

**PLANT COMMUNITY CLASSIFICATION AND
ENVIRONMENTAL GRADIENT CORRELATES ALONG
THE EASTERN PORTION OF THE MKUZE SWAMPS**

by

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ABSTRACT

The aim of this study was to describe the plant communities within the eastern portion of the Mkuze Wetland, including only those systems that have a substantial input of water from the Mbazwane Stream, and to determine environmental factors that control distribution. The Mbazwane Wetland has a catchment of reworked sandy marine sediments, and its gradient is very shallow, such that water moving downstream through this system is free of suspended sediment and is clear. In addition, it has low conductivity suggesting a low solute load.

A total of nine communities were identified in the study, based on the TWINSpan cluster analysis. These are: *Ficus trichopoda*/*Scleria angusta* Swamp Forest Community; *Rubus rigidus* Disturbed Swamp Forest; *Phragmites australis*/*Ficus trichopoda* Precursor Swamp Forest; *Typha capensis*/*Pycnus mundii*/*Leersia hexandra* Marsh Community; *Phragmites australis*/*Cladium mariscus*/*Ficus verruculosa* Swamp Community; *Cyperus papyrus* Swamp Community; *Echinochloa pyramidalis* Floodplain Community; *Ischaemum fasciculatum*/*Centella asiatica* Floodplain Community; *Paspalum distichum* Floodplain Community. These communities can be divided into three broad groups, swamp forest, emergent herbaceous swamp/marsh and grassland floodplain communities. One of the main environmental variables influencing distribution was duration and depth of flooding, which separated the permanently flooded swamp and emergent swamp/marsh communities from the seasonally/ periodically inundated floodplain communities. Environmental variables that account for further division of the communities within these two groups, appear to be disturbances from fire and substratum differences related to sediment deposition from the Mkuze River, which enters the lower Mbazwane Wetland from the west.

The permanently flooded swamp forest communities, are largely restricted to the northern parts of the study area, while the emergent swamp/ marsh communities, are restricted to the southern part of the study area. The swamp forest community is fringed to the west by an extremely high and steep dune, while the swamp/marsh communities are fringed to the west by much lower and more gently sloping dunes. It

is suggested here that wildfires in conjunction with topography influence the distribution of these two groups of communities. An analysis of diurnal variation in temperature in the winter months (June – August) for winds (greater than 1.0m/s) reveals that winds blowing from the west to north-west are associated with extremely high temperatures that persist during the day and well into the night. These are berg wind conditions that have been strongly linked to the desiccation of vegetation and promoting its susceptibility to burning in wildfires, and it is during these conditions that fires are most likely to occur in the study area. Swamp forest is situated in areas that are protected from direct exposure to these winds by the high, steep dune immediately to the west. These are thus likely to be naturally protected from fire. In contrast the herbaceous swamp/marsh communities are not protected from wind or fire by a similar topographic feature. Mature swamp forests were restricted to these 'berg wind shadow' areas, where there is complete protection from fire. Precursor and disturbed swamp forests occur where they are less protected and thus are infrequently exposed to fire.

The distribution of the permanently flooded swamp/marsh communities in the areas exposed to fire appears to be related to the input of nutrients. The *Cyperus papyrus* Swamp Community was rooted in clay rich peat in the area around the Mkuze Delta that receives an input of clay from the Mkuze River during very high floods. In contrast, the *Phragmites australis/Cladium mariscus/Leersia hexandra* Swamp Community was rooted in peat with low ash content, as there is little or no input of clay from the Mkuze River, even during high floods. The seasonally/periodically-flooded communities included the *Echinochloa pyramidalis* Floodplain Community, the *Ischaemum fasciculatum/Centella asiatica* Floodplain Community and the *Paspalum distichum* Floodplain Community. The *Echinochloa pyramidalis* Floodplain Community was restricted to seasonally flooded areas receiving an input of clastic sediment from the Mkuze River during high floods, while the other floodplain communities occurred in areas receiving water from the relatively sediment free Mbazwane Stream. The distribution of these two communities appears to be influenced by the duration of inundation, with the *Ischaemum fasciculatum/Centella asiatica* Floodplain Community being at higher elevation and therefore less frequently flooded than the *Paspalum distichum* Floodplain Community.

PREFACE

The experimental work described in this dissertation was carried out in the School of Life and Environmental Sciences (MTB Branch), University of Natal, Durban, from January 1999 to December 2000, under the supervision of Professor W.N. (Fred) Ellery.

This study represents original work by the author and has not otherwise been submitted in any form or for any other degree or diploma to any tertiary institution. Where use has been made of the work of others it is duly acknowledged in the text.

Ashleigh Schoultz

Date

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CHAPTER 1: INTRODUCTION

The varied climate and geomorphology of South Africa have resulted in wetlands that are remarkably diverse despite being limited in number (Cowan 1995). The Greater Mkuze Wetland, located in southern Maputaland, is one of Southern Africa's largest and most complex wetland systems. The principal source of water for this wetland system is the Mkuze River, which joins with the southerly flowing Mbazwane Stream and several smaller streams in the Manzibomvu area to drain into Lake St Lucia (Stormanns 1987). The St Lucia lagoon system and the swamps along the lower Mkuze River form part of the Greater St Lucia Wetland System, which has been designated by South Africa as a Wetland of International Importance in terms of the Ramsar Convention (Cowan 1995).

In addition to being the largest supplier of fresh water to Lake St Lucia, the diverse wetlands of the Greater Mkuze Wetland system provide an abundance of natural resources and habitats as well as important ecological services. Stormanns (1987) identified eight different types of wetlands in the Greater Mkuze Wetland, which are characterised by 14 plant communities and 671 species. Additionally, at least 32 Red Data Book Species have been identified in the wetland (Bourquin 1986, Johnson 1986). The Greater Mkuze Wetland provides valuable resources for the local inhabitants. These resources include water for irrigation, areas for grazing and cultivation, food and a variety of plant species used as building material and for craftwork (Stormanns 1987). Human impact on the wetland has increased dramatically since the 1950's (Taylor 1986). These largely negative impacts include encroachment into the wetland by cultivation, the construction of several canals to divert water from the Mkuze River and the removal of riparian fig forest along the banks of the Mkuze River (Taylor 1986).

In order to appropriately conserve and manage wetlands it is necessary to have an understanding of both wetland structure and function. This provides a basis for evaluating the likely effects of perturbations on the system. Fundamental to understanding wetland structure and function is knowledge of wetland vegetation composition and the environmental factors controlling vegetation distribution. There have been few quantitative studies on plant communities in southern African wetland

(Rogers 1997), and the Mkuze Wetland is no exception. Stormanns (1987) study on plant communities of the Mkuze Swamp system was largely descriptive in its approach to plant community composition and distribution, and afforded relatively little insight into the underlying environmental determinants of community distribution.

Much theoretical insight of wetlands and their dynamics has come from northern temperate systems, and there are opportunities in tropical and subtropical areas to test and reflect on this body of theoretical knowledge. Rogers (1997) has attempted to integrate theoretical insights from southern Africa into existing knowledge of northern temperate systems, but numerous opportunities exist to conduct new studies to add to this. As such, the diverse wetland types found in southern Africa provide ecologists the opportunity to investigate wetland community structure and function that has largely been based on a relatively narrow range of studies of northern temperate systems (Rogers 1997). Studies on southern African wetlands have included a range of wetland types such as the Nyl River Floodplain (Coetzee and Rogers 1991), the Okavango Delta (Ellery 1987, Ellery *et al.* 1991, Ellery *et al.* 1993a), and the swamp forest of the eastern shores of Lake St. Lucia (Wessels 1991). These studies have generally corroborated the established view that wetland plant community composition and structure are primarily a function of hydrological conditions (Rogers 1997). This study forms part of a broad interdisciplinary study of the Greater Mkuze Wetland including researchers from a variety of disciplines and institutions (Dalhberg *et al.*, 1999).

Thus, the aim of this study was to:

- describe plant communities within the eastern portion of the Mkuze Wetland, including only those systems which have a substantial input of water from the Mbazwane Stream, and to determine environmental factors that control distribution

The objectives were to:

- classify the main plant communities in the Mbazwane Wetland,
- map the distribution of each of these communities, and relate community distribution to a range of environmental factors, and
- integrate the findings of this study with general theories of wetland ecosystems.

CHAPTER 2: STUDY AREA

2.1 Introduction

Extending north of, and including Lake St. Lucia, the Greater Mkuze Wetland System (GMWS) covers approximately 42 000 ha on the Zululand Coastal Plain and encompasses a variety of wetland habitats including open water, floodplains, hygrophilous grasslands, swamps and marshes (Stormanns 1986). The Mkuze wetland system forms a large part the GMWS and, includes the Mkuze River and its floodplain, the 6 Manzibomvu streams draining from the north into the Mkuze River, and the southerly flowing Mbazwane Stream which joins with the Mkuze River to form the Mkuze swamps (Fig. 1).

The Mkuze swamp occupies a drowned river valley cut by the Paleo-Mkuze River during the Pleistocene. Its present day morphology is due to sedimentation within this valley as a consequence of a rise in sea level, and therefore the geomorphic base level, since the last Ice Age (van Heerden 1986). The southern end of the swamps lies just north of Lake St. Lucia, while its northern extreme is found north of the delta formed by the Mkuze River as it discharges into the swamps. This study included only the areas of the Mkuze wetland that receive a substantial amount of water from the Mbazwane Stream as indicated in Figure 1. This area will be referred to throughout thesis as the Mbazwane Wetland

2.2 Hydrology

The Mbazwane Stream contributes 5–8 % of the Mkuze River's mean annual flow into Lake St. Lucia (Hutchinson and Pitman 1973). It flows as a channel or series of braided channels along its northern and middle sections, however, upon entering the northern part of main swamp (Fig. 1), it is no longer confined to a channel. Deriving its water solely from rainfall and groundwater recharge from the coastal plain, the Mbazwane Stream has low conductivities and a very low clastic sediment load (McCarthy and Hancox 2000). Additionally it comprises extensive peat deposits due

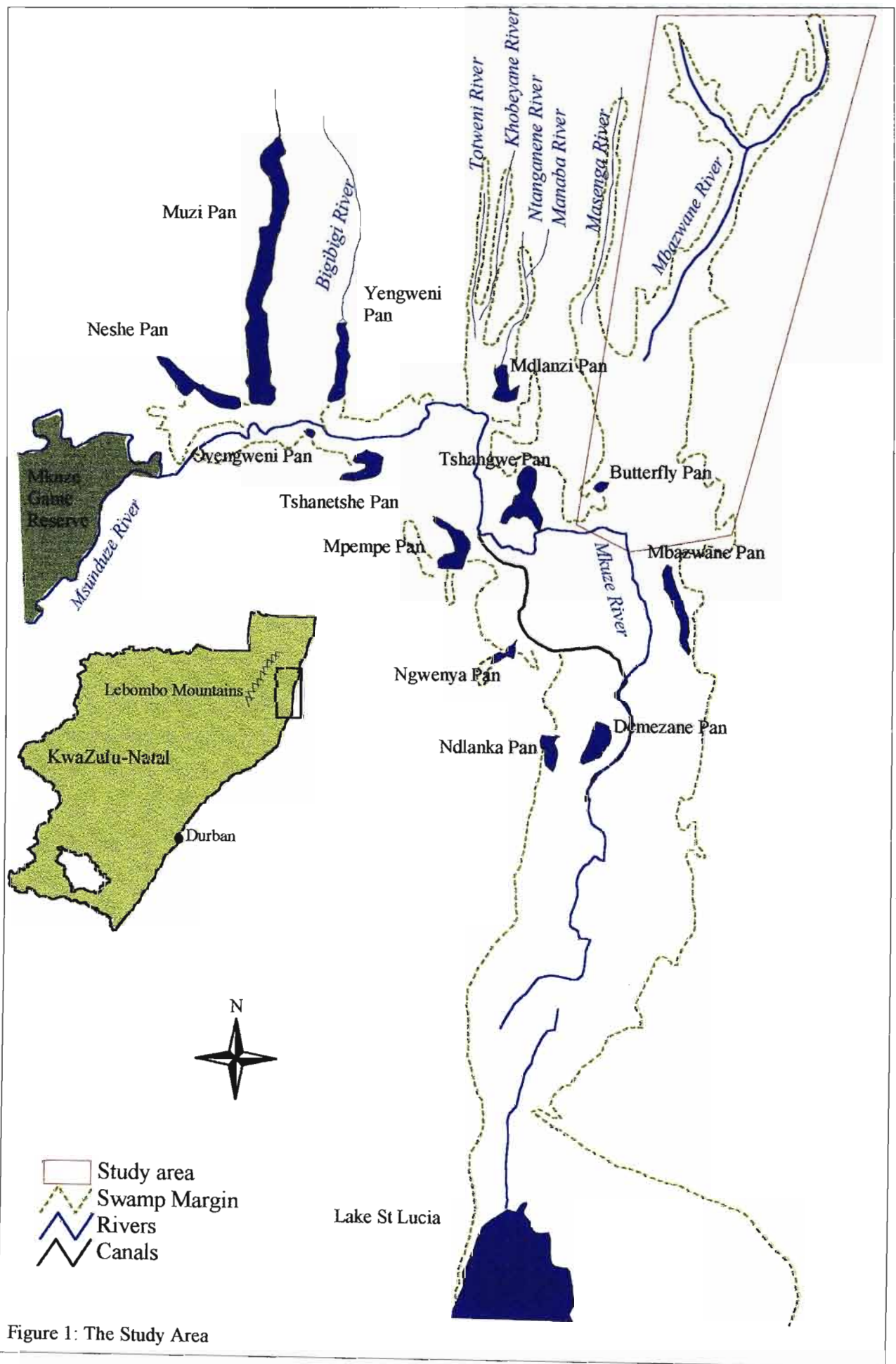


Figure 1: The Study Area

to the lack of decomposition of organic material below the water surface (Stormanns 1987).

The Mbazwane Stream seldom floods and maintains a regular and persistent flow throughout the year, with discharge increasing downstream due to continual groundwater input (Stormanns 1987; McCarthy and Hancox 2000). With the exception of inputs from rainfall and groundwater, the Mbazwane Stream is the only source of water to the northern section of the swamps (McCarthy and Hancox 2000).

2.3 Geomorphology

The northern portion of the Zululand Coastal Plain consists of two major landscape units: the Lebombo Mountains and the coastal plain (Watkeys *et al.* 1993). The coastal plain has an undulating topography that is interspersed with a series of parallel low beach ridges and dune cordons (McCarthy and Hancox 2000). Geologically recent deposits of unconsolidated dune sand overlies much of the coastal plain, while the Mkuze River, which drains areas underlain predominantly older Ecca, Dwyka and lower Beaufort Groups is associated with deposits of silty alluvium (Stormanns 1987; Watkeys *et al.* 1993). Reworking of the unconsolidated dune sand by wind action during the late Pleistocene and recent times has resulted in the formation of the extensive north-south dune topography (Stormanns 1987).

In general, water table levels in the high lying dune crests are elevated relative to the interdune depressions, resulting in the movement of subsurface water into the interdune depressions. This is associated with the formation of lakes, pans and swamps in the low-lying depressions on the sandy coastal plain (McCarthy and Hancox 2000). Thus the dune cordons and the interdune areas play an important role in the development of coastal wetlands through impeding and controlling drainage, acting as local groundwater recharge areas and forming areas for sedimentary fill (McCarthy and Hancox, 2000).

A particularly large dune cordon reaching an altitude of approximately 30m above sea level, extends in a northeast-southwest direction along the western border of the Mbazwane Stream in its northern section. At the southern end of its course the

Mbazwane Stream enters the northern portion of the Mkuze swamps, and this dune feature is no longer discernible.

2.4 Climate

Northern KwaZulu-Natal experiences its greatest temperatures, humidity and rainfall during the summer months (Watkeys *et al.* 1993). Rainfall averages between 1000 – 1100 mm annually along the coast and decreases to 600 mm at the base of the Lebombo Mountains (Schulze 1982). Flooding along the Mkuze River is seasonal, with periodic flooding caused by the presence of occasional cut-off lows moving up the coast, which are associated with very high rainfall at high intensity (Tyson and Preston-Whyte 2000). Even more occasionally, tropical cyclones cause extreme flooding (McCarthy and Hancox 2000). Mean annual temperatures range from 21 °C to 22 °C, while mean humidity values for the wet months are 97.9% (08h00) and the dry months 91.8% (08h00) (Schulze 1982; Watkeys *et al.* 1993). The prevailing winds are northeasterly and southwesterly (McCarthy and Hancox 2000), and berg winds occur mainly in the winter months, being associated with high temperatures that prevail for a few days (Tyson and Preston-Whyte 2000).

2.5 Vegetation

The coastal margin of the northern KwaZulu-Natal coast falls under Acocks' (1953) Coastal Forest and Thornveld (Type A1), consisting of open grassland interspersed with numerous and extensive patches of forest. The Mbazwane Wetland is comprised of two of the forest types typical of this region as described by Acocks (1953), namely, Type 1b. Zululand Palm Veld and Type 1d. Dune Forest.

The Zululand Palm Veld is mainly found north of the Tuglea River and is associated with sandy soils on the poorly drained coastal plain (Acocks 1953). The forests of the Zululand Palm Veld are characterised by woody lianas, palms and trees, and include species such as *Brachylaena* spp., *Trichilia emitica*, *Strelitzia nicolai*, *Syzygium cordatum*, *Acacia karoo* and *Phoenix reclinata*. The grasslands within the Zululand Palm Veld are usually open and characterised by species such as *Aristida junciformis*,

Eragrostis spp., *Sporobolus* spp., *Hyparrhenia* spp., *Digiteria* spp., *Setaria* spp., and occasionally *Themeda triandra* (Low and Rebelo 1996).

Dune Forests within this region are found on the high lying dunes running down the coast and are characterised by trees, shrubs, climbers and grasses (Acocks 1953). Typical canopy species include *Mimusops caffra*, *Diospyrus rotundifolia*, *Euclea natalensis*, *Brachylaena discolor* and *Apodytes dimidata* (Acocks 1953; Low and Rebelo 1996). Shrubs and climbers include *Scutia myrtina*, *Allophylus natalensis* and *Dracaena hookeriana*, while typical grass species include *Dactyloctenium australe* and *Ehrharta erecta* (Acocks 1953).

CHAPTER 3: WETLAND VEGETATION DYNAMICS: A REVIEW OF THE LITERATURE

3.1 Introduction

Wetlands are found along a gradient at the margins of terrestrial uplands and deepwater aquatic systems. They are distinguished from the two by a combination of three features: the presence of standing water either at the surface or within the root zone; the presence of hydric soils; and vegetation that is adapted to or tolerant of saturated soils (Cowardin *et al.* 1979). The hydrological conditions, which can vary from permanent to intermittent flooding, are known to exert the greatest influence on the structure and function of a wetland (Mitsch and Gosselink 1993). Defined by the depth, duration and frequency of flooding above the surface or in the root zone, the hydrological regime impacts spatial heterogeneity in wetlands, by influencing oxygen supply, nutrient availability and the concentration of toxins in the soil. These secondary factors in turn determine the site specific conditions to which biota respond, and thus strongly influence ecosystem characteristics such as organic matter accumulation, primary production and nutrient cycling (Gosselink and Turner 1978).

Plant communities are characterised by changes in species composition over time as species decline or appear over time, or as environmental conditions are altered (Mitsch and Gosselink 1993). When species in a community are replaced in a predictable, orderly sequence and change is directed towards a stable community, the process is known as succession (Begon *et al.* 1990; Mitsch and Gosselink 1993). The concept of succession has been widely applied in plant ecology, including wetland ecology, to explain the establishment and subsequent development of plant communities. According to classic successional theory, changes in the environment, and therefore, changes in species composition, are primarily directed by biological processes within the community. This is generally referred to as autogenic succession (Begon *et al.* 1990). When the serial replacement of species occurs as a result of external influences, such as fire or sediment deposition, succession is referred to as allogenic succession (Begon *et al.* 1990). The typical mechanism of succession in wetlands involves the autogenic accumulation of organic matter, which reduces water depth and therefore favours species tolerant of decreased depth and duration of

inundation. Organic matter accumulation is considered to be the overriding factor changing environmental conditions within wetlands, and the conversion of a shallow open water body to a terrestrial community rooted in peat, is known as a hydrarch succession (Mitsch and Gosselink 1993).

Wetland vegetation typically exhibits a distinct pattern of zonation along the elevation gradient from open water to terrestrial (Denny 1985a). This reflects environmental gradients in oxygen supply, nutrient availability and toxin concentrations along the gradient from permanently flooded (open water) to seasonally flooded to terrestrial (Gosselink and Turner 1978). In classical successional theory these environmental gradients are considered to result from changes to the hydrological regime brought about by peat accumulation. The accumulation of peat is seen to alter surface elevation to the point where it is no longer permanently flooded and can support flood tolerant species (Mitsch and Gosselink 1993). As mentioned previously, this succession from an open water body to terrestrial vegetation as a result of mainly organic matter accumulation, is known as hydrarch succession, and the sequence of communities as a hydrosere (Denny 1985a). However, Walker (1970) showed that succession did not necessarily follow a predictable and linear sequence and that external factors are often instrumental in changing community composition. Thus, an alternate view to classic succession is that allogenic factors are the dominant agents in determining wetland vegetation composition and distribution. Here the observed patterns of zonation are considered to simply reflect species response to underlying environmental gradients, and changes in species composition are not necessarily directed towards a single terrestrial climax (Mitsch and Gosselink 1993; Breen *et al.* 1988).

The contrasting models of biotic (autogenic) and abiotic (allogenic) succession are considered below. Given that these two models are largely derived from studies done in northern temperate environments, consideration is also given to insights gained from studies in southern Africa. However, first the role of the hydrological regime as a determinant of community distribution is discussed.

3.2 The hydrological regime as a determinant of community distribution

The hydrologic regime of a wetland is conventionally considered the most important environmental variable influencing plant community composition and distribution (Breen *et al.* 1988; Mitsch and Gosselink 1993; Rogers 1995). The hydrological regime modifies or influences a range of secondary abiotic parameters, such as nutrient availability, degree of substrate anoxia, soil salinity and the solubility and toxicity of metals. This results in spatial and temporal variations in the physical and chemical environment, creating different niches along both the horizontal and vertical dimensions to which biota respond (Mitsch and Gosselink 1993; Breen *et al.* 1988, Rogers 1995; Gosselink and Turner 1978).

Wetland vegetation distribution is limited by spatial variation in oxygen concentration and chemical conditions of the substrate brought about by hydrologic conditions, which range from intermittent to permanent soil saturation (Kotze *et al.* 1994). Wetland soils are classified as hydric soils, which are defined as: "soil that in its undrained condition is saturated or flooded long enough during the growing season to develop anaerobic conditions that favour the growth and regeneration of hydrophytes" (Kotze *et al.* 1994). In addition to limiting the oxygen available to plant roots and underground stems for respiration and growth, soil saturation results in transformations to minerals in the soil. A number of metals such as iron and manganese are reduced in anoxic conditions and become soluble, potentially reaching concentrations that are toxic to plants. Additional transformations occur to nitrogen, phosphorus and sulphur which affect their availability and may lead to their removal from the soil by leaching. Organic carbon constitutes a substrate that is readily oxidised, but in the absence of oxygen, organic matter accumulates. Wetland soil conditions thus create a stressful environment for plants, and only plants which have developed mechanisms to cope with these conditions are able to survive (Kotze *et al.* 1994).

The degree of soil saturation within a wetland, and thus the degree and persistence of anaerobic conditions, is dependent on where on the continuum between aquatic and terrestrial systems the area lies (Kotze *et al.* 1994). Breen *et al.* (1988) consider

swamps, which are characterised by the presence of standing water among vegetation, to lie at one extreme of the continuum, while at the opposite end are floodplains which have alternating periods of submergence and exposure. Kotze *et al.* (1994) have described this continuum in terms of three soil saturation classes which correspond to the water regime, and have included the dominant vegetation types associated each class. The soil saturation classes and their vegetation types are as follows (Table 1):

- Permanently/Semi-permanently saturated/flooded soils, characterised by reeds, sedges and/or bulrushes.
- Seasonally saturated/flooded soils, characterised by sedges and grasses; and
- Temporarily saturated/flooded soils, characterised by hygrophilous grasses.

Table 1. A provisional basis for differentiation between the main types of wetlands, other than floodplains, in KwaZulu-Natal (from Kotze *et al.* 1994)

	Type 1 Wetland	Type 2 Wetland	Type 3 Wetland
Hydrological indicators			
Duration of inundation *	short	long	very long
Depth to water table **	> 500 mm	150 – 500 mm	< 150 mm
Pedological indicators			
Colour/texture	light grey	dark grey, clayey	black heavy clay
Mottling of A horizon	none	slight	present, plus rust like stains in root canals
Subsoil/gley	slight mottling	distinct mottling	heavy mottling
Botanical indicators ***			
Dominant plants	hygrophilous grasses	sedges	reeds, bulrushes and/or woody plants

* short duration = saturated for 7 days to 1 month
 long duration = saturated for 1 month to 6 months
 very long duration = saturated and frequently inundated, for more than 6 months

** For the major part of an average rainfall season

*** Frequently, vegetation alone, which is a reflection of hydrological and soil conditions, will suffice in determining the presence and boundaries of a wetland.

Typical wetland biota therefore consists of plants adapted to, or tolerant of varying degrees of inundation, and predictable patterns of vegetation distribution are often evident. Plants intolerant of flooding are found in areas at relatively high elevation, while those more tolerant of flooding but less tolerant of prolonged dry periods are found in areas of less variable water levels at lower elevation (Breen *et al.* 1988). Areas subject to floods of shorter duration and depth, are thought to have greater plant species diversity than those that are permanently flooded (Gosselink and Turner

1978). Biota however are not passive to the hydrological regime. By increasing clastic sedimentation and peat building in areas experiencing prolonged flooding, biota alter the basin morphology, thereby modifying the hydrological conditions. This would in turn result in changes to species composition and richness (Mitsch and Gosselink 1993). When the changes in species and community composition are primarily directed by the accumulation of organic material, community development forms part of an autogenic successional sequence.

