The vegetation ecology of the lower Mkuze River floodplain, northern KwaZulu-Natal:

A landscape ecology perspective.

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PREFACE

The work described was carried out between January 1999 and December 2001, in the School of Life and Environmental Sciences (previously the Department of Geographical and Environmental Sciences) at the University of Natal-Durban, under the supervision of Prof. W.N. Ellery. The study represents original work by the author and has not been submitted in any other form to another university. Where use was made of the work of others, it has been duly acknowledged in the text.

ACKNOWLEDGEMENTS

ABSTRACT

The overall aim of this study was to develop an understanding of the vegetation ecology of the lower Mkuze River floodplain from a landscape ecology perspective. The lower Mkuze River floodplain and its associated wetlands are located east of the Lebombo Mountains and north of Lake St. Lucia on the Maputaland Coastal Plain in northern KwaZulu-Natal. This system is defined as a storage floodplain wetland and comprises a mosaic of different wetland types. In addition it has a complex history of resource use and management.

Landscape ecology proved to be an ideal theoretical framework for this study because it enables the examination of complex ecological processes and phenomena in an integrated and holistic manner. It achieves this by explicitly recognizing the spatial heterogeneity, dynamics and hierarchical organization of the landscape; concepts that proved useful in developing an understanding of the ecological patterns and processes operating within the lower Mkuze River floodplain.

The vegetation of the study area was classified, using multivariate techniques, into six plant communities. The distribution of these plant communities was correlated with underlying environmental gradients that summarized the interactions between hydrology, substrate properties and topography within the floodplain system. Within the study area the *Phragmites mauritianus* reed swamp community was found where there was slow moving water, in semi- to permanently saturated soil. This was usually around the edges of pans or in extensive stands in low-lying areas in the distal reaches of the floodplain. The *Imperata cylindrica* hygrophilous grassland community was uncommon and was found in isolated stands towards the edge of the region of seasonal flooding. The *Echinochloa pyramidalis* backswamp community was the most extensive of all the plant communities identified. This community was tolerant of flooding and was found in damp places such as seasonal pans, backswamps and riverbanks as well as in standing water. The distribution of the *Ficus sycomorus* riparian forest community was restricted to elevated levees adjacent to the river channel that experienced inundation when floods were large enough to overtop channel banks. The *Cynodon dactylon* floodplain community was generally found towards the floodplain-terrestrial upland boundary in elevated areas with sandy well-drained soils.

The *Acacia xanthophloea* woodland community was distributed on the floodplain margin in elevated areas on sandy soils, primarily fringing the linear pans draining towards the Mkuze River from the north. The description of the plant community types and the underlying environmental determinants of their distribution provided a useful foundation for the examination of ecological processes and phenomena operating at spatially coarser levels within the landscape hierarchy.

Plant communities were aggregated into functional types based on criteria such as exposure to similar flooding and sedimentation regimes. The identification and mapping of these functional types, using a Geographical Information System (GIS), enabled one to identify a hydrogeomorphic continuum that described the interaction between floodplain processes and vegetation distribution. Within the study area the proximal-seasonally inundated functional type comprised plant community types found on channel levees and within backswamp areas. These areas were functionally connected to the Mkuze River in that they were exposed to seasonal flood events and associated sedimentation. The distal-permanently inundated functional type was typically found in the lower reaches of the floodplain that were rarely exposed to hydrological and sedimentological inputs from the Mkuze River. This functional type was permanently inundated and characterized by standing water and/or permanently saturated soils that were generally associated with the large floodplain pans. The distal-infrequently inundated functional type was typically located in sandy areas along the southern distal reaches of the floodplain. These areas were infrequently inundated by overbank floodwaters from the Mkuze River and were not characterized by substantial clastic sedimentation. The distribution and interaction between these functional types made it possible to develop process-based understanding of the ecosystem patterns and processes operating within the lower Mkuze River floodplain.

Landscape ecology theory emphasises the importance of a temporal analysis of spatial heterogeneity and the role of disturbance in ecosystem patterns and processes. Therefore a temporal analysis of the landscape mosaic from 1937 to 1996 was undertaken, using a GIS, in order to quantify landscape change over time. The landscape characteristics utilised to examine this change were total category area, percentage contribution to the total landscape area, number of patches, mean patch size, median patch size, patch size standard

deviation and the mean perimeter-area ratio. These spatial statistics were calculated for each year using PATCH ANALYST, an ArcView GIS extension and they were used to illustrate the role of anthropogenic disturbance on the landscape mosaic at a variety of levels within the landscape hierarchy. Anthropogenic disturbance was found to affect landscape content and configuration and therefore had the potential to undermine the underlying environmental determinants of landscape patterns and processes. Once the underlying functional processes are undermined, irreversible ecosystem degradation is a possible outcome.

The examination of the different levels within the landscape hierarchy and the dynamics of ecosystem patterns and processes operating within the Mkuze River floodplain made it possible to develop deeper insights into ecosystem patterns and processes than a conventional vegetation ecology study that typically focuses primarily on plant community classification. The use of landscape ecology as an overarching theory that guided the research process and aided the interpretation of findings by explicitly recognising the importance of examining spatial heterogeneity, hierarchical organisation and dynamics, proved invaluable in developing process-based understanding of the lower Mkuze River floodplain.

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CHAPTER 1 INTRODUCTION

Vegetation ecology studies generally focus on landscapes that comprise a mosaic of landforms, vegetation types and landuses. An understanding of the relationships that exist between these components of the landscape is essential in order to develop insights into the fundamental patterns and processes that govern ecosystem structure, function and evolution. A theoretical framework that explicitly recognizes these relationships is that of landscape ecology. Landscape ecology is a relatively new discipline in the field of ecology. It evolved primarily out of a need to explain complex ecological patterns and processes in an integrated and holistic manner (Urban *et al.*, 1987).

Landscape ecology is the study of the heterogeneity and dynamics of a landscape, a thorough understanding of which incorporates scale dependent explanations of the components of the landscape and the role of natural and anthropogenic disturbances in the development of the landscape mosaic (Forman, 1995). Landscape ecology is underpinned by the concepts of heterogeneity and hierarchy. Landscapes vary in heterogeneity and this variability has important consequences for the interpretation and understanding of ecological processes such as community structure and functioning, and how disturbance affects ecosystem integrity. Hierarchy theory emphasizes the importance of scale. Explanations of spatial and temporal heterogeneity and ecological processes differ when examined across a range of scales. Therefore the explicit recognition of hierarchical organization and scale are critical to understanding landscape mosaics (Allen & Starr, 1982; Turner *et al.*, 1991; Wu & Loucks, 1995).

This study utilizes these concepts as a means to explore the ecological patterns and processes operating within the lower Mkuze River floodplain. The vegetation ecology of the lower Mkuze River floodplain has not been thoroughly researched. Previous studies have largely focused on plant community descriptions (Tinley, 1976; Stormanns, 1986; Stormanns *et al.*, 1987; Stormanns & Breen, 1987, Schoultz, 2000; Taylor, 2000). The lower Mkuze River floodplain is a dynamic ecosystem comprising a complex mosaic of different wetland types within a floodplain environment. It comprises a rare combination of both lacustrine and palustrine wetlands and is classified as a storage floodplain wetland

(Noble & Hemens, 1978) characterized by a riverine area and an adjacent seasonally inundated floodplain. This varied geomorphological and hydrological setting has resulted in a centre of high floral and faunal biodiversity and a wetland system that provides many direct and indirect benefits to surrounding landusers. These include *inter alia*, the use of natural resources, such as reeds for crafts; the provision of sites for ecotourism and recreation; hydrological benefits such as flood attenuation and stream flow regulation; and erosion control (Taylor, 1986; Goodman, 1987; Holland *et al.*, 1989; Koaleli, 1999).

In order to gain insight into the ecological patterns and processes that govern this floodplain system, ecosystem structure and functioning was examined through the lens of landscape ecology theory. Few other studies in southern Africa have explicitly examined wetland and/or floodplain environments from a landscape ecology perspective, therefore this study provides insight into the usefulness of this approach.

The overall aim of this study was to develop an understanding of the vegetation ecology of the lower Mkuze River floodplain from a landscape ecology perspective. In order to achieve this aim the following objectives were set:

- To classify the vegetation of the study area,
- To determine the relationships between vegetation distribution and underlying environmental gradients,
- To produce a detailed vegetation map illustrating the spatial distribution of vegetation,
- To broadly classify, map and examine the ecological patterns and processes operating within the floodplain landscape,
- To use a Geographical Information System (GIS) to quantify the change of landscape characteristics over time, and
- To examine the role of anthropogenic disturbance through a spatio-temporal analysis of the landscape mosaic.

CHAPTER 2 THEORETICAL FRAMEWORK

2.1 Introduction

Landscape ecology provides the ideal theoretical framework for this study of the lower Mkuze River floodplain and its component wetlands because it allows one to examine complex ecological processes and phenomena in an integrated and holistic manner. In addition it explicitly recognizes the spatial heterogeneity, dynamics and hierarchical organization of the landscape; concepts that are central to landscape ecology studies and are essential in order to gain insight into landscape patterns and processes (Urban *et al.*, 1987; Forman, 1995).

This chapter briefly describes the roots of landscape ecology, its underpinning theories and basic principles, and then provides a framework for understanding wetland and floodplain patterns and processes from a landscape ecology perspective.

2.2 The Emergence of the Hierarchical Patch Dynamics Paradigm

2.2.1 The Equilibrium Paradigm

The concepts of balance-of-nature, steady-state, stability and homeostasis are central to the equilibrium paradigm. These concepts promulgate the idea that all factors and processes that affect ecological systems are balanced. The stability of a system is maintained through its ability to return to a previous equilibrium after some form of change or perturbation. The equilibrium-centered view has been widely accepted in ecology for decades and is evident in theories of equilibrium in community ecology, biogeography, ecosystem ecology, the Gaia hypothesis, deep ecology and conservation biology (Wu & Loucks, 1995).

The popularity of the equilibrium concept in vegetation ecology during the early part of the 20th century can be largely attributed to the ideas of F.E. Clements who argued that the vegetation climax represented a state of equilibrium in plant community development (Crawley, 1986). Clements described this process of plant community development through a number of predictable stages of succession. Two central principles of this process of succession were that communities are regarded as superorganisms capable of

self-regulation and that an ecosystem is characterized by emergent properties resulting from whole ecosystem organization rather than from its individual components (Huston, 1994). In addition, Clements suggested that this process of succession had a homogeneous, fixed end point, referred to as the climatic climax, which represented the stable plant community in equilibrium with macroclimatic conditions. All other plant communities were viewed as developmental stages in the ontology of the climatic climax (Van der Valk, 1998). This theory of succession allowed for all plant communities to be classified within a single, intuitively attractive framework that aided the understanding of plant community development.

H.A Gleason offered an alternative view of succession. He argued against the superorganism concept stating that an ecosystem can be understood by examining its individual components. He envisaged plant communities distributed along a continuum that constantly changes in time rather than as distinctly bounded, static units. Succession resulted from individual species' responses to environmental gradients. In other words a community was viewed as an assemblage of individual species that responded independently to changing environmental conditions (Ricklefs, 1990). The appeal of this more reductionist view has been that the search for explanations to processes or phenomena at one level of organization may be found by studying mechanisms that operate at lower levels. The success of this individualistic approach, over the Clementsian view, depends on the avoidance of excessive reductionism (Huston, 1994).

Many ecologists have challenged the theories underpinning the equilibrium paradigm since its inception. Advocates for an alternative paradigm have pointed out that equilibrium conditions are rare in nature and the failure of the classical equilibrium view to explain heterogeneity, dynamics, stochasticities and perturbations in ecological systems (Wu & Loucks, 1995).

2.2.2 The Alternative Paradigm

The search for explanations of ecological processes and phenomena that the classical equilibrium view failed to account for resulted in the emergence of a number of alternative paradigms. In the mid to late 20th century a battle of semantics emerged between the

theories of ecosystem resilience, persistence and homeorhesis that comprised the non-equilibrium viewpoint. All these theories however recognized two main concepts. Firstly, they described the ability of an ecosystem to absorb change and disturbance. Secondly, they emphasized a dynamic equilibrium i.e. they recognised fluctuations in ecosystem stability (Wu & Loucks, 1995).

The idea of a dynamic equilibrium led to the development of the multiple-equilibia perspective, which developed from the thermodynamic principles of entropy, dissipative structures and non-linear mathematics. This course of development introduced the concepts of heterogeneity, hierarchical structures and stratified stability. The dynamics of multiple equilibria systems are determined primarily around threshold boundaries caused by disturbances. Chaos and catastrophe theory focused on these boundaries, resulting in increased awareness in the complex dynamics and unpredictability of non-linear systems (Wu & Loucks, 1995).

The equilibrium, non-equilibrium and multiple-equibria perspectives have provided the theoretical foundations towards a greater understanding of ecosystem development, dynamics and the role of disturbance. However there was still a need for a conceptual framework that integrated these ideas and that explicitly recognized landscape heterogeneity, hierarchical organization, and the multiplicity of spatial and temporal scales that characterize ecological processes and phenomena (Urban *et al.,*1987).

2.2.3 The Hierarchical Patch Dynamics Paradigm

Hierarchical patch dynamics has been proposed as providing this integrative conceptual framework (Urban *et al.,*1987; Wu & Loucks, 1995). It essentially comprises the combination of two concepts, namely, hierarchy theory and heterogeneity (Rogers & Bestbier, 1997). Hierarchy theory, as mentioned in the previous section, has its roots in non-equilibrium thermodynamics and provides the theoretical basis for explaining scale when examining patterns and processes in ecological systems (Wu & Loucks, 1995). The concepts of patch dynamics and biodiversity that emphasize both spatial and temporal aspects of ecological systems are concepts that underpin heterogeneity (Noss, 1990; Wu & Loucks, 1995).

Hierarchy theory describes systems as structurally organized into functional components operating at different scales (Urban *et al.,*1987). These functional components or levels interact with adjacent levels in such a manner that each level in the hierarchy contains the levels below. In other words, lower levels interact to generate higher, slower and spatially coarser levels while higher levels constrain lower, faster and finer levels. Ecological processes are therefore functionally and spatially hierarchically nested (Urban *et al.,*1987; Wu & Loucks, 1995). The appeal of a hierarchical paradigm is that it allows one to study an event at a specific scale while the next lower level provides the mechanistic explanation for ecological patterns and processes and the next higher level provides the context for the study (Urban *et al.,*1987).

A heterogeneous landscape is said to comprise a mosaic of patches, the basic ecological unit of the hierarchical patch dynamics paradigm, differing in size, origin, diversity and spatial configuration (Urban *et al.,*1987; Forman, 1995). A reciprocal relationship exists between the landscape mosaic and ecological processes that operate within it. Ecological processes are responsible for the formation of the landscape, while the landscape imposes structural constraints on ecological processes. This relationship results in a dynamic mosaic of patches that operate at different hierarchical levels and over a wide range of scales (Wu & Loucks, 1995).

The development of the hierarchical patch dynamics paradigm has led to the emergence of the discipline of landscape ecology (Urban *et al.,*1987). The explicit recognition of landscape heterogeneity and dynamics, and the hierarchical organization of both the landscape mosaic and ecological processes, especially disturbance, comprises a conceptual framework that provides a sound theoretical basis for examining complex ecological patterns and processes.

2.3 Landscape Ecology

According to Forman (1995) a landscape is a mosaic of ecosystems that occur over a kilometers wide area. Landscapes are however, not size specific. Rather they can be delimited by the ecological patterns and/or processes that are of interest to the investigator (Naveh & Lieberman, 1994; Forman, 1995). Landscape ecology is the study of the

heterogeneity and dynamics of a landscape, a thorough understanding of which incorporates scale dependent explanations of the spatial configuration of the landscape and the role of natural and anthropogenic disturbances in the development of the landscape mosaic (Forman, 1995). The appeal of landscape ecology as a theoretical and analytical framework is that it enables one to examine landscapes in such a way that the most integrative explanation of the ecology of the landscape can be elucidated. The theoretical concepts of landscape ecology are best examined *via* the two theories that underpin it, namely hierarchy and heterogeneity.

2.3.1 Hierarchy

Hierarchy theory emphasizes the importance of scale. Explanations of spatial and temporal heterogeneity and ecological processes differ when examined across a range of scales. Therefore the explicit recognition of hierarchical organization and scale are critical to understanding landscape mosaics (Allen & Starr, 1982; Turner *et al.,* 1991; Wu & Loucks, 1995).

The smallest spatial scale to which the ecological patterns and processes of interest can be deconstructed is referred to as the grain. These first order landscape elements are by definition homogeneous with relatively discrete boundaries (Kotleir & Wiens, 1990). At the next higher level in the hierarchy, second order landscape elements comprise clusters of first order elements. Third order landscape elements contain the two lower levels and are formed by variation within and among the first and second order landscape elements. This process of inclusion continues until the uppermost level in the hierarchy is reached. This upper level is defined as the extent and is the largest scale of heterogeneity to which the grain responds or is constrained (Kotleir & Wiens, 1990). This nested hierarchical organization of scale is illustrated in Figure 2.1. As a consequence of reduced interaction and influence between levels as the number of intervening levels increases, a minimum of three adjacent levels in the hierarchy should be examined in order to gain some insight into landscape heterogeneity and its underlying ecological processes (Forman, 1995; Wu & Loucks, 1995).

The reference level is the level at which the processes or phenomena under study characteristically operate. The next higher level provides the significance or context for, and imposes constraints on, the spatial heterogeneity and ecological processes operating at the reference level. The adjacent lower level comprises the grain of, and provides the mechanistic explanation for, the reference level (Forman, 1995; Wu & Loucks, 1995).
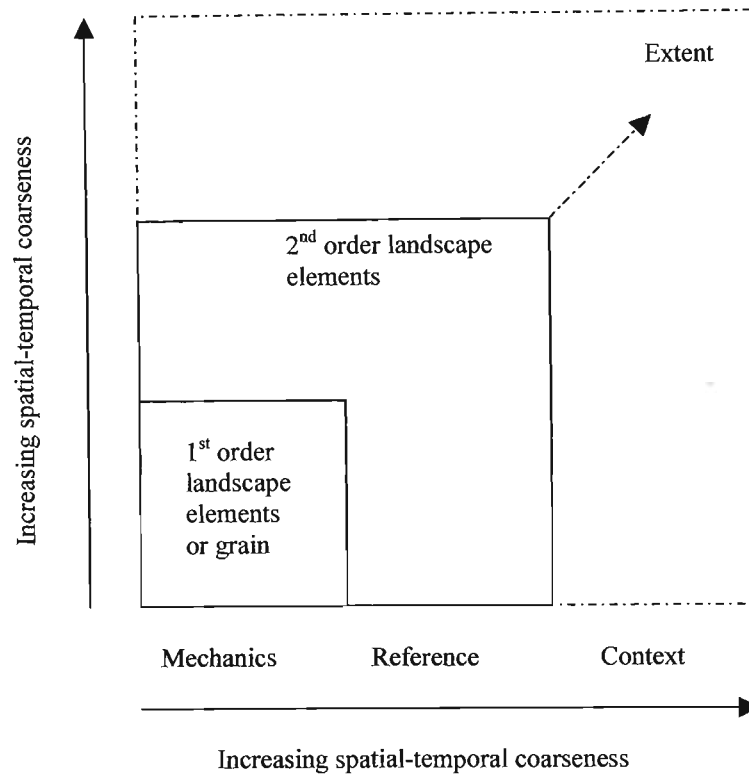
Figure 2.1 The nested hierarchical organization of the landscape mosaic.

2.3.2 Heterogeneity

Landscapes vary in heterogeneity and this variability has important consequences for the interpretation and understanding of ecological processes and phenomena such as community structure and functioning, and how disturbance affects ecosystem integrity (Forman, 1995; Kamada & Nakagoshi, 1996). Heterogeneity can be defined by (1) content - the different landscape elements that comprise the landscape mosaic, (2) configuration - the spatial arrangement or functional connectivity of the landscape elements in relation to one another and (3) dynamics - the change in content and configuration over time.

Content

The basic ecological unit of the landscape mosaic is the landscape element or patch (Forman, 1995). A patch at a given scale has an internal structure that is a reflection of patchiness at finer scales and the mosaic containing that patch has a structure that is determined by patchiness at coarser scales (Kotleir & Wiens, 1990). Landscape content can be described in terms of patch types and their characteristics (Wu & Loucks, 1995).

Patches are usually identified and defined by the investigator and normally reflect the purpose of the study. In most cases patches are plant or animal communities, i.e. an assemblage of species (Forman & Godron, 1986). Forman & Godron (1986) have defined five generic patch types based on their differing origins or causative mechanisms. These include disturbance patches, which are produced by local disturbances or perturbations in a small area; remnant patches, which appear when a small area escapes widespread disturbance surrounding it; environmental resource patches, which are produced by the heterogeneous distribution of resources; introduced patches, which are created by human disturbance; and ephemeral patches, which are produced by transient fluctuations in resource availability (Wu & Loucks, 1995).

Patches can be characterised by *inter alia* their size, shape and number (Turner *et al.,* 1991; Wu & Loucks, 1995). These characteristics play a significant ecological role in determining landscape patterns and processes. Patch size, for example influences the amount of minerals and nutrients stored within a patch, and the numbers, types and flows of species within patches (Forman & Godron, 1986). Patch shape affects the movements and flows of species between adjacent patches. Compact patches are effective in conserving resources, they protect the internal resources of the patch against surrounding detrimental effects. In contrast, convoluted patches are effective in enhancing interactions with the surrounding mosaic. Generally the boundaries of natural patches are curved while those of human created or introduced patches contain one or more straight lines (Forman, 1995). Patch size and shape are characteristics of individual patches. However, patches seldom exist singly in a landscape, therefore the number of patches within a landscape is an important characteristic to consider. The number of patches is important in terms of

maintaining and maximizing species diversity within a landscape (Forman & Godron, 1986).

Configuration

Configuration refers to the spatial arrangement of patches in a landscape mosaic. The concept of configuration explicitly recognizes the juxtaposition of these spatial elements or patches by providing an intermediate level of exploration between the grain and context levels in the hierarchical organization of the landscape i.e. the reference level. This intermediate level is defined by clusters or aggregations of landscape elements that are functionally connected by common attributes such as dispersal mechanisms, geomorphic landforms or disturbance regimes. This configuration of spatial elements has more influence on the ecological functioning of the landscape than individual landscape elements. A configuration is spatially recognizable but depends on being functionally connected (Forman, 1995; Noss, 1987).

Dynamics

Change is characteristic of all landscapes and is usually driven by a combination of natural, social, economic and political forces. These forces create disturbance regimes that operate at different spatial and temporal scales, resulting in a constantly changing landscape mosaic (Dunn et al., 1991). Landscape heterogeneity is maintained through a balance between natural and anthropogenic disturbance regimes (Kamada & Nakagoshi, 1996). According to Forman (1995) landscape dynamics are evident through the following spatial processes: perforation, which is the process of puncturing holes within a patch; fragmentation, which is the breaking up of a patch into smaller portions; shrinkage, which is the decrease in size of a patch; and attrition, which is the disappearance of a patch.

These spatial processes have distinctive spatial attributes as well as significant effects on a range of ecological characteristics. Perforation and fragmentation may affect either the whole area or a patch within it, while shrinkage and attrition generally apply to an individual patch. Patch number in the landscape generally increases with fragmentation and decreases with attrition. Mean patch size decreases with perforation, fragmentation and shrinkage, and typically increases with attrition because small patches are most likely to

disappear first. Connectivity between patches typically decreases as fragmentation increases (Forman, 1995). A further two spatial processes not recognised by Forman (1995) that were considered important are those of augmentation and consolidation. These processes refer to introduced patches, which with increasing anthropogenic disturbance result in an increase in patch number and then the consolidation of patches into a few larger patches.

The driving force behind landscape transformation is disturbance. Therefore, in order to understand the spatial processes of landscape transformation and their impact on landscape content and configuration, one needs to examine the properties of disturbance. White & Pickett (1985) identified a number of properties that can be used to describe disturbance regimes. They include:

- The spatial distribution of a disturbance, especially in relation to environmental gradients. A disturbance within a more environmentally sensitive area has a potentially larger impact than the same disturbance in a less sensitive area.
- The frequency or mean number of disturbance events per time period. The more frequent the occurrence of the disturbance the more severe the impact.
- The area disturbed. This can be expressed as area per disturbance event. The larger the area the more severe the impact.
- The synergism or cumulative impact of the disturbances. The effects of a disturbance on the occurrence of other disturbances. The higher the synergism of disturbance events the more severe the potential impact due to cumulative effects.

In conclusion, a thorough understanding and utilization of the concepts of hierarchy and heterogeneity are necessary when conducting studies within the discipline of landscape ecology. Explanations of spatial heterogeneity and landscape dynamics, including the role of disturbance, must take into account scale or the level at which ecological processes and phenomena occur within the hierarchical structure of the landscape.

2.4 Wetland Ecology

2.4.1 Wetland Patterns and Processes

In order to understand the mechanical functioning or the grain of wetlands in general, one needs to examine the interaction between hydrology, substrate and vegetation. Gosselink & Turner (1978) proposed a conceptual model describing the role of hydrology in wetland ecosystems, which examines these interactions. Hydrology is regarded as the primary determinant of wetland patterns and processes (Mitsch & Gosselink, 1993) and has an important influence on wetland substrate properties. The substrate allows the growth of specific vegetation, which in turn can alter the hydrology, resulting in a dynamic feedback system (Gosselink & Turner, 1978; Fig. 2.2). Thus, for example, flooding of a soil may lead to the establishment of dense emergent vegetation that slows the flow of water, increasing the duration of inundation.
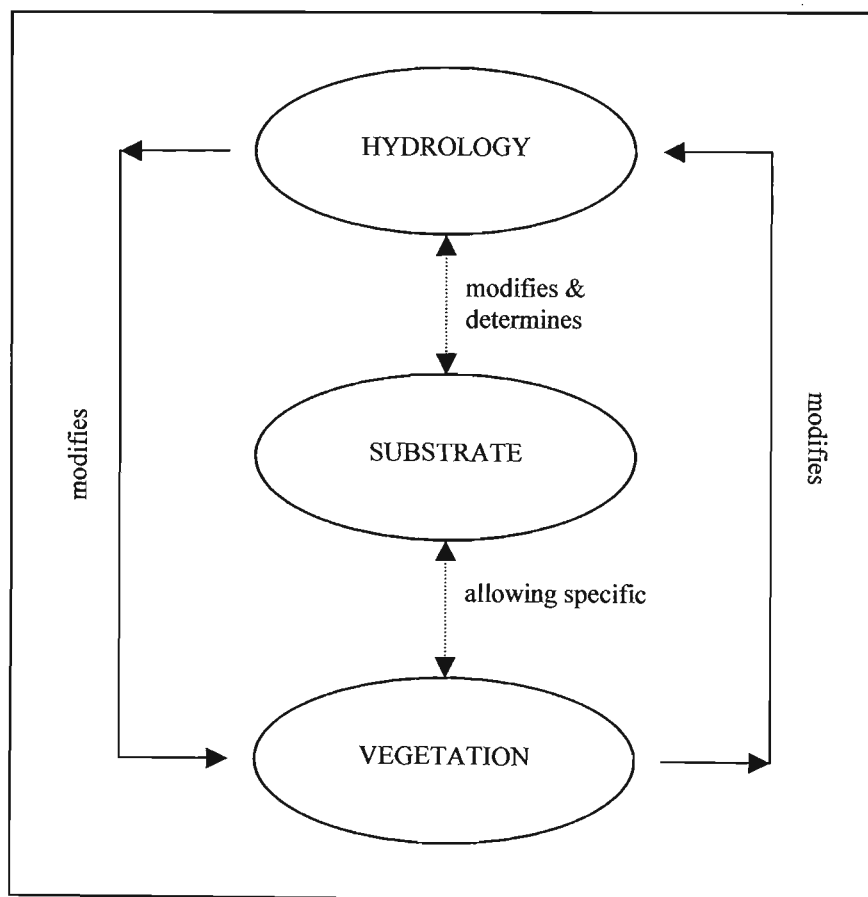
Figure 2.2 A conceptual model of wetland pattern and process (adapted from Gosselink & Turner, 1978).

The hydrological regime can be characterized by four attributes: source, velocity, renewal rate and timing (Gosselink & Turner, 1978). The source and velocity components play an important role in determining the solute composition of wetland inflow and the ability of that flow to transport suspended material that contributes to depositional and/or erosional processes. The renewal rate and timing (the hydroperiod) of a wetland describes the frequency and depth of inundation. The rise and fall of surface and subsurface water determines the characteristics of each type of wetland and the consistency of this pattern ensures stability of wetland patterns and processes (Mitsch & Gosselink, 1993).

The hydrological regime of a wetland strongly influences the physical and chemical components of the substrate, primarily through limiting oxygen availability. When soils become saturated, anaerobic conditions occur. The reduction of oxygen diffusion within the soil usually manifests itself as a decrease in redox potential, which in turn influences biogeochemical processes by initiating chemical transformations (Mitsch & Gosselink, 1993; Mohanty & Dash, 1982). Transformations of nitrogen, phosphorous, sulphur, iron, manganese and carbon occur within this anaerobic environment and impact on plant growth and development (Armstrong, 1975). The alternation of aerobic and anaerobic conditions also reduces the decomposition rate of organic matter, leading to an increase in the accumulation of organic matter in the soil. The organic matter content of a soil is therefore a good indicator of inundation frequency (Mitsch & Gosselink, 1993).

The vegetation component is reliant on the combination and interaction of both hydrological and substrate conditions. These two variables influence the spatial heterogeneity of the landscape by creating a diverse range of environmental conditions, which are reflected in the distribution of plant communities. These communities also reflect internal interactions between component species that buffer and isolate the community from extreme fluctuations in external environmental conditions (Breen *et al.,* 1988). This feedback can result in the modification of the original hydrological and substrate variables (Fig. 2.2). A change or perturbation in any of the three component variables can thus be expected to alter wetland patterns and processes.

2.4.2 Floodplain Patterns and Processes

An examination of wetland patterns and processes at the next higher, spatially coarser level (the reference level) allows one to consider the interactions between hydrology, substrate and vegetation at a broader scale of observation. First order landscape elements, which in this study comprise plant communities, examined at the level of the grain, can be clustered at the reference level by considering units that are functionally similar. In this study hydrology, substrate and vegetation interactions are examined against the template of a floodplain environment.

Many recent studies of floodplain environments have established that vegetation distribution is correlated to hydrological gradients (Heeg & Breen, 1982; Breen *et al.,*1988; Rogers & van der Zel, 1989; Coetzee *et al.,*1993; Ellery *et al.,*1993; van Coller *et al.,*1997; Selinger-Looten *et al.,*1999). Floodplain hydrology is characterized by a flooding regime in which the river overtops its banks and inundates the surrounding floodplain (Malanson, 1993). Distinct changes in frequency, duration and depth of flooding exist along a gradient from the river channel to terrestrial upland (Rogers, 1997; van Coller *et al.,*1997). The physical and chemical properties of wetland substrates are determined by this inundation gradient, which leads to the aggregation of tolerant vegetation types with distance away from and elevation above the thalweg (Rogers, 1995; Higgins *et al.,*1996; Higgins *et al.,*1997; Diederichs & Ellery, 2001). In studies where there is a scarcity of hydrological information vegetation distribution and micro-topography are often used as surrogates for hydrological characteristics (Rogers, 1995; van Coller *et al.,*1997; Diederichs & Ellery, 2001).

Sedimentation patterns and sediment properties within the floodplain environment are dependant on, and influenced by, the nature of the hydrological regime. Floodplains are located in the lower reaches of drainage systems where gradients are typically low, resulting in the deposition of sediment (Reineck & Singh, 1975; Malanson, 1993). Sediment is deposited when the flow velocity falls below the minimum velocity required to keep particles of a certain size in motion. Thus, when current velocity is reduced by a shallower gradient, or when overbank flooding occurs, the coarsest sediment particles are deposited first and progressively finer particles are deposited further away as current

velocity continues to decrease (Knighton, 1984; Hamblin, 1992). This deposition process results in a mosaic of different textured sediments across the floodplain surface, which in turn influences substrate properties (Malanson, 1993). Coarse-grained soils or sands are more permeable and thus better drained than fine-grained clays, resulting in concomitant zones of soil saturation that are suitable to specifically adapted plant community types (Mitch & Gosselink, 1993; Rogers, 1995; Higgins *et al.,*1997).

These hydrological and sedimentological processes interact to create a unique floodplain topography comprising a diverse range of geomorphic landforms. These include *inter alia*:

(1) Meander scroll bars, which are a series of elevated depositional features separated by depressions on the convex side of channel bends. They are formed as the channel migrates laterally across the floodplain.

(2) Oxbow lakes, which are bodies of standing water that are formed as a result of the cutoff of a meander bend by erosional and depositional processes typical of meandering rivers.

(3) Natural levees, which are elevated depositional features adjacent to the channel that are formed when coarse materials are deposited on the channel rim during overbank flow.

(4) Backswamps, which are low-lying basins characterized by the accumulation of fine sediments and saturated soils that occur in areas behind channel levees.

(5) Lateral lakes, which are formed when levees of the main channel are deposited across the mouths of tributary streams, resulting in permanent open water bodies (Leopold *et al.,*1964; Wetzel, 1983; Mitch & Gosselink, 1993).

Such fluvial landforms are spatially and temporally dynamic, thereby creating a constantly changing template of environmental conditions that is reflected in a mosaic of vegetation types (Rogers, 1995; Higgins *et al.,*1996; Rogers & Bestbier, 1997; van Coller *et al.,*1997).

The ecological patterns and processes that operate within the floodplain environment are determined by the interaction and feedback between inundation patterns, sedimentation processes, topography (and therefore geomorphology), and vegetation distribution. A change in any one of these components can have a knock-on effect, resulting in the alteration of other components in the landscape, and ultimately can lead to alteration of

floodplain patterns and processes. Wetlands in general, and floodplains in particular, are prone to change and disturbance because they are dynamic ecosystems. They also tend to be extremely productive systems and are therefore heavily utilized by humans in a variety of ways (Bruwer & Ashton, 1989; Davies & Day, 1998; Heeg & Breen, 1982; Klimas, 1988; Kotze & Breen, 1994). According to Bootsma (2000) anthropogenic disturbances cause three major types of pressures on wetland / floodplain ecosystems, namely, the transformation of the land surface, for example through drainage and canalization; the alteration of biogeochemical cycles, for example by pollution with nutrients and pesticides; and the modification of biological resources such as over-utilization of renewable resources, overgrazing and/or the introduction of alien species displacing indigenous species.

2.5 Conclusion

Very little research in southern Africa explicitly examines wetland and floodplain environments from a landscape ecology perspective. The few exceptions include studies by Rogers & Bestbeir (1997) on the Sabie River and Higgins *et al.* (1996) on the Nyl River floodplain. As was evident in these studies, in order to gain a broad understanding of the heterogeneity and dynamics of an ecological system such as a floodplain, one must take cognizance of the hierarchical organization of the landscape. The grain of the floodplain environment can be examined via the component variables of wetland patterns and processes. These variables can give rise to functionally similar units when examined against the template of a floodplain environment, thus providing insight into ecological patterns and processes operating at the reference level of the landscape mosaic.

CHAPTER 3 STUDY AREA

3.1 Introduction

Ecological patterns and processes operating at larger scales within a landscape serve to define and constrain spatial heterogeneity and dynamics within the finer levels of the landscape hierarchy (Urban et al., 1987; Kotleir & Wiens, 1990; Higgins et al., 1996). In this chapter, two of these larger or higher levels are described, namely the extent and context (Fig. 2.1), which together provide the background to the study area. The upper most level, the extent, is the largest scale of heterogeneity to which the grain responds and is constrained, while the context defines ecological patterns and processes operating at the reference level (Kotleir & Wiens, 1990). Descriptions of the climate, geology, geomorphology, hydrology, vegetation and landuse that constrain and define the ecological interactions operating within the lower Mkuze River floodplain provide a template that is crucial to our understanding of the finer scale functioning of the system.

3.2 Location

The lower Mkuze River floodplain and its associated wetlands are located east of the Lebombo Mountains on the Maputaland Coastal Plain in northern KwaZulu-Natal, South Africa (approximate location: 27° 45'S; 32° 30'E). This study focuses on that part of the lower Mkuze River floodplain from Muzi Pan in the west to the Mkuze Swamps in the east. The northern boundary includes the southern portion of the Manzibomvu Streams that drain towards the Mkuze River from the north, while the southern boundary is defined by the confluence between the Mkuze River and the Mpempe Canal (Fig. 3.1).

