13!
 20!  82  ! 104  44  45!  306  42  13!  376  63  28!  -15   0   0!
 21!  83  ! 155  46  27!  330  86  16!  290  66  17!   66   3   1!
 22!  91  ! 357  42  42!  798 290  87!  130   8   3!  362  60  26!
 23!  92  ! 564  43  63! 1040 340 152!  369  43  26!  759 181 117!
 24!  93  ! 401  36  69! 1141 307 151!  290  20  13!  559  74  53.
---+------+-------------+--------------+--------------+--------------+
---+------+-------------+--------------+--------------+--------------+
 JS! NAME! QLT MAS INR!  k=1 COR CTR!  k=2 COR CTR!  k=3 COR CTR!
---+------+-------------+--------------+--------------+--------------+
 25!  11  !   2  22 871!   -7   0   0!  356   1  13!   49   0   0!
 26!  13  !  12  30 265!  -83   0   1!  371   7  19!  296   5  12!
 27!  43  ! 501  28 193! -987  65  89!-1237 102 194! 2244 334 663!
---+------+-------------+--------------+--------------+--------------+
```

APPENDIX 2.5

ORDINATION OF TREE SPECIES QUANTITY IN 25 TRANSECTS

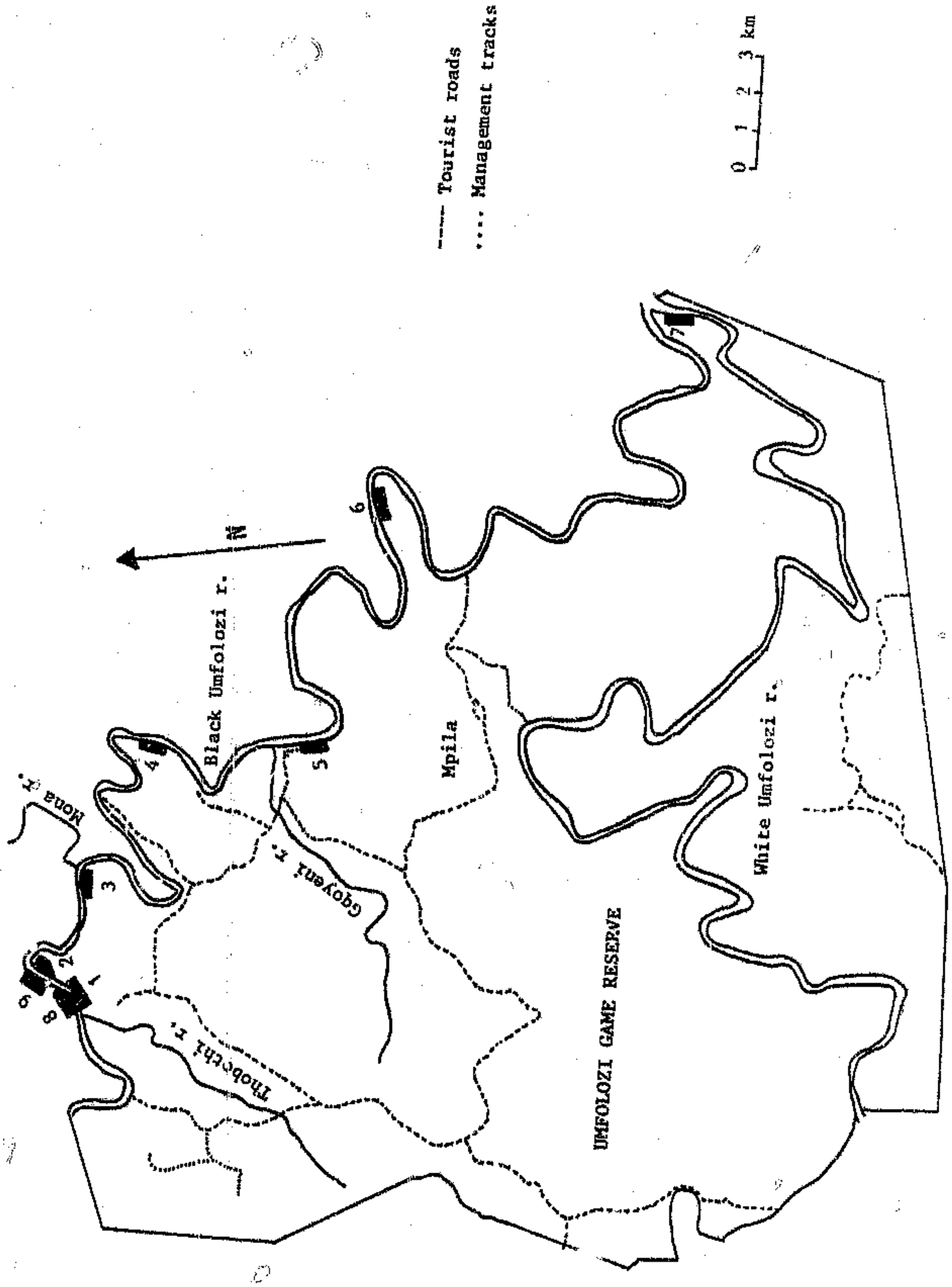
```
INERTIAS AND PERCENTAGES OF INERTIA
-----------------------------------

 1 1.124515  29.80%  ************************************************
 2 0.630558  16.71%  *********************************************
 3 0.528295  14.00%  ***********************************
   xxxxxxxxxxxxxxx
   --------
   3.773542

COLUMN CONTRIBUTIONS
--------------------

---------+--------------+--------------+--------------+--------------+
   J! NAME! QLT MAS INR!  k=1 COR CTR!  k=2 COR CTR!  k=3 COR CTR!
---+-----+--------------+--------------+--------------+--------------+
   1! 11  ! 320  55  38! -671 171  48!  625 149  46!  -29   0   0!
   2! 12  ! 193   8   4! -627 175   6!  -27   0   0! -201  18   1!
   3! 13  ! 858  92  96!-1546 675 425!  644 117  82! -485  66  55!
   4! 21  ! 411  46  54!  518  62  24!  225  12   5! 1213 338 173!
   5! 22  ! 169  72  38! -531 140  39!   11   0   0! -240  29  10!
   6! 23  ! 462  81  45! -368  65  21!  529 134  49!  742 264 113!
   7! 31  ! 580  57  46!  152   8   3!-1320 572 214!   28   0   0!
   8! 32  ! 366  52  41!   29   0   0!-1029 352 117!  201  13   5!
   9! 33  ! 343  74  34! -113   7   2! -758 333  91!  -72   3   1!
  10! 41  !  97  41  28!  359  50  10!  -82   3   1! -337  44  12!
  11! 42  ! 218  26  23!  524  84  14! -134   5   1! -649 128  28!
  12! 43  ! 241  22  14!  467  92   9! -256  28   3! -534 121  16!
  13! 51  !  39  25  26!    3   0   0! -356  32   7! -156   6   2!
  14! 52  ! 196  55  79!   52   0   0!-1003 186 120! -237  10   8!
  15! 53  ! 188  23  31! -538  61  14! -489  51  13! -596  74  22!
  16! 61  !  92   5   5!  495  49   2!   63   1   0!  279  26   1!
  17! 62  ! 240  20  12!  394  65   6!  224  21   2!  608 155  18!
  18! 63  ! 304  32  40!  393  32  10!  387  31  10! 1073 240  93!
  19! 7   ! 186  31  60!  879 104  46!  139   3   1! -766  79  45!
  20! 81  ! 547  36  22!  152  10   2!  471  96  17! 1007 441  91!
  21! 82  ! 168  26  14!  429  91   9! -342  58   6!  192  18   2!
  22! 83  ! 272  34  58!  658  66  28!  493  37  17! 1053 169  94!
  23! 91  ! 622  39  97! 1647 290 205! 1432 219 172!-1032 114 105!
  24! 92  ! 174  18  37!  935 109  30!  437  24   7! -578  42  15!
  25! 93  ! 267  32  68!  874  96  48!  514  33  18!-1047 138  89!
---+-----+--------------+--------------+--------------+--------------+
```

APPENDIX 3 Map of the Umfolozi Game Reserve showing the locations of the 9 study sites



APPENDIX 4 The distribution of species along the soil moisture gradient as percentages obtained from their distribution at 10 m intervals on 26 transects

(A) woody species in order of their distribution from the river outwards