3.3 Autogenic succession – The classical idea of succession

Wetlands are traditionally considered to be seres in a hydrarch successional sequence from an open water body to a terrestrial forest climax (Mitsch and Gosselink 1993). In this view, characteristic and distinct plant communities replace one another along a linear and directed path mediated by autogenic processes. The submerged plant zone is seen as a pioneer colonisation stage, in which rooted plants act to reduce water velocity resulting in an increase in sedimentation. Clastic sedimentation and/or concurrent deposition of organic matter decreases the water depth and enables the establishment of emergent vegetation in place of the submerged plants (Denny 1985a). Organic matter deposition from within the system rapidly increases with the presence of emergent vegetation, further raising the surface elevation and reducing the depth and duration of flooding. This creates habitats suitable for vegetation tolerant of periodic dry periods, which then succeed the emergent vegetation. Ultimately, shrubs and small trees occur, which in addition to adding organic material to the soil, assist in the conversion of the site to a terrestrial one by enhancing evapotranspiration (Mitsch and Gosselink 1993). The final community to occupy the site in this sequence is a climax terrestrial forest. The important factor is that changes in this successional sequence are driven by the biota, which alter the surface elevation and consequently the hydrological regime, by increasing sedimentation through reducing water velocity and by contributing to organic matter accumulation.

An autogenic successional sequence requires that the changes in community composition and structure at a site are linear and directed towards a stable climax. However, while examples of this sequence have been documented, several studies have shown that the pattern of submerged to floating leaved to emergent plant to

terrestrial forest is not universal. Other factors, including local topography, water balance and individual plant tolerances, play a role in changing floristic composition in wetlands (Walker 1970). In addition, Ellery *et al.* (1990) illustrated that peat accumulation in the Okavango Delta in Botswana did not necessarily lead to a terrestrial climax, but rather it increased the likelihood that other environmental factors such as fire and differential sedimentation would alter ecological processes and therefore community composition and structure.

3.4 Allogenic succession – The continuum idea and the environmental sieve model

The continuum idea stems from the individualistic hypothesis put forward by Gleason (1917) and states that the distribution of a species is governed by its response to the environment (Mitsch and Gosselink 1993). In this view no explicit plant communities exist. Rather, aggregations of plants reflect similar tolerances or adaptations in a number of species, as such, changes in the ecosystem over time are thought to result from simple changes in the environment. In addition, these changes are not necessarily directed towards a particular stable climax community. Thus, the zonation of plants is considered to reflect underlying environmental gradients to which plants respond, which, in wetlands often have abrupt boundaries (Mitsch and Gosselink 1993). Changes in the environment in this view are considered to largely be the result of allogenic processes.

Van der Valk (1981) proposed the environmental sieve model, which holds that the presence and abundance of a species at a site are determined by the individual life histories and their adaptations to the environment. Each species has a unique life history type and therefore unique characteristics through which it responds to the controlling environmental factors. As discussed above, the hydrological regime is the dominant allogenic force operating to create and modify the chemical and physical properties of a wetland. As hydrological conditions vary, so do other environmental factors, thus forming an “environmental sieve”. As the environmental conditions change, so does the sieve and thus the type and number of species present. The changes are therefore dependent on the environmental conditions and are not necessarily directed towards a specific climax (Mitsch and Gosselink 1993).

3.5 Allogenic vs. autogenic factors

Allogenic succession and autogenic succession as separate concepts are limited in their usefulness when applied to wetland dynamics (Niering 1989). Rather, both are important factors in the development and final characteristics of wetland vegetation (Mitsch and Gosselink 1993). Generally the hydrological regime is dominant in influencing wetland structure and function, and therefore species composition and distribution. Biota function as part of a feedback loop, whereby the hydrological regime is modified by increased sedimentation and by organic matter accumulation (Gosselink and Turner 1978). The relative importance of each of these forces appears to be influenced by the nature of the inflows and outflows of the hydrological regime.

In high-energy wetlands, such as areas adjacent to high order rivers, much of the organic production is removed and the floodplain microtopography and sediment characteristics reflect the pattern of overflow from the adjacent river (Gosselink and Turner 1978; Mitsch and Gosselink 1993). In these systems, allogenic forces appear to overwhelm autogenic forces. In contrast, in low-energy systems, such as some freshwater marshes and swamps, vegetation composition and distribution appear to reflect biotic processes. Here organic matter is able to accumulate and thereby modify the hydrological regime. Thus both abiotic and biotic processes combine in varying degrees, depending on the fluvial setting, to produce the observed patterns in wetland vegetation.

3.6 Insights into southern African wetlands

The description of key factors and processes in wetland ecosystems reflects a strong bias towards northern temperate wetlands, where most wetland research has been done. It is therefore appropriate to consider insights in tropical and subtropical systems, including southern Africa. The number of studies conducted on plant community structure and dynamics in southern African wetlands is limited, and therefore there is little basis for regional generalisations (Rogers 1997). However, a few recent studies on plant community structure and correlations between species distribution and environmental gradients in different wetland types, provide some

important insights into wetland vegetation processes in southern African wetlands (Rogers 1997).

Studies on highveld vleis in South Africa have illustrated that both autogenic and allogenic factors are influential in influencing community structure and change in these systems (Rogers 1997). Highveld vleis are generally permanently flooded marshes, with peat accumulations of 6 meters or more and are dominated by mono-specific stands of *Phragmites australis*. In a study on the changes in the distribution of communities dominated by *Phragmites australis* or *Typha capensis* in the Daggafontein vlei over the period 1968 to 1989, Venter (1991) found that the area covered by *Phragmites australis* increased 132% while areas covered by *Typha capensis*, open water and grassland decreased significantly. This indicated a successional sequence to the hypothesised *Phragmites australis* dominated climax community. Venter (1991) proposed that the superior ability of *Phragmites australis* to capture light and root space was particularly important in influencing its establishment late in the successional sequence. There were however, instances where community change did not follow the predicted successional sequence and open water bodies or *Typha capensis* dominated communities increased in size. These changes appeared to be the result of waterfowl grazing and fire. Areas dominated by *Typha capensis* were converted to open water by the extensive feeding of waterfowl on the rhizomes and young shoots of *Typha capensis*, while fire appeared to reduce the competitive ability of *Phragmites australis*, enabling the encroachment of *Typha capensis* (Venter 1991).

Several studies conducted on vegetation change in different wetland types in the Okavango Delta have provided insights into wetland processes and have made important contributions to wetland ecology in southern Africa (Rogers 1997). The Okavango delta contains several habitats including permanent swamps, seasonal swamps and islands (Ellery and McCarthy 2000), and complex changes in community composition, which occur in response to the longitudinal hydrological gradient, are evident in the downstream direction (Rogers 1997). Such vegetation response to longitudinal gradients have been observed in river systems in northern temperate regions, but the unique combination of high evapotranspirational losses, low local rainfall and highly seasonal inflows in the Okavango Delta result in this longitudinal

hydrological gradient being manifest over much shorter distances than elsewhere (Rogers 1997).

In a study on back-swamp successional dynamics in the Okavango Delta, Ellery *et al.* (1991) found that back-water swamp communities occur as floating mats of vegetation that form on floating peat layers. These floating mats of vegetation, which arise on floating mats of organic material, differed in species composition when compared to the emergent communities found at the end of a classic successional sequence recorded in open water bodies (Ellery *et al.* 1991). Additionally, the formation of these floating vegetation mats was found to be unaffected by water depth because of their buoyancy and as the effects of fluctuations in water level are eliminated on these floating mats, autogenic processes become the main agents directing community change (Ellery *et al.* 1991). While these floating mats provide an exposed surface for the colonisation by short emergent vegetation, and these communities are insulated from environmental variables such as water level fluctuations, light availability, variation in water chemistry and soil conditions, they become increasingly exposed to other environmental variables such as fire (Ellery *et al.* 1991). This overall insulation of the community to temporal variation in environmental conditions means that autogenic processes become, with the exception of fire, the main agents directing community change (Ellery *et al.* 1991).

3.7 Conclusion

It seems that in tropical and subtropical systems where overall climatic conditions are variable in space and time, the conventional view that autogenic processes play a predominant role in community change over time, may be inappropriate. The present study can be seen as simply a case study in which some of these ideas will be tested.

CHAPTER 4: METHODOLOGY

4.1 Introduction

Data collection was carried out in two phases, as a preliminary visit (pilot study) during and after which field methods and also data analysis techniques were tested, and species/area curves compiled. The second phase, in July 1999, was the main data collection phase. This time was chosen so the effects of local rainfall would be reduced in the measurement of water level and conductivity, since this is the height of the dry season.

4.2 Data Collection

4.2.1 Plant Community Description

Stand selection

The vegetation within the study area was initially sub-divided into different vegetation strata (stratification) using aerial photographs and knowledge of the study area obtained during an initial reconnaissance visit. Strata identified were forested, swamp and grassland. Vegetation sampling took the form of continuous plots along transects within the study area, with transects placed at relatively uniform intervals with each stratum, depending on accessibility. The eastern edge of the swamp was completely inaccessible by road, while access to the western edge was restricted by the absence of existing roads. Personal safety made it difficult to walk great distances from the vehicle. Therefore, sampling was conducted mainly from the western edge of the Mbazwane Wetland.

Stand size

Stand size was established by determining the minimum sample area, which is defined as the smallest area on which the community being sampled is adequately represented (Mueller-Dombois and Ellenberg 1974). This was accomplished by constructing species richness - sample area curves, as described by Mueller-Dombois and Ellenberg (1974), for each of the three vegetation strata identified from the aerial

photographs. Within each of these strata, all species within a 1m X 1 m plot were recorded. The plot size was then doubled in size and all species within that plot recorded. The process was then repeated, with the doubling of plot size continuing until very few new species were recorded. The species numbers were then plotted against stand size resulting in species richness - sample area curves for each vegetation type. The point on the graph where a 10 % increase in stand size resulted in 5 % more species being encountered was located. This was the plot size selected. The forested areas had a stand size of 100 m², while the swamp and grassland areas had a stand size of a 25 m².

Measurement of species cover

A modification of the Braun-Blanquet (1965) cover abundance scale was used to estimate the cover of species in the sample plots. Six cover classes were used and for the purposes of data entry and analysis in the classification and ordination, the cover abundance was converted to approximately the midpoint of each cover interval (Table 2).

Table 2. Percentage cover interval, scale value and corresponding cover value used in data analysis.

Scale value (data collection)	Percentage cover interval	Cover value (data analysis)
1	0-2	1
2	3-5	3
3	6-10	7
4	11-25	15
5	26-50	35
6	51-100	75

4.2.2 Environmental Variables

Distance and Elevation

Distance and elevation are considered useful indices of depth and duration of flooding, in that, sites close to the water and/or at a lower elevation will be flooded

more frequently and to a greater depth than a point further away and at a higher elevation (Voortman 1997; Coetzee and Rogers 1991).

The distance from and relative elevation above the water level for each sample plot were determined from cross-sectional topographic profiles constructed for each transect, using data collected with optical surveying equipment. Survey points were located at regular intervals along transects, such that a survey point was located at the centre of each sample plot. In instances where there was more than one channel along the transect, the distance and height above the channel of the sample plot were measured relative to the closest channel.

Peat Thickness

In the classical view of succession, the accumulation of organic matter in wetlands results in a reduction in water depth until the site is able to support emergent and finally terrestrial vegetation (Mitsch and Gosselink 1993). Thus a measurement of peat depth was considered a surrogate measure of the depth at which the initial colonisers of the area became established (Ellery 1987). In sample plots where there was peat accumulation, measurements of peat thickness were taken at the centre of the plot. Since the substratum beneath the peat was sandy and that peat has low bulk density, the point of refusal was considered to represent thickness.

Peat/Soil Samples

Approximately 1 kg of peat and inorganic soil were collected manually to a depth of up to 10cm, by collecting small subsamples of approximately 100 g from random points within each plot.

Water Samples and Depth to Water Table

Certain aspects of water chemistry, such as electrical conductivity, have been found to influence wetland vegetation distribution (Howard-Williams 1979). Additionally the depth below the surface of the water table can have an important influence on the distribution of vegetation (Ellery *et al.* 1993). Water samples were collected from every second plot along each transect, although several additional samples were also collected. In plots found in standing water, water samples were taken from just below the water surface and the water table surface was considered to be at 0 m. In plots

that were dry at the surface at the time of sampling, holes were augered to the water table and a sample extracted at this depth. Measurements of water table depth in such cases were also made after leaving the water table for approximately 30 minutes to equilibrate. Conductivity was measured immediately after sampling using a Corning 311 Conductivity Meter. No other analyses were conducted on the water samples.

4.3 Data entry and analysis

In order to describe the vegetation of the eastern portion of the Mkuze wetland and to examine the relationships between community distribution and environmental conditions, two multivariate techniques were used, namely classification and ordination.

Classification involves extracting similar entities from a set of raw data and placing them into groups (Gauch 1982; Jongman *et al.* 1995). The classification of communities helps to detect structure in complex multivariate data sets such as matrices of samples by species and samples by environmental data (Jongman *et al.* 1995). Classification therefore assists in extracting information on the occurrence of species and establishing community types for descriptive analysis (Jongman *et al.* 1995).

Ordination is a statistical technique that allows communities to be separated in a two (or map) dimensional manner such that those communities most similar in species composition and relative abundance are closest together, while those most dissimilar are furthest apart (Begon *et al.* 1990). It also frequently enables the interpretation of environmental variables most strongly correlated with species and community distribution.

4.3.1 Classification

Plant community classification was done using the TWINSpan (Two Way Indicator Species Analysis) program devised by Hill (1979a). The program uses a polythetic divisive classification technique, where division is based on the presence and cover of more than one species. All sample units are considered at the outset and are repeatedly

divided into smaller groups of increasing similarity (Ellery 1987). In addition to the classification of sites, TWINSpan also creates an ordered two-way table from a sample-by-species matrix.

The TWINSpan program default values were used in all instances with the exception of the pseudospecies cut levels and the pseudospecies weightings. Six pseudospecies cut levels were selected: 0, 2, 5, 10, 25 and 50, while pseudospecies weightings were assigned as follows: 1, 2, 4, 6, 6, and 6. This means that pseudospecies at cut levels 2, 3, 4, 5 and 6 were given 2, 4, 6, 6, and 6 times the weight respectively of the pseudospecies at the lowest level. This was considered justified as species with greater cover were considered more important in classifying communities than those with lower scores.

4.3.2 Ordination

For the purposes of gradient analysis, the detrended correspondence analysis (DCA) option of the DECORANA program (Hill 1979b) was used. Ordination refers to various multivariate techniques that arrange sites along axes based on species composition (ter Braak 1995). The output from an ordination is a graphical summary of the data, in which sites that are similar in species composition are arranged close to one another in two dimensional space, while those with dissimilar species composition are arranged far apart. The DCA ordination program extracts the ordination axes from the species data by maximising the dispersion of species scores based upon theoretical environmental variables (ter Braak 1995). Environmental data can then be superimposed on the ordination diagram to provide a framework in which to interpret the theoretical environmental variables (ter Braak 1995). The ordination axes are termed eigenvectors and have corresponding eigenvalues that give a measure of the importance of the ordination axes. Eigenvalues range between 0 and 1, with values greater than 0.5 indicating a good separation of species along the axes (ter Braak 1995). Species importance values used in this analysis were abundance values. The axes generated by the program were displayed graphically to enable interpretation.

4.3.3 Environmental Variables

Peat samples

Organic matter content or conversely ash content of each peat sample collected was determined by measuring the weight loss on combustion at 500°C and was expressed as a percentage of the total weight.

Soil samples

A simple particle size analysis was conducted on each sample using the pipette method as described in the laboratory manual for the Practical course in Soil Science at the School of Life and Environmental Sciences, University of Natal, Durban. This method is based on Stokes Law, which states that when settling through a fluid of known density, large particles travel more rapidly than small ones. Since the relationship between particle diameter and settling velocity are known, it is possible to determine the diameters of settling particles. Percentages of sand, silt and clay were determined for each sample.

Water samples

A Corning conductivity meter was used to measure the conductivity of the water samples. The temperature of all samples was 20°C at the time of measurement.

4.3.4 Vegetation mapping

The Atlas GIS program was used to develop a contour map of the study area from 1:10 000 ortho-photographs. The TWINSPAN communities were then mapped onto the contour map, using data from sample locations in conjunction with aerial photographs, ortho-photographs and direct field observation. Based on the combination of these activities the wetland boundaries were delineated.

CHAPTER 5: RESULTS

5.1 Introduction

Classification and ordination are useful ways of summarising complex multivariate data sets, and offer one the opportunity to meaningfully classify samples, display relationships between groups of samples and investigate the underlying environmental conditions that might contribute to heterogeneity within the floristic data (Gauch 1982). Plant communities were classified using the TWINSpan program (Hill 1979a) based on a combination of high Eigenvalues (> 0.4) and field experience, as well as on comparative work by Stormanns (1986). The results from this analysis are described first. This is followed by the DCA sample ordination (ter Braak 1995), which aimed to link community distribution and environmental characteristics. A description of the topography and general environmental characteristics of the study area is also provided. Finally, detailed descriptions of each community and their distributions are given.

5.2 Plant Community Classification

Nine plant communities were identified in the TWINSpan cluster analysis (Fig. 2). The output table (Appendix A) is summarised in Table 3.

The first level of division separated samples indicated by *Thelypteris spl.* and *Cyperus prolifer* (Group 2, $n=87-$) from samples indicated by *Ischaemum fasciculatum*, *Cyperus longus* and *Centella asiatica* (Group 3, $n=28+$). At the second level of division the samples in Group 2 were separated into two groups. *Ficus trichopoda* (cover greater than 5 %) and *Scleria angusta* were indicators of samples in the negative group of this division (Group 4, $n= 13-$). Further divisions of this group did not produce any meaningful groupings of samples and therefore it was taken to represent the *Ficus trichopoda/Scleria angusta* Swamp Forest Community (Group A). The positive group of this division (Group 5) was separated based on the indicator species *Phragmites australis*, *Leersia hexandra* and *Cyperus prolifer* (Group 5,

Table 3. Summary of TWINSpan two-way output table showing those species that occurred in 50% or more of the samples in one or more of the communities identified in this study. Indicator species of the relevant communities are in bold type.

spp. #	Species name	Group A	Group B	Group C	Group D	Group E	Group F	Group G	Group H	Group I
	No of samples	13	11	15	20	11	14	3	22	6
288	<i>Bridelia micrantha</i>	5	9	11					2	
77	<i>Dissotis canescens</i>		1	8					1	
206	<i>Rubus rigidus</i>	1	10	5					2	
259	<i>Voacanga thouarsii</i>	4	8	7						
304	<i>Cyperus alternifolius</i>	4	7	1						
52	<i>Commelina africana</i>	1	2	8	2		2			
68	<i>Cyperus prolifer</i>		5	13	19	11	3			
97	<i>Ficus verruculosa</i>				3	10	3			
155	<i>Mikania natalensis</i>			5	11	9	3		1	
179	<i>Phragmites australis</i>		8	13	19	11	5		1	1
248	<i>Typha capensis</i>		6	7	16	7	4			
296	<i>Cladium mariscus</i>					9				
383	<i>Polygonum senegalense</i>				2		2	2		
384	<i>Polygonum serrulatum</i>			6	14	7	14			
421	<i>Thelypteris sp1</i>	2	10	15	17	11	9		2	
67	<i>Cyperus papyrus</i>				10	9	14		1	
393	<i>Pycnus mundii</i>				14	2	3			1
71	<i>Cyperus textilis</i>		2	9	3		4	2	1	
79	<i>Echinochloa pyramidalis</i>						2	3	2	
142	<i>Leersia hexandra</i>		1	8	17	9	14	2	4	1
96	<i>Ficus trichopoda</i>	11	2	10			2			
196	<i>Rauvolfia caffra</i>	7		1						
246	<i>Trichilia dregeana</i>	6								
247	<i>Trichilia emetica</i>	6								
282	<i>Bahia racemosa</i>	6								
289	<i>Burchellia bubalina</i>	7								
349	<i>Keetia gueinzii</i>	6								
364	<i>Microsporium sp.</i>	7	2							
388	<i>Psychotria capensis</i>	7		1						
405	<i>Scleria angusta</i>	11	1	2						
178	<i>Phoenix reclinata</i>	5	6	1					2	1
119	<i>Imperata cylindrica</i>		5		1				5	3
172	<i>Paspalum distichum</i>				1				2	5
324	<i>Fimbristylis complanata</i>		1						2	3
376	<i>Panicum deustum</i>								2	3
41	<i>Centella asiatica</i>								14	2
317	<i>Eragrostis inamoena</i>								7	3
66	<i>Cyperus longus</i>								12	4
75	<i>Digiteria eriantha</i>								6	3
130	<i>Ischaemum fasciculatum</i>	1	1	2					19	3
239	<i>Themeda triandra</i>								7	
419	<i>Syzygium cordatum</i>	7	7	7		1			7	

n=74+). The samples in Group 5 were further divided at the subsequent level of division. Samples in the positive group (Group 11, n=3+) were separated based on the indicator species *Echinochloa pyramidalis* (high cover, > 25%). This group was not divided in a meaningful way at subsequent levels of division, and these samples were considered to represent the *Echinochloa pyramidalis* Floodplain Community (Group G). The negative group of samples in the division of Group 5 was not indicated by any species (Group 10, n=71-). At the fourth level of division samples in Group 10 were divided into two groups. Samples in the negative group (Group 20, n=26-) was indicated by *Bridelia micrantha*, *Rubus rigidus*, *Voacanga thourasii* and *Syzigium cordatum*; and the positive group (Group 21, n=45+) by *Cyperus papyrus*, *Polygonum serrulata* and *Leersia hexandra*.

At the fifth level of division, samples in Group 20 were separated into two groups one with sample on the negative group (Group 40, n=1-), with the remaining samples in the positive group (Group 41, n=25+). However this was not considered to be meaningful and the sample in Group 40 was included in the positive side of the division (Group 41). It was therefore ultimately included in Group 82 as it had a large proportion (50%) of its species in common with samples in that group. The second division at the fifth level of division separated samples in Group 21 into two groups based on the indicator species *Cyperus papyrus* with high cover (>25%) in the positive group (Group 43, n=14+), while the samples in the negative group of that division were indicated by *Cyperus proliifer* (Group 42, n=31-). Samples in Group 43 were not divided again in a meaningful way and these samples represent the *Cyperus papyrus* Swamp Community (Group F).

At the sixth level of division, samples in Group 41 and Group 42 were each split into two groups. Group 41 (n=26) was divided, based on the presence of *Rubus rigidus* with high cover (>2%) in the samples in the negative group (Group 82, n=11-) and *Phragmites australis* and *Ficus trichopoda* in the samples in the positive group (Group 83, n=15+). These groups were not divided again and are considered to represent the *Rubus rigidus* Disturbed Swamp Forest Community (Group B), and the *Phragmites australis*/*Ficus trichopoda* Precursor Swamp Forest Community (Group C), respectively. Group 42 (n=31) was separated based on the indicator species

Cladium mariscus, *Phragmites australis* and *Ficus verruculosa* in the positive group (Group 85, n=11+). This group represents the *Phragmites australis*/*Cladium mariscus*/*Ficus verruculosa* Swamp Community (Group E). The samples on the negative side of this division (Group 84, n=20-) were not indicated by any particular species, but had preferential species *Typha capensis*, *Pycnus mundii* and *Leersia hexandra* with cover greater than 2%. This grouping therefore represents the *Typha capensis*/*Pycnus mundii*/*Leersia hexandra* Marsh Community (Group D).

The samples in the positive group of the first division (Group 3) were separated at the second level of division based on the presence of *Ischaemum fasciculatum* (cover >5%) and *Centella asiatica* in the negative group (Group 6, n= 22-), forming the *Ischaemum fasciculatum*/*Centella asiatica* Floodplain Community (Group H). Species in the positive group had *Paspalum distichum* (cover >5%) as an indicator species (Group I, n=6+), representing the *Paspalum distichum* Floodplain Community. Although these groupings were divided further at subsequent levels of division, the divisions were not considered meaningful.

Based on the TWINSpan cluster analysis it was possible to distinguish 9 communities. These ranged from tall emergent swamp forest (Group A) and its precursors (Groups B and C) to herbaceous marsh communities typical of permanently flooded conditions (Groups D, E and F), to those typical of seasonally flooded settings (Groups G, H and I).

5.3 Sample ordination: linking community distribution and environmental characteristics.

The results of the detrended correspondence analysis (DCA) ordination of samples indicates that axes 1 and 2 account for a large proportion of variation in the data, while axes 3 and 4 account in a less meaningful way to variation in the data (Eigenvalues of axes 1-4 are 0.77, 0.53, 0.38 and 0.28 respectively). Thus only the first two ordination axes are presented here.