Following the Cowardin wetland classification system adapted for South Africa (Dini et al., 1998), the lower Mkuze River floodplain is classified as a combination of both lacustrine and palustrine wetlands. Lacustrine wetlands include permanently flooded lakes such as those located north of the Mkuze River i.e. the Muzi, Yengweni and Mdlanzi Pans. The rest of the system falls within the palustrine category, subsystem floodplain. Floodplain systems can be further divided into type according to Noble & Hemens (1978). They classified the Mkuze River as a storage floodplain wetland characterized by a riverine area and an adjacent seasonally inundated floodplain that retains water for long periods
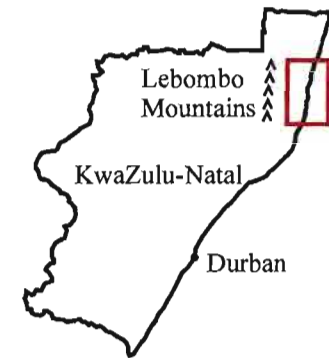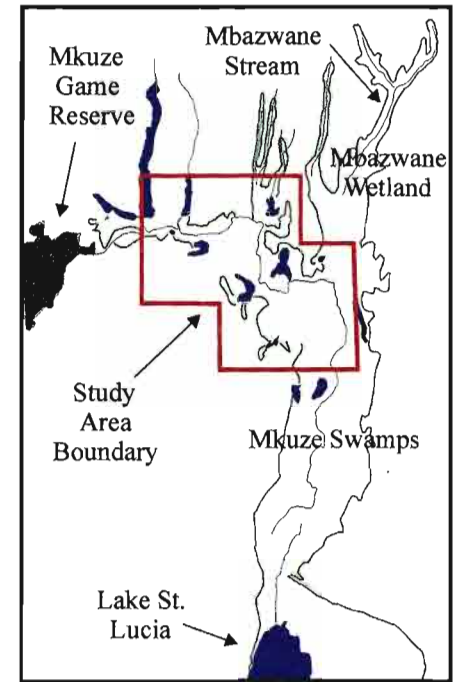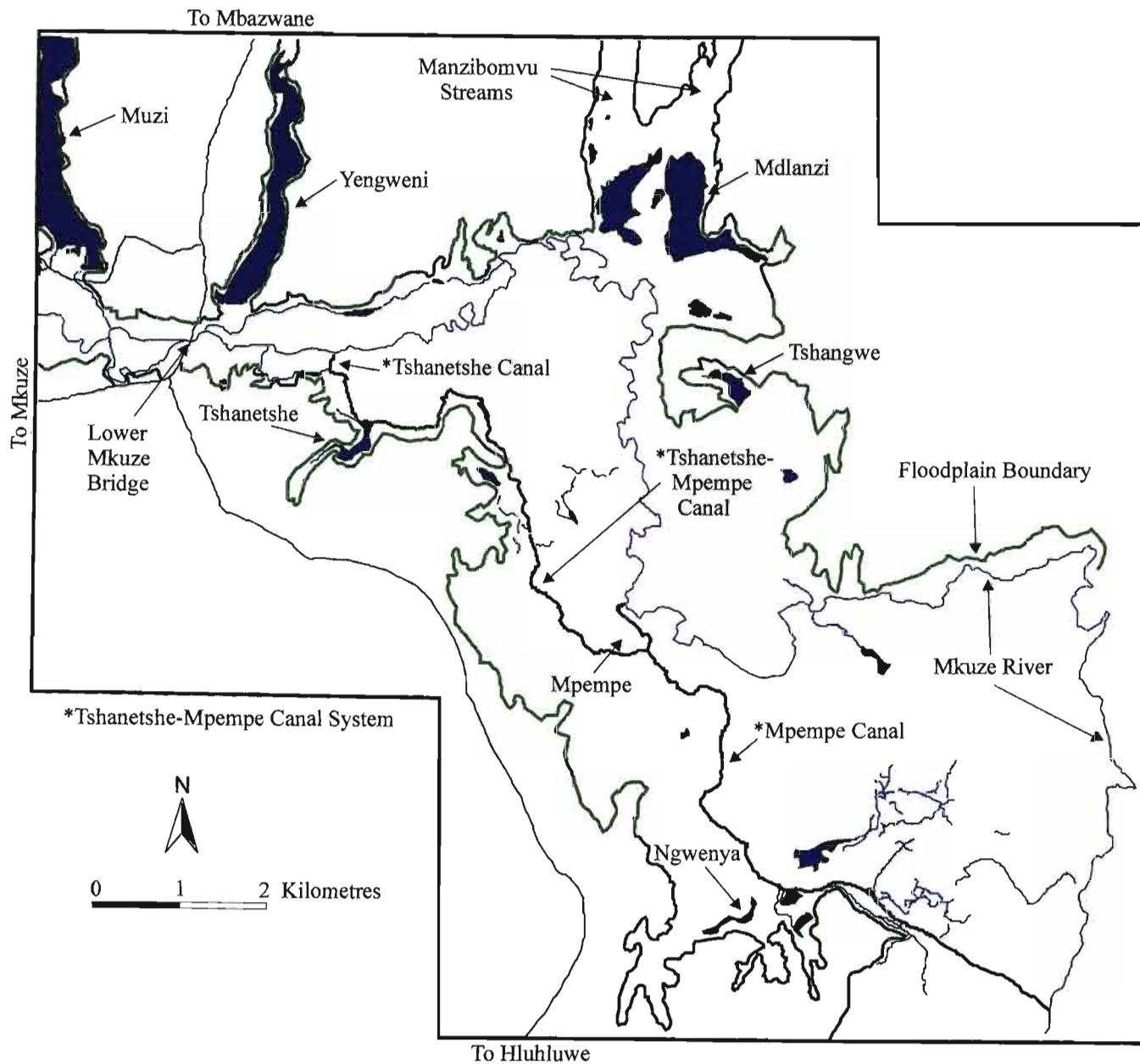
Figure 3.1 Location of study area.

between floods. Thus the lower Mkuze River floodplain comprises a mosaic of different wetland types (Rogers, 1995).

3.3 Extent

3.3.1 Climate

The climate of Maputaland is subtropical with hot, wet summers and mild, drier winters. The mean annual temperature of the coastal plain ranges from 20 to 23°C (Low & Rebelo, 1996). Maximum summer temperatures occur in January, with typical values of approximately 30°C, while minimum winter temperatures, averaging approximately 17°C, occur between June and July (Low & Rebelo, 1996). High temperatures are usually accompanied by high humidities. Average humidities range from 97.9% (8am) to 76.6% (2pm) in the summer months and between 91.8% (8am) and 50.8% (2pm) in the winter months. Evapotranspiration rates are high with a maximum of 189.4 mm in January and a minimum of 82.3 mm in June. The prevailing winds tend to be sub-parallel to the coast i.e. blow in a north-easterly or south-westerly direction (Watkeys et al., 1993).

An east-west rainfall gradient is apparent across the coastal plain. Along the coast annual rainfall averages 1000 mm.yr^{-1}. This progressively decreases to 600 mm.yr^{-1} at the foot of the Lebombo Mountains and then increases again to 800 mm.yr^{-1} at the mountain crest (Maud, 1980; McCarthy & Hancox, 2000). Approximately 60% of the rain falls in the summer months and is usually attributed to cold fronts moving northwards along the coast. Floods result from prolonged rainfall events associated with either cutoff lows or tropical cyclones. The most severe cyclone in recent history that affected the Maputaland Coastal Plain within South Africa was Cyclone Domoina that resulted in widespread flooding in 1984 (Taylor, 1991).

3.3.2 Geology

Maputaland is underlain by Mesozoic, Tertiary and Quaternary sequences (Watkeys et al., 1993; Fig. 3.2). The development of the Maputaland Coastal Plain was initiated by the break-up of Gondwanaland, approximately 180 Ma during the Mesozoic (Watkeys, 2000). The Lebombo Mountains, which fringe the western boundary of the coastal plain in northern KwaZulu-Natal, were formed during this period by the extrusion of volcanic lava
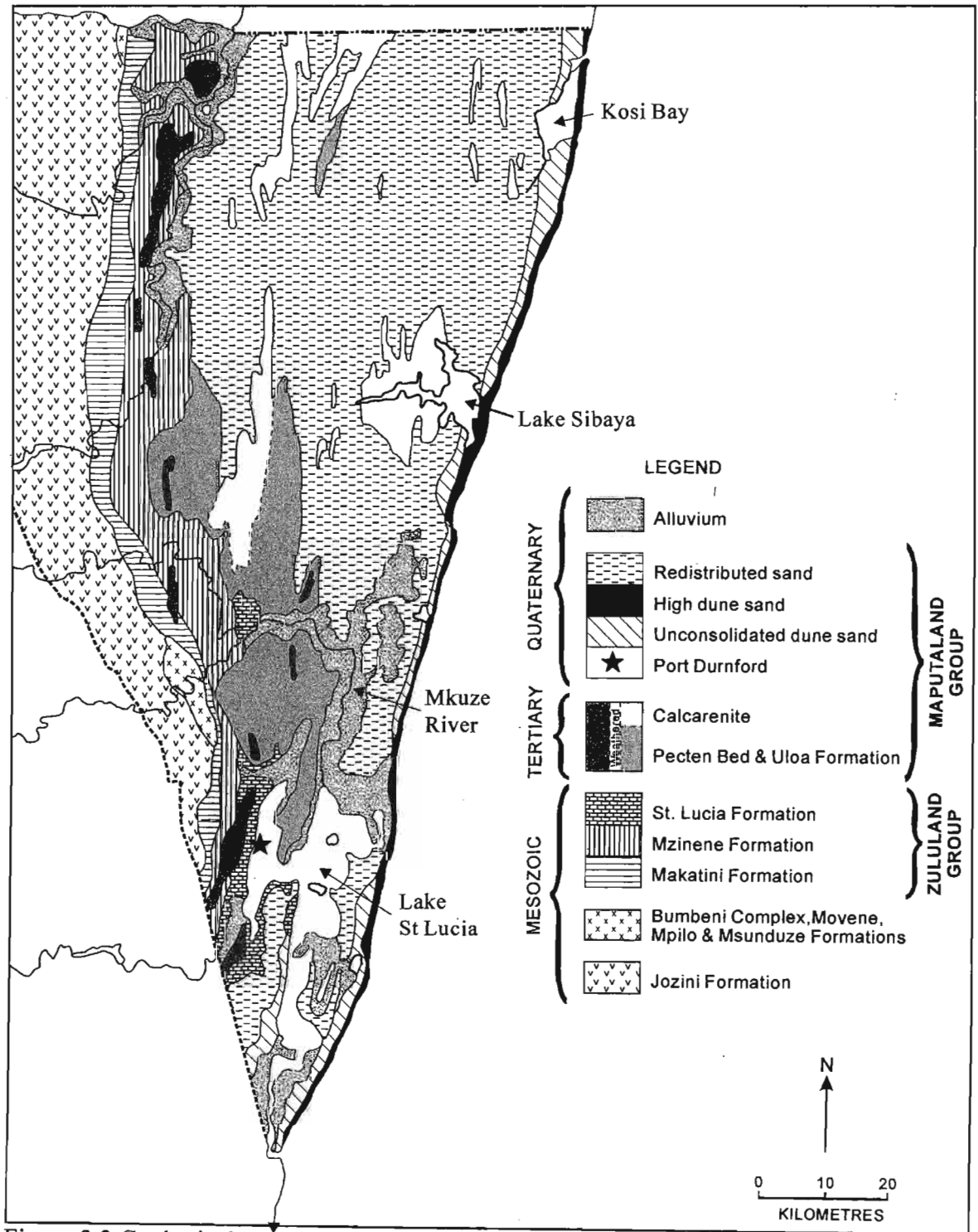
Figure 3.2 Geological sequences of the Maputaland Coastal Plain
(adapted from Watkeys *et al.*, 1993)

along the continental rift line. The oldest outcrops from the Lebombo Mountains comprise the Jozini Formation rhyolites (179 Ma) of the Lebombo Group, which falls within the upper part of the Karoo sequence (Watkeys *et al.*, 1993).

These igneous rocks are unconformably overlain by terrestrial and marine sediments of the Zululand Group, which comprise three formations exposed in north-south striking zones that abut the eastern foothills of the Lebombo Mountains (Hobday, 1979). These formations include the lower Cretaceous Makatini Formation (120 to 114 Ma), the Mzinene Formation (112 to 91 Ma) and the St Lucia Formation (85 to 65 Ma; Watkeys *et al.*, 1993).

These Cretaceous rocks are overlain by the Maputaland Group sedimentary rocks of the Neogene (10 Ma) and Quaternary periods. The Maputaland Group comprises the richly fossiliferous Uloa Formation that is overlain by coquina limestone with calcareous debris of the Pecten Beds. This in turn is overlain by calcarenite beach deposits. Pleistocene sediments of the Port Durnford Formation overlay these Neogene formations and consist primarily of mudstone, lignitic clay, sand and corals laid down about 120 000 years BP. The age of this formation co-incides with the Eemain high sea levels and it is largely covered by unconsolidated and redistributed dune sand (Maud, 1980; Watkeys *et al.*, 1993).

From the Eemian high (120 000 years BP) to 20 000 years BP a series of marine regressions and transgressions took place (Watkeys *et al.*, 1993). In combination with the cyclic deposition and erosion of the unconsolidated Quaternary sands, this resulted in the formation of linear north-south trending dune ridges, representing former shorelines (Natal Parks Board, 1996). These marine regressions resulted in the rejuvenation of the lower courses of rivers draining the coastal plain. The resultant incised valleys were flooded during subsequent transgression periods (Hobday, 1979; van Heerden, 1986; Botha, 2000).

3.3.3 Vegetation

The vegetation of the Maputaland Coastal Plain is classified by Low & Rebelo (1996) as Coastal Bushveld-Grassland, which comprises a mosaic of forest patches set in a grassland-savanna matrix. This vegetation type has a high biodiversity because it lies

within a tropical / sub-tropical transition zone and is exposed to east-west environmental variation, such as the rainfall gradient, across the coastal plain. According to Watkeys *et al.* (1993) this variation, especially in the underlying geology, has produced six distinct vegetation zones (Fig. 3.3). Grassland on shallow upland soil, forest on deeper soils and mixed woodland on soils of Cretaceous origin characterize the western most region, the Lebombo Zone. The vegetation of the Cretaceous-Tertiary Zone varies from *Acacia* dominated wooded grasslands on upland sites to low but dense thicket on the valley floors dominated by *Acacia spp* and *Euclea spp.* The Sand Forest Zone occurs on poorly developed soils of Tertiary and Quaternary origin. The vegetation of this zone comprises three types; mixed bushveld occurring on red sands, a mixed broad-leafed woodland that occurs on paler sands with a high water table, and a short, dry deciduous forest community occurring as a mosaic of forest patches within a matrix of open woodland.

The Palm Zone is found in low-lying gently undulating terrain with poorly drained sandy to sandy-clay soils. The vegetation comprises scattered Ilala palms (*Hyphaene natalensis*) in a grassland matrix. The Coastal Lakes and Wetland Zone is found where the terrain is gently undulating and the water table is generally high, resulting in the formation of numerous shallow seasonal pans in interdune depressions. The vegetation comprises a mosaic of different wetland types. The Coastal Dune Zone forms the eastern margin of Maputaland and consists of a cordon of high coastal dunes that are densely vegetated with coastal dune forest (Watkeys *et al.,* 1993). The current study area straddles both the Palm Zone and the Coastal Lakes and Wetland Zone.

3.4 Context
3.4.1 Local Geology and Geomorphology
The formation and configuration of the present lower Mkuze River floodplain is the result of a series of marine regressions and transgressions that took place from 120 000 to 20 000 years BP. The resultant dune cordons, representing former shorelines, impeded the flow of the paleo-Mkuze River causing it to alter its flow from a seaward bound easterly orientation to a southerly direction draining into Lake St Lucia (Meyer, 2000; McCarthy & Hancox, 2000).
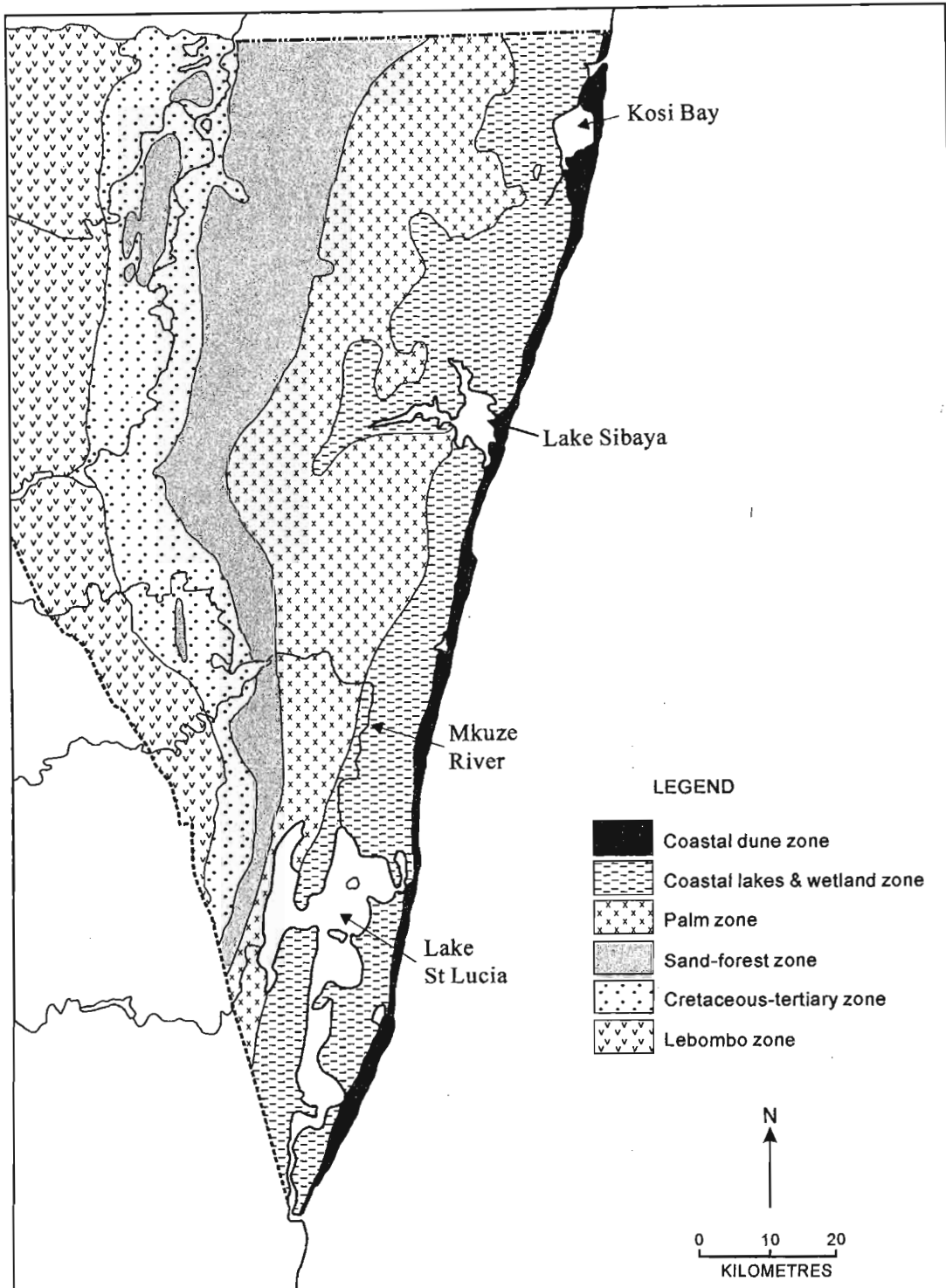
Figure 3.3 Vegetation zones of the Maputaland Coastal Plain
(adapted from Watkeys *et al.*, 1993).

The lower Mkuze River floodplain occupies a drowned valley incised into Quaternary deposits (van Heerden, 1986). Valley infilling continues at present as the river attempts to establish a graded equilibrium after the last marine transgression (approximately 9000 years BP). This process is evident in the west to east progradation of the lower reaches of the Mkuze River floodplain into the Mkuze Swamps. It is this progradation that has blocked off interdune tributaries resulting in the formation of linear pans and swamps such as Muzi and Yengweni Pans (McCarthy & Hancox, 2000).

Not only is the floodplain aggrading laterally but also vertically. The low gradients of the coastal plain and the moderate clastic loads transported across the floodplain surface by the Mkuze River have contributed to levee formation and vertical floodplain aggradation. During flooding these levees are overtopped, resulting in inundation of the floodplain that is accompanied by sediment deposition (Watkeys *et al.,*1993). Gradually, as a consequence of differential sedimentation on the floodplain, channel avulsion occurs (McCarthy & Hancox, 2000). This process of avulsion has a long history in the lower Mkuze River floodplain and has created a number of interchannel depressions that contain pans such as the Mpempe Pan (Maud, 1980; McCarthy & Hancox, 2000). As the river switches its course new pans are created and others destroyed. Thus, pan formation and subsequent infill are a dynamic process within this system (van Heerden, 1986). The major geomorphic landforms present within the lower Mkuze River floodplain are the river channel, the floodplain and its associated pans and swamps.

After being constrained by the Lebombo Mountains, the floodplain east of Muzi Pan widens and channel shape and orientation is highly variable. Based on this variation the Mkuze River can be divided into three reaches. The first reach extends in an east-west direction from Muzi Pan to Mdlanzi Pan. Here the channel is straight, relatively wide and deep, with high levees. In the second reach (between Mdlanzi and Mpempe Pans) the channel orientation is north-south. Here the channel becomes highly sinuous and narrower, although it maintains the same depth and levee height. The third reach extends from Mpempe Pan to the margin of the Mkuze Swamps. Once again the channel is east-west orientated and is relatively straight. However, it becomes increasingly shallower and less distinct (McCarthy & Hancox, 2000).

The geologic nature of the Mkuze River catchment plays an important role in the chemical composition and the physical characteristics of surface inflows across the floodplain surface. The Mkuze River is characterised by moderate clastic loads with high conductivities, ranging between 0.3 to 3.2 $mS.cm^{-1}$, with a mean value of 1.5 $mS.cm^{-1}$ (Stormanns *et al.,*1987). Clastic sediment entering the floodplain via the Mkuze River consists primarily of suspended silt and clay. Sedimentation in the upper section of the lower Mkuze River floodplain is evident in levee formation, and in the lower sections by the prograding nature of the floodplain eastwards into the Mkuze Swamps (McCarthy & Hancox, 2000).

3.4.2 Hydrology

The hydrology of the Mkuze River has not been examined in detail and there is only descriptive hydrological information for the floodplain and associated wetlands below the lower Mkuze River Bridge. The primary hydrological input into the lower Mkuze River floodplain is surface inflow, with direct rainfall onto the floodplain and groundwater inflows playing minor roles. Surface inflows primarily originate from the Mkuze River, which is approximately 300km in length, with a drainage basin covering $4820km^2$ (Watkeys, 2000). The source of the Mkuze River lies east of Vryheid in KwaZulu-Natal, runs through the Lebombo Mountains across the coastal plain and into Lake St Lucia (Watkeys *et al.,*1993). The Mkuze River is characterized by highly variable flows with mean annual flows that vary from 211 to 326 x 10^6 m^3 (Stormanns *et al.,*1987). This variation is due to the rainfall gradient that exists across the coastal plain and the seasonal nature of rainfall within the Mkuze River catchment. During the summer rainfall season the Mkuze River regularly overtops its banks and inundates the surrounding floodplain. During the winter months of most years there is little to no flow (McCarthy & Hancox, 2000).

Other sources of inflow include those from the Manzibomvu Streams draining into Mdlanzi Pan and the eastern fringes of the floodplain (Stormanns *et al.,* 1987). These streams are predominantly groundwater fed and are located between paleo-dune ridges north of the Mkuze River where the water table, relative to the surrounding floodplain, is elevated. This elevation causes localized groundwater seepage into interdune depressions

forming and recharging wetlands (Watkeys *et al.,*1993; McCarthy & Hancox, 2000). The Mbazwane Stream, the largest of the Manzibomvu Streams, contributes approximately 5 to 8 % to the Mkuze River's mean annual flow (Stormanns *et al.,*1987).

3.4.3 Vegetation

Very few studies specifically investigating vegetation distribution and ecology have been undertaken in the lower Mkuze River floodplain and surrounding areas. These studies include a descriptive account of vegetation distribution across the northern section of the lower Mkuze River floodplain by Tinley (1976), a semi-quantitative account of the vegetation ecology of the Greater Mkuze Wetlands by Stormanns *et al.* (1987), the classification and distribution of plant communities within the Mbazwane Wetland by Schoultz (2000) and the relationship between plant community distribution and environmental conditions surrounding Mdlanzi Pan by Taylor (2000).

Tinley (1976) provided a detailed description of the distribution of eight vegetation types that were encountered along a cross-section that extended from the foothills of the Lebombo Mountains to the Mbazwane River that lies to the east of the present study area. Approximately a quarter of the area covered by Tinley (1976) falls within the current study area, the majority of which includes the pans north of the Mkuze River i.e. Muzi, Yengweni and Mdlanzi Pans. Reeds such as *Phragmites mauritianus* and *Echinochloa pyramidalis* fringed the edges of both the Muzi and Yengweni Pans. *Acacia xanthophloa* formed a boundary between floodplain and terrestrial upland along the edges of Muzi Pan. *Cyperus spp., Imperata cylindrica* and small patches of reeds dominated the area surrounding the Manzibomvu Streams and Mdlanzi Pan.

The Greater Mkuze Wetlands as defined by Stormanns *et al.* (1987) includes the lower Mkuze River floodplain of the current study, the Mbazwane Wetland, north-east of the lower reaches of the Mkuze River floodplain, and the Mkuze Swamps, north of Lake St Lucia. This study identified 14 plant communities within four broad vegetation types; hygrophilous grassland, marsh, swamp and forested wetland habitats. Four of these 14 communities were found within the current study area, namely a *Ficus sycomorus-Rauvolfia caffra* community, an *Echinochloa pyramidalis* community, a *Cyperus papyrus*

community and an *Acacia xanthophloea-Cynodon dactylon* community. Vegetation distribution was related to water source (Mkuze River vs Manzibomvu Streams) as well as dune formation, sea level fluctuations, flooding, subsidence, channel switching and sedimentation (Stormanns *et al.,* 1987).

Schoultz (2000) examined plant community distribution within the eastern portion of the Mbazwane Wetland, which forms the north-eastern boundary of the current study area. Nine plant communities were identified in this study and were clustered into three broad groups, namely swamp forest, emergent herbaceous swamp/marsh and grassland floodplain. Depth and duration of flooding, substratum type and the occurrence of fire determined the distribution of plant communities.

The study by Taylor (2000) comprised a small section within the current study area, focusing primarily on the Mdlanzi Pan and its associated drainage lines to the north of the Mkuze River. Five plant communities were identified including two swamp communities, a swamp fringe community, a grassland community and an open woodland community. The environmental determinants of plant community distribution were related to substratum type, depth to water table and distance to water's edge.

3.4.4 Land Ownership and Use

The primary landowners and users within and surrounding the lower Mkuze River floodplain are the rural community of Mnqobokazi and the Ezemvelo KwaZulu-Natal Wildlife (formerly Natal Parks Board; Andren, 2001). The floodplain to the west and south of the Mkuze River falls under the jurisdiction of the Mnqobokazi tribal authority. The village of Mnqobokazi has a population of approximately 5800 inhabitants, the majority of which are under the age of 15 years. Just less than half the population is unemployed and those that are employed earn very low incomes (Andren, 2001). The most common means of income generation is through the selling of agricultural products and raw materials for the craft industry. Subsistence agriculture is the main landuse in this area. Crops such as sugar cane, maize, bananas and vegetables are cultivated within the floodplain, and the wetlands are used as winter grazing for cattle and goats. Wetland resources such as water,

soil, reeds, medicinal plants, fish and waterfowl are utilized by the residents of the village (Taylor, 1986; Goodman, 1987; Holland *et al.*, 1989; Koaleli, 1999).

In recent years two major changes in agricultural practice on tribal land have occurred. Firstly farming has recently become more mechanized as tractors are being used for ploughing. This has led to the planting of cash crops and the expansion of land under cultivation including land within the lower Mkuze River floodplain (Taylor, 1986). Secondly an increasing number of households cultivate gum trees (*Eucalyptus saligna*) in small woodlots of less than 1 ha. Community members enter into a partnership with commercial forestry organizations to which they resell grown trees. Community members have already noticed the impact of these woodlots on local water supply (Andren, 2001).

The portion of the lower Mkuze River floodplain that is controlled by the Ezemvelo KwaZulu-Natal Wildlife lies to the east of Muzi Pan and to the north of the Mkuze River (Holland, Alletson & Leitch, 1989). One of the roles of Ezemvelo KwaZulu-Natal Wildlife is to conserve and manage state land that is not formally within protected areas. One of the significant values of the Greater Mkuze Wetland System is that it is one of the major sources of freshwater to Lake St Lucia (Stormanns *et al.*, 1987). However a history of mismanagement in this regard has resulted in the alteration of the hydrological regime within the lower Mkuze River floodplain (Alexander, 1986; Taylor, 1986; Goodman, 1987).

In the late 1960s Lake St Lucia experienced hypersaline conditions as a result of severe drought that was thought to pose a threat to the lake ecosystem. In order to increase the supply of freshwater to St Lucia, the Natal Provincial Administration's Reclamation Unit excavated the Mpempe Canal during 1970-71 (Fig. 3.1). The purpose of the canal was to shorten the route of flow into Lake St Lucia by circumventing the northern portion of the lower Mkuze River floodplain and wetlands. In so doing, the increased inflow of fresh water from the Mkuze River would dilute the high salinity levels. However, the canal was poorly designed and resulted in a number of negative impacts. These included:

- The formation of an actively eroding canal and its subsequent enlargement (Goodman, 1987).

- The deposition of large volumes of sediment in the area surrounding Ngwenya Pan (Alexander, 1986; Goodman, 1987).

- The conversion of Mpempe Pan from a permanent water body in 1973 to a dry pan (Alexander, 1986).

- The alteration of natural flooding regimes of certain wetlands including Tshangwe and Ngwenya Pans (Alexander, 1986; Goodman, 1987).

- The prevention of the free movement of people and animals between fields and residences during high flow periods when the canal acts as a barrier (Loudon *et al.,*1987; Goodman, 1987).

- The initiation of an active nick point, eroding in a north-westerly direction along the southern floodplain boundary towards Tshanetshe Pan, which resulted in the formation of a distinct channel that has been termed the Tshanetshe-Mpempe Canal (Ellery *et al.,*in prep.; Fig. 3.1).

Management attempts to rectify the situation have proved ineffective and temporary (Alexander, 1986; Taylor, 1986; Goodman, 1987).

The area to the south of the Mkuze River channel and west of Tshanetshe Pan used to be privately owned farmland that with the aid of irrigation supported a variety of crops such as sugar cane, cotton and bananas (Goodman, 1987). The portion that falls within the study area consisted primarily of riparian forest that had a history of disturbance (Holland, Alletson & Leitch, 1989). In 1981 a large portion of the riparian forest below the lower Mkuze River Bridge was cleared by the landowner for the establishment of cotton plantations (Taylor, 1986; Goodman, 1987). This resulted in the activation of a scour channel that redirected floodwaters towards the Tshanetshe Pan and the backswamps south of the Mkuze River (Alexander, 1986). In 1986 a private farmer in the Tshanetshe area excavated a canal from the Mkuze River into Tshanetshe Pan for irrigation purposes. As a consequence water now passes freely from the Mkuze River into the Tshanetshe Pan and leaves via the Tshanetshe-Mpempe Canal. As a result approximately 80% of water during low flow periods is now being diverted from the north down to the southern portion of the floodplain. This new flow route has been termed the Tshanetshe-Mpempe Canal System (Ellery *et al.,*in prep.; Fig. 3.1).

CHAPTER 4 VEGETATION ECOLOGY

4.1 Introduction

One of the aims of vegetation ecology is to describe vegetation through classification and/or ordination in order to establish meaningful causal explanations of vegetation distribution in terms of underlying environmental variables (Mueller-Dombois & Ellenberg, 1974). Ecologists have used many techniques to achieve this aim. These techniques commonly form an integral part of ecological studies and are used to reduce and order large, multivariate data sets, into meaningful descriptions and explanations of ecological patterns and processes (ter Braak, 1996).

The vegetation ecology of the lower Mkuze River floodplain has not been thoroughly researched. Previous studies have largely focused on plant community descriptions of the area (Tinley, 1976; Stormanns, 1986; Stormanns et al.,1987; Stormanns & Breen, 1987; Schoultz, 2000; Taylor, 2000). This chapter aims to classify and describe the vegetation of the study area and determine the relationships between vegetation distribution and underlying environmental gradients.

4.2 Methodology

4.2.1 Data Collection

In April 1999 a reconnaissance survey of the study area was undertaken in order to familiarise the investigator with access routes, the range of possible plant assemblages, environmental gradients and the necessary sampling techniques. This initial knowledge was used to design appropriate sampling procedures to be used during the intensive data collection phase conducted in July 1999.

One hundred and ninety-eight plots were sampled in 14 transects within the study area. Transects were placed perpendicular to the local thalweg (the lowest point in a channel) and terminated at the wetland-terrestrial boundary, which was readily identifiable in the field by a change in vegetation and soil characteristics. Detailed delimitation of the wetland boundary using the soil morphology characteristics as ascribed by Kotze et al. (1994) was not carried out due to the large extent of the study area and time constraints. Transects

were placed at locations throughout the study area that took cognisance of the floristic diversity and environmental heterogeneity that was encountered during the reconnaissance survey (Fig. 4.1). Placement depended largely on accessibility, which was severely limited due to lack of roads and dense, impenetratable vegetation. Vegetation cover and environmental variables were sampled in plots that were distributed at approximately even intervals along each transect.

Plot size was established by determining the minimum plot size, which according to Mueller-Dombois & Ellenberg (1974) is defined as the "smallest area on which the species composition of the community in question is adequately represented". A nested system of sample plots indicated that a plot size of a 10m radius within forested areas and of a 3m radius in reed and grassland areas was adequate.

Mean species richness per sample plot was calculated for each plant community type. Although plot size varied, it was calculated according to the species-area curve i.e. plot size was determined when species richness reached a point when increasing size resulted in few additional species. Therefore a varying plot size should not negate comparisons of mean species richness per sample plot for each plant community type.

4.2.2 Vegetation Data

At every plot within each transect floristic composition and cover was recorded. A species list was compiled for each plot and voucher specimens of species not recognised in the field were collected for later identification. Plant species nomenclature follows Arnold and de Wet (1993). Estimated percentage cover of plant species was recorded using a modified version of the Braun-Blanquet Cover-Abundance Scale (Table 4.1; Mueller-Dombois & Ellenberg, 1974). This scale provided a simple, time efficient and quantitatively acceptable method of estimating plant cover, and is a useful sampling approach that is used to recognise and describe vegetation communities through classification and/or ordination (Mueller-Dombois & Ellenberg, 1974; Smith, 1990).
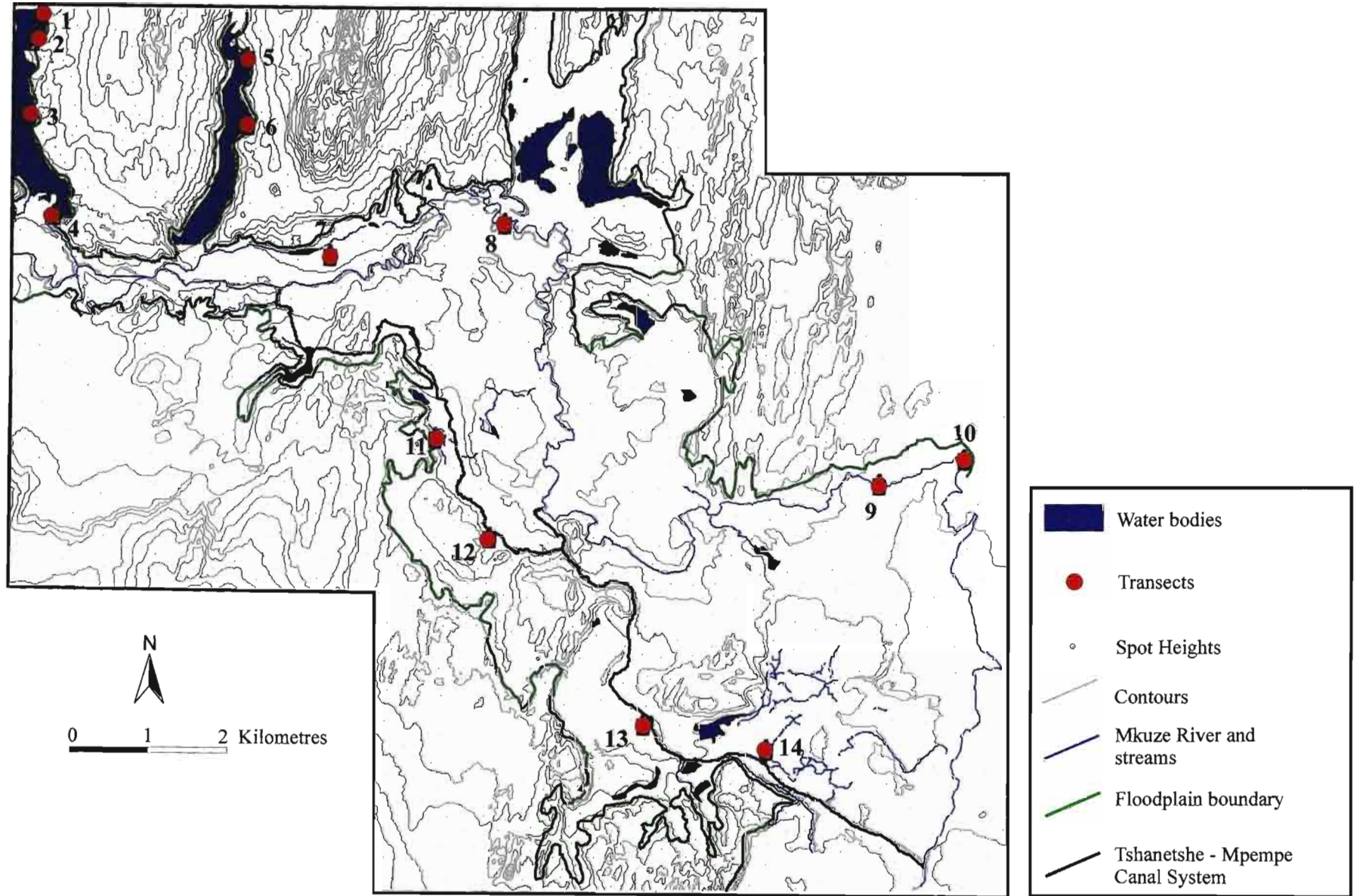
Figure 4.1 Location of transect sites.

