Ecosystem engineering by the wetland plant palmiet: does it control fluvial form and promote diffuse flow in steep-sided valleys of the Cape Fold Mountains

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Abstract

Ecosystem engineering refers to the way that organisms control the structure and function of ecosystems. It has been suggested that palmiet (*Prionium serratum*, Thurniaceae) works as an ecosystem engineer, shaping peat wetlands in South Africa. However, there is currently a paucity of evidence supporting this claim. Palmiet has a dense root, rhizome and stem system that forms dense stands, growing from channel banks into fast flowing river channels. This slows river flows, traps sediment, which builds up riverbeds and ultimately blocks river channels, turning the river into a wetland. The aim of this study was to determine if palmiet is an ecosystem engineer and to document its pattern of colonisation and the nature of its control of a fluvial system. This was achieved by undertaking vegetation surveys in the Kromrivier Wetland in the Eastern Cape. The data was analyzed using vegetation classification and ordination, where vegetation communities were linked to environmental factors. It was found that palmiet occupied three distinctive habitats; 1) on near-horizontal valley- bottom habitats filled with sediments that are a mixture of autochthonous organic sediment and allochthonous clastic fines, 2) the bed of gullies that have recently filled with coarse grained clastic sediment, and 3) open water bodies. Three conceptual models were developed, one that accounts for the process of gully bed colonisation, sediment trapping and gully filling, another involving rapid colonisation of sedimentary fill from tributary sediment sources that block a gully, and the third involving colonisation of open-water areas that form in former gullies upstream of the blockage. The study suggests that the wetland has been characterised by repeated cutting and filling cycles, despite which, palmiet has repeatedly reinstated diffuse flow conditions across the valley floor. Palmiet was indicated to exert a key control on fluvial form and dynamics of the wetlands in the Kromrivier valley.

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1 Introduction

1.1 The prevailing conceptual model of wetlands

A conceptual model developed by Gosselink & Turner (1978) has been the foundation for wetland science for many years. The model suggests that hydrology is the main driver of wetland structure and function, which modifies soil biogeochemistry. The biogeochemical processes associated with the creation of anaerobic soils due to flooding, in turn, influence the biotic response in selecting for plants that can tolerate flooding of the root zone and animals that can exist in flooded habitats. The model has been modified in different contexts and presented in various forms, with the standard presentation being in the classic textbook "Wetlands" by Mitsch & Gosselink (2015), as illustrated in Figure 1.1.

Wetlands are therefore viewed as having three characteristics in common. Firstly, wetlands have shallow water above the surface of the Earth, or the water table is within 0.5 m of the surface. Secondly, soils undergo a range of biogeochemical reactions when they are flooded that gives rise to a distinct soil morphology in which metals become soluble and are leached from parts or all of the flooded soil profile. Thirdly, all wetlands support a variety of plants and animals adapted to saturated conditions.

It is therefore generally accepted that hydrology is the primary factor controlling wetland formation, as hydrology affects soil characteristics, which then influence wetland biota. However, there are feedback processes between these factors. Vegetation growth due to flooding increases plant productivity, which exerts a feedback on the hydrology by increasing roughness and slowing the flow of water through the landscape (Kotze *et al.*, 2008). Prolonged flooding also encourages organic accumulation due to reduced decomposition rates of organic matter, increasing soil organic matter content and raising the elevation of the wetland (Gründling *et al.*, 2015). In some cases, plants may confine stream width (Ellery *et al.*, 2003b) or even block and divert flow (Corker, 2000).

The model suggests that the formation, persistence, size, and function of wetlands are controlled by hydrologic processes, while geomorphology and climate exert controls external to the wetland and in ways to which the wetland simply "responds". Thus, the climate and geomorphology are "given" and the wetland simply responds to these external controlling factors. As such, climate and geomorphology provide a template for wetlands in that they control the water balance and basin shape in which wetlands exist.

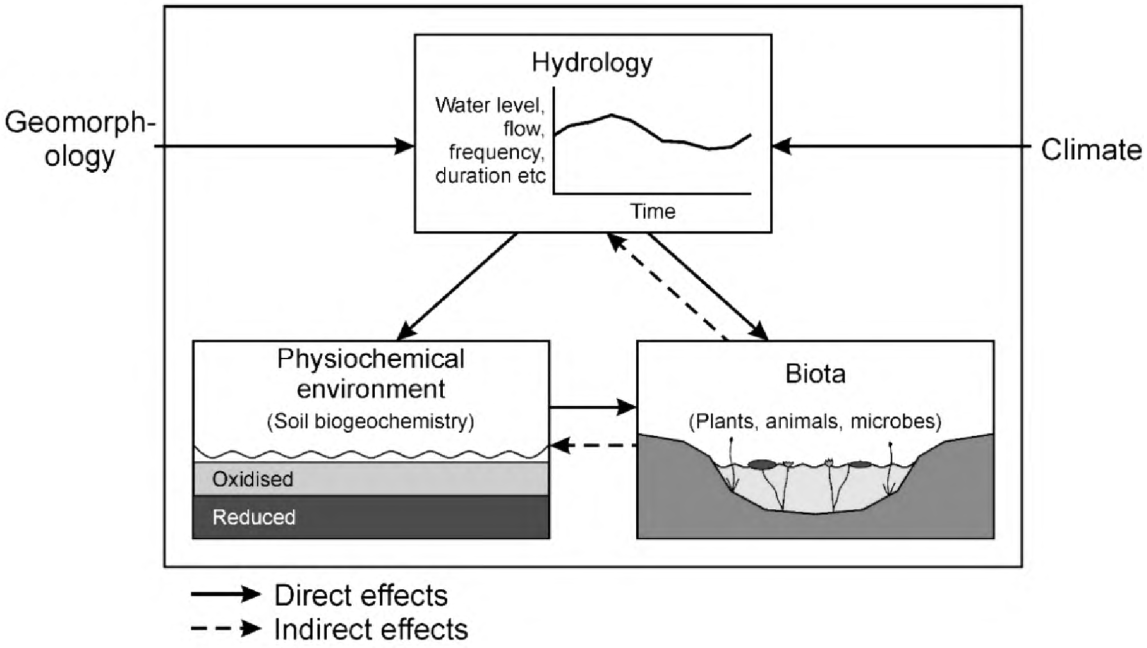

Figure 1.1: The three components of wetland structure and function: hydrology, soil physiochemistry and biota. After Mitsch & Gosselink (2015).

1.2 Controls on wetland distribution in southern Africa

Wetlands occur at the interface between terrestrial and aquatic environments, and between surface water and groundwater systems (Ellery *et al*., 2009). However, uplift events over the last 20 million years have raised the elevation of the southern African land surface by approximately 1400 m in the east and by 400 m in the west, creating an elevated subcontinent that is undergoing erosion at a subcontinental scale (McCarthy & Rubidge, 2005). The erosional landscape of southern Africa, which is characterised by incising rivers and a semi-arid climate results in many wetlands being integrated with the fluvial network and shaped by fluvial processes (Ellery *et al*., 2009; Job, 2014). Despite this, wetlands are generally considered as independent ecosystems, rather than as fluvial geomorphic entities (Edwards *et al*., 2016). It is important to consider wetlands as geomorphic sub-systems connected to, and integrating with, the fluvial system in southern Africa, in order to understand their structure and function. When the study of wetlands includes the whole host of fluvial and geomorphic processes associated with rivers, the impacts of climate, hydrology, flora and fauna can be better understood.

The sediment eroded, transported and deposited by moving water plays an important role in shaping the earth's surface (Anderson & Anderson, 2010). Understanding how moving water and sediment work to produce landforms and landscape features will provide insight into the occurrence, morphology and dynamics of wetlands in a subcontinent dominated by net erosion (Ellery *et al.,* 2009).

A base level is defined as the elevation below which a stream cannot erode its bed. Sea level is a base level for all rivers as no river entering the open ocean can ever erode its bed below sea level. As erosion lowers the slope of the bed of the stream, velocity declines such that the stream loses power to the point where it is no longer able to erode. Local base levels exist throughout landscapes, including lakes, impoundments, resistant lithologies and even landslides that block streams (Ellery *et al.*, 2009). Typically, floodplain and valley-bottom wetlands in South Africa are formed as a result of the presence of a local base level that limits the depth of incision in an upstream direction and promotes lateral planing of the valley floor (Tooth *et al.*, 2002; 2004). Such lateral planing of the valley floor by a meandering stream upstream of the local base level causes not only valley widening, but also longitudinal slope reduction upstream of the local base level. These processes illustrate how wetland formation and evolution are a direct consequence of geomorphic processes, and signify the importance of understanding geomorphic and fluvial processes in the study of wetlands (Garden, 2008).

The influence of vegetation on channel form and dynamics is often neglected; however, there is a growing scientific interest in these plant-river interactions (Franklin, 2008; Gurnell *et al.*, 2010; Larsen & Harvey, 2011; Nepf, 2012; Schoelynck *et al.*, 2014; Zong & Nepf, 2010). Mackin (1956) observed that the Wood River in Idaho, USA, alternated between a meandering and braided planform as its marginal vegetation changed from forest to prairie vegetation. Riparian vegetation is being increasingly recognised to exert a fundamental influence on fluvial form and dynamics, rather than being a response to the constraints imposed by fluvial processes and forms (Gurnell *et al.*, 2013). Macrophyte patches, for instance, reduce flow velocity as friction is increased, and consequently the flow velocity adjacent to such patches increases due to the deviation of flow around them (Franklin, 2008; Schoelynck *et al.,* 2012; Tooth *et al.*, 2014). Macrophyte patches thus create spatial variability in stream velocity and bring about geomorphological changes including bank stabilisation and sediment deposition (Gurnell *et al.,* 2013; Schoelynck *et al.*, 2014).

1.3 Concepts of ecosystem engineering by palmiet

It is well known that organisms can have significant impacts on the physical and chemical processes occurring in their environments. Some of these impacts are with regard to trophic interactions, and some involve organisms altering the physical structure or chemical reactivity of materials in their environment (Wright & Jones, 2006). It is the latter impacts, which are independent of the transfer of materials and energy via the food chain, to which ecosystem engineering refers. Therefore, an ecosystem engineer is an organism (or guild of organisms) that alters its habitat through modifying the flow of matter (other than via the food chain) and thereby influences the structure and functioning of entire ecosystems (Jones *et* *al.,* 1997). An example of an ecosystem engineer is the North American beaver (*Castor canadensis*), which constructs beaver dams along streams, thereby controlling the structure and function of the stream reach over which the beaver dam has been constructed.

It is thought that palmiet is an ecosystem engineer that is able to control fluvial form and valley morphology in wetlands in which it occurs (Sieben, 2012; Job, 2014). The role of biological factors in influencing wetland form and dynamics has not been extensively documented or studied in South Africa, and the precise role of palmiet in wetland recovery and controlling fluvial form has only been superficially examined (Sieben, 2012; Job, 2014).

1.4 Fluvial form and dynamics

Alluvial streams are ones that flow over material deposited on the streambed or that are flanked by floodplain deposits; they do not have their form controlled by bedrock alone (Schumm, 2005). Given that they flow on or alongside material that has been deposited by the stream itself, they are not entirely controlled by bedrock (Schumm, 1981). The relative proportions of bed load (sand and gravel), and suspended load (silt and clay), as well as flow variability, are the most important factors that determine not only the cross-sectional shape of the stream but the width-to-depth ratio and planform pattern (Schumm *et al.,* 2002). It is generally accepted that fluvial processes in alluvial streams form four distinct channel patterns along a continuum as shown in Figure 1.2, from straight, meandering, braided and anabranching (sometimes referred to as anastomosing; Schumm *et al.,* 2002).

According to Charlton (2008), stream type depends on stream gradient, bank stability (often as the result of riparian vegetation), and sediment supply. Braided rivers tend to occur on steeper gradients, where bars are formed because of the large supply of coarse (bed load) sediment, while single thread channels occur where there is a lower bed load sediment supply for bar formation. Anastomosing channels are multithreaded, but are much more stable than braided streams and commonly have thick clay and silt banks that are well vegetated (Nanson, 2013). Anastomosing streams form where bed load sediment is the main sediment available for transport. These streams would typically lead to a braided channel pattern, however in the case of anastomosing streams, the flow regime is relatively constant, and vegetation grows permanently and is sufficiently robust to colonise bars and stabilise them such that and the course of the channel is fixed (Brooks & Brierley, 2002; Lord *et al.*, 2009; Nanson, 2013; Polvi & Wohl, 2013).

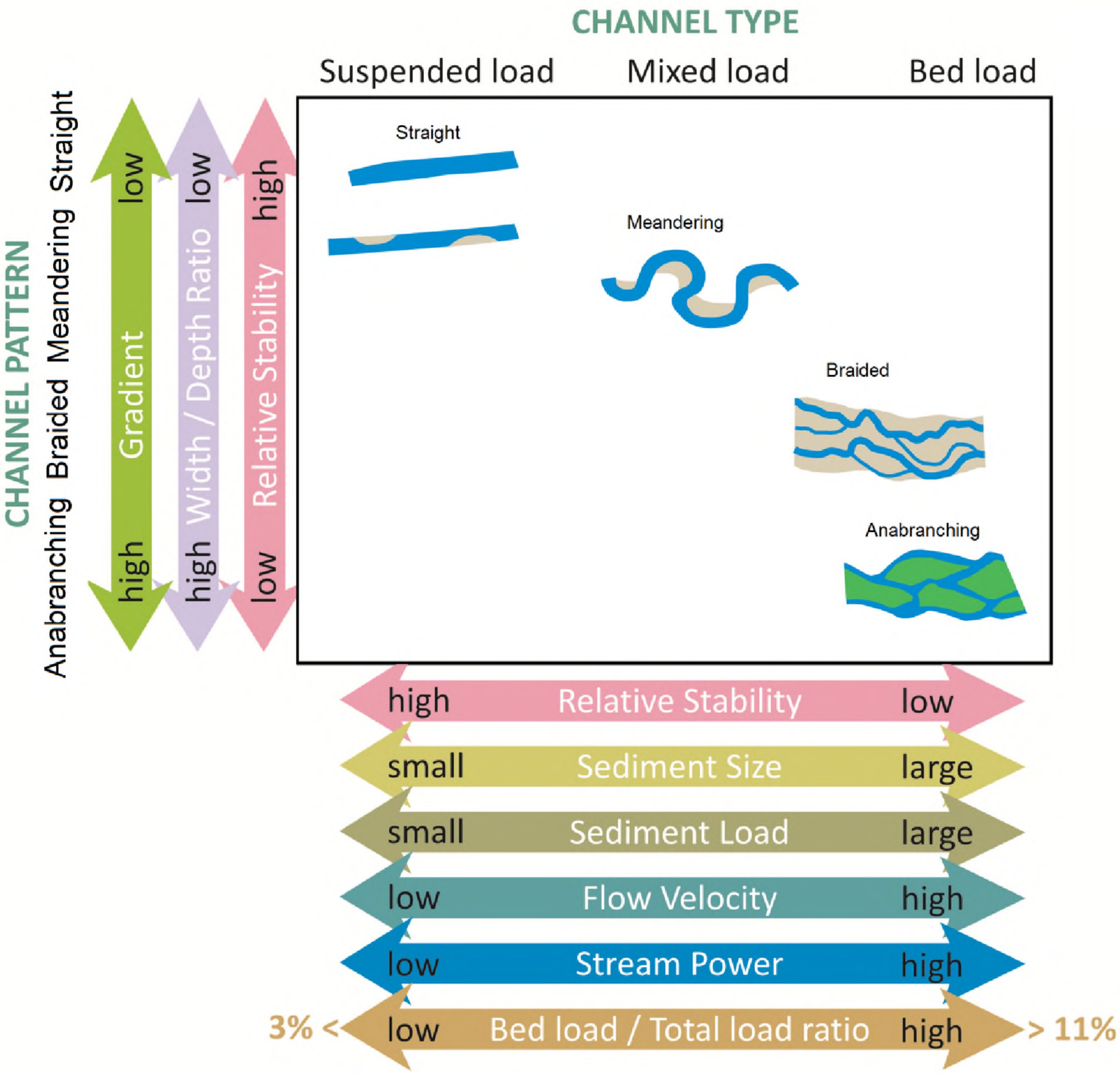

Figure 1.2: Alluvial channel classification based on channel planform and sediment load, with associated variables and stability specified. After Bently (2010) and Rinaldi *et al*. (2015).

The Kromrivier wetland is a valley-bottom wetland without a channel and is characterised by diffuse flow, despite being a stream that exhibits extremely variable, permanent flow (Rebelo, 2012). Given this, it does not fit any of the four channel patterns described above. The Kromrivier is dominated by palmiet, which is thought to grow from the stream margins, across them, blocking their course and causing diffuse flow (Rebelo, 2012; Job, 2014). This could explain why the Kromrivier does not follow traditional fluvial form. Plant growth affects channel development in two ways: firstly, impedance to sediment transport, and secondly, increasing bank strength (Millar, 2000).

There has been limited work investigating the possibility that diffuse valley-bottom wetlands may be the end product of vegetation control on a fluvial system. This work aims to investigate this by examining the possibility that palmiet might control channel pattern in a fluvial system. Species that control the structure of an ecosystem in this way are known as "ecosystem engineers" (Jones *et al.,* 1997). Palmiet has been referred to as an ecosystem engineer as it appears to control stream form and valley morphology in the unchannelled valley-bottom wetlands in which it occurs, however, there is no formal evidence that has been presented to support this claim (Job, 2014; Sieben, 2012). If palmiet is shown to exert a fundamental control on the structure of this wetland, it will be considered an ecosystem engineer.

1.5 Aim

To determine the role of palmiet as an ecosystem engineer and document the nature of its control of a fluvial system.

1.6 Key question

To what extent does palmiet influence fluvial structure and function in the Kromrivier wetland, and can it be classified as an ecosystem engineer?

1.7 Objectives

1. Map vegetation communities of the Kompanjiesdrif basin of the Kromrivier wetland and relate vegetation distribution to hydrological factors and indicators of wetland degradation by gullying.
2. Determine patterns of colonization of eroded gullies by palmiet and examine its role in sediment trapping and gully restoration.
3. Develop a conceptual model of the role of palmiet in wetland evolution in the Kompanjiesdrif basin of the Kromrivier wetland to clarify its role as an ecosystem engineer.

2 Literature Review

2.1 Hydrology as a driver of wetland structure and function

In this section, the relationship between the hydrological regime (the depth, duration and timing of flooding) will be examined in greater detail than in Chapter 1.

2.1.1 Hydrology and the physiochemical environment

The hydrological regime of wetlands, with varying frequency, depth and duration of flooding is what distinguishes them from terrestrial and aquatic ecosystems (Acreman & Miller, 2006). The hydrological regime influences the establishment and development of wetland ecosystems, including species composition and ecological functions (Ellery, 1988; Acreman & Miller, 2006).

According to Gosselink & Turner (1978), the most important attributes of the hydrological regime include the source, velocity, timing and renewal rate of the flow. The source of the water's flow is viewed as determining the chemical composition of influent waters. The velocity affects turbulence and the flows ability to transport suspended particulate matter. The renewal rate refers to the rate of replacement of the water, which is dependent on the volume, inundation frequency, and velocity. Timing refers to the frequency and season of inundation. These hydrological attributes are influenced by the climate and geomorphology of the wetland and catchment system.

The hydrology in turn influences soil properties, as flooded soils are anaerobic (Gosselink & Turner, 1978; Mitsch & Gosselink, 2015). The reduction and oxidation properties of flooded soils fundamentally influence solubility of many elements (mainly metals), which are stable in the solid phase under oxidising conditions, but which become soluble under reducing conditions (Metcalfe, 1931; Armstrong, 1967). In the first instance, the solubility of metals (especially iron) when soils are first flooded, makes these metals available for plant uptake, rendering these soils toxic to plant species (Armstrong, 1967). However, over prolonged periods, metals are leached from wetland soils such that they become increasingly gleyed (uniform grey in colour; Kotze *et al*., 1996). These soil geochemical properties influence the plants that are able to colonise a site, mainly because plants require oxygen in the root zone.

2.1.2 Biotic ecosystem responses to hydrology

Shallow flooding is a prerequisite for the formation of wetlands, requiring a sufficient water input for sufficiently long on a broad zone, where the longitudinal slope is suitably low to prevent rapid water loss (Gosselink & Turner, 1978). These conditions promote inundation of the land surface for periods that are sufficiently long to lead to anaerobic conditions in the soil, which is associated with biogeochemical transformations that give flooded soils distinctive biogeochemical and morphological characteristics. Flooded (anaerobic) soil is extremely stressful for plants, which need oxygen in the root zone in order to survive (Mitsch & Gosselink, 2015). Thus, only plants that are able to transport oxygen into the soil are able to tolerate these conditions and therefore wetland vegetation is quite distinctive.

The hydrological attributes and the physiochemical environment affect the biota, through ecosystem responses. Primary productivity for instance is affected and often limited by the substrate parameters listed above, the availability of dissolved nutrients being possibly the most limiting in terms of plant growth (Acreman & Miller, 2007). The availability of dissolved nutrients is vital for plant growth and is controlled by the source of the nutrients and of renewal. Toxins are also carried into wetlands by floodwaters. The extent to which herbicides and pesticides are made available to wetland plants and animals is determined by the frequency and velocity of flooding waters (Acreman & Miller, 2007).