(B) herbaceous species in alphabetical order

	DISTANCE FROM RIVER (m)											
SPECIES	10	20	30	40	50	60	70	80	90	100	110	120
Thespesia acutiloba	100	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sesbania punicea	100	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Nuxia oppositifolia	100	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Combretum erythrophyllum	100	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Salix woodii	95.2	4.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sesbania sesban	35.0	27.5	14.7	7.2	7.8	1.4	1.2	0.0	0.3	1.2	2.0	1.7
Ficus sycomorus	24.5	20.1	12.6	11.3	17.0	9.4	1.9	0.6	1.9	0.6	0.0	0.0
Cassia didymobotria	20.0	20.0	40.0	0.0	20.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Trema orientalis	16.7	33.3	8.3	8.3	16.7	16.7	0.0	0.0	0.0	0.0	0.0	0.0
Melia azedarach	9.5	57.1	14.3	9.5	4.8	4.8	0.0	0.0	0.0	0.0	0.0	0.0
Acacia gerrardii	7.1	28.6	3.6	7.1	10.7	10.7	3.6	0.0	3.6	0.0	21.4	3.6
Acacia karroo	6.9	6.2	11.7	16.6	5.5	29.7	5.5	6.2	1.4	5.5	4.1	0.7
Phyllanthus reticulatus	6.0	20.3	13.2	33.7	11.5	6.6	1.4	0.5	1.1	2.2	1.6	1.9
Ziziphus mucronata	3.1	6.3	3.1	6.3	25.0	46.9	3.1	0.0	0.0	3.1	0.0	3.1
Spirostachys africana	2.0	6.5	10.9	10.8	7.0	12.6	12.5	18.5	5.7	6.7	6.2	0.6
Dichrostachys cinerea	1.5	1.0	9.7	14.0	10.5	12.2	25.0	12.0	3.1	7.9	2.3	0.8
Sideroxylon inerme	0.0	66.7	33.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Rhus gueinzii	0.0	25.0	25.0	0.0	50.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Rhus pentheri	0.0	20.0	0.0	33.3	46.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Dovyalis caffra	0.0	18.2	32.5	49.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Acacia tortilis	0.0	15.6	34.4	3.1	0.0	9.4	3.1	9.4	0.0	9.4	15.6	0.0
Acacia schweinfurthii	0.0	12.5	12.5	37.5	12.5	0.0	25.0	0.0	0.0	0.0	0.0	0.0
Terminalia phanerophlebia	0.0	11.1	0.0	22.2	33.3	33.3	0.0	0.0	0.0	0.0	0.0	0.0
Acacia robusta	0.0	7.3	7.3	36.6	4.9	31.7	7.3	0.0	0.0	2.4	2.4	0.0
Pappea capensis	0.0	6.3	0.0	6.3	0.0	37.5	0.0	6.3	25.0	18.8	0.0	0.0
Maytenus heterophylla	0.0	5.7	0.0	20.0	34.3	22.9	2.9	14.3	0.0	0.0	0.0	0.0
Grewia villosa	0.0	5.3	11.6	22.1	16.8	6.3	4.2	3.2	1.1	3.2	4.2	22.1
Croton menyhartii	0.0	5.1	11.7	7.5	4.5	10.8	16.3	5.7	0.3	1.5	19.0	17.5
Acacia nigrescens	0.0	5.0	11.2	8.7	12.4	23.0	6.8	12.4	1.2	3.1	11.8	4.3
Commiphora neglecta	0.0	4.2	4.2	12.5	8.3	33.3	16.7	4.2	0.0	8.3	8.3	0.0
Plectroniella armata	0.0	2.7	53.8	22.3	8.7	7.6	0.5	0.0	0.0	3.3	1[illegible]	0.0
Manilkara concolor	0.0	0.0	100	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pouzolzia mixta	0.0	0.0	50.0	50.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Euphorbia tirucalli	0.0	0.0	22.2	22.2	11.1	44.4	0.0	0.0	0.0	0.0	0.0	0.0
Schotia capitata	0.0	0.0	16.7	0.0	16.7	50.0	0.0	0.0	0.0	0.0	0.0	16.7
Grewia flavescens	0.0	0.0	12.5	37.5	12.5	6.3	0.0	0.0	0.0	0.0	6.3	25.0
Grewia monticola	0.0	0.0	8.7	34.8	8.7	21.7	13.0	4.3	0.0	0.0	0.0	8.7
Capparis tomentosa	0.0	0.0	8.0	4.0	8.0	4.0	0.0	0.0	4.0	12.0	12.0	48.0
Azima tetracantha	0.0	0.0	7.1	5.5	7.5	16.9	30.5	7.7	0.0	4.3	8.2	12.3
Maytenus senegalensis	0.5	0.0	1.6	7.6	1.1	17.4	16.8	7.1	32.1	15.8	0.0	0.0
Strychnos madagascariensis	0.0	0.0	0.0	100	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cussonia paniculata	0.0	0.0	0.0	50.0	0.0	50.0	0.0	0.0	0.0	0.0	0.0	0.0
Sclerocarya birrea	0.0	0.0	0.0	42.9	14.3	0.0	0.0	28.6	0.0	14.3	0.0	0.0
Ehretia amoena	0.0	0.0	0.0	34.6	11.5	19.2	15.4	3.8	0.0	0.0	7.7	7.7
Grewia occidentalis	0.0	0.0	0.0	25.0	50.0	0.0	0.0	0.0	0.0	0.0	0.0	25.0
Maerua rosmarinoides	0.0	0.0	0.0	17.6	52.9	0.0	17.6	0.0	0.0	0.0	0.0	11.8
Grewia bicolor	0.0	0.0	0.0	14.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	85.7
Schotia brachypetala	0.0	0.0	0.0	8.3	25.0	50.0	8.3	0.0	0.0	0.0	0.0	8.3