Table 4.1 Modified Braun-Blanquet Cover-Abundance Scale.

Cover Class	Percentage Cover (%)	Cover Interval Midpoint (%)
1	0-2	1
2	2-5	3
3	5-10	8
4	10-25	19
5	25-50	39
6	>50	76

4.2.3 Environmental Data

Data on a variety of environmental variables were collected from each plot. The topographical profile for each transect was surveyed using a dumpy level and staff. Survey points corresponded to the centre of each sample plot. Distance from and relative elevation above the nearest thalweg were measured from these profiles for each plot. Surface soil samples (excluding surface litter) were randomly collected from each plot at a depth of approximately 10cm. Samples collected in the field were sub-sampled prior to further analysis based on similar aggregate stability, colour and texture. Soil sample characteristics of particle size and organic matter content were measured in the laboratory.

4.2.4 Data Analysis

4.2.4.1 Soil Characteristics

Soil texture characteristics were measured using the pipette particle size method. The underlying principles of this method are based on Stokes' Law which describes the relationship between particle diameter size and settling velocities. This law states that large particles settle more rapidly than small particles through a fluid of known density, allowing one to calculate the relative proportions of sand, silt and clay within a sample (Geographical & Environmental Sciences, 1998).

Each soil sample was prepared so that only the mineral fraction at a grain diameter size of finer than 2mm remained. This sample of known weight (40-50g) was mixed with distilled water and poured into a measuring cylinder and allowed to settle. At prescribed times, determined from Stokes' Law, aliquots of known volume were extracted, dried and

weighed. From these weights the percentage sand, silt and clay in the sample was calculated.

Organic matter content was measured using the Walkley-Black method. This is a chemical method where potassium dichromate digests organic carbon at a known rate. Potassium dichromate was added to soil samples weighing between 0.10 and 0.13g. A titration process measured the quantity of unused dichromate, from this the percentage of organic carbon in the soil samples was calculated (Geographical & Environmental Sciences, 1998).

Details of sample preparation, the pipette method and the Walkley-Black method are provided in Appendices 4.1, 4.2 and 4.3.

4.2.4.2 Classification

The primary aim of classification is to identify recurring patterns in vegetation composition and cover. These recurring combinations of similar species associations form the basis of plant community identification (Mueller-Dombois & Ellenberg, 1974; Gauch, 1982; Begon et al., 1990). The concept of the plant community has evolved over the years from a Clementsian view, where the ecological limits of each plant species comprising the community, coincides with the distribution of the community as a whole; to the now commonly accepted individualistic view originally espoused by Gleason who believed that each species is distributed independently of others along an environmental gradient (Ricklefs, 1990). In the latter case such communities are not precise entities with distinct boundaries. Therefore their delimitation is often solely determined for the practical consideration of vegetation description (Noss, 1987). In this study the purpose of the identification of plant communities was to provide a basis for a generalised description and summary of community level organisation within the landscape mosaic.

The diverse range of classification methods available to ecologists can be divided into two major approaches, namely non-hierarchical versus hierarchical. Non-hierarchical classification assigns each sample (or species) to a cluster, placing samples (or species) together based on their similarity. In addition to grouping similar entities, hierarchical methods arrange data in a hierarchical structure (Gauch, 1982). Hierarchical classification

can be either agglomerative or divisive. Agglomerative methods initially consider each sample (or species) as a separate group and then repeatedly combine similar samples (or species) until only a single group remains. Divisive methods initially assume all samples (or species) as one group and then proceed by repeatedly dividing groups of samples into two until all the units are individually separated (Digby & Kempton, 1987; Jongman *et al.,*1995). Divisive methods can be further described as either monothetic or polythetic depending on the technique of division employed. In monothetic methods each group division is based on the degree of dissimilarity of individual species. Polythetic divisions are based on all species, where groups are divided according to their score on the principal axis of an ordination. In 1975 a hybrid of these two methods was developed and was termed 'indicator species analysis'. It was subsequently modified and termed '**T**wo **W**ay **IN**dicator **SP**ecies **AN**alysis' (TWINSPAN; Hill, 1979; Gauch, 1982; Digby & Kempton, 1987). This technique first classifies samples, which in turn are used to obtain a classification of species according to their ecological preferences. These two classifications are then combined to produce a two-way table that arranges clusters in sequence according to their similarity (Hill, 1979).

Samples were classified on the basis of their species composition using the computer programme TWINSPAN (Hill, 1979). All default options were chosen with the exception of the following:

1. Six pseudospecies cut levels (0, 2, 5, 10, 25 and 50) were indicated instead of the recommended five, where the chosen cut levels corresponded to the cover-abundance scale used in this study (Table 4.1),

2. A number of samples were excluded from the analysis, including:
   - Samples 1 to 18 and 159-167, which initially fell within the defined study area but were subsequently excluded as the boundary limits of the study area were redefined.
   - Samples 95, 102, 110, 118, 168 and 177 were omitted as they formed a distinct aquatic community, which unduly influenced the TWINSPAN output,

3. The pseudospecies weightings were modified such that species cover values at the lowest level had a default weighting of 1, while those with cover values of 2-25%

had a weighting of 2 and those with cover values greater than 25% had a weighting of 3.

4.2.4.3 Ordination

Efforts to understand vegetation patterns along environmental gradients have led to a range of methods that aid the determination of vegetation-environment relationships (Mueller-Dombois & Ellenberg, 1974; Smith, 1990). Ordination is one method that allows the investigator to summarise community patterns and relate the distribution of sample sites to environmental gradients underlying plant species distribution (Begon et al., 1990; Ricklefs, 1990).

Ordination is an ecological tool that attempts to recover the underlying structure of species compositional data that is assumed to arise as a consequence of environmental heterogeneity (Jongman et al., 1995). The graphical output of ordination is a two dimensional arrangement of points, the coordinates of which are the sample (or species) scores computed during the ordination process (ter Braak, 1996). The arrangement of sample sites along the ordination axes is such that those samples close together correspond to samples of similar species composition and those samples far apart correspond to samples of dissimilar species composition. The ordination axes correspond to an assumed underlying environmental gradient(s) and are constructed in a way that maximises the dispersion of the sample (or species) scores. The ordination process also generates an eigenvalue for each axis which ranges from 0 to 1. Axes with eigenvalues greater than 0.5 are considered useful when trying to elucidate the environmental determinants of plant community distribution (Jongman et al., 1995). The ordination process also generates biplot scores for each environmental variable that can be superimposed on the ordination diagram. These variables are represented by vectors in relation to the ordination axes. The direction and length of the vector indicates a correlation between the distribution of sample (or species) scores and the rate of change of the environmental variable (ter Braak, 1996). The ordination process also generates a weighted correlation matrix that aids in the interpretation of the correlation between each ordination axis and the environmental variables.

Ordination techniques can be divided into two main groups, namely direct and indirect gradient analysis. Direct methods use species and environment data in a single, integrated analysis. Indirect methods use species data only and environmental interpretation is done as a separate step in the process. Both techniques can be further subdivided, on the basis of the underlying species response along environmental gradients, into linear or unimodal methods (ter Braak, 1996). The ordination techniques most widely used by community ecologists are the indirect techniques of principal components analysis (PCA), correspondence analysis (CA) and techniques related to CA such as detrended correspondence analysis (DCA; Jongman *et al.*, 1995). DCA, an indirect, unimodal ordination technique, was used to analyse the present data set and was carried out using the computer programme CANOCO (**CANO**nical **C**ommunity **O**rdination; ter Braak, 1988).

Species and sample data were written in FORTRAN format suitable for input into CANOCO. All programme defaults except the following were used:

(1) Samples omitted from analysis were the same as for the TWINSPAN classification,

(2) Square root transformation of species data was used and

(3) Rare species were down-weighted.

After the extraction of the ordination axes, sample dispersion was analysed in terms of the environmental variables measured in the field i.e. percent sand, clay and organic matter, and distance from and relative elevation above the local thalweg.

4.3 Results

4.3.1 Classification

Six plant communities, two of which include additional sub-communities, were identified from the TWINSPAN classification. These are indicated in bold within the following description of the dendrogram illustrating the TWINSPAN classification (Fig. 4.2). The full TWINSPAN output is presented in Appendix 4.4 and is summarised in Table 4.2, which includes species that occurred in more than 50% of the sites within any of the plant communities or sub-communities.

At the first level of division (eigenvalue = 0.692) the TWINSPAN classification divided the 165 samples into two groups (Group 2: n= 93-; Group 3: n= 72+). Group 2 was
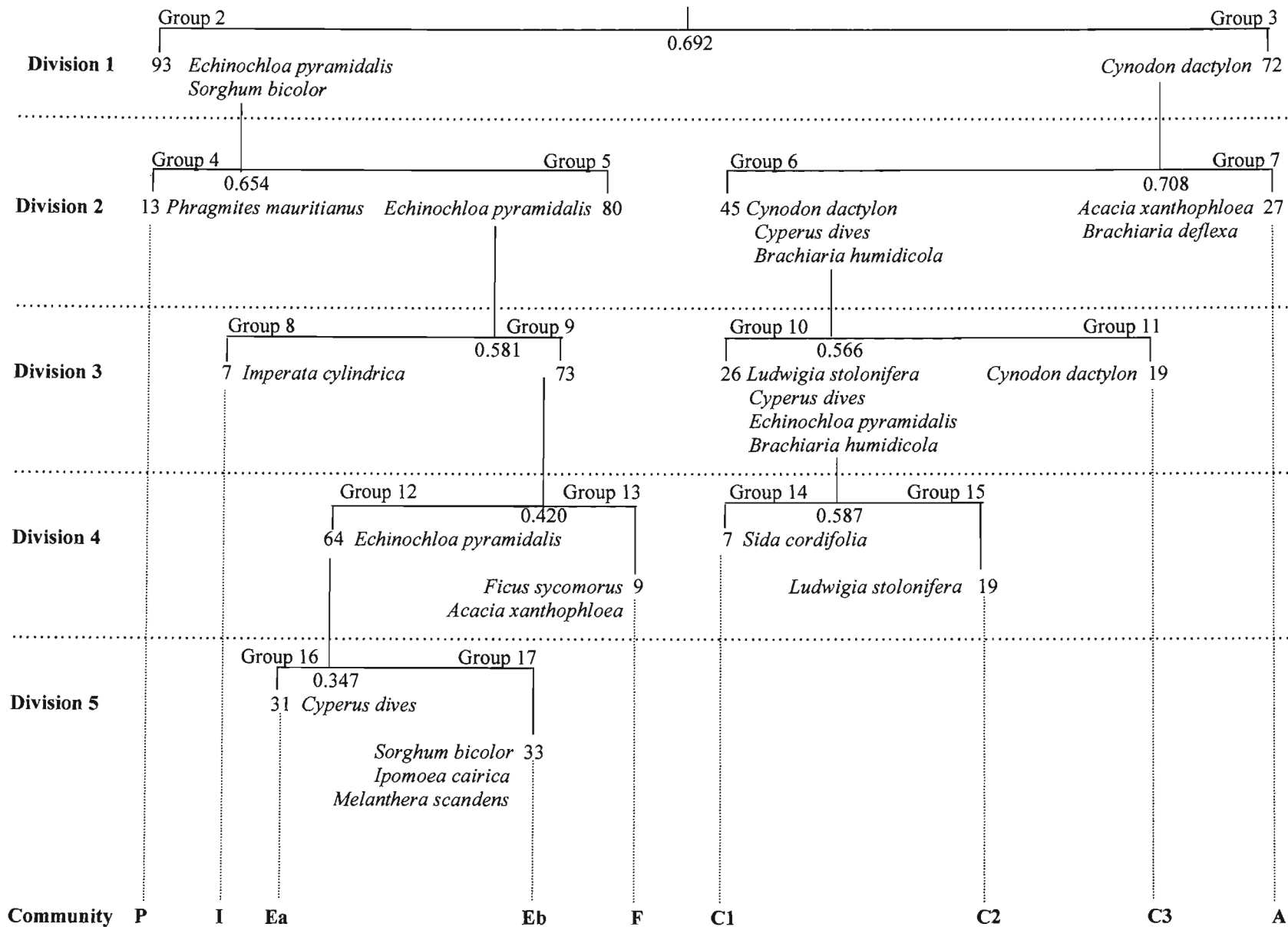
Figure 4.2 TWINSPAN dendrogram illustrating the hierarchical arrangement of plant community types (see text for full plant community names).

indicated by *Echinochloa pyramidalis* and *Sorghum bicolor* and Group 3 by *Cynodon dactylon*. These two groups represent two broad vegetation complexes within the study area, namely a marsh/swamp complex and a floodplain complex respectively.

The marsh/swamp complex (Group 2: n=93-) was further divided into a negative group (Group 4, n=13-) and a positive group (Group 5, n=80+). The latter group was indicated by *Echinochloa pyramidalis* and the former by *Phragmites mauritianus*. Samples indicated by *Phragmites mauritianus* could not be divided in a meaningful way at subsequent levels of division, and thus this group (Group 4: n=13-) was considered to represent the **Phragmites mauritianus reed swamp community (P)**. The floodplain complex (Group 3: n=72+) was divided at the second level of division into a negative group (Group 6, n=45-) with the following indicators: *Cynodon dactylon, Cyperus dives* and *Brachiaria humidicola,* and a positive group (Group 7, n=27+), indicated by *Acacia xanthophloea* and *Brachiaria deflexa*. Group 6 (n=45-) represents the **Cynodon dactylon floodplain community (C)** and comprises three sub-communities that are described at divisions three and four. Group 7 (n=27+) could not be divided in a meaningful way at subsequent levels of division, and thus was considered to represent the **Acacia xanthophloea woodland community (A).**

At the third level of division the samples in Group 5 (n=80+) were divided into a negative group indicated by *Imperata cylindrica* (Group 8, n=7-) and a positive group with no indicators (Group 9, n=73+). Subsequent divisions of the negative group (Group 8, n=7-) were not meaningful and thus this group was considered to represent the **Imperata cylindrica hygrophilous grassland community (I).** Also at division three the samples in Group 6 (n=45-) were divided into a negative group (Group 10, n=26-) indicated by the following common species: *Ludwigia stolonifera, Cyperus dives, Echinochloa pyramidalis* and *Brachiaria humidicola;* and a positive group indicated by *Cynodon dacylon* (Group 11, n=19+). *Sida cordifolia*, an indicator of disturbed areas, was preferentially associated with samples in Group 11 (n=19+) and was thus considered to represent a sub-community of the **Cynodon dactylon floodplain community (C)**, namely the **Cynodon dactylon moderately disturbed floodplain community (C3).**

Table 4.2: Summary of the TWINSPAN output showing species that occur in more than 50% of the sites within each plant community type.

Species Name	P $n=13$	I $n=7$	Ea $n=31$	Eb $n=33$	F $n=9$	C1 $n=7$	C2 $n=19$	C3 $n=19$	A $n=27$
Ipomoea mauritiana	12(1-5)								
Phragmites australis	8(1-3)								
Phragmites mauritianus	13(3-6)				4(1-2)				
Imperata cylindrica		7(4-6)							
Rhynchosia totta		4(1-3)							
Alysicarpus rugosus		7(1-2)							
Paspalum distichum		7(3-6)							
Setaria sphacelata		4(1-2)							
Chloris gayana		5(2-4)							
Echinochloa pyramidalis			31(3-6)	33(2-6)	9(1-5)		11(1-4)		
Persicaria senegalensis			16(1-3)						
Ipomoea cairica	6(1-4)			26(1-3)	6(1-3)				
Sorghum bicolor		3(1-2)		28(2-6)	6(1-3)				
Melanthera scandens	11(1-4)			17(1-3)					
Ficus sycomorus					6(3-4)				
Cyperus dives			15(1-5)			6(2-3)			
Cynodon dactylon						7(1-3)	16(2-6)	19(2-6)	
Brachiaria humidicola						7(1-4)			
Ludwigia stolonifera							14(1-3)		
Phyla nodiflora							13(1-4)		
Sida cordifolia				18(1-4)		7(5-6)		14(1-4)	
Brachiaria deflexa									18(2-6)
Acacia xanthophloea					4(1-6)				18(1-5)

The numbers (eg 4(1-2)) on the table indicate that the species occurs in 4 sites with a cover value ranging from 1 to 2 on the cover abundance scale. Refer to the text for full plant community type names.

At the forth level of division the samples in Group 9 (n=73+) were divided into a negative group indicated by *Echinochloa pyramidalis* (Group 12, n=64-) and a positive group (Group 13, n=9+) characterised by the common species *Ficus sycomorus* and *Acacia xanthophloea*. Group 12 (n=64-) represents the **Echinochloa pyramidalis backswamp**

community (E) and comprises two sub-communities that are described at division five. Samples in Group 13 (n=9+) could not be divided in a meaningful way at subsequent levels of division, and thus was considered to represent the **Ficus sycomorus riparian forest community (F)**. Also at level four, the samples in Group 10 (n=26-) were divided into a negative group indicated by *Sida cordifolia* (Group 14, n=7-) and a positive group described by *Ludwigia stolonifera* (Group 15, n=19+). Both groups were considered to represent sub-community types of the **Cynodon dactylon floodplain community (C)**, namely the **Cynodon dactylon highly disturbed floodplain community (C1)** and the **Cynodon dactylon undisturbed floodplain community (C2)** respectively.

At the fifth level of division the samples in Group 12 (n=64-) were divided into a negative group described by *Cyperus dives* (Group 16, n=31-) and a positive group (Group 17, n=33+), characterised by the following species: *Sorghum bicolor, Ipomoea cairica* and *Melanthera scandens*. Both groups were considered to represent sub-communities of the **Echinochloa pyramidalis backswamp community (E)**, namely the **Echinochloa pyramidalis-Cyperus dives undisturbed backswamp community (Ea)** and the **Echinochloa pyramidalis-Sorghum bicolor disturbed backswamp community (Eb)** respectively.

4.3.2 Ordination

Eigenvalues for each ordination axis are presented in Table 4.3. The first axis of the ordination was the most useful in terms of accounting for variation in the community data. The second and third axes accounted for less variation but were still considered useful while the forth axis, with an eignvalue less than 0.5, was not considered particularly useful.

Table 4.3: Eigenvalues of the DCA ordination axes.

Ordination Axis	Eigenvalue
Axis 1	0.68975
Axis 2	0.58348
Axis 3	0.52024
Axis 4	0.31334

The sample scores for axes 1 and 2 were plotted against each other in order to illustrate the arrangement of samples based on their species composition (Fig. 4.3). Sample scores on the first ordination axis ranged from −3.48 to +3.52 and on the second ordination axis from 2.55 to +3.46. Each sample score was labelled with the initial of the plant community type identified in the TWINSPAN classification in order to illustrate the relationship between plant communities and the arrangement of samples in the ordination diagram.

The *Phragmites mauritianus* reed swamp community (P) had low sample scores for axis 1 and scores close to zero for axis 2. The *Ficus sycomorus* riparian forest community (F), the *Imperata cylindrica* hygrophilous grassland community (I), the *Echinochloa pyramidalis-Cyperus dives* undisturbed backswamp community (Ea) and the *Echinochloa pyramidalis-Sorghum bicolor* disturbed backswamp community (Eb) were grouped within a fairly narrow range of site scores ranging from −1.85 to +0.65 on axis 1 and from −0.82 to +1.97 on axis 2. The *Cynodon dactylon* undisturbed floodplain community (C2), the *Cynodon dactylon* highly disturbed floodplain community (C1) and the *Cynodon dactylon* moderately disturbed floodplain community (C3) had positive scores on axis 1 and generally negative values on axis 2. The *Acacia xanthophloea* woodland community (A) was grouped with positive values for both axes 1 and 2.

The distribution of sample scores for axes 1 and 3 are illustrated in Figure 4.4. Sample scores on the third ordination axis ranged from −1.23 to +5.25. The *Phragmites mauritianus* reed swamp community (P) had low sample scores for axis 1 and scores close to zero for axis 3. The *Imperata cylindrica* hygrophilous grassland community (I) formed a distinct group with high sample scores for axis 3 and scores approximately between 0 and −1.00 for axis 1. The *Ficus sycomorus* riparian forest community (F), the *Echinochloa pyramidalis-Cyperus dives* undisturbed backswamp community (Ea) and the *Echinochloa pyramidalis-Sorghum bicolor* disturbed backswamp community (Eb) are centrally grouped on the ordination diagram with sample scores ranging from approximately −2.00 to +0.35 along axis 1 and from −1.00 to +1.50 for axis 3. The *Acacia xanthophloea* woodland community (A) and the *Cynodon dactylon* floodplain community (C) form a mixed group with positive scores along axis 1 and samples scores ranging from −1.23 to approximately +3.50 along axis 3.
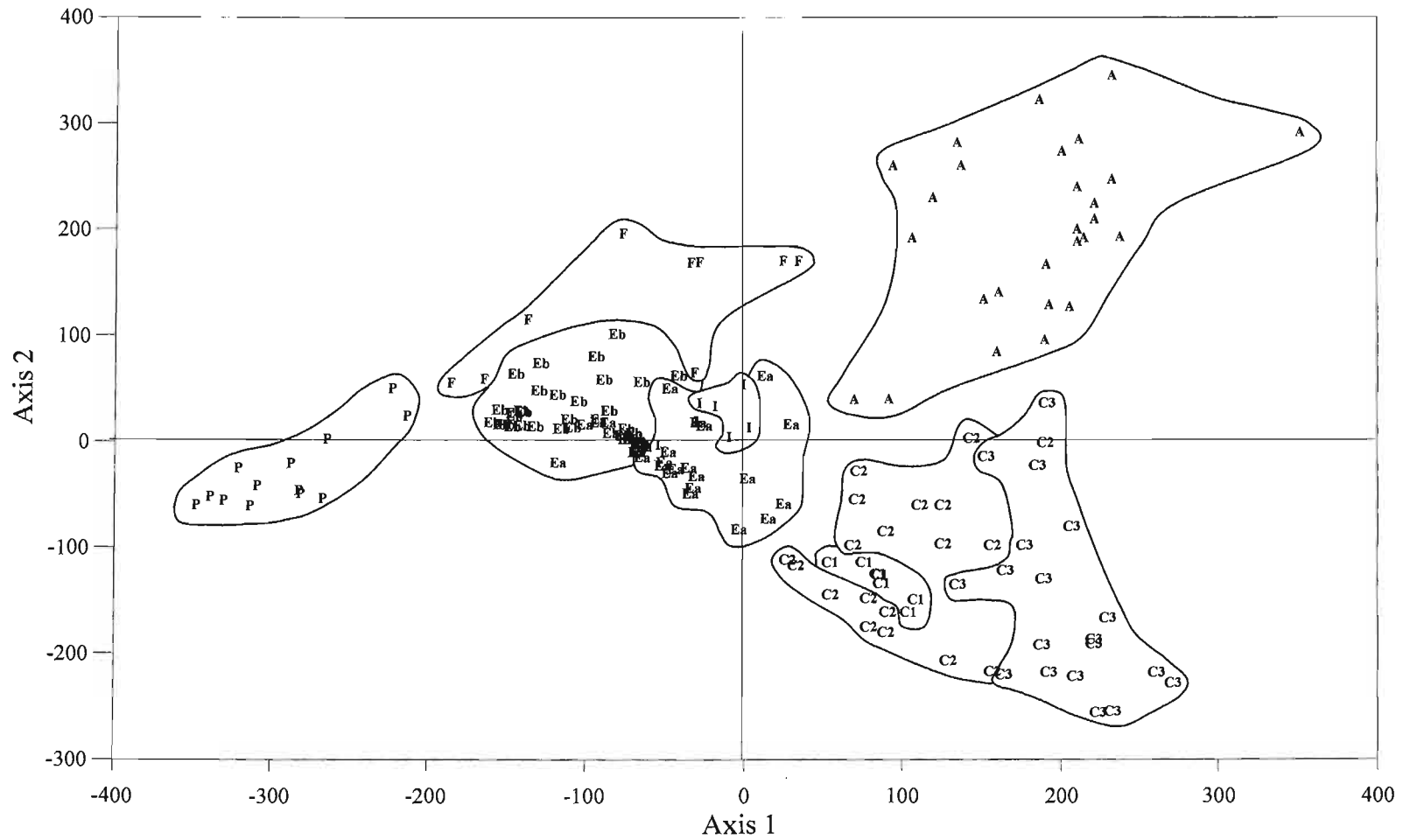
Figure 4.3 Sample scores of DCA ordination axes 1 and 2 illustrating plant community clusters
(units are standard deviations x 100; see text for full plant community names).
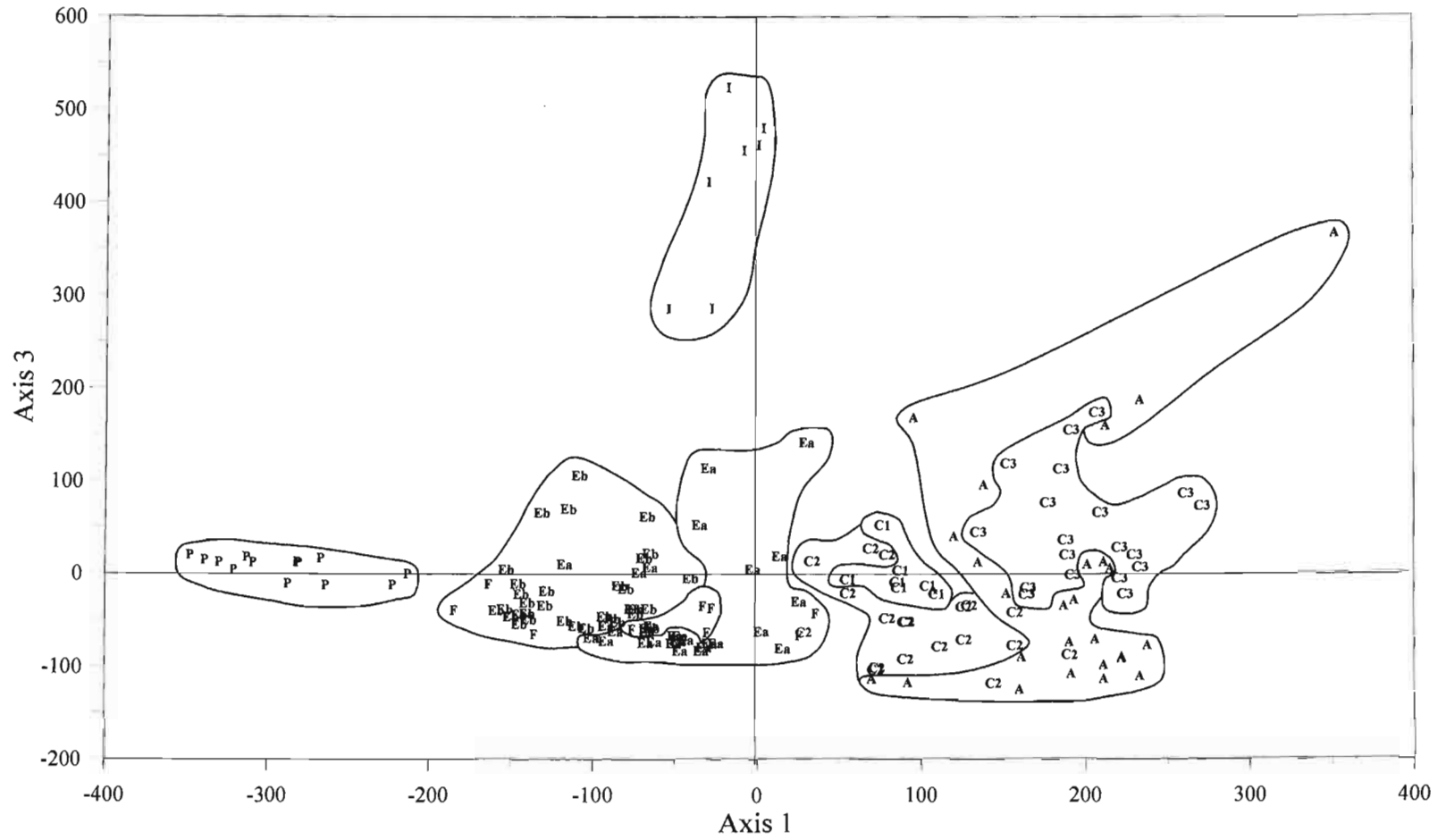
Figure 4.4 Sample scores of DCA ordination axes 1 and 3 illustrating plant community clusters
(units are standard deviations x 100; see text for full plant community names).

Biplot scores of the measured environmental variables were generated as part of the ordination and these were superimposed on the ordination diagrams (Figs. 4.5 & 4.6). Regression analysis was used in order to determine the significance of the correlation between the biplot and sample scores (Table 4.4). The first axis of ordination was strongly positively correlated with sandy soils and relative elevation above the local thalweg with correlation coefficients of 0.4196 (F=45.03; P=<0.01) and 0.5581 (F=72.15; P=<0.01) respectively. Organic matter and clay content were negatively correlated to axis 1 with correlation coefficients of –0.4986 (F=39.98; P=<0.01) and –0.2026 (F=7.15; P=<0.01) respectively. Relative elevation above the local thalweg was the only environmental variable that correlated significantly to sample score distribution on the second ordination axis (r^2=0.1554; F=7.15; P=<0.01). Distance from the local thalweg was most significantly correlated to axis 3 (r^2=0.4817; F=45.02; P=<0.01). Percentage clay and organic matter content contributed to the variation in the sample scores to a lesser extent with correlation coefficients of 0.2003 (F=5.01; P=<0.01) and –0.2343 (F=14.83; P=<0.01) respectively.

Table 4.4: Correlation matrix showing the relationship between the ordination axes and environmental variables.

Environmental Variables	Axis 1	Axis 2	Axis 3
Percent sand content	0.4196**	0.0977	0.0283
Percent clay content	-0.2026**	-0.1358	0.2003*
Percent organic matter content	-0.4986**	0.0878	-0.2343**
Distance from thalweg	0.1164	-0.0691	0.4817**
Relative elevation above thalweg	0.5581**	0.1554**	-0.0750

** = 99% Confidence Limits * = 95% Confidence Limits

Based on these analyses it was evident that the environmental variables of percentage sand content and relative elevation above the local thalweg were the primary determinants of the distribution of sample scores on the positive side of the first ordination axis. This suggests that the *Acacia xanthophloea* woodland community (A), the *Cynodon dactylon* undisturbed floodplain community (C2), the *Cynodon dactylon* highly disturbed floodplain community (C1) and the *Cynodon dactylon* moderately disturbed floodplain community (C3) were characterised by sandy soils and high elevations relative to the local thalweg. The
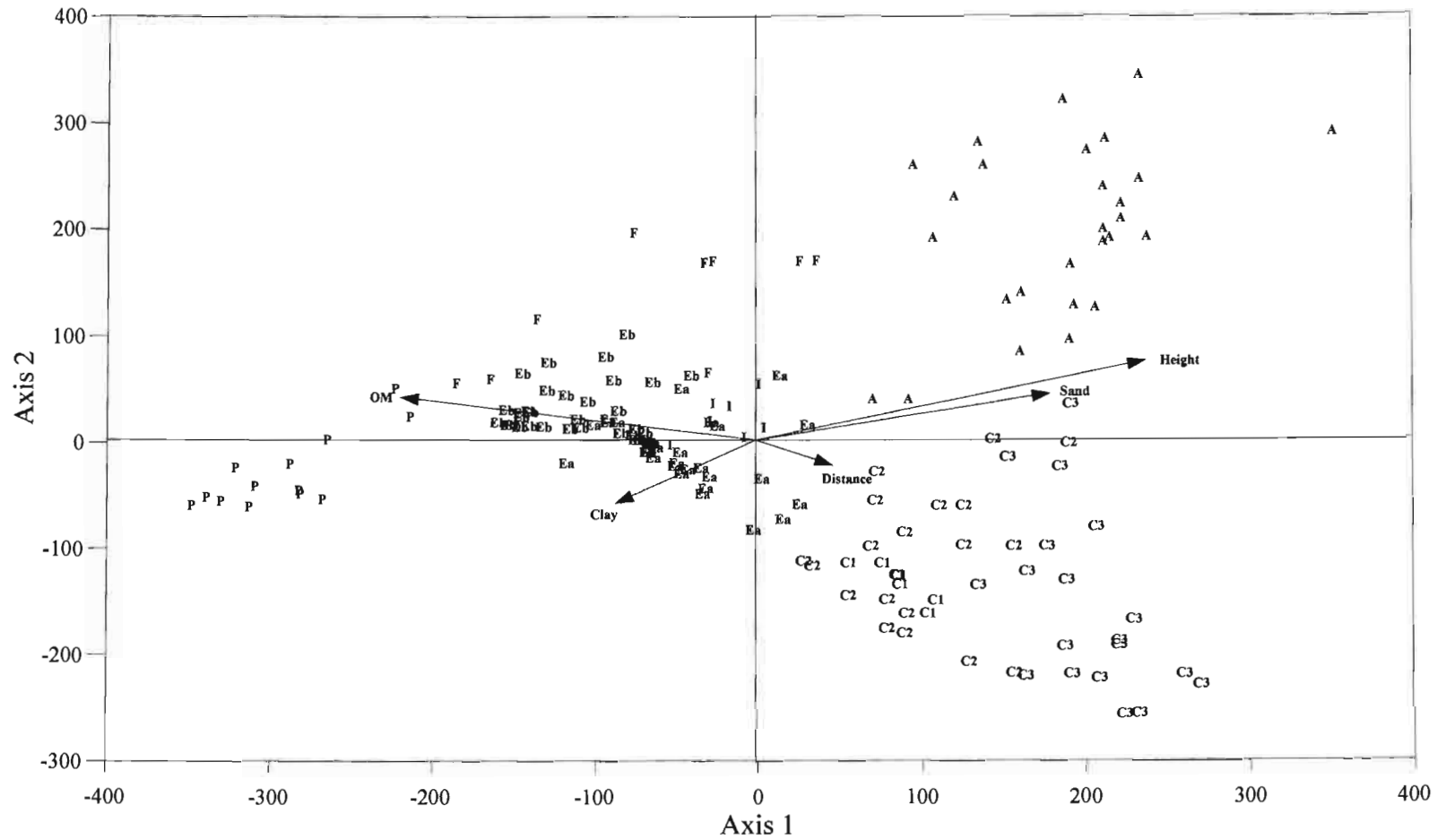
Figure 4.5 Sample and biplot scores for ordination axes 1 and 2 (units are standard deviations x 100; see text for full plant community names).
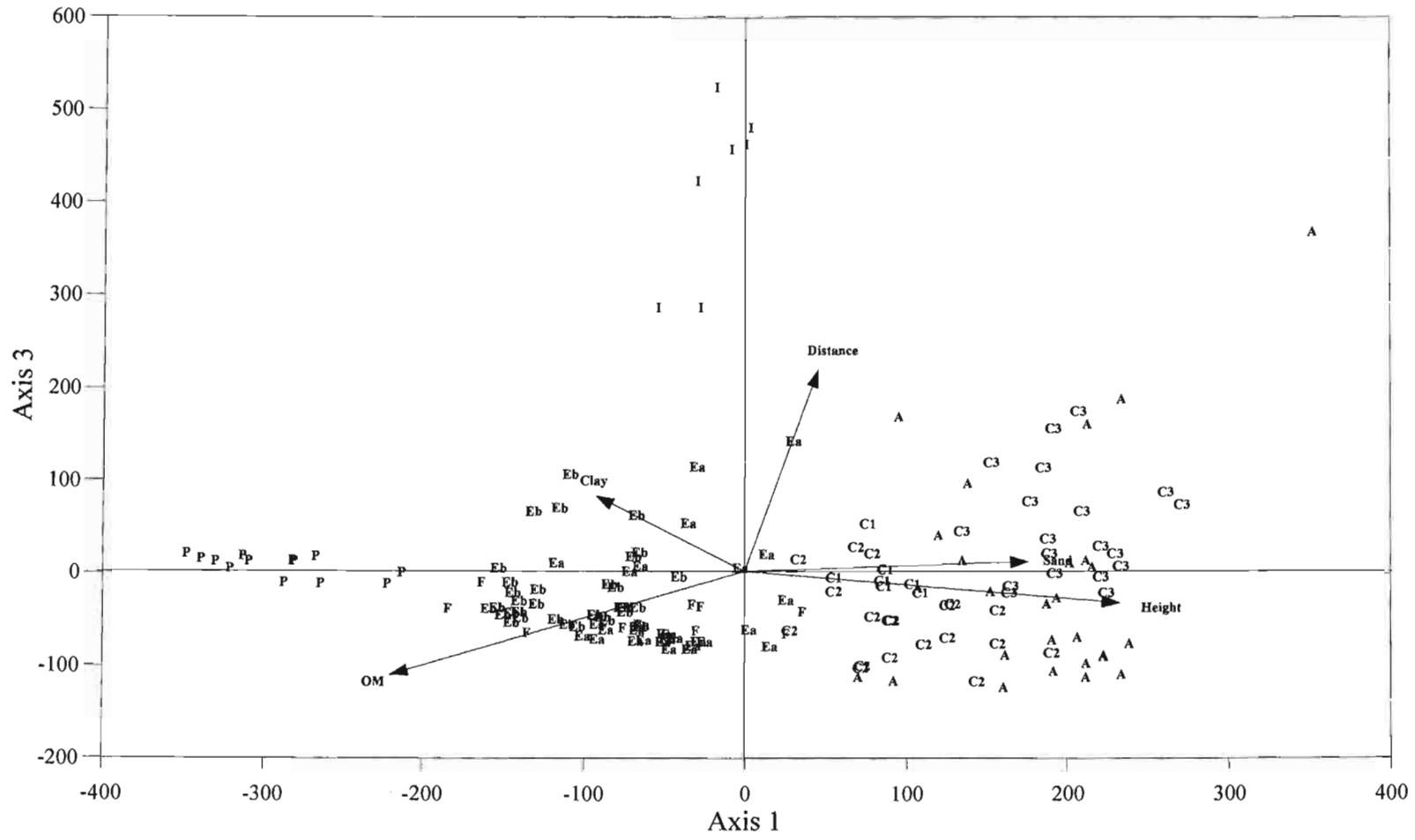
Figure 4.6 Sample and biplot scores of ordination axes 1 and 3 (units are standard deviations x 100; see text for full plant community names).

arrangement of samples with low axis 1 scores was associated with high organic matter and clay content, and they occurred at low elevations relative to the thalweg. High organic matter and clay contents were thus typical of the *Phragmites mauritianus* reed swamp community (P). When axis 1 was plotted against axis 3 (Fig. 4.6) it is evident that the *Imperata cylindrica* hygrophilous grassland community (I) was distributed on clayey soils situated at relatively large distances from the local thalweg.