Wetland species richness is largely affected by spatial heterogeneity, which in turn is determined by hydrology and local-scale elevation, as these factors interact to increase the number of niches available, and therefore the opportunity for successful invasion by a plant or animal species. The large *Phragmites australis* marshes at the mouth of the Mississippi river are an example of low species richness due to low spatial diversity (Gosselink & Turner, 1978). Here, floodwaters provide transportation for dissolved or suspended material, and due to uniform mixing, cause spatial heterogeneity to decrease (Gosselink & Turner, 1978). The hydrological regime interacts with topography to contribute to elevational and substrate differences, which are related to habitat and species diversity or uniformity. Where water rises over stream banks and spreads out, current velocity lessens such that coarse sediment is deposited close to the stream and becomes progressively finer laterally, resulting in an elevation gradient that is associated with variation in sediment particle size (Ellery *et al.*, 2012). Plant zonation in these wetlands occurs as a result of such habitat differences.

According to Cook (2015), due to the landscapes in which wetlands occur, the hydrological regime is not constant throughout the entire wetland. For instance, there are regions that are permanently flooded throughout the year, regions that are seasonally saturated, and regions that are temporarily saturated. These areas of different flooding duration are referred to as hydrological zones. Depending on hydrology, a wetland can possess all three hydrological zones, any two of them, or only one. These conditions allow for an environment where the distribution of hydrophytes varies in space.

Wetland vegetation is usually divided into three types, being; emergent, floating-leaved and submerged plants (Cronk & Fennessy, 2016). The distribution of these plant guilds is dependent on the hydrological regime of the wetland. The plants in a typical wetland are arranged in distinct, yet often overlapping zones from submerged vegetation in deeper and more permanently flooded areas, to floating-leaved vegetation in areas flooded to a shallower depth for shorter periods, to emergent vegetation in areas flooded to the shallowest depth (Noon, 1996; Ellery & Ellery, 1997). The hydrosere (zones) reflects differences in the degree of adaptation to aquatic life of different plant species. These zones, moving from dry land to open water consist of dry land plants, marsh plants, swamp plants, rooted floating plants, free-floating plants and submerged plants. The spatial distribution of plants represents a successional sequence that takes place over time as sediment (often organic sediment) accumulates and increases elevation of the land surface over time (Mitsch & Gosselink, 2015).

2.1.3 Feedback effects

The succession of different plant species can be observed in individual areas of a wetland, and is a good example of how biotic factors such as wetland vegetation can exert a strong effect on the hydrological regime that determines the existence of wetlands. Vegetation provides important feedbacks to hydrology through transpiration and the increase of flow resistance, as well as to the physicochemical environment by affecting soil properties and elevation, which is modified through the accumulation of organic matter and by trapping sediment (NRC, 1995). Animals such as North American beavers (*Castor canadensis*) and Atlantic salmon (*Salmo salar*) can also significantly affect hydrology, soils, and other biota (NRC, 1995; Moore, 2006).

According to Corker (2000), plants established in a particular region of a wetland will alter local environmental conditions through processes such as trapping sediment. This causes aggradation, often reducing the frequency of flooding, making it more suited to a different set of plant species. Typically, open water regions are colonised by plants suited to deep water areas. Clastic sediment becomes trapped among the roots and old leaf bases of these plants, gradually raising the level of the wetland. This allows rooted plants with floating leaves to establish. As clastic or organic sediment accumulates, the area becomes more suited to the establishment of emergent plant species. This continual succession process associated with increased elevation of the land surface may extend over many years until eventually dry land exists where once there was open water and wetlands.

2.1.4 Climate and geomorphology

In the model presented by Gosselink & Turner (1978) and the subsequently updated version by Mitsch & Gosselink (2015), climate and geomorphology are not viewed as playing a fundamental role in shaping wetland structure and function. However, geomorphic processes modify basin shape on an ongoing basis over timescales of decades, modifying hydrological processes to different degrees, such that it exerts a fundamental control on hydrological, edaphic and ecological processes in wetlands (McCarthy *et al.*, 1986; 1988; McCarty & Ellery, 1994; 1997; Ellery *et al.*, 1992; 1993; 1995; 2003a; Smith *et al.*, 1997; Tooth *et al.,* 2002; 2004). In southern Africa (at least), geomorphic processes have a large influence on the structure, functioning and dynamics of wetland ecosystems as a whole.

2.2 The creation of broad, gently sloping valleys in fluvial systems

2.2.1 Streams as integrated systems with feedback: the logarithmic longitudinal profile

Streams move water and sediment, which shapes the surface of the earth through erosion and deposition. Where the ability of a stream to transport sediment is greater than its sediment load, erosion occurs, and where sediment load exceeds the ability of the stream to transport sediment, deposition occurs (Ellery *et al.*, 2009). Where the transport ability of the stream and the sediment load are equal, there is no erosion or deposition. A combination of stream velocity and discharge enables running water to erode and transport sediment, where high velocities are required to move large particles, while lower velocities are required to move smaller particles (Kotze *et al.*, 2008).

Where erosion and deposition take place in a stream, a longitudinal profile is built in which the stream gradient is appropriate for the available discharge and sediment supply (Ellery *et al.*, 2009). Streams typically have a concave upward longitudinal profile from their headwaters to the sea. This is because streams erode material in relation to their velocity and discharge, and erosion lowers the slope on the bed of the stream. Thus, where velocity is high but discharge is low, such as in the headwaters of a catchment, stream power is low and erosion creates a stream with a steep longitudinal slope. However, as discharge and stream power increase downstream, erosion is able to erode material and create a much lower gradient on the bed of the stream. Thus, as discharge in a stream increases systematically downstream, the slope decreases. This concave-upward longitudinal profile is determined by the fact that rivers that flow into the sea cannot erode their beds below the sea level, which acts as a base level (Knighton, 2014). Local base levels can occur along the course of a stream where a tributary enters the main stream or at impoundments along the course of a river (Leopold & Bull, 1979). Base levels can change as sea levels change over time and impoundments are not constant, thereby altering the longitudinal profile of the stream (Leopold & Maddock, 1953).

A change in discharge, velocity, sediment load or base level will cause changes to the longitudinal profile, and the river will compensate to restore equilibrium. A river is in equilibrium when the channel form and gradient are balanced to transport water and sediment. A graded stream is a river in equilibrium, and tends to have a uniform concave upward longitudinal profile (Knighton, 2014). However, most rivers do not have entirely consistent concave upwards longitudinal profiles because variations in rock type across which the stream flows as well as the presence of tributaries or lakes, which create local base levels that cause steps to occur in the longitudinal profile.

2.2.2 Stream response to variation in discharge

Although streams are not able to control discharge and sediment supply, they are able to modify their longitudinal slope by altering width and depth, and therefore velocity (Leopold & Maddock, 1953). Streams respond to variation in discharge and sediment supply by altering their width or depth through erosion or deposition (Knighton, 2014). Typically, width and depth increase with increasing discharge, while velocity is mainly affected by the longitudinal slope (Leopold & Maddock, 1953). Streams usually increase in size downstream, as a larger channel is required to carry the increasing discharge.

2.2.3 Channel planform patterns in relation to sediment supply

2.2.3.1 Introduction

Alluvial channels are categorized based on sediment load and channel stability (Hogan & Luzi, 2010). Sediment is transported in the form of bed load or suspended load (Chanson, 1999). Bed load moves by rolling, sliding, and saltating (bouncing) over the bed, and moves at velocities lower than the surrounding fluid flow (Church, 2006). Bed load is generally thought to constitute 5 to 10 % of the total sediment load in a stream, making it less important in terms of the mass of sediment transported by streams. Suspended load, which is where particles are kept in suspension by turbulent eddies in the stream, usually makes up the rest, although this is not always the case (Leopold *et al.*, 1964). Three broad types of stream are recognised in terms of their sediment load: (1) suspended load dominated, (2) mixed load, and (3) bed load dominated. Between these three alluvial channel types, 14 channel patterns (forms) are recognized and described by Schumm (1986). Sediment load is the main driver of variation in channel planform pattern, and is thus important to examine.

Channels dominated by suspended load are narrow and deep and have low stream power and range from straight single channels to sinuous single channels (Lord *et al.*, 2009).

Suspended load dominated channels are defined as channels that transport less than 3 % bed load (Schumm, 1981). According to Schumm (1986), mixed load channels range from straight channels with coarse-grained bars to sinuous channels with coarse-grained bars. They transport larger quantities of coarse sediment than suspended load dominated channels. Mixed load channels have higher stream power, higher sediment transport rates and higher width-to-depth ratios than suspended load dominated channels (Schumm, 2005). Mixed load channels carry between three and 11 % bed load (Schumm, 1981). Bed load dominated channels have high stream power, high gradients, high width-to-depth ratios, and high sediment transport rates (Schumm, 2005). Schumm (1981) defines bed load channels as channels that transport more than 11 % of their total sediment load as bed load.

Based largely on the nature of the sediment load being transported, it is generally accepted that there are four main patterns (forms) of alluvial channels: straight, meandering, braided, and anabranching (Charlton, 2008). These four categories are often subdivided into a greater number of channel patterns. Patterns are based on sediment grade (size), sediment load, flow velocity, stream power and gradient (Charlton, 2008).

2.2.3.2 Straight channels

Schumm (1981) classified straight channels as either straight with migrating sand waves, or migrating alternate bars with a sinuous thalweg. Many rivers have been artificially straightened but naturally occurring straight rivers that are not bedrock controlled, are rare (Charlton, 2008). Straight channels are static, with low energy and high bank strength, which together limit channel migration.

2.2.3.3 Meandering Channels

Meandering channels form on a variety of bedrock and alluvial substrates. Alluvial meanders are associated with moderate stream power and develop in gravels, sands, and fine-grained silts and clays (Charlton, 2008). Meanders form and evolve over time as the individual bends migrate across the floodplain, with erosion focused on the outside of the bends and deposition focused on the inside of bends (Charlton, 2008). Meander cut-offs are formed when a bend is breached by a channel that connects the two closest parts of the bend, causing the river to flow along a straight path, abandoning the meander (Klein & Zellmer, 2014). The degree of meandering varies so greatly that some divide the category into two forms, those that deviate only slightly from a straight line, to those with highly convolute bends (Charlton, 2008). Meandering streams can be divided into passive and active meandering, which are often used in categorising channel planform pattern (Schumm, 2005). Streams that have a meandering form but are not actively meandering and therefore devoid of features associated with active meandering streams, such as point bars, cut banks and oxbow lakes, are generally referred to as sinuous (Stanistreet *et al.,* 1993).

2.2.3.4 Braided Channels

Braided channels consist of two of more channels divided by islands or bars, usually with a single dominant channel (Leopold *et al.,* 1964; Knighton, 1984). They are characterised by wide, shallow channels and are dominated by bed load sediment (Smith & Smith, 1984). According to Knighton (1984), the conditions required for the development of the form is an abundant bed load supply, erodible banks, and a highly variable discharge (Charlton, 2008). In addition to an abundant bed load, the load should contain size fractions which the stream is generally unable to transport (transport occurs during large floods), supporting initial deposits which form bars. These bars divert the flow against the channel banks, causing bank erosion, which in turn causes the wide, shallow channels associated with bed load transport. It has been suggested that steep slopes are not necessarily needed for braiding to occur (Parker, 1976; Chang, 1979; Charlton, 2008; Knighton, 1984). Braided streams are divided into bar-braided and island-braided channels. They are highly dynamic and experience frequent shifts in channel position, which can occur over the space of just days, or more slowly over years to decades (Charlton, 2008).

2.2.3.5 Anabranching Channels

Anabranching channels have flow that is divided into separate channels, called anabranches, by large, stable alluvial islands (Charlton, 2008). Individual anabranches can be straight, meandering, or braided (Charlton, 2008). The rate of lateral channel migration is low, and the inter-channel floodplain areas are relatively permanent, which is unlike that of braided channels (Lord *et al*., 2009). Thus, the islands are relatively stable, and are often well vegetated (Charlton, 2008). Deltas often form an anabranching pattern as the river adjusts to move sediment across low gradients before it enters a lake or the sea (Nanson, 2013). River planforms characterised by channels that branch and then rejoin were first described by Crist (1932) from the Llanos of Venezuela, and then by Whitehouse (1944) in central Australia.

The terminology of anabranching channels has resulted in some confusion, particularly when making distinctions between anabranching and anastomosing channels. Anastomosing channels are often referred to as the fourth channel pattern (Lord *et al*., 2009), when in fact they are a subset (and the most studied) of anabranching channels. According to Nanson (2013), the first group of streams that were described with an alluvial ‘anabranching’ pattern were associated with mostly fine-grained or organic sedimentation and were termed ‘anastomosing’ (e.g. Smith, 1976; Smith & Smith, 1980; Smith 1983; Knighton & Nanson, 1993). For a time, the two terms were used synonymously, but sedimentologists were reluctant to include higher energy, coarse grained rivers in the same category as the low energy, fine grain anastomosing channels. Consequently, the term ‘anabranching’ has become the umbrella term for multiple channel systems where stable vegetated islands divide river flow (Knighton & Nanson, 1996). Anastomosing refers to the subcategory of low energy, fine grained, and often organic rich anabranching channels (Nanson, 2013).

The channel planform of the Kromrivier is unlike any of those described by Charlton (2008), but it is an unchannelled valley-bottom wetland. It is therefore imperative to revise wetlands and wetland classification, in order to include unchannelled valley-bottom wetlands.

2.2.4 Definition of a wetland

The South African National Water Act (1998) defines wetlands as “lands which are transitional between terrestrial and aquatic systems where the water table is usually at or near the surface, or the land is periodically covered with shallow water, and which land in normal circumstances supports or would support vegetation typically adapted to life in saturated soil” (National Water Act, 1998: 18).

2.2.5 Wetland origin in southern Africa

Multiple uplift events that took place over the last 20 million years elevated the interior escarpment by approximately 400 m in the southern Cape (McCarthy & Rubidge, 2005; Marker & Holmes, 2010; Job, 2014). This uplift has produced an erosional landscape, causing the majority of coastal rivers to be in a state of incision (McCarthy & Rubidge, 2005; Marker & Holmes, 2010; Job, 2014). Erosion is considered to lead to the destruction of wetlands as it enhances the flow of water downstream and therefore reduces the residence time of water in the landscape, including wetlands. Therefore, wetlands should be rare in the region.

Despite these conditions, a wide variety of wetlands exists in southern Africa (Rogers, 1997). The formation of wetlands in southern Africa, as well as their distribution and structure, is recognised to be influenced by geomorphological factors that control the patterns of water distribution and retention in the landscape (Ellery *et al.*, 2009). As such, it is appropriate to investigate wetlands in southern Africa within the broad framework of fluvial geomorphology (Garden, 2008).

2.2.6 Wetland classification

Distinguishing between wetland types is important for continuing wetland research, management, and wetland conservation in a changing climate (Driver, 2010). Ollis *et al.* (2013) classified wetlands that occur in South Africa into six types: floodplain wetlands, channelled valley-bottom wetlands, unchannelled valley-bottom wetlands, depressions, seeps, and wetland flats. The classification system relates to the way water arrives at and flows through a wetland, and the source, volume and reliability of water and sediment supply (Tooth *et al.*, 2015). Because the present study occurs in a fluvial setting, only those wetlands that are integrated into the fluvial network will be described here, namely seeps, floodplains, channelled valley-bottom and unchannelled valley-bottom wetlands.

2.2.6.1 Floodplain wetlands

Floodplain wetlands occur on plains or gently sloping land that is entirely a product of fluvial processes associated with an alluvial river channel (Ollis *et al.*, 2013). These wetlands are characterised by geomorphological features linked to fluvial erosional and depositional processes that result from channel migration, including point bars, scroll bars, oxbow lakes and levees. In southern Africa, most floodplains form where a stream flowing across lithologies that are not particularly resistant to weathering and erosion, such as sedimentary rocks of the Karroo Supergroup, encounters a resistant lithology across its path (Tooth *et al.*, 2002; 2004). The resistant lithology acts as a local base level below which the stream cannot incise, such that the stream uses available energy to plane the valley laterally, as illustrated in Figure 2.1. Such lateral planing is associated with the development of a meandering stream, and a broad valley with a gentle longitudinal slope (Tooth *et al.*, 2002). Although these systems are sites of sediment accumulation, the sedimentary deposits in these systems are shallow (< 2 m thick), and the sediment storage in these features is generally temporary, as the wetlands are erosional in the long term as the dolerite dyke is eroding, albeit slowly.

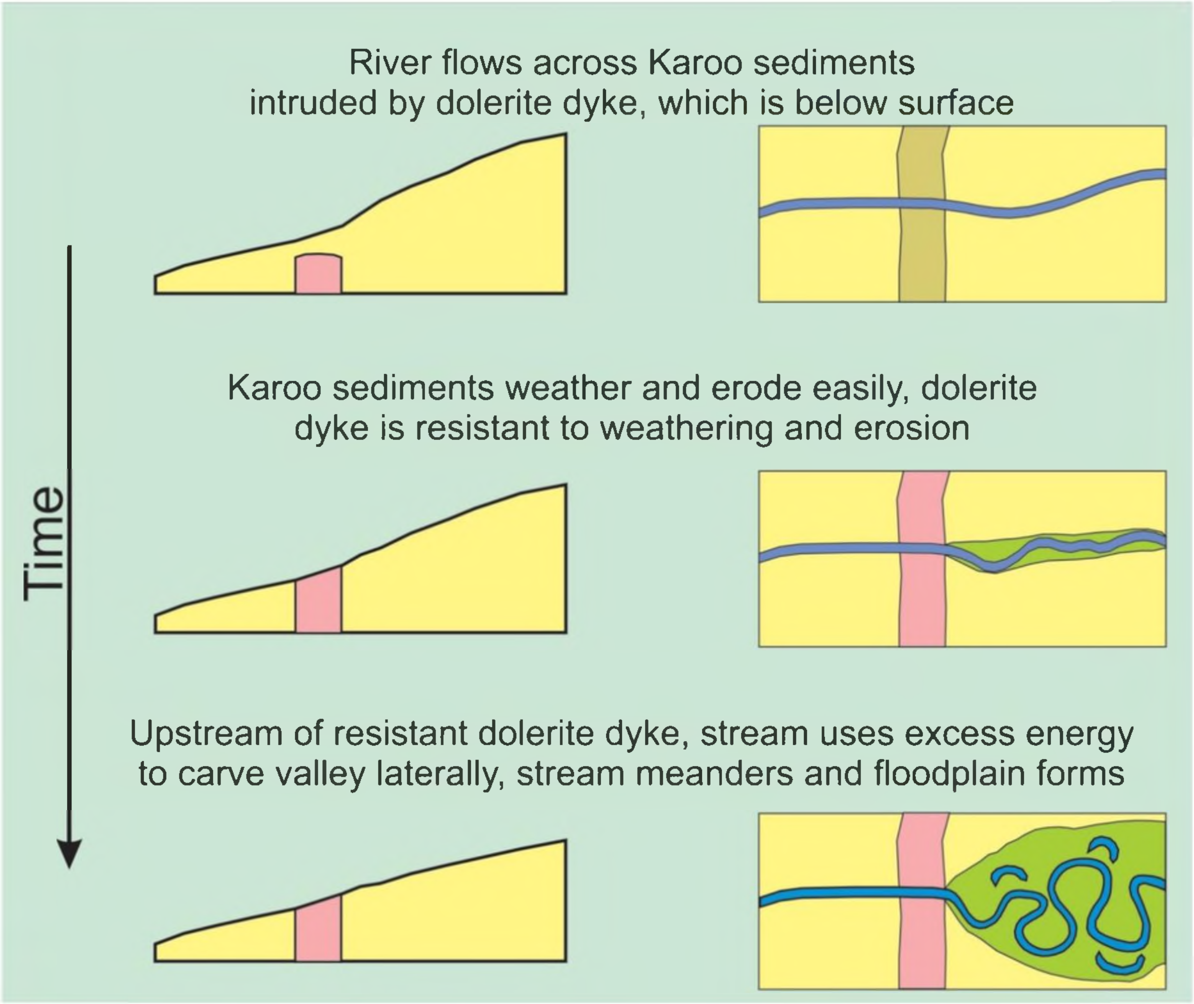

Figure 2.1: The Tooth *et al*. (2002) model of floodplain formation on the Highveld of South Africa.

2.2.6.2 Channelled valley-bottom wetland

Valley-bottom wetlands are located along a flat valley floor, and more often than not, are connected to an upstream or adjoining river channel (Ollis *et al.*, 2013). Channelled valley-bottom wetlands are sites of sediment accumulation; however, there is an absence of characteristic floodplain features such as oxbow lakes, although erosional features relating to riverine processes may be present. They tend to be narrower and have somewhat steeper gradients than floodplain wetlands, and the contribution from lateral groundwater input in relation to the mainstream channel is generally greater. Channelled valley-bottom wetlands have not been studied well and little is known about their formation.