Dombeya rotundifolia	0.0	0.0	0.0	0.0	50.0	50.0	0.0	0.0	0.0	0.0	0.0	0.0
Ehretia rigida	0.0	0.0	0.0	0.0	50.0	0.0	0.0	50.0	0.0	0.0	0.0	0.0
Euclea natalensis	0.0	0.0	0.0	0.0	25.0	25.0	0.0	50.0	0.0	0.0	0.0	0.0
Tarchonanthus camphoratus	0.0	0.0	0.0	0.0	9.1	0.0	0.0	0.0	0.0	0.0	9.1	81.8
Capparis fascicularis	0.0	0.0	0.0	0.0	0.9	0.0	0.0	0.0	0.0	69.6	23.5	6.1
Ozoroa engleri	0.0	0.0	0.0	0.0	0.0	100	0.0	0.0	0.0	0.0	0.0	0.0
Dombeya cymosa	0.0	0.0	0.0	0.0	0.0	33.3	0.0	0.0	0.0	0.0	0.0	66.7
Diospyros whyteana	0.0	0.0	0.0	0.0	0.0	25.0	20.0	55.0	0.0	0.0	0.0	0.0
Boscia foetida	0.0	0.0	0.0	0.0	0.0	16.7	0.0	0.0	0.0	0.0	66.7	16.7
Boscia albitrunca	0.0	0.0	0.0	0.0	0.0	5.0	0.0	0.0	0.0	30.9	59.1	5.0
Euclea schimperi	0.0	0.0	0.0	0.0	0.0	0.0	100	0.0	0.0	0.0	0.0	0.0
Combretum apiculatum	0.0	0.0	0.0	0.0	0.0	0.0	0.0	100	0.0	0.0	0.0	0.0
Berchemia zeyheri	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	75.0	25.0	0.0
Cussine transvaalensis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	66.7	33.3

SPECIES	DISTANCE FROM RIVER (m)											
	10	20	30	40	50	60	70	80	90	100	110	120
Asclepias fruticosa	47.7	37.2	2.2	2.2	0.0	6.5	2.2	0.0	2.2	0.0	0.0	0.0
Asclepias sp.	0.0	0.0	41.2	0.0	0.0	20.6	0.0	38.2	0.0	0.0	0.0	0.0
Asparagus macowanii	0.0	0.0	100	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Aster squamatus	46.5	44.9	2.6	1.6	4.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Asytasia natalensis	0.0	0.0	0.0	0.0	0.0	100	0.0	0.0	0.0	0.0	0.0	0.0
Abutilon angulatum	0.0	11.3	43.5	11.3	0.0	11.3	0.0	22.6	0.0	0.0	0.0	0.0
Abutilon austro-africanum	2.9	5.4	5.8	5.8	0.0	11.2	16.1	14.0	2.9	16.5	16.5	2.9
Abutilon grandiflorum	0.0	0.0	29.9	10.4	0.0	0.0	20.9	19.4	0.0	0.0	19.4	0.0
Abutilon sonneratium	0.0	0.0	0.0	0.0	0.0	0.0	0.0	50.0	0.0	50.0	0.0	0.0
Acalypha glabrata	0.0	100	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Acalypha peduncularis	100	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Acalypha sp.	0.0	33.3	66.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Acanthospermum glabrum	50.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	50.0	0.0	0.0
Achyranthes aspera	3.0	6.2	9.2	12.2	16.9	16.9	15.5	3.0	12.5	4.6	0.0	0.0
Achytopsis leptostachya	0.0	0.0	0.0	0.0	0.0	100	0.0	0.0	0.0	0.0	0.0	0.0
Acokanthera oblongifolia	0.0	0.0	0.0	100	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ageratum houstonianum	0.0	0.0	50.0	50.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Andropogon eucomus	75.0	0.0	0.0	0.0	0.0	25.0	0.0	0.0	0.0	0.0	0.0	0.0
Aneilema dregeanum	0.0	0.0	0.0	0.0	0.0	100	0.0	0.0	0.0	0.0	0.0	0.0
Argyrolobium sp.	0.0	100	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Aristida congesta	0.0	7.3	14.2	6.5	4.9	16.9	16.9	12.5	4.6	3.0	12.5	0.0
Aristida diffusa	0.0	0.0	0.0	0.0	0.0	0.0	79.4	20.6	0.0	0.0	0.0	0.0
Barleria crossandriformis	0.0	0.0	35.0	65.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Barleria elegans	0.0	0.0	26.7	9.3	0.0	0.0	0.0	18.7	0.0	9.3	0.0	36.0
Bidens bipinnata	8.0	2.8	16.4	27.2	5.6	8.0	0.0	2.8	10.8	13.2	0.0	5.2
Bidens biternata	0.0	0.0	0.0	0.0	25.9	74.1	0.0	0.0	0.0	0.0	0.0	0.0
Bidens pilosa	0.0	0.0	0.0	0.0	74.1	25.9	0.0	0.0	0.0	0.0	0.0	0.0
Blepharis integrifolia	0.0	0.0	0.0	0.0	35.0	0.0	0.0	0.0	0.0	0.0	65.0	0.0
Blumea caffra	60.5	23.8	15.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Botriochloa bladhii	0.0	0.0	0.0	0.0	100	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Botriochloa insculpta	7.4	17.0	4.6	0.0	7.1	14.1	11.7	7.4	7.1	18.7	2.5	2.5
Brachiaria dictyoneura	66.7	0.0	0.0	0.0	33.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Brachiaria eruciformis	0.0	0.0	0.0	8.6	8.6	0.0	8.6	33.3	16.0	16.0	8.6	0.0