4.3.3 Plant Community Distribution in relation to Topography

Transects 1 to 6

Muzi and Yengweni Pans are perennial linear shaped pans that occupy shallow north-south orientated interdune depressions north of the Mkuze River. Transects 1 to 6 were placed along the eastern shores of the southern reaches of these pans (Fig. 4.1), the topographic profiles of which are illustrated in Figure 4.7. None of the transects were longer than 100m indicating that the floodplain fringe surrounding these pans was extremely narrow. The banks of both pans were gently sloping and as one progressed from the waters edge to terrestrial upland three bands of vegetation were apparent. The shallow waters along the shoreline were characterised by floating aquatic vegetation described as the *Potamogeton thunbergii-Ludwigia stolonifera* aquatic community (Aq) (see Section 4.3.4 for full description). The second band of vegetation was typically grassy and was identified as belonging to either the *Echinochloa pyramidalis-Cyperus dives* undisturbed backswamp community (Ea) or the *Cynodon dactylon* undisturbed floodplain community (C2). The floodplain boundary was fringed with the *Acacia xanthophloea* woodland community (A).

Transects 7 and 8

Transects 7 and 8 were located on a part of the floodplain where the Mkuze River flows in an east-west direction. Transect 7 was situated north-east of Tshanetshe Pan while transect 8 was south-west of Mdlazi Pan (Fig. 4.1). Both transects extended from the southern bank of the Mkuze River, northwards towards the floodplain boundary covering a distance of between 600 and 800m (Fig. 4.8). Along this section of the Mkuze River the channel banks formed well developed levees that typically supported riverine vegetation, in this case the *Ficus sycomorus* riparian forest community (F). As elevation decreased away from the levees, the backswamp depressions were characterised by either the *Echinochloa*

Transect 1
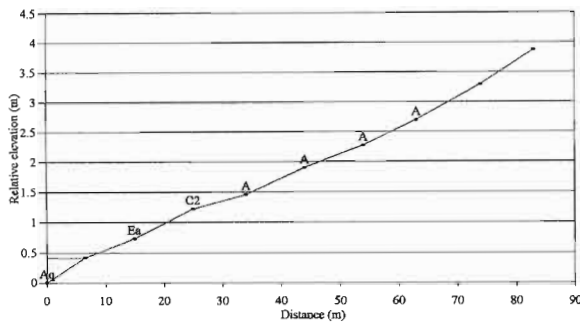
Transect 5
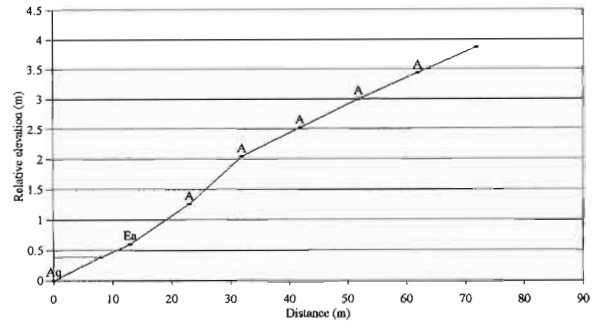
Transect 2
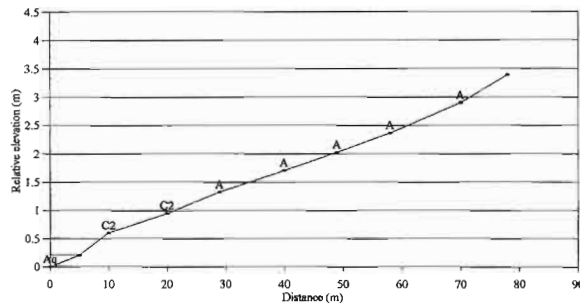
Transect 6
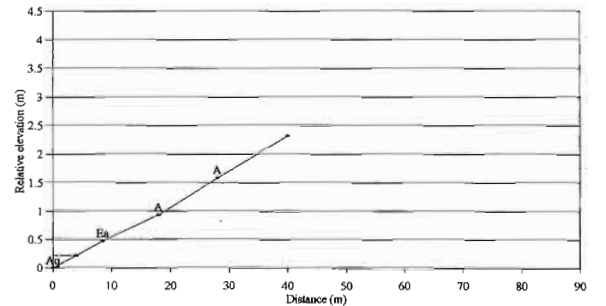
Transect 3
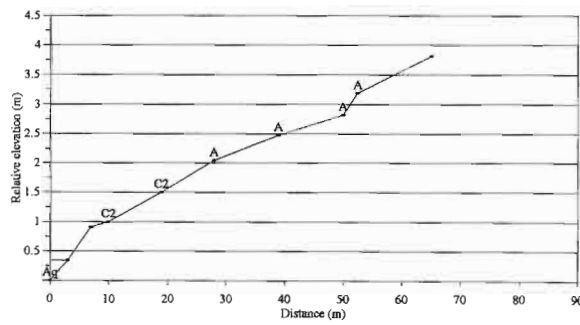
Transect 4
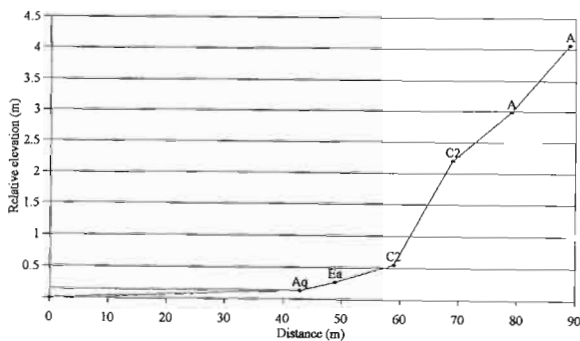
Figure 4.7 Transects 1 to 6 showing topographic profiles and plant community distribution (see text for full plant community names).

Transect 7
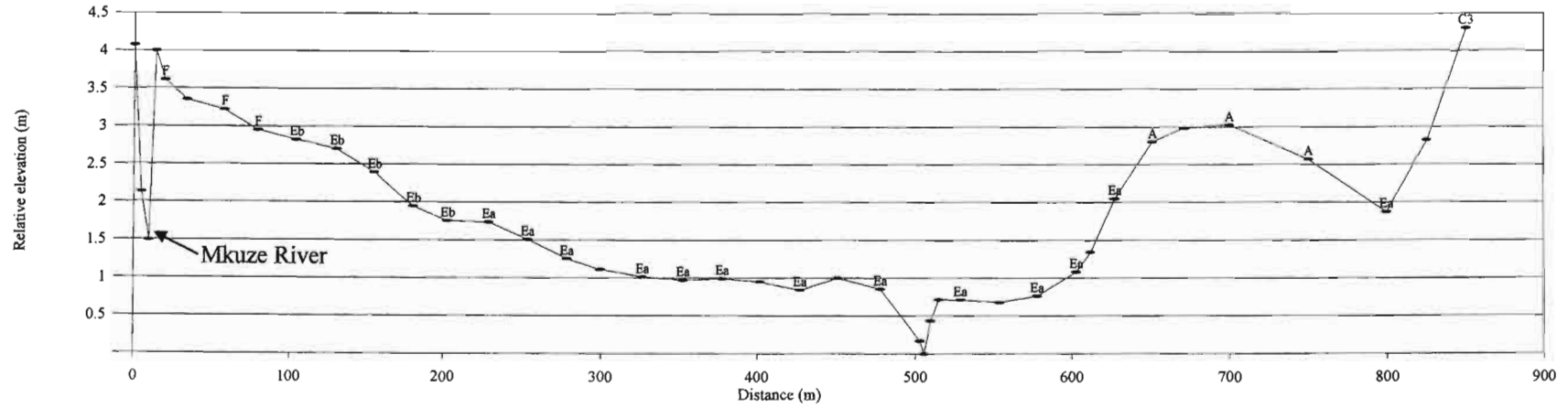
Transect 8
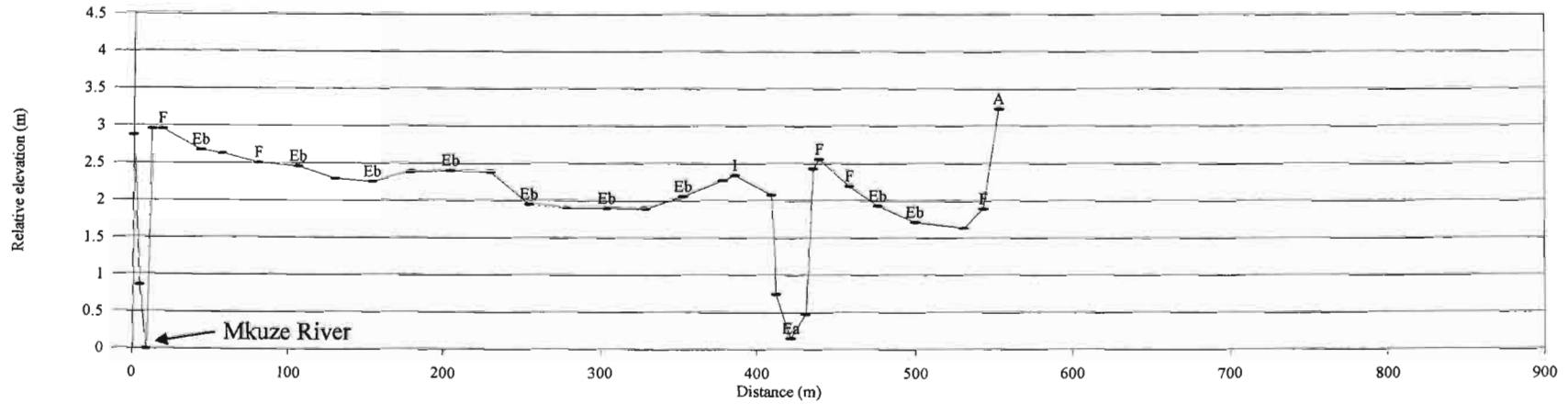
Figure 4.8 Transects 7 and 8 showing topographic profiles and distribution of plant communities (see text for full plant community names).

pyramidalis-Cyperus dives undisturbed backswamp community (Ea) or the *Echinochloa pyramidalis-Sorghum bicolor* disturbed backswamp community (Eb).

Both transects illustrate possible evidence of channel migration across this section of the lower Mkuze River floodplain. At approximately 500m along transect 7 a secondary channel was encountered; while at 400m along transect 8 a cut-off meander or oxbow lake was evident. Both of these features were flanked by either the *Echinochloa pyramidalis-Cyperus dives* undisturbed backswamp community (Ea) or the *Echinochloa pyramidalis-Sorghum bicolor* disturbed backswamp community (Eb). The northern bank of the oxbow lake supported remnant vegetation belonging to the *Ficus sycomorus* riparian forest community (F). As one progressed towards the floodplain boundary elevation increased, these higher lying areas were characterised by the *Acacia xanthophloea* woodland community (A).

River channel depth decreased from 3.580m to 2.955m and channel width decreased marginally from 14 to 12m as one progressed downstream from transect 7 to transect 8.

Transects 9 and 10

Transects 9 and 10 were located along the lower reaches of the Mkuze River west of the Mbazwane Wetland (Fig. 4.1). The channel banks and even the channel itself are elevated relative to the surrounding floodplain (Fig. 4.9). Vegetation along transect 9 comprised two plant communities namely the *Echinochloa pyramidalis-Sorghum bicolor* disturbed backswamp community (Eb); and as one progressed away from the channel the *Imperata cylindrica* hygrophilous grassland community (I) was the dominant vegetation. Transect 10 ran in an east-west direction and vegetation was dominated by the *Phragmites mauritianus* reed swamp community (P). The Mkuze River at the time of sampling was dry in both transects, however the soils along transect 10 were highly saturated.

The Mkuze River channel decreased in both depth (1.1m to 0.8m) and width (13m to 5m) as one progressed downstream.

Transect 9
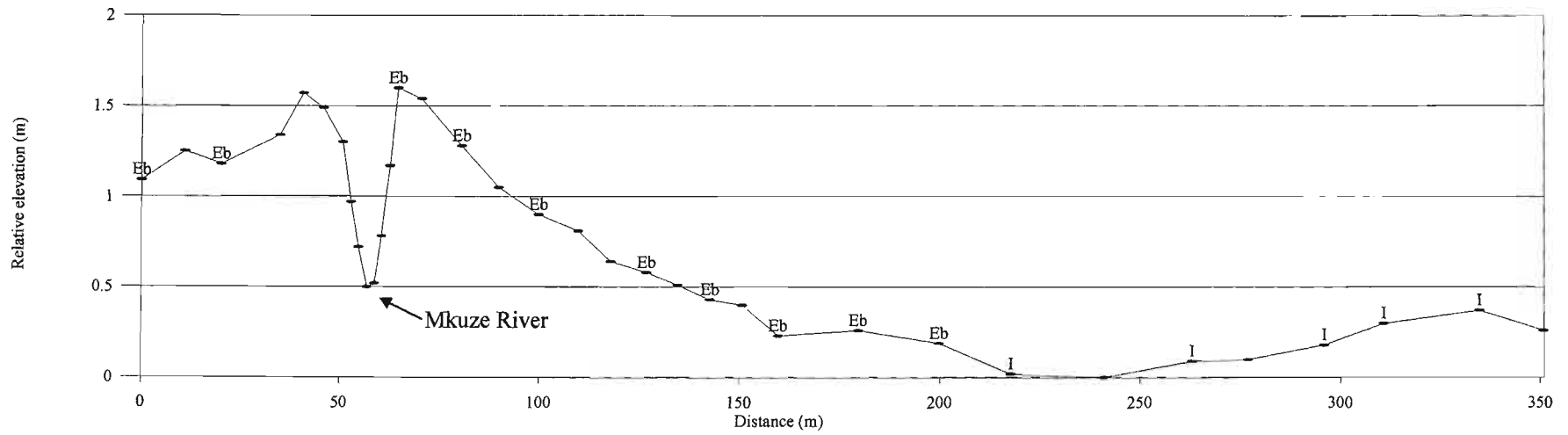
Transect 10
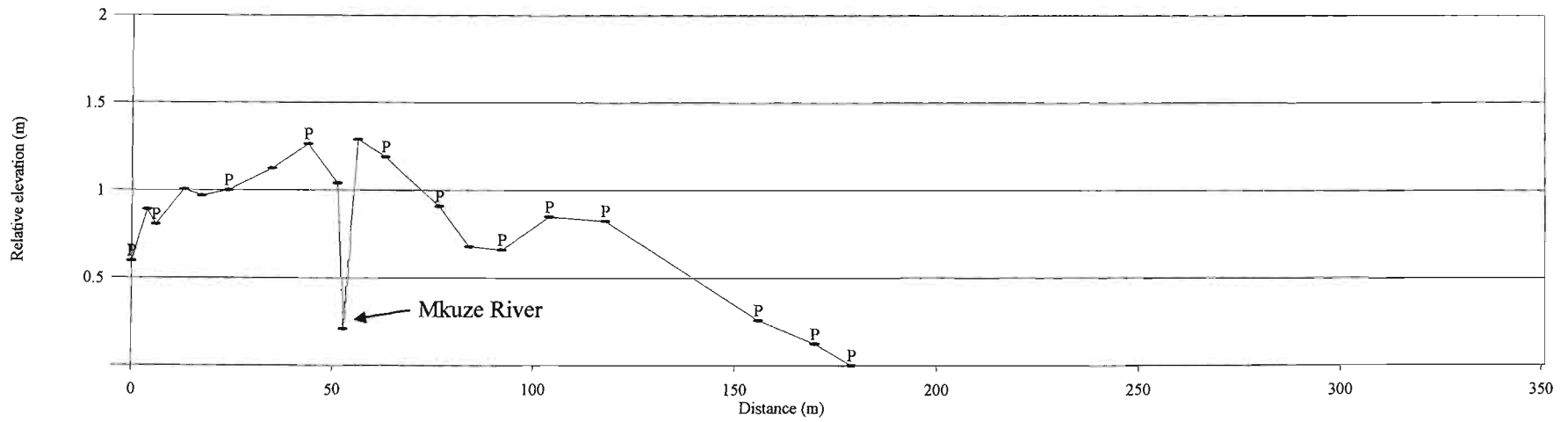
Figure 4.9 Transects 9 and 10 showing topographic profiles and distribution of plant communities (see text for full plant community names).

Transects 11 to 14

Transects 11 and 12 were located along the Tshanetshe-Mpempe Canal while transects 13 and 14 were located along the Mpempe Canal (Fig. 4.1). Transects 11 and 12 were placed north of Mpempe Pan and ran from the eastern bank of the canal, westwards towards an elevated terrestrial island within the floodplain (Fig. 4.10). The canal in transect 11 was fringed with a narrow band of the *Echinochloa pyramidalis-Cyperus dives* undisturbed backswamp community (Ea) and then dominated by vegetation from the *Cynodon dactylon* undisturbed floodplain community (C2) and the *Cynodon dactylon* moderately disturbed floodplain community (C3) towards the terrestrial upland. The source of disturbance was primarily cattle grazing and trampling. Transect 12 was located south of transect 11 and the vegetation was either the *Cynodon dactylon* highly disturbed floodplain community (C1) or the *Cynodon dactylon* moderately disturbed floodplain community (C3). Disturbance in this case could again be attributed to cattle. The canal at the time of sampling was dry with a few isolated puddles.

Transects 13 and 14 were located further downstream; transect 13 was northwest and transect 14 east of Ngwenya Pan. Transect 13 ran in a northeast-southwest direction from the northern bank of the canal, across one of the arms of Ngwenya Pan and towards the southern floodplain boundary. The surrounding floodplain was very flat and dominated by grassy lawns comprising a combination of the *Cynodon dactylon* undisturbed floodplain community (C2) and the *Cynodon dactylon* moderately disturbed floodplain community (C3). The edges of Ngwenya Pan were fringed with the *Echinochloa pyramidalis-Cyperus dives* undisturbed backswamp community (Ea). Transect 14 ran from the southern bank of the canal in a northerly direction into the surrounding floodplain. The topography was relatively flat and dominated by vegetation belonging to the *Echinochloa pyramidalis-Cyperus dives* undisturbed backswamp community (Ea).

4.3.4 Plant Community-Environment Descriptions

This section aims to summarise the observations and information elucidated from the TWINSPAN, DCA and topographical profiles in order to describe each plant community and explain its distribution. The summary of the TWINSPAN output (Table 4.2) forms the

Transcript 11
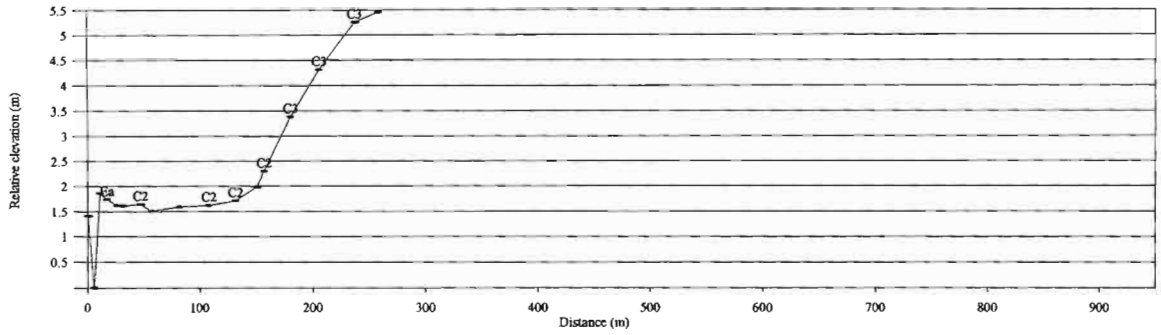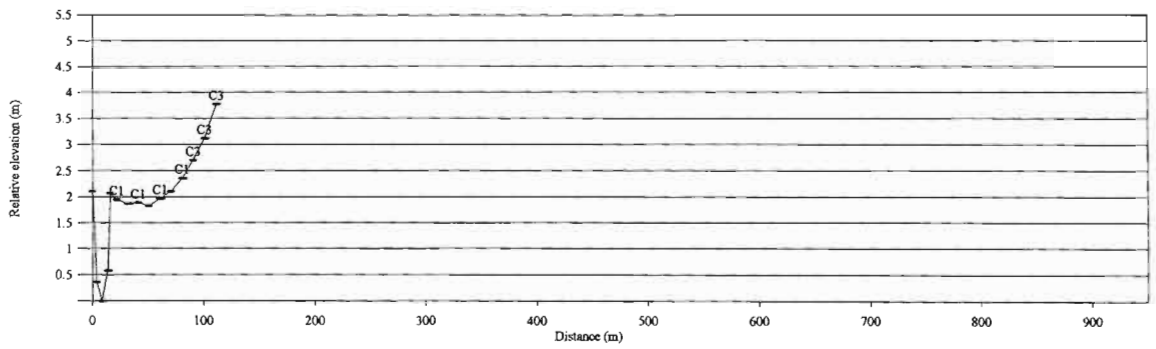
Transect 12

Transect 13
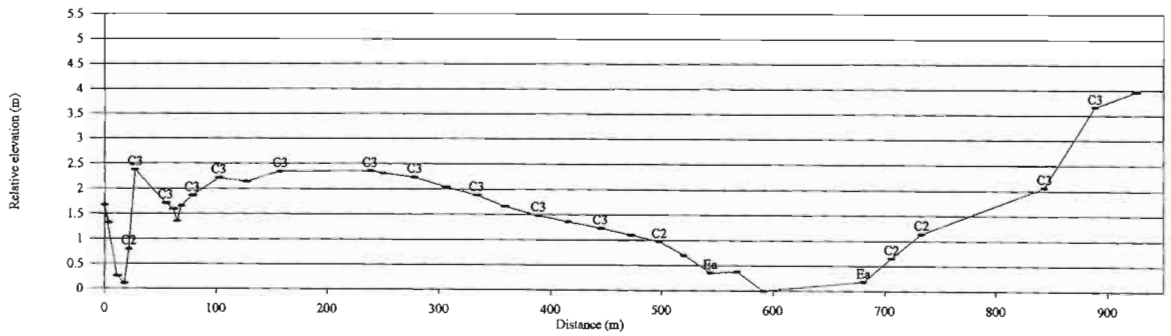
Transect 14
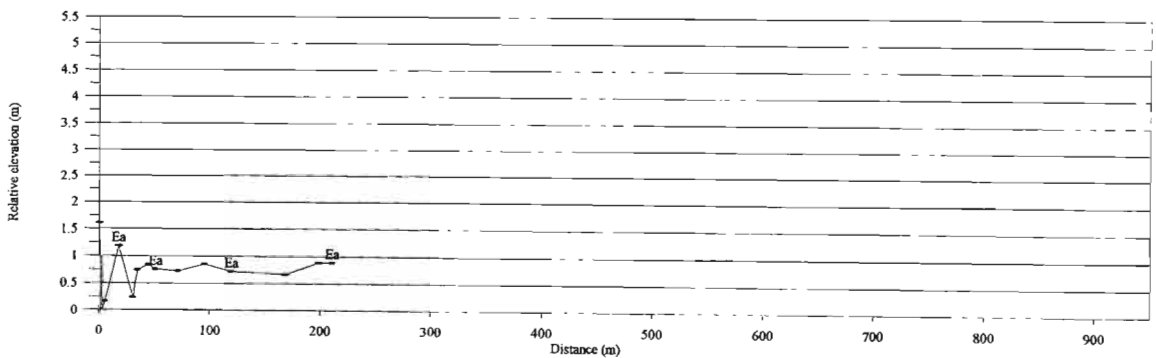
Figure 4.10 Transects 11 to 14 showing topographic profiles and distribution of plant communities (see text for full plant community names).

basis of the descriptions that follow since it illustrates all the plant species that occur in more than 50% of the sites within each plant community type.

The *Phragmites mauritianus* reed swamp community (P)

All sample plots that comprised this community were dominated by dense stands of *Phragmites mauritianus.* Cover values were high, ranging from 5 to over 50%. This community was usually associated with a stratum of herbs and creepers such as *Ipomoea mauritiana*, which occurred in 92% of the sample plots with cover values of up to 50% and *Melanthera scandens*, which occurred at low abundances in 85% of the sample plots. Another common species was *Phragmites australis*, which occurred in approximately 60% of the plots at low covers (0-10%). Mean species richness per sample was low at 8.31 species per sample plot (Fig. 4.11). This community is typically associated with saturated clayey soils (66.2% clay) that have the highest organic matter content (8.8%) of all the plant communities in this study (Table 4.5). This community occurs at low elevations relative to the local thalweg primarily in the distal reaches of the floodplain, generally north of the Mkuze River, fringing pans and minor watercourses.

The *Imperata cylindrica* hygrophilous grassland community (I)

This community was dominated by the grass *Imperata cylindrica*, which formed dense stands that grew to a height of approximately 1m. Common species included the grasses *Paspalum distichum*, which occurred in all sample plots with cover values ranging from 5 to greater than 50%, *Setaria sphacelata*, which occurred in approximately 60% of the sample plots with very low covers, *Sorghum bicolor*, which had cover values of less than 5% in 43% of the samples, *Chloris gayana*, which occurred in approximately 71% of the plots with cover values that ranged from 2 to 25%, and the herb *Alysicarpus rugosus*, which occurred at low covers in all the sample plots. Mean species richness was 8.57 species per sample (Fig. 4.11). This community is limited to soils with high clay content (67.8%) with relatively low organic matter content (5.5%; Table 4.5). It is typically found in areas far away from the local thalweg, towards the edge of the reach of seasonal flooding, at relatively low elevations on flat, open floodplain.
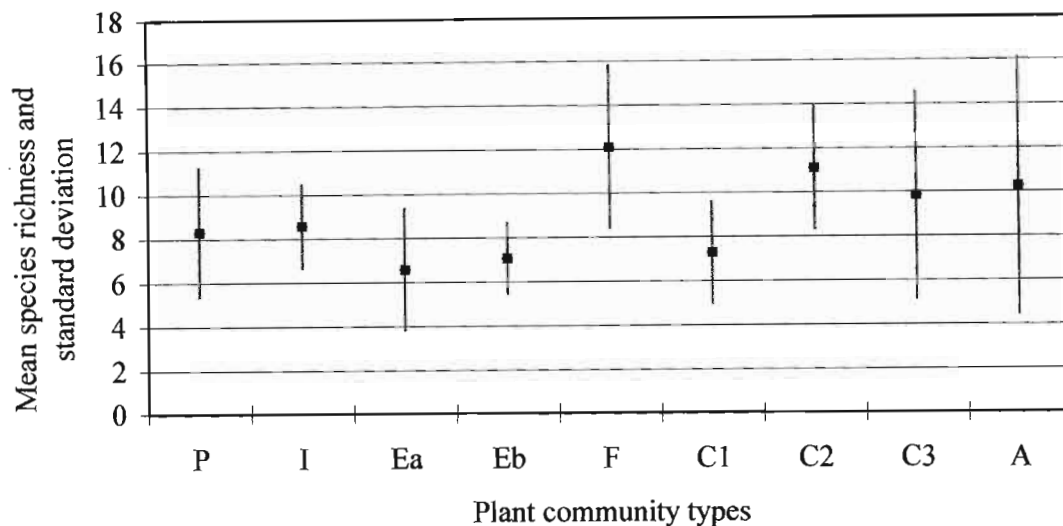
Figure 4.11 Mean species richness and standard deviations for each plant community type identified in the TWINSPAN analysis (refer to text for full plant names).

The *Echinochloa pyramidalis* backswamp community (Ea & Eb)

This community was the most extensive plant community type and was dominated by the grass *Echinochloa pyramidalis,* which had high cover values that ranged from 2 to greater than 50% and occurred in all sample plots. It was divided into two sub-communities based primarily on the presence of alien plant species, indicative of disturbance. The *Echinochloa pyramidalis-Cyperus dives* undisturbed backswamp community (Ea) was characterised by the Giant Sedge *Cyperus dives*, which occurred in approximately 50% of the sample plots with cover values that ranged from less than 1 to 50%. Another common species was *Persicaria senegalensis*, a robust perennial that also occurred in 50% of the samples with low cover values. This sub-community is typically found in marshy areas at low elevation relative to the thalweg and in silty soils (64.1% silt) with relatively high organic matter content (7.4%; Table 4.5). Mean species richness for this sub-community is very low at 6.58 species per sample (Fig. 4.11).

The *Echinochloa pyramidalis-Sorghum bicolor* disturbed backswamp community (Eb) had high cover values for the grass *Sorghum bicolor,* that ranged from 2 to greater than 50% in 85% of the sample plots. Other common species included *Ipomoea cairica*, a creeper found in disturbed riverine settings, which occurred in 79% of the plots with low cover values,

the herb *Melanthera scandens,* which occurred in approximately 50% of the samples, also with low cover values, and *Sida cordifolia,* a shrub indicative of disturbed areas, which had cover values that ranged from less than 1 to 25% in 55% of the sample plots. This sub-community is limited to clay soils (60%) with relatively high organic matter content (7.3%; Table 4.5). Mean species richness for this sub-community is slightly higher than the undisturbed sub-community at 7.06 species per sample plot (Fig. 4.11). Both sub-communities form extensive stands located in the backswamp areas of the Mkuze River forming a corridor through of the floodplain, primarily fringing watercourses and pans.

Table 4.5 The mean value of each environmental variable for each plant community type identified in the TWINSPAN analysis.

	Sand (%)	Silt (%)	Clay (%)	Organic matter (%)	Distance from thalweg (m)	Relative elevation above thalweg (m)
P	10.5	23.3	66.2	8.8	56.31	0.51
I	18.0	14.2	67.8	5.5	209.71	0.06
Ea	24.0	64.1	11.9	7.4	97.94	0.79
Eb	16.5	23.6	59.9	7.3	100.1	1.23
F	35.8	23.1	41.1	7.3	48.11	2.18
C1	10.6	8.2	81.2	6.0	42.29	2.00
C2	27.2	31.1	41.7	6.2	67.11	1.33
C3	49.6	11.1	39.3	4.9	171.37	2.7
A	41.1	23.7	35.2	6.6	70.93	2.43

The *Ficus sycomorus* riparian forest community (F)

The dominant species, *Ficus sycomorus,* which occurred in approximately 70% of the sample plots with cover values that ranged from 5 to 25%, formed a tall canopy layer along with other tree species such as *Voacanga thouarsii,* which occurred in 44% of the sample plots with cover values that ranged from 2 to 25%, and *Acacia xanthophloea,* which also occurred in approximately 44% of the plots with cover values that ranged from less than 1 to over 50%. A further two strata were evident, namely a shade tolerant shrub layer characterised by *Achyranthes aspera,* with cover values that ranged from 2 to 25% in 44%

of the plots, and *Ipomoea cairica*, with low cover in approximately 70% of the plots, and a grass stratum that comprised two grass species; *Echinochloa pyramidalis*, which occurred in all the sample plots with cover values that ranged from less than 1 to 50% and *Sorghum bicolor*, which occurred in 67% of the samples with low cover values. Mean species richness is high at 12.11 species per sample plot (Fig.4.11). This community occurs on predominately clay soils (41.1% clay) at relatively high elevations above the local thalweg (Table 4.5). Generally this community is found close to the riverbanks or on levees adjacent to the river channel.

The *Cynodon dactylon* floodplain community (C1, C2 & C3)

This community was dominated by the grass *Cynodon dactylon*, which formed extensive lawns within the floodplain. *Cynodon dactylon* occurred in 93% of the sample plots with cover values that ranged from less than 1 to over 50%. Three sub-communities were identified on the basis of level of disturbance. The *Cynodon dactylon* highly disturbed floodplain community (C1) had high cover values (25 to >50%) for *Sida cordifolia*, which occurred in all sample plots and was an indicator of disturbed areas. Other common species included the grass *Brachiaria humidicola*, with cover values that ranged from less than 1 to 25% in all sample plots, and the sedge *Cyperus dives*, which occurred in 86% of the plots with low cover values (2 to 10%). This sub-community is found adjacent to the Tshanetshe-Mpempe Canal System in areas with clayey soils (81.2% clay; Table 4.5) that are heavily utilised by people and cattle and has a mean species richness of 7.29 species per sample plot (Fig. 4.11).

The *Cynodon dactylon* undisturbed floodplain community (C2) was characterised by *Ludwigia stolonifera*, a creeping herb found in damp areas, which occurred in 74% of the sample plots with low cover values (0 to 10%). Other common species included the grass *Echinochloa pyramidalis*, which occurred in approximately 60% of the sample plots and had a cover value ranging from less than 1 to 25% and the herb *Phyla nodiflora*, which had similar cover values and occurred in 68% of the plots. The mean species richness for this sub-community is 11.11 species per sample (Fig.4.11) and is generally found in areas with silty-clay soils (31.1% silt ; 41.7% clay; Table 4.5) typically close to the local thalweg, which in this case is the Tshanetshe-Mpempe Canal System.

The *Cynodon dactylon* moderately disturbed floodplain community (C3) was characterised by *Sida cordifolia,* which occurred in 74% of the sample plots with cover values that ranged from less than 1 to 25%. This community is typically found on sandy soils (49.6% sand) with relatively low organic matter content (4.9%) and at a high elevation above the local thalweg (Table 4.5). It occurs primarily towards the distal reaches of the floodplain to the south of the Mkuze River. Mean species richness is 9.85 species per sample (Fig. 4.11). Thus mean species richness for the three sub-communities decreases with increasing disturbance.

The *Acacia xanthophloea* woodland community (A)

This community comprised two strata, a tree stratum dominated by *Acacia xanthophloea,* which occurred in 67% of the sample plots with cover values that ranged from less than 1 to 50% and a second layer that comprised low growing grasses such as *Brachiaria deflexa,* which also occurred in 67% of the plots with cover values that ranged from 2 to over 50% and *Panicum maximum* which occurred in 41% of the sample plots and had cover values ranging from 2 to 25%. Mean species richness is high at 10.27 species per sample (Fig. 4.11), however the majority of species tend to have low covers, ranging from less than 1 to 10%. This community is typically found fringing the floodplain-terrestrial upland boundary, especially adjacent to the linear pans, Muzi and Yengweni Pans and is characterised by sandy soils (41.1% sand) and situated relatively high above the thalweg (Table 4.5).

The *Potamogeton thunbergii- Ludwigia stolonifera* aquatic community (Aq)

This community was excluded from the multivariate analysis since it formed a discrete aquatic community with very few samples that were considered to be outliers. Such samples tend to strongly influence the TWINSPAN output and it is therefore recognised that they should be omitted from the analysis (Gauch, 1982). This community was dominated by the aquatic species *Potamogeton thunbergii,* which occurred in 60% of the sample plots with cover values that ranged from 2 to greater than 50%, and the floating creeper *Ludwigia stolonifera,* which occurred in all the plots with cover values that ranged from 2 to 25%. Other common species included *Trapa natans,* which occurred in 40% of the plots with a cover of 5 to 10% and *Nymphaea nouchali,* which occurred in all plots at

low covers (0 to 5%). This community is predominately found in still water along the edge of the Muzi and Yengweni Pans to the north of the Mkuze River.