2.2.6.3 Unchannelled valley-bottom wetland

Unchannelled valley-bottom wetlands are valley-bottom wetlands without a river channel. Unchannelled valley-bottom wetlands are identified by their location on valley floors, an absence of channel banks, and the occurrence of diffuse flows (Ollis *et al.*, 2013). Water inputs into the unchannelled valley-bottom wetland are usually from an upstream channel, but water moves through the wetland as diffuse surface or subsurface flow and exits the wetland via stream flow.

According to Joubert & Ellery (2013), the formation of the Wakkerstroom valley-bottom wetland in the South African Highveld interior can be attributed to geological, geomorphic and vegetation controls on alluvial stream behaviour. The early development of this wetland was similar to that of other dolerite-controlled systems in the Highveld, but today buried meander channel belt and flooded backswamp floodplain sediments can be found. The more recent development of the system is largely due to the interaction between trunk and tributary stream alluvial processes, where tributary streams deposit sediment on the trunk valley and block the flow of water down the wetland such that flow changes from being in a floodplain stream to diffuse flow. The elevation of the base level of the wetland over time therefore reduces flow in the stream to becoming more diffuse, following which, dense vegetation stands form across the entire valley floor. The Wakkerstroom Vlei trunk river thus loses its channel as it “floods out” along the valley-bottom component due to a “trunk-by-tributary” impoundment dynamic, which has been enhanced and preserved by the dense growth of *Phragmites australis* along these reaches. This results in a widespread, diffuse flowing unchannelled valley-bottom wetland, where conditions support the accumulation of peat.

2.2.7 Changes in wetland type

Tooth *et al.* (2014) describe how it is possible to change from one wetland type to another, based on environmental changes. Tooth *et al.* (2014) found that floodplains are able to change into unchannelled valley-bottom wetlands based on rainfall variation in the Blood River, northern KwaZulu-Natal. Between 800 and 100 years ago, the Blood River floodplain wetlands were characterised by a meandering channel flowing through the floodplain. During the last 100 years, there have been major morphological and sedimentary changes up-valley and the meandering channel has been replaced by a straight channel that narrows downstream, and terminates in an unchannelled valley-bottom wetland, characterised by an extensive reedbed. The reedbed consists of a dense stand of reeds and sedges (predominantly *Phragmites australis*). Thick layers of organo-clastic sediment have accumulated in the floodplains as lobes, in places burying the former meander sediments. Small headcut channels move water that filters through the reedbeds on the down-valley side of these lobes. If headcutting through the lobes continues, a through-going channel may re-establish up-valley, and could possibly link to the sinuous channel that flows in the lower part of the wetland.

The initial causes of the changes along the Blood River are unknown, although the establishment of the reedbed could be a key component of channel and floodplain development (Tooth *et al*., 2014). It is well known that the establishment of permanent water can encourage the growth of wetland vegetation, especially sedges and reeds. *Phragmites australis* is able to invade rapidly from the channel margins of slow flowing or inactive sections of channels. Once a dense stand of reeds is established, the trapping efficiency and channel roughness increase, due to their extensive rhizome and deep root network, which could result in channel diversion as well as channel abandonment and filling. It has been observed in other South African floodplain wetlands that once the rhizomes and rooting zone of reedbeds are undermined, headcuts form through the underlying clastic sediments (Tooth *et al*., 2014). As *Phragmites australis* colonises areas of former channel, it changes the system from a floodplain to an unchannelled valley-bottom, thereby modifying the structure of the entire wetland. There have been many cases of flora and fauna affecting wetland flow and sediment dynamics, resulting in changes in the channel (Smith *et al.,* 1997; Ellery *et al.,* 2003a; Tooth *et al.,* 2009; Tooth *et al*., 2014). The plants that modify wetland structure and function are termed “ecosystem engineers”, and could be key in highlighting the fact that hydrology is not the only factor to be considered when studying wetlands.

2.3 The role of vegetation and geomorphology in wetland ecosystems

2.3.1 The effect of vegetation on stream and wetland structure

Historically, vegetation has not been considered in classical models as a driver of channel form. Smith (1976) estimated a 20 000-fold increase in resistance to erosion offered by an 18 % volume root mass in riverbanks. Smith & Smith (1980) identified the importance of vegetation in structuring three anastomosing streams in the Banff River, Canada. It was found that the key characteristics of anastomosing channels were rapid aggradation conditioned by downstream control and channels that were stabilised by bank vegetation. Since the start of the 21st century, the impact of vegetation on fluvial processes and dynamics, including studies of bank processes, channel dynamics, channel planform styles and the development of particular landforms has been well-documented (Mackin, 1956; Franklin *et al*., 2008; Gurnell *et al*., 2010; Zong & Nepf, 2010; Larsen & Harvey, 2011; Nepf, 2012; Gurnell, 2013; Schoelynck *et al*., 2014). Despite the advances of the last decade, there is still much to learn about plants and fluvial geomorphology (Rowntree, 2000; Tabacchi *et al*., 2000; Smith-Adao & Scheepers, 2007; Gurnell, 2013).

Vegetation has been identified as a key control on channel planform, particularly in relation to transitions between multi-thread and single-thread planforms. Recent studies have documented the role of vegetation in affecting channel morphology and response over multiple spatial and temporal scales, by controlling channel width, grain size, bedforms, roughness, sediment transport, and rates of landscape lowering (Buffington, 2012). The importance of coherent banks supported by riparian vegetation for stable anabranches to form has been particularly well documented (Lord *et al.*, 2009; Nanson, 2013; Polvi & Wohl, 2013). Brooks & Brierley (2002) have shown how, prior to human disturbance, vegetation had a major role to play in maintaining naturally forested systems with low width-to-depth ratios and stable channels. Nanson (2013) has shown that on smaller rivers, vegetation is usually essential for maintaining the necessary bank strength for anabranching to develop. The significance of vegetation for bank stability and erosion resistance is dependent on the size, structure and biomechanical properties of both the above and belowground biomass in relation to the size of the stream (Gurnell, 2013).

Vegetation is also thought to cause channel narrowing and bring about single thread flow (straight or meandering) in streams that would otherwise be braided (Knighton & Nanson, 1996; Gran & Paola, 2001; Murray & Poala, 2003). According to Murray & Poala (2003), bank stability, which is often the result of plant growth, is the main cause of single-channel streams. Vegetation is able to reduce flow velocity and trap sediment on a bank, preventing the formation of channels. In the absence of vegetation, flow divisions and braiding arise from the formation of bars and the associated flow divergence in the stream. One such example of this is the once single-channelled Plum Creek in Colorado, USA. In 1965, a flood uprooted the majority of the vegetation, removing much of the silt and clay, transforming Plum Creek into a wider and steeper braided channel (Friedman *et al.,* 1996). A study conducted by Nevins (1969) reported how the Turandanui River in New Zealand, changed over the course of one year from a braided stream into a single meandering channel by planting willow shrubs on channel bends. Similarly, Tal & Paola (2007) showed that single thread channels could be formed and stabilised by vegetation.

There has been limited work investigating the possibility that wetlands may be the end product of vegetation control on a fluvial system. One such example is a study of the distribution of marsh vegetation in the Okavango Delta, Botswana, in which Ellery *et al.* (2003b) show the link between vegetation distribution in the channel margin, and channel characteristics. *Cyperus papyrus* was found to thrive in two situations. Firstly, it was able to occupy and invade areas of open water by floating as an entangled mat of rhizomes at the channel margin, thereby reducing channel width. A decrease in flow along the Okavango River as a result of an avulsion further upstream, allowed *Cyperus papyrus* to invade the partially abandoned channel, and in doing so has caused a decrease in width of the Okavango River.

The second occurrence of papyrus dominance was where water was being lost from channels as a consequence of aggradation over time due to the deposition of sediment on the bed of the channel. As a result, the channel became elevated above the surrounding areas that flanked the channel prior to aggradation. This allowed papyrus to invade permanently flooded areas and grow as an entangled mass of rhizomes on a relatively unconsolidated substratum with high hydraulic conductivity. Despite the channels water loss there was little apparent steepening of the hydraulic gradient away from the aggrading channel because the hydraulic conductivity through papyrus beds is very high. In general, water loss through papyrus swamps is high compared to water loss through channel margins dominated by other plant species as papyrus culms are spaced widely along the rhizome and thus water moves freely between them. Other plants found in the Okavango such as *Miscanthus junceus* have densely packed shoots, leading to lower hydraulic conductivity and steeper hydraulic gradients perpendicular to the channel.

A remarkable feature of channels in the Okavango Delta is that despite an order of magnitude variation in discharge from the upper Delta (140 $m^3.s^{-1}$ to just 17 $m^3.s^{-1}$) in the distal permanent swamps, the depth and current velocity of streams vary by approximately 20 % (Ellery *et al.*, 2003b). Interactions between current velocity and channel margin vegetation growth result in variation in channel width that is highly correlated to variation in discharge. The width of streams in the Okavango delta is largely controlled by vegetation, particularly *Cyperus papyrus*.

2.3.2 Ecosystem engineers and geomorphology in relation to wetland structure

Vegetation clearly has an important influence on stream structure, as well as wetland structure and function, although present models display biota as having only indirect effects on the hydrology and soil biochemistry. Current models also perceive climate as not being central to structuring wetland ecosystems. However, climate can play a large role in shaping both fluvial and wetland ecosystems, through its effect on runoff and therefore the ability of streams to erode and deposit sediment.

The physical architecture of wetlands is clearly shaped by geomorphological processes, which involve the movement and deposition of sediment, water and organic matter (Tooth *et al.*, 2015). This movement of mass associated with the shaping of wetlands can involve tectonic activity and the weathering, erosion, transportation, and deposition of surface materials. Most wetlands form where surface and groundwater flow is concentrated and drainage is impeded. Despite the evident importance of geomorphology as a process that contributes to wetland structure and function, the study of the contribution of geomorphology for wetland studies is limited. Instead, hydrologists and ecologists have focused on the local, short-term process interactions between hydrology, soils and biota, downplaying the geomorphological and climatic factors shaping wetlands (Tooth *et al.*, 2015). The study of geomorphology has tended to ignore wetlands and, consequently, the geomorphology of wetland science is not well understood by wetland scientists, policy makers, or land managers. Accordingly, it is essential to consider wetlands in the context of the wider geomorphic landscape in which they occur, particularly their local catchment. This study will highlight the effect that ecosystem engineers and geomorphology have in relation to wetland structure and function, particularly examining the influence that plants have on geomorphology.

2.4 Ecosystem engineering

2.4.1 Definition

Ecosystem engineering refers to the role that organisms play in the structuring of ecosystems through their influence on the flow of materials other than via the food web. This role has been studied for hundreds of years. Darwin (1881), for example, studied the effects that earthworms have on soil formation, an activity that later became known as bioturbation. Jones *et al.* (1994), however, was the first to coin the term ‘ecosystem engineer’, using the example of the creation and maintenance of wetlands by the North American beaver (*Castor canadensis*). When beavers construct dams, they alter the hydrology of rivers, from fast flowing streams to ones with diffuse flow, ultimately contributing to wetland formation (Naiman *et al.,* 1988; Jones *et al.*, 1994). This definition is useful as all organisms modify their environments in some way, but ecosystem engineering differentiates organisms that have an impact on ecosystem structure and those that work through trophic interactions.

2.4.2 Plants as ecosystem engineers in wetlands

Plants often act as ecosystem engineers in fluvial environments such as wetlands. For example, plants are known to assist in the removal of nitrogen, phosphorous and metals in wetlands (Tanner, 2001; McCarthy & Rubidge, 2005). The role of plants as ecosystem engineers in wetlands is most obvious in surface-flow systems. In these cases, plant shoots and leaf litter moderate water flow, stabilise sediments, shade and shelter the water column and provide habitats for other biota (Tanner, 2001). An example of a plant as an ecosystem engineer is that of the semi-floating *Cyperus papyrus* growing in the channel margin of streams of the Okavango Delta, which is able to create a vegetated levee in the absence of fine sediment that would typically be deposited on the channel margin (Ellery, 1988). The formation of levees by papyrus promotes the diffuse flow of water through the channel margin and through this, maintains thousands of square kilometres of permanent wetland in the Okavango Delta. In this way, papyrus controls fluvial form, and alters its environment as an ecosystem engineer.

Similarly, *Phragmites australis* controls the fluvial form of the stream in which it grows (Tooth *et al.*, 2014). *Phragmites australis* is known to invade slow moving streams from the channel margins, and through the trapping of sediment, causes channel abandonment and filling. In this way, *Phragmites australis* alters the system from a floodplain to an unchannelled valley-bottom. The examples of *Cyperus papyrus*, and *Phragmites australis,* both show how plants are able to modify and even "control" fluvial pattern, and in this way, behave as an ecosystem engineer.

2.5 Palmiet *(Prionium serratum)*

2.5.1 Description

Palmiet (*Prionium serratum*, Thurniaceae) is a common riparian wetland plant, occurring in river floodplains and along river fringes in the Eastern Cape, Western Cape, and Kwazulu-Natal Provinces of South Africa (Boucher & Withers, 2004; Rebelo 2012). The plant is evergreen and semi-aquatic and grows clonally to form extensive monotypic stands about 2 m tall (Figure 2.2; Munro & Linder, 1997). The leaves are stiff, leathery and pale green, with toothed edges. The main stem (which functions as a rhizome) is usually covered with the fibrous remains of old leaves. It grows throughout the year, flowering in spring and summer, with fruit appearing in March (Boucher & Withers, 2004; Rebelo, 2012). It is intolerant of saline water and cannot survive in full shade (Boucher & Withers, 2004).

Palmiet is a hydrophytic plant. Therefore, it has adaptations that allow it to survive in saturated environments. Hydrophytes have morphological, physiological and life history adaptations that enable survival in saturated or flooded soil (Ernst, 1990; Jackson, 1990; NRC, 1995).

Figure 2.2: Palmiet, *Prionium serratum*, growing across the Kromrivier in a clonal stand with *Phragmites australis* (common reed) sticking through it.

2.5.2 Palmiet as an ecosystem engineer

It has been suggested that palmiet is an ecosystem engineer with peat-forming properties (Job, 2014; Sieben, 2012). As well as providing the organic material that builds peatlands, palmiet also changes the hydrology of an ecosystem, slowing the flow of water in fluvial systems (Sieben, 2012). Palmiet has a dense root, rhizome and stem system, and forms dense stands, growing from the banks and from islands into fast flowing streams. This provides frictional resistance to flood flows, dissipating their energy and trapping any sediment, which builds up riverbeds and ultimately blocks river channels (Job, 2014).

The ability of palmiet to control fluvial systems has been recognised in palmiet peatlands in the Western Cape, where gully erosion greatly increases the flood risks to communities downstream (Ngetar, 2012; Job, 2014). Although these gullies are widely attributed to anthropogenic factors, Ngetar (2012) speculated that wetlands in South Africa might naturally experience valley widening through repeated cutting and filling processes. Job (2014) assumed that the formation of extensive peat deposits in the upper Goukou River appears to be controlled by palmiet. In the Goukou Wetland, the plant grows across the full width of the valley floor, and Job (2014) speculated that it ‘takes hold’ of the river, trapping sediment and slowing down the flow of the river. Palmiet is also able to withstand high energy floods. The remains of old leaves drape down, enclose the stems, and appear to protect the plants from damage during floods when rocks moving downstream would collide with and damage the plants (Boucher & Withers, 2004; Job, 2014). Palmiet is also able to bend sideways against the banks during excessive water flows, shielding the banks from erosion and lowering silt loads in the river (Gull, 2012).

Palmiet is peat forming and organic sedimentation leads to the formation of a deep peat basin across the valley floor (Sieben, 2012). Peat is defined as “a sedentarily (*in-situ*) accumulated material comprising of at least 30 % (dry mass) of dead organic matter” (Joosten & Clark, 2002). Peat wetlands form when the rate of production and accumulation of organic matter exceeds that of decomposition (Rydin & Jeglum, 2006). These conditions occur where plant productivity is high, due to an abundant water supply, and the rate of organic matter decomposition is low because soils are starved of oxygen. Additionally, a slow flow of water through the wetland (so that organic matter can accumulate), and a limited input of clastic sediment are required for the formation of peat (Rydin & Jeglum, 2006; Ellery *et al.*, 2012). The extensive rooting system of palmiet is also thought to play a role in ‘‘leaking’’ oxygen into the otherwise anoxic peat. This would result in the habitat being suitable for other species and other functional groups that do not usually occur in peatlands (Pugnaire & Valladares, 2007). In that sense, palmiet forms the foundation of a complete ecosystem.

2.5.3 Threats to palmiet

Palmiet plays a role in influencing fluvial style and forming extensive peatlands that hold water in the landscape for extended periods and therefore reduce flood risk for people living downstream. Despite the value of palmiet, it is viewed as a pest plant by farmers as it is believed to be a high water user and to block waterways, promoting flooding of arable land and infrastructure (Rebelo, 2012). Many landowners therefore actively remove palmiet from peatlands, threatening the integrity of these wetlands (Job, 2014). They use water found in the peatlands for irrigation, but simultaneously clear palmiet in an effort to limit its encroachment into their fields. Clearing palmiet has negative consequences for palmiet wetlands, landowners, and for people living downstream. The loss of palmiet wetlands leads to degradation of rivers due to its effect on reducing water quality and limiting the duration of base flows, as well as increasing flood risk (Rebelo, 2012; Sieben, 2012). Loss of palmiet will also make land more vulnerable to erosion during floods (Sieben, 2012). Proper management of these wetlands is therefore vital for the benefit of human well-being.

3 Study Area

3.1 Location

The Kromrivier is located in the Eastern Cape Province of South Africa (33°S; 24°E; Figure 3.1). It is about 100 km in length from its upper reaches (550 m above sea level) to its estuary. The Kromrivier Catchment (15 5631 ha) is narrow and steep, bordered by the Suuranys Mountains (±1 050 m) to the north, and the Tsitsikamma Mountains (±1 500 m) to the south, both oriented east to west. The river flows into the Indian Ocean through an estuary to the north of St Francis Bay, west of Port Elizabeth.

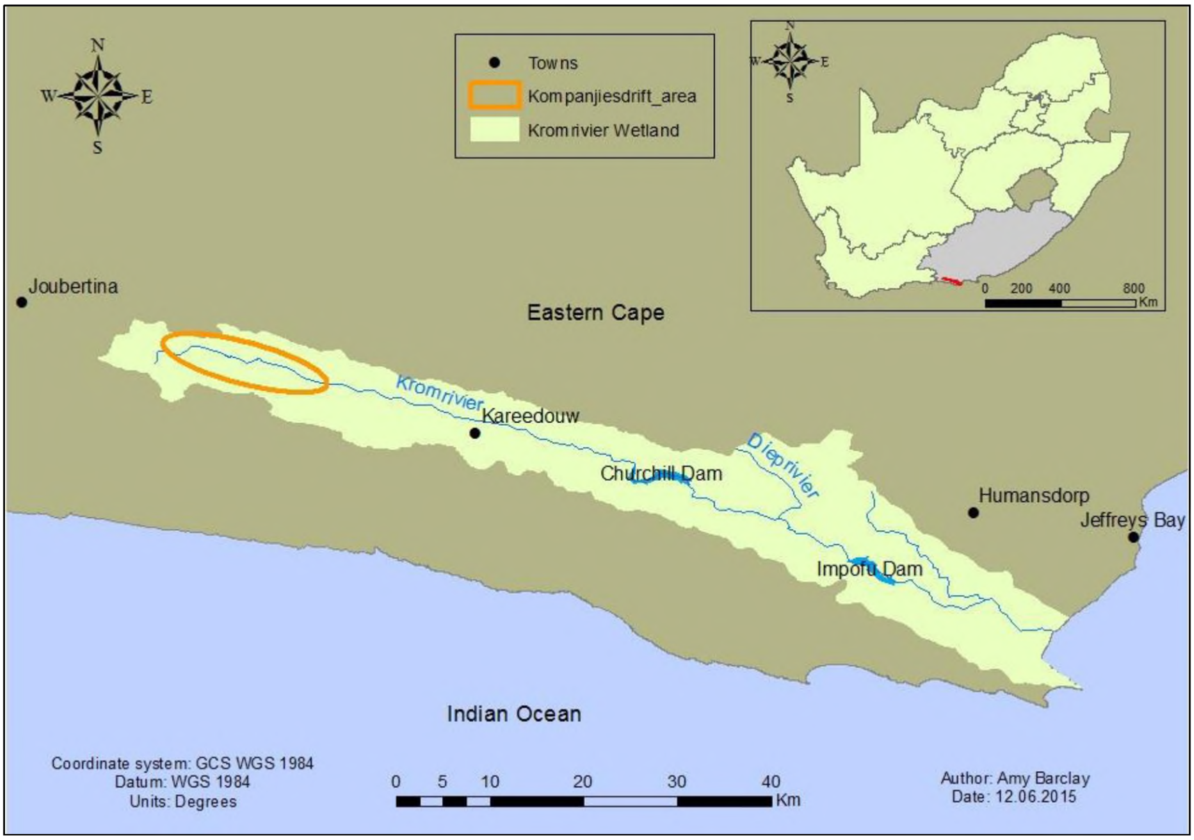

Figure 3.1: Vicinity map showing the Kromrivier catchment.