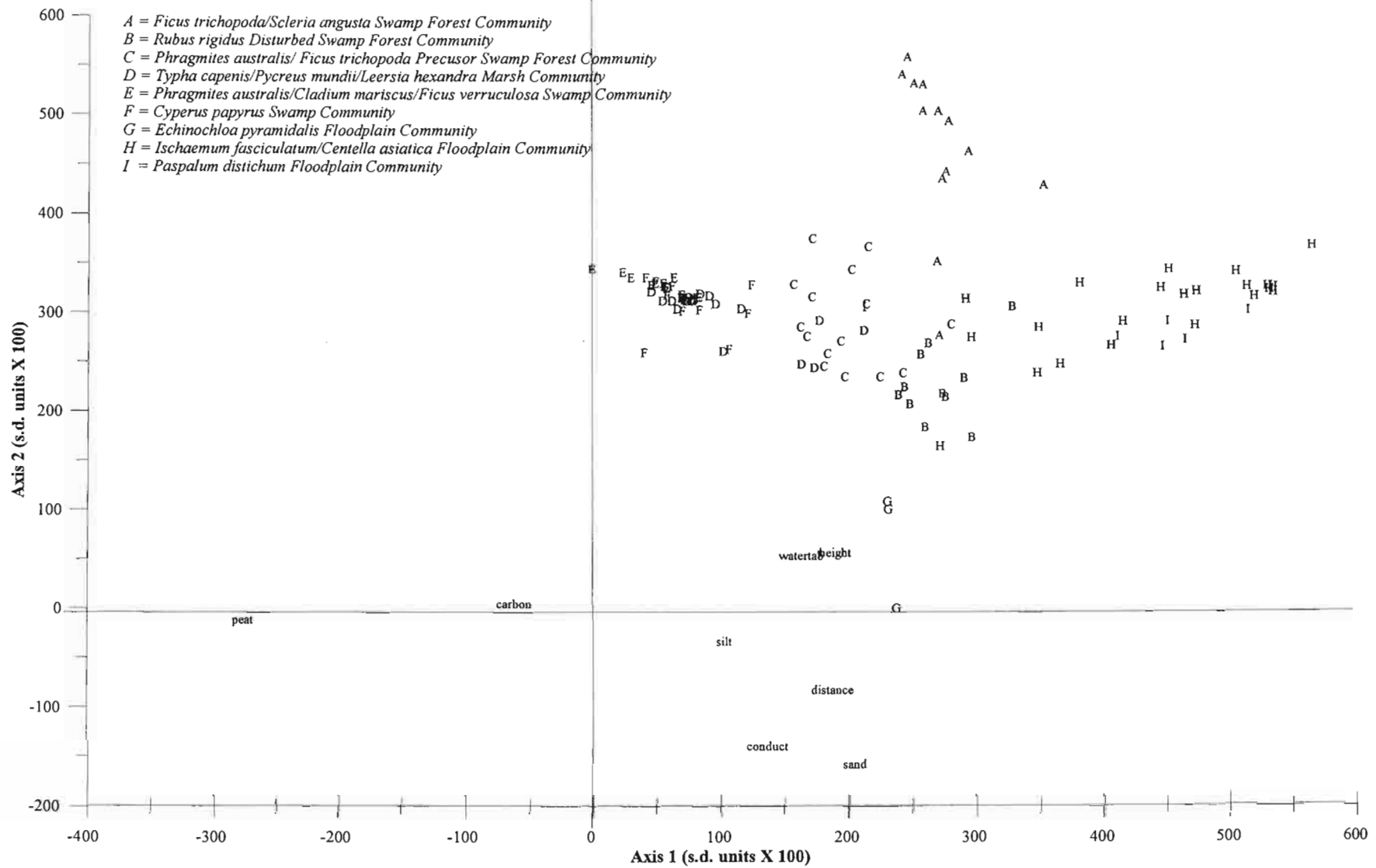


Figure 3. DCA ordination of samples along axes 1 and 2 with each sample displaying the community type as identified in the TWINSpan cluster analysis, and with biplot scores for each of the measured environmental variables.

Sample scores for axes 1 and 2 of the DCA ordination are displayed in Figure 3. Samples are distributed evenly along the horizontal axis over the range of sample scores from 0 to 6 standard deviation units, although samples were concentrated in the region of 2.5 standard deviation units. In contrast most samples occur within a narrow range of scores along axis 2. The axis 2 scores range from 0 to 6 standard deviation units, with most samples occurring in the region of 3 standard deviation units. By labelling samples with their community groupings from the TWINSpan classification on axes 1 and 2 of the ordination diagram, it is clear that the arrangement of samples in ordination space shows good agreement with the results of the TWINSpan cluster analysis. Two of the seasonally flooded communities (Groups H and I), have high positive scores along axis 1, while the emergent marsh communities (Groups D, E and F) are clustered together and have low scores. The permanently flooded swamp forest communities (Groups A, B, and C) are found midway along axis 1, as is the *Echinochloa pyramidalis* Floodplain Community (Group G). These swamp forest and seasonally flooded grassland communities (Groups A, B, C and Group F respectively) are separated along axis 2. The swamp forest community (Group A) had high scores along the second ordination axis, whereas the disturbed and precursor swamp forests (Groups B and C) had intermediate scores. The three samples of the *Echinochloa pyramidalis* Floodplain Community (Group G) had low scores.

Biplot scores for the environmental variables for axes 1 and 2 were plotted together with the sample scores (Fig 3). The distribution of samples along the horizontal axis appeared to be strongly related to peat depth. The peat depth biplot score had an axis 1 score of -277 and an axis 2 score that was close to zero, suggesting that samples with low axis 1 scores occurred on thick peat deposits, while those with high axis 1 scores occurred on plots with low peat thickness. This relationship is clearly evident when the measured values for peat depth for each sample are superimposed on the axis 1 and 2 sample scores (Fig 4). Samples with no peat accumulation had high axis 1 scores and those with the greatest peat depths had low axis 1 scores. The other measured environmental variables (namely, % carbon, depth to water table, height above thalweg, distance from thalweg, % silt, % sand and surface water/groundwater

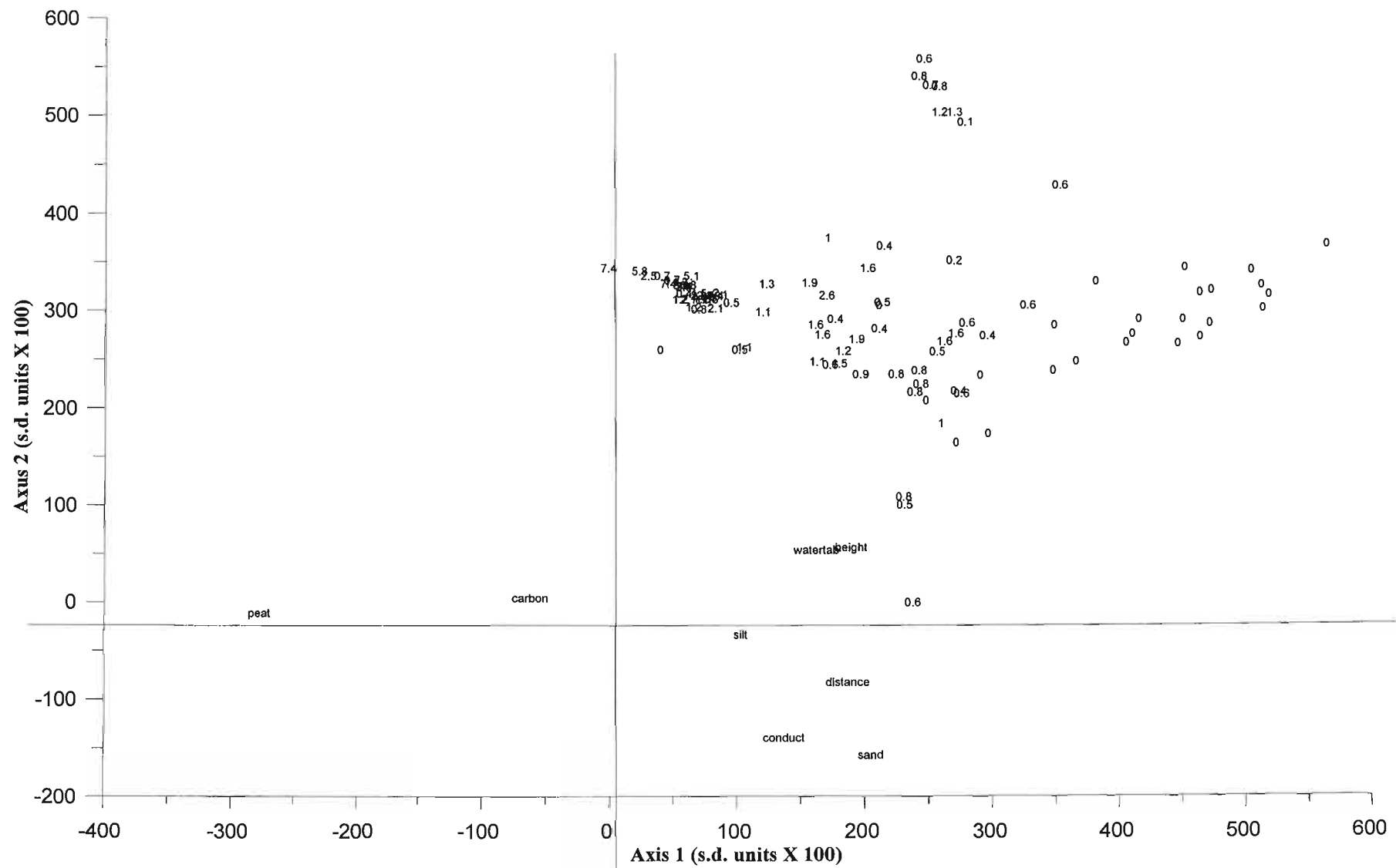


Figure 4. DCA ordination of samples along axes 1 and 2 with each sample displaying peat thickness

conductivity) had low axis 1 and 2 scores, and therefore do not appear to be related to variation in species composition along either axis.

The environmental factors contributing to the distribution of samples along the second axis is not clear from the present analysis, suggesting that the selection of measured environmental variables was inadequate for the separation of samples along axis 2.

5.4 Topographic and cross-sectional profiles: local scale environmental variation

Topographic cross-sectional profiles of each transect (Fig. 5) are presented in Figures 6-14. The cross-sectional profiles show the location of each sample plot in relation to the environmental variables peat thickness, depth to the water table and relative elevation. The corresponding TWINSpan community classification is superimposed on each plot. In addition, these data provide a basis for an analysis of regional trends and for mapping of various features in the study area.

Transect 1: Northwest Drainage Line

The northernmost transect was placed across a drainage line leading into the Mbazwane Stream from the north. The east bank of the drainage line was steeper and at a slightly lower elevation than the more gradually sloping west bank (Fig. 6). The area between the two banks was approximately 60 meters wide and relatively flat. At the time of sampling, this area was saturated with water to the surface and a small channel fringed with trees was located roughly in the middle of the main peat filled depression. Peat occurred from the base of the east bank through to the crest of the west bank, with the greatest accumulation (2.6 m) found east of the channel. The east bank was dry at the surface, and the substratum was composed of fine sand. In contrast, the west bank comprised shallow peat deposits that were saturated and water was flowing over the peat towards the central peat filled depression. Just below the crest of the west bank (Fig 6), a small pool of standing water was observed where the water table intersected the surface. These features suggested an extremely high water table on the western side of the wetland.

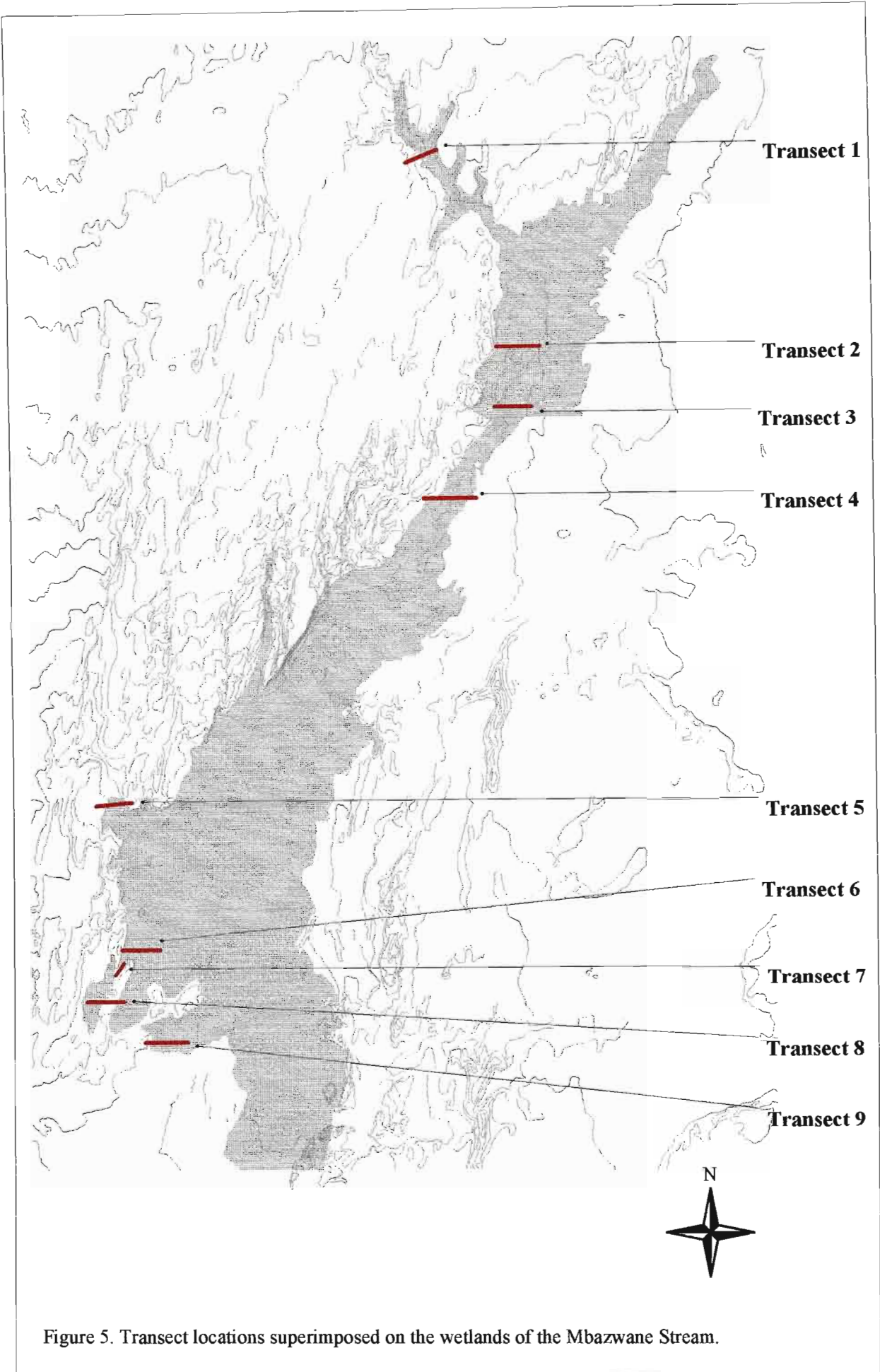


Figure 5. Transect locations superimposed on the wetlands of the Mbazwane Stream.

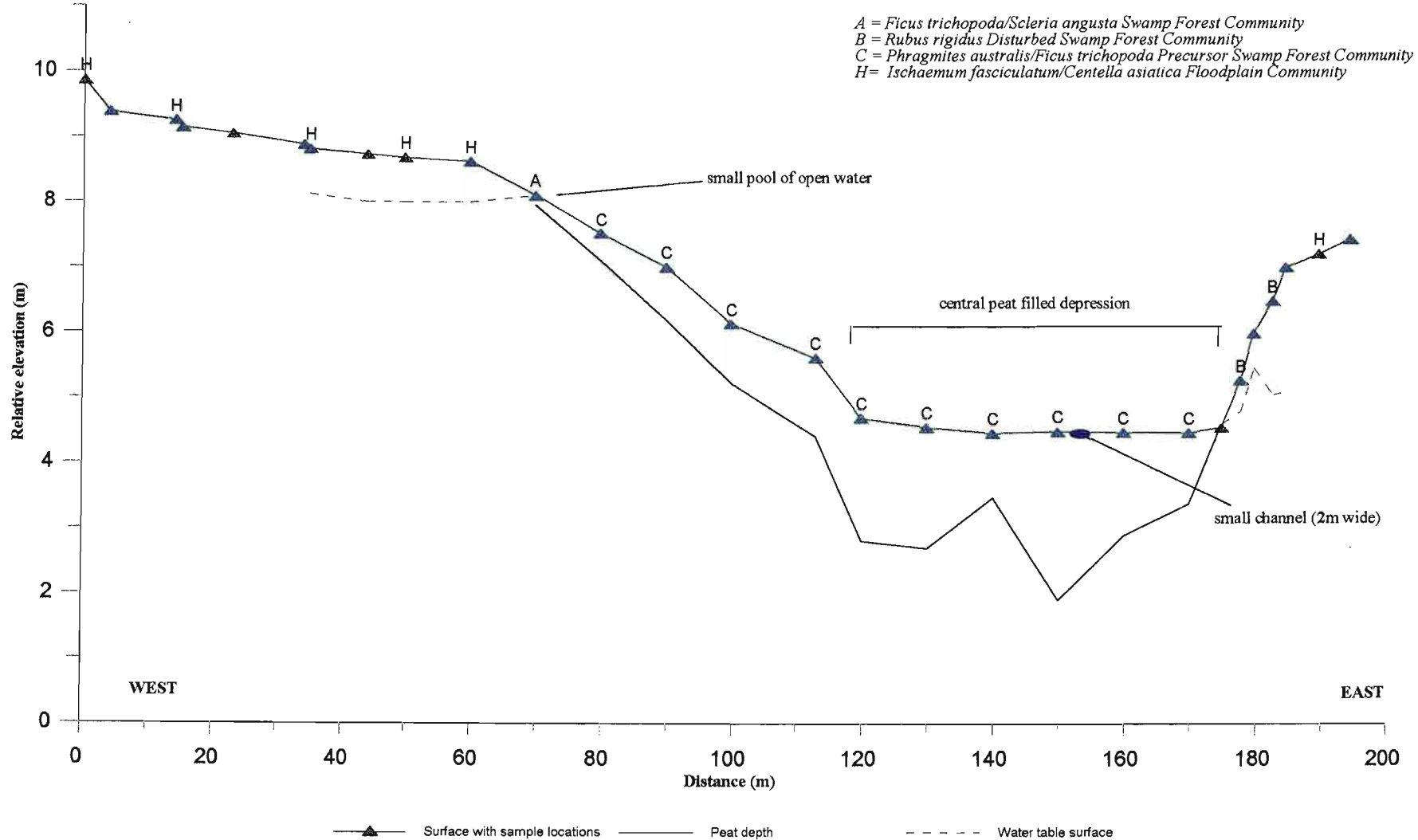


Figure 6. Topographic cross-section of transect 1 in the northern drainage line, with sample points, community distribution, ground water depth and peat thickness.

The water table surface slopes towards the drainage line on both banks, suggesting continual discharge of groundwater into the wetland. This wetland must thus receive much of its water supply from groundwater. Samples on top of both banks were in the *Ischaemum fasciculatum*/*Centella asiatica* Floodplain Community, while the samples along the eastern bank slope were classified as *Rubus rigidus* Disturbed Swamp Forest Community. Samples found at the base of the east bank through to just below the crest of the west bank are part of the *Phragmites australis*/*Ficus trichopoda* Precursor Swamp Forest Community. A single sample of the *Ficus trichopoda*/*Scleria angusta* Swamp Forest Community was found near the crest of the west bank at the point where standing water was observed.

Transect 2: Northern Mbazwane Stream Floodplain

This transect was located across the main axis of the Mbazwane Stream and its swamps in the northern region of its drainage area. Topographically there was little variation in elevation along the transect with local relief varying by less than 0.8m (Fig 7). The eastern edge of the transect was located along a low bank flanking a narrow channel-like depression. Moving westwards from the eastern bank of this depression, surface elevation did not change appreciably until the western edge of the transect, where there was a steep bank. The water table surface was found to be between 0.1 m and 0.5 m below the surface for the first 150 m of the transect, after which it was at or above the surface. The water table level was undetectable at the western edge of the transect due to the auger hole repeatedly collapsing before the water table was reached. However it appears that the water table surface had a very gentle east to west slope along the length of the transect. Peat was found along most of the length of the transect, with the greatest accumulation being on the western edge of the transect where depth to the substratum beneath the peat was approximately 1.5 meters. Samples along this transect were the *Rubus rigidus* Disturbed Swamp Forest Community on slightly elevated sites and the *Phragmites australis*/*Ficus trichopoda* Precursor Swamp Forest Community on sites of slightly lower elevation.

Transect 3: East of the Mbazwane Stream (northern region)

This transect was located on the eastern floodplain of the Mbazwane Stream, just south of Mbazwane Crossing. The survey line started at the water's edge on the east

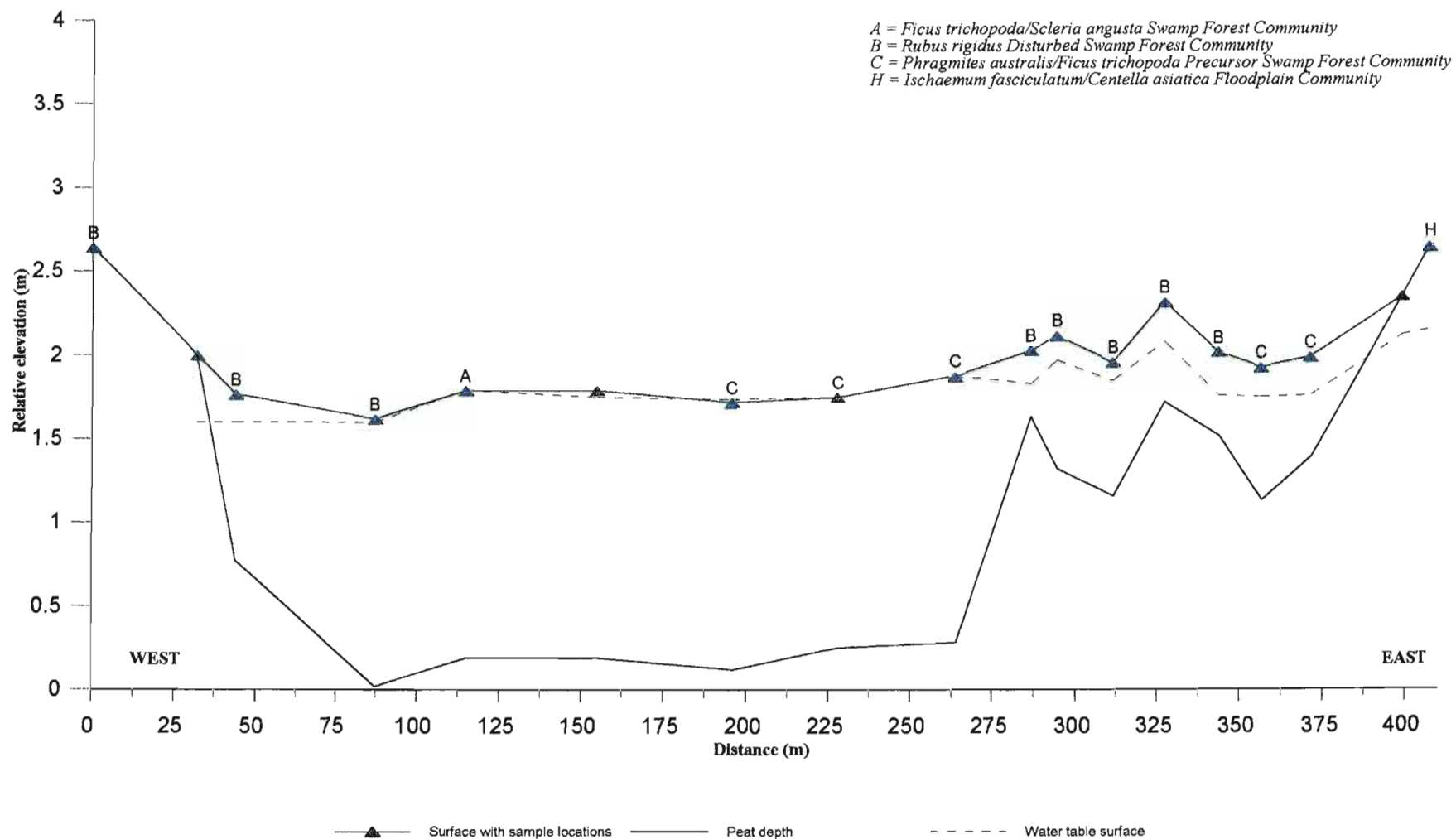


Figure 7. Topographic cross-section of transect 2 in the northern Mbazwane Stream floodplain, with sample points, community distribution, ground water depth and peat thickness.