Bulbostylus hispidula	11.5	54.1	11.5	11.5	0.0	11.5	0.0	0.0	0.0	0.0	0.0	0.0
Cyperus articulatus	100	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cyperus difformus	51.9	48.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cyperus esculentus	40.2	37.8	0.9	1.6	5.7	8.1	4.9	0.0	0.0	0.9	0.0	0.0
Cyperus immensus	47.7	47.7	0.8	0.0	1.6	0.8	0.0	1.6	0.0	0.0	0.0	0.0
Cyperus laevigatus	51.7	46.6	1.1	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cyperus rotundus	0.0	0.0	0.0	100	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cyperus sexangularis	44.7	43.8	2.8	2.8	2.8	0.8	0.4	1.6	0.4	0.0	0.0	0.0
Cyphostemma sp.	0.0	0.0	0.0	100	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cassia capensis	6.2	53.1	40.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cassia floribunda	11.6	30.1	12.0	16.4	22.6	2.4	2.4	0.0	0.0	0.0	2.4	0.0
Cenchrus ciliaris	3.0	11.1	17.0	11.4	10.2	9.9	2.6	9.0	8.9	8.0	8.1	0.9
Centella asiatica	33.3	33.3	33.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ceratotheca triloba	10.3	0.0	38.2	20.6	10.3	0.0	0.0	0.0	10.3	10.3	0.0	0.0
Chamaesyce hirta	0.0	0.0	0.0	100	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cheilanthes involuta	0.0	0.0	100	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Chenopodium album	6.4	9.2	18.8	9.2	21.6	25.2	3.2	0.0	0.0	3.2	3.2	0.0
Chenopodium ambrosiodes	0.0	36.0	18.7	26.7	0.0	9.3	0.0	9.3	0.0	0.0	0.0	0.0
Chenopodium carinatum	16.1	23.0	0.0	23.0	14.9	23.0	0.0	0.0	0.0	0.0	0.0	0.0
Chenopodium opulifolium	2.3	4.6	7.0	17.5	31.1	37.4	0.0	0.0	0.0	0.0	0.0	0.0
Chloris gayana	8.0	13.2	8.8	19.8	18.9	8.7	2.9	2.3	7.4	10.0	0.0	0.0
Chloris virgata	11.3	6.1	12.2	6.1	6.1	23.5	6.1	0.0	11.3	11.3	6.1	0.0
Chromolaena odorata	0.0	0.0	0.0	12.5	12.5	50.0	12.5	0.0	12.5	0.0	0.0	0.0
Cissampelos mucronata	15.9	44.1	7.6	15.9	8.2	4.1	0.0	0.0	4.1	0.0	0.0	0.0
Cissus rotundifolia	0.0	7.3	12.5	16.8	27.1	36.3	0.0	0.0	0.0	0.0	0.0	0.0
Clerodendrum glabrum	0.0	0.0	0.0	100	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Clutia sp.	0.0	0.0	0.0	50.0	0.0	0.0	0.0	0.0	0.0	0.0	50.0	0.0
Coddia rudis	0.0	0.0	0.0	0.0	0.0	100	0.0	0.0	0.0	0.0	0.0	0.0
Commelina benghalensis	0.0	0.0	0.0	33.3	66.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0

SPECIES	DISTANCE FROM RIVER (m)											
	10	20	30	40	50	60	70	80	90	100	110	120
Commelina modesta	0.0	0.0	100	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Commicarpus africanus	0.0	0.0	0.0	0.0	0.0	26.7	30.0	30.0	13.3	0.0	0.0	0.0
Commicarpus fallacissimus	0.0	0.0	0.0	0.0	0.0	0.0	100	0.0	0.0	0.0	0.0	0.0
Commicarpus pentandrus	0.0	0.0	0.0	16.7	72.5	10.8	0.0	0.0	0.0	0.0	0.0	0.0
Commicarpus sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	65.0	35.0	0.0
Convolvulus farinosus	0.0	33.3	66.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Conyza bonariensis	19.9	23.7	23.7	17.6	2.4	6.3	3.7	1.3	0.0	1.3	0.0	0.0
Conyza scabrida	100	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Conyza sumatrensis	26.5	35.2	16.8	5.4	2.2	9.5	2.2	1.1	0.0	1.1	0.0	0.0
Corbichonia decumbens	0.0	0.0	0.0	100	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Corchorus tridens	41.2	38.2	0.0	0.0	0.0	20.6	0.0	0.0	0.0	0.0	0.0	0.0
Corchorus trilocularis	15.6	4.6	8.9	4.3	15.6	35.4	2.3	4.3	0.0	6.6	2.3	0.0
Crossandra fruticulosa	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	42.6	57.4
Crotalaria lanceolata	6.9	26.5	0.0	46.1	13.7	0.0	0.0	0.0	0.0	0.0	0.0	6.9
Crotalaria monteiroi	0.0	0.0	100	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Crotalaria pallida	15.4	16.4	9.5	5.2	10.2	17.4	13.3	6.1	1.1	1.1	3.2	1.1
Crotalaria sp.	0.0	0.0	0.0	0.0	0.0	50.0	50.0	0.0	0.0	0.0	0.0	0.0
Crotalia monteiroi	50.0	50.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cryptolepsis oblongifolia	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	100	0.0