3.2 Upper Kromrivier wetland

The Kromrivier wetland is extensive, making up 1 077 ha of the catchment; however most of the catchment and the wetland is heavily degraded or completely transformed (Rebelo, 2012). The upper Kromrivier Wetland is a peat wetland system located near the town of Kareedouw. The peatland complex consists of a main basin, three peat sub-basins and various tributaries (Haigh *et al.*, 2002). These peatlands can be classified as valley-bottom fens. The altitude of the upstream basin ranges from 300 to 350 m above mean sea level, with an average slope of 0.6%. The total volume of peat within the three basins is approximately 6 000 000 m^3 (Rebelo, 2012).

3.3 Climate and rainfall

Rainfall in the region follows a bimodal pattern, with maximum rainfall in spring and autumn, however, it is often unpredictable (Nsor, 2007). Mean annual precipitation for the entire catchment is ±614 mm. Mean annual surface runoff for the catchment is ±75 mm, which is ±11 % of the rainfall (Middleton & Bailey, 2008). The catchment experiences occasional flooding. The largest flood recorded at the Churchill Dam, occurred on the 22 November 1997, when floodwaters deeper than 900 mm overflowed the dam wall.

3.4 Land use

Kareedouw is the largest town in the catchment, and has a population of fewer than 1 000 people (Rebelo, 2012). Apart from Kareedouw, there are a few small towns and settlements, such as Joubertina. The catchment has been heavily transformed by agriculture and alien invasion, with the upper catchment comprising mostly privately owned and farmed land. Farming in the catchment is largely intensive fruit, vegetable and large livestock farming. Poor farming practices are a major threat to wetlands in the area. These practices include clearing wetland vegetation, such as palmiet, and constructing drainage ditches in order to plant orchids. Overgrazing is also a serious threat to the catchment. Ecotourism is growing in the area, with a few game and holiday farms having been developed in the lower catchment to attract tourists.

The Kromrivier System has two major impoundments; the Churchill Dam (with the adjacent Churchill Water Treatment Works) and the Impofu Dam (with the adjacent Elandsjagt Water Treatment Works; Figure 3.1; Gull, 2012).

3.5 Geology

The catchment consists predominantly of shales and sandstones of the Cape Supergroup (Figure 3.2). The Cape Fold Belt is part of an intensely folded range with dipping beds forming a trellis drainage pattern (Boshoff *et al.*, 2000). The major geological formations are the Late Precambrian Nama Group (Cango Formation), the Ordovician to Denovian Cape Supergroup and Tertiary to recent deposits (Haigh *et al.*, 2002). Of the Cape Supergroup, Table Mountain Group rocks are the main mountain-forming lithologies. The core rock type is quartzite with subordinate shale horizons forming the bedrock of the Kromrivier basin. The prime soil type is dark organic-rich loam within the immediate vicinity of the peat basin.

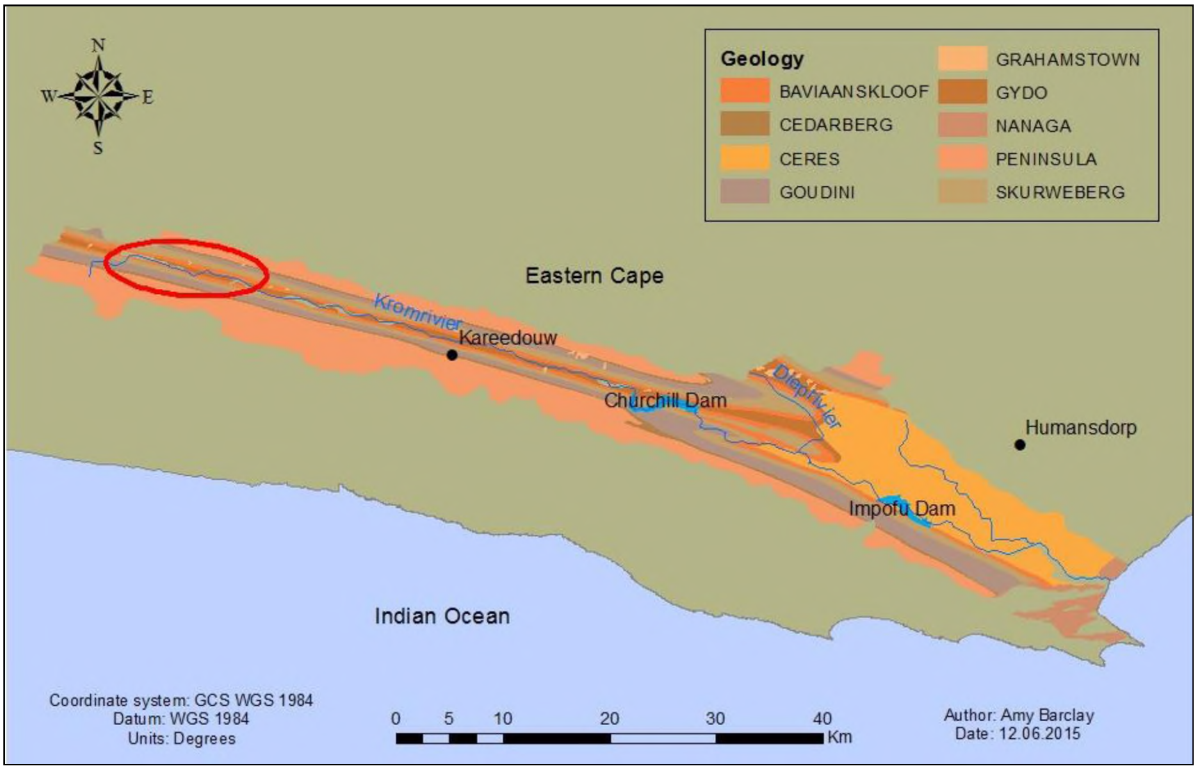

Figure 3.2: Geological map of the Kromrivier catchment.

3.6 Vegetation

The Kromrivier catchment vegetation is dominated by grassy and mountain fynbos (Mucina & Rutherford, 2006). This fynbos has been degraded severely in the lower slopes of the mountains, as well as in the wetlands, mainly due to grazing. Other vegetation types found in the catchment include grassland, thicket, renosterveld and forest (Vlok *et al*., 2008). The dominant vegetation of the peat basin is palmiet, with smaller areas of grasses, reeds, sedges and ferns (Haigh, *et al.,* 2002; Gull, 2012; Nsor & Gambiza, 2013).

There is alien vegetation in the catchment, particularly black wattle (*Acacia mearnsii*), which has invaded the catchment and parts of the wetland are completely dominated by it. This plant has been viewed as using large quantities of water and as being responsible for the collapse of palmiet wetlands across the range where palmiet occurs (Rebelo, 2012). Black wattle began invading the Kromrivier catchment in the 1930s and the wetland's health has deteriorated since then (Rebelo, 2012). By 2007, more than 11 % of the Kromrivier was invaded, mostly along the riverbanks. Working for Water has been clearing black wattle since 1996 and has made substantial progress since 2007 (Rebelo & Cowling, 2013).

3.7 Hydrology

There are six major and five minor tributaries entering from the southern mountain range, and seven large and numerous minor tributaries (seasonal) entering from the drier northern mountain range in the upper catchment (Haigh *et al.,* 2002). Several of the tributaries have alluvial fans that constrict the trunk valley and thus limit the extent of the palmiet wetlands. Groundwater recharge rates are estimated to be high despite the relatively low rainfall, largely because of the shallow soils in the mountain slopes and the low water-use of fynbos vegetation (Rebelo, 2012).

Peat beds develop along the trunk stream upstream of tributary alluvial fans. Two western peat basins cover 240 ha, whilst an eastern peat basin covers 150 ha (Rebelo, 2012). Peat beds are being destroyed by agriculture, ploughing of the wetlands, the removal of palmiet, water abstraction, draining, and gully erosion, the construction of dams, roads, railway lines and fences, alien plant invasion and peat fires (Haigh *et al.,* 2002).

3.8 Wetland health

Poor farming techniques, the invasion of black wattle on the floodplains and wetlands, the construction of tarred roads and bridges, and the channelling of the river, have escalated degradation and caused the health of the wetland to decline. In recent years, some riparian landowners also channelized the river using bulldozers, causing the river to incise further. This has resulted in water flowing down the river with unnaturally large amounts of sediment. As a result of these interventions, it is estimated that about 60 % of the system's peat basins were lost over the last century.

Headcuts have formed in the Kromrivier because of activities that have disturbed the Kromrivier's path, such as the building of a provincial road (the R62) and the building of the railway line through the wetlands (Rebelo, 2012). This, and damage caused by poor farming techniques and over grazing, created flow paths leading to erosion. The erosional nick-points have migrated upstream and created wider and deeper headcuts over time (Rebelo, 2012). The channels formed by the headcuts are detrimental because they drain groundwater, drying out the wetland, and leading to degradation.

Alluvial fans are a feature of the Kromrivier valley floor, and are apparent at the distal ends of tributaries. These fan-shaped deposits extend into the palmiet wetlands and restrict the area of these wetlands. These fans cause the increased rate of sediment delivery at these places (Haigh *et al.*, 2008). Flooding erodes the distal ends of the alluvial fans, which result in steep banks developing and contributes towards the advancement of headcuts (Gull, 2012; Figure 3.3).

Figure 3.3: A headcut in the upper Kromrivier wetland, above the Kompanjiesdrif basin.

Despite the loss of many of its wetlands, the Kromrivier still contains several extensive peat deposits, which continue to contribute to the improvement of water quality, attenuation of floods and maintenance of flow in the river. The catchment has also been the subject of extensive wetland rehabilitation by the statutory agency Working for Wetlands and invasive alien plant control by Working for Water since 2001. Working for Wetlands rehabilitation structures are designed to trap some of the massive amounts of sediment that move in pulses down the system every time there is a flood. Gabion structures, such as those used in the Kromrivier are thought to assist in bank and soil stabilisation, reducing erosion and decreasing the speed of water flow (Figure 3.4). They can also provide an area for vegetation to establish.

Figure 3.4: A gabion structure installed by Working for Wetlands in the upper Kromrivier wetland, above the Kompanjiesdrif basin, built to restore the river by stopping the headcut from proceeding backwards up the river.

4 Methods

4.1 Objective 1

Map vegetation communities of the Kompanjiesdrif basin of the Kromrivier and relate vegetation distribution to hydrological factors and indicators of wetland degradation associated with erosion.

4.1.1 Data collection

The study focussed on a single basin, the Kompanjiesdrif Basin, in which 150 samples were located (Figure 4.1). Two other locations were used, the farm Krugersland (in the Kompanjesdrif Basin to the west of the area shown in Figure 4.1, which was actively eroding (18 samples) and the farm Hudsonvale (east of the area shown in Figure 4.1), which comprised of vegetated wetland adjacent to a recently (two to three decades) eroded gully (15 samples). At each site, samples were placed systematically in an arrangement that approximated a grid, with spacing longitudinally down the valley being much greater than across the valley. Between five and six transects were located longitudinally at each site. Each sample had a radius of 2 m. Palmiet 'islands' in a gully below an erosion control structure were also sampled.

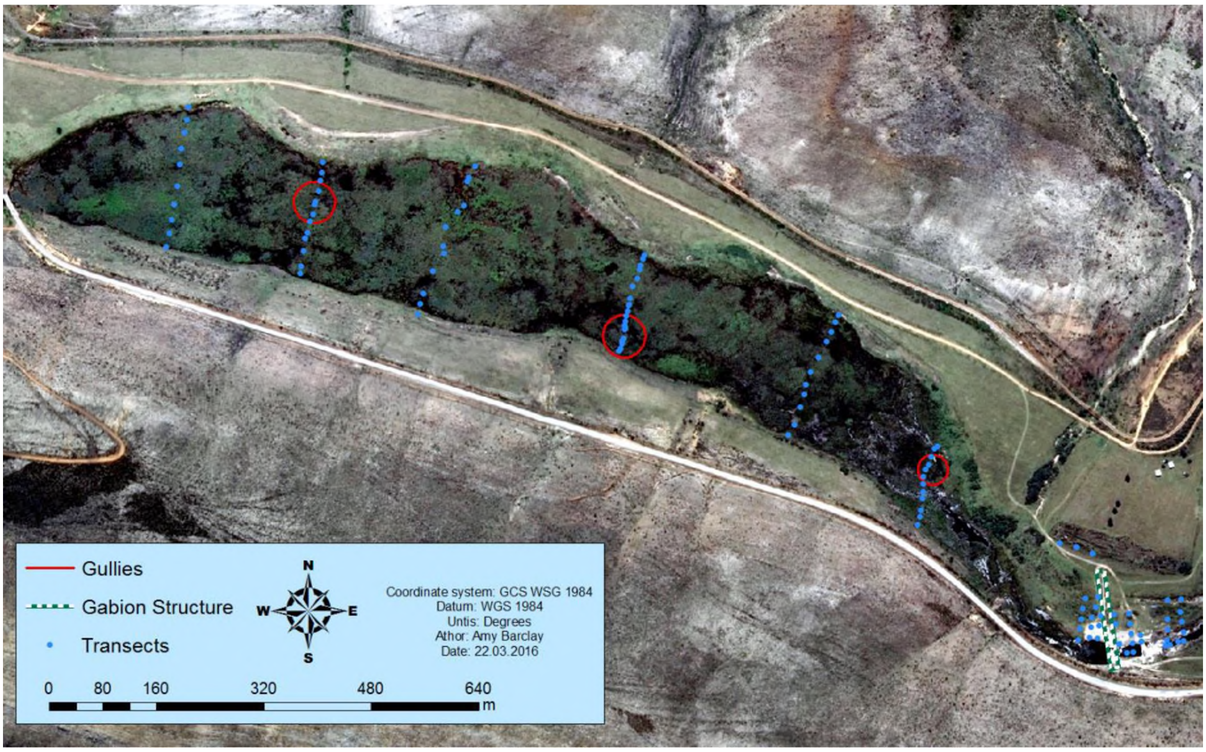

Figure 4.1: An orthophotographic image showing sample sites at the Kompanjiesdrif basin.

In each sample, an estimate of cover-abundance of plant species was made using a cover-abundance scale. All plants in each of the samples were identified to species level. At each sample, water depth, or depth to the water below the wetland surface was measured, as was distance of the sample to the nearest gully and distance of the sample to the nearest wetland margin. In addition to this, the elevation of each sample, in relation to the lowest point in the transect was measured using a Differential Global Positioning System (DGPS).

Sediment cores were collected systematically along each transect such that about 30% of samples were coredto a depth of 2.2m. The organic content of each sample was measured following low temperature combustion at 450 °C for four hours in a muffle furnace. Particle size was measured following combustion using a Malvern Mastersizer that measures diffraction of a laser beam passed through a dispersed sample. The median particle size values (dsv_{50}) for samples are presented.

4.1.2 Data analysis and presentation

Vegetation composition in each sample was analyzed using a multivariate approach; firstly by classification, using a Two-Way Indicator Species Analysis (TWINSPAN), and secondly by ordination, using a Detrended Correspondence Analysis (DECORANA). The ordination approach was undertaken using the statistical package canonical correspondence analysis (CANOCO). Simpson's diversity index, Shannon Diversity index, as well as species richness were calculated for each sample.

4.1.2.1 Classification

Classification is the process of grouping samples based on their similarity in respect of a large number of factors. In the case of the TWINSPAN, samples are classified on the basis of their species composition. The classification technique devised by Hill (1979) was used to classify samples in this study. The divisive method starts with the entire set of samples, and progressively divides it into smaller groups of increasing similarity (Gauch, 1982). In addition to grouping samples, TWINSPAN also identifies indicator species for these groups and creates a two-way table of their occurrence. Eigenvalues provide an indication of the fidelity of divisions in the TWINSPAN cluster analysis, and in this study, the threshold Eigenvalue of greater than 0.40 was considered sufficient to justify a division.

TWINSPAN is one of the most widely used cluster analysis techniques used in ecological studies of this kind for classifying samples based on their species composition, and organizing them into a two-way table that can be summarized as a dendrogram. Major groupings are provided along with indicator species, which are species that occur in a minimum of 80 % of the samples in one group of the division, and less than 20 % of the samples in the other group. For this study, any species occurring in a single sample only was not included in the analysis, as recommended by Gauch (1982).

4.1.2.2 Ordination

Ordination summarizes data sets by identifying similarity between samples based on their species composition, and presents this in relation to two or more axes of variation in the multidimensional data set. This was done using DECORANA. Results were then projected onto two dimensions in such a way that samples with similar species composition are plotted close together, while samples that did not have similar species composition are placed far apart. Ordination was also used to describe relationships between species composition patterns and environmental factors that might underlie these patterns.

4.2 Objective 2

Determine patterns of colonization of eroded gullies by palmiet, and examine its role in sediment trapping and gully restoration.

4.2.1.1 *Field work*

Current and former gullies were identified in the field and vegetation surveys were conducted at each site. Environmental factors such as water depth, depth to the water surface, elevation, and distance to the nearest wetland margin were recorded at each site. The sizes of individual colonies were measured and their elevation relative to the local water surface determined.

4.2.2 Data analysis and presentation

A map was created to display vegetation communities in the basin.

5 Results

The approach used in this study to start examining the question of whether palmiet is an ecosystem engineer was to examine its distribution in as wide a range of geomorphic settings as was evident in the study area. The approach was to classify samples based on species composition using classification and ordination, and relate plant community distribution to environmental conditions, particularly the geomorphic settings in which palmiet dominates. In this way, the role of palmiet as an ecosystem engineer could be examined in relation to the range of geomorphic contexts in which it is the dominant species.

5.1 Classification

The two-way table created from the TWINSPAN cluster analysis (Table 5.1) in conjunction with the output from the statistical analysis, especially the use of Eigenvalues, formed the basis for the classification of samples into communities based on their species composition (Figure 5.1). A summary of indicator and preferential species occurrences in each of the communities is provided in Table 5.2. The samples were divided into five major communities after four levels of division.

At the first level of division, the 183 samples (Group A; n= 183) were divided into two groups. This was based on the presence of the indicator species *Prionium serratum* in the negative group (Group B; n= -146) and the presence of the indicator species *Pennisetum clandestinum* in the positive group (Group C; n= 37), with an Eigenvalue of 0.854 associated with the division. Group B was characterised by the indicator species *Prionium serratum* (palmiet) which occurred in 76 % of the samples and was only found in two samples from Group C. Group C was not divided further in a meaningful manner and it was characterised as Community 5 by the indicator species *Pennisetum clandestinum*, which occurred in 35 of the 37 samples. *Arctotis arctotoides* occurred in 32 of the 37 samples in the *Pennisetum clandestinum* community, and both *Athanasia trifurcate* and *Leersia hexandra* occurred in 27 of the 37 samples. Species found in the *Pennisetum clandestinum* community were terrestrial or semi-terrestrial grasses and herbaceous groundcover, whereas those common in the negative were mainly hydrophytic plants.

At the second level of division, Group B (n= -146) was divided further based on the presence of *Prionium serratum* in 95 % of the samples in the negative group (Group D; n= -111), while *Miscanthus capensis* was found in 66 % and *Juncus Kraussii* in 60 % of the 35 samples in the positive group (Group E; n= 35). This division had an eigenvalue of 0.463. Group D was not divided further in a meaningful manner and it represents the *Prionium serratum* community (Community 1). This community is dominated by diverse vegetation such as the wetland plant palmiet (*Prionium serratum*), the single-stemmed tree, *Rhus rehmanniana*, the water-loving shrub, *Conyza scabrida,* and the herbaceous *Helichrysum odoratissimum*.

Group E (n= 35) was further divided at the third level of division, with 32 samples in the negative group (Group F; n= -32), and three samples in the positive group, forming Group G (n= 3). Group G was not divided further in a meaningful manner and it represents the *Metalasia densa* community (Community 4), distinctive only by the occurrence of the shrub *Metalasia densa.*

Group F was further divided at the forth level of division into Group H (n= -16), which was characterised by the indicator species *Miscanthus capensis* and Group J (n= 16) was characterised by the presence of *Juncus kraussii* in 88 % of samples. The *Miscanthus capensis* community (Community 2) was characterised by a presence of the grass species *Miscanthus capensis* in 94 % of samples and *Prionium serratum* that was present in 69 % of samples. The *Juncus kraussii* community (Community 3) was characterised, not only by *Juncus kraussii*, but also by the presence of *Clifortia strobilifera* and *Pteris dentata* in 56 % of samples.

Table 5.1: Cover abundance (TWINSPAN divisions), axis X shows sample numbers and axis Y shows species numbers.