4.4 Discussion
4.4.1 Plant Community Classification and Distribution-Comparative Studies

Extensive floodplain systems are uncommon in South Africa because most rivers are short with low mean annual runoff (Breen *et al.,* 1993). Those floodplains that do occur generally develop in the mid to lower reaches where a river attains grade and floods overtop the channel banks. Noble and Hemens (1978) classified South African floodplains into three types, namely Karoo salt flats, floodplain vleis and storage floodplains. The Mkuze and Pongola River floodplains, both located on the Maputaland Coastal Plain, are examples of storage floodplains. A comparison between the present study and previous research on the Mkuze and the Pongola River systems provides useful insight into the similarities and differences of plant community classification, description and distribution (Tinley, 1976; Furness & Breen, 1980; Heeg & Breen, 1982; Stormanns *et al.,* 1987; Schoultz, 2000; Taylor, 2000).

The study by Tinley in 1958 (published in 1976) is the earliest report on Mkuze River floodplain vegetation. He described eight vegetation types encountered along a transect line that extended from the eastern edge of the Mbazwane River, across the northern portion of the Mkuze River floodplain, to the foothills of the Lebombo mountains. Two of the vegetation types described resemble communities identified in the current study, namely a Riparian Forest Type and an Aquatic Vegetation Type. The Riparian Forest Type was dominated by *Ficus sycomorus* and was distributed along the length of the Mkuze River, similar to the *Ficus sycomorus* riparian forest community (F) in the current study. The Aquatic Vegetation Type was a broad grouping of aquatic, floating-leaved and emergent plants. Three sub-divisions of this type that are comparable to communities in the current study include a *Cyperus papyrus* and *Phragmites mauritianus* dominated swamp, an *Echinochloa pyramidalis* marsh and a *Nymphaea sp* aquatic community. These correspond respectively to the *Phragmites mauritianus* reed swamp community (P), the *Echinochloa pyramidalis* backswamp community (E) and the *Potamogeton thunbergii-Ludwigia stolonifera* aquatic community (Aq) found in the current study.

Other vegetation types identified by Tinley (1976) that were found adjacent to the floodplain boundary of the current study include those vegetation types found on upland or terrestrial areas. These include an Open Grassland and Lala Palm Vegetation Type, an Acacia and Bush Vegetation Type, an Open and Closed Woodland Vegetation Type, a Coastal Forest Vegetation Type and a Sand Forest Vegetation Type.

A study of the vegetation of the Greater Mkuze Wetlands, of which the present study area is only a part, was undertaken by Stormanns *et al.* (1987). Physiognomically distinct vegetation formations were identified from aerial photographs in order to aid the selection of sample sites. Vegetation was sampled in 42 plots using the Braun-Blanquet method of sampling and plant communities classified using TWINSPAN. In their study Stormanns *et al.* (1987) identified 14 plant communities, three of which correspond closely to those identified in the current study. These included the *Ficus sycomorus-Rauvolfia caffra* community, which fringed the Mkuze River; extensive stands of *Echinochloa pyramidalis,* with a similar distribution within the floodplain backswamps as in the present study; and an *Acacia xanthophloea-Cynodon dactylon* community which corresponds to the *Acacia xanthophloea* woodland community (A) and the *Cynodon dactylon* floodplain community (C), found along the margins of the floodplain in the current study.

Other plant communities identified by Stormanns *et al.* (1987) that were not found in the current study area included a *Phragmites australis* community, found to the north of Mpempe Pan and towards the lower reaches and eastern margin of the floodplain, and a *Cyperus papyrus* community, found predominantly surrounding Mdlanzi, Tshangwe and Ngwenya Pans. The occurrence of *Phragmites australis* was uncommon in the current study. It was however found north of Mdlanzi Pan according to Taylor (2000). Although the occurrence of *Cyperus papyrus* within the floodplain in the current study was uncommon in the areas sampled, it was identified during aerial photograph analysis as a dominant species that constituted a distinct plant community type. This community has been mapped and described in Chapter 5.

Schoultz (2000) examined the underlying environmental determinants of plant community distribution within the eastern portion of the Mbazwane Wetland. Although this study falls

outside the current study area boundary, it does lie adjacent to the northeastern boundary of the lower reaches of the Mkuze River floodplain. Vegetation was sampled in 87 plots using the Braun-Blanquet method of sampling, plant communities were classified using multivariate techniques and mapped with the aid of aerial photographs. Nine plant communities were identified, two of which were similar to those found within the current study. They included an *Echinochloa pyramidalis* floodplain community and a *Cyperus papyrus* swamp community. Other vegetation types included coastal forest, floodplain grassland and swamp forest.

A study by Taylor (2000) focused on the Mdlanzi Pan and its associated drainage lines to the north of the Mkuze River. Vegetation was sampled in 76 plots using the Braun-Blanquet method of sampling and plant communities were classified and mapped using multivariate techniques and GIS. Five plant communities were identified, however because the scale of sampling and mapping was finer than the current study, communities were not comparable.

The Pongola River floodplain, which comprises a low-lying area adjacent to the river channel with numerous depressions or pans (Heeg & Breen, 1982), appears to be structurally and functionally very similar to the lower Mkuze River floodplain. Six plant communities and two sub-communities were recognised by Furness & Breen (1980). Physiognomically distinct vegetation areas were identified from aerial photographs and vegetation sampled in 106 plots using the Braun-Blanquet method of sampling. After the communities were ground truthed, they were transcribed from the aerial photographs onto a map of the same scale.

Of the six communities identified by Furness & Breen (1980) five were currently found in the lower Mkuze River floodplain. Although species composition differed slightly, the indicator species and geomorphic distribution were similar. The *Phragmites mauritianus* community of Furness & Breen (1980) corresponds with the *Phragmites mauritianus* reed swamp community (P) of the current study. The *Ficus sycomorus-Rauvolfia caffra* community is similar to the riparian forest of Tinley (1976) and the present study. The *Acacia xanthophloea* woodland community (A) described in the present study and the

Acacia xanthophloea-Dyschoriste depressa community of the Pongola are structurally similar in that they both comprise an open tree stratum interspersed with low growing grasses and herbs. Both the Pongola and Mkuze River floodplains are characterised by short grass lawns dominated by *Cynodon dactylon,* the community species composition of which varies according to disturbance, usually the result of grazing. Heeg & Breen (1982) also describe the occurrence of a variety of aquatic plant communities. Those communities found in the perennial pans within the Pongola River floodplain had similar species composition to the *Potamogeton thunbergii-Ludwigia stolonifera* aquatic community (Aq) of the current study. The last comparable community is described by Furness & Breen (1980) as a *Cyperus fastigiatus-Echinochloa pyramidalis* community. Although no *Cyperus fastigiatus* was identified on the lower Mkuze River floodplain in the current study, the presence of the grass *Echinochloa pyramidalis* was widespread and often disturbed by cattle. The only community identified by Furness & Breen (1980) that was not found in the current study was a *Phragmites australis* community. Although this species was found within the floodplain, it was not common and thus did not form a community type. It was however widespread in the area to the north of eastern margin of the floodplain, within the Mbazwane Wetland (Schoultz, 2000).

It is useful to compare vegetation types and plant communities from different studies since they can provide confirmation of plant community types, insight into how vegetation has changed over time and/or a broader, more inclusive picture of vegetation types and distribution. However plant community classifications are partly an outcome of the selection of one's study area boundary, sampling design and data analysis techniques. For example, the inclusion of a larger study area may lead to recognition of distinct communities that may only be sampled superficially in a smaller study area. Samples are therefore clustered according to the heterogeneity of the samples within the data set. Furthermore, stratification of vegetation prior to sampling may influence the analysis to the extent that the output is an expression of the stratification process. The choice of divisive or agglomerative, of monothetic or polythetic cluster analysis techniques may also influence the identification of plant communities. The concern in this study was not to unequivocally classify the vegetation of the lower Mkuze River floodplain but to use the classification process as a heuristic tool. Therefore, the identification of plant community

types provides a foundation from which insights into process orientated questions on ecosystem patterns and processes could be elucidated i.e. it constitutes the grain from which the reference level within the landscape hierarchy can be explored.

4.4.2 Environmental Determinants of Plant Community Distribution

According to Gosselink & Turner (1978) the interaction between hydrology, substrate and vegetation determines the structure and functioning of wetland systems. Specific environmental variables were measured in this study in order to illustrate the nature and complexity of these interactions (Fig. 2.2).

Substrate properties are determined by *inter alia* soil texture characteristics. The floodplain surface is a mosaic of different textured sediments. This mosaic is formed largely through the deposition of sediments on the floodplain during flood events (Malanson, 1993). The Mkuze River introduces a sediment load dominated by fine clays that are deposited on the floodplain surface during flood events (McCarthy & Hancox, 2000). Substratum type plays an important role in determining soil chemistry and hydraulic properties. Fine-grained clays have low infiltration rates and thus contribute to saturated soil conditions. When soils become saturated, anaerobic conditions result, initiating chemical transformations within the substrate (Armstrong, 1975) in which only vegetation tolerant of these conditions flourishes. Anaerobic conditions also slows down the decomposition rate of organic matter in the soil, thus soils with high organic matter content (>5%) typify areas that are at least periodically inundated (Mitsch & Gosselink, 1993). The measurement of soil texture and organic matter content within soil samples thus provided a useful indication of the influence of flooding and soil chemical processes on plant community distribution.

Distance from, and elevation above, the thalweg are often measured as indicators of the hydrological regime of floodplain systems (Rogers, 1995; Higgins *et al.,* 1996; Higgins *et al.,* 1997; Diederichs & Ellery, 2000). Topography controls the frequency and duration of inundation. Low-lying areas such as backswamps usually store floodwaters and slow down flow velocity, resulting in the deposition of fine sediments. These topographic depressions

are often characterised by saturated sediments with high organic matter content. Elevated areas are conversely flooded less frequently and for shorter duration (Malanson, 1993).

A dendrogram summarising how the underlying environmental variables determine plant community classification and impact on distribution provides a useful means of examining vegetation-environment relationships within the lower Mkuze River floodplain (Fig. 4.12). The first level of division in the dendrogram can be attributed to the fluvial influence of the Mkuze River on substratum type. Two vegetation complexes were apparent, a swamp/ marsh complex dominated by clay soils and a floodplain complex characterised by sandy soils.

The *Phragmites mauritianus* reed swamp community (P) community was found in semi- to permanently saturated soils with high clay and organic matter content. Those communities periodically inundated during seasonal flooding were further divided by distance from the thalweg. This suggests that those communities such as the *Imperata cylindrica* hygrophilous grassland community (I), which are situated further away from the thalweg than other communities, are less tolerant of flooding. Geomorphological landforms within the floodplain such as elevated levees were characterised by the *Ficus sycomorus* riparian forest community (F), while the *Echinochloa pyramidalis* backswamp community (E) was typically found in the low-lying areas or backswamp depressions fairly close to the Mkuze River channel. The presence or absence of alien plant species indicative of disturbance determined the sub-communities of the *Echinochloa pyramidalis* backswamp community (Ea & Eb)

Those plant communities that are less influenced by the sediment input from the Mkuze River i.e. the *Acacia xanthophloea* woodland community (A) and the *Cynodon dactylon* floodplain community (C) were dominated by sandy soils in areas where there is little or no fluvial sedimentation taking place. The degree of inundation or relationship to elevation above, and distance from, the thalweg separated these communities. The *Cynodon dactylon* floodplain community is infrequently inundated while the *Acacia xanthophloea* woodland community (A) is rarely inundated. The level of disturbance, whether from human or

	Swamp / Marsh Complex			Floodplain Complex

Division 1 — Fluvial Sedimentation — Present (Clay Soils) / Absent (Sandy Soils)

Division 2 — Hydrology — Semi - to Permanently Inundated / Periodically Inundated / Infrequently Inundated / Rarely Inundated

Division 3 — Distance from Thalweg — Far / Close / Close / Far

Division 4 — Geomorphology — Backswamp / Levee — Disturbance — Yes / No

Division 5 — Disturbance — No / Yes

Community P   I   Ea   Eb   F   C1   C2   C3   A

Figure 4.12 Dendrogram illustrating underlying environmental determinants of plant community types (see text for full plant community names).

animal sources, also played an important role in determining the distribution of the sub-communities of the *Cynodon dactylon* floodplain community (C1, C2 & C3).

4.4.3 Conceptual Model of Vegetation-Environment Relationships

Based on the results of the vegetation analysis, a conceptual model of the relationship between plant community distribution within the study area and the underlying environmental gradients was developed (Fig. 4.13). In general the *Phragmites mauritianus* reed swamp community (P) is found where there is slow moving water, in semi- to permanently saturated soil. This is usually around the edges of pans or in extensive stands in low-lying areas on the distal reaches of the floodplain. The *Imperata cylindrica* hygrophilous grassland community (I) is uncommon and is found in isolated stands towards the edge of the region of seasonal flooding. The *Echinochloa pyramidalis* backswamp community (Ea & Eb) is the most extensive of all the plant communities. This community is tolerant of flooding and is found in damp places such as seasonal pans, backswamps and riverbanks, as well as in standing water. The distribution of the *Ficus sycomorus* riparian forest community (F) is restricted to elevated levees adjacent to the river channel that experience inundation when floods are large enough to overtop channel banks. The *Cynodon dactylon* floodplain community (C1, C2 & C3) is generally found towards the floodplain-terrestrial upland boundary in elevated areas with sandy well-drained soils. However the *Cynodon dactylon* highly disturbed floodplain community (C1) is also found at slightly lower elevations with more clayey soils and is extremely disturbed by cattle and humans. The *Acacia xanthophloea* woodland community (A) is distributed on the floodplain margin in elevated areas on sandy soils, primarily fringing the linear pans (Muzi and Yengweni Pans) draining towards the Mkuze River from the north.

4.5 Conclusion

The vegetation of the study area was classified into six plant communities namely the *Phragmites mauritianus* reed swamp community, the *Imperata cylindrica* hygrophilous grassland community, the *Echinochloa pyramidalis* backswamp community, the *Ficus sycomorus* riparian forest community, the *Cynodon dactylon* floodplain community and the *Acacia xanthophloea* woodland community. The distribution of these plant communities
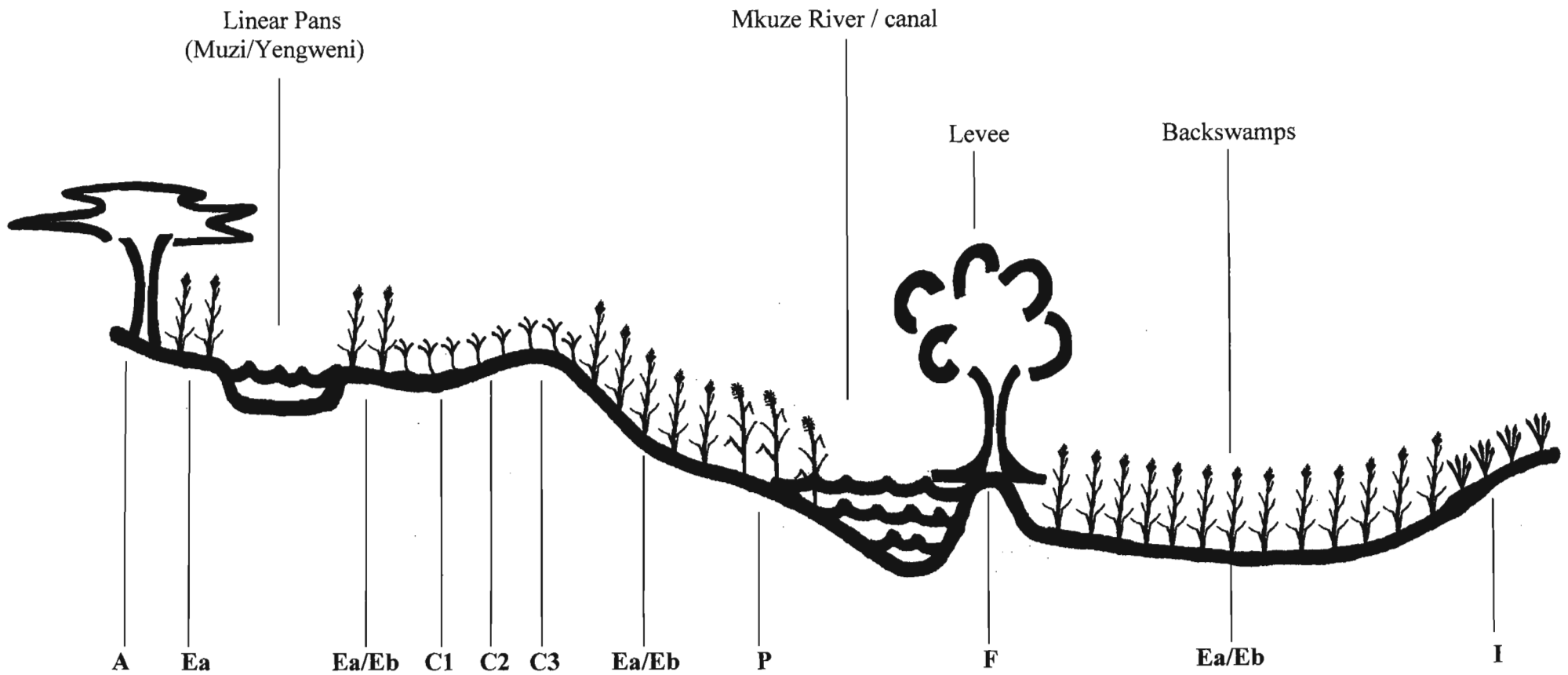
Figure 4.13 Conceptual model of plant community distribution (see text for full plant community names).

was correlated with an underlying inundation-sedimentation gradient that summarized the interactions between hydrology, substrate properties and topography.

This chapter provided an explanation of vegetation-environment relationships at the plant community level within the landscape hierarchy. From a landscape ecology perspective this level of analysis corresponds to the grain of the landscape. The description of the plant community types and the underlying environmental determinants of their distribution provides a useful foundation for the examination of ecological processes and phenomena at the next higher, spatially coarser level within the landscape hierarchy, the reference level.

CHAPTER 5 LANDSCAPE ECOLOGY

5.1 Introduction

The results presented in the previous chapter show that vegetation distribution is correlated with an inundation-sedimentation gradient that summarizes the interactions between hydrology, substrate properties, sedimentation and geomorphology. These results provide an explanation of vegetation-environment relationships at the plant community level within the landscape hierarchy. From a landscape ecology perspective this level of analysis corresponds to the grain of the landscape, which provides the mechanistic explanation of plant community distribution.

This distribution has previously been illustrated in a generic spatial context, as was evident in the conceptual model of plant community distribution described in Chapter 4. Only once these communities are mapped, thus placing them in the specific context of the lower Mkuze River floodplain, is one able to build on the knowledge of vegetation-environment relationships in such a way that allows one develop process-based understanding. The aim of this chapter is therefore to describe the grain in a spatially explicit context and to examine the ecological patterns and processes operating at the next higher, spatially coarser level within the landscape hierarchy, the reference level.

5.2 Methodology
5.2.1 The Spatial Distribution of Plant Community Types

In order to determine the spatial configuration of the landscape at the grain, plant community types or patches were mapped from 1:30 000 black and white aerial photographs taken in August 1996. Aerial photographic analysis for mapping purposes usually involves the identification and delimitation of specific features recognizable by a combination of image characteristics, including tone, texture, shape, size, shadow height and spatial relationship (Lyon & McCarthy, 1995). Patches of vegetation were distinguished on the basis of these image characteristics. Stereoscopic magnification is commonly used as an aid to detect boundaries that coincide with changes in topography and/or vegetation (Johnston *et al.*, 1992). This proved invaluable in this study, especially for the delimitation of the floodplain boundary, which was identified by a change in

vegetation structure and topography. Plant community types were traced onto transparent overlays. Each polygon was labeled according to the plant community type identified in the TWINSPAN classification process.

Inaccuracies are inevitable during aerial photograph based mapping. Accuracy depends on the quality of the photograph, the efficiency of the photo analyst, the amount of ground truthing and the degree of registration and distortion problems (Dunn *et al.*, 1991; Lyon & McCarthy, 1995). Aerial photographs have been routinely used for resource mapping during the last half century. During this time the inaccuracies of aerial photograph interpretation and mapping have been thoroughly documented. The reduction of these inaccuracies was not considered a priority in the past because area errors were less than those associated with the technology used to measure map area. However, as technologies have advanced these errors have become more obvious especially since the inception of geographical information systems (GIS) where maps are routinely used in spatial analyses involving multiple overlays (Lyon & McCarthy, 1995). Two major distortions commonly encountered when mapping from aerial photographs are tilt and camera lens distortions of the photographed landscape. These inaccuracies, although considered quite small in large format aerial photographs, can influence mapping accuracy.

The aerial photographs used in this study were not orthometrically corrected. However, a degree of rectification was obtained through transferring co-ordinates for recognizable reference points from 1986 orthophotographs to each aerial photograph. Although this did not eliminate all distortion and registration problems, the remaining inaccuracies were considered acceptable for present mapping purposes. Ground truthing is a necessary process that reduces photo interpretation inaccuracies. It is commonly used to identify potential gaps in the plant community classifications and may result in corrections that update and enhance the quality of the final map (Mueller-Dombois & Ellenberg, 1974). Logistically it was impossible to cover the entire study area due to lack of access roads, difficulty in crossing wetland areas due to dense vegetation, the presence of standing water and hazards posed by wild animals such as crocodiles and hippopotami. Therefore ground truthing took the form of the examination of colour slides taken during a single aerial survey from a light aircraft.

The next step in the mapping process involved digitizing the vegetation polygons into a GIS. The GIS software Atlas version 4.0 was used for this purpose as well as for editing and cleaning the maps. GIS is a computerized mapping system used for the capture, storage, management, analysis and display of spatial and descriptive data and is recognized as one of the principal technologies available for landscape ecology studies (Coulson *et al.*, 1991). The development of GIS technology has provided landscape ecologists with an analytical tool that can be used to examine the spatial complexity of heterogeneous landscapes (Haines-Young *et al.*, 1993; Aspinall, 1999).

In order to provide a regional overview of topography of the study area, a digital elevation model (DEM) was constructed. The elevation data, obtained by digitising the contour lines and spot heights from 1986 orthophotographs, was converted into a grid-based DEM using SURFER software and the kringing method. A grid spacing of 20 x 20m was chosen and imported into ArcView version 3.1. Five valley cross-sectional profiles were constructed from the DEM from the southern or western to the northern or eastern floodplain boundary. They were plotted with standardized x and y axes in order to illustrate changes in floodplain width, elevation and topography in a downstream direction. Bearing in mind that the contour lines and spot heights of the orthophotographs are not entirely accurate, the topography is not precise. Inaccuracies are further compounded during the digitizing process and the overlaying of themes from different data sources. Nevertheless the DEM provided a reasonable impression of the regional topography of the floodplain system.

5.2.2 The Determination of Functional Landscape Units

Ecosystems are complex systems that can be described and classified in many different ways. The nested model describing the hierarchical nature of landscapes (described in Chapter 2) allows one to derive a framework for understanding this complexity. The plant community types identified in Chapter 4 comprise the finest level within the landscape hierarchy, having been classified according to species composition and then related to environmental determinants underlying their spatial distribution. This spatial heterogeneity in plant community distribution is a reflection of the functional heterogeneity within the landscape mosaic (Breen *et al.*, 1988; Mitsch & Gosselink, 1993). The clustering of plant communities based on functional criteria can be used as a means of simplifying and

exploring the complexities of ecological patterns and processes at the reference level within the landscape hierarchy.

In recent years ecologists have placed increasing emphasis on the use of functional classifications when describing the structure and functioning of ecosystems (Gitay & Noble, 1997). The functional group (or type) concept stresses the importance of process orientated ecological questions and focuses on describing the landscape according to common functional attributes (Solbrig, 1994; Hobbs, 1997; Sala *et al.*, 1997). These functional attributes are commonly based on criteria such as the utilisation of similar resources, response to specific perturbations, or relationship to limiting or dominating ecosystem processes (Gitay & Noble, 1997; Hobbs, 1997). It is however recognised that when identifying functional types, the similarity criteria chosen by the investigator usually reflects the purpose of the study (Korner, 1994; Solbrig, 1994; Westoby & Leishman, 1997).

In this study vegetation functional types were identified by examining plant community similarity (or dissimilarity) along the first ordination axis. The Euclidean distances between the mean sample scores of each plant community provides a commonly used, simple yet effective index of community similarity (Gauch, 1982; Mentis & Ellery, 1994). Plant communities were aggregated into vegetation functional types and mapped using a GIS as a means to explore ecological patterns and processes operating at the reference level within the landscape hierarchy.

5.3 Results

5.3.1 The Spatial Distribution of Plant Community Types

The process of mapping in this case necessitated the inclusion of categories not previously identified in the classification process and the omission of categories too fine for the scale of mapping. The sub-communities: the *Echinochloa pyramidalis-Cyperus dives* undisturbed backswamp community and the *Echinochloa pyramidalis-Sorghum bicolor* disturbed backswamp community were indistinguishable on the aerial photographs and were therefore mapped as one vegetation unit. Similarly the sub-communities of the *Cynodon dactylon* floodplain community were mapped as a single entity. The *Imperata*

cylindrica hygrophilous grassland community was absorbed into the *Echinochloa pyramidalis* backswamp community because it occurred in patches too fine for the scale of mapping. Similarly, the *Acacia xanthophloea* woodland community was eliminated since it only occurred along the floodplain edges and was not readily observable at the scale of mapping utilized. Three new categories were identified during the mapping process. Firstly a *Cyperus papyrus* swamp community (Cy) was included. This community is described in other research conducted within the study area (Schoultz, 2000; Taylor, 2000). *Cyperus papyrus* is a sedge that commonly grows in extensive monospecific stands in permanently saturated soil and/or shallow water conditions. A second addition was that of terrestrial islands within the floodplain. These are areas of elevated basement sand that project through the silt dominated floodplain deposits (McCarthy & Hancox, 2000) and are typically vegetated with *Hyphaene coriacea* (Lala Palm). The third category was agricultural fields, this included land presently under cultivation, fallow land and recently abandoned and recovering fields.

The distribution of plant community types is illustrated in Figure 5.1. The *Cyperus papyrus* swamp community (Cy) and the *Phragmites mauritianus* reed swamp community (P) are generally found along the north-eastern and eastern edges of the floodplain, especially in areas surrounding permanent standing water such as the Mdlanzi and Tshangwe Pans or in saturated soils such as those along the edges of the fan adjacent to the Mbazwane Wetland. The *Echinochloa pyramidalis* backswamp community (E) occurs widely throughout the floodplain but tends to follow the Mkuze River forming a broad, central corridor through the floodplain system. The *Cynodon dactylon* floodplain community (C) is found along the southern edges of the floodplain boundary, particularly in the region of Mpempe and Ngwenya Pans. It appears to occur in that region of the floodplain where there is little or no active sedimentation i.e. in the southern-middle reaches of the floodplain. The *Ficus sycomorus* riparian forest community (F) is restricted to a narrow band fringing the Mkuze River, concentrated in the section of the river below Muzi and Yengweni Pans. Isolated patches are evident further downstream but agricultural land dominates the southern banks of the Mkuze River in this area.

Legend:

- Cyperus papyrus swamp
- Phragmites mauritianus reed swamp
- Ficus sycomorus riparian forest
- Echinochloa pyramidalis backswamp
- Cynodon dactylon floodplain
- Water bodies
- Terrestrial islands
- Agricultural fields
- Mkuze River and streams
- Floodplain boundary
- Tshanetshe - Mpempe Canal System

N

0   1   2 Kilometres
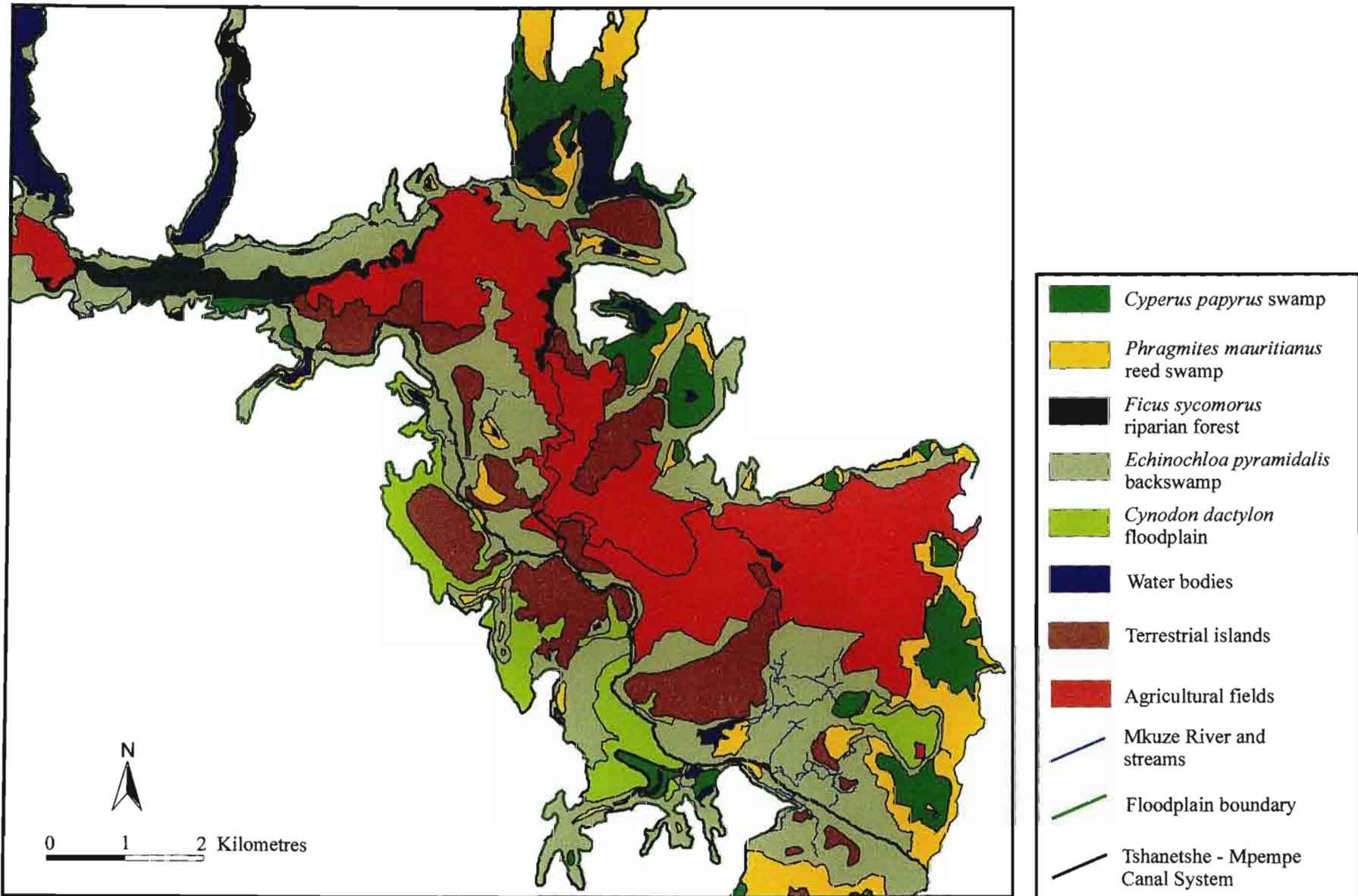
Figure 5.1 Plant community landscape mosaic in 1996.

5.3.2 The Description of the Functional Mosaic

5.3.2.1 The Identification of Functional Types

Three clusters of similar plant communities or vegetation functional types are readily identifiable when one compares the similarities and dissimilarities of community types based on the Euclidian distances of the centroid of each community relative to each other in ordination space (Table 5.1). The first comprises the *Echinochloa pyramidalis* backswamp community (E), the *Ficus sycomorus* riparian forest community (F) and the *Imperata cylindrica* hygrophilous grassland community (I), all of which have small Euclidean distances between them, indicating a high degree of community similarity. The mean sample scores of the *Cynodon dactylon* floodplain community (C) and the *Acacia xanthophloea* woodland community (A) are also situated close together in ordination space, forming a second group of similar plant community types. Also evident are the large distances separating the *Phragmites mauritianus* reed swamp community (P) from the other communities, indicating the high degree of dissimilarity between these communities. The *Phragmites mauritianus* reed swamp community (P) therefore forms a third cluster.

Table 5.1 Euclidean distances between plant community types based on mean axis 1 sample scores from the DCA output (Fig. 4.3; standard deviation units x 100).

	P	I	E	F	C
I*	271.03				
E	211.92	**59.12**			
F	224.57	**46.46**	**12.66**		
C	**430.84**	159.81	218.93	206.27	
A	**474.09**	203.06	262.18	249.52	**43.25**

*see text for full community names

5.3.2.2 The Spatial Distribution of Functional Types

The spatial distribution of the three vegetation functional types is illustrated in Figure 5.2. The vegetation functional type comprising the *Echinochloa pyramidalis* backswamp community (E), the *Ficus sycomorus* riparian forest community (F) and the *Imperata cylindrica* hygrophilous grassland community (I) dominates the functional landscape mosaic. This functional type forms a broad corridor flanking the Mkuze River forming a

Legend:

- **Distal - permanently inundated swamp** (*Cyperus papyrus* swamp and *Phragmites mauritianus* reed swamp communities)

- **Proximal - seasonally inundated marsh** (*Ficus sycomorus* riparian forest, *Echinochloa pyramidalis* backswamp and *Imperata cylindrica* hygrophilous communities)

- **Distal - infrequently inundated swamp** (*Cynodon dactylon* floodplain community)

- **Water bodies**

- **Terrestrial islands**

- **Agricultural fields**

- **Mkuze River and streams**

- **Floodplain boundary**

- **Tshanetshe - Mpempe Canal System**

Figure 5.2 The spatial distribution of vegetation functional types.

central corridor through the floodplain system. The functional group comprising the *Phragmites mauritianus* reed swamp community (P) has been grouped with the *Cyperus papyrus* swamp community (Cy) since these two communities share similar environmental determinants of their distribution. This functional type is predominantly distributed along the northern fringes of the floodplain towards the distal edge of the floodplain and is generally associated with the larger, more permanent floodplain pans. The functional type comprising the *Cynodon dactylon* floodplain community (C) is located in the middle to distal reaches of the floodplain forming a narrow band along the southern boundary.

5.3.2.3 The Definition of Functional Types

The three vegetation functional types are clearly illustrated in Figure 5.3. Axis 1 of the DCA output corresponds to the inundation-sedimentation gradient described in Chapter 4 and in conjunction with the community similarity indices and spatial distribution described above, one is able to describe the distribution of the three functional types from a hydrogeomorphic perspective:

- **The distal[*]-permanently inundated swamp**

  This functional type comprises the *Phragmites mauritianus* reed swamp community (P) and the *Cyperus papyrus* swamp community (Cy). Typically it is found in the distal reaches of the floodplain that are rarely exposed to hydrological and sedimentological inputs from the Mkuze River. This functional type is permanently inundated and characterized by standing water and/or permanently saturated soils that are generally associated with the large floodplain pans such as Mdlanzi and Tshangwe Pans.