Cryptolepsis obtusa	23.6	26.1	26.1	9.6	12.1	2.5	0.0	0.0	0.0	0.0	0.0	0.0
Cymbopogon excavatus	30.0	30.0	30.0	0.0	0.0	0.0	10.0	0.0	0.0	0.0	0.0	0.0
Cynodon dactylon	12.8	13.5	13.5	15.2	10.7	11.7	5.4	4.6	5.4	4.6	1.4	1.1
Cynodon nlemfuensis	5.3	13.4	18.9	13.6	16.7	8.3	4.2	2.0	10.1	7.5	0.0	0.0
Dactyloctenium australe	5.4	17.8	16.8	15.5	15.5	18.4	3.3	2.5	3.3	1.4	0.0	0.0
Dactyloctenium sp.	0.0	6.9	13.7	26.5	46.1	0.0	6.9	0.0	0.0	0.0	0.0	0.0
Datura stramonium	12.8	28.9	13.3	16.1	12.8	12.8	3.3	0.0	0.0	0.0	0.0	0.0
Desmodium incanum	100	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Digitaria debilis	50.2	30.1	10.0	4.8	4.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Digitaria didactyla	38.2	0.0	0.0	20.6	0.0	0.0	0.0	0.0	0.0	20.6	20.6	0.0
Digitaria eleusine	8.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	8.8	16.3	66.3
Digitaria eriantha	17.2	4.5	13.4	13.4	0.0	8.9	4.5	0.0	12.7	17.2	0.0	8.3
Digitaria natalensis	60.6	39.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Dinebra retroflexa	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	50.0	50.0	0.0	0.0
Diplachne fusca	50.0	24.1	13.0	13.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Echinochloa colona	0.0	50.0	0.0	0.0	0.0	50.0	0.0	0.0	0.0	0.0	0.0	0.0
Enneapogon cenchroides	0.0	15.1	15.1	0.0	31.4	38.4	0.0	0.0	0.0	0.0	0.0	0.0
Enneapogon sp.	0.0	17.1	34.1	17.1	0.0	0.0	0.0	31.7	0.0	0.0	0.0	0.0
Equisetum sp.	68.1	17.4	6.0	8.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Eragrostis aspera	0.0	25.9	0.0	48.1	25.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Eragrostis cilianensis	0.0	20.6	0.0	20.6	38.2	20.6	0.0	0.0	0.0	0.0	0.0	0.0
Eragrostis ciliaris	17.1	48.8	0.0	17.1	0.0	0.0	17.1	0.0	0.0	0.0	0.0	0.0
Eragrostis curvula	13.1	9.9	7.1	13.6	10.0	7.8	11.4	4.9	3.8	7.6	7.0	3.8
Eragrostis gummiflua	100	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Eragrostis inamoena	0.0	0.0	0.0	100	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Eragrostis lappula	100	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Eragrostis plana	100	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Eragrostis racemosa	0.0	0.0	50.0	50.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Eragrostis sp.	0.0	0.0	100	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Eragrostis superba	0.0	5.6	7.7	7.6	8.9	9.8	11.9	15.0	7.6	6.5	9.7	9.7
Eriochloa meyerana	79.4	0.0	0.0	0.0	20.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Eriosema psoraleoides	18.2	8.8	31.8	36.5	4.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Fimbristylis ferruginea	69.1	20.6	10.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Flaveria bidentis	0.0	14.9	14.9	0.0	0.0	0.0	0.0	27.7	42.6	0.0	0.0	0.0
Gisekia africana	0.0	0.0	0.0	0.0	25.9	24.7	0.0	49.4	0.0	0.0	0.0	0.0
Glycine wightii	0.9	14.2	14.2	27.1	30.1	6.3	0.0	4.5	0.0	2.7	0.0	0.0
Gomphrena celosioides	0.0	10.7	20.6	16.0	10.7	0.0	5.3	15.3	0.0	5.3	10.7	5.3
Heliotropium ovalifolium	20.6	38.2	0.0	0.0	0.0	0.0	20.6	0.0	0.0	0.0	20.6	0.0
Heliotropium steudneri	0.0	100	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Hemarthria altissima	100	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Heteropogon contortus	0.0	0.0	100	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Hibiscus cannabinus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	100	0.0	0.0	0.0	0.0
Hibiscus dongolensis	4.5	0.0	21.7	13.4	21.7	13.4	0.0	0.0	4.5	8.3	0.0	12.7

SPECIES	DISTANCE FROM RIVER (m)											
	10	20	30	40	50	60	70	80	90	100	110	120
Hibiscus micranthus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	100	0.0
Hibiscus pusillus	0.0	4.8	8.8	0.0	13.6	36.1	0.0	0.0	0.0	4.8	13.6	18.4