(See Appendix A for species names)

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   234901567872456802068579134501234589014345689581277829538906789236171363467213790347895664568914535490124680129 2013733201725124 1236366847912587 407 9018927010456450539898227703561468903
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74 --------------------------------------------------------------------------------------------------------------4 ---------------- ---------------- --- 4-------4----------------------------
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Community:                                                    One                                                         Two            Three       Four                Five
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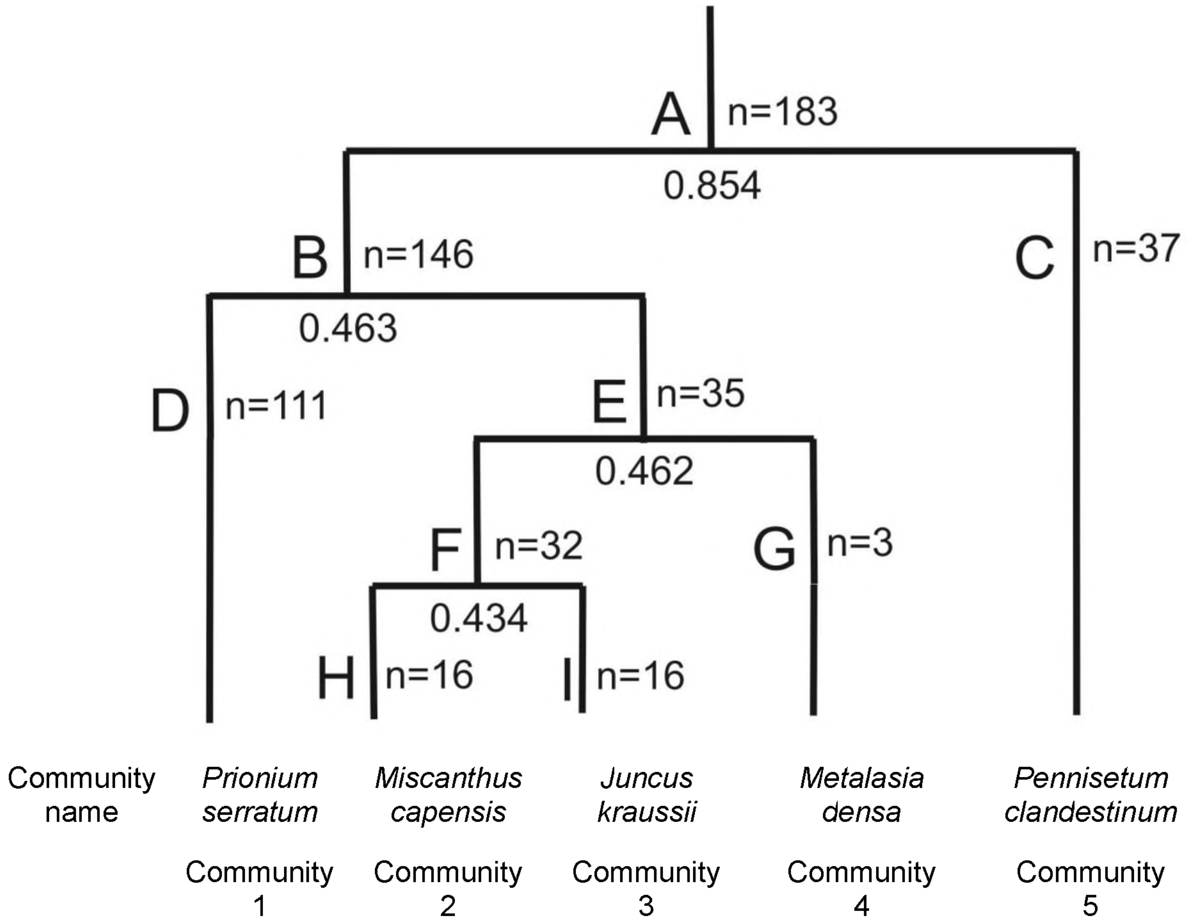

Figure 5.1: Classification of plant communities based on the TWINSPAN cluster analysis.

Table 5.2: Indicator and preferential species and their occurrence in each plant community identified in this study.

Species		**Community name and number (n= number of samples)**				
		Prionium serratum 1 (n= 111)	*Miscanthus capensis* 2 (n= 16)	*Juncus kraussii* 3 (n= 16)	*Metalasia densa* 4 (n= 3)	*Pennisetum clandestinum* 5 (n= 37)
Prionium serratum	A	**105 (2-6)**	**11 (1-6)**	1 (1)	0	2 (5)
Rhus rehmanniana	B	**52 (1-5)**	5 (3-5)	0	0	0
Conyza scabrida	C	**33 (1-6)**	5 (2-3)	1 (2)	0	1 (2)
Helichrysum odoratissimum	D	**30 (1-5)**	7 (1-4)	6 (3-4)	1 (1)	1 (1)
Miscanthus capensis	E	11 (3-6)	**15 (2-6)**	5 (2-4)	0	1 (4)
Clifortia strobilifera	F	21 (2-6)	**9 (1-4)**	**9 (2-5)**	0	0
Juncus kraussii	G	19 (1-6)	4 (3-4)	**14 (4-5)**	1 (5)	0
Pteris dentate	H	13 (4-5)	8 (2-5)	**9 (3-6)**	1 (3)	0
Metalasia densa	I	0	1 (4)	0	**3 (1-3)**	1 (2)
Pennisetum clandestinum	J	1 (5)	1 (5)	0	1 (2)	**34 (3-6)**
Arctotis arctotoides	J	1 (3)	0	0	1 (1)	**29 (1-6)**
Athanasia trifurcate	L	3 (2-3)	2 (3-4)	0	0	**27 (1-5)**
Leersia hexandra	M	2 (2-3)	0	1(2)	0	**26 (2-5)**
Trifolium burchellianum	N	0	1 (1)	0	0	**23 (1-3)**

5.2 Vegetation distribution

Figure 5.2 shows that the distribution of plant communities in the wetland does reflect a systematic spatial pattern from which it is possible to divide the study into three distinct regions: The terrestrial fringe, the wetland fringe, and the central wetland zone.

The *Prionium serratum* community is spread throughout the entire central wetland zone, upstream of any of the erosion control structures where the wetland forms a broad valley-bottom feature. In addition, palmiet dominates small and isolated monospecific islands on the bed of the gully downstream of any erosion control structures. This is the most widespread community in the wetland, both in respect of the extent of its distribution, and of habitats in which it is found.

The *Miscanthus capensis* community is restricted to the inner edge of the wetland fringe region. The *Juncus kraussii* community is also restricted to the wetland fringe region, although is not found in great abundance in this part of the Kompanjiesdrif basin, but the majority of the samples from this community are found in the same basin further upstream of where the Provincial road (R62) crosses the Kompanjiesdrif basin, on the Krugersland farm. The *Metalasia densa* community is restricted to the riverbank of the Kompanjiesdrif basin on the Krugersland farm, and the *Pennisetum clandestinum* community is restricted primarily to the terrestrial margin of the wetland, as well as, in two cases, occurring on a semi-attached island on the gully bed.

Overall, there is a generalised pattern of community change perpendicular to the flow in the wetland. Community 1 (*Prionium serratum* community) is found in the centre of the wetland, community 2 (*Miscanthus capensis* community) is found towards the edge of the wetland, followed by community 3 (*Juncus kraussii* community). Community 4 (*Metalasia densa* community) is found on the terrestrial margin of the wetland, as is community 5 *(Pennisetum clandestinum* community). This pattern has been explored further using ordination.

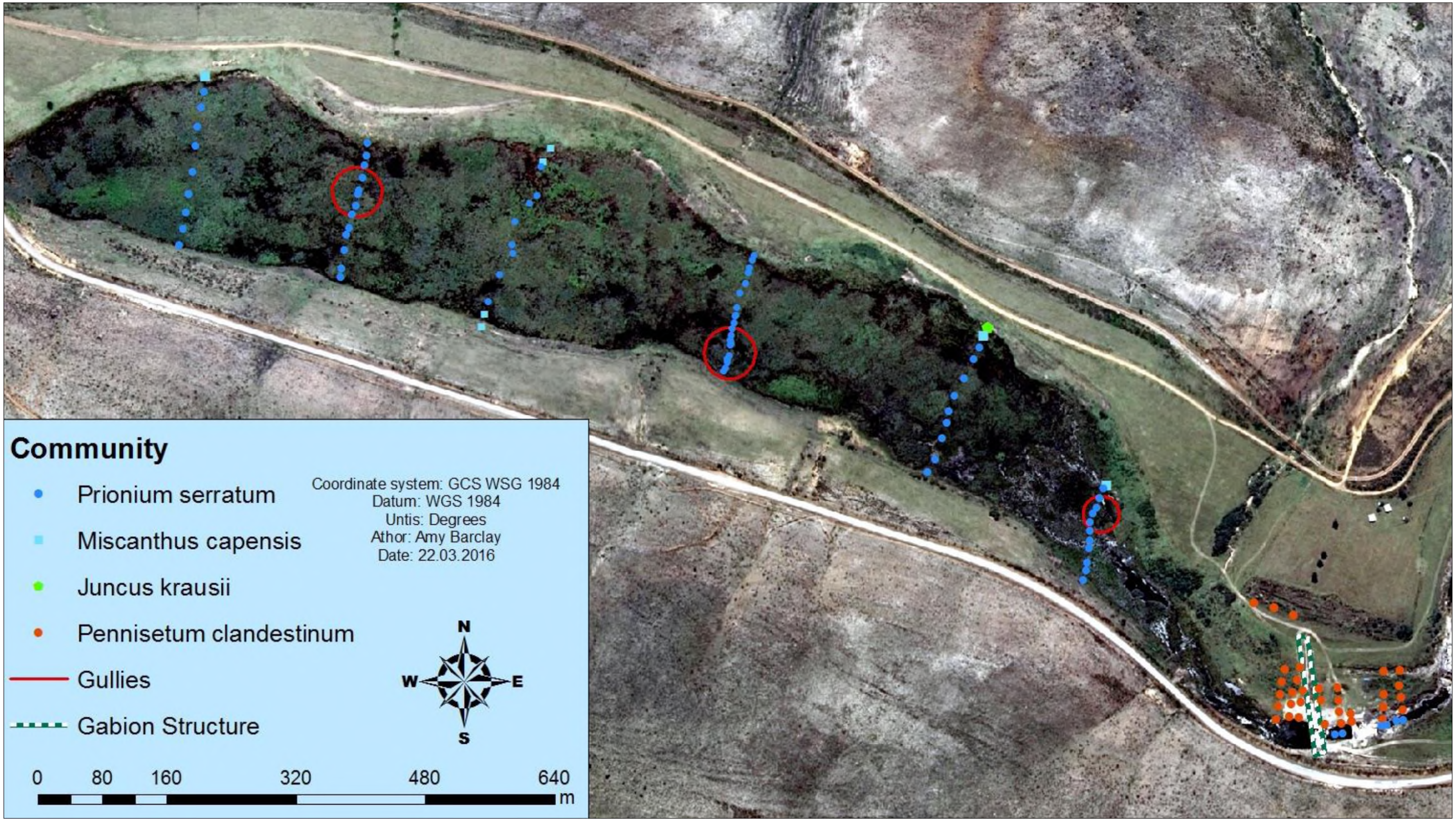

Figure 5.2: The distribution of vegetation communities in the wetland (several samples fell outside of the pictured area, including the three samples of the Metalasia densa community).

5.3 Ordination

5.3.1 Vegetation community distribution

Figure 5.3 shows the similarity and dissimilarity of samples along the first two axes of the detrended correspondence analysis (DCA) ordination. Samples are arranged with scores from zero to less than five on the first ordination axis, and from zero to less than four on the second axis. The proximity of samples to each other on an ordination diagram reflects their similarity to each other on the basis of their species composition. Communities identified in the TWINSPAN are generally clustered, reflecting that they have similar species compositions.

The samples were arranged in a manner such that samples of the *Prionium serratum community* in the centre of the wetland had low Axis 1 scores, while those on the terrestrial margin had high Axis 1 scores. The samples formed two distinct clusters along Axis 1, with the *Pennisetum clandestinum* community having a higher Axis 1 score than the cluster of communities one to four. Two samples from the *Pennisetum clandestinum* community occurred together with the samples of the first cluster. These two samples are island samples on the bed of the gully, possibly explaining why they had different scores to the rest of the *Pennisetum clandestinum* community.

Communities dominated by *Prionium serratum* (the *Prionium serratum* and *Miscanthus capensis* communities) had low Axis 1 scores and variable Axis 2 scores. These communities are dominated by palmiet and herbaceous vegetation and are found within the wetland itself. Transitional communities, i.e. the *Juncus kraussii* and *Metalasia densa* communities, where the vegetation is a mixture of terrestrial and hydrophytic species, had a range of Axis 1 scores. However, the *Juncus kraussii* community samples fell over a narrow range of scores on Axis 2. Similarly, the *Metalasia densa* community had a wide range of Axis 1 scores but a restricted range of Axis 2 scores. It is clear from the indirect gradient analysis that vegetation distribution is related to the position of samples in relation to a wetness gradient from wet (low Axis 1 scores) to dry (high Axis 1 scores). This was examined further by examining the environmental factors determining the distribution of vegetation.

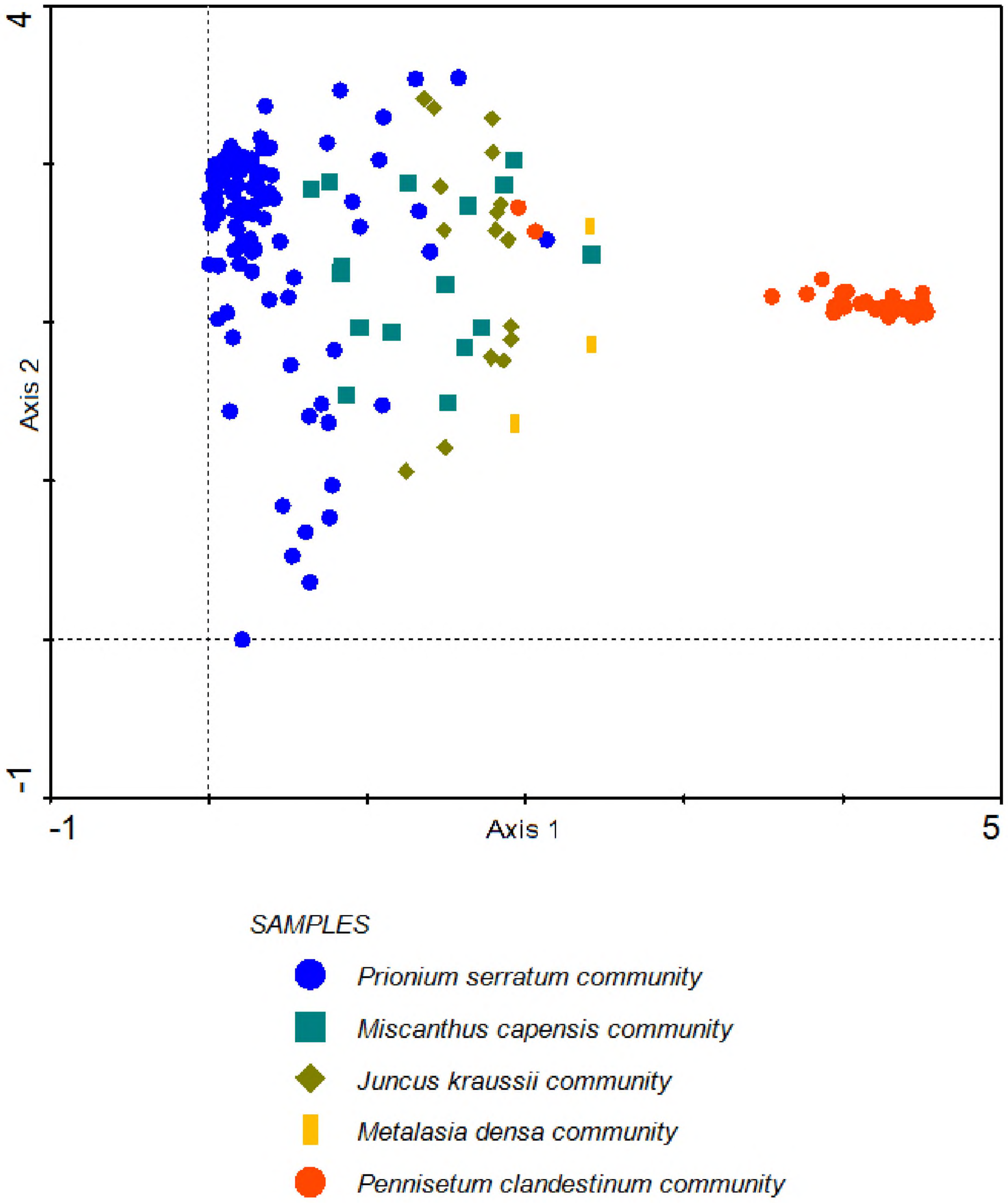

Figure 5.3: DCA-ordination diagram of the five plant communities identified in the TWINSPAN cluster analysis.

5.3.2 The influence of environmental variables on vegetation distribution

Figure 5.4 is an ordination of samples upon which variation in environmental factors has been superimposed. The distribution of samples in this scatter plot is identical to the scatter plot shown in Figure 5.3, given that the environmental variables were passively superimposed on the DCA ordination. The distribution of the *Prionium serratum* community is, with a few exceptions, positively related to water depth and the position of samples in the wetland, while distribution was negatively related to the distance of the sample to the nearest gully.

The communities with palmiet as the indicator species are widely scattered along the two axes of the ordination, indicating that palmiet is able to tolerate a range of environmental conditions.The *Miscanthus capensis* community samples also seem to be associated with variable environmental conditions, with sample points being fairly scattered along the first two axes of the ordination. The *Juncus kraussii* community is positively related to elevation and distance from the nearest gully and negatively related to distance of the sample to the nearest wetland margin and water depth, indicating that samples in this community are found towards the edge of the wetland at a high relative elevation. The *Metalasia densa* community and the *Pennisetum clandestinum* community are positively related to distance from the nearest gully and elevation, while they are negatively related to their distance to the nearest wetland margin and water depth.

Axis 1 was positively correlated with the distance of samples from the gully and elevation, and negatively related to distance to the nearest wetland margin and water depth. Axis 2 was negatively related to the size of the island. The species-environmental correlation of the four axes was somewhat low at 0.494, 0.386, 0.230, and 0.423 respectively (Table 5.3). Axis 1 had the highest correlation, meaning that species distribution could be meaningfully attributed to the measured environmental factors. The percentage variance of the species data is given cumulatively as well as for the species-environment relation (Table 5.3). Axis 1 captures 9.1 % of the variance of species data . Axis 1 accounts for 35.8 % of the cumulative percentage variance of species-environment relationship, and the first two axes account for 41 % of the cumulative percentage variance of species-environment relationship.

In general, communities found where water depth was high, are found in the centre of the wetland with high scores for "distance to the nearest wetland margin" and low scores for elevation and distance to the nearest gully. Communities where depth of the water was low (a negative water depth) were found on the terrestrial margins of the wetland where elevation and distance to the gully in the wetland were high. This confirms that communities are situated in order from Community 1 (*Prionium serratum* community) in the centre of the wetland, having greatest water depth, to Community 5 (*Pennisetum clandestinum* community) having the highest Axis 1 scores and restricted to areas where the water table was below the land surface, elevation was high and distance to nearest gully was also high.

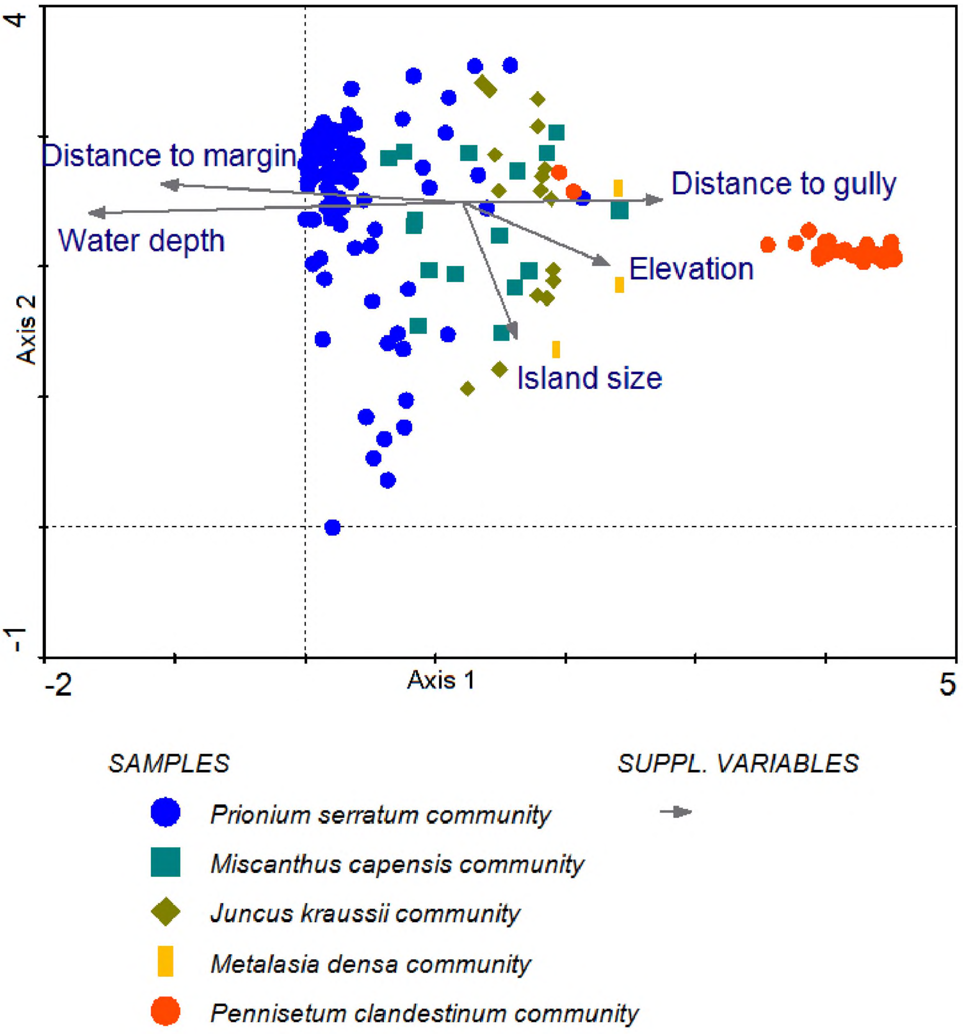

Figure 5.4: DCA-ordination diagram of the five plant communities identified in the in relation to environmental variables.