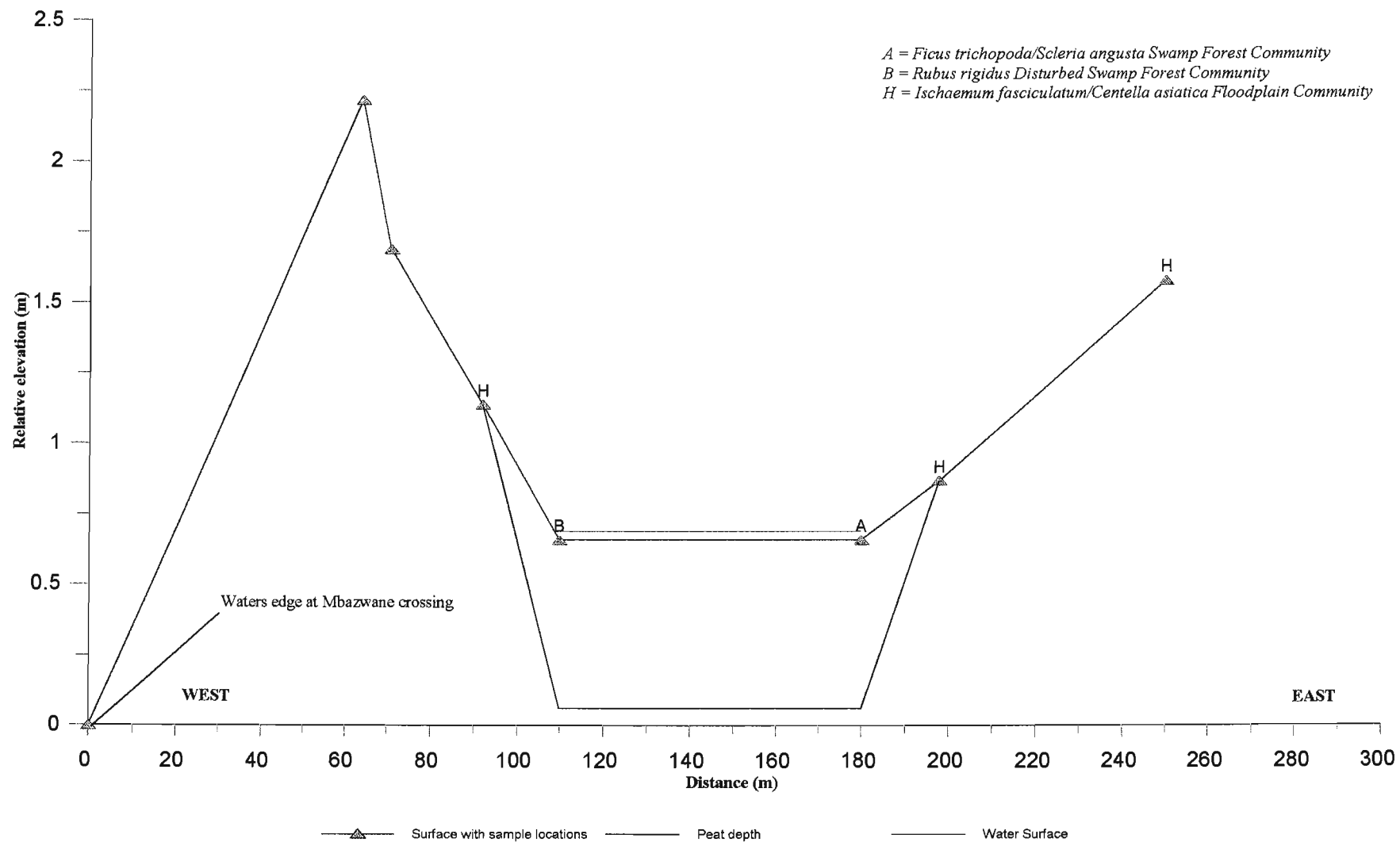


Figure 8. Topographic cross-section of transect 3, east of the Mbazwane Stream (northern region), with sample points, community distribution and peat thickness.

side of the Mbazwane Stream, and extended for approximately 250 m to the east (Fig. 8). The east bank of the river consists primarily of sandy soils with little ground cover and coastal forest tree species. Vegetation sampling started at approximately 95 m from the water edge of the Mbazwane Stream. A slight depression was found in the floodplain running roughly parallel to the Mbazwane Stream. It contained surface water at a higher elevation than the water surface in the Mbazwane Stream itself, suggesting that the Mbazwane Stream receives groundwater from the surrounding landscape. This is supported by the gradual seepage of water into the river from groundwater on both the east and west banks of this crossing. Vegetation along the sampled area consisted mostly of short grasses and herbs. Sample plots on the banks of this depression were classified as part of the *Ischaemum fasciculatum*/*Centella asiatica* Floodplain Community, while samples in the middle were grouped as part of the *Rubus rigidus* Disturbed Swamp Forest and *Ficus trichopoda*/*Scleria angusta* Swamp Forest communities.

Transect 4: Samango Crossing

This transect was located along the Mbazwane Stream at Samango Crossing. In this area the Mbazwane Stream was not confined to a single channel, but rather it flowed as a series of unconnected channels within a broad depression (Fig. 9). The elevated areas between the channels were topographically flat and consisted of forested areas on peaty soils saturated with water, but that were slightly elevated above the water table. The water table surface sloped down towards the river from the east and west banks and was at a relatively constant elevation across the depression. The greatest depths to the substratum were measured in the two outer channels (1.5m and 1.6 m on the west and east sides respectively). The entire transect was within a forested area and all samples were classified as *Ficus trichopoda*/*Scleria angusta* Swamp Forest Community.

Transect 5: Northern line in the permanent swamps

This transect was located where a shallow north-south drainage line joins the permanent swamps from the north (Fig 5). The transect extended from the western boundary of the swamps, across an area of emergent vegetation to a small peninsula which extended southwards into the permanent swamps (Fig 10). The gently sloping

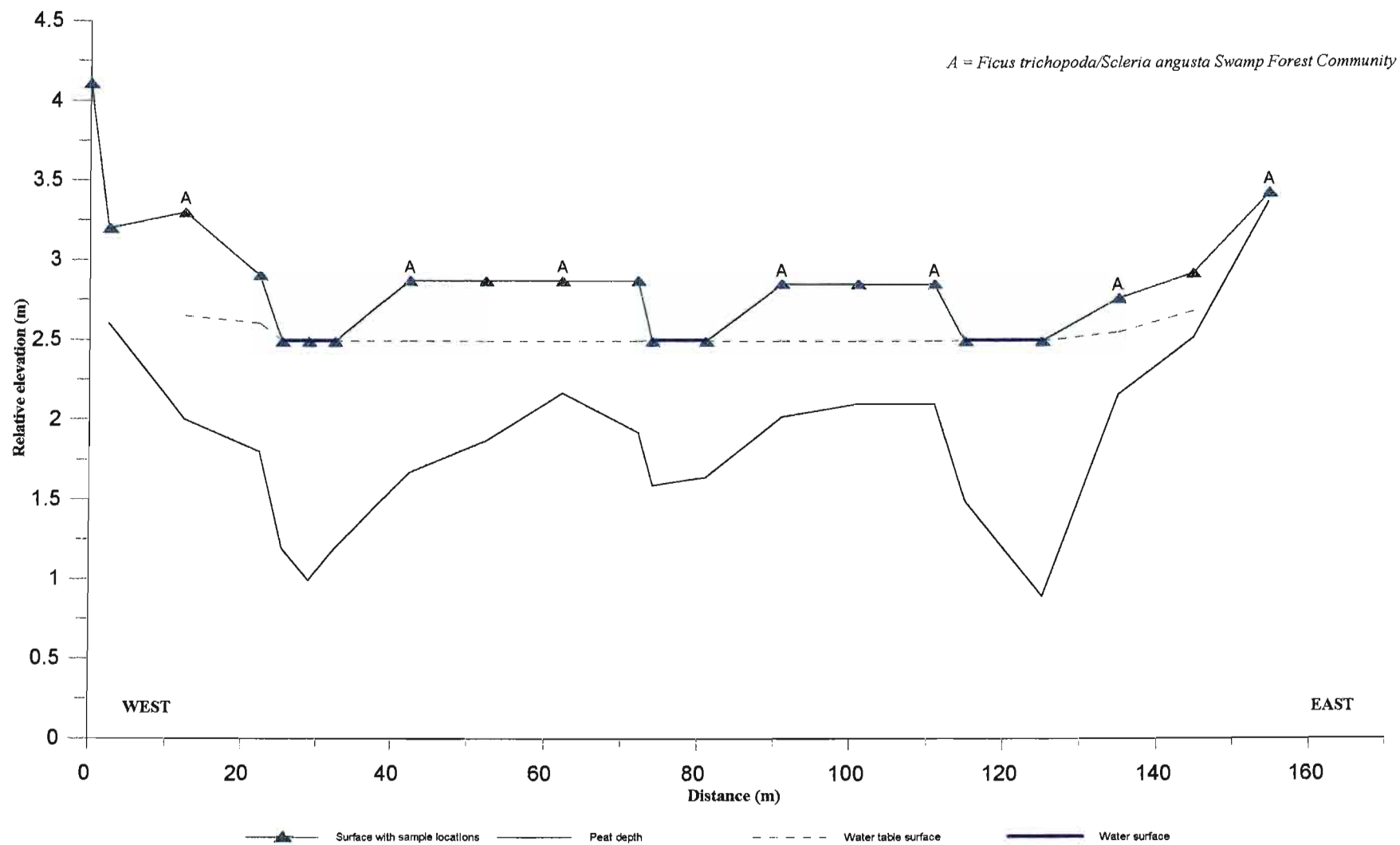


Figure 9. Topographic cross-section of transect 4 at Samango Crossing, with sample points, community distribution, ground water depth, and peat thickness.

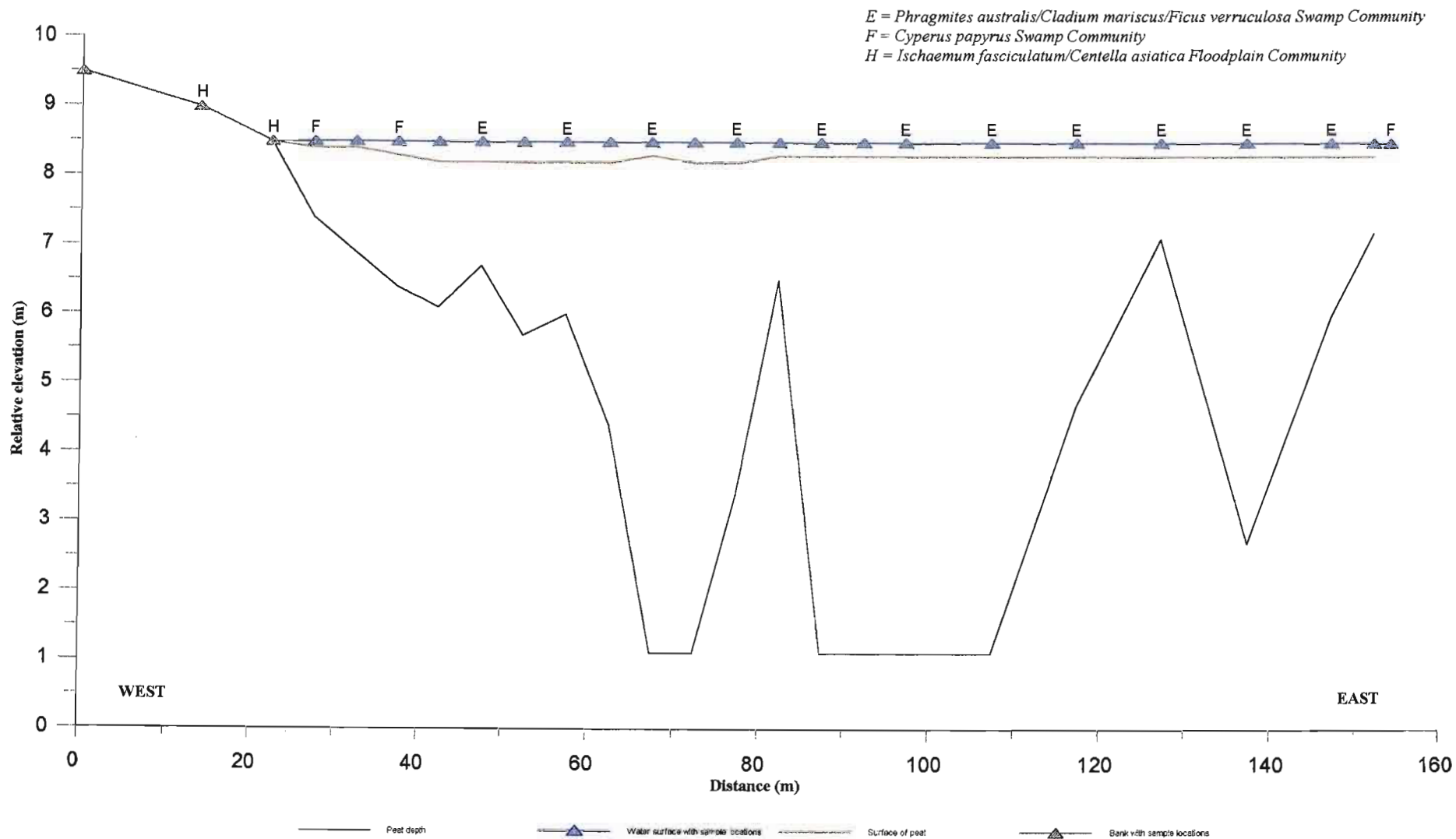


Figure 10. Topographic cross-section of transect 5 at the northern line in the permanent swamps, with sample points, community distribution and peat thickness.

west bank was covered with hygrophilous grassland, and was classified as part of the *Ischaemum fasciculatum*/*Centella asiatica* Floodplain Community. The east bank was not sampled. The area between the two banks had shallow water at the surface (between 0.1 m and 0.2 m in depth) and vegetation was rooted in peat. Depths to the substratum along this transect were the greatest recorded in the study, with depths greater than 7 m occurring at several places. This suggests the presence of a deeply incised valley at some time in the history of this wetland that has subsequently become filled with peat. Two emergent communities were found in the permanently flooded areas of this transect. The samples nearest the banks were classified as the *Cyperus papyrus* Swamp Community and in the main swamp were classified as the *Phragmites australis*/*Cladium mariscus*/*Ficus verruculosa* Swamp Community.

Transect 6: North of Butterfly Pan

This transect was located north of Butterfly Pan, north of where a small peninsula extended northwards into the swamps. The western edge of the transect was at the western boundary of the swamps, and all samples occurred in water of depths between 0.1 m and 0.2 m (Fig. 11). The cross-sectional profile of the peat illustrates that peat depth increased gradually eastwards for a distance of approximately 85 m, after which it decreased as the northward sloping peninsula extended out beneath the peat deposits. Beyond a distance of 170 m peat thickness once again increased as the transect extended into open swamp. Average peat depth was 1.5 m. Vegetation from the swamp edge to approximately 200 m was classified as part of the *Typha capensis*/*Pycreus mundii*/*Leersia hexandra* Marsh Community. The samples at the eastern end of the transect were dominated by *Cyperus papyrus*, being classified as the *Cyperus papyrus* Swamp Community. The dominance of *Cyperus papyrus* was observed to continue eastwards out into the open swamp.

Transect 7: Southwest Drainage Line

This transect was located approximately 500 m south of transect 6, along a drainage line running from south-west to north-east, entering the permanently flooded swamp at the north-eastern limit of the transect. Only 5 stands were sampled over a distance of approximately 120m (Fig. 12). Topographically the drainage line slopes towards the north-east, although the slope was not uniform. The thalweg occupies a shallow

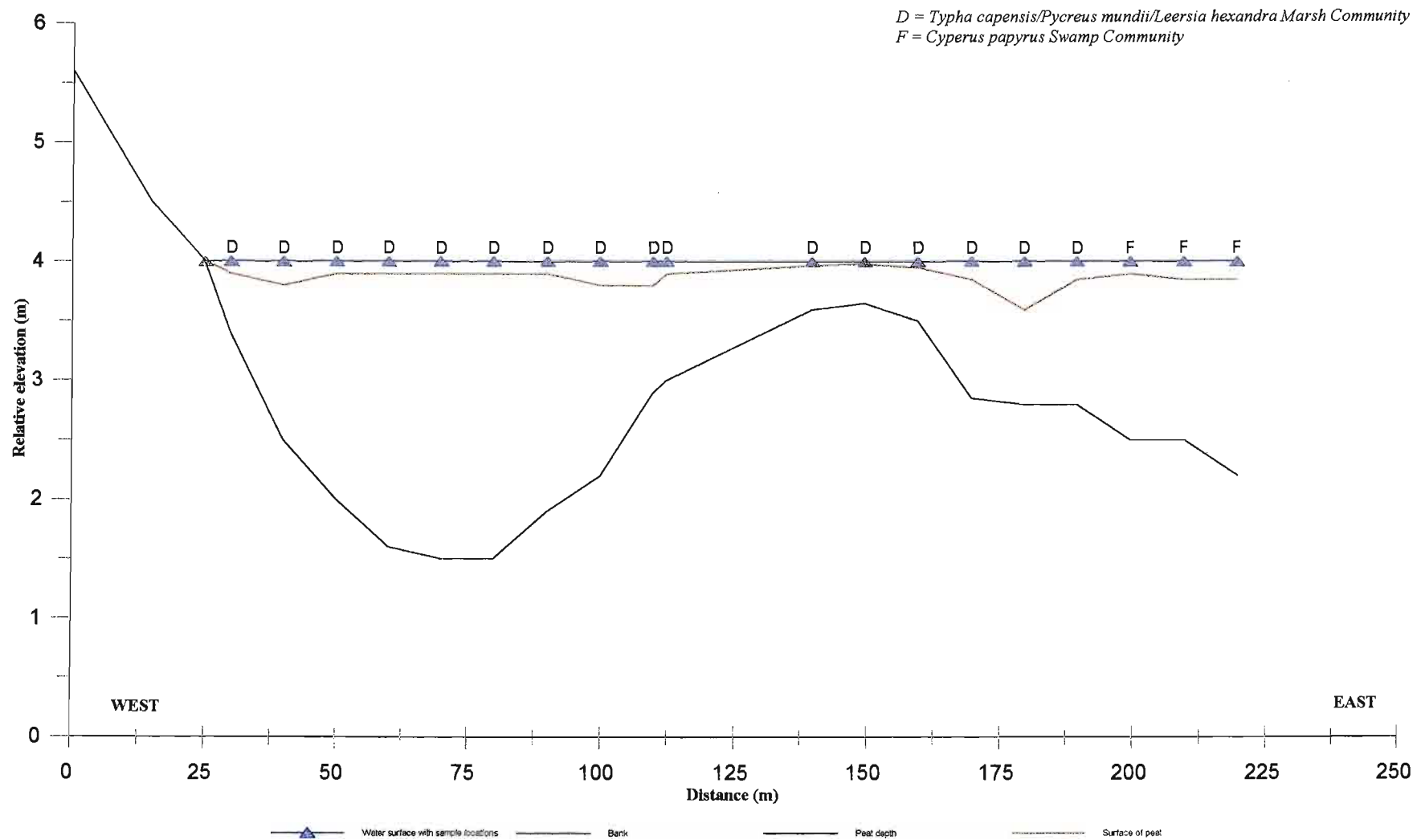


Figure 11. Topographic cross-section of transect 6 north of Butterfly Pan, with sample points, community distribution and peat thickness.

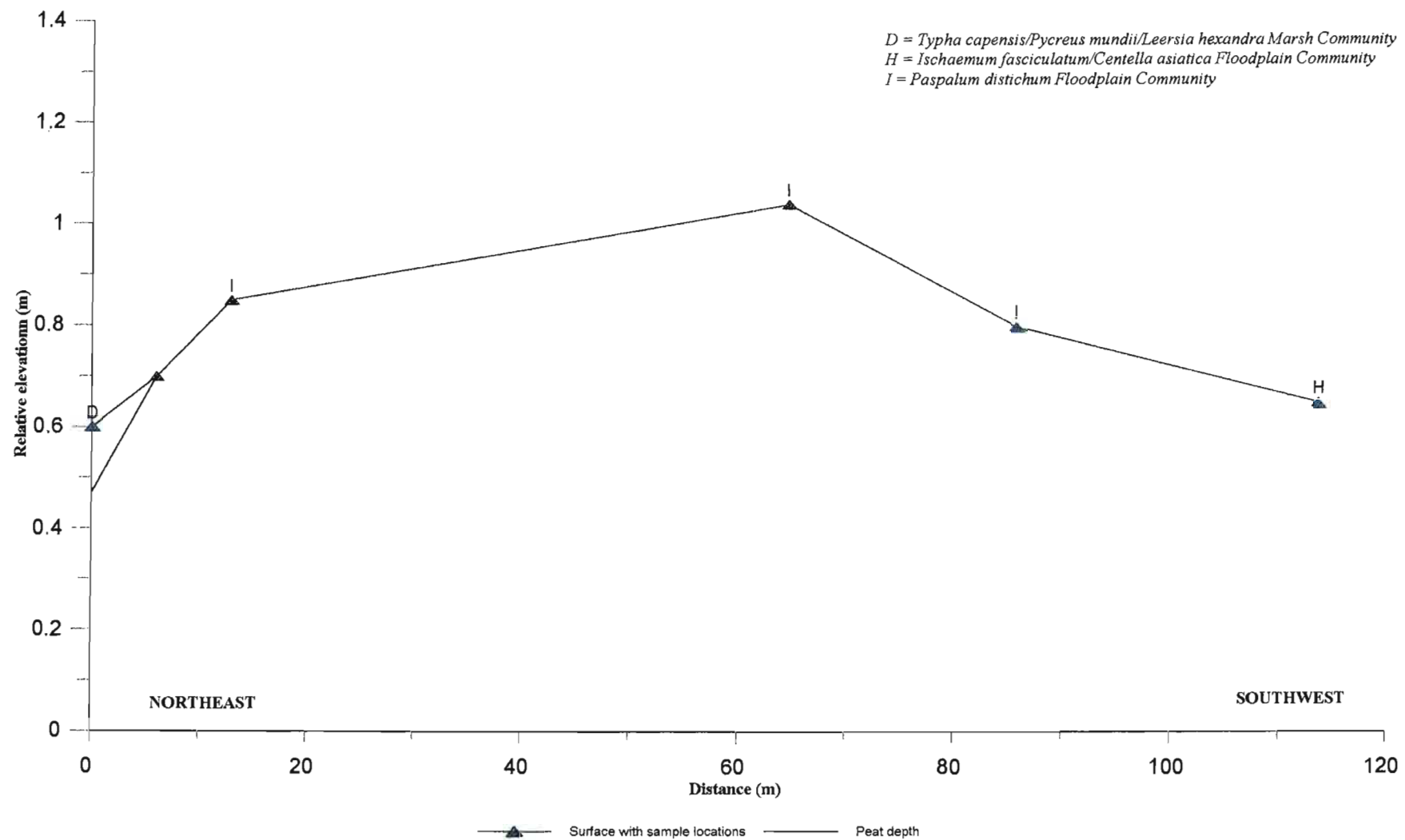


Figure 12. Topographic cross-section of transect 7 in the southwest drainage line, with sample points, community distribution and peat thickness.

depression at its southernmost end, rising gradually some 0.3m over a distance of 50 m, and then sloping more or less uniformly into the permanent swamp. The northernmost sample was dominated by emergent vegetation and was grouped with the *Typha capensis*/*Pycreus mundii*/*Leersia hexandra* Marsh Community. The remaining five samples were dominated by grasses and thus were grouped in the two seasonally flooded grassland communities. Samples closest to the swamps were part of the *Paspalum distichum* Floodplain Community, with the sample furthest away being grouped with the *Ischaemum fasciculatum*/*Centella asiatica* Floodplain Community. Peat accumulation was only observed along this transect at the edge of the swamp, extending to a depth of 0.5 m.

Transect 8: West of Butterfly Pan

Transect 8 was located in a north-south orientated drainage line west of Butterfly Pan, with the easternmost samples occurring in the fringe of vegetation on the western shore of Butterfly Pan (Fig. 13). Samples at the north-south orientated depression at the western end of the transect were separated from the main swamps by a ridge of high lying ground. The western depression contained a mono-specific stand of *Echinochloa pyramidalis*. Samples occurring along the ridge up to the swamp edge were dominated by grasses, and were a mixture of the floodplain grassland communities. The samples at the edge of the main swamp were dominated by *Echinochloa pyramidalis*, while those further in the main swamp were part of the *Cyperus papyrus* Swamp Community. Peat accumulation increased moving eastward from the edge of the main swamp. Measurements of the water table surface on either side of the ridge suggested that the water table surface sloped towards the swamp.

Transect 9: East off the fan

The southernmost transect extended in an eastward direction into the permanent swamps, from the tip of the delta/alluvial fan formed by the Mkuze River (Fig. 14). There was little variation in vegetation composition between samples, with *Cyperus papyrus* being the dominant vegetation in all samples. All samples occurred in shallow water and peat thicknesses were greater than 0.5 m. During measurement of peat accumulation, the presence of organic-rich clay deposits in the substratum made accurate measurements of depth to the substratum difficult. This was the first transect

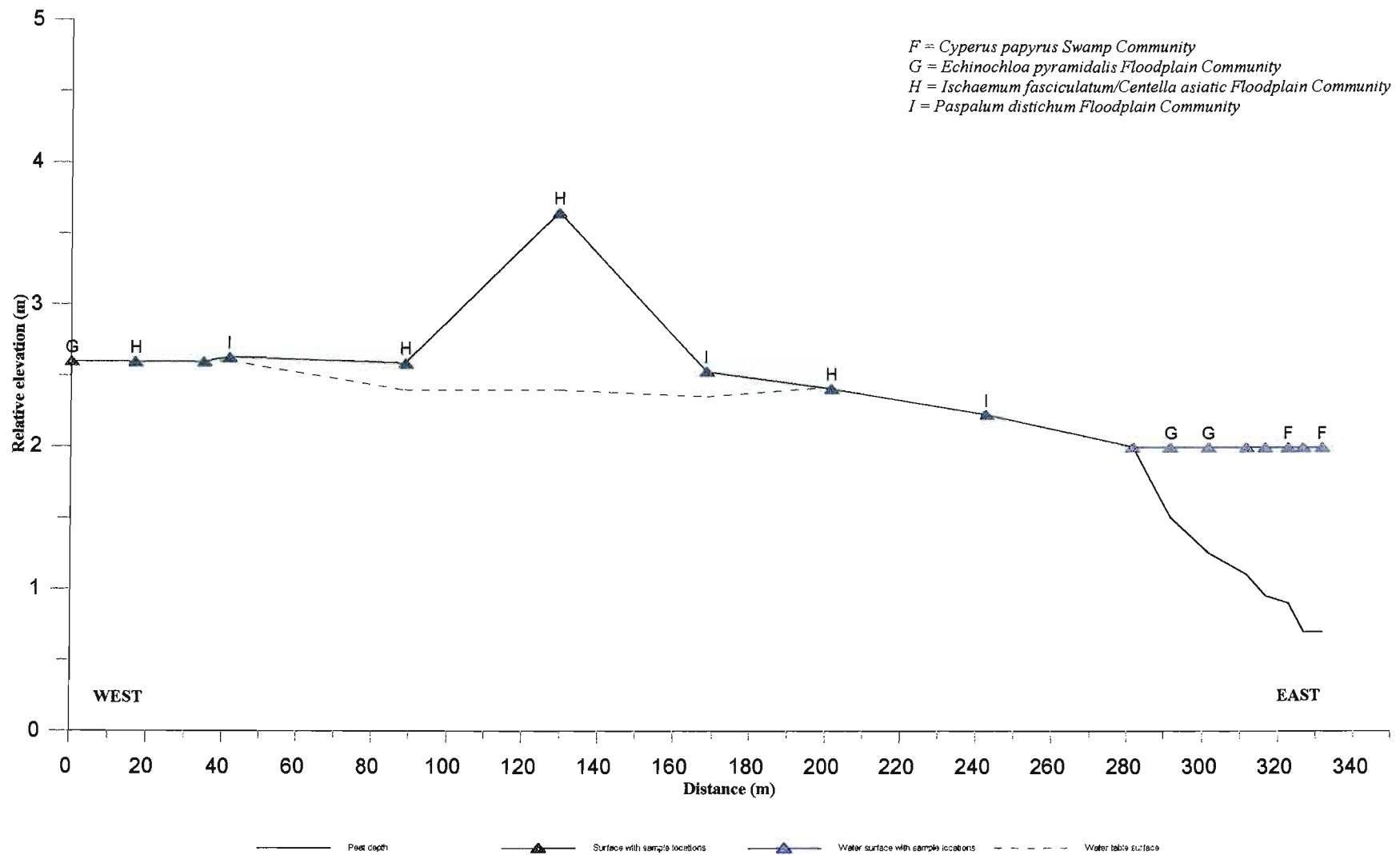


Figure 13. Topographic cross-section of transect 8 west of Butterfly Pan, with sample points, community distribution, ground water depth and peat thickness.