Hibiscus sp.	0.0	0.0	0.0	0.0	0.0	0.0	100	0.0	0.0	0.0	0.0	0.0
Hyparrhenia filipendula	0.0	20.6	0.0	20.6	0.0	0.0	0.0	0.0	0.0	58.8	0.0	0.0
Hypertelis sp.	0.0	0.0	0.0	100	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Imperata cylindrica	100	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Indigofera costata	4.7	0.0	0.0	4.7	13.4	9.4	26.8	22.1	4.7	0.0	4.7	9.4
Indigofera spicata	1.7	16.4	19.9	14.9	14.9	5.2	5.2	5.0	6.7	3.2	5.0	1.7
Ipomea crassipes	8.5	14.0	25.5	18.7	15.5	3.9	5.4	8.5	0.0	0.0	0.0	0.0
Ipomea magnusiana	0.0	0.0	0.0	0.0	0.0	100	0.0	0.0	0.0	0.0	0.0	0.0
Ipomea plebeia	7.4	0.0	7.4	0.0	7.4	0.0	13.7	21.1	0.0	35.8	7.4	0.0
Ipomea sp.	16.7	0.0	16.7	19.7	16.3	10.3	13.3	0.0	0.0	3.4	3.4	0.0
Ipomea wightii	0.0	18.9	18.9	33.6	9.8	18.9	0.0	0.0	0.0	0.0	0.0	0.0
Jasminum stenolobum	0.0	100	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Juncus exsertus	45.9	31.8	22.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Juncus fraussii	100	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Justicia flava	5.5	0.0	26.0	21.3	0.0	31.5	15.7	0.0	0.0	0.0	0.0	0.0
Justicia odora	0.0	0.0	100	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Justicia protracta	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	40.3	59.7
Justicia sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	100
Kyphocarpa angustifolia	0.0	0.0	0.0	0.0	0.0	0.0	50.0	50.0	0.0	0.0	0.0	0.0
Lantana camara	0.0	0.0	50.0	50.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Lantana rugosa	0.0	0.0	0.0	100	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Leersia hexandra	100	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Lepidagathis scabra	0.0	0.0	0.0	0.0	0.0	50.0	0.0	0.0	0.0	0.0	50.0	0.0
Leucas glabrata	0.0	50.0	0.0	0.0	50.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Leucas martinicensis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	100	0.0	0.0
Leucas sp.	100	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Lippia javanica	14.4	7.2	21.6	13.4	14.4	21.6	0.0	0.0	7.2	0.0	0.0	0.0
Lycium acutifolium	0.0	0.0	0.0	17.3	17.3	16.0	0.0	16.0	0.0	0.0	33.3	0.0
Malvastrum coromandelianu	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	100
Mariscus capensis	50.0	0.0	50.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Melhania didyma	0.0	0.0	0.0	100	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Melhania forbesii	0.0	0.0	0.0	100	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Melhania suluensis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	13.0	0.0	13.0	74.1
Momordica balsamina	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	60.6	39.4	0.0
Momordica involucrata	50.0	0.0	0.0	0.0	50.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Monsonia sp.	0.0	21.2	39.4	39.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Nesaea radicans	100	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Nidorella resedifolia	17.1	0.0	15.9	0.0	17.1	25.6	8.5	0.0	0.0	15.9	0.0	0.0
Ocimum canum	0.0	0.0	0.0	34.1	0.0	65.9	0.0	0.0	0.0	0.0	0.0	0.0
Ocimum urticifolium	8.9	1.9	14.6	16.7	5.7	9.2	1.9	8.9	17.8	3.5	3.8	7.3
Oenothera parodiana	0.0	35.0	65.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Panicum deustum	18.3	6.1	16.2	28.7	16.5	4.3	0.0	0.0	0.0	4.0	6.1	0.0
Panicum maximum	4.2	9.4	11.0	14.4	16.6	18.6	8.2	7.1	4.3	3.7	3.1	1.3
Paspalum dilatatum	31.0	34.0	13.7	7.1	3.6	7.1	0.0	0.0	0.0	3.6	0.0	0.0
Paspalum paspalodes	53.7	18.0	17.1	6.7	2.0	0.5	1.5	0.0	0.0	0.5	0.0	0.0
Paspalum scrobiculatum	18.6	14.8	18.6	22.4	0.0	3.8	0.0	3.8	0.0	3.8	7.1	7.1
Paspalum urvillei	42.5	20.8	21.2	6.2	6.2	3.1	0.0	0.0	0.0	0.0	0.0	0.0
Pavonia burchellii	0.0	0.0	0.0	0.0	50.0	0.0	0.0	32.5	0.0	17.5	0.0	0.0