Table 5.3: Summary of DCA of species and environmental data for the Kromrivier.

Axes	**1**	**2**	**3**	**4**	**Total inertia**
Species-environment correlations	0.494	0.386	0.230	0.423	
Cumulative % variance of species data	9.1	15.6	20.7	24.4	
Cumulative % variance of species-environment relationship	35.8	41.0	0.0	0.0	
Sum of all eigenvalues					7.534

5.4 Substratum characteristics

A typical core in the *Prionium serratum* community (Figure 5.5a) was greater than 2.5 m thick. Bedrock could generally not be reached due to the presence of a sand layer at a depth of 2.5 m that collapsed, and could not be penetrated. The upper material contained layers of organic matter that had either a sludge-like consistency (organic sludge), or a compact consistency (organic compact). These substantial organic layers were interspersed with layer of clastic sediment varying from coarse sand to clay. The sand layer at the base of the cores had a greater particle size and lower organic matter content than the organic layers. The sand layer was found across the entire wetland at an approximate depth of 2 to 2.3 m and was often associated with a layer of fine material (silt and clay) directly above it. A second layer of finer sand was found in some cores as well; primarily along transect six, just above the engineered structure on the eastern edge of the Kompanjiesdrif Basin. Plant matter, often in the form of roots, but also in the form of palmiet stems, was often found within the core samples.

On six occasions in the Kompanjiesdrif basin, palmiet was found growing across a former gully that had been blocked with sediment further downstream, and was filled with water (Figure 5.5b). Gullies such as the one illustrated in Figure 5.5b, from transect two, were greater than 7.5 m deep and had a fine organic-rich sand layer at the base and coarser sand above it. Above these layers on the bed of the former gully, water was found, and palmiet had grown across the water surface such that without detailed and systematic coring, such overgrown former gullies would never have been found. Similarly, a gully in transect two was found to be filled with water from 0 to 470 cm, with organic sediment at 470 to 490 cm and sand at 490 to 496 cm. A second layer of organic matter occurred at 496 to 520 cm.

In cases where palmiet formed large clumps ("islands") on the bed of the gully below the gully stabilisation structures, it was growing on sand immediately above bedrock. In gullies such as the one in Figure 5.5c, there was a mound of sediment of coarse sand, gravel and rounded cobble trapped by the palmiet, and the area surrounding the clump was bedrock. Downstream of the island of palmiet there was often a lag of coarse gravel and cobble (Figure 5.6).

On these islands in particular, although this is generally the case in the palmiet wetlands in this study area, the old leaf bases in close proximity to the stem contain significant accumulations of sand. Palmiet is extremely good at trapping sediment, perhaps as an adaptation to reduce fire damage to stems when palmiet wetlands burn. This sediment trapping ability is associated with aggradation, which would occur rapidly on the beds of former gullies given sufficient sediment supply (Figure 5.7).

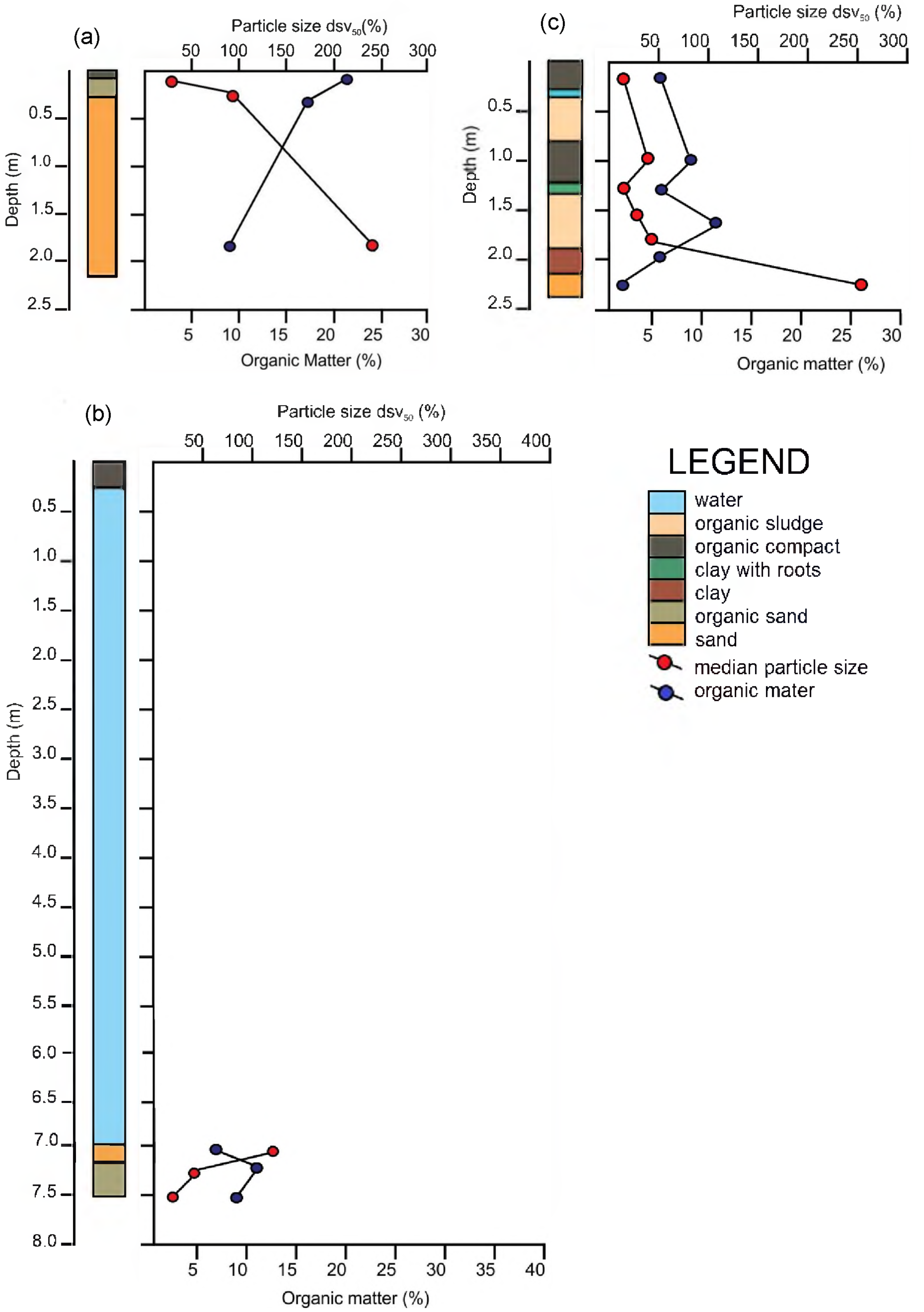

Figure 5.5: A core section showing the sedimentary stratigraphy of typical cores of the *Prionium serratum* community (a) (b) (c).

Figure 5.6: A palmiet stand growing on the bed of a gully, in the form of an island. Flow is from top-left to bottom-right of the photograph. To the right of the island is bedrock and to the left is sand and gravel. Downstream of the palmiet a bar of gravel and cobble is evident.

Figure 5.7: Sandy sediment trapped in the leaf bases of palmiet leaves from a plant on a sandy palmiet-dominated island on the bed of the gully downstream of erosion control structures on the eastern end of the Kompanjiesdrif basin.

Typical cores in the *Miscanthus junceus* community (Figure 5.8a) and the *Juncus kraussii* community (Figure 5.8b) were less than 2.5 m thick above a sandy substratum, with organic sludge found in both sediment cores. Clay layers were found in the *Miscanthus junceus* community cores (Figure 5.8a). Typical cores of the *Metalasia densa* community (Figure 5.8c) and *Pennisetum clandestinum* community (Figure 5.8d) were on substratum material of tributary alluvial fans and not on valley fill sediment associated with the valley-bottom, as indicated by their largely clastic nature.

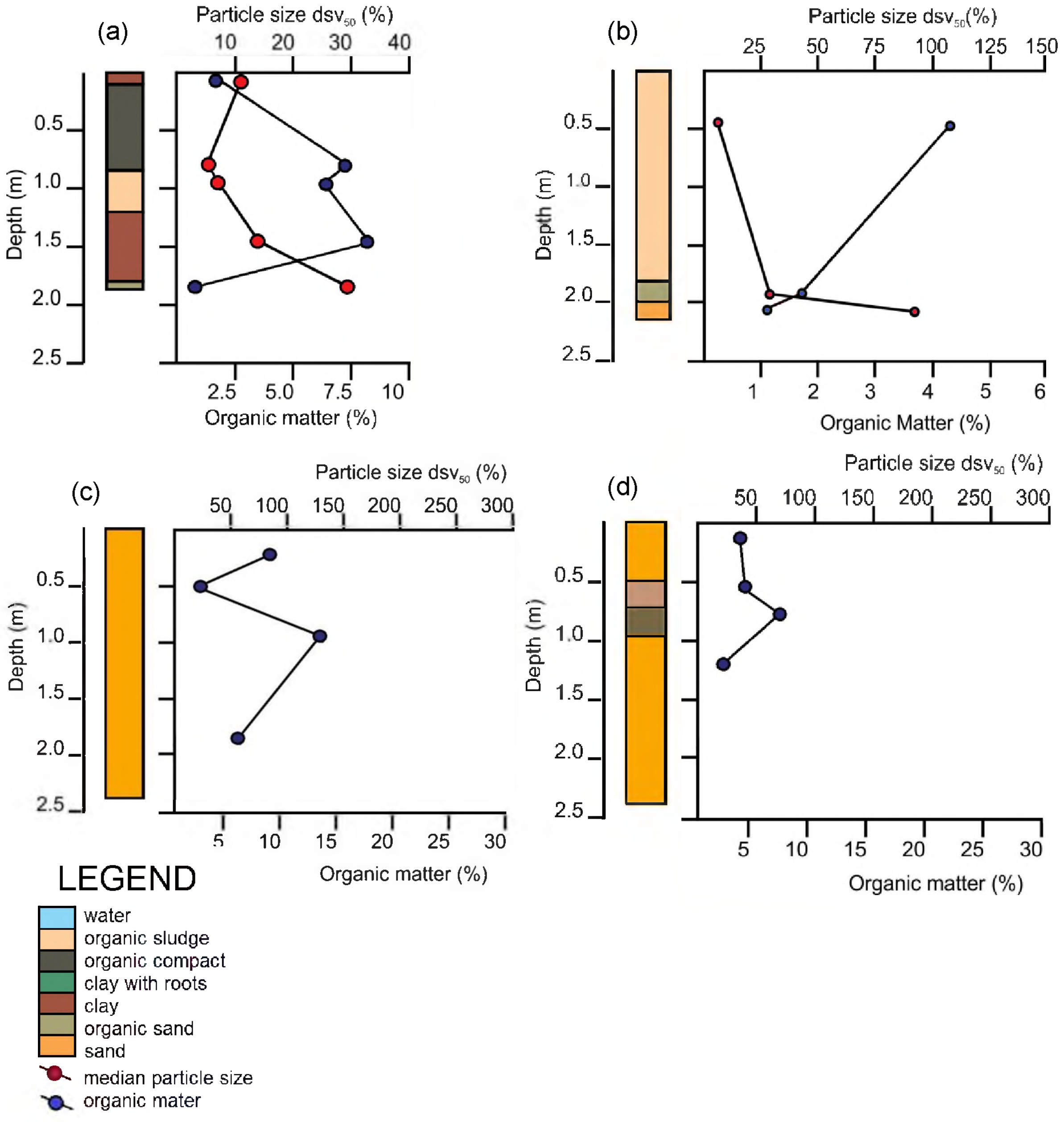

Figure 5.8: A core section showing the sedimentary stratigraphy of typical cores of the *Miscanthus junceus* community (a), the *Juncus kraussii* community (b), the *Metalasia densa* community (c) and the *Pennisetum clandestinum* community (d) in the Kompanjiesdrif basin.

5.5 Community descriptions

Based on the TWINSPAN analysis, it was possible to distinguish five communities, while the DCA provided insight into the environmental factors that were related to community distribution. The communities included herbaceous marsh communities with palmiet as an important dominant species, *Miscanthus capensis,* and *Juncus kraussii* communities and grassy-fynbos vegetation along the edge of the wetland and the terrestrial margin (*Metalasia densa* and *Pennisetum clandestinum* communities).

5.5.1 Prionium serratum community

The average number of species per sample was lowest in the *Prionium serratum* community, at four species (Table 5.4). This community contained a surprisingly wide range of species such as the wetland plant *Prionium serratum*, the single-stemmed shrub *Searsia rehmanniana*, the water-loving shrub *Conyza scabrida,* and the herbaceous *Helichrysum odoratissimum*. The Simpson diversity index (D) was 0.08904, which was the highest of all the communities. The Shannon diversity index (H') was 2.963, which was the lowest score of all the communities (Table 5.4). As the Simpson diversity index weights dominant species and the Shannon diversity index does not, it was possible, using these two indices to see the impact that the dominant *Prionium serratum* had on these measures of community-level diversity.

The *Prionium serratum* community occupied the entire centre wetland zone highlighting the ability of *Prionium serratum* to colonize and dominate permanently flooded conditions within the wetland. Palmiet's dominance was a product of its ability to occupy three distinct habitats in the wetland. Firstly, palmiet was able to clonally invade areas of open water that remained as a result of the blockage of a former gully due to sedimentation from tributary alluvial fans further downstream. Secondly, palmiet colonised local areas of permanently flooded sediment on the gully floor downstream of the gabion structure designed to stabilise headward erosion of a gully. Because of its dense root, rhizome and stem system, palmiet was able to grow into dense stands on the gully bed of eroded valley sections. Over time, palmiet trapped sediment, which played a role in stabilising the gully bed. The third habitat where palmiet was found was on organic and clastic sedimentary fill that has accumulated to substantial depths across the wetland, where there was no evidence of former gullies.

5.5.2 Miscanthus capensis community

The *Miscanthus capensis* community had an average species number per sample of seven. The community was restricted to the wetland fringe region, where the palmiet decreases in abundance and gives way to more terrestrial communities, including species such as the grass *Miscanthus capensis* and the shrub *Cliffortia strobilifera* and the herb *Helichrysum* *odoratissimum*. The Simpson diversity index (D) of this community was 0.0503, and the Shannon diversity index (H’) was 3.105 (Table 5.4).

5.5.3 Juncus kraussii community

The *Juncus kraussii* community was restricted to the wetland fringe region. The *Juncus kraussii* rush occurred in high density in the shallow waters of the edge of the wetland. Dominated by *Juncus Kraussii* and to a lesser extent, the terrestrial fern, *Pteris dentata*, the community was a transitional community between wetland communities and terrestrial communities. The average species number per sample of the *Juncus kraussii* community was six, which was similar to the *Miscanthus capensis* community. The Simpson diversity index (D) score of this community was 0.0568, and the Shannon diversity index (H’) score was 2.971 (Table 5.4).

5.5.4 Metalasia densa community

The *Metalasia densa* community had an average of 11 species per sample (Table 5.4). The Simpson diversity index (D) score of this community was 0.01852, and the Shannon diversity index (H’) score was 3.016. It was restricted to the wetland/terrestrial interface on the outermost fringe of the wetland.

5.5.5 Pennisetum clandestinum community

The *Pennisetum clandestinum* community had an average of seven species per sample. Four of the species found in this community occur only in the *Pennisetum clandestinum* community and ten species were encountered infrequently. This community consisted predominantly of grassy-fynbos vegetation. The Simpson diversity index (D) score of this community was 0.06715, and the Shannon diversity index (H’) score was 2.984, which was the lowest of all the communities (Table 5.4). The *Pennisetum clandestinum* community was also restricted to the slopes outside of the wetland, in the upland zone, except for occurring on two islands below the gabion structure. These were the only two samples of the *Pennisetum clandestinum* community where palmiet was growing.

Table 5.4: Results of the community distribution analysis, showing species richness, diversity index values, and population size.

	Prionium serratum	*Miscanthus capensis*	*Juncus kraussii*	*Metalasia densa*	*Pennisetum clandestinum*
Species richness:	46	32	28	22	35
Simpson diversity index: (D)	0.08904	0.0503	0.0568	0.01852	0.06715
Shannon diversity index: (H’)	2.963	3.105	2.971	3.016	2.984

5.6 Longitudinal profile and cross-sections

Examination of the longitudinal profile of the entire length of Kompanjiesdrif basin from transect one, immediately downstream of the provincial road bridge (R62) to immediately upstream of the gabion structure on the eastern edge of the basin, shows the wetland to have a relatively uniform and gentle slope of 0.85 % (Figure 5.9). At a distance of about 600 m from the upper part of the wetland, the valley steepens.

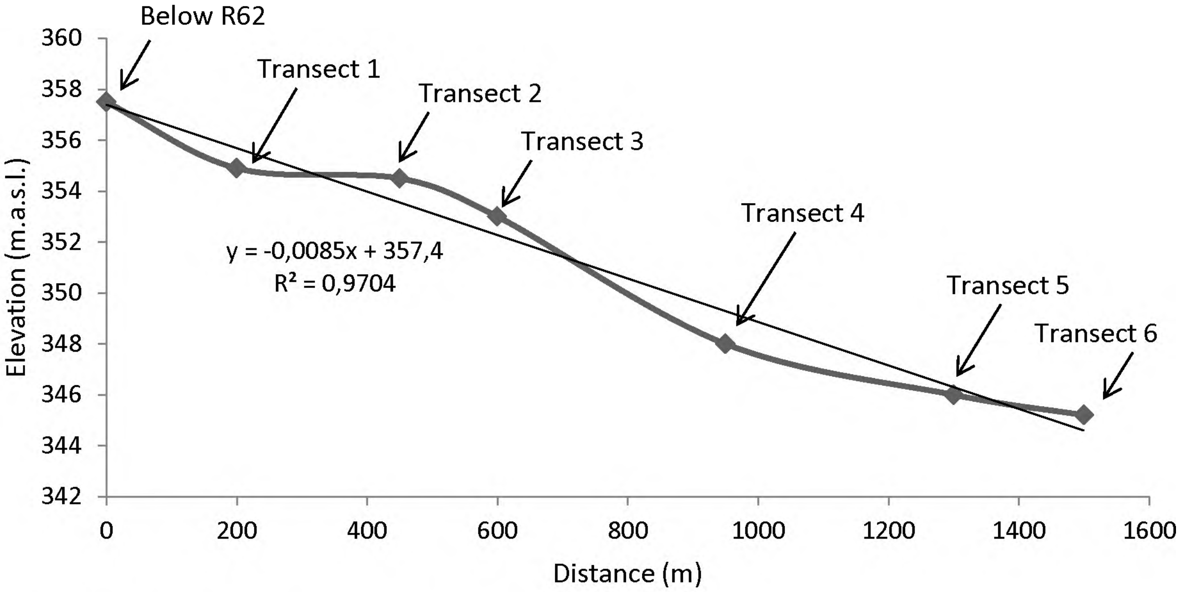

Figure 5.9: Longitudinal profile of the Kompanjiesdrif basin.

The slope from the north into the wetland at all sites is more gentle than to the south of the wetland, reflecting the influence of the large number of north-bank tributary alluvial fans on wetland morphology. From the head of the wetland below the provincial road (R62) bridge, where the wetland is approximately 40 m wide, the wetland widens considerably to about 110 m at transect one (Figure 5.10a). At transect two, which is opposite a northern tributary alluvial fan, the wetland width is similar to transect one at about 110 m (Figure 5.10b). The width of the wetland increases to about 240 m at transect three (Figure 5.10c). Opposite a second alluvial fan, the width of the wetland at transect four is narrower at about 170m (Figure 5.10d). Transect five shows the wetland to be about 200 m in width (Figure 5.10e). The wetland at transect six is about 120 m in width (Figure 5.10f). The wetland surface is near-horizontal for all transects and variation in local relief across each transect is generally limited (0.1 to 0.2 m over horizontal distances of tens of metres).