- **The proximal-seasonally inundated marsh**

  This functional type comprises the *Echinochloa pyramidalis* backswamp community (E), the *Ficus sycomorus* riparian forest community (F) and the *Imperata cylindrica* hygrophilous grassland community (I). The geomorphology of this functional type is very varied, comprising plant community types found on channel levees and within

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[*] According to the Concise Oxford Dictionary of Earth Sciences proximal applies to a sedimentary environment close to the source of the deposit and distal applies to a depositional environment sited at the furtherest position from the source area (Allaby & Allaby, 1990). In this case the source area is considered to include the entire length of the Mkuze River within the study area.
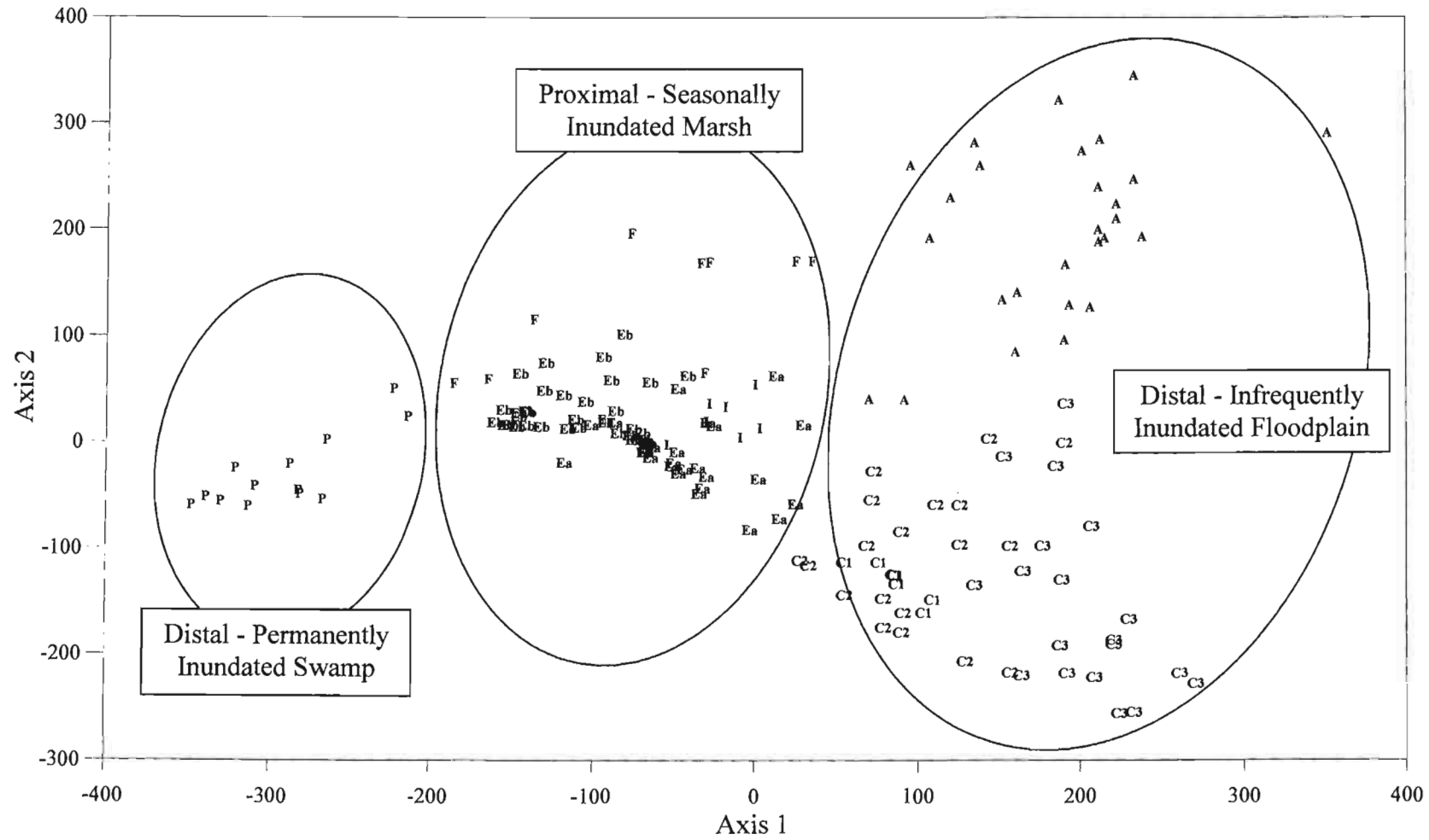
Figure 5.3 Sample scores of DCA ordination axes 1 and 2 illustrating vegetation functional types (units are standard deviations x 100; see text for full plant names).

backswamp areas. However, these areas are all functionally connected to the Mkuze River in that they are exposed to seasonal flood events and associated sedimentation.

- **The distal-infrequently inundated floodplain**

  This functional type comprises the *Cynodon dactylon* floodplain community (C) and the *Acacia xanthophloea* woodland community (A). This functional type is typically located in elevated, sandy areas along the southern, distal reaches of the floodplain. It is infrequently inundated by overbank floodwaters from the Mkuze River and is not an area characterized by substantial clastic sedimentation.

5.3.3 Regional Topography

The digital elevation model (DEM) of the floodplain and surrounding areas, the cross-sectional profiles and the relationship between topography and the distribution of vegetation functional types is shown in Figure 5.4.

The elevation within the floodplain is relatively uniform, the majority of which is less than 20m above sea level (asl). Small, isolated patches of higher lying ground, between 20 and 30m asl, are found within the floodplain, predominantly in the upper reaches below Muzi and Yengweni Pans. Generally however the upper and middle reaches of the floodplain lie between 10 to 20m asl while the lower reaches, towards the margin of the floodplain fan, lie between 0 and 10m asl. The higher lying areas outside the floodplain comprise terrestrial upland that lies between 20 and 30m asl and the paleo-dune ridges east of Muzi and Yengweni Pans that in places reach an elevation of between 60 and 70m asl.

Floodplain width steadily increases from approximately 1500m at profile A(c)-A(m) to approximately 4000m at profile E(c)-E(m). The positions of the Mkuze River and the Tshanetshe-Mpempe Canal System are labeled on each profile. In all profiles it is evident that the Mkuze River is situated on an elevated ridge relative to the surrounding floodplain. Although this is unusual it is not due to mapping error and is in fact a phenomenon that provides insight into the sedimentation processes operating within the floodplain system. Also evident in all the profiles is the canal system, which occupies a basin depression lying to the south and west of the elevated ridge and at a lower elevation than the Mkuze River. The presence of this ridge-basin feature is continuous down the length of the floodplain
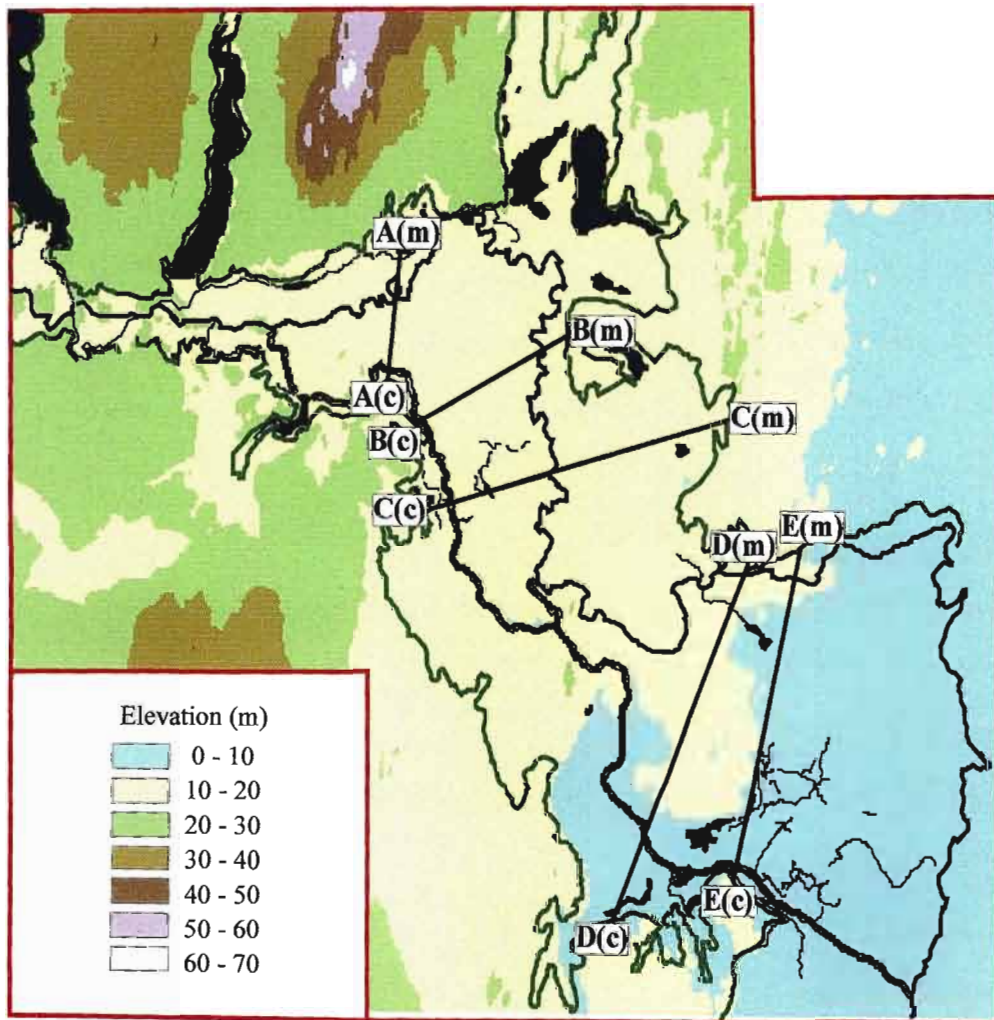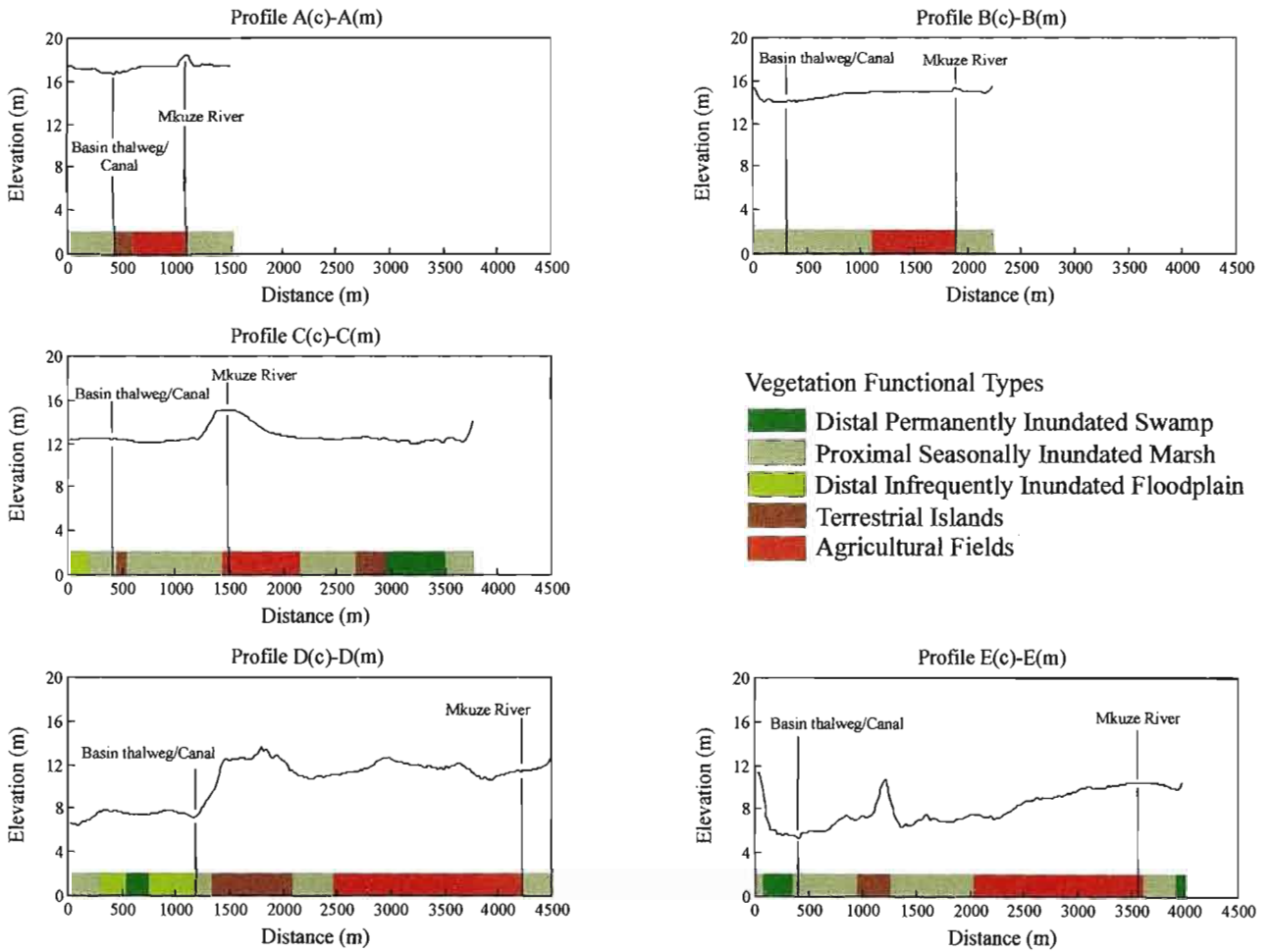
Figure 5.4 DEM, cross-sectional profiles and distribution of vegetation functional types.

and provides insight into the geomorphic setting of the lower Mkuze River floodplain system.

To further illustrate this ridge-basin feature, the elevations and valley distances from the confluence of the Mkuze River and the Tshanetshe Canal were measured at each point where profiles A(c)-A(m) to E(c)-E(m) intersected with the river and canal (Fig. 5.5). There are substantial differences in elevation between these two topographic features. From the confluence of the Tshanetshe Canal and the Mkuze River to where the canal intersects with Profile E(c)-E(m) there is an elevation difference of 9.3m, while from the confluence to where the Mkuze River intersects with Profile E(c)-E(m) the elevation difference is approximately 7m. This difference in elevation between the ridge and basin has important implications for hydrological and sedimentological processes operating within the floodplain system.
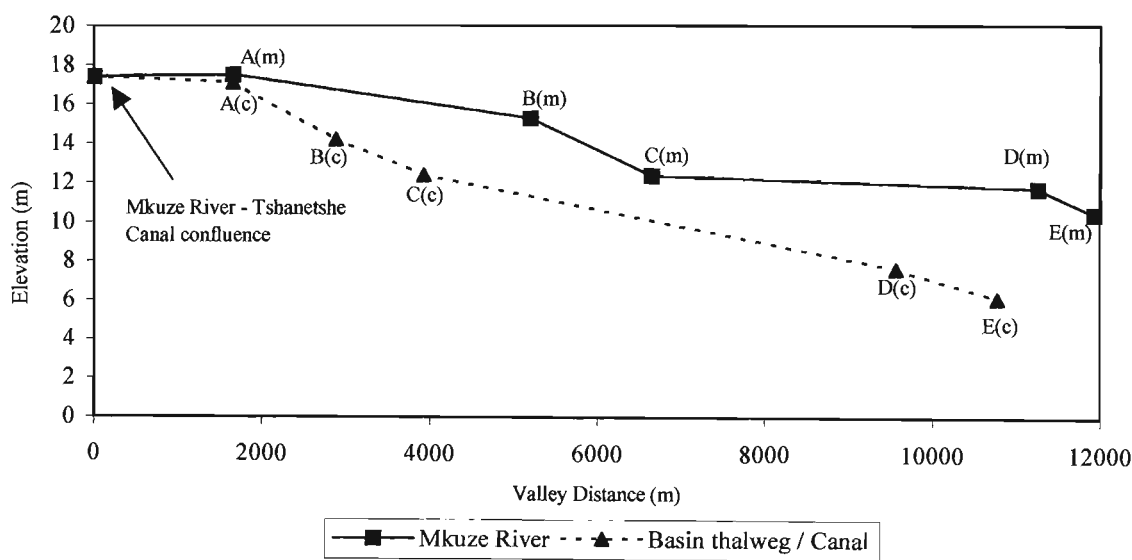
Figure 5.5 Elevation differences along the Mkuze River and the Tshanetshe-Mpempe Canal System (Profiles A(c)-A(m) – E(c)-E(m).

Narrow map sections, corresponding to the position of each cross-sectional profile, were taken from Figure 5.2 and inserted along the bottom of each profile in Figure 5.4 in order to illustrate the distribution of vegetation functional types in relation to the basin-ridge feature described above. In all profiles, except B(c)-B(m), the Mkuze River and canal are separated by areas of terrestrial island, while in profiles C(c)-C(m) and D(c)-D(m) the

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canal is in close proximity to the distal-infrequently inundated floodplain functional type. The ridge, on which the Mkuze River is situated, is typically characterised by either the proximal-seasonally inundated marsh functional type or agricultural fields in all profiles.

5.4 Discussion

5.4.1 The Spatial Distribution of Functional Types

Floodplain systems and their associated wetlands typically exhibit a continuum of variation in their ecological patterns and processes (Malanson, 1993). In order to gain insight into this variation some researchers have attempted to classify floodplains and floodplain wetlands. This has often resulted in an artificial typology that invariably offers superficial explanations of floodplain processes (Breen *et al.*, 1988; McCarthy & Hancox, 2000; Kotze *et al.*, 2001). A move away from this approach towards one that focuses on process-based understanding of floodplain systems becomes apparent when examining recent literature on floodplain structure and functioning.

In a study examining vegetation processes in swamps and flooded plains Breen *et al.* (1988) identified a continuum of floodplain types based primarily on hydrological regime. Swamps were located on one end of the continuum and defined by the persistence of standing water; while flooded plains were located at the opposite extreme, being characterized by the regular alternation of wet and dry phases. Marshes occupied an intermediate position on the continuum and contained water-saturated sediments but little to no standing water among vegetation. Higgins *et al.* (1996) identified three flood event sizes that inundated various geomorphological zones within the Nyl River floodplain. These were a hydromorphic zone flood, a floodplain zone flood and a channel zone flood. The hydromorphic zone flood was characterized by floods that occurred in approximately three out of 10 years. Flooding occurred to such an extent that inundation reached the height of the floodplain-terrestrial upland boundary. The floodplain zone flood was one that occurred every four in 10 years and inundated interchannel depressions and backswamp areas of the floodplain. In contrast, the channel zone flood occurred in approximately seven out of 10 years and was restricted to within the channel confines.

Selinger-Looten *et al.* (1999) in a study examining the relationship between plant community structure and landscape patterns in floodplains identified three types of areas within the floodplains examined. These were a hygrophilic type where surface water was present for extended periods; a mesophilic type, which was a seasonally waterlogged area where substrates were saturated for extended periods but surface water was seldom present; and a xerophilic type, which was an intermittently inundated area where surface water was only present for short periods and the water table was otherwise well below the soil surface. These three studies illustrate the use of a process driven identification of a continuum of functional types that provided useful insight into floodplain patterns and processes. All three continua were primarily hydrologically based but either implicitly or explicitly recognized the importance of geomorphological processes.

In this study a similar continuum was identified within the lower Mkuze River floodplain, namely the distal-permanently inundated type and the distal-infrequently inundated type, which occupied the extremes of the continuum, while the proximal-seasonally inundated type occupied an intermediate position. The definition of these functional types ties in with Gosselink & Turner's (1978) conceptual model described in Chapter 2, where wetland patterns and processes are determined by the interaction between hydrological regime, sediment inputs (and therefore local geomorphology) and vegetation distribution. The identification and distribution of the three functional types provides a useful framework for examining ecological processes operating within the lower Mkuze River floodplain.

Overbank flooding of the Mkuze River is the primary input of water and sediment into the floodplain system. Mean annual flow varies between 211 and 326 x 10^6 m^3 (McCarthy & Hancox, 2000). Daily discharge measurements of the Mkuze River taken at the lower Mkuze River bridge from 1970 to 1988 (Fig. 5.6) clearly illustrate that flooding is seasonal, is characterized by large pulses of high flows and that there is little to no flow during the winter months of most years. Thus, hydrological and consequently sedimentological inputs onto the floodplain occur during these high flow events. The distribution of functional types is therefore determined primarily by a flood based inundation gradient, similar to that described in the study by Higgins *et al.* (1996). The distal-permanently and the distal-infrequently inundated functional types are exposed to
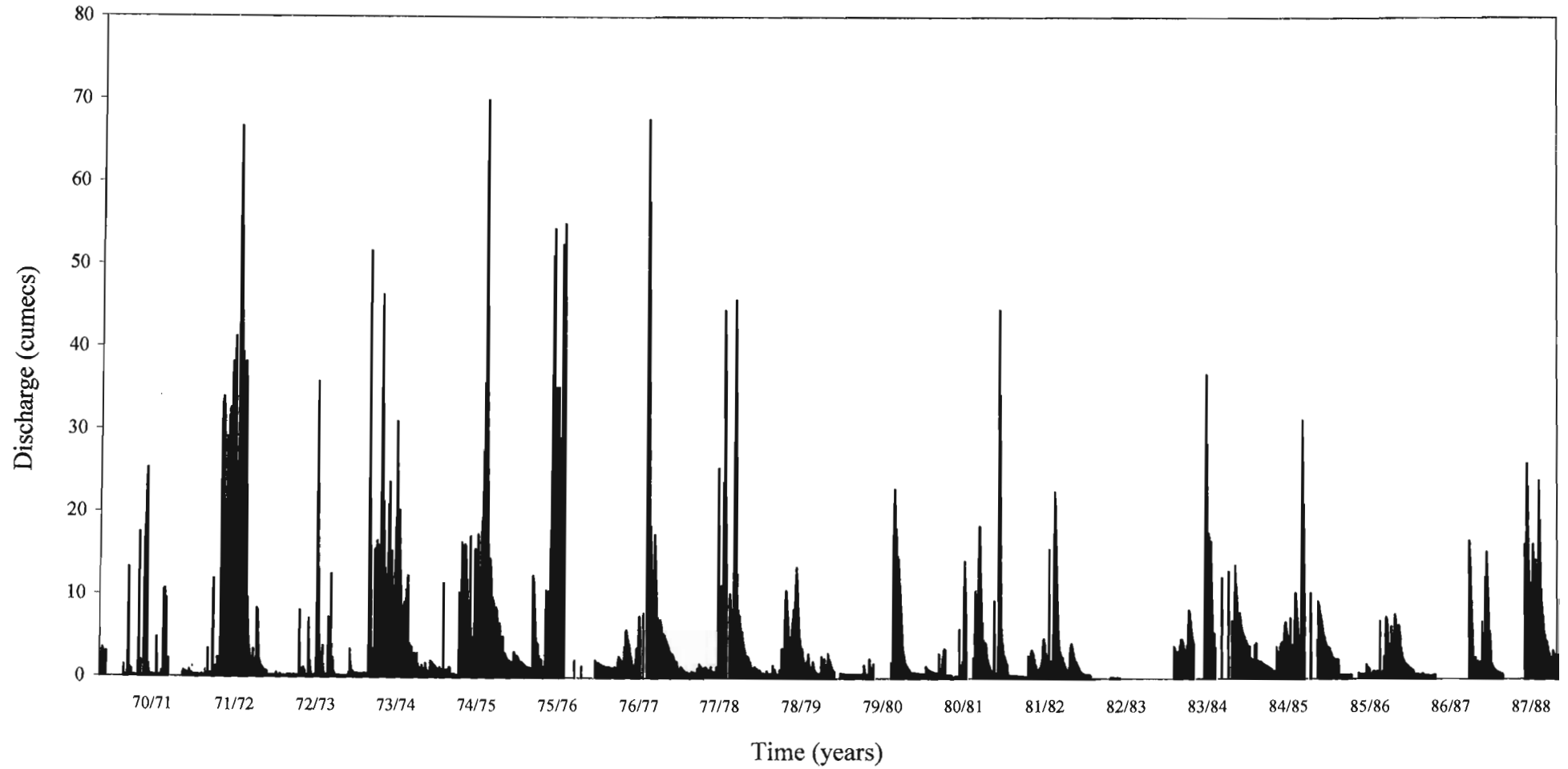
Figure 5.6 Daily discharge readings of the Mkuze River taken at the lower Mkuze River Bridge for the years 1970 to 1988.

Mkuze River water and sediment inputs during exceptionally large flood events, whereas the proximal-seasonally inundated type is exposed to all flood events large enough to overtop channel levees.

Both the distal-permanently and distal-infrequently inundated functional types are located towards the margins of the floodplain. Although these functional types receive water and sediment inputs very infrequently from the Mkuze River, the Mkuze River has played an important role in their evolution and development. The lower Mkuze River floodplain is prograding in a west-east direction into the Mkuze Swamps as a result of sediment transported by the Mkuze River to the eastern floodplain margin during large flood events (McCarthy & Hancox, 2000). This advancement has progressively blocked off interdune tributaries and isolated abandoned channels within the floodplain, giving rise to a mosaic of wetland types. This process continues today, providing the geomorphic setting for the formation of the distal-permanently inundated swamps. This functional type is distributed in areas of permanent standing water or highly saturated soils. As such hydrological inputs must always be in excess of outputs. Inputs from the Mkuze River, as already mentioned, only occur during large flood events. Therefore another hydrological input exists that is sustaining this functional type. Those distal-permanently inundated swamps located along the eastern margin, adjacent to the Mkuze Swamps are fed by the Mbazwane River and associated wetlands, while those situated along the northern boundary of the floodplain are fed by the Manzibomvu Streams. Both the Mbazwane and Manzibomvu Streams are groundwater fed, therefore they seldom flood and provide the regular and continuous source of inflow required to sustain the distal-permanently inundated swamps.

The distal-infrequently inundated functional type is found on elevated, well drained sandy soils. The input of coarse-grained sediments onto the floodplain is not via the Mkuze River. This functional type is typically located along the terrestrial upland-floodplain boundary or in the vicinity of terrestrial islands where projections of basement sand predominate since there has been little input of clastic sediment from the fluvial system in these areas.

A lateral rather than a longitudinal zonation of functional types dominates the floodplain surface. This zonation in relation to the Mkuze River and other external inputs, is summarized schematically in Figure 5.7. The proximal-seasonally inundated functional type is influenced primarily by the input of water and sediment from the Mkuze River. The distal-permanently inundated functional type is influenced by a combination of water and sediment input from the Mkuze River as well as the southward draining Mbazwane and Manzibomvu Streams. The distal-infrequently inundated functional type receives its water supply from the Mkuze River during extreme flood events but by the time this water reaches the southern floodplain margins it appears to be relatively sediment free, thus the substratum is typical of the underlying basement sand.

5.4.2 Floodplain Patterns and Processes

The lower Mkuze River floodplain is an aggrading system (McCarthy & Hancox, 2000). Little to no sediment originating from the Mkuze River is entering Lake St Lucia (Taylor, pers. comm.). Therefore the floodplain and its associated wetlands are acting as major sediment sinks. Aggradation has resulted in levee formation and over time has contributed to the formation of an alluvial ridge. The Mkuze River channel is situated on this alluvial ridge and is progressively attaining grade downstream. This has resulted in a decrease in channel slope, reducing flow velocities and resulting in a reduction in the ability of the river to transport sediment. Sediment is therefore deposited along the channel bed. This process is confirmed when examining changes in channel depth downstream within the study area (Table 5.2). Channel depth decreases progressively as one moves downstream to such an extent that in the distal reaches of the floodplain the channel becomes indistinct. During large flood events the channel is unable to accommodate floodwaters, especially in these distal reaches, resulting in a diffuse flow over the channel banks and across the floodplain surface.

Table 5.2 Downstream changes in channel depth of the Mkuze River.

Transect Number *	Channel Depth (m)
7	3.6
8	3.0
9	1.1
10	0.8

*See Figure 4.1 for location within study area.
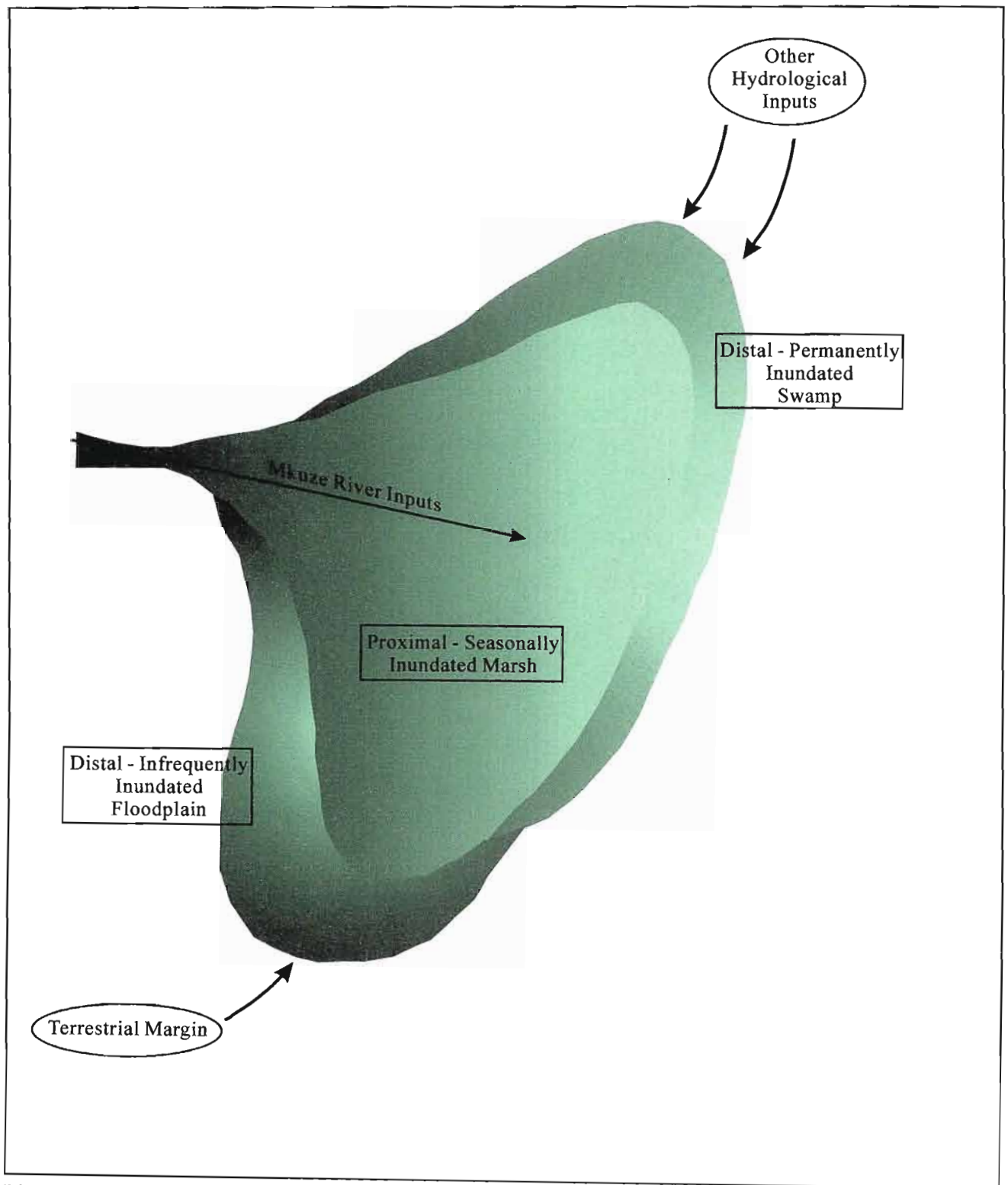
Figure 5.7 The distribution of vegetation functional types in relation to Mkuze River inputs.

This phenomenon where the influent river channel increasingly loses definition downstream and flow becomes diffuse has been described in Australian fluvial systems as floodouts (Tooth & Nanson, 2000). Floodouts occur along that part of the river profile where there is a marked reduction in channel capacity compared with reaches further upstream and where overbank flows become increasingly more common (Tooth, 1999a). In addition, floodouts occur in systems with high sediment inputs where vertical accretion of the floodplain is common (Tooth, 1999b) and along rivers characterized by variable discharge (Tooth & Nanson, 2000). According to Tooth (1999a) floodouts are a feature of arid and semi-arid areas in Australia. However, many of the characteristics of these Australian floodouts are evident in the lower Mkuze River floodplain, which is located in a moist subtropical setting. If the lower Mkuze River floodplain is a floodout, the concept of floodouts would have be extended beyond the semi-arid systems in which they were first described. Further investigation is required if the hydrological, sedimentological and geomorphological processes operating within floodouts are to be fully understood.

Floodplains are dynamic systems, primarily because hydrological inputs and the fate of sediments within the system are constantly changing. From the data presented in this study it appears that sedimentation has been primarily confined to the channel margins and to the northern side of the floodplain system, creating a channel that is substantially elevated relative to the surrounding floodplain and a floodplain that itself forms an elevated alluvial ridge along the northern side of the floodplain. The basin depression along the southern margin of the system appears to have received less sediment and thus it occurs at a much lower elevation than the northern margin for a given valley distance. Within a system of this kind, given this pattern of sedimentation and the resultant differences in elevation between the basin and alluvial ridge features, channel avulsion is likely, if not inevitable. Avulsion is initiated by breaches in channel banks or levees resulting in the establishment of a new distributary channel along a hydraulically more efficient pathway. Breaching of the channel levees was initiated at two points along the Mkuze River during the excavation of the Mpempe and Tshanetshe canals. These canals joined to form the Mpemepe-Tshanetshe Canal System that runs the length of the basin along the southern floodplain boundary. Although this avulsion process was catalyzed by human intervention, there is

evidence within the lower Mkuze River floodplain that this process could have been initiated by natural processes (Loudon *et al.,* 1987; Ellery *et al.,* in prep.).

Along the reach of the Mkuze River south of Yengweni Pan and at the confluence of the Tshanetshe Canal and the Mkuze River there is evidence of hippo trails leading from the Mkuze River into the surrounding floodplain areas (Loudon *et al.,* 1987; Ellery *et al.,* in prep.). Hippo trails were found to have a catalytic effect on local geomorphological change, including the development of new channel systems during the process of channel avulsion, within the Okavango Delta in northern Botswana (McCarthy *et al.,* 1998). Behavioral studies have shown that hippos tend to use the same pathways repeatedly to access their grazing areas, resulting in the development of semi-permanent trails (O'Connor & Campbell, 1986). These trails are typically orientated along a local thalweg parallel to the regional hydraulic gradient, resulting in the localised concentration of flow along this pathway (McCarthy *et al.,* 1998). Erosive widening and deepening of these hippo trials may occur and ultimately they may develop into a primary distributary channel.

This process of avulsion, initiated by hippo trails and accelerated by canal excavation, has resulted in the redistribution of primary flows from along the Mkuze River to along the Mpemepe-Tshanetshe Canal System. The average low flows are channeled down the canal system and only large flows will flow down the original Mkuze River channel. This redistribution of the majority of flows along the basin thalweg has resulted in active erosion along the Mpempe-Tshanetshe Canal System, thereby increasing its width and depth along its entire length. This has resulted in an increase in the canal's capacity to accommodate larger discharges, thereby reducing the frequency of overbank flooding and consequently altering the pattern of sedimentation across the floodplain surface. These erosional processes are exacerbated by overgrazing and cattle trampling that result in reduced vegetation cover within and adjacent to the canal. All these factors have contributed to the more rapid movement of water through the floodplain system, the redistribution of seasonal flows across the floodplain surface and consequently the redistribution of sediments (Alexander, 1986). Thus natural and anthropogenic disturbances are causing a shift within the hydrogeomorphic continuum that determines the

distribution of vegetation functional types. The possible consequences of this will be examined in more detail in Chapter 6.

5.5 Conclusion

The plant communities identified and described in Chapter 4 were aggregated into three functional types namely the proximal-seasonally inundated functional type, the distal-permanently inundated functional type and the distal-infrequently inundated functional type. The identification and mapping of these functional types, using a GIS, enabled one to identify a hydrogeomorphic continuum that described the interaction between floodplain processes and vegetation distribution. This interaction allowed one to develop process-based understanding of ecosystem patterns and processes operating within the lower Mkuze River floodplain. From a landscape ecology perspective this scale of analysis corresponds to the reference level within the landscape hierarchy.

CHAPTER 6 LANDSCAPE DYNAMICS

6.1 Introduction

The results in the previous two chapters show that the mechanistic explanation of plant community distribution, at the hierarchical level of the grain, is determined by an inundation-sedimentation gradient. The clustering of these plant communities, based on functional criteria, enabled one to identify a hydrogeomorphic continuum that provided insight into floodplain patterns and processes operating at the reference level within the landscape hierarchy. In addition, landscape ecology theory emphasises the importance of a temporal analysis of spatial heterogeneity and the role of disturbance in ecosystem patterns and processes (Urban *et al.*, 1987). This chapter aims to use a GIS to quantify landscape change over time and to examine the role of anthropogenic disturbance through a spatio-temporal analysis of the landscape mosaic.

6.2 Methodology

6.2.1 Aerial Photograph Based Mapping

Temporal changes of vegetation patterns are commonly documented by mapping a series of aerial photographs from different years (Haines-Young *et al.*, 1993; Lyon & McCarthy, 1995). In addition to the several drawbacks of aerial photograph based mapping mentioned in Section 5.2.1, the most problematic when undertaking temporal analyses is the scarcity of aerial photographs from before the mid- to late 1930s (Dunn *et al.*, 1991). For the present study, the earliest aerial photographs available were from 1937 and the most recent from 1996, thus the temporal analysis was limited to a 59-year time span. Four sets of aerial photographs separated by approximately 20-year intervals, were selected for temporal analyses, the details of which are presented in Table 6.1. Rectification of tilt and camera lens distortions were minimised, and map categories classified and digitised into a GIS for all aerial photographs using the same techniques described in Section 5.2.1.

6.2.2 Spatial Statistics

Landscape ecology theory emphasizes the importance of the spatio-temporal relationship between landscape pattern and ecological processes. Landscape patterns provide the template for ecological processes such as flooding regimes, erosional and depositional

processes, and the occurrence of disturbance within a landscape. Spatial statistical analysis is a recognised method for quantifying and examining the temporal change of landscape patterns (Dunn *et al.,* 1991; Turner *et al.,* 1991). An in-depth study of the relationship between patch characteristics, such as *inter alia* the number, size and shape of patches that comprise landscape pattern, and associated ecological processes operating within the lower Mkuze River floodplain was beyond the scope of this study. Rather, landscape pattern was quantified in order to allow for the comparison of the floodplain landscape over the 59-year time period. This was then used as a tool to examine the role of anthropogenic disturbance within the landscape mosaic.

Table 6.1 Aerial photographic coverage of the study area.

Date of Photographs	Photograph Interval (years)	Scale of Photograph	Percentage Cover of Study Area
Sep 1937	-	1 : 21 000	~99%
May 1957	20	1 : 12 000	100%
May-July 1979*	22	1 : 10 000	~90%
August 1996	17	1 : 30 000	100%

*Orthophotograph

The spatial statistics of the four sets of plant community distribution maps were calculated using PATCH ANALYST, an ArcView GIS extension. PATCH ANALYST consists of several scripts written in Avenue and C code and it incorporates a modified version of the Fragstats Spatial Pattern Analysis programme commonly used in the generation of spatial statistics in landscape ecology studies (Elkie *et al.,* 1999). The statistics calculated for this study were as follows:

- **Total category area (TCA)** - The sum of areas of all patches within each map category (ha).
- **Contribution to total landscape area (%CTLA)** - The percentage area that each map category contributes to total landscape area (%).
- **Number of patches (No.P)** - The total number of patches within each map category.