Perotis patens	65.0	35.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Phragmites australe	49.1	16.2	3.1	10.0	11.5	8.4	0.8	0.0	0.8	0.0	0.0	0.0
Pluchea dioscoridis	23.4	23.2	18.9	17.9	6.9	4.3	1.4	1.4	0.0	0.0	2.6	0.0
Polygala amatymbica	0.0	0.0	0.0	0.0	0.0	11.5	0.0	32.8	0.0	0.0	11.5	44.3
Polygonum lapathifolium	49.2	13.2	35.3	2.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pogonarthria squarrosa	0.0	0.0	0.0	0.0	0.0	0.0	50.0	0.0	50.0	0.0	0.0	0.0
Pouzolzia mixta	0.0	0.0	0.0	0.0	100	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Priva africana	0.0	0.0	0.0	100	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Priva cordifolia	0.0	12.7	25.5	23.6	12.7	12.7	0.0	0.0	0.0	12.7	0.0	0.0
Protasparagus natalensis	0.0	0.0	0.0	9.4	3.6	16.9	31.2	29.6	0.0	1.9	7.5	0.0
Protasparagus setaceus	0.0	0.0	0.0	21.3	7.4	21.3	35.1	14.9	0.0	0.0	0.0	0.0
Pteris vittata	100	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

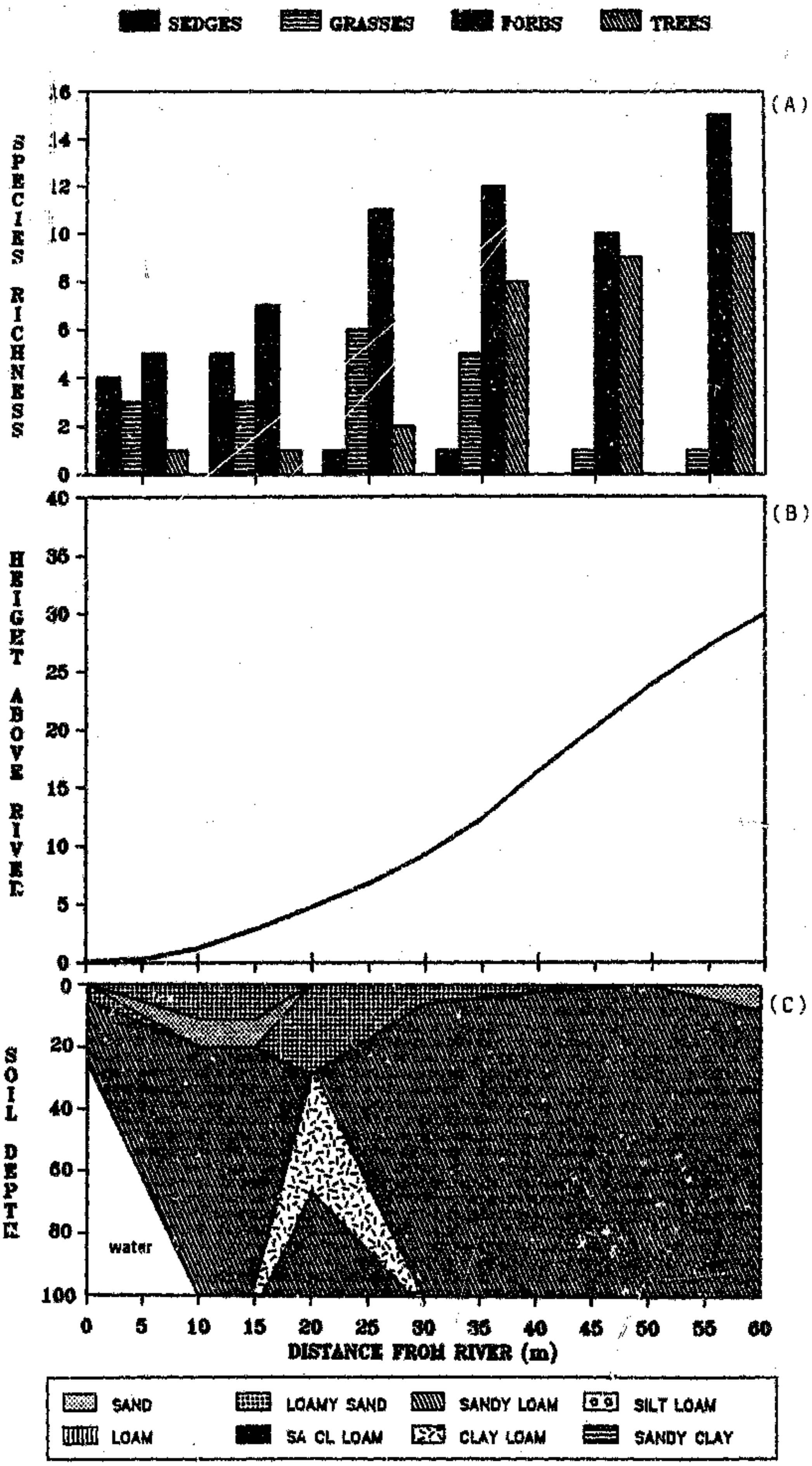
SPECIES	DISTANCE FROM RIVER (m)											
	10	20	30	40	50	60	70	80	90	100	110	120
Pycreus mundii	100	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pycreus polystachyos	58.0	24.4	15.7	1.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Rhoicissus tridentata	0.0	0.0	0.0	0.0	0.0	25.9	0.0	74.1	0.0	0.0	0.0	0.0
Rhynchelytrum repens	1.3	16.2	25.8	10.2	10.2	9.7	5.4	7.2	3.0	5.4	3.0	3.0
Rhynchosia minima	2.5	19.5	5.1	12.3	14.4	0.0	2.5	17.0	7.2	17.0	2.5	0.0
Rhynchosia sp.	0.0	0.0	6.1	23.5	23.5	0.0	0.0	40.9	0.0	0.0	0.0	6.1
Rhynchosia totta	0.0	0.0	0.0	100	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Richardia brasiliensis	4.4	6.3	8.5	17.0	17.4	14.5	2.2	12.6	8.5	6.3	2.2	0.0
Ricinus communis	19.0	16.2	10.4	16.2	14.7	6.4	5.9	1.5	5.3	4.3	0.0	0.0
Ruellia cordata	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.8	55.8	38.3
Ruellia patula	0.0	0.0	0.0	50.0	0.0	50.0	0.0	0.0	0.0	0.0	0.0	0.0
Sansevieria hyacinthoides	0.0	0.0	17.5	0.0	0.0	32.5	50.0	0.0	0.0	0.0	0.0	0.0
Scadoxus puniceus	0.0	0.0	0.0	0.0	50.0	0.0	0.0	50.0	0.0	0.0	0.0	0.0
Schkuhria pinnata	1.8	1.8	1.8	6.7	10.5	10.5	8.5	13.6	15.4	15.4	6.7	5.1
Senecio madagascariensis	54.1	11.5	11.5	0.0	11.5	0.0	0.0	11.5	0.0	0.0	0.0	0.0
Sesbania bispinosa	26.0	20.3	16.4	12.4	13.8	4.3	2.6	2.8	0.0	0.0	0.0	1.4
Setaria chevalieri	30.3	60.0	4.8	0.0	0.0	4.8	0.0	0.0	0.0	0.0	0.0	0.0
Setaria sphacelata	16.7	8.3	16.7	0.0	8.3	8.3	0.0	0.0	8.3	16.7	16.7	0.0
Setaria sp.	64.1	0.0	0.0	0.0	0.0	35.9	0.0	0.0	0.0	0.0	0.0	0.0
Sida cordifolia	0.0	0.0	0.0	0.0	50.0	50.0	0.0	0.0	0.0	0.0	0.0	0.0
Sida dregei	10.1	0.0	10.1	0.0	0.0	10.1	10.1	10.1	10.1	18.8	20.3	0.0
Sida rhombifolia	50.0	0.0	50.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sida sp.	0.0	18.2	0.0	36.4	9.1	27.3	0.0	0.0	0.0	0.0	9.1	0.0
Solanum geniculatum	0.0	0.0	0.0	0.0	25.9	0.0	0.0	0.0	0.0	0.0	0.0	74.1
Solanum mauritianum	7.2	7.2	14.4	14.4	21.6	27.8	7.2	0.0	0.0	0.0	0.0	0.0
Solanum nigrum	0.0	0.0	100	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Solanum panduriforme	6.8	15.2	14.9	14.6	10.4	18.8	7.2	2.4	3.8	3.6	2.4	0.0
Solanum sp.	0.0	0.0	50.0	0.0	0.0	0.0	0.0	50.0	0.0	0.0	0.0	0.0
Sonchus sp.	62.2	9.5	0.0	18.9	9.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sphedamnocarpus sp.	14.6	14.2	8.8	11.7	0.0	14.2	8.3	8.8	10.8	5.8	2.9	0.0
Sporobolus nitens	11.3	11.3	0.0	11.3	11.3	32.3	0.0	0.0	0.0	0.0	22.6	0.0
Sporobolus pyramidalis	14.1	17.6	11.4	11.2	13.0	6.6	11.1	2.9	4.6	4.7	1.8	1.0
Striga elegans	0.0	0.0	100	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Stylosanthes fruticosa	0.0	0.0	100	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Tagetes minuta	12.7	23.6	12.7	25.5	12.7	0.0	0.0	0.0	0.0	12.7	0.0	0.0