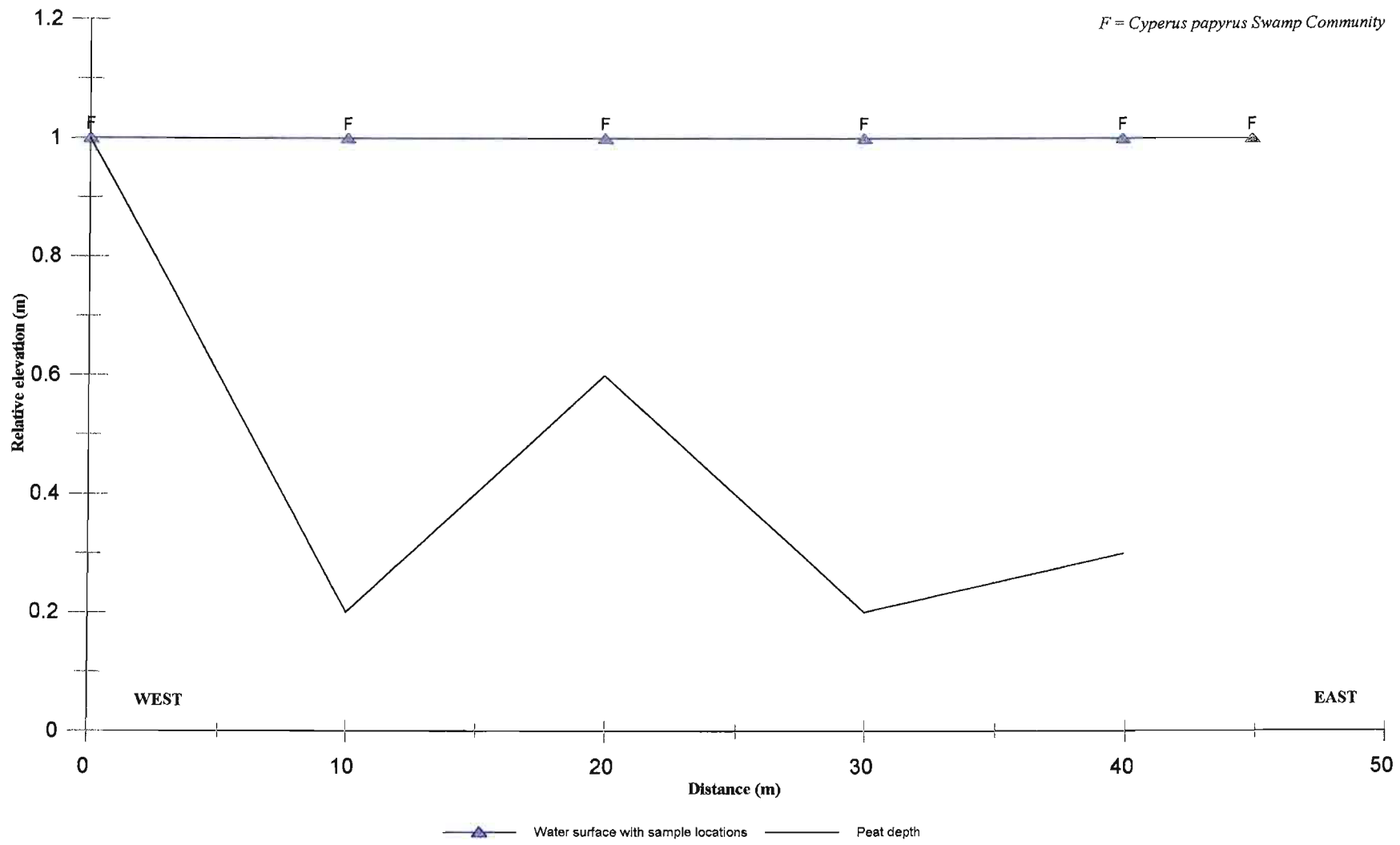


Figure 14. Topographic cross-section of transect 9 east off the Mkuze Delta, with sample points, community distribution and peat thickness.

in which clay was encountered, clearly reflecting the influence of the Mkuze River which must deposit fine sediment (silt and clay) into the Mbazwane drainage line during high floods.

5.5 Regional scale environmental gradients

Regional Topography

The topography of the basin as a whole is shown in Figure 15. The northern drainage area has an elevation between 19 m and 32 m above sea level, and the slope on the land surface is relatively steep. In the middle region of the drainage area the elevation ranges between 12 m and 32 m, and once again relief is very steep, particularly immediately to the west of the drainage line itself. In contrast, the southern region of the basin has an elevation range between 5 m and 15m, and the relief is relatively flat.

In addition to this longitudinal gradient it is also evident that areas to the west of the study area lie at elevations that range between 20 m and 55 m, with areas in the north-west at the highest elevation. Often the slope from the high-lying land to the west into the wetland is considerably steeper than from the east. The areas to the east are more gently undulating with elevations generally between 20 m and 35 m.

The northern part of the drainage line is relatively narrow with steep sided banks that are approximately of similar elevation, or with the western bank at higher elevation than the eastern bank (Fig. 16a and 16b). Along the middle section of the northern drainage area the Mbazwane flows as a series of braided channels surrounded by swamp forest. The drainage area is broader, with the western bank considerably steeper and at higher elevation than the eastern bank (Figs. 16c and 16d). This is particularly noticeable at locations such as Samango Crossing where the road descends steeply down a dune face into the drainage line from the west, while the road to the east has a gentle gradient. The southern part of the drainage area occupies a broad basin with relatively shallow banks (Fig. 16e and 16f).

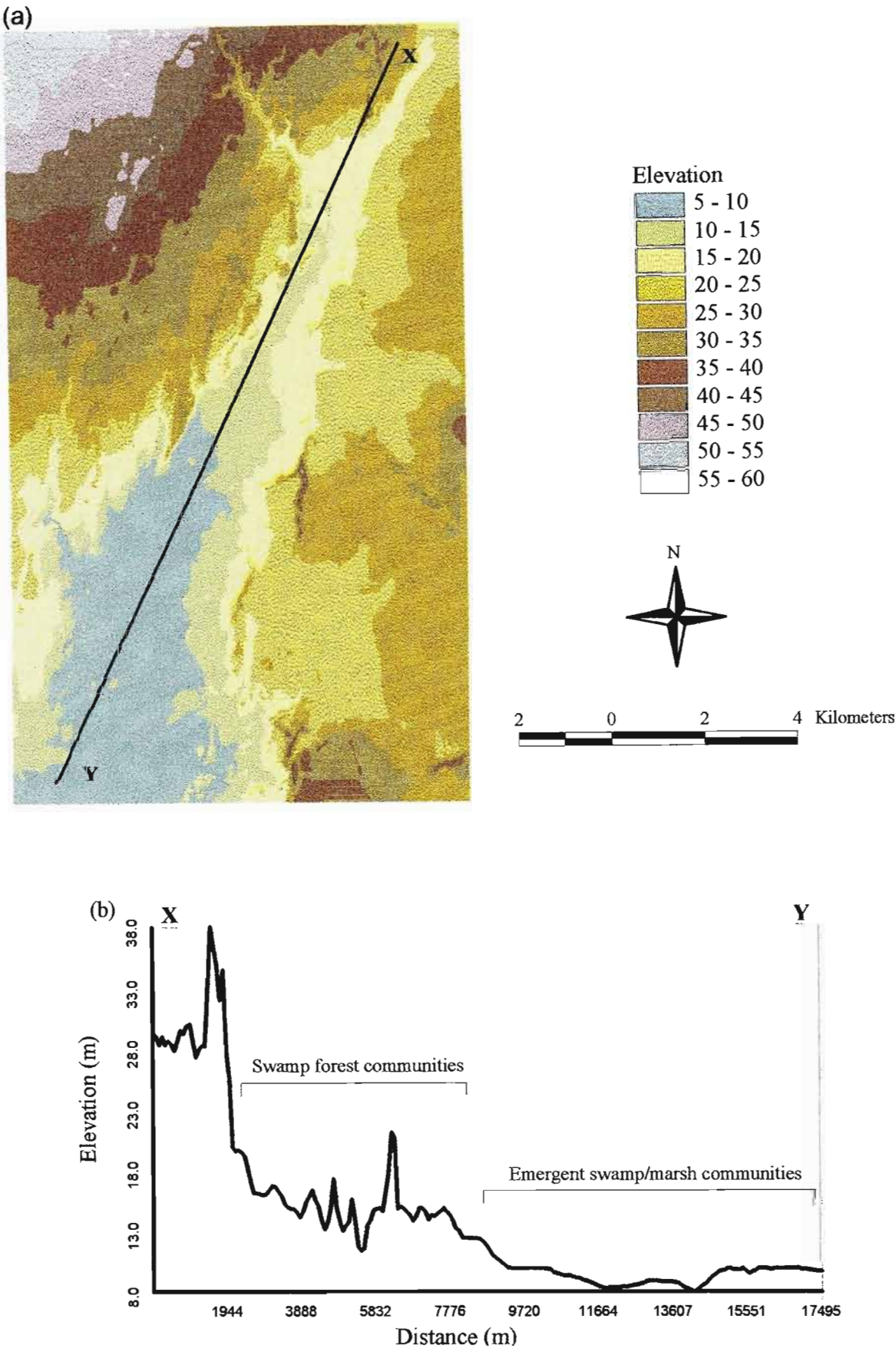


Figure 15. Topographic map (a) and longitudinal profile (b) of the Mbzawane Drainage line and a portion of its catchment.

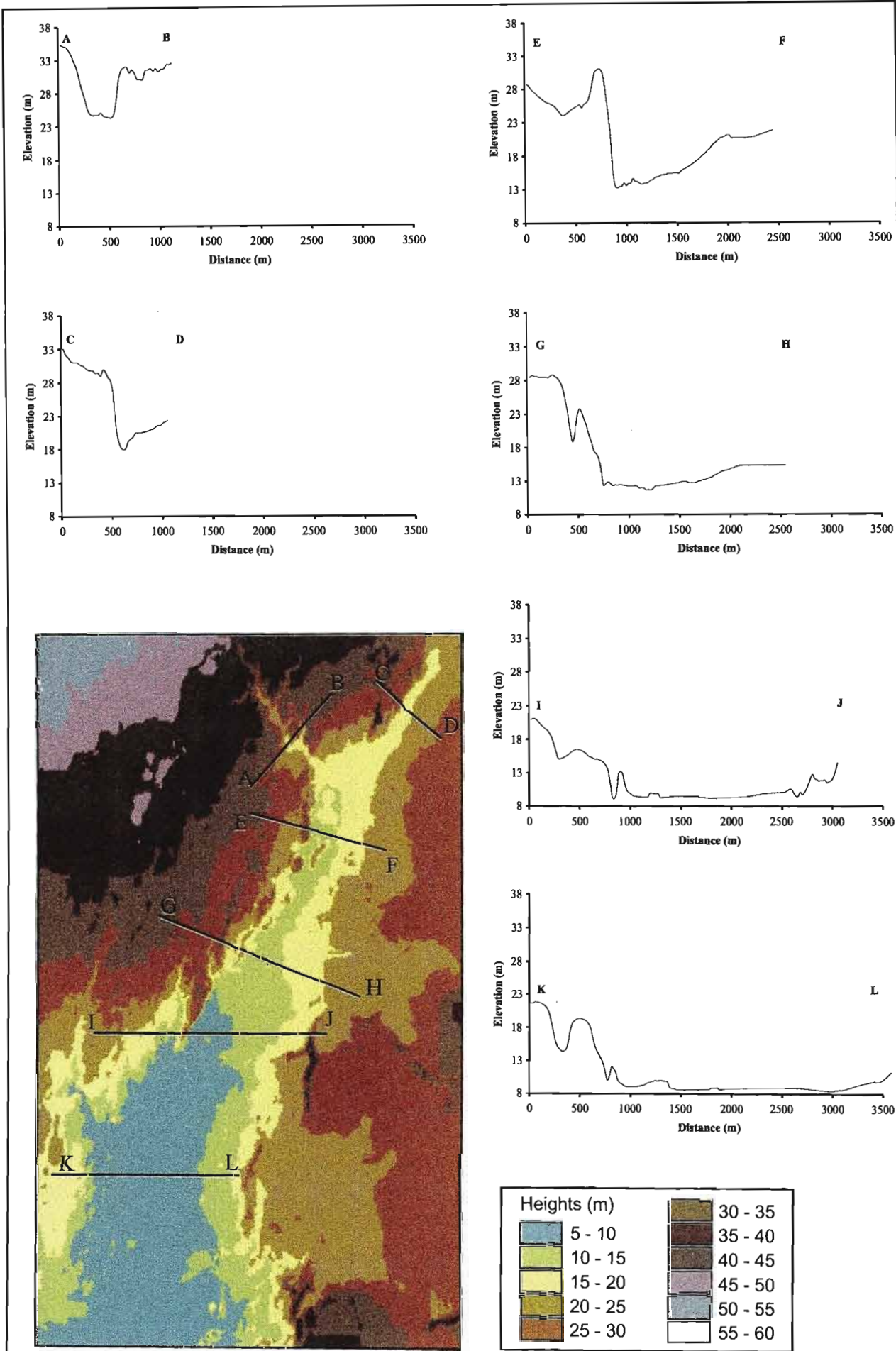
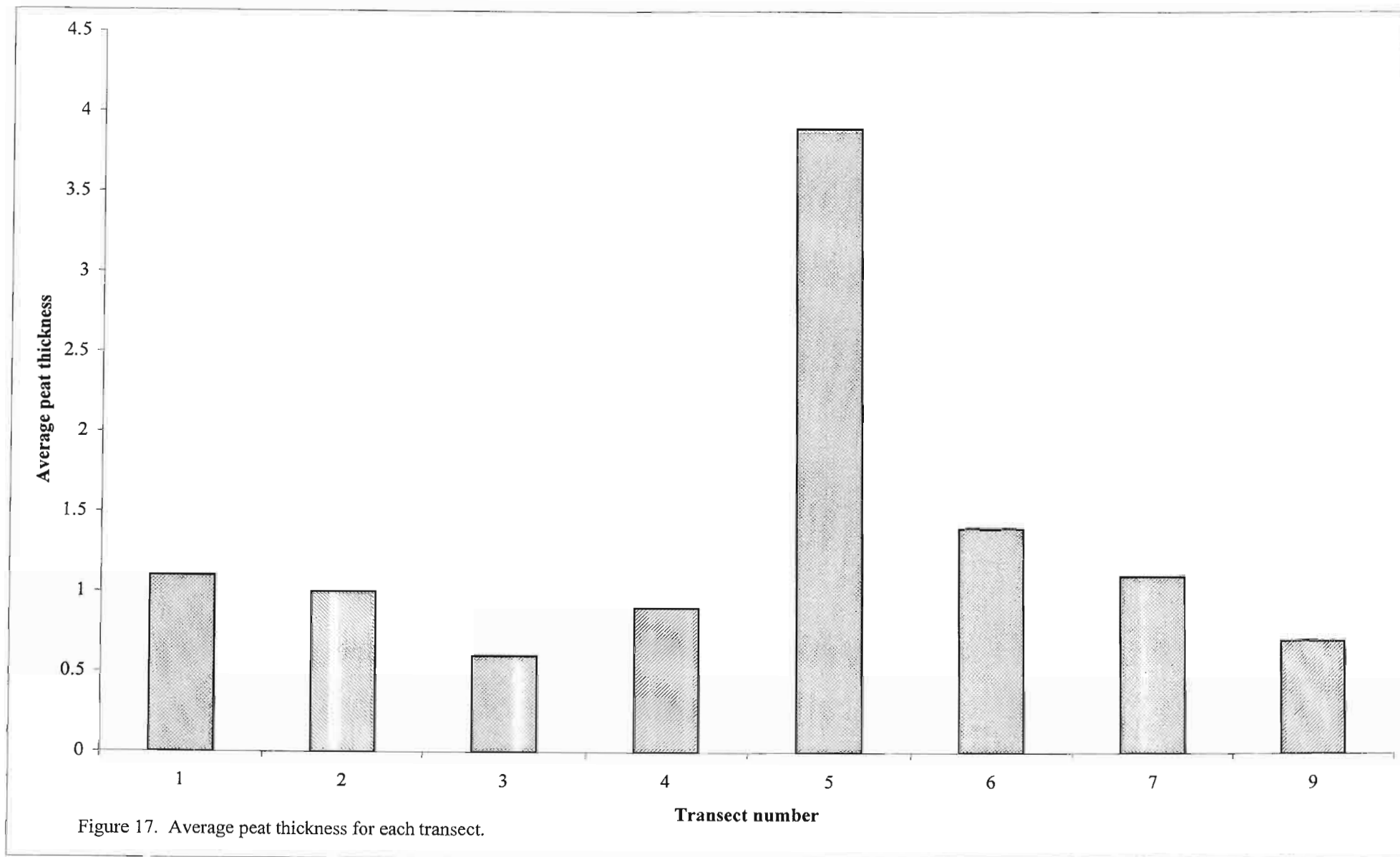


Figure 16: Cross-sectional profiles at different locations along the Mbazwane Stream.



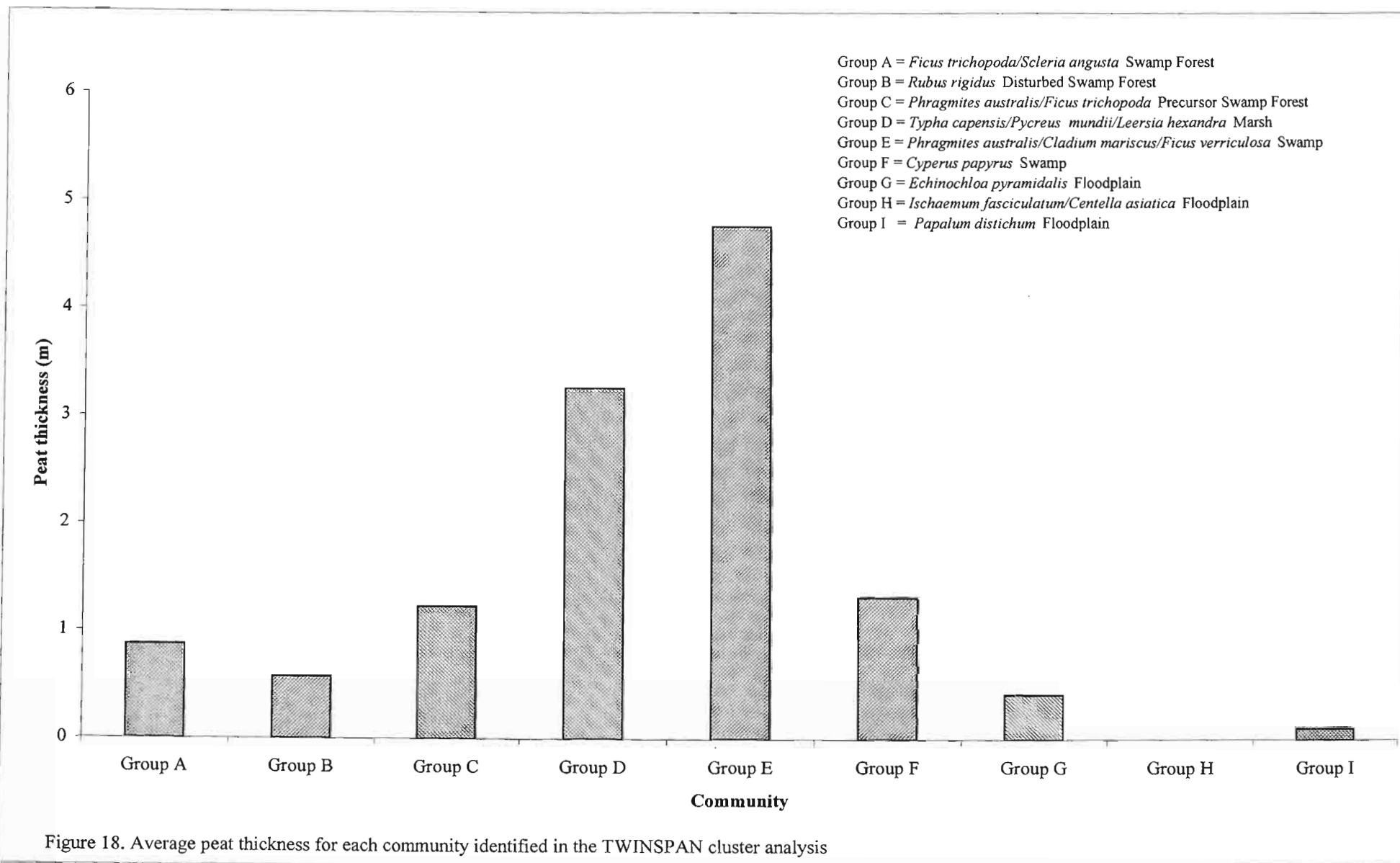
Peat Depth

Average peat accumulations for each transect are shown in Figure 17. Overall peat accumulation was generally greater in the main section of the swamp than in the areas sampled in the northern drainage area. Peat thicknesses in the northern drainage areas were typically in the region of 0.6 m to 1.0 m, with little variation. Average peat thickness in transect 5, which was located in the middle region of the study area, was substantial at nearly 4 m. Accumulations declined southwards in the study area, being 1.4 m, 1.2 m and 0.7 m in transects 6, 7 and 9 respectively. It is presumed that the pre-existing valley deepens southwards and therefore it would be expected that peat deposits would increase. However, the input of sediment from the Mkuze River would decrease peat thickness in the southern part of the study area.

The average peat thickness for each community was calculated as shown in Figure 18. The greatest accumulations were found in the *Phragmites australis/Cladium mariscus/Ficus verruculosa* Swamp Community (Group E) and the *Typha capensis/Pycnus mundii/Leersia hexandra* Marsh Community (Group D) with average thicknesses of 4.77 m and 3.27 m respectively. The average peat accumulations of these two communities were substantially greater than the remaining communities. The rankings of the remaining communities were as follows: *Cyperus papyrus* Swamp Community (1.32 m); *Phragmites australis/Ficus trichopoda* Precursor Swamp Forest (1.23m); *Ficus trichopoda/Scleria angusta* Swamp Forest (0.87m); *Rubus rigidus* Disturbed Swamp Forest (0.57 m); *Echinochloa pyramidalis* Floodplain Community (0.42); *Paspalum distichum* Floodplain Community (0.11m); and *Ischaemum fasciculatum/Centella asiatica* Floodplain Community (0 m).

5.6 Community and habitat descriptions

Using information obtained from the multivariate analyses, the cross-sectional profiles and broad scale environmental patterns in conjunction with aerial photography and field observations, a description of the communities and their distribution is provided in this section. For the purposes of mapping, some communities have either been grouped with another community, or have been excluded in the regional mapping of the communities where their distribution has



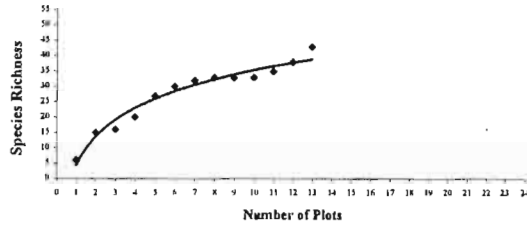
been of extremely limited extent. The two emergent communities indicated by *Phragmites australis*/*Cladium mariscus*/*Ficus verruculosa* and *Typha capensis*/*Pycneus mundii*/*Leersia hexandra*, were grouped together as the *Phragmites australis* Emergent Community, as their distribution could not be separated on aerial photographs. Furthermore, the *Rubus rigidus* Disturbed Swamp Forest Community was found to occur as extremely isolated local patches along the borders of other communities, and it was therefore not mapped.