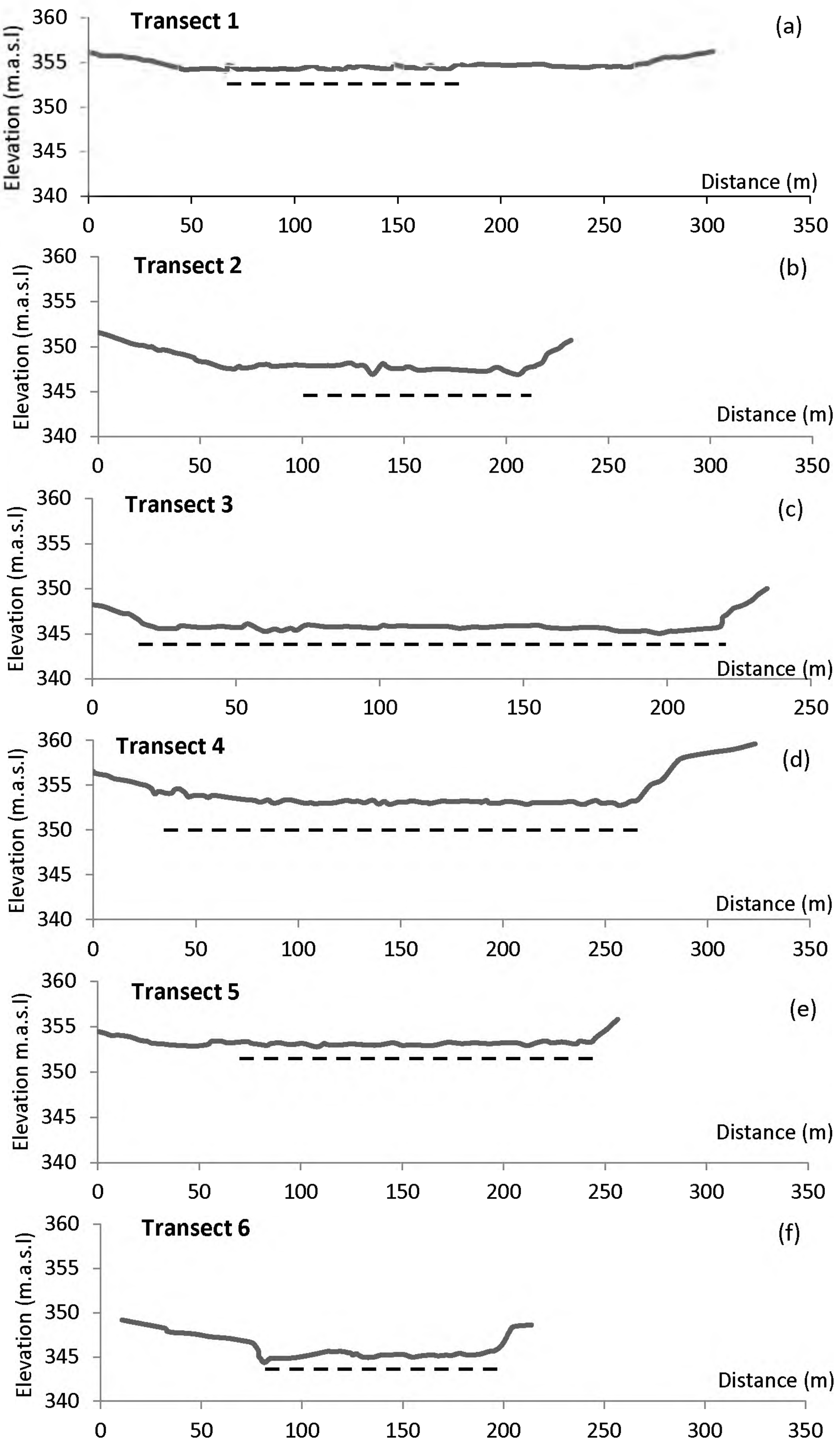

Figure 5.10: North-south cross sections of the Kromrivier wetland plotted downstream from transect one to transect six. The horizontal lines below each cross-section show the extent of the wetland across the valley.

6 Discussion

6.1 Introduction

This discussion attempts to demonstrate that firstly, while palmiet occupies distinctive hydrological settings that are permanently flooded, it occupies a range of geomorphic settings. It occurs on:

1. The permanently flooded bed of a recently formed (approximately three decades old) gully, where it exists as isolated islands that are less than 5 m wide;
2. The broad sedimentary valley-fill deposits that occur across hundreds of meters of valley-bottom wetland;
3. On the surface of drowned former gullies that have filled with water to depths of about 7.5 m;
4. On the clastic sedimentary material of filled portions of former gullies.

The same is not true for any other plant communities, which all occur on valley-fill sedimentary sequences across the unchannelled valley-bottom wetland, from the permanently flooded zone to the terrestrial margin. The role of palmiet in stabilising gully beds and trapping sediment leads to filling of gullies and the creation of a broad valley-bottom wetland in an environment where channels might be expected. The argument is then made that palmiet is an ecosystem engineer that controls the pattern and form of the Kromrivier fluvial system. Finally, it is argued that models that attempt to explain wetland structure and function need to include geomorphology as a key factor.

6.2 Channel patterns

Alluvial channels, the bed and banks of which are composed of sediment transported and deposited by the stream itself, are susceptible to major pattern change as the alluvium is eroded, transported, and deposited, and as the sediment load and discharge change (Schumm, 1985; Hogan & Luzi, 2010). The channel planform patterns are single, meandering, braided and anabranching. Since alluvial rivers are open channels, formed by the water conveyed by the channel, channel patterns should depend largely on hydrologic conditions. However, according to Schumm (1985) all channel types can be formed at similar discharges, and while discharge influences channel dimensions such as width and depth, the quantity of water moving through a channel does not affect the basic channel pattern. Sediment type plays the largest role in determining channel pattern such that channels that transport relatively low quantities of bed load sediment are more likely to be straight or meandering, while those transporting high quantities of bed load are likely to be braided.

While it is expected for a river dominated by bed load sediment to follow a braided pattern, braided rivers are not a result of coarse sediment alone. Schumm & Khan (1972) studied the evolution of channels at the same discharge, to determine the effect of slope on channel pattern. Where slopes and sediment loads were low, the channels remained straight. As the slope of the channel was increased, velocity, stream power, and sediment transport all increased. Bank erosion became significant, and a sinuous pattern, with alternate marginal bars on the convex sides of the stream, developed. At the highest slopes, where energy and sediment load were high, the channel became braided. From this experiment, it is clear that sediment load as well as stream power, determined by slope, play a role in determining channel patterns.

Typically, a steep channel dominated by bed load will be associated with a braided stream (Schumm, 1985). Braided streams usually occur in wide valleys with steep slopes, where alluvial and colluvial fans contribute to sediment input. Bed load dominated channels tend to have high stream power, high gradients, high width-to-depth ratios, and high sediment transport rates. These channels are highly dynamic with bars eroding and re-forming continuously (Lord *et al*., 2009). Generally, a change in channel pattern is the result of a change in the nature of the sediment load, for instance, a meandering stream that experiences an increased quantity of bed load sediment would most likely become braided. The lower William River, Canada, is an example of a rapid channel adjustment in response to abrupt additions of sandy bed load sediment (Smith & Smith, 1984). A relatively narrow and deep single-channel stream flows into Lake Athabasca, and the river picks up a 40-fold increase in bed load as it encounters a large dune field just south of the lake. Consequently, the channel undergoes a five-fold increase in width and a ten-fold increase in width-to-depth ratio, and develops a thoroughly braided pattern in response to the increase in bed load.

In addition to sediment and stream power, vegetation has received increasing attention in respect of its effect on channel pattern (Mackin, 1956; Smith, 1976; Smith & Smith, 1980; Franklin *et al*., 2008; Gurnell *et al*., 2010; Zong & Nepf, 2010; Larsen & Harvey, 2011; Nepf, 2012; Gurnell, 2013; Schoelynck *et al*., 2014). The occurrence of bank and riparian vegetation increases bank stability due to root reinforcement and sediment accumulation, thereby reducing erosion of channel banks (Smith, 1976). Vegetation has been identified as a key factor controlling channel planform, particularly in relation to transitions between multithread and single thread planforms. Beaumont (1981) reported that the removal of catchment and channel vegetation caused a previously meandering channel to become straight, due to increased flood effects and channel erosion and enlargement.

Vegetation has been observed to cause channel narrowing and induce single-thread flow in streams that would otherwise be braided (Mackin, 1956; Knighton & Nanson, 1996; Gran & Paola, 2001; Tal & Paola, 2007). Tal *et al.* (2004) concluded that in the absence of stabilised banks, usually due to an absence of vegetation, the flow tends to create new channels until a braided system develops. A study conducted by Nevins (1969) reported how the Turandanui River in New Zealand changed over the course of one year from a braided stream into a single meandering channel by planting willow shrubs on channel bends. The Wood River, Idaho, USA, meanders in a forest for many miles, braids in a 3-mile segment where the valley floor is prairie, and returns to a meandering habit where the river re-enters the forest (Millar, 2000). The cause of the drastic difference in channel characteristics in the three segments is a difference in bank resistance due to presence or absence and type of bank vegetation.

Vegetated banks have greater stability than non-vegetated ones, and this is suggested to be the reason for the transition from braiding to anastomosing streams (Smith, 1976). Smith & Smith (1980) identified the importance of vegetation in structuring anastomosing channels as they found that the key characteristics of anastomosing channels were rapid aggradation conditioned by downstream control and channels that were stabilised by bank vegetation. The three anastomosing channels of the Banff River, Canada were all found downstream of braided reaches composed of mainly bed load sediment, with small islands where vegetation cover was negligible. The braided channels merge downstream into the anastomosed zone where channels are stable due largely to an increase in vegetation cover.

The role of vegetation in influencing the rate of lateral migration of channels is documented by Hickin & Nanson (1989). Their study of western Canadian rivers has shown that riverbanks that are well bound by roots can offer far greater resistance to lateral erosion than non-vegetated banks of alluvium, when exposed to the same erosive forces. It was found that if discharge, slope, size of bank materials, and bank heights are constant, a river with non-vegetated banks may erode at almost twice the rate of a forested floodplain.

An example of fluvial pattern in systems dominated by bed load is provided by the Baviaanskloof Valley, a valley that is situated in a similar geological and geomorphic context immediately to the north of the Kromrivier. It is also characterised by steep mountainsides and a flat valley floor, with alternating confined and unconfined reaches Unconfined sections are about 900 m wide while confined sections are less than 100 m wide (Bobbins, 2011; Holmes & Meadows, 2012). In the unconfined section, the channel generally takes on a braided form (Figure 6.1), with elevated ephemeral floodplains and terraces on either side. The channel has a high width-to-depth ratio (Smith & Smith, 1984; Holmes & Meadows, 2012). The coarse cobble and gravel bed load support a groundwater aquifer that only intersects the channel surface during flood periods. The channel bed is dry except when floods recharge the ground water table. The abundant bed load, erodible banks, highly variable discharge, and steep channel longitudinal slopes, are all characteristics of a braided stream (Knighton, 1984; Charlton, 2008).

Figure 6.1: An oblique aerial view of the Baviaans River flowing down a broad valley in the Baviaanskloof. The steep mountainous terrain flanking the valley floor, the sparsely vegetated floodplain floor, and the typically braided nature of the stream are evident. Photo: Japie Buckle (3 November 2008).

A key feature of the Baviaanskloof is that it occurs in a semi-arid setting with a mean annual rainfall of approximately 300 mm, being highly variable intra- and inter-annually, with infrequent extremely heavy rainfall events (Jansen, 2008). Given that rainfall is low and variable, vegetation that requires permanent flooding of the land surface is absent, such that the role of vegetation in modifying fluvial planform in systems like this may be limited.

In contrast to the semi-arid Baviaanskloof, the Duiwenhoks River near Heidelberg in the Western Cape Province immediately south of the Langeberg Mountains (part of the Cape Fold mountains), receives approximately 600 mm per annum (DWA, 2014). Once again, intra- and inter-annual rainfall variability are very high. The collapse of the palmiet-dominated

Duiwenhoks Wetland following floods in the Western Cape Province of South Africa in December 2004, resulted in the conversion of a palmiet-dominated valley-bottom wetland with diffuse flow into a braided stream (DWA, 2014; Figure 6.2). Prior to the flood event of December 2004, the entire valley floor was dominated by palmiet, but following the flood and associated erosion, the Duiwenhoks stream was converted to a braided stream, illustrating the type of stream that might exist in the absence of vegetation that colonises and stabilises stream banks.

Vegetation is clearly a key element in the transition from braided to anastomosing channels, through its ability to stabilise banks. Based on the present study and other studies in other palmiet-dominated wetlands (Sieben 2012; Job 2014), palmiet may be responsible for the conversion of a braided to anastomosing stream to an unchannelled valley-bottom wetland.

Figure 6.2: The Duiwenhoks River following floods of 2004, flanked by palmiet beds that occupy the non-eroded portion of the valley floor. Photo: Japie Buckle (7 June 2005).

6.3 The distribution of vegetation in relation to hydrological regime

The Kompanjiesdrif wetland is densely vegetated, with the plant community on the valley floor dominated by the tall (>2 m) and robust palmiet plant. Plant communities in the study area are arranged from being dominated by dry land plants at the edge of the wetland where flooding frequency and duration are low, to marsh vegetation in the permanently flooded centre of the wetland.

The distribution of species and plant communities within a wetland is primarily a function of depth and duration of flooding (Spence, 1982; Urban, 2005), being that plants in a typical wetland are arranged in zones moving from dry land to open water with increased depth (Noon, 1996). Plant zonation develops to the varying properties of different plant species that enable them to establish and colonize the water-depth gradient (Buttery & Lambert, 1965; van der Valk & Welling, 1988; Coops *et al*., 1996; Zelnik & Carni, 2008). There have been many studies examining this link between the hydrological regime and plant distribution within wetlands (Keddy 1983; van den Brink *et al*., 1995; van der Valk *et al*., 1994; Pennings *et al.,* 2005; Driver, 2010).

One such study was conducted in the Klamath Basin, Oregon, USA, to evaluate the dependency of riparian plant communities on infrequent flooding (Chapin *et al*., 2002). The magnitude and frequency of flood flows needed to inundate the riparian zone at nine sites in the upper Klamath Basin was examined. To study the relationship between flood frequency and riparian plant community distribution, sites that represented a range of stream and floodplain settings were chosen. Plant communities were sampled along established cross-sections in the field. Data collected included channel and floodplain elevations and water surface elevations associated with specific discharges.

Plant communities were classified as “riparian” based on the wetland indicator status of species within a community type, or otherwise as “upland” plant communities. Plant communities at each site showed a general decrease in hydrophytic plant species and an increase in upland plant species from lower elevations to higher elevations. Near the channel edge, community types were typically dominated by common wetland, herbaceous species such as sedges (*Carex spp.*) and spikerush (*Eleocharis palustris*). Willows typically occurred in the middle-elevation to upper-elevation range of a riparian zone. Although still dominated by hydrophytic plant species, composition of the uppermost riparian communities was highly variable. The correlation of plant species and community distribution with elevation found at the riparian sites over a wide range of conditions indicates a close functional relationship between riparian vegetation patterns and depth and duration of flooding.

Wassen *et al*. (2002) compared vegetation composition and distribution, to factors such as flood duration and inundation depth during floods of the floodplain of the Biebrza River, Poland. The Biebrza River is a lowland river surrounded by peatlands with gradients of vegetation types running the length and breadth of the valley. The river is characterised by fairly natural hydrological patterns, making it a suitable reference site for the study of the effects of hydrological conditions. A vegetation gradient along a transect starting at the river, crossing the floodplain and finally ending at the valley margin was examined. This transect was compared with two other transects which crossed fen gradients in the Biebrza valley not flooded by the river.

Wassen *et al*. (2002) found that river flooding and groundwater discharge were the dominant hydrological processes determining vegetation distribution. The distribution of vegetation types followed a clear pattern parallel to the river; the reed swamp vegetation *Glycerietum maximae* in the zone closest to the river, followed by tall sedge communities *Caricetum gracilis* and *Caricetum elatae* and finally low growing type with herbs, small sedges and grasses *Calamagrostietum strictae* at the margin of the river plain, bordering the dunes.

Species richness increased away from the river towards the dunes. Elevation of the ground surface rose with increasing distance from the river; flood duration and flooding depths in spring decreased in the same direction. There was a clear gradient from the river towards the dune area with decreasing flood duration and lower flooding depths in spring and higher groundwater tables in summer. Absence and presence of species and the variation in species composition of the vegetation was explained best by flood variables, which were determined by elevation. It was concluded that river hydrology and to a lesser extent nutrient release from the soil are clearly related to vegetation composition, species richness and productivity of the vegetation.

Coops *et al*. (1996) studied the distribution on shorelines of helophyte species in relation to growth responses in the water depth gradient in The Netherlands. Four helophyte species were selected, two of which were grass species, *Phalaris arundinacea* and *Phragmites australis*, while the other two were sedge species, *Bolboschoenus maritimus* and *Schoenoplectus lacustris*. Stands of *Schoenoplectus lacustris* were found at lower depths relative to the mean water level (average fringe depth of 69 ± 19 cm) than stands of *Phragmites australis* (45 ± 20 cm), *Bolboschoenus maritimus* (36 ± 8 cm), and *Phalaris arundinacea* (25 ± 8 cm). The growth responses to a gradient of water depth were studied by planting the four species at five distinct water depths, and determining morphological parameters and biomass distributions of the species grown for two years. Results show that the biomass of *Phalaris arundinacea* was reduced below 30 cm water depth, while the biomass of *Phragmites australis* and *Bolboschoenus maritimus* was only reduced at 80 cm water depth. *Schoenoplectus lacustris* showed no biomass reduction. An increased aboveground-belowground biomass ratio in deeper water was demonstrated for each of the species under study. Mean basal stem diameter as well as mean stem length increased with water depth in all four species. The similarity of responses to water depth was greatest within each of the groups of gramineous and cyperacean species. The responses reflect the zonation of the species along the water-depth gradient: *Schoenoplectus lacustris* in relatively deep water, *Phragmites australis* and Bolboschoenus maritimus in shallower water, and *Phalaris arundinacea* in very shallow water.

Vegetation zonation in wetlands is undoubtedly related to the depth and duration of flooding, which reinforces the Mitsch & Gosselink (2015) model of the role of the hydrological regime in controlling wetland structure and function. However, a surprising finding in this study was that with the exception of the palmiet plant community, the distribution of the remaining plant communities was strongly correlated to the geomorphic setting in which they occurred. With the exception of palmiet, the plant communities all occur on valley fill sequences on or adjacent to the near horizontal, broad valley floor. However, the palmiet community was found in permanently flooded conditions on the valley floor as well as permanently flooded conditions on the bed of gullies, where it was found as isolated small islands.

6.4 The effect of vegetation on hydrological and geomorphological processes

The role of vegetation in controlling channel form and focusing the deposition of sediment to in-channel areas has been well-documented (Ellery *et al.*, 1990; 1995; Holmes *et al.*, 2005). Holmes *et al.* (2005) found that dense vegetation, in the form of alien invasive trees along the Huis River, Western Cape, could lead to reduced flow velocity and volume. With increased flow resistance, turbulence decreases and sediment deposition is aided by the incidence of dense stands of invasive trees within flooded areas of Western Cape Rivers. Changes to channel shape follows, with the type of change related to the particular geomorphological reach in which the invasion occurs. It was found that the trees along the Huis River have a damming effect, and by slowing the flow of water through the stream, the watercourse widens and the conversion of well-defined rivers into systems of diffuse flow and shallow channels occurs (Holmes *et al.*, 2005).

According to Larsen & Harvey (2011), interactions between vegetation and flowing water can produce landscape patterns distinct from the standard river channel patterns described by Schumm (1985). For instance, vegetation is able to inhibit the development of braided streams by increasing the bank's resistance to erosion (Millar, 2000; Larsen & Harvey, 2011; Murray & Paola, 2003; Tal & Paola, 2007). This in turn leads to a high degree of channel stability and the formation of anastomosing channel systems (Smith, 1976; Smith & Smith, 1980).

Nanson & Knighton (1996) found that riparian vegetation is an important factor in the formation of anastomosing channels in Magela Creek, Northern Australia. The conditions essential for the formation of anastomosing rivers include resistant bank material relative to flow strength and flow variability (Knighton & Nanson, 1993; Nanson & Knighton, 1996). The

Magela Creek riverbanks consist of fine to medium sands, with limited cohesion, and the strength of banks that lead to lateral stability and anastomosis is due to the presence of vegetation (Nanson & Knighton, 1996).

Smith (1976) and Smith & Smith (1980) emphasised, through their work in the Banff National Park, Canada, that bank stabilisation by vegetation can lead to the creation of channel systems with a particular planform configuration, which was not predicted by pre-existing models. It was noted that the characteristics of the Alexandra River in the Banff National park are distinct from those of the nearby braided Saskatchewan River. These differences include a thick accumulation of silt, clay, and sand from overbank flood deposition, the absence of buried channel and point-bar deposits, and the absence of lateral channel migration. From these differences, it is evident that the Alexandra River has a sedimentation history and channel processes distinct from the classic sedimentary models for braided streams (Allen, 1969; Hein, 1974; Walker, 1975), and it is in fact an anastomosing stream.

Experiments were carried out on bank materials of the anastomosed channels in floodplain silt deposits of the Alexander River, to determine the effect that vegetation could have on bank erodibility (and conversely, bank stability). A mat of roots flanked the channel banks and provided protection from river erosion, whereas the banks of the braiding Saskatchewan River were not protected by roots and sediment grain sizes were larger. The results suggest that in a river undergoing aggradation, vegetation roots and plant matter are able to accumulate, thus affording protection to banks from erosion.