- **Mean patch size (MPS)** - The average patch size within each map category (ha).

- **Median patch size (MedPS)** - The 50th percentile within each map category (ha).

- **Patch size standard deviation (PSSD)** - The standard deviation of patch areas within each map category (ha).

- **Mean perimeter-area ratio (MPAR)** - The average shape complexity of patches within each map category (m/ha).

6.3 Results

6.3.1 The Description of Past Landscape Mosaics

1937

The 1937 landscape mosaic is illustrated in Figure 6.1 and the corresponding spatial statistics are presented in Table 6.2. At the plant community level or the grain, the landscape mosaic is dominated by the *Echinochloa pyramidalis* backswamp community (E), which accounts for 39.6% of the total landscape area (2137ha). The distal reaches of the floodplain are dominated by the *Phragmites mauritianus* reed swamp community (P), which covers 20.9% of the total landscape area (1128.7 ha).

Mean patch size, median patch size and patch size standard deviation give an indication of the range of patch sizes within each plant community, while the mean perimeter-area ratio indicates shape. The *Ficus sycomorus* riparian forest community (F) has a mean patch size of 56.7ha, however the median patch size is 4.1ha and the standard deviation 79.2ha, indicating that 50% of the patches are less than 4.1ha, while the variance of patch size about the mean is high (Table 6.2). Thus there is a mixture of very small and large riparian forest patches within this mosaic. In addition, the mean perimeter-area ratio is 253.1 m/ha, which is high. Thus the mean shape is either a convoluted, compact shape or an elongated, linear shape. In this case, as is evident from Figure 6.1, the latter shape is more likely since this community forms a corridor flanking the Mkuze River. Conversely, the mean and median patch sizes for the *Cynodon dactylon* floodplain community (C) are similar and the patch size standard deviation relatively small, indicating that the majority of patches are of similar size. The mean perimeter-area ratio is one of the lowest (Table 6.2), indicating that the patches have a short perimeter and a large area. Thus mean shape tends to be compact

No aerial photo coverage

Legend:

- *Cyperus papyrus* swamp
- *Phragmites mauritianus* reed swamp
- *Ficus sycomorus* riparian forest
- *Echinochloa pyramidalis* backswamp
- *Cynodon dactylon* floodplain
- Water bodies
- Terrestrial islands
- Mkuze River and streams
- Floodplain boundary

N

0   1   2 Kilometres

Figure 6.1 Plant community landscape mosaic in 1937.

Table 6.2 Spatial statistics for the 1937 landscape mosaic.

Functional Type*[1]	Plant Community*[2]	Other	Spatial Statistics						
			TCA	%CTLA	No.P	MPS	MedPS	PSSD	MPAR
Distal - permanent			1468.4	27.2	44				
	Cy		339.7	6.3	26	13.1	5.0	22.0	248.7
	P		1128.7	20.9	18	62.7	24.6	102.5	184.6
Proximal - seasonal			2704.0	50.2	24				
	F		567.1	10.5	10	56.7	4.1	79.2	253.1
	E		2137.0	39.6	14	152.6	14.3	376.3	266.1
Distal - infrequent			219.4	4.1	6				
	C		219.4	4.1	6	36.6	32.5	21.7	132.9
		Water Bodies	210.0	3.9	69	3.0	0.7	7.5	863.1
		Terrestrial Islands	789.8	14.6	16	49.4	25.8	52.2	123.4
Totals			5391.6		159				

*[1]Distal - permanent = distal - permanently inundated functional type; Proximal - seasonal = proximal - seasonally inundated functional type; Distal - infrequent = distal - infrequently inundated functional type.

*[2]Cy = *Cyperus papyrus* swamp community; P = *Phragmites mauritianus* reed swamp community; F = *Ficus sycomorus* riparian forest; E = *Echinochloa pyramidalis* backswamp community; C = *Cynodon dactylon* floodplain community

with smooth edges. No part of the floodplain was identified as agricultural fields within the 1937 landscape mosaic.

At the reference level, a total of 159 patches were identified, of which 44, 24 and 6 patches were categorised as the distal-permanently inundated swamp, the proximal-seasonally inundated marsh and the distal-infrequently inundated floodplain respectively (Table 6.2). Although the distal-permanently inundated swamp had the greatest number of patches within the functional mosaic, the proximal-seasonally inundated marsh accounts for the largest percentage contribution to the total landscape area.

1957

The 1957 landscape mosaic is illustrated in Figure 6.2 and the corresponding spatial statistics are presented in Table 6.3. At the grain level, the landscape mosaic is dominated by the *Echinochloa pyramidalis* backswamp community (E), which occupies 44.6% of the total landscape area (2448.9ha). Agricultural fields contribute the least to the total area (2.6%), comprising only five patches with a mean patch size of 28.3ha. The mean perimeter-area ratio for agricultural fields is 163.8m/ha, indicating that the patches have a low perimeter to area ratio, with the mean shape tending to be compact with smooth edges.

At the reference level, the percentage contribution to the total landscape area of the distal-permanently inundated swamp, the proximal-seasonally inundated marsh and the distal-infrequently inundated floodplain is 20.3%, 52.5% and 4.5% respectively (Table 6.3). The remainder of the area comprises water bodies, terrestrial islands and agricultural fields. The water bodies' mean size and mean perimeter-area ratio is 8.5ha and 524m/ha respectively, indicating the presence of numerous, small, convoluted patches within the landscape mosaic (Fig. 6.2).

1979

The 1979 landscape mosaic is illustrated in Figure 6.3 and the corresponding spatial statistics are presented in Table 6.4. An obvious addition to the landscape mosaic is the Mpempe Canal, which was excavated in 1971 from the Mkuze River through the northern portion of Mpempe Pan and then in a south-easterly direction before rejoining the Mkuze

Legend:

- *Cyperus papyrus* swamp
- *Phragmites mauritianus* reed swamp
- *Ficus sycomorus* riparian forest
- *Echinochloa pyramidalis* backswamp
- *Cynodon dactylon* floodplain
- Water bodies
- Terrestrial islands
- Agricultural fields
- Mkuze River and streams
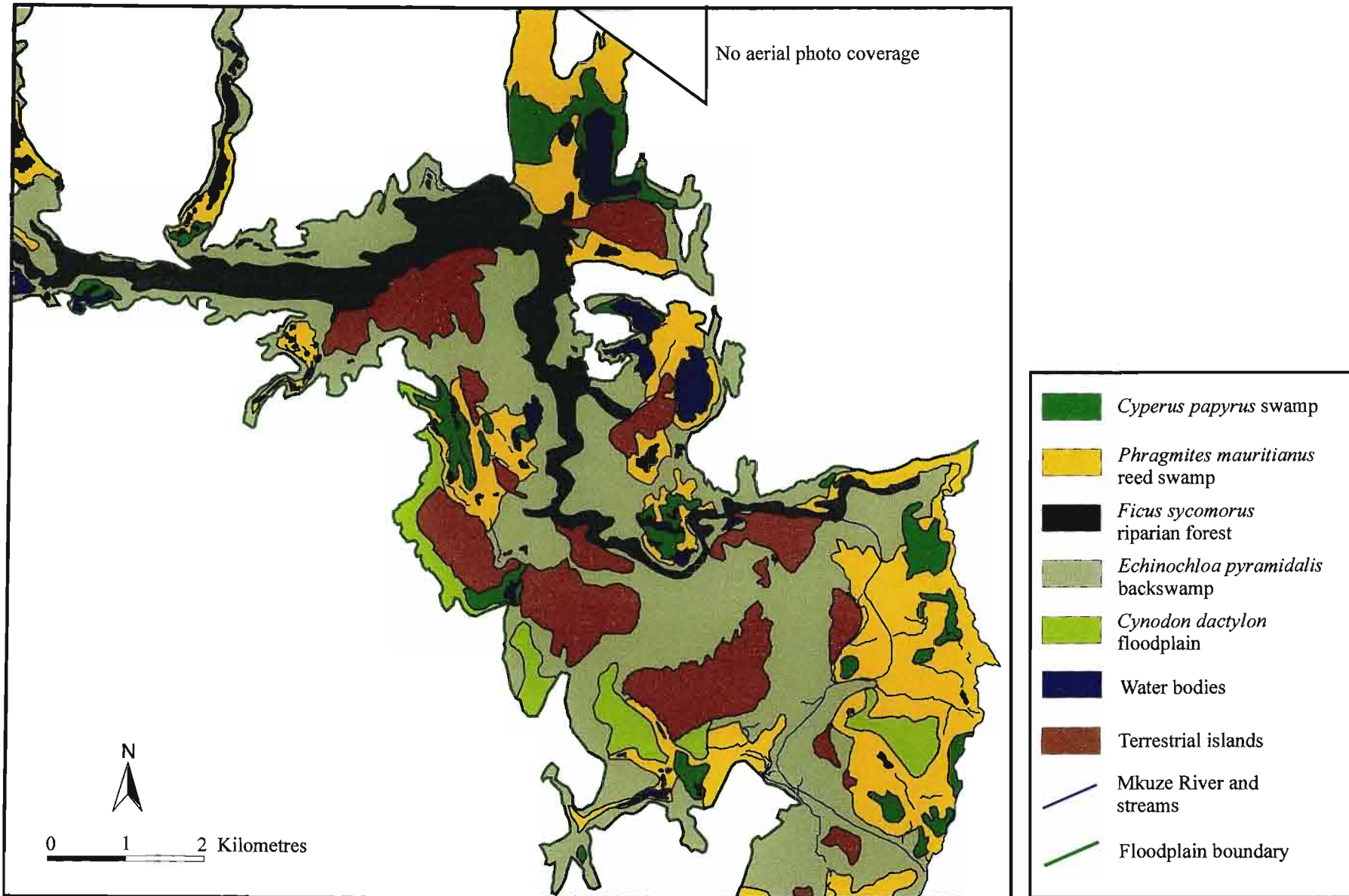- Floodplain boundary

0   1   2 Kilometres
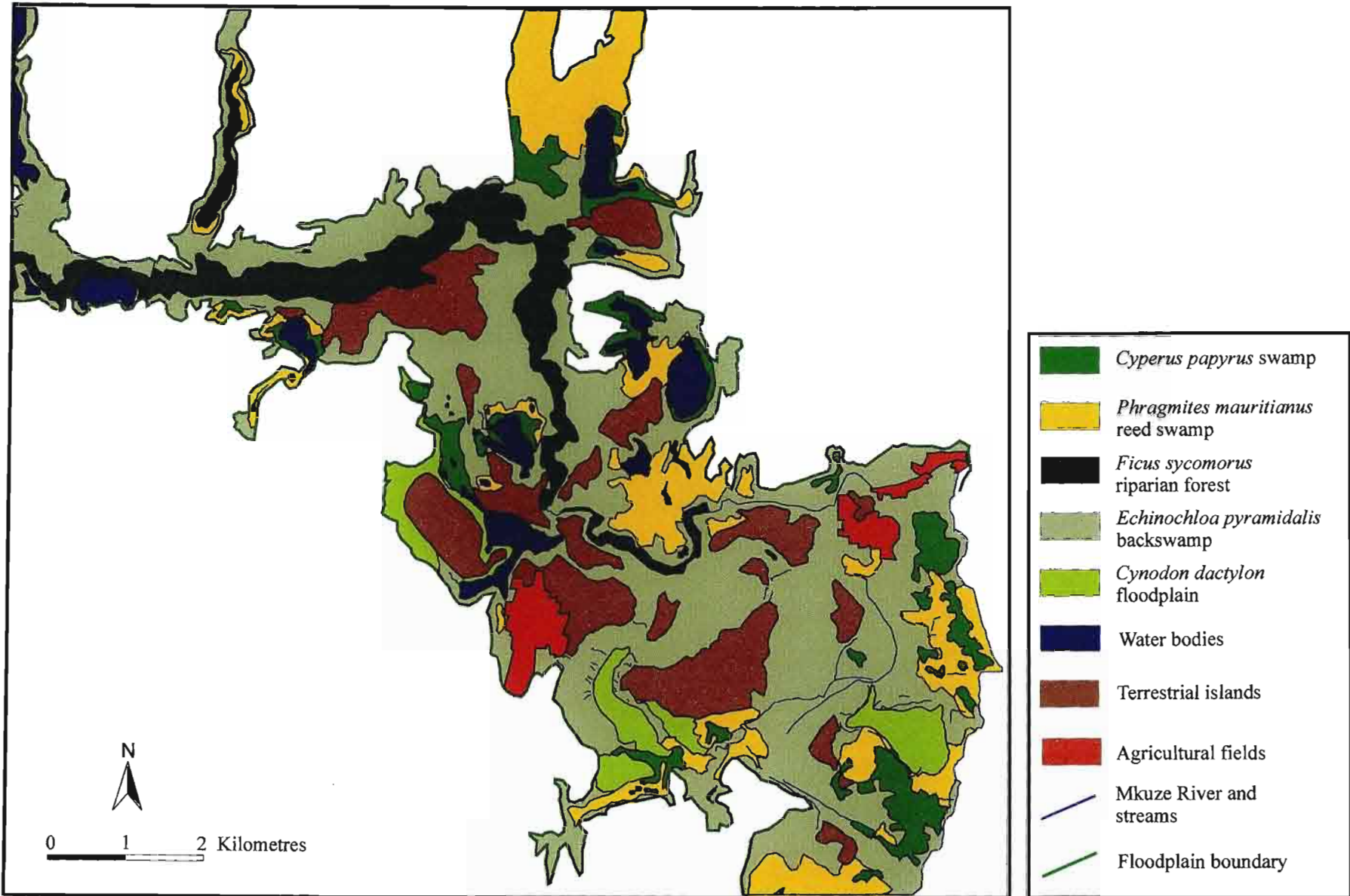
Figure 6.2 Plant community landscape mosaic in 1957.

Table 6.3 Spatial statistics for the 1957 landscape mosaic.

Functional Type*[1]	Plant Community*[2]	Other	Spatial Statistics						
			TCA	%CTLA	No.P	MPS	MedPS	PSSD	MPAR
Distal - permanent			1116.7	20.3	54				
	Cy		362.0	6.6	27	13.4	5.1	16.4	260.5
	P		754.7	13.7	27	28.0	10.8	44.6	212.4
Proximal - seasonal			2880.8	52.5	27				
	F		431.9	7.9	13	33.2	7.7	53.4	301.8
	E		2448.9	44.6	14	174.9	44.0	372.4	349.6
Distal - infrequent			245.7	4.5	6				
	C		245.7	4.5	6	41.0	26.2	26.3	164.6
		Water Bodies	313.4	5.7	37	8.5	0.8	13.9	524.0
		Terrestrial Islds	793.9	14.5	21	37.8	15.1	43.5	151.0
		Fields	141.3	2.6	5	28.3	11.1	28.5	163.8
Totals			5491.8		150				

*[1]Distal - permanent = distal - permanently inundated functional type; Proximal - seasonal = proximal - seasonally inundated functional type; Distal - infrequent = distal - infrequently inundated functional type.

*[2]Cy = *Cyperus papyrus* swamp community; P = *Phragmites mauritianus* reed swamp community; F = *Ficus sycomorus* riparian forest; E = *Echinochloa pyramidalis* backswamp community; C = *Cynodon dactylon* floodplain community
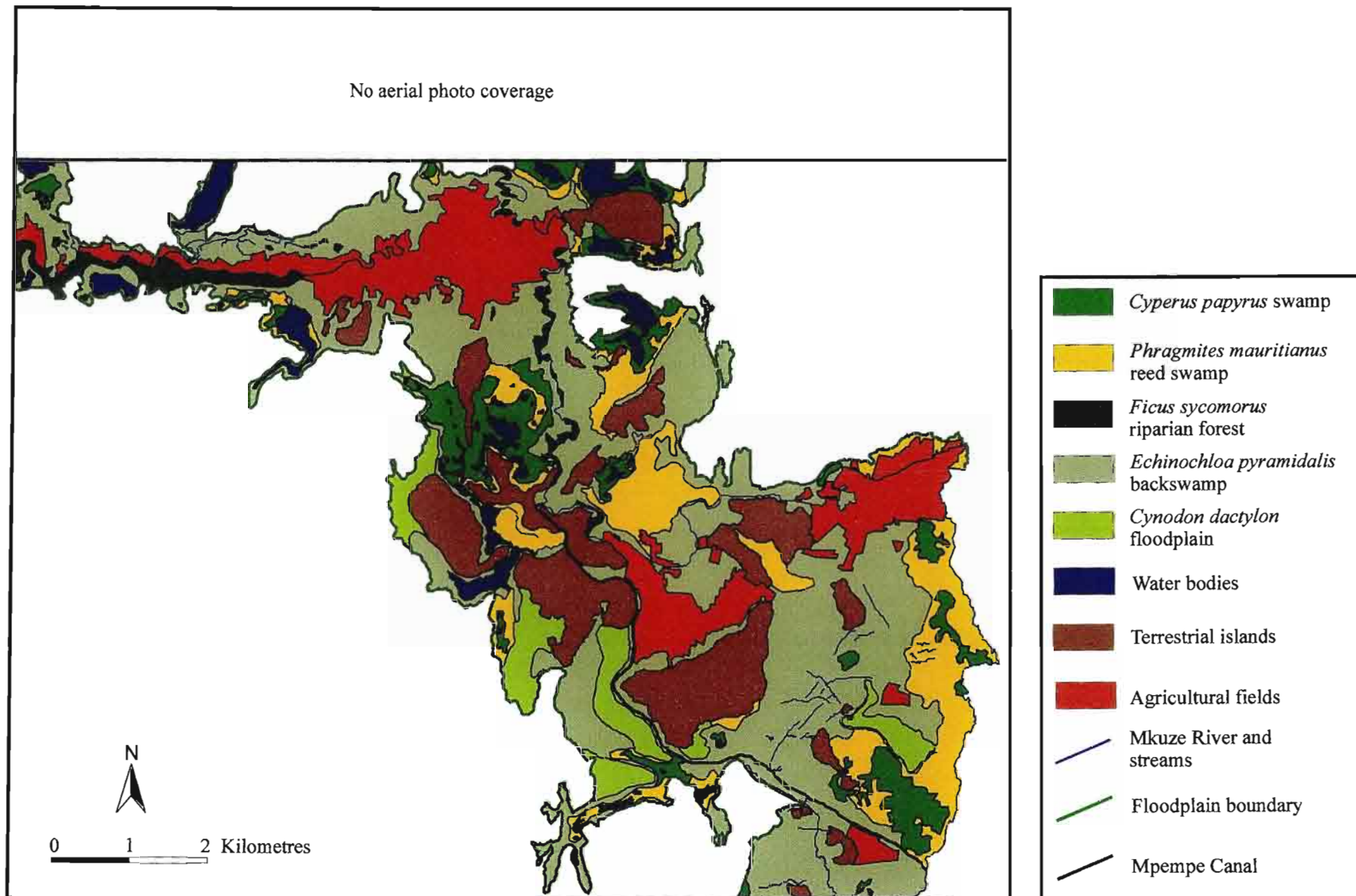
Figure 6.3 Plant community landscape mosaic in 1979.

Table 6.4 Spatial statistics for the 1979 landscape mosaic.

Functional Type*[1]	Plant Community*[2]	Other	Spatial Statistics						
			TCA	%CTLA	No.P	MPS	MedPS	PSSD	MPAR
Distal - permanent			1018.3	20.3	47				
	Cy		381.1	7.6	25	15.2	4.9	27.1	367.3
	P		637.1	12.7	22	29.0	12.0	53.2	280.3
Proximal - seasonal			2141.0	42.6	38				
	F		105.3	2.1	21	5.0	1.0	10.4	521.6
	E		2035.8	40.5	17	119.8	16.6	187.5	322.4
Distal - infrequent			244.1	4.9	7				
	C		244.1	4.9	7	34.9	40.0	21.6	160.5
		Water Bodies	204.8	4.1	72	2.8	0.3	6.7	919.8
		Terrestrial Islds	723.4	14.4	22	32.9	14.0	42.1	205.0
		Fields	696.2	13.8	21	33.2	6.3	66.3	240.8
Totals			5027.8		207				

*[1]Distal - permanent = distal - permanently inundated functional type; Proximal - seasonal = proximal - seasonally inundated functional type; Distal - infrequent = distal - infrequently inundated functional type.

*[2]Cy = *Cyperus papyrus* swamp community; P = *Phragmites mauritianus* reed swamp community; F = *Ficus sycomorus* riparian forest; E = *Echinochloa pyramidalis* backswamp community; C = *Cynodon dactylon* floodplain community

River at the south-eastern margin of the floodplain fan. At the plant community level or grain the percentage contribution to the total landscape area of the *Ficus sycomorus* riparian forest community (F) is 2.1% (105.3ha). The mean patch size of which is 5ha, the median patch size 1ha and the standard deviation 10.4ha (Table 6.4), indicating that there are many, very small patches within this mosaic. In addition, the mean perimeter-area ratio is 521.6m/ha indicating that mean shape complexity is convoluted and compact.

At the reference level the proximal-seasonally inundated marsh, comprising 42.6% of the total landscape area (2141ha), dominates the functional landscape mosaic (Table 6.4). The distal-permanently inundated swamp and distal-infrequently inundated floodplain occupy 20.3% (1018.3ha) and 4.9% (244.1ha) of the landscape area respectively. The number of patches of agricultural fields is 21, occupying approximately 14% of the total landscape area (~700ha). A mean and median patch size of 33.2 and 6.3ha respectively, and a patch size standard deviation of 66.3ha indicates that there are a variety of patch sizes, ranging from small plots to extensive fields under cultivation.

1996

The 1996 landscape mosaic is illustrated in Figure 6.4 and the corresponding spatial statistics are presented in Table 6.5. Evident in Figure 6.4 is the Tshanetshe Canal, which was excavated in 1986 for the purposes of irrigation and which subsequently joined up with the Mpempe Canal to form the Tshanetshe-Mpempe Canal System, a hydraulically more efficient pathway than the Mkuze River. At the level of the grain, the *Ficus sycomorus* riparian forest community (F) has a mean patch size of 13.1ha, a median patch size of 1.1ha and a standard deviation of 18ha, indicating that over 50% of the patches are less than 1.1ha. In addition, the mean perimeter-area ratio is 785.5m/ha indicating a long perimeter and small area. Thus the mean shape is a highly convoluted, compact shape (Table 6.5). The plant community landscape mosaic is dominated by the *Echinochloa pyramidalis* backswamp community (E), which accounts for 32.5% of the total landscape area (1829.7ha). The mean size, median patch size and mean perimeter-area ratio are 130.7ha, 50.1ha and 244.4m/ha respectively, indicating the presence of relatively large, elongated patches within the landscape mosaic (Fig. 6.4).
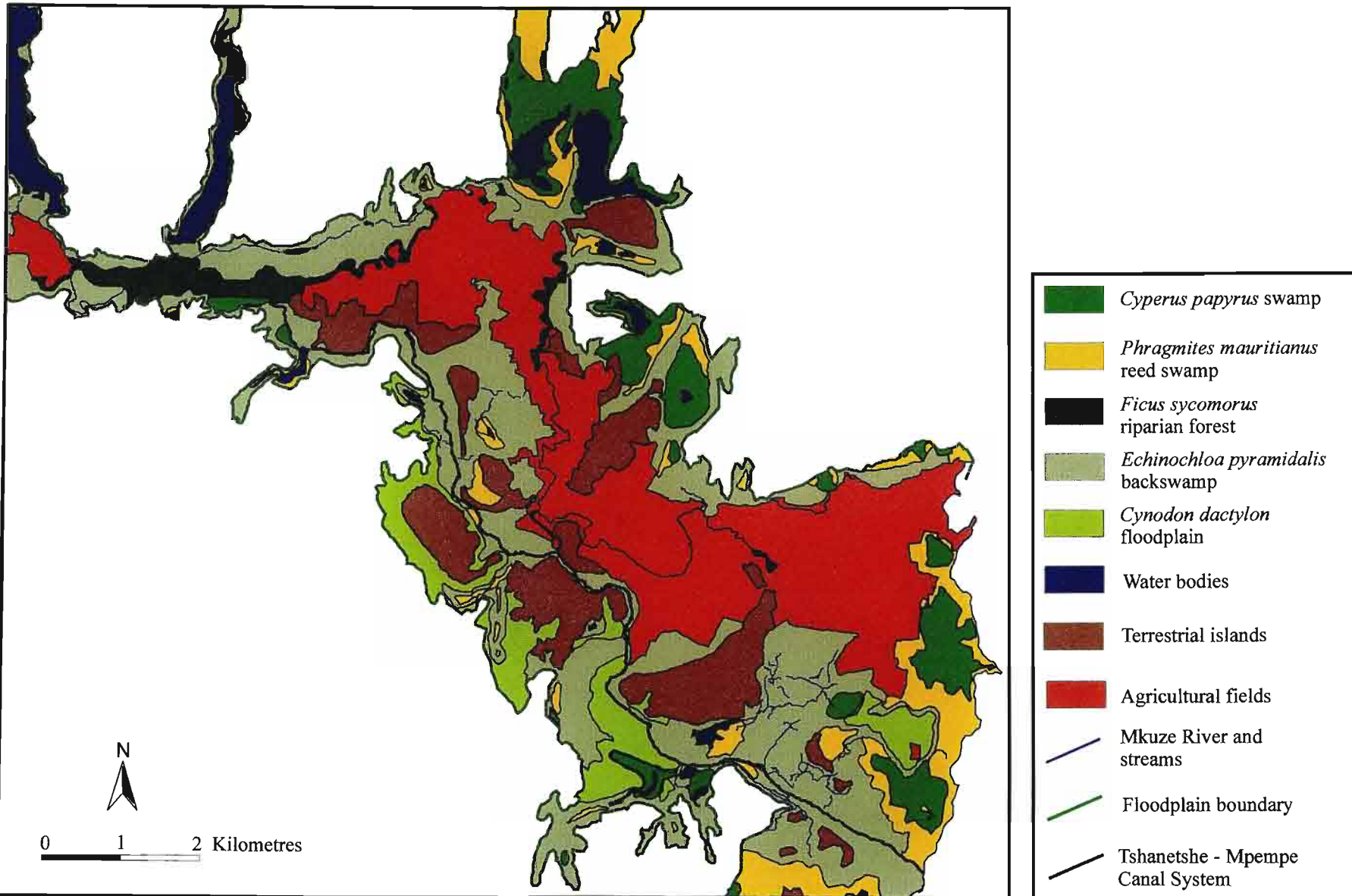
Figure 6.4 Plant community landscape mosaic in 1996.

Legend:
- *Cyperus papyrus* swamp
- *Phragmites mauritianus* reed swamp
- *Ficus sycomorus* riparian forest
- *Echinochloa pyramidalis* backswamp
- *Cynodon dactylon* floodplain
- Water bodies
- Terrestrial islands
- Agricultural fields
- Mkuze River and streams
- Floodplain boundary
- Tshanetshe - Mpempe Canal System

N

0 1 2 Kilometres

Table 6.5 Spatial statistics for the 1996 landscape mosaic.

Functional Type*[1]	Plant Community*[2]	Other	Spatial Statistics						
			TCA	%CTLA	No.P	MPS	MedPS	PSSD	MPAR
Distal - permanent			911.3	16.2	55				
	Cy		436.4	7.8	20	21.8	4.5	33.4	222.7
	P		474.8	8.4	35	13.6	3.6	29.5	344.6
Proximal - seasonal			1973.7	35.1	25				
	F		144.0	2.6	11	13.1	1.1	18.0	785.5
	E		1829.7	32.5	14	130.7	50.1	148.1	244.4
Distal - infrequent			408.0	7.3	6				
	C		408.0	7.3	6	68.0	11.8	84.3	174.4
		Water Bodies	283.1	5.0	31	9.1	1.4	20.4	598.8
		Terrestrial Islds	666.1	11.8	18	37.0	12.3	42.6	159.9
		Fields	1382.5	24.6	7	197.5	43.7	43.7	235.7
Totals			**5624.7**		**142**				

*[1]Distal - permanent = distal - permanently inundated functional type; Proximal - seasonal = proximal - seasonally inundated functional type;
   Distal - infrequent = distal - infrequently inundated functional type.
*[2]Cy = *Cyperus papyrus* swamp community; P = *Phragmites mauritianus* reed swamp community; F = *Ficus sycomorus* riparian forest;
   E = *Echinochloa pyramidalis* backswamp community; C = *Cynodon dactylon* floodplain community

The functional landscape mosaic or reference level comprises a total of 142 patches (Table 6.5). The percentage contribution to the total landscape area for the distal-permanently inundated swamp, the proximal-seasonally inundated marsh and the distal-infrequently inundated floodplain is 16.2%, 35.1% and 7.3% respectively. A central corridor, flanking the Mkuze River, comprises agricultural fields (Fig. 6.4). These fields contribute 24.6% to the total landscape area (1382.5ha). The mean patch size is 197.5ha, the median patch size and standard deviation is 43.7ha and mean perimeter-area ratio is 235.7m/ha. This indicates that there are a range of field sizes, but that a few patches constitute the larger proportion of the total category area.

6.3.2 General Patterns of Landscape Change

6.3.2.1 The Plant Community Landscape Mosaic

The Cyperus papyrus swamp community (Cy)

The percentage contribution to the total landscape area has remained relatively stable over the analysis period but the number of patches has decreased. Therefore a few patches are increasing in area (Figs. 6.5 & 6.6) and the patch size standard deviation is increasing (Fig. 6.7). Therefore some patches are shrinking, while others are augmenting. Between 1937 and 1979 the mean perimeter-area ratio increased (Fig. 6.8), indicating that mean shape complexity has become increasingly convoluted. However between 1979 and 1996 the mean perimeter-area ratio decreased, indicating that shapes were becoming increasingly simple (Fig. 6.8).

The Phragmites mauritianus reed swamp community (P)

A decrease in the percentage contribution to the total landscape area and an overall increase in the total number of patches over the analysis period was evident for this community type (Figs. 6.5 & 6.6), indicating the fragmentation and shrinkage of patches. Differences between the mean patch size and the patch size standard deviation are declining, suggesting that patches are becoming increasingly more similar in size (Fig. 6.7). The perimeter length relative to the area is increasing, indicating that mean shape complexity is generally becoming either more elongated or more convoluted (Fig. 6.8). Evidence from Figures 6.1-6.4 indicates a combination of both possibilities.
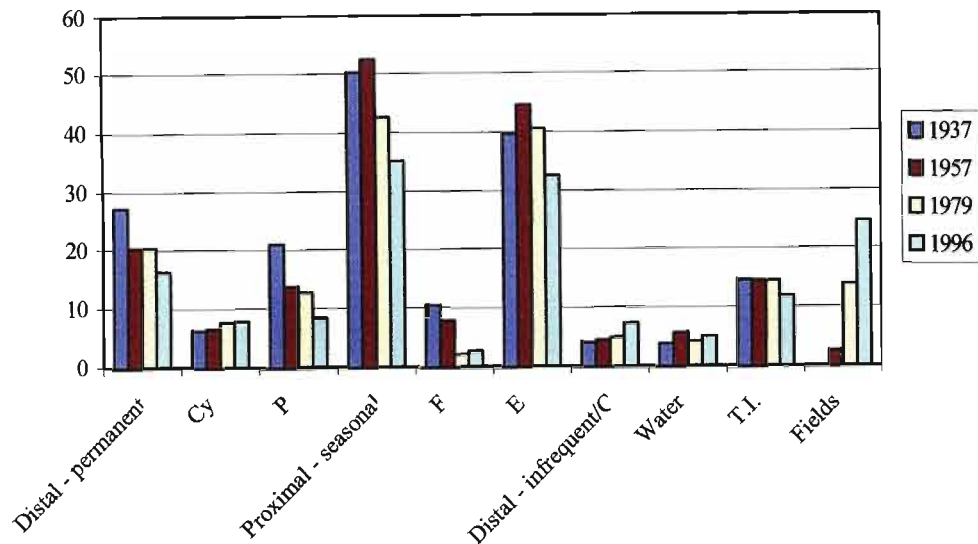
Figure 6.5 The percentage contribution to the total landscape area (%) of plant community and functional types for the years 1937, 1957, 1979 and 1996.

The Ficus sycomorus riparian forest community (F)

A dramatic decrease in the percentage contribution to the total landscape area indicates attrition of this community type over time (Fig. 6.5). The number of patches increased between 1937 and 1979, while mean patch size decreased, indicating increasing fragmentation (Figs. 6.6 & 6.7). From 1979 to 1996 there was a decrease in patch numbers and a slight increase in mean patch size indicating mild recovery. The range of patch sizes steadily decreased from 1937 to 1979, indicating that patch sizes were becoming increasingly similar over time. A slight increase in patch size standard deviation from 1979 to 1996 confirms the possibility of a slight recovery (Fig. 6.7). Mean perimeter-area ratio increased markedly over time, indicating that mean shape complexity has changed from elongated linear shapes to smaller, more convoluted shapes (Fig. 6.8).

The Echinochloa pyramidalis backswamp community (E)

After a slight increase in the percentage contribution of this community type to the total landscape area between 1937 and 1957, a steady decrease from 1957 to 1996 is evident (Fig. 6.5). This is possibly due to the introduction of other patch types such as agricultural fields over time. Although total area for this community types is decreasing, the number of patches has remained relatively constant, suggesting shrinkage of patches over time (Fig. 6.6). From 1937 to 1979 median patch size rarely exceeded 50ha. This trend changed

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dramatically between 1979 and 1996 where median patch size increased to approximately 150ha. This indicates that small patches were becoming smaller, possibly declining towards attrition. This trend is supported by the fact that patch size standard deviation is decreasing (Fig. 6.7). Mean shape complexity has also declined since 1957 from a wide continuous corridor to one comprising fragmented, perforated blocks (Fig. 6.8).
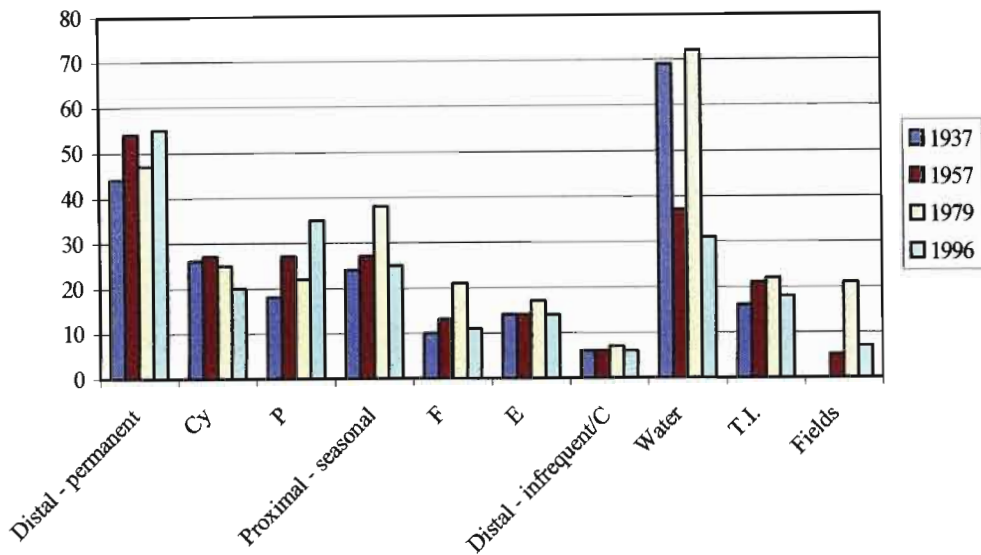
Figure 6.6 The total number of patches of plant community types for the years 1937, 1957, 1979 and 1996.