***Ficus trichopoda*/Scleria angusta Swamp Forest**

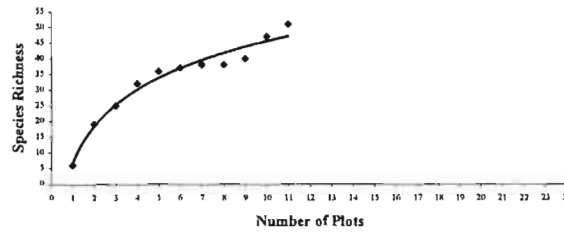
This community was dominated by trees and shrubs and had a poorly developed herbaceous layer. *Ficus trichopoda* dominated the canopy layer with cover values of 10% or greater in all the samples, with two samples having cover values of 50% or more. More than 50% of the samples in this community had *Syzygium cordatum* occurring in them, however cover values were low. *Rauvolfia caffra*, *Trichilia dregeana* and *Trichilia emetica* were common in this community, but absent from other communities. Their cover values were generally lower than 10%. The shrub layer was composed of swamp forest shrubs such as *Psycotria capensis*, *Kraussia floribunda* and *Keetia gueinzii* and coastal shrubs *Baphia racemosa* and *Burchellia bubalina*, each of which occurred in approximately 50% of the samples. The ground layer was dominated by *Scleria angusta*, which occurred in more than 80% of the samples, with cover values that ranged from less than 2% to greater than 50%. There were several other species found in this community, but in relatively few samples and with low cover values. These included common swamp forest species such as *Bridelia micrantha*, *Voacanga thouarsii*, *Cyperus alternifolius* and *Phoenix reclinata*. Species diversity in this community was relatively high with an average of 12.2 species per sample (Table 4). Species richness was also comparatively high with the total number of species sampled in this community being 43 (Fig. 19a).

This community was largely confined to the northern drainage area of the Mbazwane Stream, occurring in a narrow band on the eastern footslope of a north-east – south-west running ridge (Fig. 20) that appears to be an ancient coastal dune cordon. The western edge of this band of swamp forest was generally bordered by lowland coastal forest, while hygrophilous grasslands were found along the eastern edge. Sites where

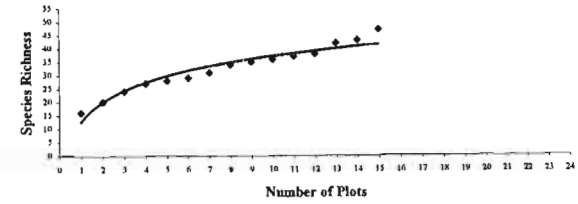
19 a. *Ficus trichopoda*/*Scleria angusta* Swamp Forest Community



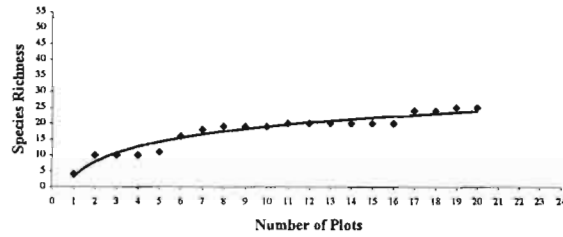
19 b. *Rubus rigidus* Disturbed Swamp Forest Community



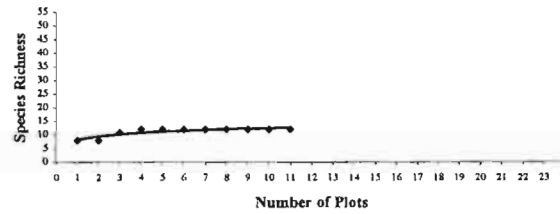
19 c. *Pragmites australis*/*Ficus trichopoda* Precursor Swamp Forest Community



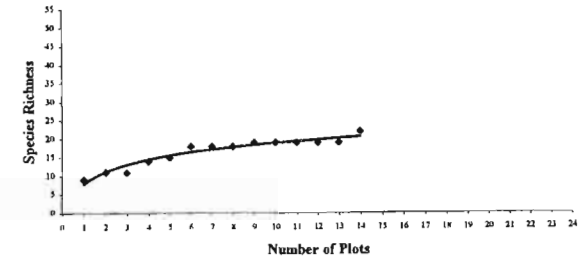
19 d. *Typha capensis*/*Pycreus mundii*/*Leersia hexandra* Marsh Community



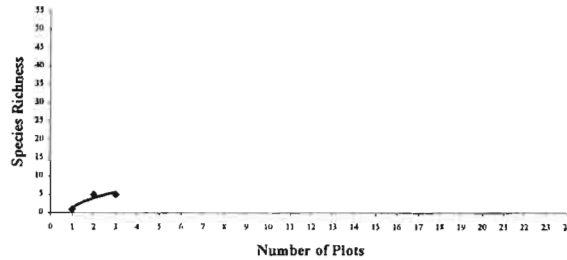
19 e. *Phragmites australis*/*Cladium mariscus*/*Ficus verruculosa* Swamp Community



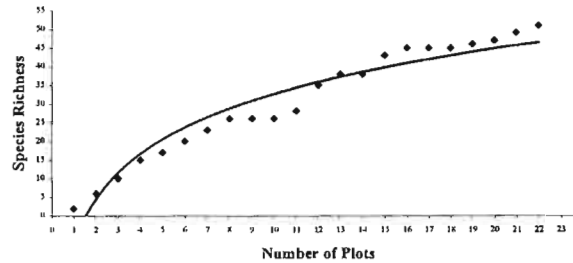
19 f. *Cyperus papyrus* Swamp Community



19 g. *Echinochloa pyramidalis* Floodplain Community



19 h. *Ischaemum fasciculatum*/*Centella asiatica* Floodplain Community



19 i. *Paspalum distichum* Floodplain Community

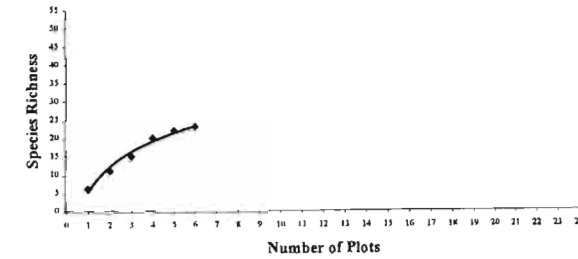


Figure 19. Cumulative species richness as a function of the number of plots sampled for each of the communities identified in the TWINSpan cluster analysis.

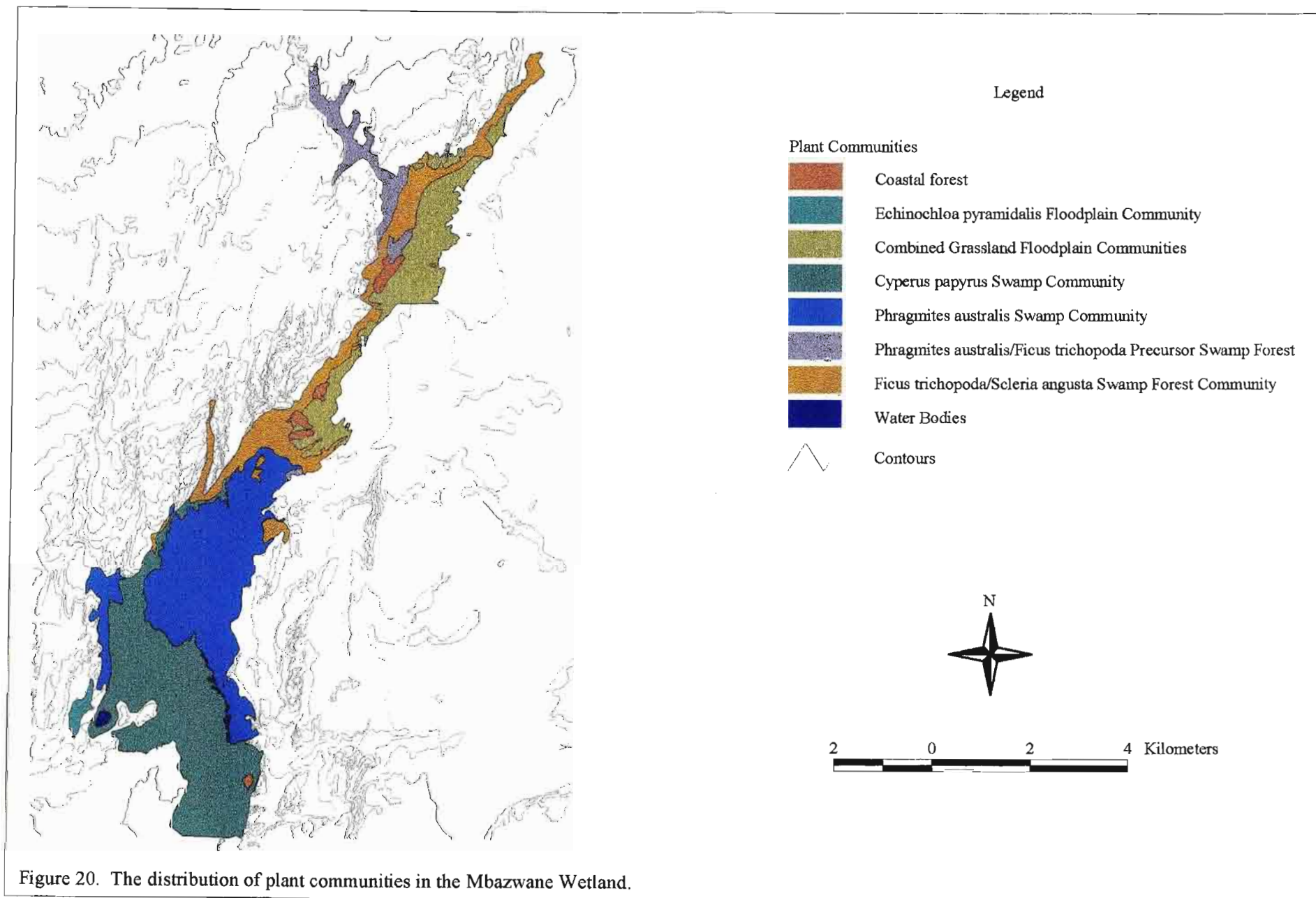


Figure 20. The distribution of plant communities in the Mbazwane Wetland.

this community was found had peaty soils that were saturated to the surface at the time of sampling. Peat accumulation ranged between 0.5 m and 1.6 m.

Table 4. Measures of species richness with each of the plant communities identified in this study.

Community	Mean species richness per plot	Standard deviation	Number of species per community
<i>Ficus trichopoda</i> / <i>Scleria angusta</i> Swamp Forest	12.2	3.6	43
<i>Rubus rigidus</i> Disturbed Swamp Forest	14.3	4.7	51
<i>Phragmites australis</i> / <i>Ficus trichopoda</i> Precursor Swamp Forest	13.1	2.4	47
<i>Typha capensis</i> / <i>Pycreus mundii</i> / <i>Leersia hexandra</i> Marsh	8.7	2.8	25
<i>Phragmites australis</i> / <i>Cladium mariscus</i> / <i>Ficus verruculosa</i> Swamp	8.6	1.4	12
<i>Cyperus papyrus</i> Swamp	6.7	2.1	22
<i>Echinochloa pyramidalis</i> Floodplain	3.7	2.3	5
<i>Ischaemum fasciculatum</i> / <i>Centella asiatica</i> Floodplain	7.7	2.7	51
<i>Paspalum distichum</i> Floodplain	8.0	1.3	23

***Rubus rigidus* Disturbed Swamp Forest**

The indicator species in this community was the shrub *Rubus rigidus* which occurred in 91% of the samples, but generally with low cover (<10%). This species, typical of disturbed areas, was largely limited to this community.

This community was characterised by a mixture of both swamp forest species and species which prefer better drained sites. Three swamp forest tree species *Bridelia micrantha*, *Syzygium cordatum* and *Voacanga thouarsii* occurred in 64% or more of the samples and had cover values ranging from 1% to 50%. *Bridelia micrantha* was the most dominant of these, with cover values that were typically between 10% and 25%. The ground layer had several species common in wet areas, including *Cyperus alternifolius*, *Cyperus prolifer*, *Phragmites australis* (low cover, <2%), *Thelypteris sp1.*, *Phoenix reclinata* and *Typha capensis*. The most frequently occurring of these was *Thelypteris sp1.*, which occurred in 91% of the samples with cover less than or equal to 10%. Species preferring better-drained areas included the shrub species *Jasminium multipartitum*, *Myrsine africana* and *Rhus nebulosa*, the grass species *Imperata cylindrica* and the herbaceous species *Senecio madagascariensis*. The 36 other species found in this community occurred in three or fewer samples and had low cover values.

Species diversity and species richness in this community were high with an average of 14.3 species per sample and a total of 51 species respectively (Table 4; Fig. 19b).

The *Rubus rigidus* Disturbed Swamp Forest Community occurred largely as isolated patches in the northern portion of the study area, or alternatively along the edges of the other forest communities (*Ficus trichopoda*/*Scleria angusta* Swamp Forest Community and the *Phragmites australis*/*Ficus trichopoda* Precursor Swamp Forest Community). Sites were generally moist at the surface and they typically had shallow peat accumulations.

***Phragmites australis*/*Ficus trichopoda* Precursor Swamp Forest Community**

This community showed overlap in its species composition both with the *Rubus rigidus* Disturbed Swamp Forest Community and the other swamp and marsh communities. Therefore, although not unique to this community, *Ficus trichopoda* and *Phragmites australis* separated this community with their higher cover values. *Ficus trichopoda* occurred in 67% of the samples and had cover values that were generally greater than 25%. *Phragmites australis* was found in all but 2 samples, with cover values of between 15 and 25%. Species common to the *Rubus rigidus* Disturbed Swamp Forest Community included *Bridelia micrantha*, *Voacanga thouarsii*, *Syzygium cordatum*, *Rubus rigidus*, *Senecio madagascariensis*, *Jasminium multipartitum*, and *Mikania africana*, while *Impomea aquatica*, *Dissotis canescens*, *Commelina africana* and *Erythrina* sp. occurred more frequently in this community than in the *Rubus rigidus* Disturbed Swamp Forest. Several other species occurring in this community occurred in the *Rubus rigidus* Disturbed Swamp Forest Community, the *Cyperus papyrus* and *Phragmites australis*/*Cladium mariscus*/*Ficus verruculosa* Swamp communities and the *Typha capensis*/*Pycneus mundii*/*Leersia hexandra* Marsh Community. However, the frequency and cover values of these species in this community were more similar to the swamp and marsh communities than the *Rubus rigidus* Disturbed Swamp Community. These included *Cyperus prolifer* and *Thelypteris* sp1. occurring in 87% and 100% of the samples respectively with cover values up to 50%, and *Leersia hexandra* and *Typha capensis* with low cover values (<10%) and in less than 55% of the samples. *Cyperus textilis*, largely restricted to

this community, occurred in 60% of the samples with cover values that ranged between 1 and 25%. *Mikania natalensis* and *Polygonum serrulatum*, which occurred frequently in the swamp and marsh communities, occurred with low cover in less than 40% of the samples in this community. Several other species were found in this community, but had low frequencies and low cover values.

This community ranked second in species diversity with an average of 13.1 species per sample (Table 4). The total number of species sampled was 47, which along with the other two forest communities was relatively high (Fig. 19c).

As with the two previous forest communities, this community was largely confined to the northern drainage areas of the Mbazwane Stream. This community predominantly occurred in the north-west running drainage line at the head of the Mbazwane system, with a few samples found bordering the section of swamp forest north of the Mbazwane Crossing (Fig 20). Samples were found in peaty areas that were saturated to the surface or had a water table below but close to the soil surface. Peat accumulation ranged from 0.5 m to approximately 2 m, and peat deposits were underlain by sand.

***Typha capensis*/*Pycneus mundii*/*Leersia hexandra* Marsh Community**

This community, which was dominated by short emergent plants, did not have any particular indicator species. However, it can be delineated by the following three preferential species *Typha capensis*, *Pycneus mundii* and *Leersia hexandra*. *Typha capensis* and *Leersia hexandra* were found in 80% and 90% of the samples in this community and had higher cover values than in samples found in other communities. *Pycneus mundii* was largely absent from other samples and was found in 70% of the samples in this community, with cover values generally between 5% and 25%. Several other species that occurred frequently included *Cyperus prolifer* (with high cover) and *Phragmites australis* (with low cover) that both occurred in 95% of the samples. *Thelypteris spl.* and *Polygonum serrulatum* were present in 85% and 70% of the samples with cover up to 25%. Two species, *Cyperus papyrus* and *Mikania natalensis* were found in 50% of the samples but both had low cover. The remaining species in this community had frequencies and cover values that were generally low.

Mean species richness in this community was 8.7 species per sample and total species richness was moderate compared to the other communities, with a total of 25 species sampled (Table 4; Fig. 19d).

This community was only found along one transect (Transect 6, Fig. 5) located at the western margin of the permanent swamps. This community extended for a distance of approximately 200 m from the western bank of the swamps, after which the *Cyperus papyrus* Swamp Community became dominant and extended eastwards into the main swamp area. All samples occurred in shallow water and vegetation was rooted in peat. Peat accumulations were on average 1.4 m thick.

For mapping purposes this community was included with the *Phragmites australis*/*Cladium mariscus*/*Ficus verruculosa* Swamp Community as they were difficult to distinguish in aerial photographs and from the air.

***Phragmites australis*/*Cladium mariscus*/*Ficus verruculosa* Swamp Community**

This community is characterised by the dominance of tall emergent herbaceous species and by the presence of the swamp fig, *Ficus verruculosa*.

This community showed a large degree of overlap in species composition with the previous community, but was separated by the occurrence of *Cladium mariscus* and *Ficus verruculosa* and by the high cover of *Phragmites australis*. The occurrence of *Cladium mariscus* was entirely restricted to this community, occurring in all but three of the samples with cover >5%. *Ficus verruculosa* only occurred in 6 samples not in this community, however it was present in 90% of the samples in this community. Its cover values in all cases were low (<5%). *Phragmites australis* was found in all samples, with its highest cover values in this group of samples. The remaining seven other species found in this community occurred in 64% or more of the samples, with the exception of *Pycnus mundii* which occurred in only two samples. Cover values for all these species were low, with most below 5%.

Species diversity in this community was intermediate compared to other communities with an average of 8.6 species per sample (Table 4). However, species richness was low with a total of 12 species sampled (Fig. 19e).

Although the occurrence of this community was restricted to one transect in this study, this community was observed to have a wide distribution. Characterised by the tall emergent grass *Phragmites australis*, this community is distinguishable on aerial photographs and was found to be the dominant vegetation over the northern portion of the permanent swamps (Fig. 20). Samples where this community was observed to occur were typically in water and vegetation was rooted in peat. Peat accumulation in areas that were sampled was substantial, with depths to a sandy substratum in some places being greater than 7 m.

***Cyperus papyrus* Swamp Community**

The high cover values of *Cyperus papyrus* (generally greater than 25%) separated this community from the other emergent communities. *Cyperus papyrus* dominated the upper layer of this community, while the lower layer was primarily composed of *Polygonum serrulatum*, *Leersia hexandra* and *Thelypteris sp1*. Cover values for these species were generally less than 10%. Other species in this community included the emergent species *Cyperus proliifer*, *Ficus verruculosa*, *Phragmites australis*, *Typha capensis*, *Cyperus textilis* and *Pycnus mundii*, which all occurred in less than 30% of the samples and with low cover. *Ipomoea cairica* occurred in three samples in this community and was exclusive to this community.

Species diversity in this community was intermediate when compared to the other communities with 6.7 species per sample (Table 4). In addition, overall species richness was intermediate, with a total number of 22 species having been sampled (Fig. 19f).

Occurring in a broad band around the fan formed by the Mkuze River, this community dominates the central and southern portions of the permanent swamps (Fig. 20). As in the case of other emergent communities, the *Cyperus papyrus*

community occurred in areas with standing water and a clay rich peat substrate. Measurements of peat depth in sites off the tip of the fan averaged 0.7 m.

***Echinochloa pyramidalis* Floodplain Community**

This community was only represented by three samples and was separated by the occurrence and high cover values of *Echinochloa pyramidalis*. One sample consisted of a mono-specific stand of *Echinochloa pyramidalis*, while the other two samples had *Panicum maximum*, *Polygonum senegalense*, *Cyperus textilis* and *Leersia hexandra*. Cover values of species other than *Echinochloa pyramidalis* were low, except for *Cyperus textilis* which had cover values greater than 25% in one or both of the samples where *Echinochloa pyramidalis* was not the only species present.

Species diversity and species richness in this community were low with 3.7 species per sample and a total of 5 species respectively (Table 4; Fig. 19g).

This community was limited to the seasonally flooded drainage line running parallel to the main swamps just west of Butterfly Pan, where *Echinochloa pyramidalis* dominated the vegetation. The substratum was clay and the land surface was dry. This area clearly received clay input from the Mkuze River, as it is the only source of clay.

***Ischaemum fasciculatum*/*Centella asiatica* Floodplain**

This community was mainly composed of grass species. Indicator species were *Ischaemum fasciculatum* and *Centella asiatica*, which occurred in > 63% of the samples and had cover values between 5% and 100% and 2% and 25% respectively. Greater than 50% of the samples had *Cyperus longus*, while 32% of the samples had *Digitaria eriantha*, *Eragrostis inamoena*, *Syzgium cordatum* and *Themeda triandra*. Occurring less frequently were *Mariscus solidus*, *Imperata cylindrica* and *Pteridium* sp. The remaining species found in this community occurred in three or fewer samples.

Species diversity in this community was intermediate with an average of 7.7 species per sample (Table 4). Species richness was high with a total of 51 species having been sampled (Fig. 19h).

This community had the greatest distribution range, occurring in floodplain areas along the northern drainage area above the permanent swamps and along the floodplain margins of the permanent swamps. The substrate at sites where this community was found were sandy and although they were dry at the time of sampling, they appeared to be seasonally flooded.

***Paspalum distichum* Floodplain Community**

Largely restricted to this community, the indicator species that separated this community was *Paspalum distichum*, which was also the most dominant species in this community, occurring in 83% of the samples with cover values generally between 25% and 50%. *Fimbristylis complanata* and *Panicum deustum*, occurring in 50% of the samples with low cover values were also largely restricted to this community. Several other species occurred in 50 % or more of the samples, but they seemed to have very wide distribution ranges, occurring more frequently in other communities. These included *Cyperus longus*, *Digitaria eriantha*, *Ischaemum fasciculatum*, *Eragrostis inamoena* and *Imperata cylindrica*, each having low cover values in the *Paspalum distichum* Floodplain Community. The remaining species found in this community were infrequent and had low cover values.

Species diversity was intermediate in comparison with the other communities with 8.0 species per sample (Table 4). In comparison to the other communities, species richness was intermediate with 23 species sampled (Fig. 19i).

This community was observed to occur in the southern portion of the study area along the western margin of the permanent swamps, where the substrate is clayey. This community was not extensive, but it tended to form a narrow border around the permanent swamps in the southern part of the study area. Sites were moist at the surface at the time of sampling, with the water table on average 0.20 m below the surface.

5.7 Landscape level heterogeneity

Beta diversity is a measure of diversity at the landscape scale, and is best quantified using a measure of community similarity or dissimilarity. Sorenson's index of community similarity, which is based on the number of shared species between two communities as a fraction of the number of species in both communities, was calculated for the communities identified in the TWINSpan cluster analysis (Table 5). Possible values are between 0.0 and 1.0, where a value of 1.0 indicates that the communities are identical in terms of their species composition, and a score of 0.0 indicates that the communities have no species in common. Thus, communities with a similarity index close to 1.0 would have large overlap in species composition, while a similarity index close to 0.0 would indicate few species common to the two communities.

Several patterns of similarity and dissimilarity were evident in Table 5. The forest communities, namely the *Ficus trichopoda*/*Scleria angusta* Swamp Forest, the *Rubus rigidus* Disturbed Swamp Forest and the *Phragmites australis*/*Ficus trichopoda* Precursor Swamp Forest, had the greatest similarity in species composition with each other, with similarity values greater than or equal to 0.5. The forest communities all had their greatest dissimilarity with the *Echinochloa pyramidalis* Floodplain, with Sorenson's similarity indices of 0.04, 0.12 and 0.11 for the *Ficus trichopoda*/*Scleria angusta* Swamp Forest, the *Phragmites australis*/*Ficus trichopoda* Precursor Swamp Forest and the *Rubus rigidus* Disturbed Swamp Forest respectively.

The marsh and swamp communities had the greatest similarity with one another, once again with Sorenson's similarity indices of 0.68.

The *Echinochloa pyramidalis* Floodplain Community had the least number of species in common with any of the other communities, while the remaining floodplain community, the *Paspalum distichum* Floodplain Community, had the highest overlap in species with the *Ischaemum fasciculatum*/*Centella asiatica* Floodplain Community, with a Sorenson's similarity index of 0.49 were similar.

Table 5. Scorensons similarity indices for the plant communities identified in the TWINSpan cluster analysis

Communities	<i>F. trichopoda</i> / <i>S. angusta</i> Swamp Forest	<i>R. rigidus</i> Disturbed Swamp Forest	<i>P. australis</i> / <i>F. trichopoda</i> Precursor Swamp Forest	<i>T. capensis</i> / <i>P. mundii</i> / <i>L. hexandra</i> Marsh	<i>P. australis</i> / <i>C. mariscus</i> / <i>F. verruculosa</i> Swamp	<i>C. papyrus</i> Swamp	<i>E. pyramidalis</i> floodplain	<i>I. fasciculatum</i> / <i>C. asiatica</i> Floodplain	<i>P. distichum</i> Floodplain
<i>F. trichopoda</i> / <i>S. angusta</i> Swamp Forest	1.0								
<i>R. rigidus</i> Disturbed Swamp Forest	0.52	1.0							
<i>P. australis</i> / <i>F. trichopoda</i> Precursor Swamp Forest	0.50	0.79	1.0						
<i>T. capensis</i> / <i>P. mundii</i> / <i>L. hexandra</i> Marsh	0.15	0.35	0.37	1.0					
<i>P. australis</i> / <i>C. mariscus</i> / <i>F. verruculosa</i> Swamp	0.04	0.16	0.24	0.54	1.0				
<i>C. papyrus</i> Swamp	0.13	0.39	0.41	0.68	0.59	1.0			
<i>E. pyramidalis</i> Floodplain	0.04	0.11	0.12	0.20	0.12	0.30	1.0		
<i>I. fasciculatum</i> / <i>C. asiatica</i> Floodplain	0.32	0.48	0.50	0.34	0.19	0.27	0.14	1.0	
<i>P. distichum</i> Floodplain	0.09	0.22	0.23	0.29	0.17	0.18	0.07	0.49	1.0

Overall, it is clear that communities can be grouped in a general way based on species composition and measures of similarity, as well as based on vegetation structure and on hydrological and substratum characteristics. Forested communities, which are permanently flooded, are similar to each other and different from non-forested communities. Of the non-forested communities, two distinct groups were evident, one that is permanently flooded (marsh and swamp communities), the other that is seasonally flooded (floodplain communities). Within the swamp/marsh communities, the *Cyperus papyrus* Swamp Community is different (least similar) to the other swamp/marsh communities. Within the floodplain communities the *Echinochloa pyramidalis* community is different from the other floodplain communities.