Talinum arnotii	0.0	0.0	0.0	65.0	35.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Talinum caffrum	0.0	0.0	0.0	100	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Themeda triandra	0.0	0.0	0.9	7.0	16.3	21.7	10.3	20.7	0.0	1.7	8.5	12.9
Thunbergia neglecta	0.0	0.0	0.0	0.0	0.0	35.0	65.0	0.0	0.0	0.0	0.0	0.0
Tragia rupestris	0.0	0.0	0.0	0.0	50.0	50.0	0.0	0.0	0.0	0.0	0.0	0.0
Tragus berteronianus	4.5	4.5	12.8	10.9	17.0	17.3	6.7	4.5	4.5	0.0	17.3	0.0
Tribulus terrestris	0.0	0.0	11.3	27.4	33.1	11.3	0.0	11.3	5.6	0.0	0.0	0.0
Tridax procumbens	0.0	14.6	14.6	0.0	14.6	14.6	41.7	0.0	0.0	0.0	0.0	0.0
Typha capensis	100	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Urochloa mosambicensis	3.5	4.0	10.1	7.0	11.4	14.9	13.6	15.2	3.1	6.1	6.6	4.4
Verbena bonariensis	38.7	11.3	27.4	0.0	5.6	11.3	0.0	0.0	0.0	0.0	5.6	0.0
Vinca rosea	14.9	29.8	0.0	27.7	0.0	0.0	0.0	0.0	27.7	0.0	0.0	0.0
Waltheria indica	0.0	0.0	0.0	0.0	100	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Waltheria sp.	0.0	0.0	0.0	100	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Withania somnifera	0.0	0.0	0.0	0.0	0.0	100	0.0	0.0	0.0	0.0	0.0	0.0
Xanthium strumarium	36.6	29.7	3.5	13.4	0.0	0.0	0.0	0.0	6.9	9.9	0.0	0.0
Zantedeschia rehmanii	0.0	0.0	0.0	0.0	0.0	0.0	74.1	25.9	0.0	0.0	0.0	0.0
Zinnia peruviana	0.0	0.0	50.0	50.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

APPENDIX 5 Sites 1 to 27 displaying

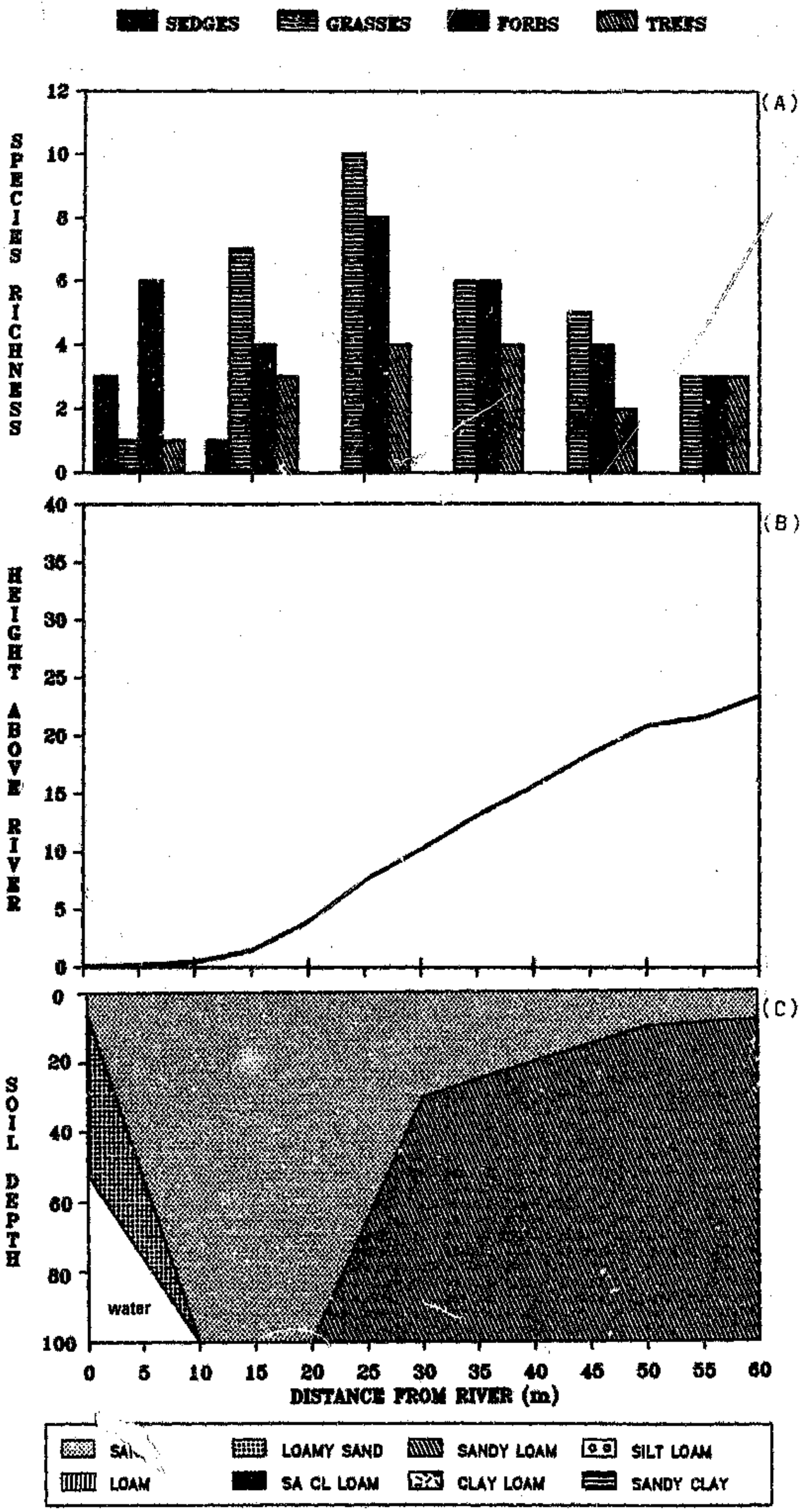
(A) direct gradient analysis of the responses of sedges, grasses, forbs and trees to the logical moisture gradient

(B) their slope profiles

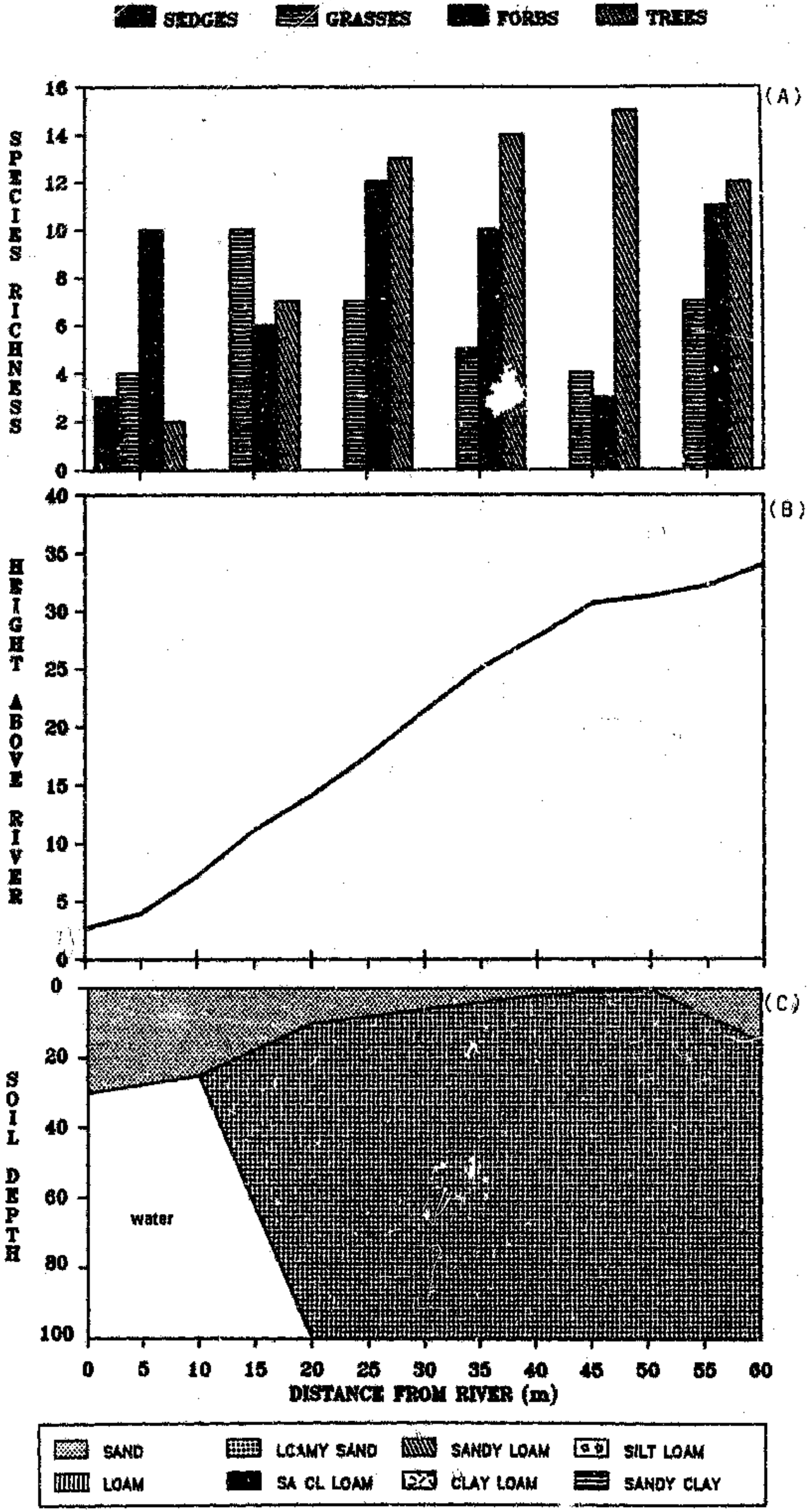
(C) their soil characteristics in terms of different soil texture classes



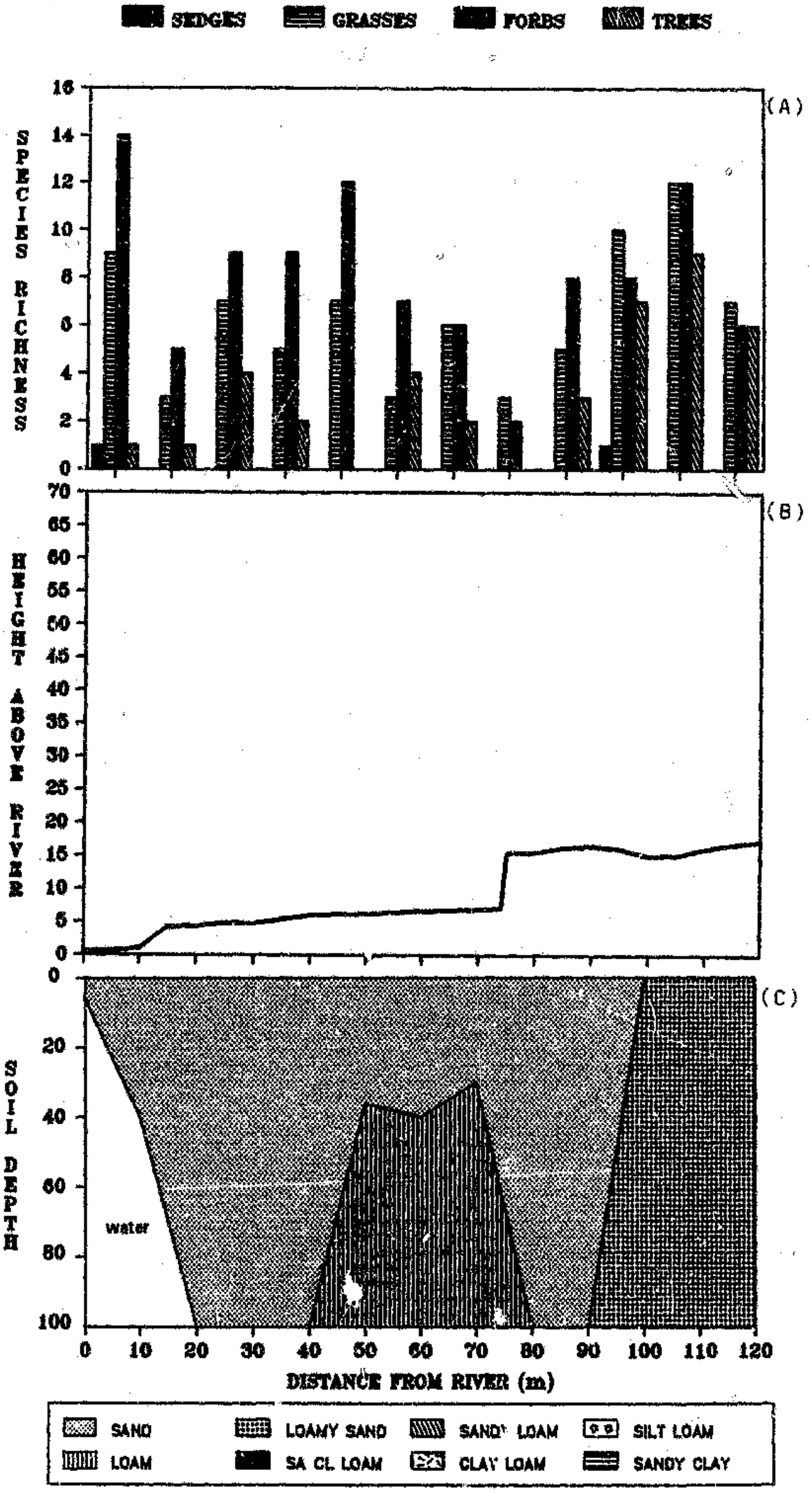
1 SITE 1 1 THOBOTHI



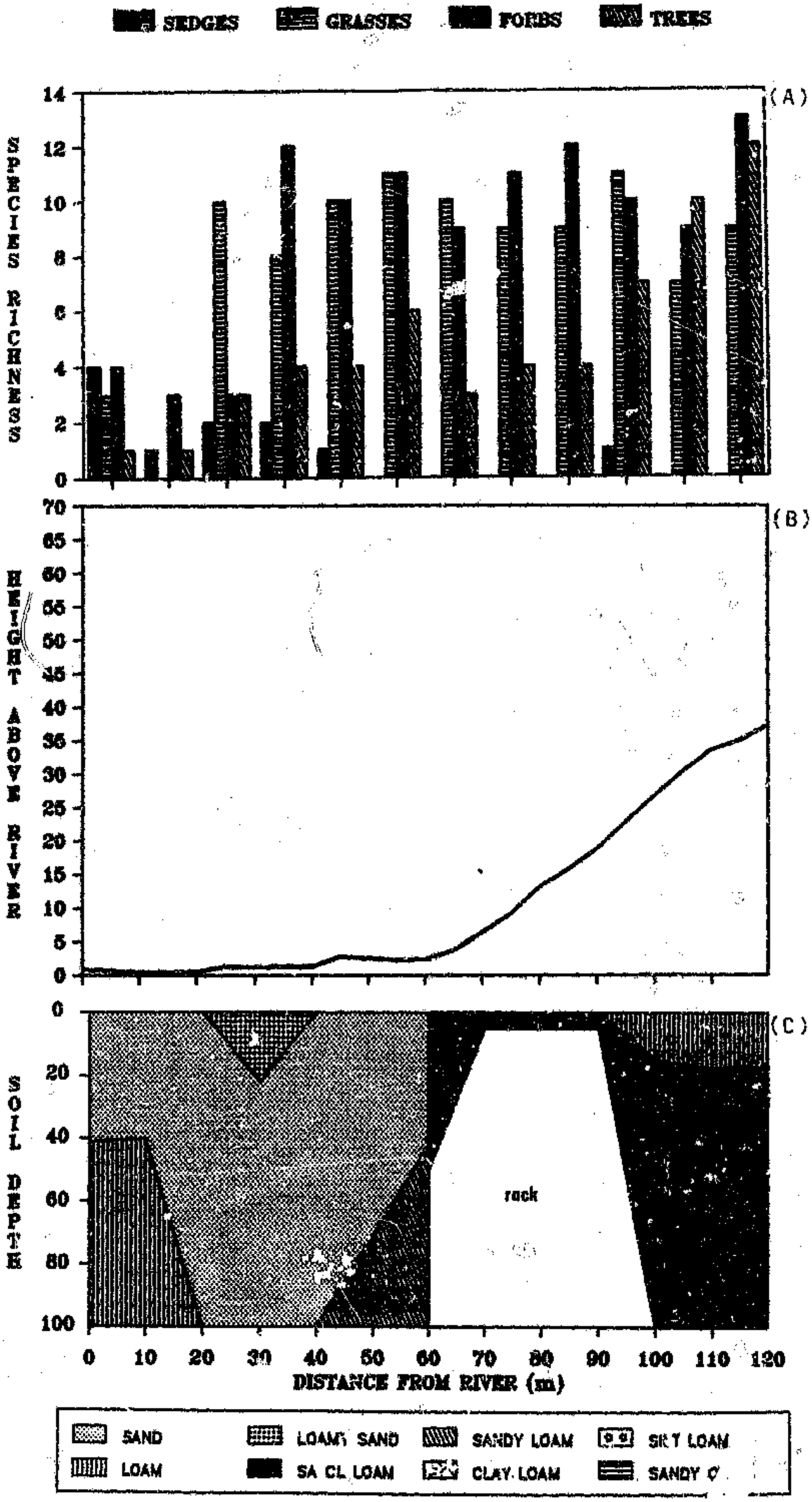
2 SITE 1 2 THOBOTHI



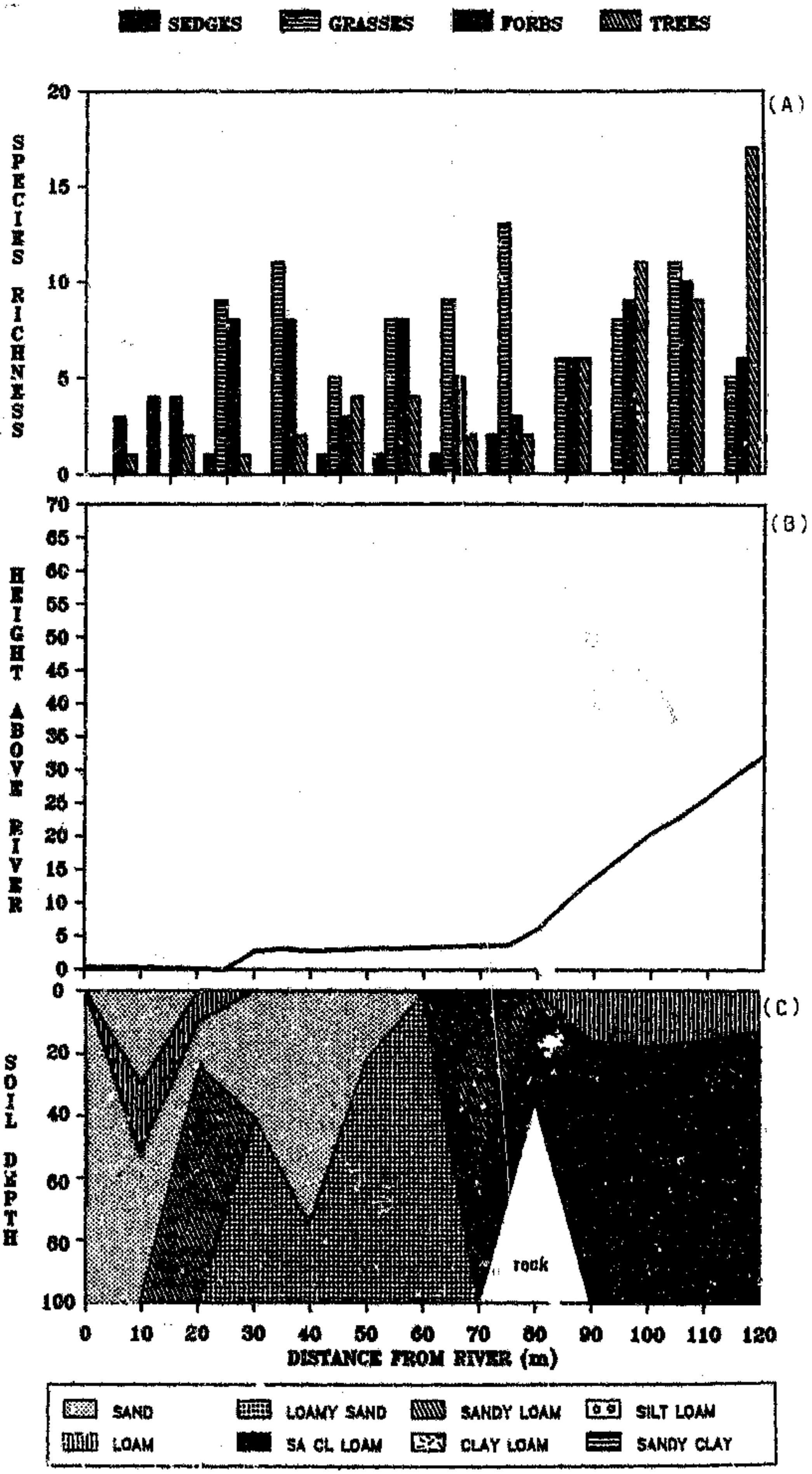
· 3 SITE 1 3 THOBOTHI



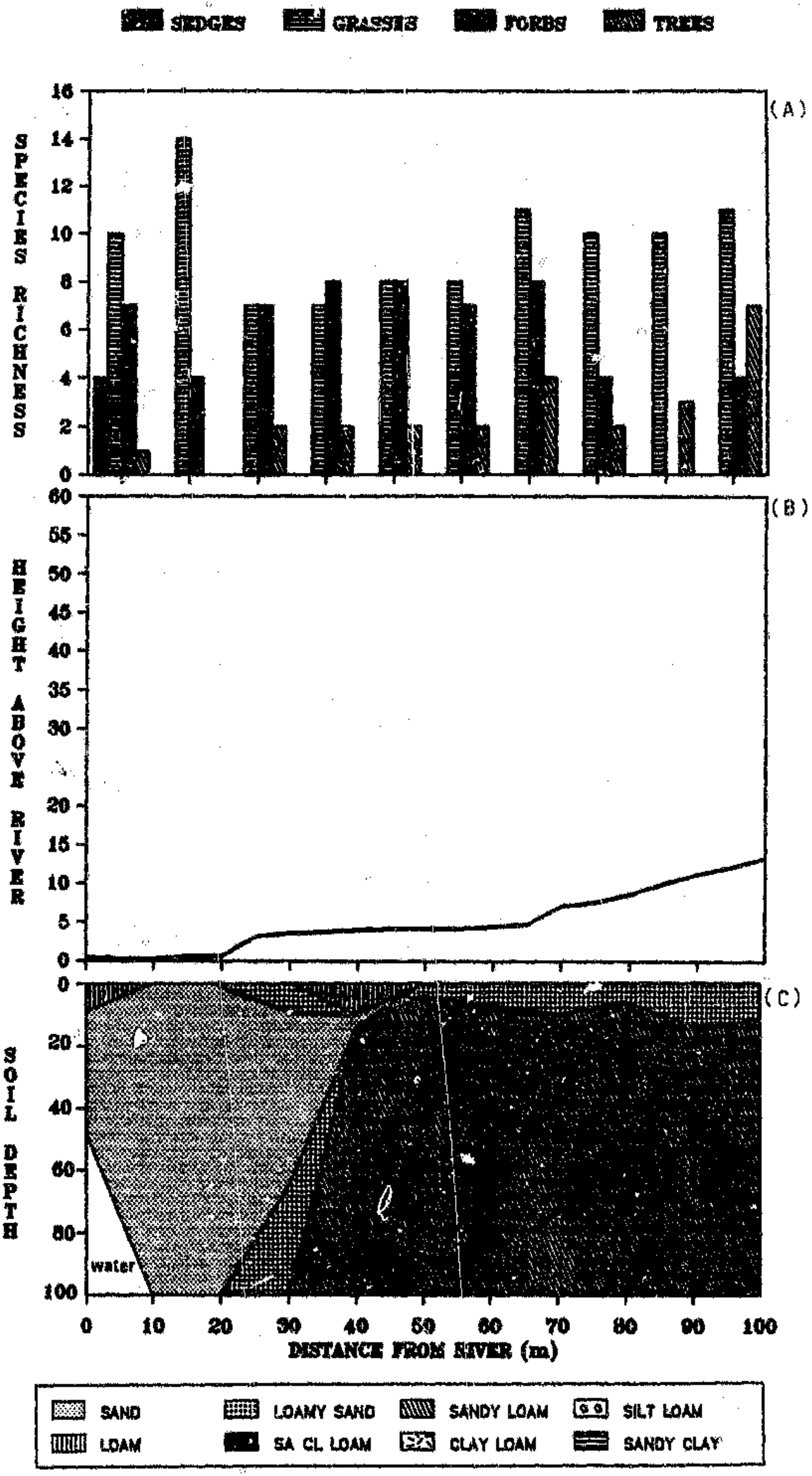
4 SITE 2 1 NGOLOTSHA



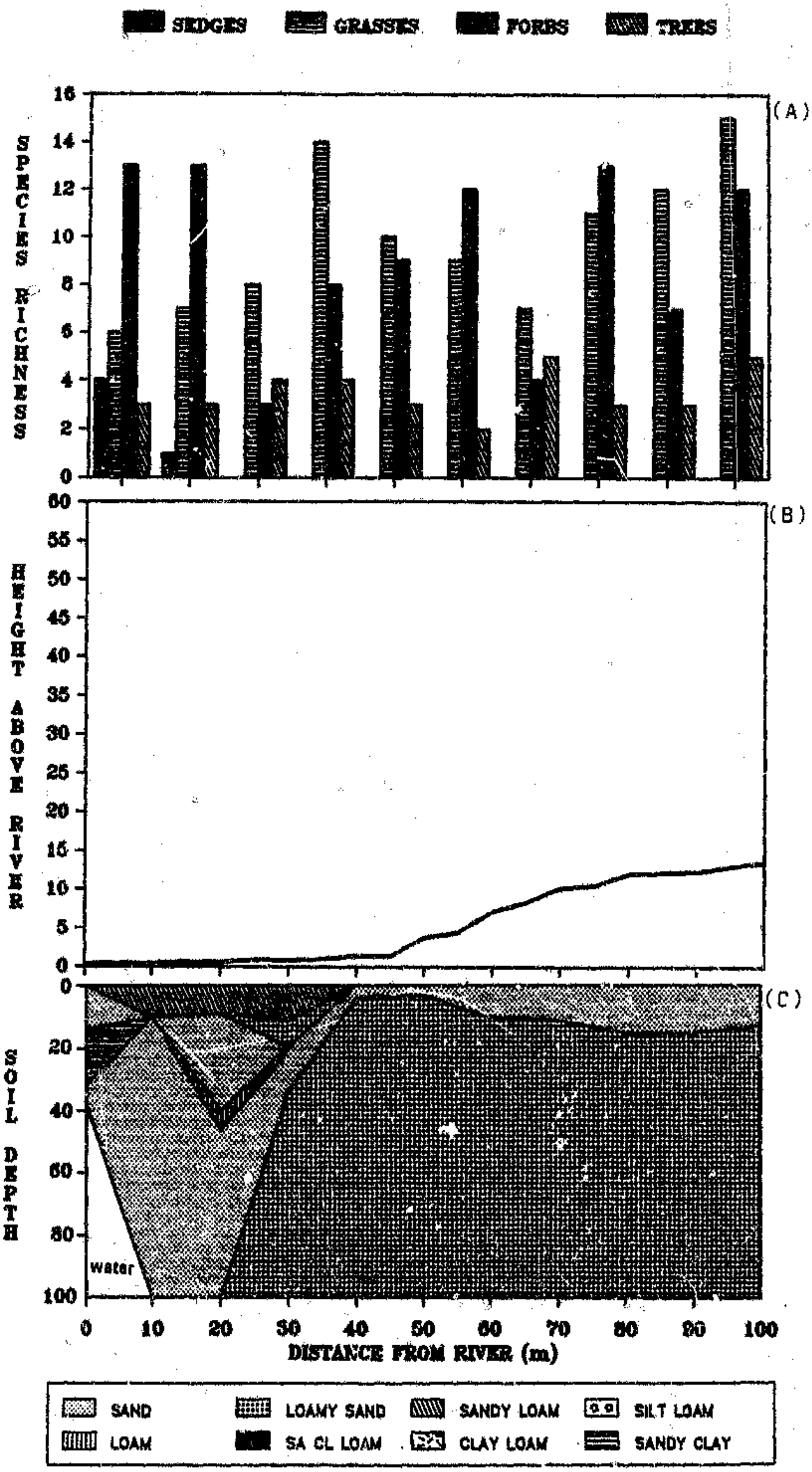
5 SITE 2 2 NGOLOTSHA



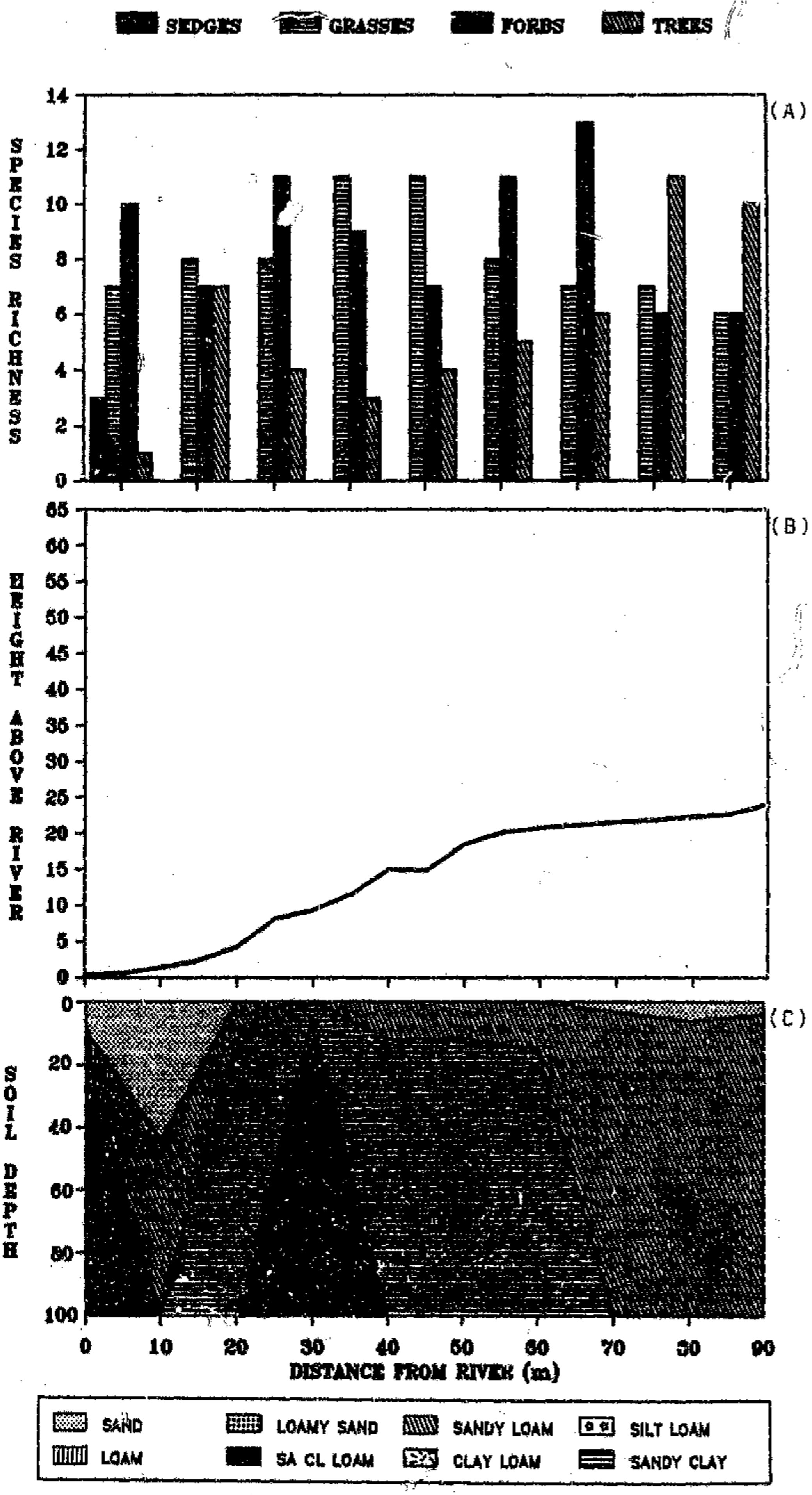
6 SITE 2 3 NGOLOTSHA



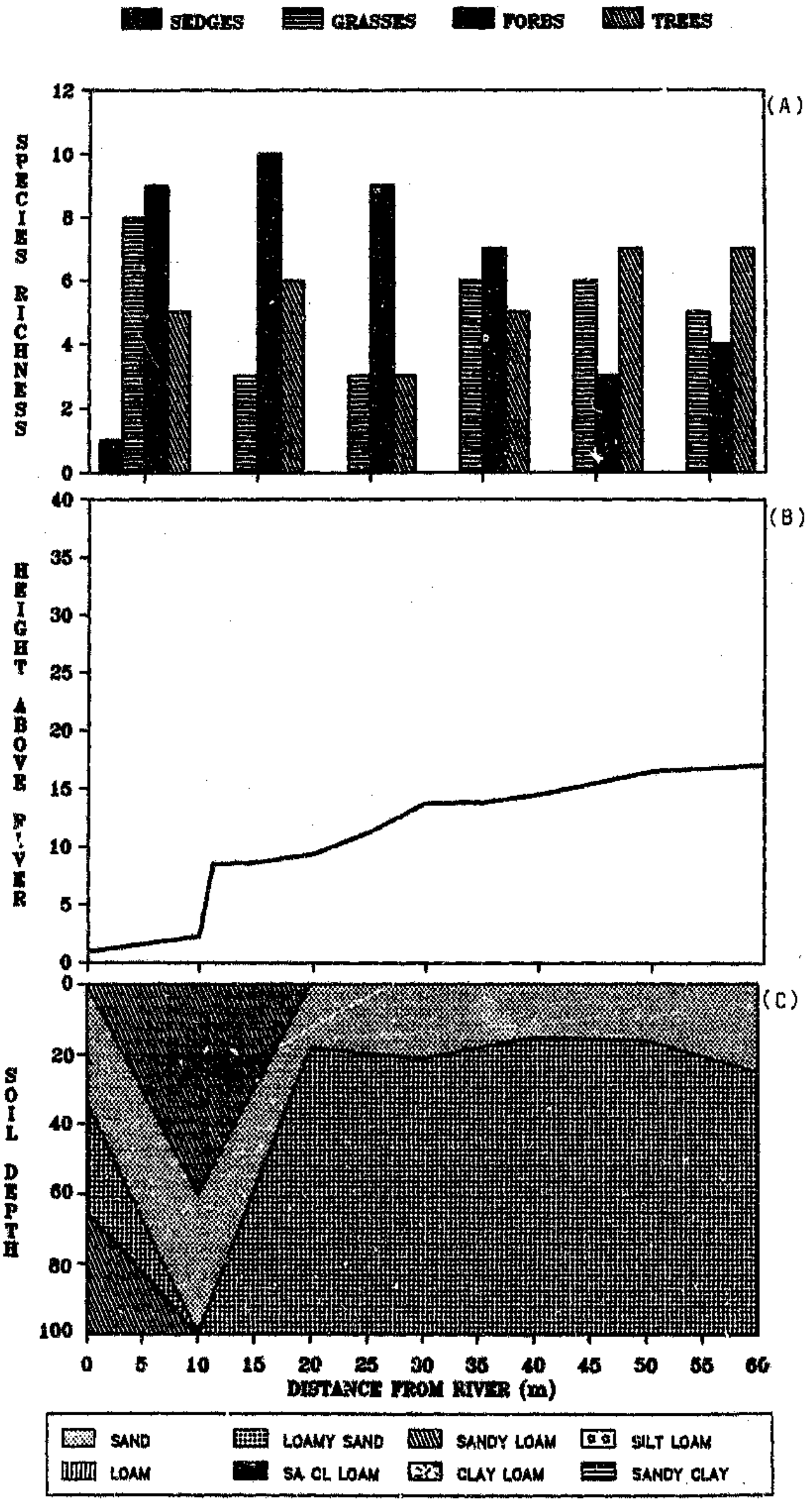
7 SITE 3 1 MBHUZANA



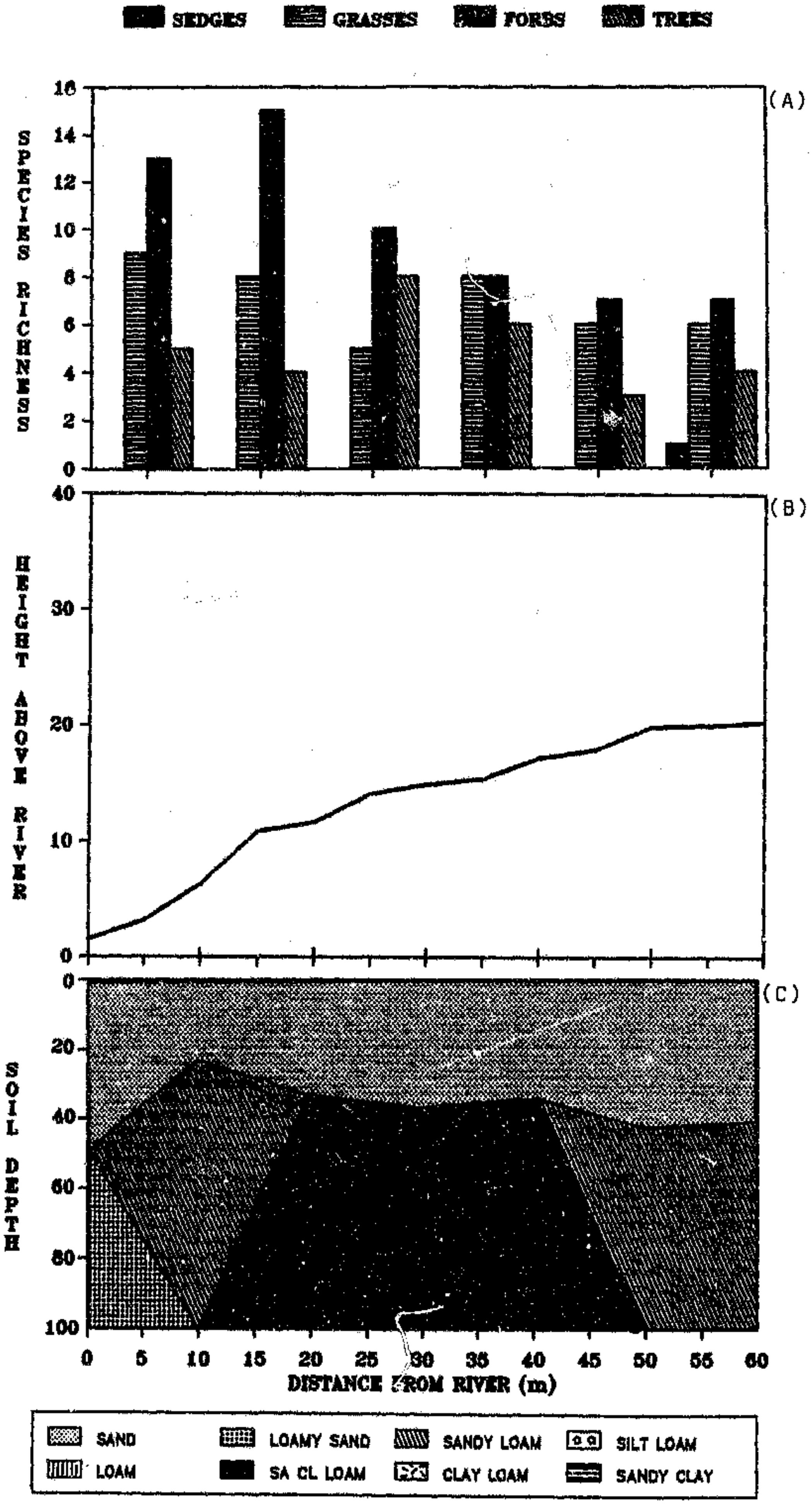
8 SITE 3 2 MBHUKANA



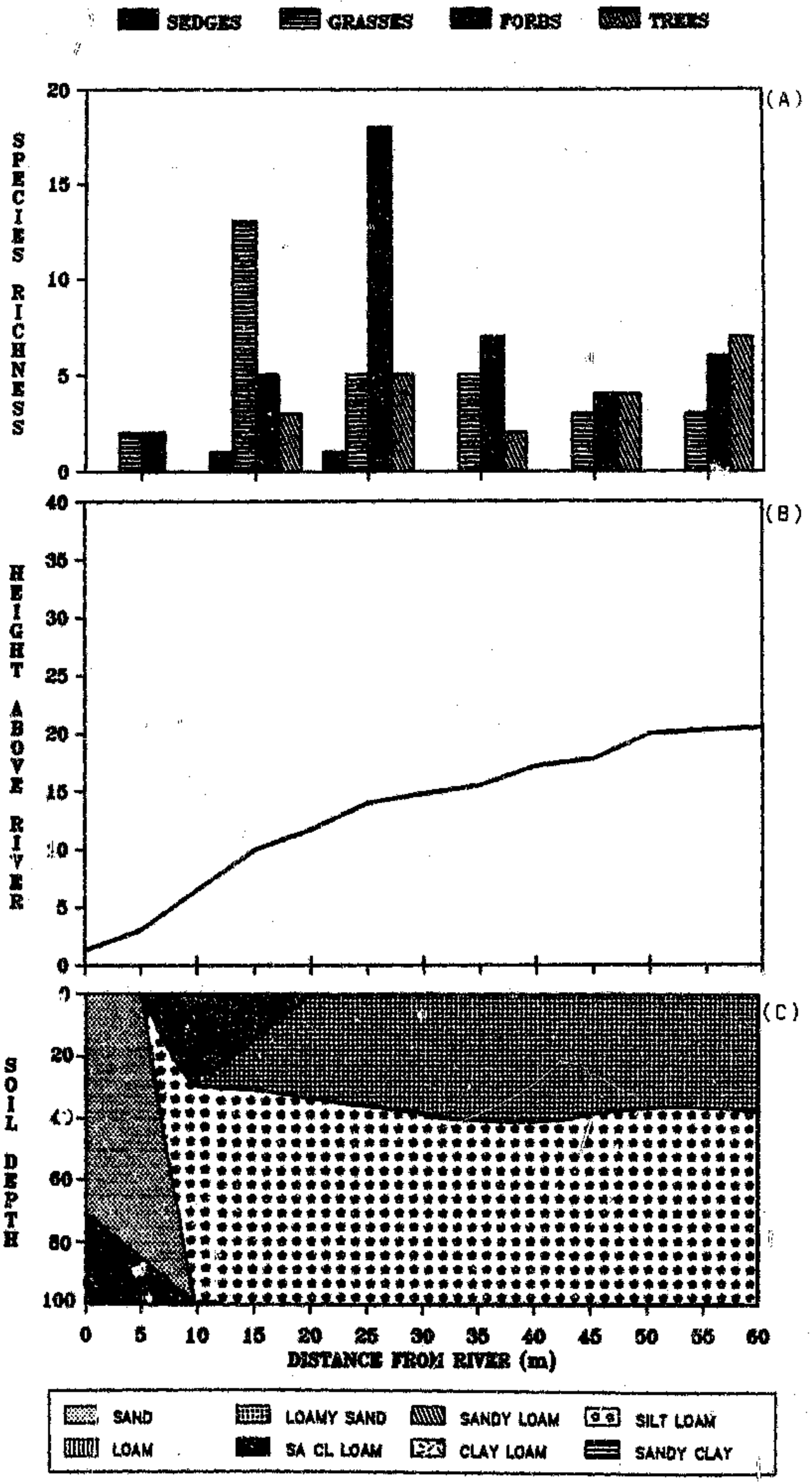
9 SITE 3 3 MBHUZANA



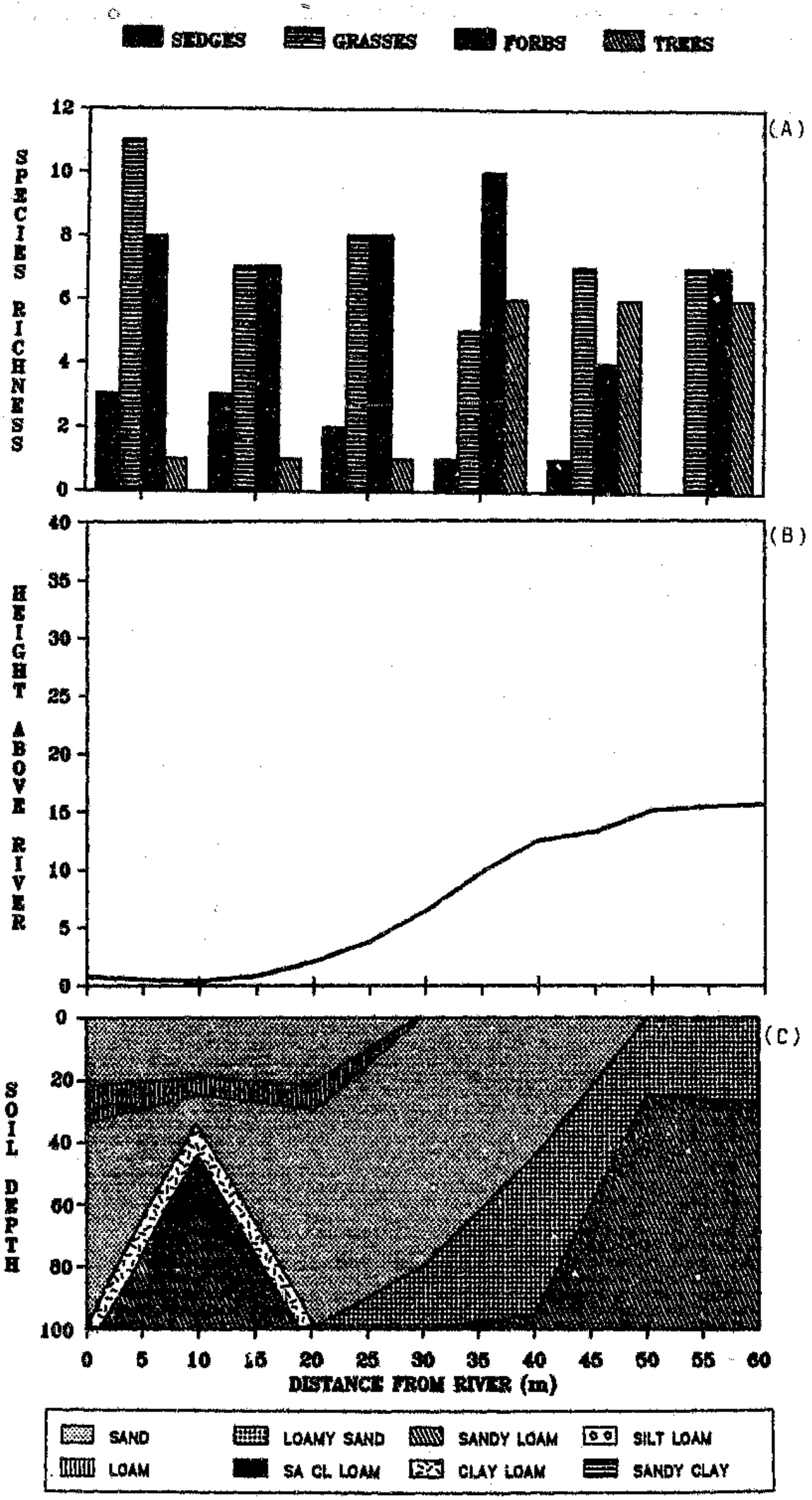
• 10 SITE 4 1 SONTULI



· 11 SITE 4 2 SONTULI



· 12 SITE 4 3 SONTULI



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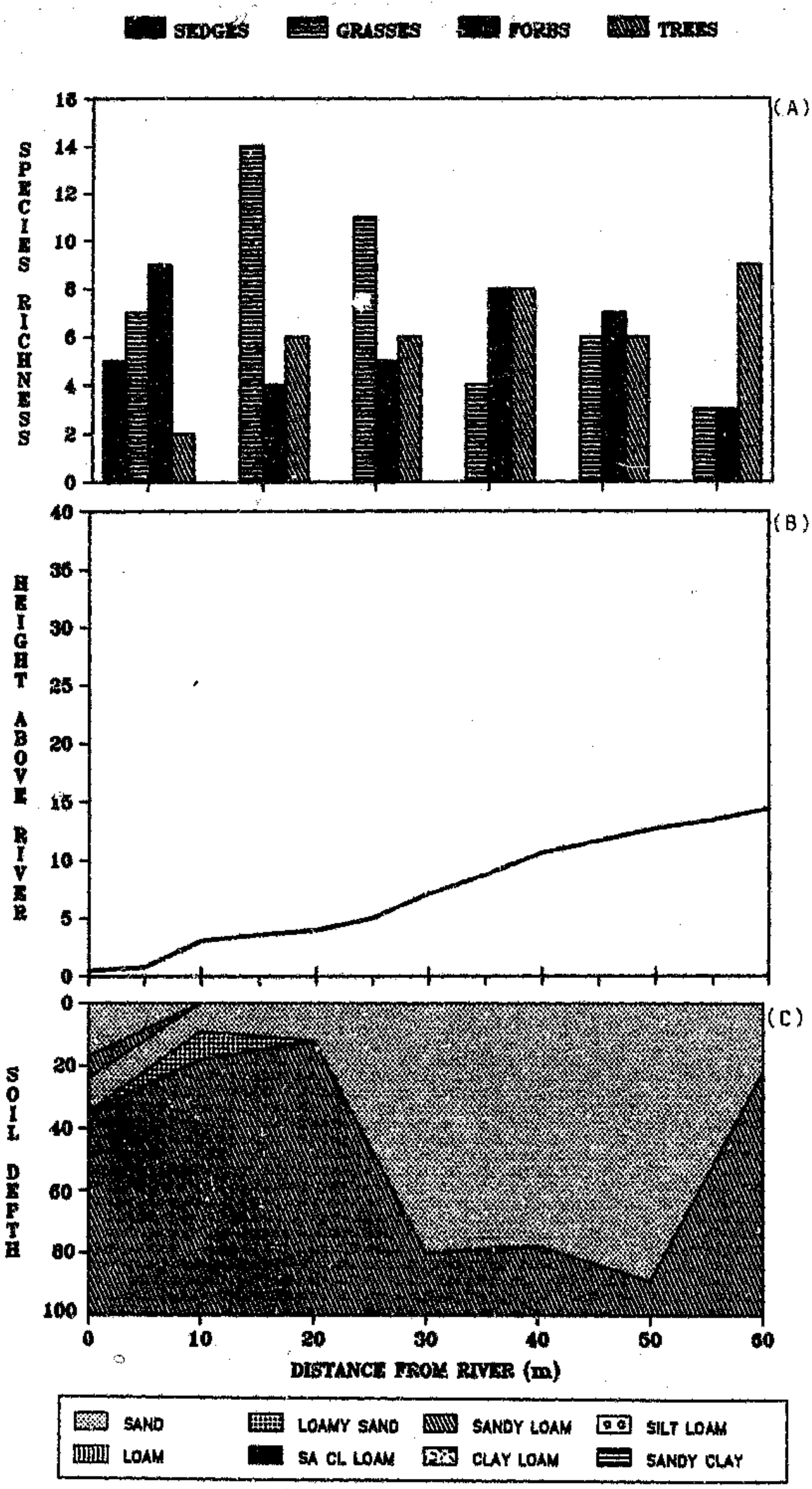

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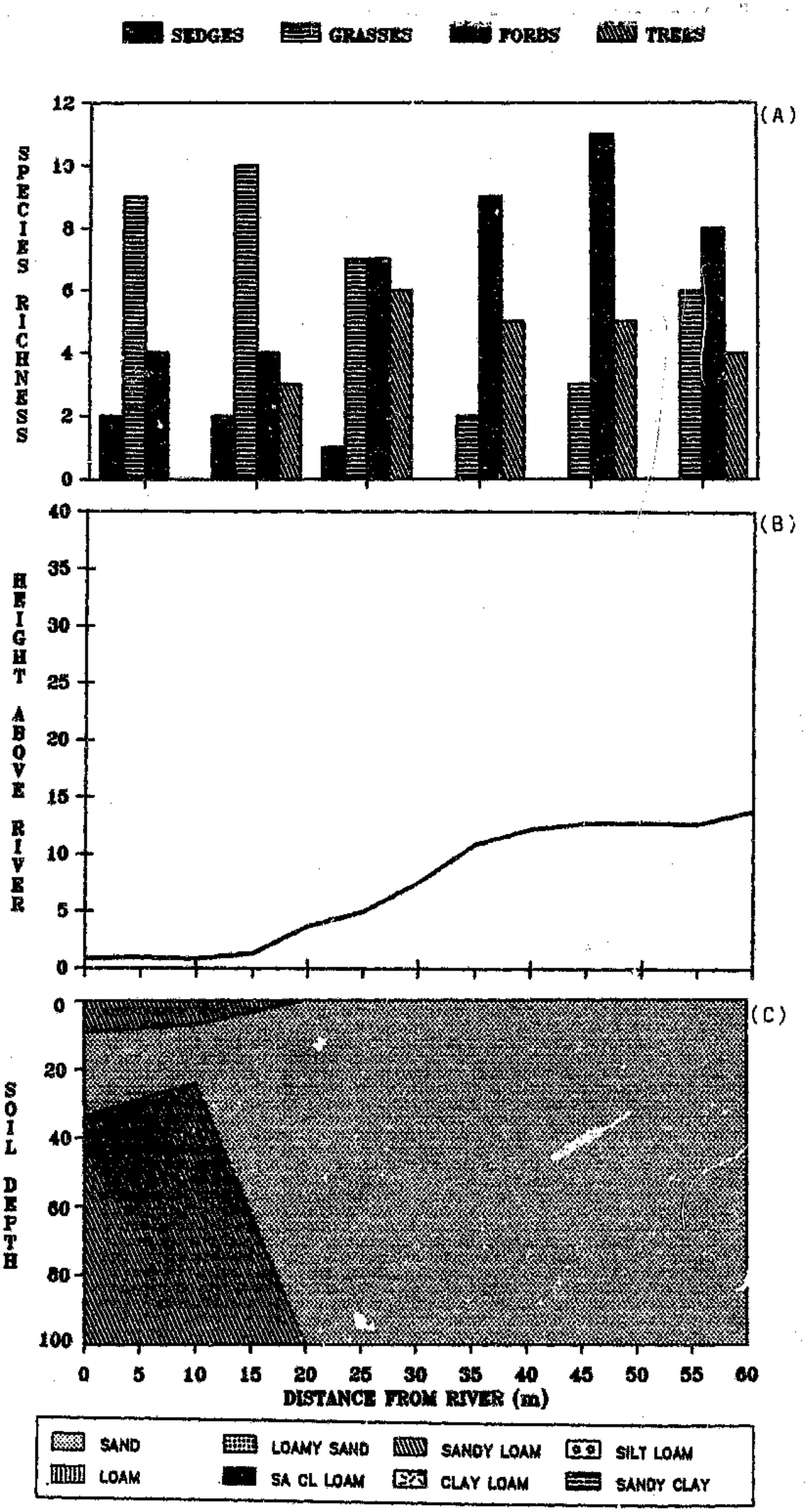

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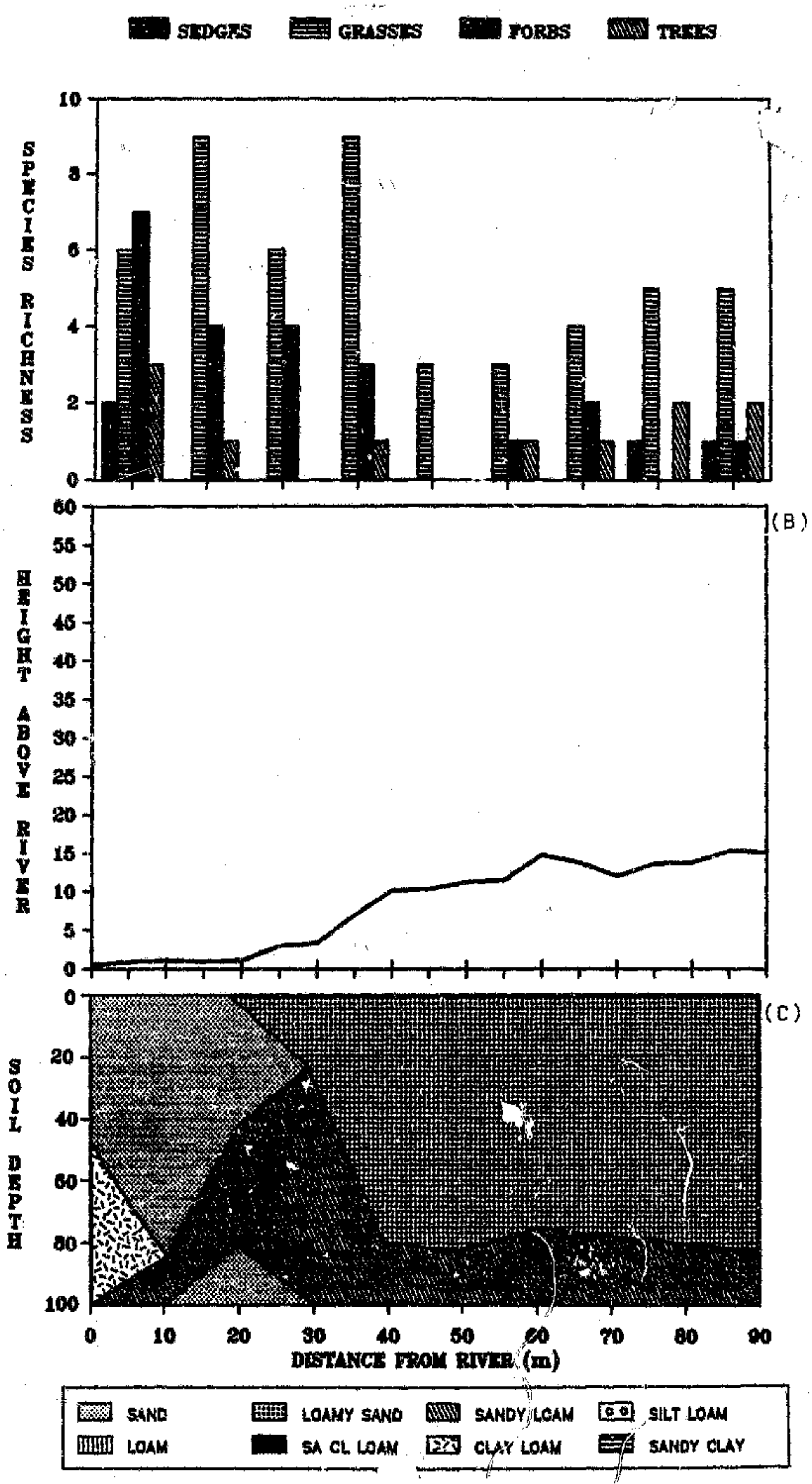

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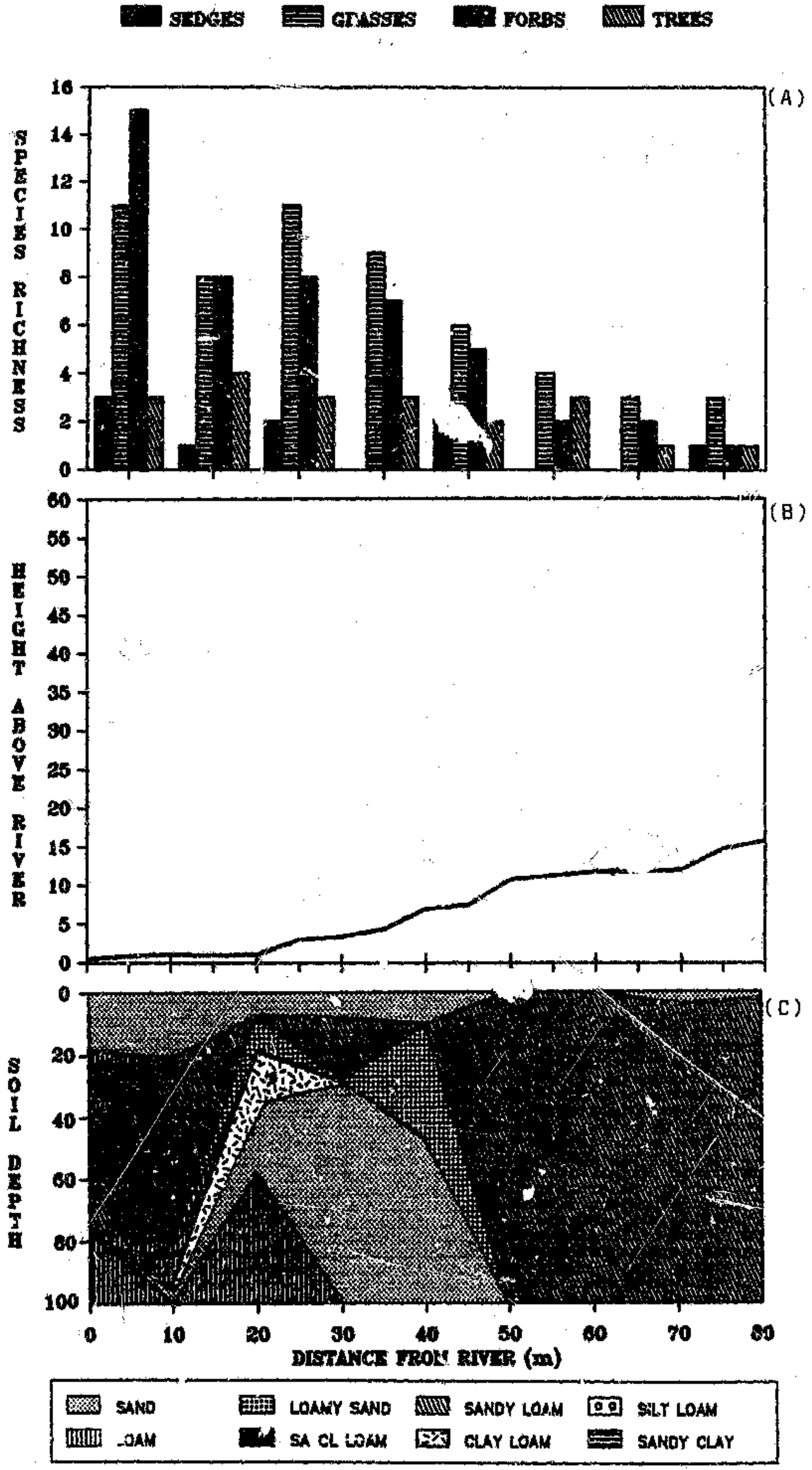

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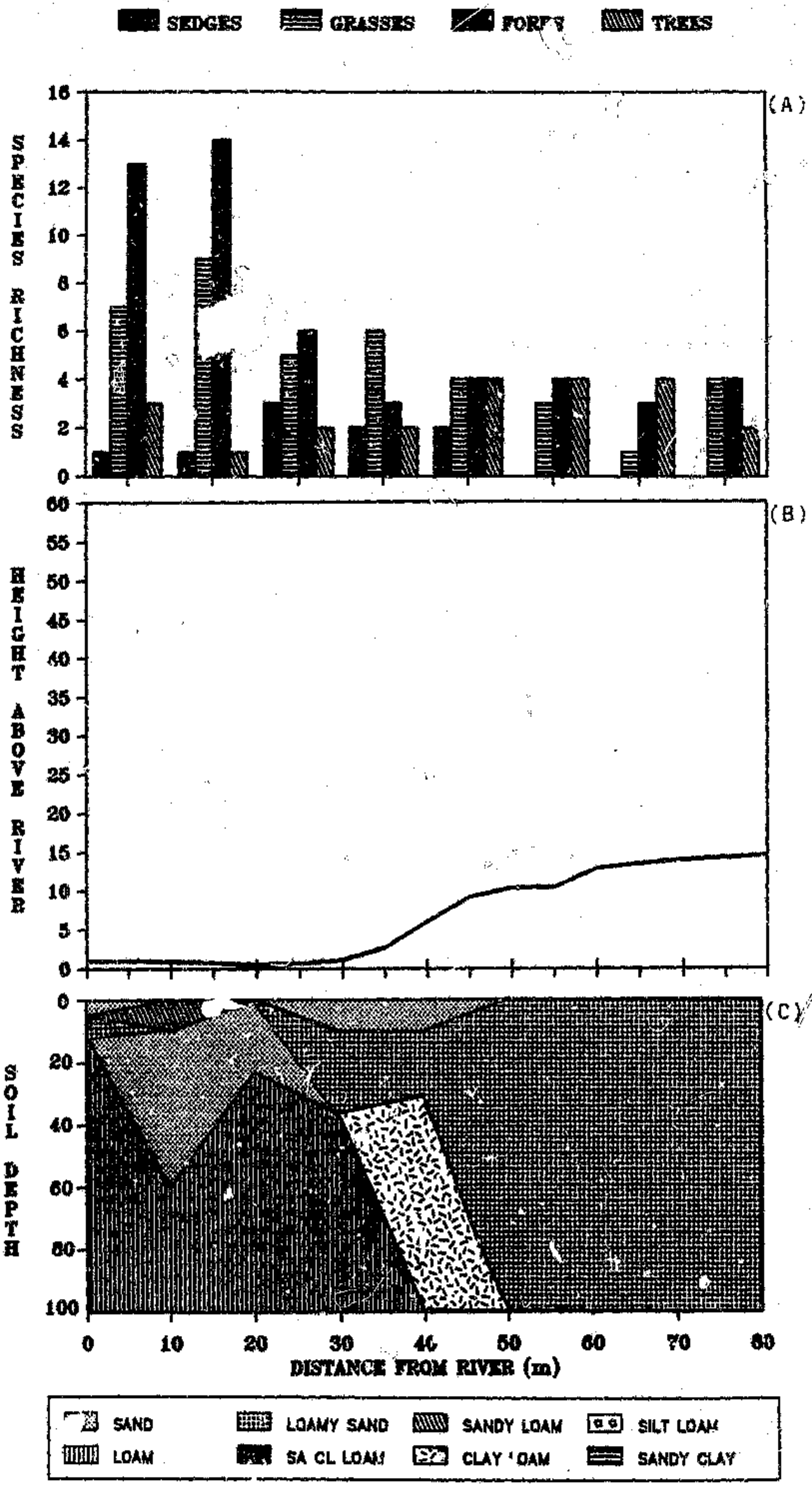

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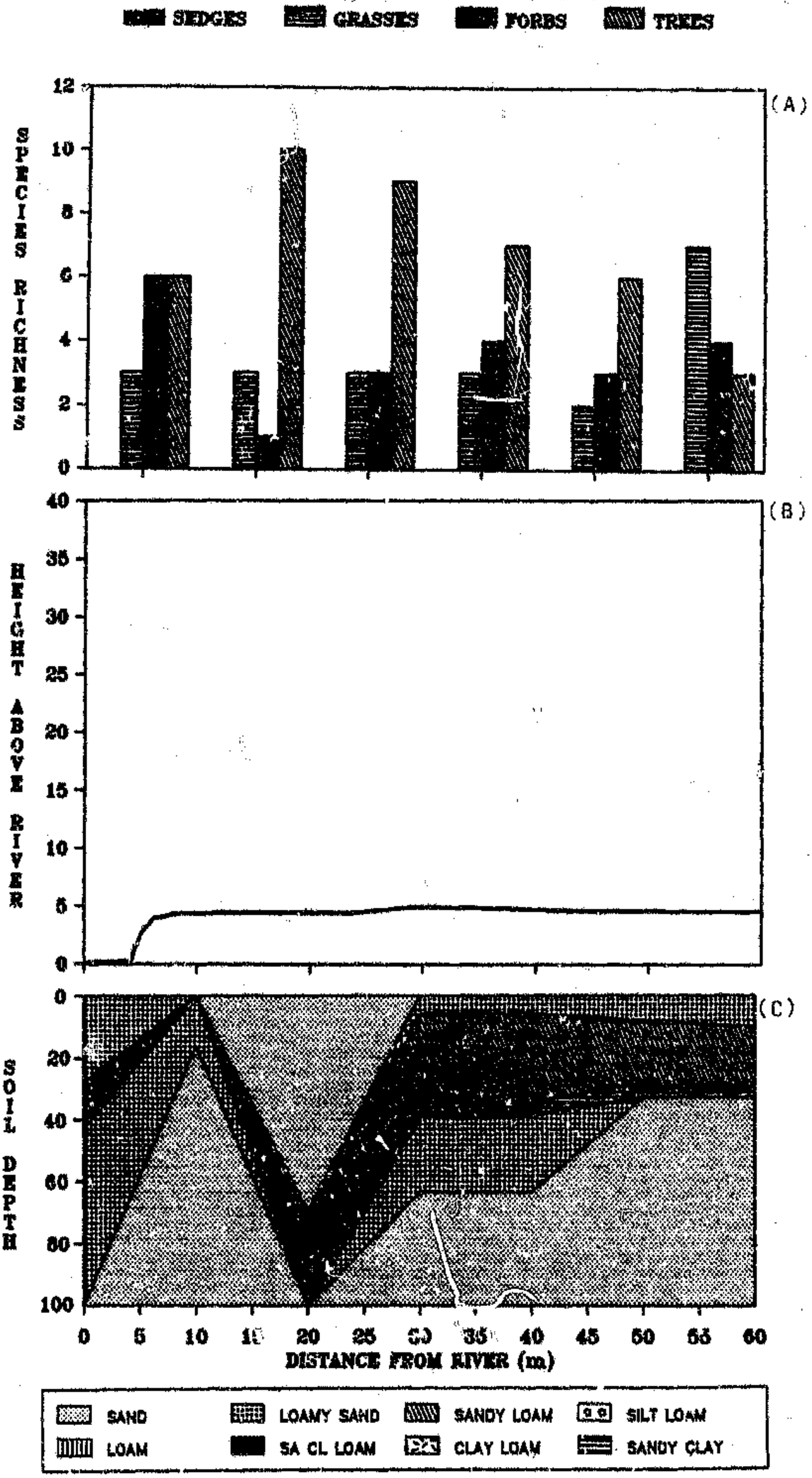

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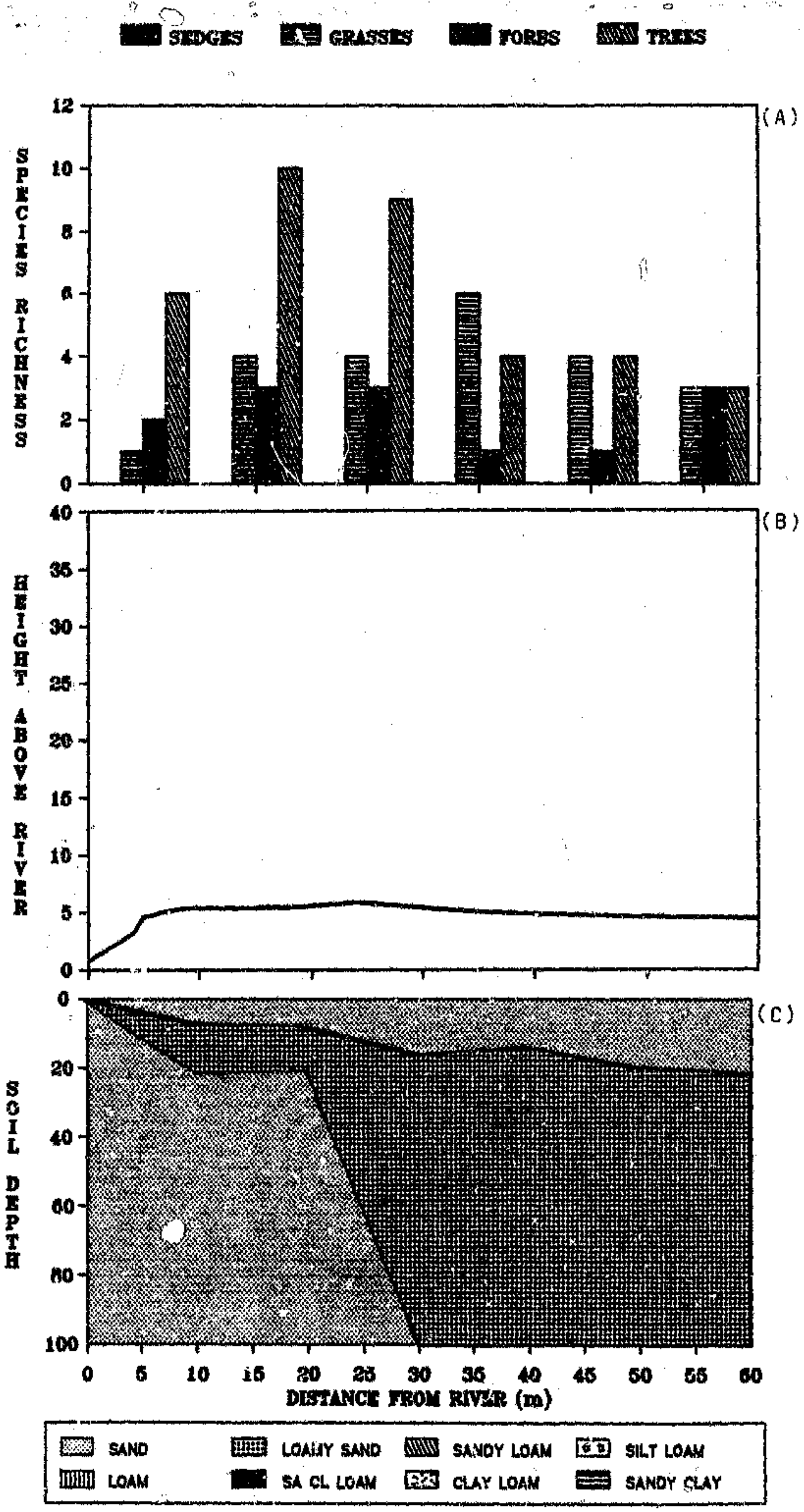

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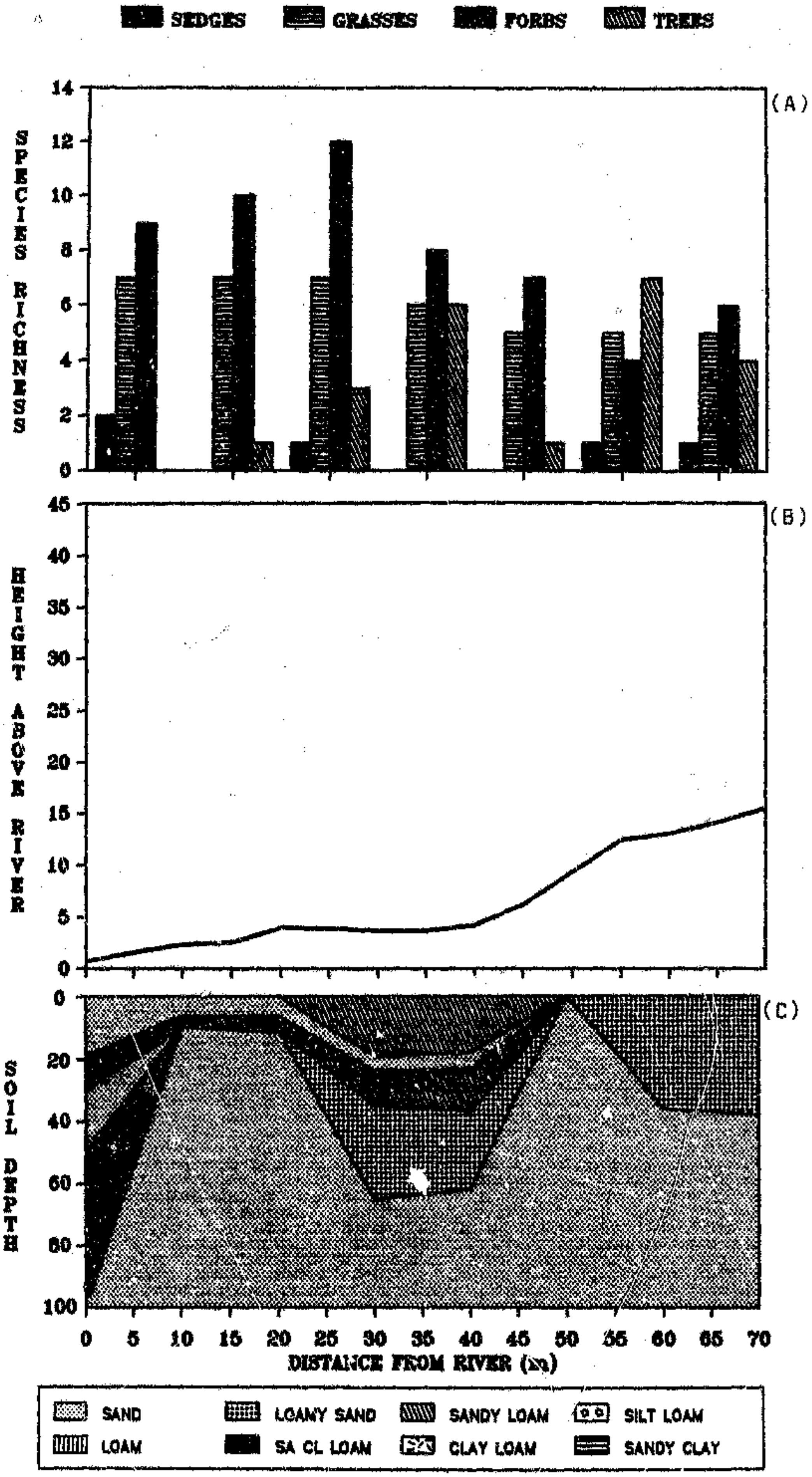

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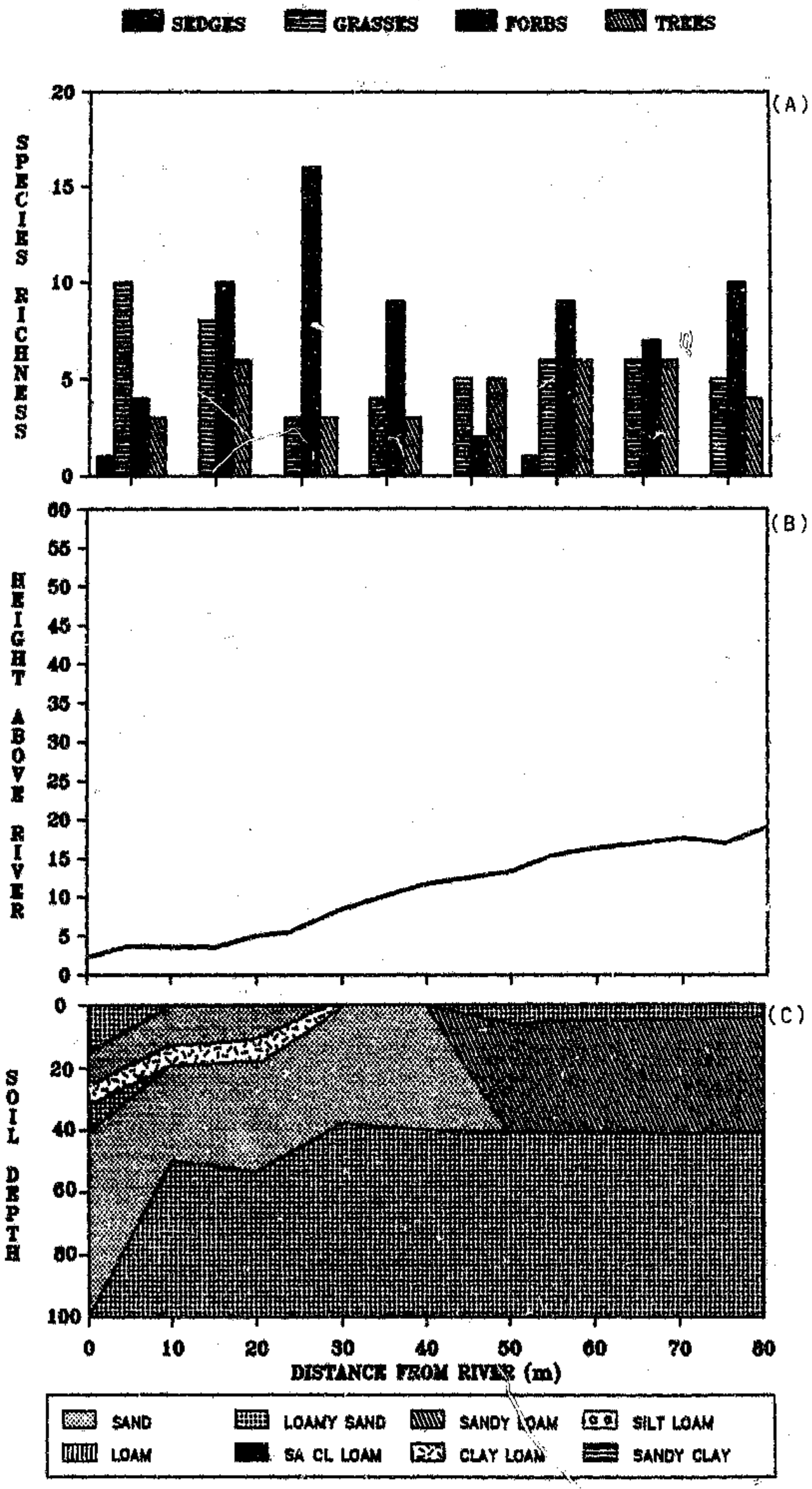

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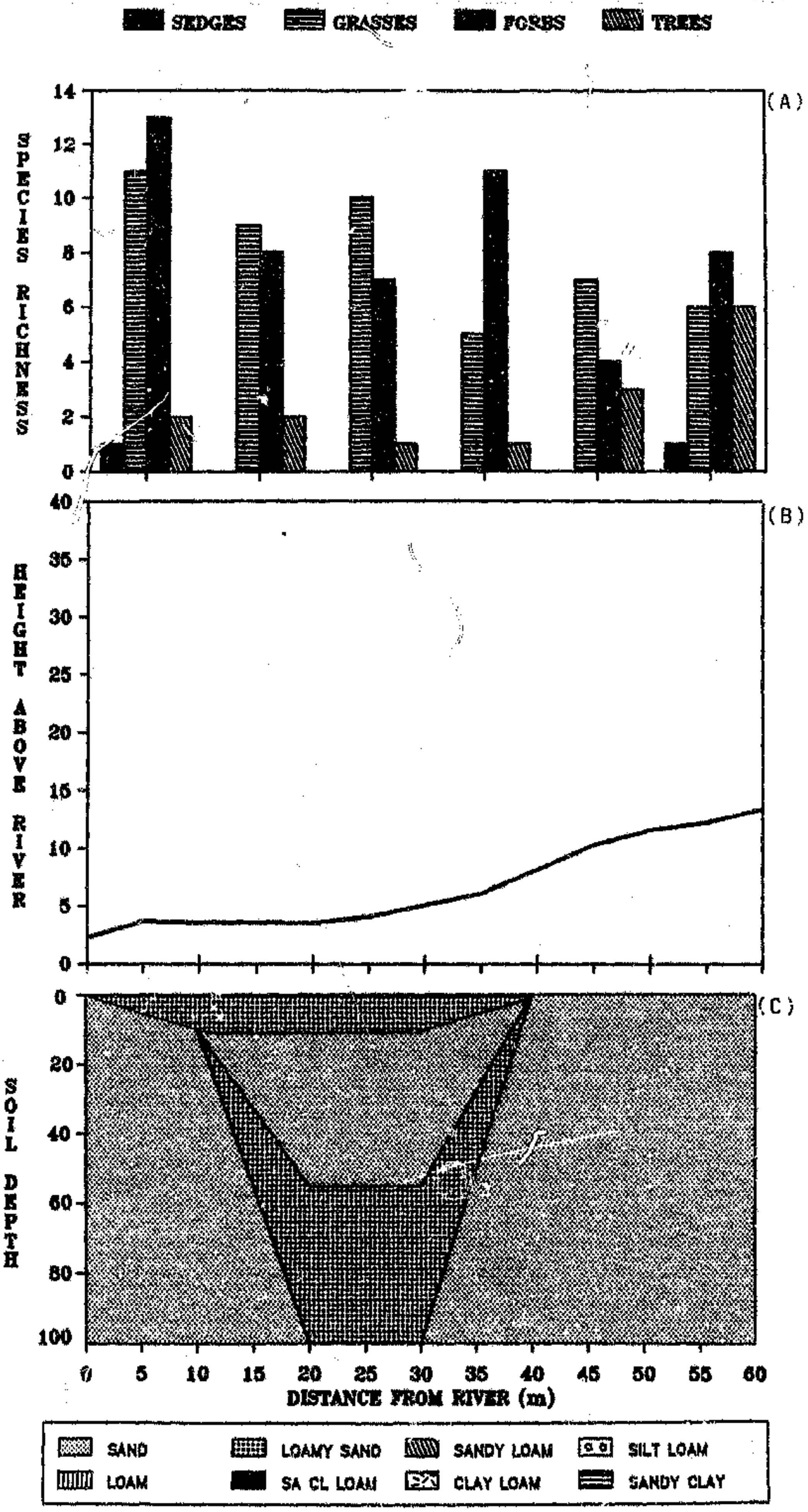

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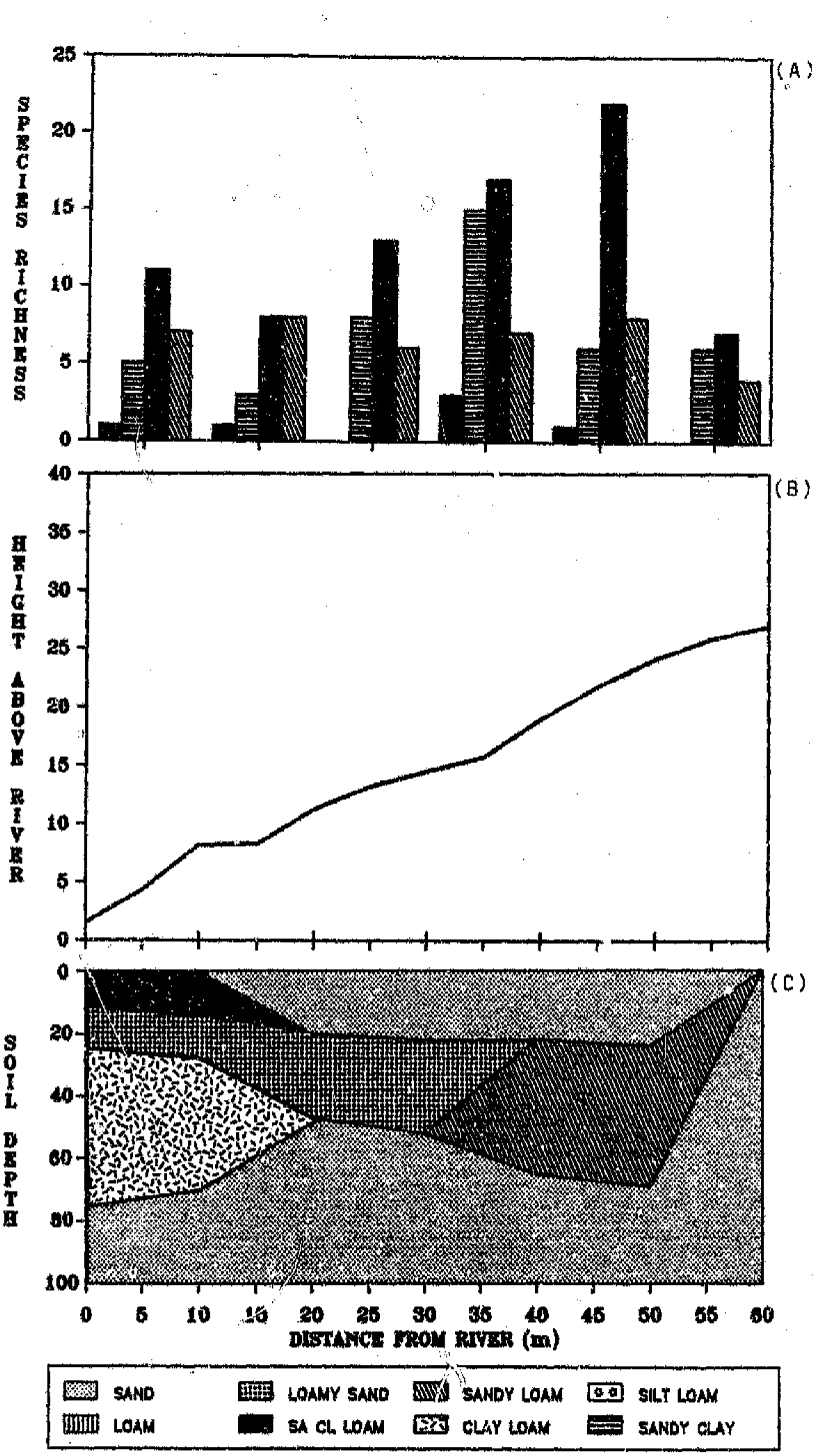
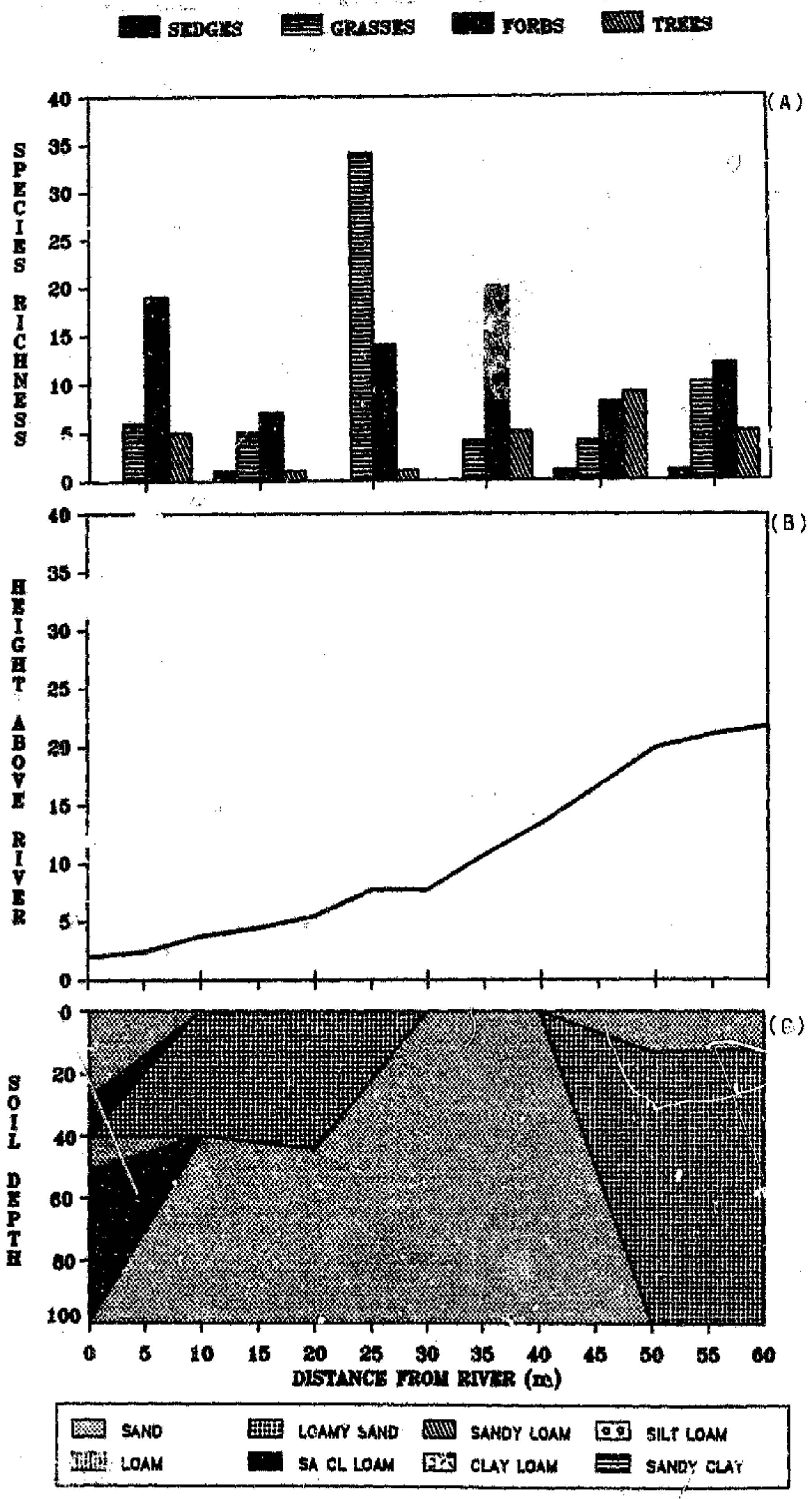


24 SITE 9 1 NGOLOTSHA WEST

25×



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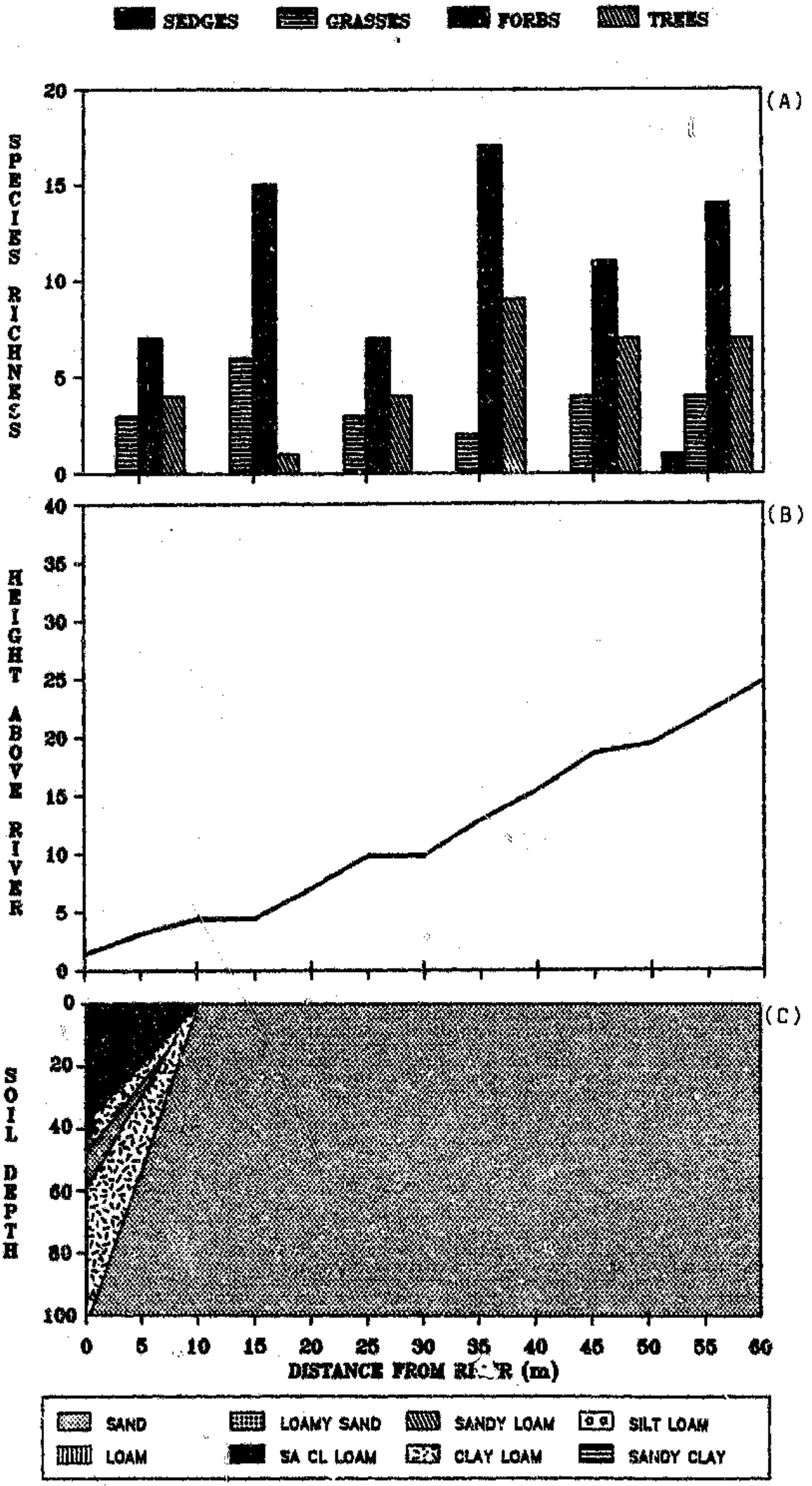

26 SITE 9 3 NGOLOTSHA WEST

Author: Kemper Nigel Palmer.

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