The Cynodon dactylon floodplain community (C)

The percentage contribution to total landscape area of this plant community type has increased slightly from 1979 to 1996 (Fig. 6.5), while the total number of patches has remained fairly constant (Fig. 6.6). Therefore patch area has increased slightly from 1979 to 1996. This is also indicated by the slight increase in mean patch size. The range of patch sizes about the mean also increased between 1979 and 1996. This, accompanied by an increase in median patch size, indicates that either small patches were becoming smaller or a few large patches were increasing slightly in area. Mean shape has remained fairly constant throughout the analysis period (Fig. 6.8).
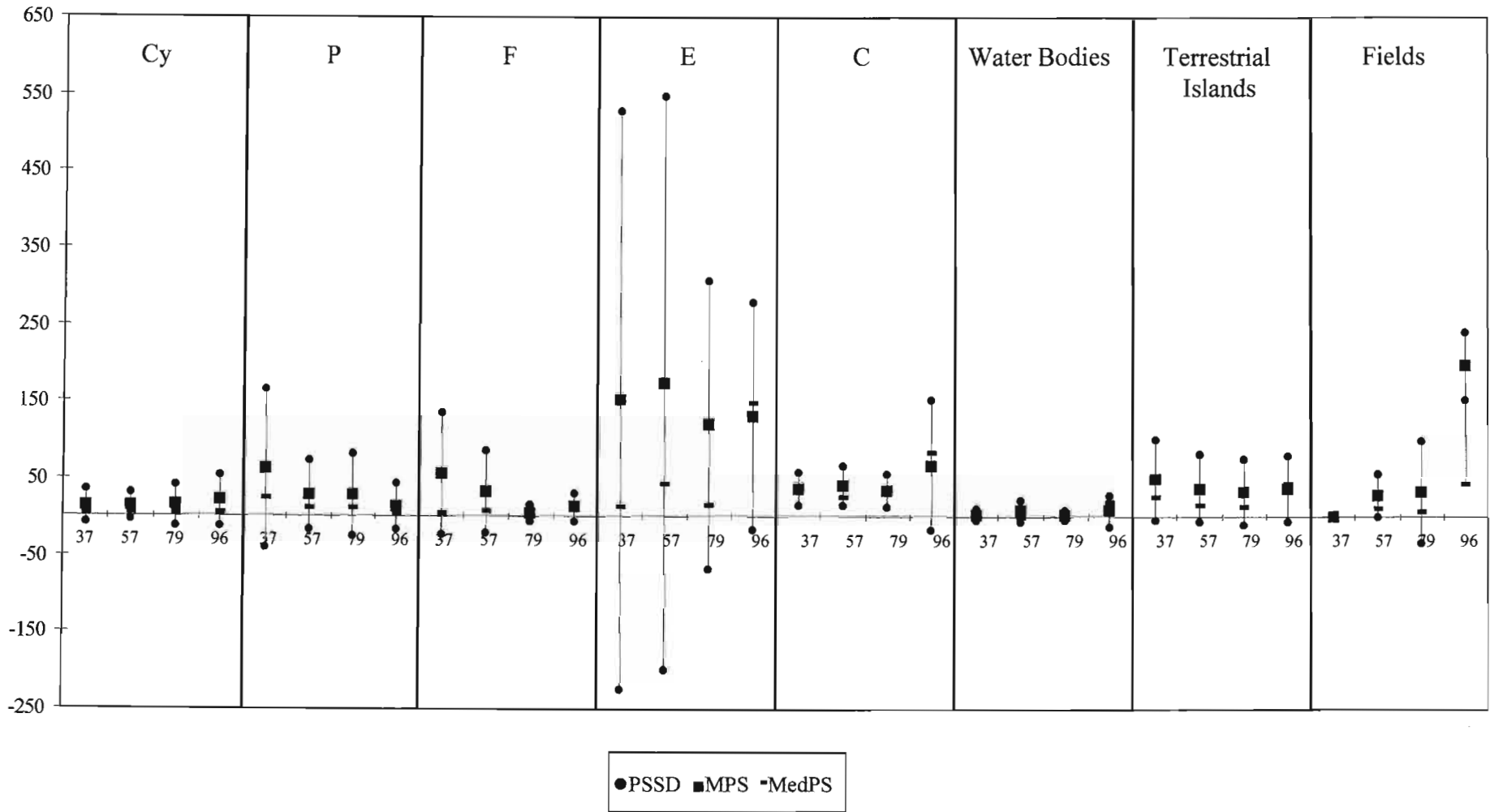
Figure 6.7 The change in patch size standard deviation, mean patch size and median patch size for each plant community type over the period 1937 to 1996 (see text for full plant names).

Water Bodies

The percentage contribution of water bodies to the total landscape area is low compared to the other mapped categories, and has remained relatively constant over the analysis period (Fig. 6.5). Patch number however is highly variable, in 1937 and 1979 approximately 70 water bodies existed, while in 1957 and 1996 only half of that occurred (Fig. 6.6), indicating that these small water bodies are a temporary feature of the landscape. Rainfall seasonality does not appear to be the determinant of this variability since all aerial photographs were flown between the months May and September (Table 6.1) and thus fall out of the rainy season. Mean patch size also remains fairly constant with only a slight increase in the range of patch sizes over time (Fig. 6.7). Mean shape complexity is highly variable (Fig. 6.8), a feature confirmed by the presence of small highly convoluted shapes in Figures 6.1-6.4.
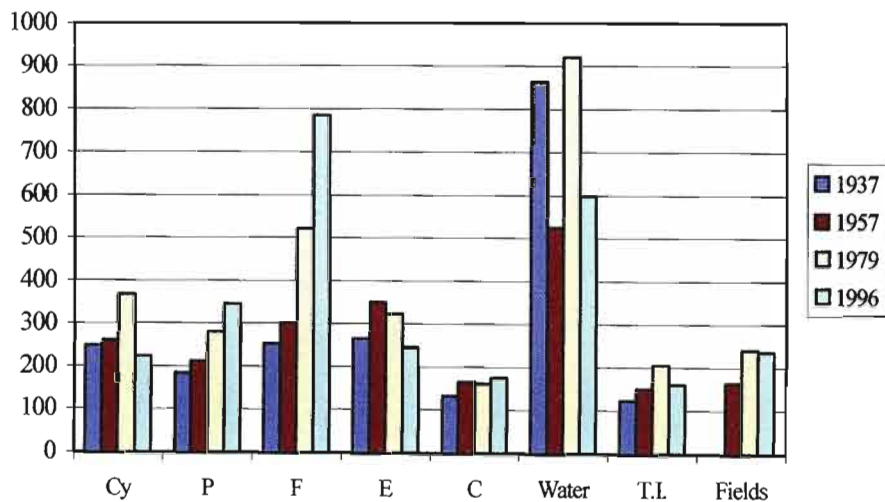
Figure 6.8 The mean perimeter-area ratio (m/ha) of plant community types for the years 1937, 1957, 1979 and 1996.

Terrestrial Islands

The percentage contribution of terrestrial islands to the total landscape area has remained constant over the time analysis period (Fig. 6.5). The number of patches has increased slightly from 1937 to 1979, followed by a decrease between 1979 and 1996 (Fig. 6.6). The patch size and shape indices show minor fluctuations over time (Figs. 6.7 & 6.8), indicating that terrestrial islands are a stable feature of the landscape mosaic.

Agricultural Fields

Agriculture was introduced into the landscape mosaic after 1937. The percentage contribution to the landscape area rose from 0% to 25% over the 60-year analysis period (Fig. 6.5). The number of patches increased steadily between 1957 and 1979, but from 1979 to 1996 patch numbers decreased dramatically (Fig. 6.6). Meanwhile mean patch size continued to increase (Fig. 6.7), indicating that the numerous, smaller patches were consolidating to form fewer, larger patches. The mean perimeter-area ratio increased until 1979 then stabilised, indicating that small fields with complex borders were being replaced by larger patches with straight, linear edges (Fig. 6.8).

6.3.2.2 The Functional Type Landscape Mosaic

In terms of its contribution to the total landscape area, the proximal-seasonally inundated marsh dominates the functional mosaic throughout the 60-year analysis period, even though it has steadily decreased from 1957 to 1996 (Fig. 6.5). The number of patches within this category is relatively low, having increased between 1937 and 1979, followed by a decrease between 1979 and 1996 (Fig. 6.6). This indicates that this functional type has become increasingly fragmented during the time period from 1937 to 1979 and that it has been replaced by other land cover types, such as agricultural fields. The percentage contribution to the total landscape area of the distal-permanently inundated swamp decreased from 27.2% in 1937 to 16.2% in 1996, while the number of patches fluctuated between 44 and 55 patches. Thus, increasing numbers of smaller patches are dominating this functional type. The distal-infrequently inundated floodplain contributes the least to the total landscape area of the three functional types. Both percentage contribution and total number of patches have remained relatively constant throughout the analysis period, although a slight increase in total area in 1996 is evident.

6.4 Discussion

6.4.1 Landscape Transformation

Landscape ecology emphasises the importance of the concepts of spatial heterogeneity and dynamics of the landscape mosaic and recognises that human impacts and modifications are an integral part of landscape content, configuration and dynamics (Forman, 1995). Factors causing landscape heterogeneity and change can be attributed to a combination of

natural and anthropogenic disturbances. The natural disturbance regime of a landscape often provides a template for anthropogenic disturbances (Kamada & Nakagoshi, 1996).

Floodplains are naturally very dynamic systems characterised by environmental gradients that are inherently changeable (Malanson, 1993). The lower Mkuze River floodplain is characterised by an inundation-sedimentation gradient that results in a continuum of floodplain functional types, the distribution of which changes with changing floodplain processes. This shifting mosaic is a natural phenomenon and is partly responsible for spatial heterogeneity within the floodplain system and therefore its functional integrity. The interaction or balance between the natural and anthropogenic disturbance regimes determines the overall dynamics of landscape patterns and processes (Kamada & Nakagoshi, 1996).

Aside from natural fluctuations, such as the constantly changing size and shape of small water bodies within the lower Mkuze River floodplain, the transformation of the landscape mosaic due to anthropogenic disturbances, appears to follow a directional pattern of change. The processes of perforation, fragmentation and shrinkage appear to steadily increase once a disturbance has been initiated, to continue until a specific threshold is reached and is then followed by complete loss of area or attrition (Table 6.6).

This loss of wetland area is being replaced primarily by agricultural land within the lower Mkuze River floodplain. The processes of perforation, fragmentation and shrinkage are initiated by disturbance events that divide patch area, such as roads, canals, footpaths and cattle tracks, all of which are present in the lower Mkuze River floodplain. Within the lower Mkuze River floodplain, the impact of three anthropogenic disturbances are especially evident over the 60-year analysis period (see Figs. 6.1-6.4), namely loss of riparian forest, an increasing percentage of land affected by agriculture and the development of the Tshanetshe-Mpempe Canal System.

Riparian forest removal
The loss of riparian forest, typically found on levees adjacent to the river channel, has a major effect on sedimentation processes and the stability of local topography (Malanson,

1993). The riparian fringe flanking the Mkuze River protects the banks of the river channel; encourages the formation of levees, which contain flow within the channel; and provides the setting for backswamp development (Alexander, 1986). Riparian forest removal exposes the channel banks to erosion, increases sediment loads within the channel, exposes backswamp areas to the deposition of coarser sediments and destabilises channel-levee topography, which can ultimately lead to channel switching (Taylor, 1986). Riparian forests in the Okavango Delta in northern Botswana have been shown to be extremely important sites of solute retention as a consequence of transpirational water loss (McCarthy *et al.*, 1993). This is likely to be true of the riparian forests of the lower Mkuze River floodplain. Removal of these forests and their conversion to bare soil may thus be extremely significant in that the ability of the wetland to remove solutes from inflowing water is reduced.

Table 6.6 Summary of landscape transformation trends for first and second order landscape elements.

Functional Type*	Plant Community*	Other	Transformation Process
Distal - permanent			Shrinkage
	Cy		Shrinkage and Augmentation
	P		Shrinkage → Attrition
Proximal- seasonal			Perforation → Fragmentation → Attrition
	F		Fragmentation → Attrition
	E		Perforation → Fragmentation → Shrinkage → Attrition
Distal- infrequent	C		Constant
		Water Bodies	Ephemeral Patch
		Terrestrial Islds	Constant
		Fields	Augmentation → Consolidation

*See text for full names

Conversion of wetlands to agricultural land

Agricultural practices impact negatively on wetland hydrology and reduce the erosion control and water purification functions of wetlands (Kotze & Breen, 1994). The conversion of wetlands to cultivated fields usually involves:

(1) The removal of the natural vegetation, in this case primarily the *Ficus sycomorus* riparian forest community (F) and the *Echinochloa pyramidalis* backswamp community (E), leading to increased erosion.

(2) The alteration of the hydrological regime, often through drainage, reducing the residence time and volume of water within wetland habitats, thereby decreasing the water purification value of wetlands.

(3) The frequent disturbance of the soil structure primarily through tillage practices, which in recent years has become increasingly mechanised within the lower Mkuze River floodplain (Taylor, 1986), leading to increased soil permeability and reduced biogeochemical transformations (Kotze & Breen, 1994).

Canal excavation

The alluvial ridge and basin feature, its associated differential sedimentation patterns and the resultant differences in elevations between these features, created a situation where channel avulsion was inevitable within the lower Mkuze River floodplain. Avulsion was initiated by breaches in the channel levees during the excavation of the Mpempe and Tshanetshe Canals and resulted in the establishment of a new distributary channel along a hydraulically more efficient pathway. The processes leading to the formation of this pathway and the consequences of this development were explored in detail in Section 5.4.2. The secondary impacts of canal construction also contribute to landscape transformation and generally include the direct elimination of wetland area due to the canal itself as well as areas where the spoil is placed, the disruption of soil structure, the alteration of runoff characteristics (Stone *et al.*, 1978) and the lowering of the surrounding water table (Alexander, 1986; Louden *et al.*, 1987).

6.4.2 Disturbance and Landscape Ecology

6.4.2.1 Hierarchy and Disturbance

Disturbance is defined as 'any relatively discrete event in time that disrupts ecosystem, community or population structure, and changes resources, substrate availability or the physical environment' (White & Pickett, 1985). However, in order to understand the impact of disturbance on ecological patterns and processes, the hierarchical nature of the landscape must be taken into account. If an ecological system is able to incorporate or

adapt to a disturbance event, at some point, it can no longer be regarded as a disturbance (Forman & Godron, 1986). In other words, what appears as a disturbance at a lower level within the landscape hierarchy might have little or no impact on ecosystem patterns and processes operating at a higher level. Lower levels within the landscape hierarchy are more prone to disturbance than higher levels, since they are characterised by processes that operate at spatially smaller scales and at temporally faster rates of change. Therefore the frequency of disturbance events is likely to be greater for lower, than for higher levels within the landscape hierarchy. The excavation and development of the Tshanetshe-Mpempe Canal System dramatically altered the distribution of surface inflows onto the lower Mkuze River floodplain and was reported to be a major ecological disaster (Loudon *et al.,* 1987). However, if this process was viewed from a higher temporal window of observation such as at a time scale of hundreds of years, then these alterations might be regarded as part of the natural disturbance regime and an integral part of floodplain processes.

6.4.2.2 Heterogeneity and Disturbance

Heterogeneity is defined by the content, configuration and dynamics of landscape elements (Noss, 1987; Forman 1995). Heterogeneity operates at all levels within the landscape hierarchy and is said to be the result of a combination of the natural and anthropogenic disturbance regime (Caswell & Cohen, 1991). In the literature there are many references that explore the impacts of disturbance in a variety of ecosystems from a structural and/or functional perspective, but there is little direct reference explicitly linking the impacts of disturbance to landscape content and configuration in an integrated way. White (1999) considered this by describing the progressive transformation of the landscape mosaic with increasing disturbance within a savanna ecosystem. Anthropogenic disturbance was found to initially alter plant species composition within patches. This process continued until patch types were lost completely and replaced by introduced patches, thus changing landscape content. In some areas, as disturbance increased, the underlying environmental variables that determined landscape configuration were overridden by an anthropogenic disturbance gradient (White, 1999). Thus the natural processes controlling functional connectivity were undermined, resulting in ecosystem degradation.

Within the lower Mkuze River floodplain, anthropogenic disturbances also appear to impact on landscape content and configuration in an ordered manner. At the grain level, disturbance appears to typically impact on the internal structure of patches. Disturbance initially altered plant species composition, as was apparent by the identification of the three sub-communities, C1, C3 & Eb (see Chapter 4), characterised by alien plant species typical of disturbed areas. However, unlike White's (1999) study where patches were altered to such an extent that they were lost and replaced by new patches, within the lower Mkuze River floodplain, landscape content remained relatively stable i.e. no patch types were lost. Rather as disturbance increased, for example as the percentage of agricultural land increased, patch size, number and shape of other patch types declined or altered.

At the reference level, the functional connectivity between landscape elements was described by a hydrogeomorphic continuum comprising the distal-permanently inundated swamp, the proximal-seasonally inundated marsh and the distal-infrequently inundated floodplain functional types. This underlying gradient is the primary controlling factor that contains and maintains ecosystem patterns and processes at this scale, and appears to be strong and dynamic enough to incorporate and adapt to the past and present anthropogenic disturbance regime.

6.4.3 Future Changes in the Landscape Mosaic

Although there has been much research investigating the impact of disturbances at all levels of ecological organisation, these have tended to focus on individual species' characteristics such as reproduction, dispersal and competition or on community characteristics such as biomass, diversity and nutrient cycling (Pickett & White, 1985). It is recognised that anthropogenic disturbances affect the spatial and temporal heterogeneity of ecosystems, but the specific effects on particular ecosystems are not always predictable (Denslow, 1985; Moloney & Levin, 1996). There is no literature that explicitly examines the impact of disturbance within wetland and/or floodplain environments at a variety of scales of observation or in the hierarchical manner as prescribed by landscape ecology theory.

Although not ecosystem specific, Forman & Godron (1986) consider the impacts of anthropogenic disturbance on landscape content and configuration from a landscape ecology perspective. They consider how an increase in the combined effects of all human disturbances over time impact on landscape characteristics such as patch size, shape and number. However, in order to determine this combined effect or overall index of disturbance, one needs to examine the properties of individual disturbances occurring within the environment under study. These properties include *inter alia* the spatial distribution of the disturbance, the frequency or mean number of disturbance events per time period, the area disturbed and the synergism or cumulative impact of the disturbances (White & Pickett, 1985). Ideally a detailed study investigating these indicators of disturbance at the grain, reference and context levels of landscape organisation is required in order to explicitly quantify the link between the anthropogenic disturbance regime and landscape heterogeneity within the lower Mkuze River floodplain. However, this was beyond the scope of the current study. Therefore, in an attempt to explore this issue in a general way, two scenarios that describe how the landscape mosaic could possibly respond to an increasing anthropogenic disturbance regime are described. These are illustrated in Figure 6.9 below.
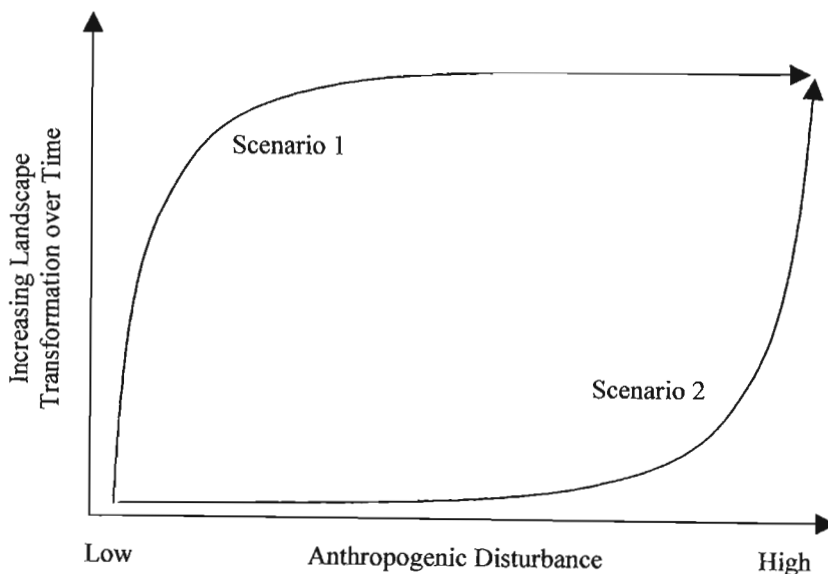

Figure 6.9 The impact of anthropogenic disturbance on landscape transformation.

The first scenario illustrates that initial low levels of disturbance have a major effect on the landscape transformation. As disturbance levels gradually increase so landscape

transformation increases rapidly. This trend continues until a stage is reached where there is minimal landscape transformation as disturbance levels continue to increase. The landscape is able to accommodate or adapt to this disturbance regime.

The second scenario describes how an initial rapid increase in the overall levels of disturbance result in minimal landscape transformation. The landscape is able to incorporate or adapt to the level of disturbance. However, as disturbance levels continue to increase, a critical threshold is reached, where the system is no longer able to cope. This is followed by a rapid change in landscape content and configuration, even when disturbance levels no longer continue to increase. This can result in possible irreversible ecosystem degradation.

Within the lower Mkuze River floodplain, over the 60-year analysis period, the overall disturbance regime has increased in the form of *inter alia* canal excavation, riparian forest removal and an increasing area of land under cultivation. When observed from a spatially coarse level, such as the reference level, it appears that the system is able to cope structurally and functionally with this current disturbance regime. This corresponds to that section of the curve of scenario 2 where high levels of disturbance result in minimal landscape transformation. However, it is possible that as disturbance levels continue to increase, the effects of cumulative disturbance will begin to impact on the ecosystems ability to adapt. The difficulty lies in identifying this critical threshold i.e. when the anthropogenic disturbance regime reaches a point where it overrides the driving forces of ecosystem patterns and processes that determine landscape content, configuration and dynamics, resulting ultimately in irreversible ecosystem degradation.

When one observes the impact of disturbances at a finer spatial level, the interpretation of the effect on landscape content and configuration might differ. For example, within the lower Mkuze River floodplain a private farmer excavated a small canal from the Mkuze River to Tshanetshe Pan (Tshanetshe Canal) in order to increase his water supply for irrigation. The synergism of this low-level disturbance event with other disturbance events, resulted in the overall redistribution of flow across the floodplain surface i.e. major landscape transformation (Scenario 1).

These two scenarios illustrate the fact that the relationship between anthropogenic disturbance and landscape transformation is not linear and that the interpretation of the impact of anthropogenic disturbance on landscape transformation depends on the scale of observation. In a system such as the lower Mkuze River floodplain, where there is more than one primary landowner / user (and therefore more than one source of anthropogenic disturbance) with diverse needs and objectives (such as the reliance on wetland resources for livelihood and the conservation and management of natural resources) one needs to constantly monitor the impacts of the utilization of resources and management decisions on ecosystem patterns and processes to ensure sustainability.

6.5 Conclusion

Landscape ecology theory emphasises the importance of a temporal analysis of spatial heterogeneity and the role of disturbance in ecosystem patterns and processes. A temporal analysis of the landscape mosaic from 1937 to 1996 was undertaken using a GIS to quantify landscape change over time. This was used to illustrate the role of anthropogenic disturbance on the landscape mosaic at both the grain and reference level within the landscape hierarchy. Anthropogenic disturbance can affect landscape content and configuration and therefore the underlying environmental determinants of landscape patterns and processes. Once the underlying functional processes are undermined, irreversible ecosystem degradation is a possible outcome.

CHAPTER 7 CONCLUSION

7.1 Synthesis of the study

Landscape ecology theory recommends that a minimum of three adjacent levels in the landscape hierarchy should be examined in order to gain insight into landscape heterogeneity and its underlying ecological processes (Forman, 1995; Wu & Loucks, 1995). This study examined the vegetation ecology of the lower Mkuze River floodplain within this hierarchical framework. The smallest spatial scale to which the vegetation of the floodplain could be deconstructed was the relatively homogeneous units of plant community types. From a landscape ecology perspective this level of analysis was referred to as the grain. The distribution of these plant communities correlated with an underlying inundation-sedimentation gradient that summarized the interactions between hydrology, substrate properties and topography within the floodplain system.

The description of this vegetation-environment relationship provided a useful foundation for the examination of ecological processes and phenomena at the next higher, spatially coarser level within the landscape hierarchy, the reference level. Plant communities were aggregated into functional types based on criteria such as exposure to similar flooding and sedimentation regimes. The identification of these functional types enabled one to identify a hydrogeomorphic continuum that described the interaction between floodplain processes and vegetation distribution. This made it possible to develop process-based understanding of the ecosystem patterns and processes operating within the lower Mkuze River floodplain.

Ecological patterns and processes operating at coarser scales within a landscape hierarchy serve to define and constrain spatial heterogeneity and dynamics within the grain and reference levels (Kotleir & Wiens, 1990). Thus two of these higher levels were described, namely the extent and context, which together provided the background to the study area. Descriptions of regional climate, geology, geomorphology, hydrology, vegetation and landuse provided a background that was crucial to the understanding of the finer scale functioning of the system.

In addition, landscape ecology theory emphasises the importance of a temporal analysis of spatial heterogeneity and the role of disturbance in ecosystem patterns and processes (Urban *et al.*, 1987). A temporal analysis of the landscape mosaic was undertaken using a GIS to quantify landscape change over time. This illustrated the role of anthropogenic disturbance in the landscape mosaic at both the grain and reference level.

The examination of the different levels within the landscape hierarchy and the dynamics of ecosystem patterns and processes operating within the lower Mkuze River floodplain made it possible to develop deeper insights into ecosystem patterns and processes than a conventional vegetation ecology study that typically focuses primarily on plant community classification. The use of landscape ecology as an overarching theory that guided the research process and aided the interpretation of findings by explicitly recognising the importance of spatial heterogeneity, hierarchical organisation and dynamics, proved invaluable in developing process-based understanding of the vegetation ecology of the lower Mkuze River floodplain.

7.2 Broadening the scope

The hierarchical nature of the landscape mosaic, as prescribed by landscape ecology theory, enables one to insert additional levels of observation within the current hierarchical structure of the study on the lower Mkuze River floodplain. There are a number of additional levels, especially at coarser spatial scales within the landscape hierarchy, that could be examined in order to place the lower Mkuze River floodplain in a broader spatial context.

The Greater St Lucia Wetland Park

The lower Mkuze River floodplain forms part of the Greater Mkuze Wetland System, which also comprises the Mbazwane Wetland to the north-east of the floodplain and the Mkuze Swamps to the north of Lake St Lucia (Fig. 3.1). In contrast to the lower Mkuze River floodplain, the Mbazwane Wetland is predominantly groundwater fed and thus receives a persistent supply of water throughout the year that can support *inter alia* swamp forest type vegetation (Schoultz, 2000). The Mkuze Swamps are supplied by a combination of inflows originating from the Mkuze River during exceptionally large flood events, and

from ground water seepage from surrounding groundwater streams (McCarthy & Hancox, 2000). The Greater Mkuze Wetland System forms part of the Greater St Lucia Wetland Park, a recognized site of international importance under the Ramsar Convention (Cowan, 1991). The lower Mkuze River floodplain thus forms part of a much larger system. These additional components of the Greater St Lucia Wetland Park could be examined within a similar framework as the lower Mkuze River floodplain and thus collectively could expand the number of intervening levels of observation between the context and extent of the current study. The sustainable management of the Greater St Lucia Wetland Park requires a multi-scale approach, which takes cognisance of spatial heterogeneity and the role of anthropogenic disturbance. This is what a landscape ecological approach can provide.

The floodplain systems of the coastal plain

The lower Mkuze River floodplain is situated on the coastal plain, which extends northwards from Mtunzini in South Africa and broadens out along the coast through central and eastern Mozambique into Tanzania and Kenya (Hobday, 1979; Haldorsen, 2001). Within South Africa the coastal plain is dominated by three floodplain systems other than the Mkuze, namely the Pongolo, the Mfolozi, and the Mhlatuze River floodplains.

The Pongola River floodplain is situated on the Makatini flats, downstream of the Pongolopoort Dam (Jozini Dam) and extends in a north-easterly direction to the confluence of the Pongolo and Usutu Rivers in Ndumu Game Reserve (Heeg & Breen, 1982). The Pongolopoort Dam was constructed in the 1960s to provide water for irrigation on the Makatini flats. The dam has had profound effects on the structure and functioning of the downstream ecosystem (Heeg & Breen, 1982). The primary impact has been on the natural flooding regime, which was seasonal prior to construction and is now dependent on artificial flood releases from the dam. Other impacts include the retention of sediments and associated nutrients within the dam, and reduced ground water flows (Heeg & Breen, 1982).

The Mfolozi River floodplain or Mfolozi swamps are situated south of the mouth of the Lake St Lucia estuary and are drained by the lower reaches of two rivers namely the

Mfolozi and the Msunduzi. These rivers are considered together since the former comprises the northern portion of the swamps while the latter comprises the southern region (Begg, 1988). Prior to any human induced modification the swamps extended over approximately 21 000ha. This system has been drastically altered by a number of anthropogenic activities, which have resulted in the reduction of wetland area. These activities include the production of sugar cane (the floodplain is one of the most fertile sugar cane producing areas in South Africa) and timber, the construction of artificial levees, canals and drains, and the diversion of the mouth of the Mfolozi away from the mouth of the Lake St Lucia estuary. These activities have altered the natural hydrological and sedimentation regimes by *inter alia* lowering the water table and impeding the distribution of sediment across the floodplain (Begg, 1988).

The Mhlatuze River floodplain system extends for approximately 24km south-westwards from the town of Richards Bay (Begg, 1989). Prior to any human influence this wetland complex occupied approximately 12 000ha. However, a large proportion of the system has been severely disturbed by a number of anthropogenic activities. These include canalisation, construction of weirs and impoundments, sugar cane and timber production, and the contamination of surface and ground water by surrounding industry (Begg, 1989). This has resulted in the reduction of wetland area, which has consequently placed a number of wetland functions, for example water purification by wetland vegetation and soils, under severe strain.

The lower Mkuze River floodplain is relatively unmodified by humans when compared to the other floodplain systems of the coastal plain. In addition, the majority of the floodplain system falls within a protected area. Thus, from a conservation perspective the lower Mkuze River floodplain is extremely valuable. The assessment of the floodplain systems on the coastal plain, from a landscape ecology perspective, can provide one with a framework for the prioritisation of areas, in this case, for conservation purposes but which could be adapted for any purpose depending on government policy and/or management objectives. The goal of conservation management has shifted from managing species to managing their habitats and ecosystems (Rogers & Bestbier, 1997). In other words conservation management is focusing on landscape heterogeneity, dynamics and the role of

disturbance within the landscape. Landscape ecology theory can therefore provide conservation managers and planners with a framework for developing strategic management plans.

7.3 Future Research

Chemical Sedimentation

An important process within wetlands that is often been overlooked in wetland research is that of chemical sedimentation (Kotze *et al.*, 2001). Dissolved chemicals are introduced into wetlands via surface flows as part of the overall sediment load. These solutes are drawn down into the root zone, where they are selectively taken up by macrophytes. Those chemicals that are excluded from uptake precipitate out of solution and accumulate in the soil. This accumulation results in a volume increase in the soil, causing vertical aggradation of the soil surface, which in turn alters local slope gradient. This can cause a change in the hydraulic characteristics of a wetland, modifying water movement and sediment dispersal (Kotze *et al.*, 2001). This process of chemical sedimentation was evident within the Okavango Delta, Botswana, and plays an important role in determining vegetation distribution (McCarthy *et al.*, 1993).

McCarthy & Hancox (2000) describe a number of fundamental processes that are considered responsible for wetland origin and evolution. These include *inter alia* changes in sea level, fluvial sedimentation, climate, vegetational succession, anthropogenic factors and chemical sedimentation (McCarthy & Hancox, 2000). According to McCarthy & Hancox (2000) of all these processes only chemical sedimentation was not considered important in the development of the Mkuze Wetland System. However, the Greater Mkuze Wetland System is known to be sink for a number of solutes, namely calcium, potassium and silicon (Barnes *et al.*, 2002). Further investigation of the mechanisms and processes of solute concentration and retention in the system is currently under way (Barnes *et al.*, 2001). Understanding these processes and their geomorphological and ecological consequences is essential in order to fully understand of the processes and dynamics operating within the Greater Mkuze Wetland System.

Floodouts

Floodouts are recognised fluvial features within the arid and semi-arid landscapes of Australia (Tooth, 1999a). These features develop where there is a marked reduction in the channels ability to accommodate flow compared with reaches further upstream and where overbank flows become increasingly common (Tooth, 1999a). In addition, floodouts commonly occur in systems with high sediment inputs that result in vertical accretion of the floodplain (Tooth, 1999b) and along rivers characterized by variable discharge (Tooth & Nanson, 2000). Floodouts have not previously been described in moist subtropical settings in general, and in South African fluvial systems in particular. However there is preliminary evidence of their existence within the lower Mkuze River floodplain. Further investigation is required if the hydrological, sedimentological and geomorphological processes operating within floodouts are to be fully understood.

Disturbance

The affect of anthropogenic activities on natural ecosystem patterns and processes is an important aspect of ecological studies that is seldom incorporated in an explicit manner. In order to determine the overall levels and impacts of disturbance that occurs within the lower Mkuze River floodplain, one needs to examine the properties of the individual disturbances. These properties include *inter alia* the spatial distribution of the disturbance, the frequency or mean number of disturbance events per time period, the area disturbed and the synergism or cumulative impact of the disturbances (White & Pickett, 1985). A detailed study investigating these properties of disturbance at the grain, reference and context levels is required in order to explicitly quantify the link between the anthropogenic disturbance regime and landscape heterogeneity within the lower Mkuze River floodplain.

Broader Context

As was previously mentioned in Section 7.2, the lower Mkuze River floodplain forms part of a larger system. There is a need to expand the current study to include those adjacent systems. This would contribute to a more in-depth understanding of ecosystem patterns and processes operating at larger, spatially coarser levels within the landscape hierarchy.

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APPENDICES

Appendix 4.1 Sample Preparation Procedure

Introduction

Before the particle sizes of a soil sample could be determined the sample was prepared to conform to the requirements of the test. The test required that the particle sizes of the mineral fraction only, finer than 2mm in diameter, with cementing agents like carbonates removed, be evaluated.

Samples collected from the field seldom conform to these requirements and therefore must be treated to remove gravel sized particles (<2mm), organic matter and in some cases cementing agents. Soil aggregates must also be chemically dispersed.

Procedure

- Between 200 and 300g of air-dried soil was ground with a pestle and mortar.
- All soil was transferred to a 2mm sieve, covered and shaken so that only particles finer than 2mm passed through the mesh and collected in the catching pan.
- All the <2mm soil was placed onto a piece of paper and mixed thoroughly with a spatula.
- Between 40 and 50g of the soil was placed into a 1000ml beaker and a little distilled water added.
- 20 ml of H_2O_2 was added to the mixture and heated gently over a hot plate.
- Once the initial reaction diminished, more H_2O_2 was added. This process was continued until with further increments of the reagent the same reaction ceased to continue, indicating that all the organic matter was digested.
- The beaker containing the mixture was filled with distilled water and stirred gently, to ensure that all the soil adhered to the sides of the beaker was brought into suspension.
- The mixture was allowed to stand overnight, after which it was oven dried at 105°C for 24 hours.
- The resultant oven-dried soil from the beaker was then ground with a pestle and mortar until a floury consistency was obtained.

- An empty 500ml beaker was oven dried for approximately one hour at 105°C, removed from oven, cooled and weighed.

- The oven dried soil was then placed into this beaker, weighed and the mass recorded.

- 100ml of the dispersing agent 0.1% Calgon (Sodium hexametaphosphate) was added to the soil and left to stand overnight in preparation for the Pipette particle size analysis (Geographical & Environmental Sciences, 1998).

Appendix 4.2 The Pipette Particle Size Method

Introduction

The particle size distribution of a soil is one of its fundamental characteristics. Cation exchange, strength, erodibility and moisture retention, among others, are determined by particle size distribution.

Procedure

- The sample prepared according to the procedure described in appendix 4.1 was transferred into a mixing cup with a mechanical stirrer and 300ml of distilled water was added to the solution. The sample was mixed for 2 minutes.

- The soil/water slurry was poured into a 1000ml measuring cylinder and topped up with distilled water to the 1000ml mark.

- The cylinder was sealed and inverted 20 times to ensure that the soil was mixed uniformly in the water.

- The temperature of the suspension was measured and the starting time of settlement recorded.

- From the table below, the time period required for the settlement of sand and silt sized particles and the concomitant times for withdrawal of the aliquots were noted.

- The aliquots were withdrawn from a point 60-70mm from the top of the liquid with a pipette and 25ml of the suspension extracted and placed it in a pre-weighed 250ml beaker. The first aliquot contains only silt and clay. It was oven dried at 105°C for 24 hours and then weighed.

- The second aliquot contains clay only and was withdrawn at the specified time, dried and weighed.

- The percentage sand, clay and silt was then calculated (Geographical & Environmental Sciences, 1998).

Temperature (°C)	Sand Settling Time	Silt Settling Time
20	4min 48sec	53min 20sec
21	4 min 41sec	52min 0sec
22	4min 28sec	50min 54sec
23	4min 24sec	49min 36sec
24	4min 22sec	48min 24sec
25	5min 15sec	47min 20sec

Appendix 4.3 The Walkley - Black Organic Matter Content Method

Introduction

The Walkley - Black method is a chemical test used to calculate the percentage of organic matter content within a soil sample. Potassium dichromate is used to digest organic matter and the amount of unused dichromate is measured by a titration process and used to calculate the percentage of organic carbon in the soil sample.

Procedure

- The ferrous ammonium sulphate solution was standardised and the volume of it needed to produce a colour change recorded.
- Between 0.10 and 0.13g of oven dried soil was placed in a 500ml conical flask, weighed and the mass recorded.
- 10ml of Potassium dichromate was added and the solution gently swirled to disperse the soil.
- 20ml sulphuric acid was added to the solution, swirled and allowed to stand for 20 minutes
- 200ml of distilled water was added to the solution.
- 10ml of orthophosphoric acid and 1 ml of diphenylamine was added.
- Ferrous ammonium sulphate was added to the flask in small increments and continually swirled until there was a colour change to green.

- The amount of ferrous ammonium used was recorded and the amount of organic matter within the soil sample calculated according to the following equation:

Percentage organic matter = $\dfrac{(0.67)(\text{Volume of ferrous ammonium used})}{\text{Mass of oven-dried soil sample}}$.

(Geographical & Environmental Sciences, 1998).

Appendix 4.4 Full TWINSPAN output table (PTO).