The data also suggest that overall heterogeneity at the landscape scale is remarkably high with these 3 broad categories of vegetation type, and as indicated by (equivalent to 3 species turnovers) the overall length of the ordination axes that cover 6 standard deviations (Jongman *et al.* 1995).

5.8 Conclusion

Nine plant communities were identified in the TWINSpan cluster analysis and they can generally be grouped into three groups based on vegetation structure and hydrological conditions. These groups were swamp forest communities, emergent swamp/marsh communities and floodplain communities. Two of these, the swamp forest and swamp/marsh communities are found in permanently flooded areas while the floodplain communities are found in seasonally or periodically flooded areas. It was not clearly evident from the measured environmental variables what environmental gradients contributed to the distribution of the communities in the permanently flooded settings.

Two general elevation gradients were evident in the study area. There was a gentle north – south gradient, with the northern part more elevated than the southern part of the system. The northern parts were also characterised by a narrower and steeper channel than the more broad and shallow southern basin. The second general elevation gradient that was evident, was a west – east elevation gradient, with the

areas to the west at a higher elevation than to the east. This gradient is particularly pronounced in the northern parts of the study area where the western edge of the wetland is bordered by a steep, high north-east – south-west orientated dune cordon.

These elevation gradients seem to influence the inundation regime, with the western edge of the northern part bordering the dune cordon as well as the southern parts of the study area being permanently flooded. The areas to the east of the wetland as well as the western edge of the southern edge were seasonally flooded.

Within the permanently flooded areas the swamp forests were restricted to the northern parts of the area. In contrast, the swamp/marsh communities were found in areas to the south of the steep, high dune cordon, where the relief to the west was gentler. Within the swamp/marsh communities, the *Cyperus papyrus* Swamp Community was restricted to the areas around the Mkuze Delta, where the substratum was a clay-rich organic deposit.

Within the seasonally flooded communities, the *Echinochloa pyramidalis* Floodplain community was restricted to areas west of the permanent swamps on the northern edge of the Mkuze Delta, where clay was abundant. The other two floodplain communities were found to north of the Mkuze Delta and to the east of the swamp forests in the northern parts, where the substratum was sandy.

CHAPTER 6: DISCUSSION

6.1 Introduction

This chapter describes and discusses the findings of this study and attempts to explain the relationship between plant community distribution and environmental variables within the Mbazwane Wetland. It also attempts to place the study within a broader framework, such that our current understanding of wetland systems is enhanced.

The nine plant communities identified in the TWINSpan cluster analysis can be grouped into three broad groups: swamp forest communities (Groups A, B and C), emergent swamp/marsh communities (Groups D, E and F) and, floodplain communities (Groups G, H and I; Fig. 2). These broad vegetation communities occupy discrete positions in the regional landscape (Fig. 5), presumably as a response to spatial variation in environmental conditions.

6.2 Duration of inundation

Axis 1 accounts for 76% of the variation in community composition and therefore probably reflects an important environmental gradient. The distribution of samples along Axis 1 appears to reflect the depth and duration of inundation, with inundation decreasing with an increase in Axis 1 score. The site specific conditions of permanently inundated swamp/marsh communities with highly negative Axis 1 scores, permanently saturated or flooded swamp forest communities with intermediate Axis 1 scores and periodically flooded floodplain communities with highly positive Axis 1 scores, were observed during three field visits during the course of the study. Two of the visits were in the drier winter months and one occurred in following heavy rains. On each occasion the swamp/marsh communities were in standing water, while the swamp forest communities were either flooded or saturated to the surface. The floodplain communities were exposed during the winter months and flooded following heavy rains early in summer. Furthermore, the communities occupy distinct topographic positions within the landscape and the depth and duration of flooding are influenced by elevation.

A north-south regional topographic gradient is clearly evident in the study area (Fig. 15). The depression in which the wetlands are situated has a gentle southward slope, with the gradient in the region in which the wetlands are situated becoming progressively shallow downstream. The cross-sectional profiles in the northern region (Figs 6-10) indicate discernible channels that contrast with the southern area where no distinct channels are evident. These channels are also evident from aerial photography in the northern region but not in the southern region. Based on these characteristics, the northern part of the study area with a steeper slope is likely to have more pronounced variation in both the lateral and vertical extent of flooding than in the permanent swamps to the south, where slope and therefore hydraulic efficiency is lower. However, the main period of sampling was during the winter months and all channels in the northern part of the study area were observed to have flowing water and areas adjacent to the channels were saturated to the surface or had shallow standing water, thus indicating permanent saturation. The area containing the herbaceous permanent swamp has a relatively flat downstream gradient (Fig. 15) and it occupies a shallow valley (Fig. 16). This basin is likely to result in weak lateral and downstream flows, and consequently there is likely to be accumulation of standing water throughout the year. Vegetation in the permanent swamps comprises emergent plants rooted in peat, reflecting permanent flooding.

In contrast, the floodplain communities are largely restricted to the eastern side of the Mbazwane Stream in the northern drainage area and in a narrow band surrounding the permanent swamps. The high lying dune cordon to the west of the Mbazwane Stream in the northern drainage area prevents seasonal floodwaters from overflowing westwards, while east of the Mbazwane Stream floodwaters inundate a fairly extensive area due to more gentle slopes to the east. Of the floodplain communities identified, the *Ischaemum fasciculatum*/*Centella asiatica* Floodplain Community was found to be the most extensive, occurring both in the northern drainage area and along the western edge of the permanent swamps. The *Paspalum distichum* Floodplain Community and the *Echinochloa pyramidalis* Floodplain Community were generally restricted to the western edge of the swamp, just north and west of Butterfly Pan. The *Echinochloa pyramidalis* Floodplain Community occurred on clay (see following section) while the other two floodplain communities occurred on sand. The

floodplain communities on sand occurred at different elevations relative to the water level at the time of sampling, with the *Ischeamum fasciculatum*/*Centella asiatica* Floodplain Community occurring at slightly higher elevations than the *Paspalum disticum* Floodplain Community.

6.3 The effect of substratum

While the swamp/marsh communities were separated from the swamp forest and the floodplain communities along the horizontal axis, the swamp/marsh communities occupy similar space within the ordination diagram and none of the measured environmental variables appears to account for their distribution (Fig 3). However, from field observations and on aerial photographs it was possible to distinguish two emergent communities occupying distinct areas within the permanent swamps. The distribution of the *Typha capensis*/*Pycnus mundii*/*Leersia hexandra* Marsh Community was not easily identified as this community was only found at one sample site (Transect 6), and site conditions were very similar to where the *Phragmites australis*/*Pycnus mundii*/*Leersia hexandra* Swamp Community was found. Thus this community appears to have a more localised distribution and the environmental variables most influential in controlling its distribution are not clear.

The other two swamp/marsh emergent communities however, appear to occupy distinct positions within the landscape. The *Phragmites australis*/*Pycnus mundii*/*Leersia hexandra* Swamp Community was found in the northern and eastern parts of the permanent swamp, while the *Cyperus papyrus* Swamp Community forms a broad band fringing the delta formed by the Mkuze River as described by McCarthy and Hancox (2000). The *Cyperus papyrus* Swamp Community was rooted in clay rich peat in the area around the delta that receives an input of clay from the Mkuze River during very high floods. In contrast, the *Phragmites australis*/*Cladium mariscus*/*Leersia hexandra* Swamp Community was rooted in peat with low ash content as there is little or no input of clay from the Mkuze River, even during high floods. Prior to its diversion along various artificial canals, the Mkuze River entered the area of permanent swamp in this study area via the northern part of the Mkuze Delta, creating a fan-shaped feature that is extending eastwards into the swamps over time as a result

of clastic sediment deposition. The permanent swamps in this study are thus maintained by water supplied mainly from the southward flowing Mbazwane Stream and the occasional input of water from the eastward flowing Mkuze River. The two rivers, which derive their waters from different sources, differ in their sediment loads. The Mkuze River, draining Ecca shale and sandstone, Dwyka tillite and fine-grained volcanic rocks of the Lebombo Mountains (rhyolite), carries a high sediment load. By the time the Mkuze River reaches the Mbazwane Stream the sediment load is mainly silt and clay (McCarthy and Hancox 2000). In contrast, the Mbazwane Stream drains the Pleistocene sands of the coastal plain and is essentially sediment free (Stormanns 1986). During periods of high floods, flow from the Mkuze River flowing along its original course, would enter the permanent swamps. The loss of flow competence as it enters the Mbazwane Wetland, mainly as a result of the presence of dense stands of emergent vegetation, results in the deposition of its sediment load. Thus, it is expected that a zone extending outwards from the Mkuze River into the permanent swamps, would contain deposits of clay within the accumulated organic matter. This contrasts with the adjacent areas to the north that are fed by the waters from the sediment free Mbazwane Stream, which would therefore have no sediment deposits within the underlying peat layer. As a consequence, the zone of swamp receiving water from the Mkuze River has a higher clay content and is more likely to contain a higher nutrient content than the more northern areas.

Ellery and McCarthy (2000) found that the distribution of *Cyperus papyrus* in the Okavango Delta was influenced by a similar set of processes. *Cyperus papyrus* standing crop was greatest along channel margins where clay and plant nutrient supplies were greatest and standing crop decreased at right angles from the channel as clay and thus nutrient supply were deposited and/or taken up by channel margin vegetation. The same set of processes would account for the distribution of *Cyperus papyrus* in the Mbazwane Wetland.

In the study area there is a relatively sharp boundary between the *Cyperus papyrus* Swamp Community and the *Phragmites australis*/*Pycneus mundii*/*Leersia hexandra* Swamp Community. It is suggested that this represents the limit of clay input into the wetlands in the study area from the Mkuze River, creating a discontinuity in the

nutrient gradient and consequently restricting *Cyperus papyrus* to nutrient enriched areas.

6.4 The role of fire

Acocks (1953) considers the areas along the eastern seaboard, which includes the present study area, to be grasslands seral to forests. Natural and anthropogenic fires have been a part of the grassland habit for millennia (Tainton and Mentis 1984). They play a major role in the development and maintenance of grasslands, with frequent fires restricting the development of trees and therefore of forests (Granger 1984). In the absence of fires or where there are prolonged periods between fires, grasslands are replaced by communities with a woody component. Depending on moisture availability, rainfall seasonality and the temperature during the dry season, the woody component is dominated by shrubs (karoo), or trees (savanna or forest), or both (fynbos; savanna and forest) (Ellery *et al.* 1993). In particularly moist settings such as along the eastern seaboard, forest is expected (Acocks 1975; Wessels 1991).

Berg winds, which are hot, dry winds blowing from the west, are a common feature of the coastal plain during late winter and early spring. Occurring late in the dry season, berg winds are likely to lead to desiccation of vegetation and render it susceptible to burning (Ellery *et al.* 1991). The susceptibility of vegetation to desiccation is further enhanced by strongly seasonal rainfall and in which there is a pronounced or prolonged dry period (Ellery and Mentis 1991). Natural fire patterns in conjunction with wind and topography are thought to have had a substantial influence on the distribution of forest patches in South Africa (van Daalen and Geldenhys 1988), and the occurrence of berg winds in grasslands that have sufficient rainfall to support forest vegetation, restricts the distribution of patches of forest to 'berg wind shadow areas'.

Wind data from the town of Mabibi located 50 km north-east of the study area has been used to establish general wind patterns in the region (Diab and Sokolic, unpublished data). The prevailing winds in this area are north-east and south-west (Fig. 21) and the occurrence of berg winds from the north-west is uncommon.

Nevertheless, their effect in promoting fires, and therefore in fundamentally affecting vegetation distribution, may be substantial. Wind direction, temperature and times of day are plotted for winds during the winter months of June, July and August (Fig. 22). Based on incoming solar radiation, one would expect warming to take place during the daytime and cooling to take place at night, irrespective of wind direction, such that temperature would be warmest during the afternoon and coolest before sunrise early in the morning (Tyson and Preston-Whyte 2000). There are two interesting anomalies to this expected trend. The first is the presence of cool temperature throughout the day at times when winds blow from the south-west (200 - 240°; Fig. 22). These winds accompany cold fronts that occur in this area during the winter months. The second is the presence of particularly warm conditions that extend well into the night and even into the early morning when winds blow from the west and north-west (275 - 310°; Fig. 22). These warm temperatures occur during berg wind conditions, when air heats as it descends from the escarpment and blows across the coastal plain. The occurrence of berg wind conditions has been strongly linked to the desiccation of vegetation and its susceptibility to burning in wildfires (Ellery *et al.* 1993), and it is during these conditions that fires are most likely to occur in the study area. It is suggested here that Axis 2 of the ordination diagram reflects a gradient of fire frequency. Communities with high Axis 2 scores have few or no fires while those with low Axis 2 scores are frequently affected by fires.

The sites with mature *Ficus trichopoda*/*Scleria angusta* Swamp Forest were restricted to the northern portion of the study area and were found in a drainage line that was bordered on its western side by a north-east to south-west orientated dune cordon, reaching an elevation of approximately 30 m (Fig. 23). This north-east to south-west dune cordon is a very prominent feature with a very steep slope towards the south-east (Fig. 24). In contrast, the area to the south-east of the drainage line was at a lower elevation and the slope into the drainage line from this area was much more gentle. It is suggested that this high lying dune cordon to the west of the drainage line serves to protect the drainage line from fire that occurs under berg wind conditions, as these fires appear only to burn to the crest of the dune cordon and do not extend down its

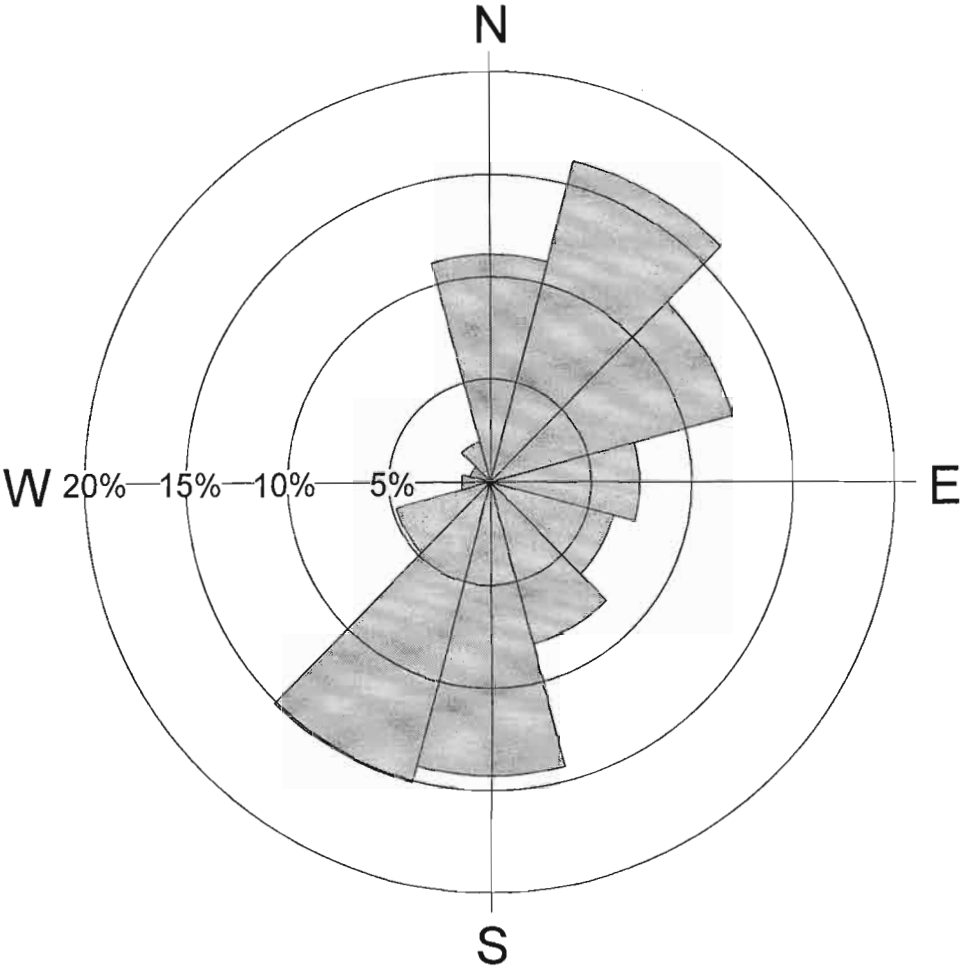


Figure 21: Wind rose showing the percentage frequency of winds for the Mabibi area, Maputaland.

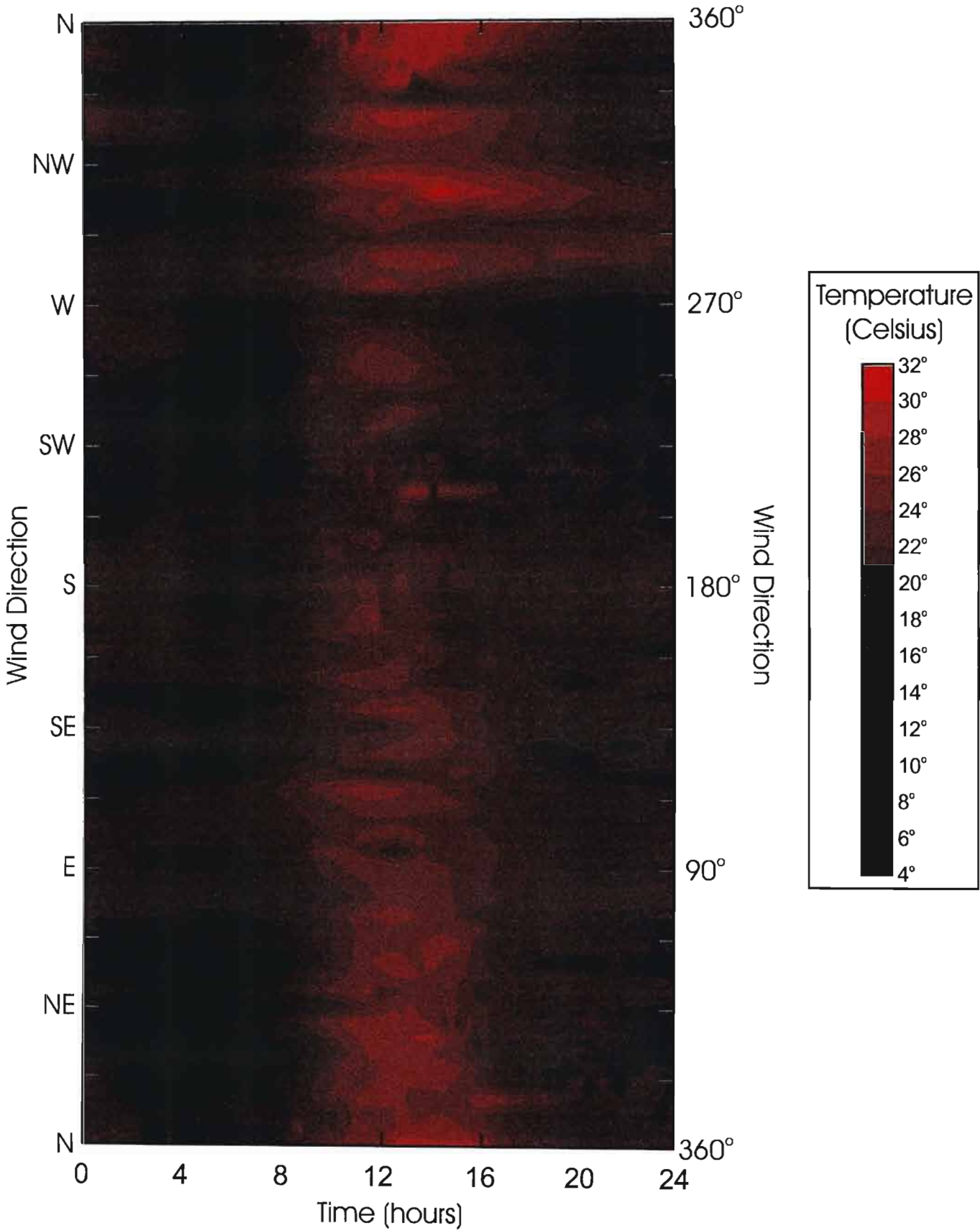


Figure 22: Mean surface temperatures for the months of June, July and August, 1996 in relation to time of day and wind direction for wind speeds greater than 1.0 m/s.

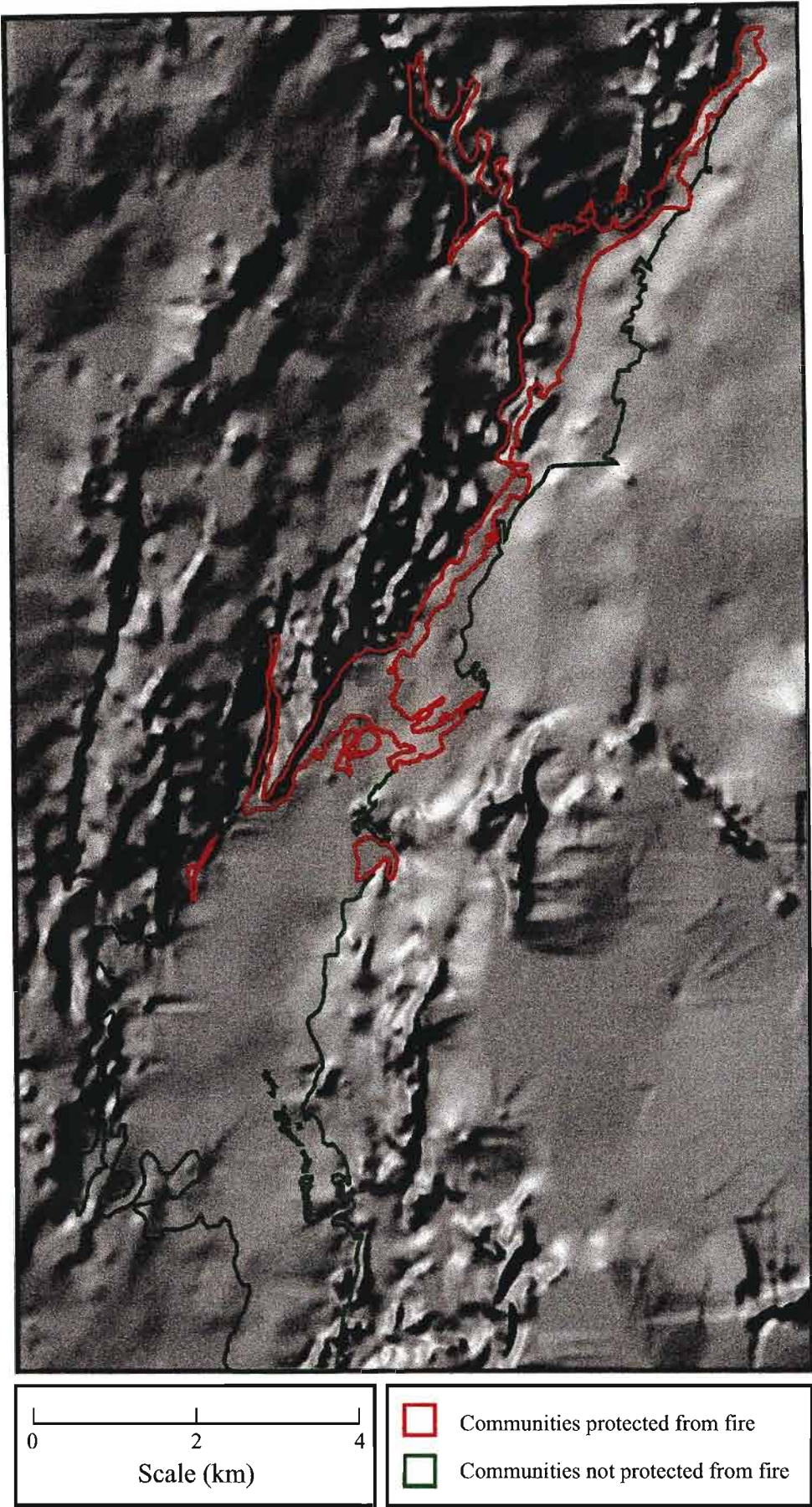


Figure 23: Community distribution of the Mbazwane Wetland in relation to topographic features.

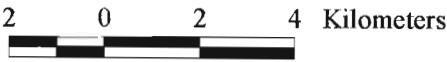
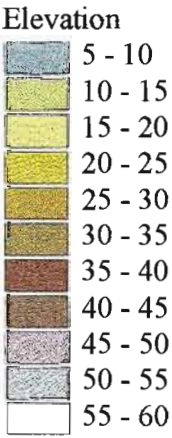
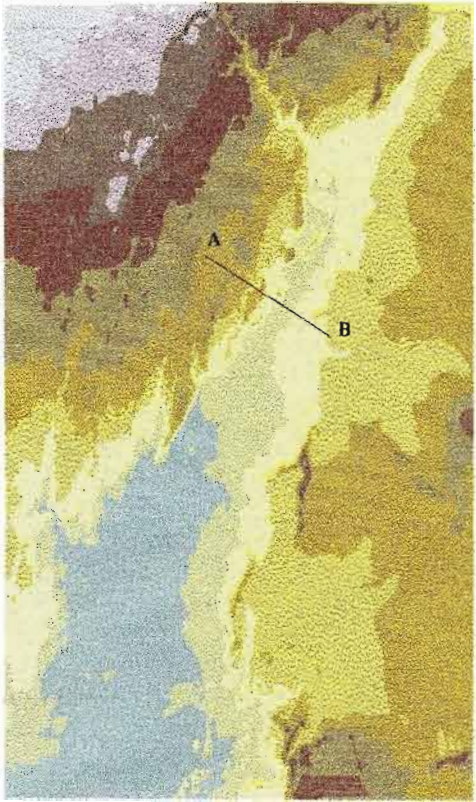
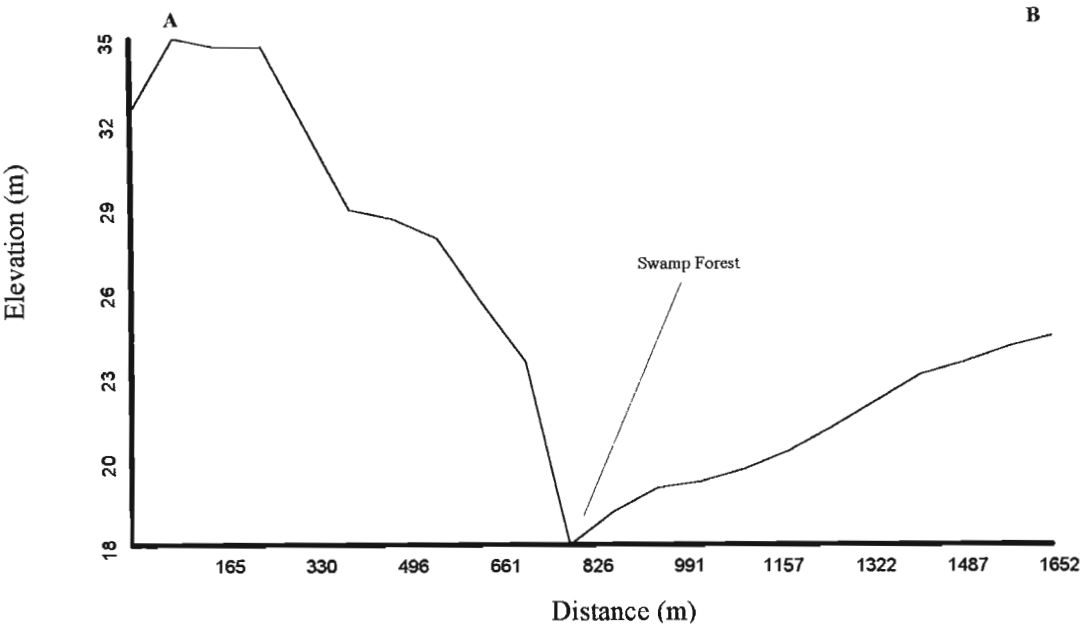


Figure 24. Topography (a) and a typical cross-sectional profile across the Mbazwane Stream in roughly the same orientation as berg wind direction, in the region where swamp forest is present.

eastern slope. Thus mature swamp forest distribution is limited to the western fringe of steep sided drainage lines in areas where there is complete protection from fires.

In his study on the factors influencing the distribution and development of swamp forests along the Maputaland coast, Wessels (1991) found that *Ficus trichopoda* Swamp Forests only occurred in areas where fire was absent. The seedlings of *Ficus trichopoda* were found to be intolerant of fire and mature forests were not penetrated at all by fire. However, while Wessels (1991) supports this contention that the absence of fire is a determinant of swamp forest communities, he does not explain the exclusion of fire from areas where swamp forest communities occur.

Within the swamp forest communities themselves it seems that the distribution of communities is either related to the time interval since the last fire and thus reflects fire frequency, or else it is related to human disturbance which includes one or more of a combination of local burning, tree felling for hardwood use, or extraction of plant products such as bark and/or plant harvesting. The *Phragmites australis/Ficus trichopoda* Precursor Swamp Forest Community was predominantly found along the north-west orientated drainage line in the northern section of the study area (Fig. 23). This drainage line has steep banks that may offer protection from fires when berg winds are not that strong. However, with stronger winds, fire is likely to extend down the banks. Thus this community would probably have long intervals between exposure to fires. This would enable the establishment of *Ficus trichopoda* seedlings (Wessels 1991). However, without complete protection from fire, the *Phragmites australis/Ficus trichopoda* Precursor Swamp Forest Community is prevented from developing into a mature swamp forest community.

The *Rubus rigidus* Disturbed Swamp Forest Community, found along the edges of the *Ficus trichopoda/Scleria angusta* and the *Phragmites australis/Ficus trichopoda* Swamp Forests, is likely to be the result of instances where fire has penetrated the edges of these communities, or they may reflect human induced disturbances. Harvesting of plant resources for a variety of uses is widespread and in many cases there was evidence of tree felling and harvesting of plants and plant parts. The distribution of this community may be related to such activities, as peripheral swamp

areas are far more accessible than the main swamp forests themselves, particularly where growth is dense and vegetation is impenetrable. It is also easier to remove products from the periphery to the more open grasslands and savannas, than from the swamp forests themselves.

In contrast, the swamp/marsh and floodplain communities are found in sites where fires are likely to occur more frequently. These communities occupy vast expanses of gently undulating terrain and are either elevated sufficiently to be exposed to berg-wind conditions (in areas east of the fire protected swamp forest communities) or alternatively, they are not fringed to the west by a steep sided dune cordon. As such, they are prone to frequent burning which maintains the floodplain and swamp/marsh communities as predominantly herbaceous vegetation. Both the emergent swamp/marsh vegetation and the grassland communities are able to re-establish following a fire, as their stems or permanent shoots occur below ground or the water level, and therefore are protected.

6.5 Predicting community distribution

Based on the above discussion it is possible to predict community distribution within the Mbazwane wetlands in the form of a decision tree (Fig. 25). The strength of presenting ecological findings in this way has merit for several reasons:

- it summarises understanding in a clear way,
- it is explicitly testable, and
- it highlights areas of uncertainty where future investigation may be desirable

Thus while it may seem an oversimplification of the complexity of the system in which the study was carried out, it has value as a heuristic tool.

The overriding environmental variable affecting the distribution of communities was the duration of inundation, which separated permanently inundated areas (swamp/marsh and forested communities) from seasonal/periodically inundated areas (floodplain communities).

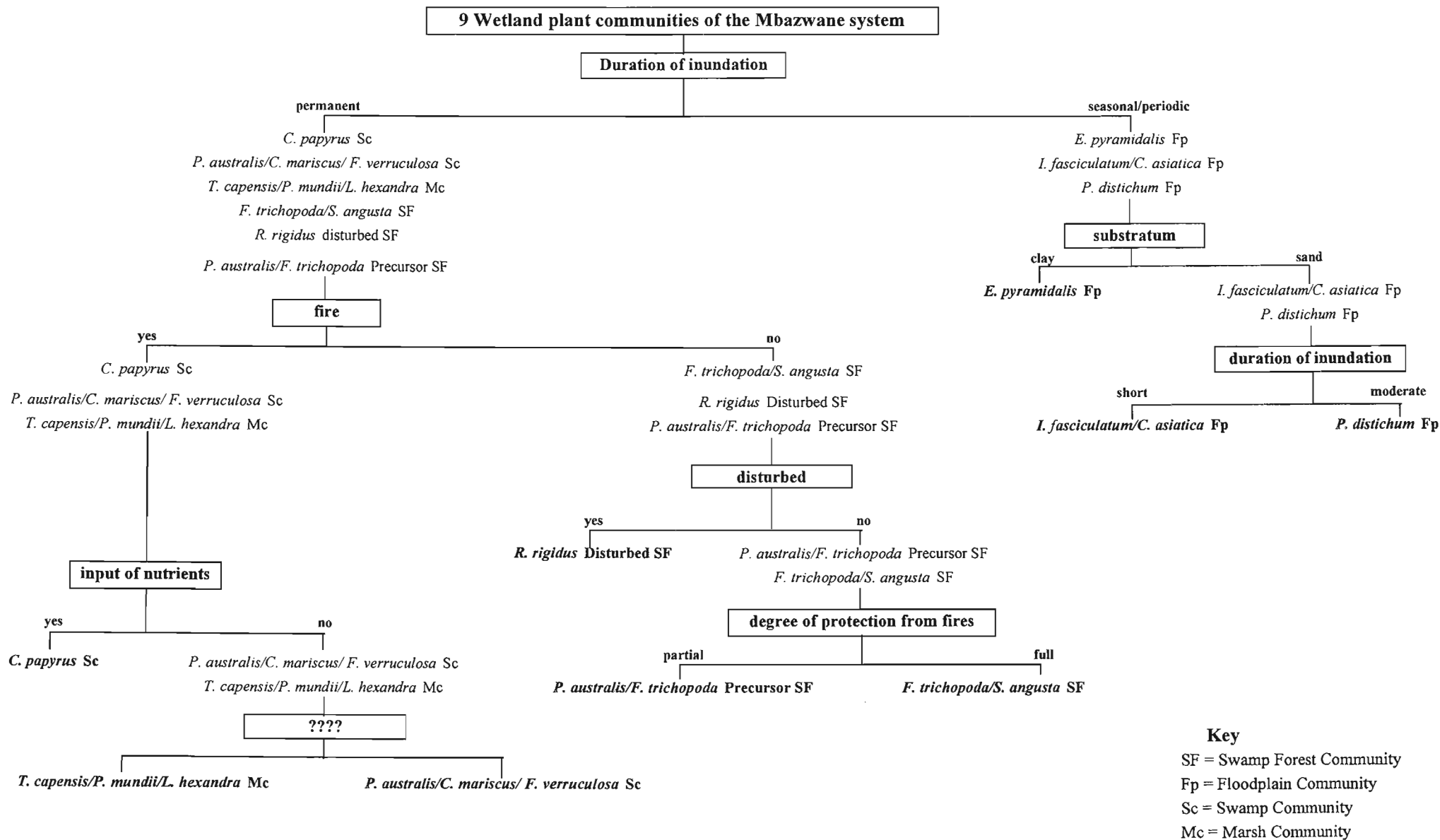


Figure 25. Decision tree predicting plant community distribution based solely on environmental characteristics in the Mbazwane Wetland

Within the seasonal/periodically inundated areas, the nature of the substratum separated the *Echinochloa pyramidalis* Floodplain Community, which was found on a substratum containing clay, from the *Ischaemum fasciculatum*/*Centella asiatica* and the *Paspalum distichum* Floodplain Communities which were found on a sand substratum. The *Ischaemum fasciculatum*/*Centella asiatica* Floodplain Community and the *Paspalum distichum* Floodplain Community were separated from each other by the duration of inundation, with the *Paspalum distichum* Floodplain community experiencing moderate periods of inundation, in comparison to the short periods of inundation experienced by the *Ischaemum fasciculatum*/*Centella asiatica* Floodplain Community.

Within the permanently flooded communities, the herbaceous emergent swamp/marsh communities were separated from the swamp forest communities by fire. The swamp/marsh communities were further divided by the input of nutrients, with the *Cyperus papyrus* Swamp Community restricted to areas receiving an input of nutrient from sediment laden Mkuze River floodwaters and the *Phragmites australis*/*Cladium mariscus*/*Ficus verriculosa* Swamp Community and the *Typha capensis*/*Pycnus mundii*/*Leersia hexandra* Marsh Community occurring in areas not influenced by floodwaters. The environmental variable separating the *Phragmites australis*/*Cladium mariscus*/*Ficus verriculosa* Swamp Community and the *Typha capensis*/*Pycnus mundii*/*Leersia hexandra* Marsh Community, is not known.

Of the permanently flooded swamp forest communities, *Rubus rigidus* Disturbed Swamp Forest Community is separated from the other two swamp forest communities by anthropogenic disturbance. The remaining swamp forest communities are separated from each other by the degree of protection from fires. The *Ficus trichopoda*/*Scleria angusta* Swamp forest was only found in areas that offer complete protection from fire, while the *Phragmites australis*/*Ficus trichopoda* Precursor Swamp Forest occurred in areas experiencing periodic burning.

6.6 Vegetation distribution in relation to allogenic and autogenic factors in the Mbazwane wetland

Classical succession, when applied to wetlands, holds that wetlands are a part of a hydrarch successional sequence from an open aquatic system to a climax forest community (Mitsch and Gosselink 1993). The change to a climax forest community is brought about by the accumulation of peat, which raises the surface elevation and thereby reduces the depth, duration and frequency of flooding. The classic sequence of succession is from submerged to floating leaved to emergent to forested climax community (Denny 1985a; Mitsch and Gosselink 1993). The TWINSpan cluster analysis revealed swamp forest, herbaceous emergent swamp/marsh and floodplain communities present in the study area (Fig. 22). The study area lies within the Tongaland-Pondoland Regional Mosaic and swamp forests are typical of permanently wet sites in this lowland region (Moll 1978; Wessels 1991). Thus the climax community in the Mbazwane Wetland is likely to be swamp forest rooted in peat (Smuts 1998).

As community change in the classical successional sequence is brought about by peat accumulation, it may be expected that community distribution would relate in some way to peat thickness, where peat accumulation would show a gradual increase in thickness from the earliest successional community to the climax community. Figure 18 shows the average peat accumulations for each community. Peat accumulations are quite varied and it is evident that the expected pattern of a consistent increase in peat thickness from the early successional emergent communities to the climax swamp forest community does not occur. The largest peat accumulations are found at sites with the swamp or marsh communities and lowest accumulations at floodplain sites. Swamp forest (the supposed climax community) occurs in areas of intermediate peat thickness, suggesting that the concept of autogenic succession as described in classical texts (Pearsall 1920; Wilson 1935), is not occurring within this system, and that there are other environmental factors influencing community composition and distribution.

It is interesting to consider the fact that peat thickness was strongly related to Axis 1 scores of the ordination (Fig. 3), but was not related to community succession in any way. Organic matter accumulation is controlled by the hydrological regime through its influence on primary productivity, decomposition and import/export of particulate organic matter (Mitsch and Gosselink 1993). The presence of a permanent water supply increases primary productivity and decreases the rate of organic matter decomposition.

The export or deposition of organic matter from a system is dependent on the hydrologic energy of the inundation regime (Gosselink and Turner 1978). High-energy hydrologic regimes remove organic material from a system, preventing its accumulation, while the opposite is true for low-energy systems where conditions enable organic matter accumulation. Thus, for a given basin shape and hydrological regime it is likely that thicker peat accumulations reflect longer time periods of accumulation (Grundling *et al.* 1998). Hydrologic energy is often indicated by flow rate or by frequency and severity (depth variation) of flooding, where high flow rates or episodic large flood events indicate a high energy regime while low flow rates or stable water levels associated with permanently flooded areas, indicate a low-energy environment (Gosselink and Turner 1978). If anything, there should be a downstream decrease in hydrological energy due to the gradual decline in slope and therefore flow velocity in the present study area (Fig. 24), and one might therefore expect peat thickness to increase downstream.

Clearly, basin physiography is also likely to influence potential peat thickness as this determines the depth of permanent flooding and therefore of potential organic matter accumulation. Basin depth must increase downstream in the study area as rivers flowed southwards through the present mouth of Lake St. Lucia during periods when sea levels dropped such as during the last ice age (McCarthy and Hancox 2000). During such periods, rivers must have incised into the pre-existing topography and created valleys, which are presently filled with peat deposits. Given the very shallow gradient on the water surface in the study area and the low hydrological energy conditions, peat depth must accumulate to a depth depending on basin physiography, since it accumulates to the mean or minimum depth of permanent flooding. The

correlation of Axis 1 scores with peat thickness (Fig. 26) may, therefore, just be coincidental.

None of the factors described above relating to peat thickness can be systematically related to community distribution or vegetation succession. As such, Axis 1 of the ordination may reflect downstream gradients in environmental factors other than peat thickness or community succession. Axis 1 may reflect a fire gradient as the northern part of the study area is protected from fire under berg wind conditions, while the southern part is not. Furthermore, the southern part of the study area receives clay from the Mkuze River, while the northern area does not. These factors, and not peat depth, are considered to be the most important determinants of community distribution in the Mbazwane Wetland.

If this interpretation is correct, then autogenic processes seem unimportant within the Mbazwane wetland system, or at least, they are not evident within the system as it is at present. This suggests that the classical theory of wetlands as part of a hydrarch succession driven by the accumulation of organic matter (Clements 1916) is not particularly valid for this system. In addition, the model of succession proposed by Mitsch and Gosselink (1993) does not appear to adequately account for the observed patterns of community distribution. Mitsch and Gosselink (1993) proposed that in permanently inundated wetland systems the initial determinants of wetland succession are allogenic, but as the system matures the system becomes 'insulated' from environmental fluctuations and disturbances as nutrients and organic matter accumulate. As discussed above, peat accumulation does not appear to be related to succession in this system, and furthermore, it has been suggested that disturbance, particularly by fire, plays an important role in community distribution.

Alternative models of wetland community succession include those of van der Valk (1981) and Breen *et al.* (1988). In his 'environmental sieve' model, Van der Valk (1981) suggested that allogenic factors, in particular fluctuations in water level, determine the site-specific conditions to which wetland plants respond - depending on their life-history features. While the findings in this study suggested depth and duration of flooding as an important environmental variable separating floodplain

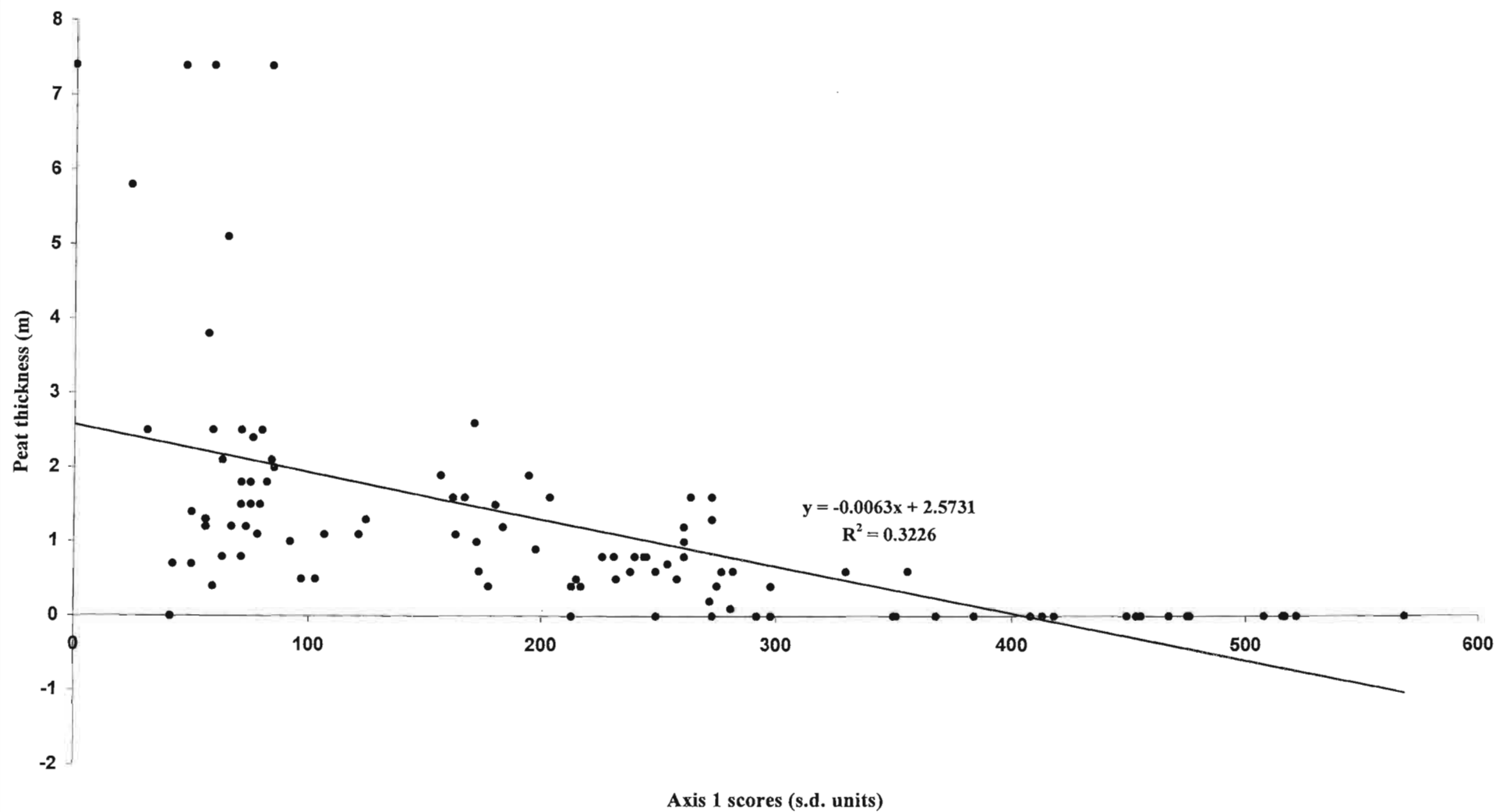


Figure 26. Peat depth in relation to axis 1 score of the ordination.

communities from permanently flooded communities, there was no evidence to suggest that hydrological conditions accounted for the distribution of communities within permanently flooded settings. Breen *et al.* (1988) proposed a model for community distribution in which vegetation patterns are considered to reflect the effects of allogenic and autogenic processes on resource distribution. The model explicitly recognises hydrogeomorphic processes as creating the environmental template that governs community distribution, since hydrological and geomorphological conditions and processes are spatially heterogeneous. However, plant communities tend in some cases to amplify spatial heterogeneity, such as the removal of fine clastic sediment and plant nutrients in the channel margins of the Okavango Delta (Ellery *et al.* 2000), which leads to the creation of a system that is extremely nutrient deficient. In some cases plant communities may reduce environmental heterogeneity, for example, by slowing down the flood wave and reducing the amplitude of the seasonal flooding in the Okavango Delta (McCarthy *et al.* 1986a). Ultimately, community distribution is a product of these processes operating together.

6.7 Conclusion

This study has demonstrated the importance of hydrogeomorphic processes in the Mbazwane Wetland, in that the depth and duration of flooding as well as the deposition of sediment around the Mkuze Delta are important determinants of community distribution. However, the role of fire is seldom considered in wetland systems and this study clearly points to it as an important determinant of community distribution. It must be seen as an important component of the “environmental template”, playing a key role in creating a disturbance regime that sets back the successional clock. As such, hydrarch succession is not as important here as it is in northern temperate systems where fire is infrequent.

This does not mean that succession has never been important in the Mbazwane Wetland. Prior to the infilling of the Mbazwane drainage line with peat and/or sediment, it is likely that during its early evolution since the last ice age, it was a shallow lake (McCarthy and Hancox 2000). The infilling of the lake by a

combination of peat in the south, must have been accomplished, at least in part, by vegetation succession in a hydrarch successional sequence. A focus on the vegetation within and fringing Lake St Lucia and other coastal lakes such as Lake Sibaya or Kosi Lake may provide greater insight into the nature and dynamics of these processes. Alternatively, peat coring and analysis of various organic remains in the Mbazwane Wetland may provide such insight.

CHAPTER 7: CONCLUSION

This study has attempted to classify and determine the environmental factors influencing the distribution of plant communities in the Mbazwane system of the Mkuze Wetland. A total of nine communities were identified in the TWINSPAN cluster analysis and these communities can be separated into three broad groups, namely, swamp forest communities, emergent swamp/marsh communities and grassland floodplain communities. The results of this study indicate that one of the main environmental variables influencing distribution is hydrological conditions, which separates the communities into permanently flooded and seasonally/periodically flooded communities. It is suggested here that the environmental variables that account for further division of the communities within these two groups, are disturbances from fire and substratum differences related to geomorphological processes of sediment deposition.

The northern part of the study area is bordered on its western side by a dune cordon, which offers protection from fires that are driven by berg winds. This enables the establishment of mature *Ficus trichopoda*/*Scleria angusta* Swamp Forest. Partial protection from fires maintains the *Phragmites australis*/*Ficus trichopoda* Precursor Swamp Forest in an earlier successional stage. The lack of protection from fire maintains the swamp/marsh communities as herbaceous.

The input of sediment from the Mkuze River during high flood events creates substratum differences that are likely to be associated with differences in nutrient supply. These substratum differences separate the *Cyperus papyrus* Swamp Community, found in areas of permanently flooded swamps receiving clastic sediment from the Mkuze River, from the adjacent *Phragmites australis*/*Cladium mariscus*/*Ficus verruculosa* Swamp Community rooted in peat in which there is little input of clastic sediment. Additionally, the *Echinochloa pyramidalis* Floodplain Community that occurs in settings that receive clastic sediment from the Mkuze River, is separated from the two other floodplain communities that occur in areas where there is little input of clastic sediment. These two floodplain communities are separated by the duration inundation, with the *Ischaemum fasciculatum*/*Centella*

asiatica Floodplain experiencing shorter periods of inundation than the *Paspalum distichum* Floodplain Community.

Given this it seems that community distribution in the Mbazwane Wetland is presently not determined by autogenic processes, but that abiotic environmental factors are important. This does not imply that autogenic processes have not been important in making the Mbazwane Wetland what it is today. However, in order to understand these fully one needs to undertake either/or a combination of paleobotanical studies and broader scale ecological studies extending into the coastal lakes in the region, such as Lake St Lucia, Lake Sibaya or Kosi Lake.

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