Large-scale changes in flow direction, called avulsion, takes place in the Okavango Delta, northern Botswana, over surprisingly short time scales (less than a century). These events involve the abandonment of one channel system, where water is diverted to a new area, leading to the formation of a new channel system (Ellery *et al.*, 1993). A set of studies (McCarthy *et al.*, 1986; Ellery *et al.*, 1993; 1995; Smith *et al.*, 1997) suggested that depositional processes controlled by vegetation, were responsible for channel avulsion in the Okavango Delta.

Ellery *et al*. (1995) described interactions between vegetation growth in the channel margin of rivers in the bed load dominated Okavango Delta. As the banks adjacent to 4 to 5 m deep channels comprised peat, and channel margins are leaky (flow through the peat and as overbank flow), sedimentation is confined to the channel bed, causing channel aggradation and an associated rise in water level in the channel. Vegetation levees are formed due to rapid aggradation of the channel margin that results from a combination of processes. Firstly, plant growth is greatest close to the channel as nutrient supply is greatest here, and thus peat formation is greatest in this region. Secondly, peat only forms below the level of permanent flooding and a rise in the water level enables peat to accumulate to a greater elevation. Thirdly, *Cyperus papyrus* is capable of growing as a floating mat of entangled roots, rhizomes and stems, such that a rise in the water level would cause the entangled floating mat to rise too. This combination of processes results in an increase in the water gradient at right angles to the channel axis. As the channel aggrades, increasing quantities of water are thus lost from the channel and current velocity and discharge in the channel decline. The decline in current velocity and discharge of the channel is accompanied by an increase in the rate of bed load sedimentation and encroachment of papyrus from the channel margin into the channel in a positive feedback that leads to channel abandonment.

On the one hand, vegetation gives rise to particular channel patterns through enhanced bank stability. On the other hand, there are threshold flows that even vegetation cannot withstand. The collapse of the palmiet-dominated Duiwenhoks Wetland following floods in the Western Cape Province of South Africa in 2004 resulted in the conversion of a valley-bottom wetland with diffuse flow into a braided stream (DWA, 2014; Figure 6.2). Prior to the flood event of 2004, the entire valley floor was dominated by palmiet, but following the flood and associated erosion, the Duiwenhoks stream was a braided stream – illustrating the type of stream that might exist in the absence of vegetation that colonises and stabilises stream banks.

The Alexandra and Saskatchewan Rivers (Banff National Park, Alberta, Canada), the Duiwenhoks River (Western Cape, South Africa), and the Baviaanskloof River (Eastern Cape, South Africa), occur in steep sided valleys with flat valley floors. They exhibit marked fluctuations in flow and discharge, and are dominated by bed load sediments. Given these characteristics, they may be expected to have a braided channel planform (Charlton, 2008; Francis *et al.*, 2009; Schumm, 2005). The Duiwenhoks and Kromrivier streams exhibit remarkably similar characteristics, such that in the absence of stable vegetated banks, should also be braided. In the presence of vegetation, they may be anastomosing. However, the Duiwenhoks and Kromrivier streams are not braided or anastomosing, but instead are unchannelled valley-bottom wetland systems typically characterised by diffuse flow.

6.5 From braided to anastomosing to unchannelled valley-bottom: palmiet as an ecosystem engineer controlling fluvial structure.

Palmiet has been observed stabilising sediment islands within river channels (Munro *et al.,* 2001; Boucher & Withers, 2004; Sieben, 2012; Job, 2014). Job (2014) further found that palmiet stands in the Goukou Wetland in the Western Cape are able to expand by vegetative propagation on deposited sediment during sustained low flows (Figure 6.3). Due to its clonal nature, the plant is able to extend into open water in a river channel, narrowing channel width, such that palmiet is able to colonise the entire width of the river channel over time. Once the channel has been colonised, surface flow is as diffuse flow through an unchannelled valley-bottom. In this way, palmiet is thought to control the form of a river channel, establishing across the entire valley floor, giving rise to diffuse flow conditions across the valley. Through its control on erosion and deposition within the river system, *Prionium serratum* creates a hydrological setting that leads to sediment accumulation

Figure 6.3: Palmiet pictured in several Cape rivers, encroaching across a channel in an inter-fingering manner (a) and (b), resisting high velocity flows and slowing waters (c), and growing in a dense mass across the full width of the channel (d). Photos: Nancy Job.

In the Kromrivier wetland, both clastic and organic sediment accumulates amongst the rhizomes of the palmiet stand, which leads to aggradation over time. Palmiet is able to bind sediment between the old fibrous leaves such that entrainment is difficult (Figure 6.4). In the absence of clastic sediment, palmiet can form peat, thus contributing to aggradation and the presence of a valley-bottom wetland that is near-horizontal in cross-section and has a very gentle longitudinal slope.

Figure 6.4: The fibrous remains of an old *Prionium serratum* leaf, which has entrapped particles. Photo: Nicholaus Huchzermeyer (2015).

6.6 The role of palmiet in the geomorphic evolution of the Kompanjiesdrif basin

The role of vegetation in gully formation and restoration has been examined in an extensive body of literature (Thornes, 1985; Prosser & Slade, 1994; Descroix *et al*., 2001; Zheng, 2006). Prosser & Slade (1994) found that changes in valley floor vegetation, particularly the reduction in vegetation cover, increase susceptibility to gully erosion. Where valley floor vegetation declines or is degraded, flow resistance is decreased and stream power is increased, and as a result, rapid gully formation occurs. Similarly, Ellery *et al.* (2009) argue that erosion may be initiated in response to climate variability as increased rainfall leads to increased runoff and therefore may increase the susceptibility of a valley to erosion.

Several generations of gully formation and filling in the Kompanjiesdrif basin have been discovered (Lagesse 2015, In Prep), dating back from 400 years BP to nearly 8 000 years

BP, suggesting that erosion and subsequent filling have taken place in the Kompanjiesdrif basin over the last 10 000 years. These gullies vary between 5 to 8 m deep and 15 to 25 m wide (Lagesse, In Prep). This cutting and filling cycle is a subject of ongoing investigation (Lagesse, In Prep), but the present study has shed light on the role of palmiet in the filling of gullies after individual erosion events, as follows:

- Colonising the bed of a gully from small islands and trapping sediment, leading to gully filling with clastic and/or organic sediment;
- Colonising a gully filled with sediment as a result of sediment input from large tributary alluvial fans;
- Encroaching areas of open water from the bank of gullies that have been blocked by sediment from tributary streams downstream.

6.6.1 Trapping sediment leading to gully filling

If, following an erosional event, a gully forms below an erosional nick point, the gully bed remains wet as a result of water flowing down the valley from upstream. Sediment, including sand, is generated through headward erosion, some of which is deposited as marginal bars. These are colonised by palmiet, possibly because of vegetative propagation from fragments of palmiet broken from the undermined substratum at the erosional nick point (Figure 6.5a). Sand bars continue to form and provide suitable habitat for palmiet (Figure 6.5b), but, at some point palmiet starts trapping clastic sediment. If there is an absence of clastic sediment supply, organic sediment accumulates to just below the water surface, causing the water surface to rise over time (Figure 6.5c), until the gully fills with sediment and the entire valley-bottom is once again flooded (Figure 6.5d). In this model, the gully fills as a result primarily of the colonisation of the gully bed by palmiet and the sediment trapping and peat forming ability of palmiet.

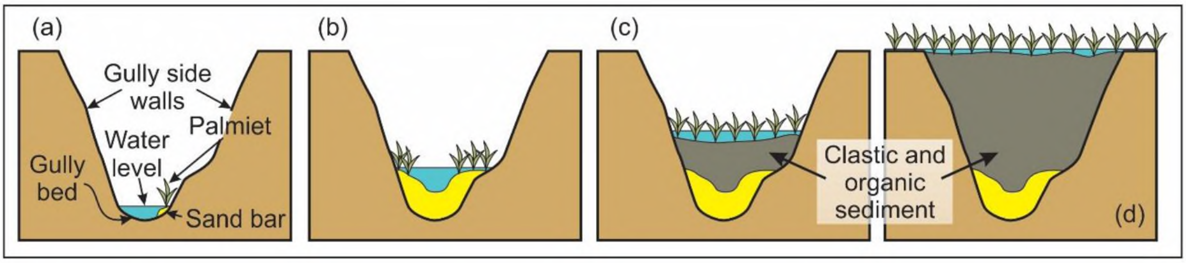

Figure 6.5: Illustration of the role of palmiet in colonising sedimentary bars and trapping sediment and/or forming peat, leading to gully filling and colonisation of the valley floor following an erosional event.

6.6.2 Colonisation of a gully filled with sediment from a tributary alluvial fan

The second manner in which palmiet colonises former gullies is where a gully has been filled with sediment that seems to be associated with lateral input of sediment from a tributary alluvial fan (Figure 6.6a). In this case, the alluvial fan is introducing sediment from its catchment, causing it to extend onto the valley floor, until it impinges upon the gully and blocks it with sediment (Figure 6.6b A-A). It is clear from the cores that clastic sedimentary deposits in former gullies are dominated by relatively coarse sediment that could not arise from sediment transport from the head of the wetland, but must be a result of sediment from a laterally impinging alluvial fan. Palmiet seems able to colonise and dominate these settings.

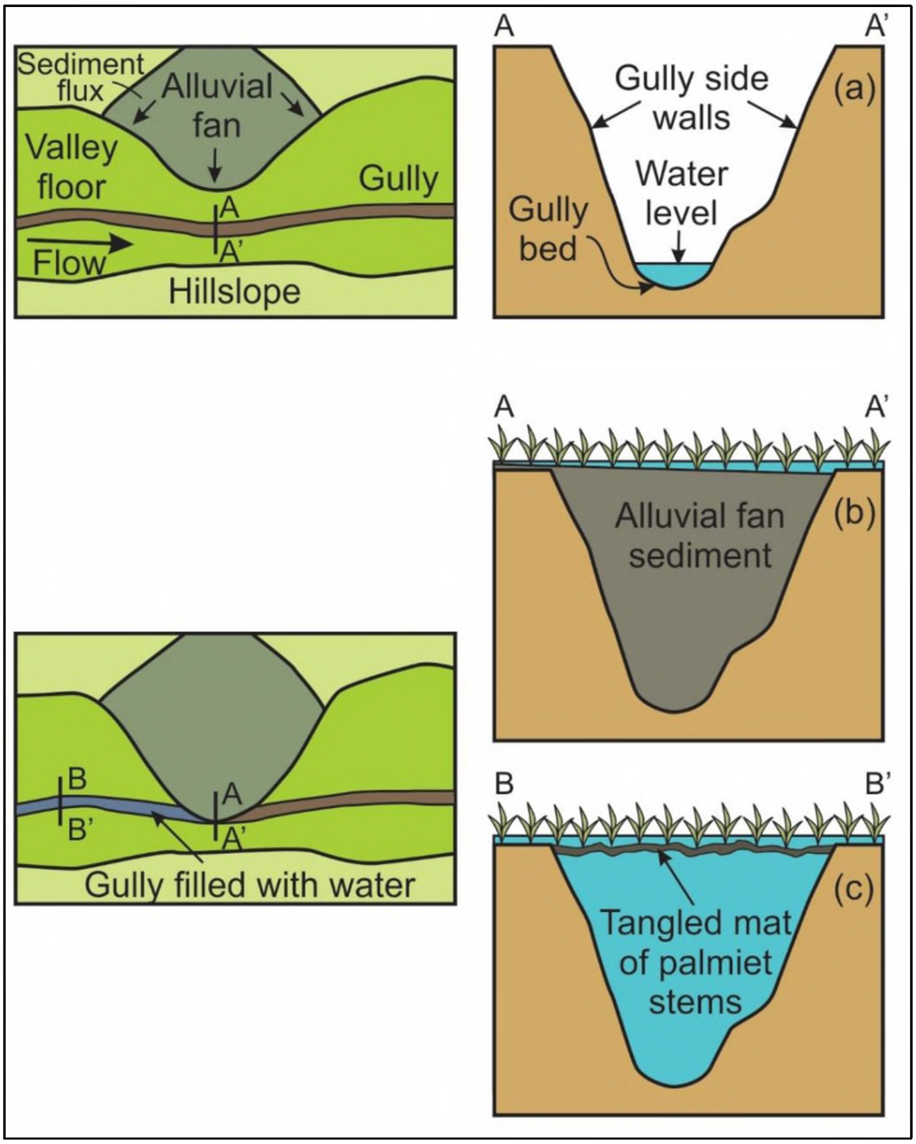

Figure 6.6: Illustration of the response of palmiet to the filling of a gully by sediment from a tributary alluvial fan (a and b) and growing across the water pond in the gully upstream of the blocked section (c).

6.6.3 Encroachment of open water areas in former gullies blocked further downstream

Upstream of a gully that is blocked by a laterally impinging alluvial fan, the gully is drowned with water. Palmiet encroaches laterally from the edge of the water-filled gully and grows over the water surface, such that there is no visible sign of the former gully from remotely sensed imagery, such as aerial photography, or from walking across the wetland surface (Figure 6.6c B-B').

6.7 Beyond anastomosis: the role of palmiet in the creation of an unchannelled valley-bottom system

The role of vegetation in controlling fluvial form from braided to anastomosing has been well described and discussed (Smith, 1976; Smith & Smith 1980; Ellery *et al.*, 1993; McCarthy *et al.*, 1993; Ellery *et al.*, 1995; Smith *et al.*, 1997). The key role played by vegetation in this respect is to stabilise depositional features that then become channel banks in a fluvial system that divides its course around these features in an anastomosing network. Vegetation may even play an active role in regulating channel width and slope (Ellery *et al.,* 2003b). In the Kromrivier, palmiet colonises gully beds and promotes sedimentation to fill gullies and create a valley-bottom wetland without a channel. It also rapidly colonises sedimentary deposits and areas of open water to convert a channeled wetland system to an unchannelled valley-bottom wetland.

In many respects, the behavior of palmiet is very similar to that of papyrus in the Okavango Delta (see Ellery *et al.,* 1995). In the event of an avulsion in the Panhandle of the Okavango Delta, for example, in which flow in a single channel system is reduced, papyrus rapidly colonises the channel from the bank and reduces channel width such that channel width is appropriate for the available discharge (Ellery *et al.,* 1995; 2003b). Although the mode of colonization by palmiet is different, the outcome is similar, but more extreme in that a potential channel is not allowed to develop, but an unchannelled wetland is formed. Therefore, it is argued here that palmiet fundamentally affects fluvial pattern, and that without the presence of this species, the Kromrivier and other fluvial systems dominated by this species would have a fundamentally different fluvial pattern than if this species was absent.

Palmiet wetlands, characterised by the dominance of palmiet, occur on a slope that is steeper than what could be expected for wetlands of a certain size (Sieben, 2012). They are distributed in acidic, nutrient-poor waters that support little life, in the Eastern Cape, Western Cape, and Kwazulu-Natal Provinces of South Africa (Boucher & Withers, 2004; Rebelo 2012). The distribution of palmiet wetlands is all but limited to Table Mountain Sandstone, as it only grows on this extremely nutrient-poor substrate (Job, 2014). Palmiet has a reported tolerance for a wide range of hydrological conditions (Job, 2014), but variations in sediment load, water depth and flow velocity are thought to limit its establishment and growth, and in particular, its association with peat accumulation.

Palmiet peatlands are found in deep valleys, typically within or at the base of mountain ranges comprised of Table Mountain Sandstone. These peat accumulations may be as deep as 8 m, for instance in the Goukou Wetland (7 m, Job, 2014), the Duiwenhoks Wetland (6 m, Gründling, 2015) and the upper Kromrivier Wetland (8 m). Palmiet peatlands are typically long (>10 km) and narrow (<1 km; Job & Ellery, 2013). Most palmiet peatlands do not have a clearly defined stream channel, which distinguishes them from typical Western Cape mountain streams fringed by palmiet. Where palmiet fringes streams, it forms sporadic clumps along the banks and is rooted in sand and cobble, with some (but not major) organic material accumulation due to the fast-flowing nature of these mountain streams (Job & Ellery, 2013).

According to Job (2014) the occurrence of palmiet peatlands has to do with the erosion of resistant quartzite lithologies of the Cape Supergroup, with shale as subsidiary lithologies. This geological setting is thought to play a key role in facilitating the expansion and persistence of large peat basins at the base of the mountains, by contributing to permanent saturation and peat formation. The sustained release of water from these fractured quartzite lithologies has been seen to contribute enormously to the formation of the Goukou Wetland, in the Western Cape.

The clastic sedimentary load in streams associated with these Cape Fold Mountain catchments is generally much lower than those streams that are associated with peat formation by trunk- or tributary-blocking interactions observed elsewhere in the country (Ellery *et al*., 2012 (Mkuze); Grenfell *et al*., 2009b; 2010 (Futululu); Joubert & Ellery, 2013 (Wakkerstroom)). The low sediment yield in Cape Fold Mountain catchments is because quartzite is extremely resistant to weathering and erosion.

7 Conclusion

This study has presented evidence that the restoration of old gullies and the creation of a wetland with diffuse flow conditions in the Kompanjiesdrif basin is controlled largely by the dominant plant species, *Prionium serratum*. The aim of this study was to determine the role of palmiet as an ecosystem engineer and document the nature of its control of a fluvial system. These aims were achieved largely in the development of two conceptual models, one that accounts for the process of gully bed colonisation, sediment trapping and gully filling, the other involving rapid colonisation of sedimentary fill from tributary sediment sources that block a gully. Palmiet is also able to colonise areas of open water that fill a gully when it is blocked further downstream by sedimentary input from tributary sources. The study suggests that the wetland has been characterised by repeated cutting and filling cycles, despite which palmiet has repeatedly reinstated diffuse flow conditions across the valley floor.

Gully erosion is common in southern Africa and various rehabilitation strategies focused at halting gully erosion have been implemented, such as the gabion structures along the Kromrivier. However, without understanding and examining the complete set of processes that control the formation and dynamics of these wetland systems, these strategies aimed at rehabilitation may not be sustainable. The natural rehabilitation of gullies in the Kromrivier can be attributed to the geomorphic processes that drive the dynamics of the ecosystem, which is strongly influenced by the ecosystem engineer palmiet. A long-term study of the processes used by palmiet in gully restoration in a variety of river systems dominated by this species would prove useful in improving our understanding of the importance of palmiet in gully restoration.

The fluvial form of the Kromrivier wetland, is largely due to the dominance and role of palmiet in modifying fluvial form and dynamics, and this concept could assist in better understanding the form and dynamics of these and other wetlands. By colonising gully beds and areas of open water along streams, palmiet is able to stabilise sediment islands within river channels and trap sediment, leading to aggradation of the riverbed and creating an unchannelled valley-bottom wetland where a single thread or braided stream may be expected. The traditional view of wetland ecology is that vegetation responds to environmental gradients and conditions that are a product of the hydrological regime. However, it is evident from the results of this study that it is not simply that the vegetation distribution is affected by environmental conditions, but that plants influence water and sediment distribution, thus affecting the architecture of a fluvial system. This model extends the original model by Gosselink & Turner (1978), by emphasizing the role that interactions between vegetation and geomorphology play in controlling processes such as the hydrological regime, and therefore, soil physiochemistry and biota.

This study therefore demonstrates that the role of geomorphology (as modified by vegetation), in controlling the landscape form of valleys that host wetlands has been neglected in wetland studies in the past. According to Tooth *et al.* (2015), a small group of southern African and Australian researchers has made enormous progress in this field. Southern Africa has a remarkable number of wetland ecosystems given the region's high altitude. Valley widening, for instance, occurs in settings where the prevailing lithologies are relatively easily erodible, but where such valleys are crossed by resistant lithologies such as dolerite dykes. In such settings, streams erode the less resistant lithologies rapidly, and once a stream has eroded its bed to an appropriate gradient over the soft sediments, streams use available energy to carve the landscape laterally, causing the valley to widen (Tooth *et al.,* 2015). While the Tooth *et al.* (2002) model of valley widening by a meandering stream does not apply in this setting, a broad flat valley with a gentle longitudinal slope has formed in a mountainous landscape.

Tooth *et al.* (2015) has proposed that the overall physical structure and hydrology of wetlands is determined by geomorphological factors, and that understanding the structure and functioning of wetlands over timescales of interest to ecologists and wetland managers needs to incorporate geomorphic understanding. Therefore, a model is proposed from the findings in this study for wetland formation, which extends the model of Mitsch & Gosselink (2015; Figure 7.1). The hydrological regime is given for a particular climatic setting, due to runoff that is generated by rainfall. Given the inevitability that moving water is likely to lift and transport sediment, fluvial systems are not simply about water. It is therefore inevitable that fluvial processes will have geomorphic outcomes and produce landforms that reflect variation in lithological and geomorphic heterogeneity. Vegetation, as shown in this study, will influence the outcomes of a given combination of hydrological and geomorphological processes and influence the prevailing landforms that will ultimately develop. By influencing landforms and "basin shape", these processes influence the distribution of water and the duration of flooding in the basin, which in turn influences soil physiochemistry. As outlined in the Gosselink & Turner (1978) and Mitsch & Gosselink (2015) models, soil physiochemistry influences the biotic response of the system.

The model is undoubtedly a model that applies to fluvially integrated wetland systems in southern Africa, as indicated by numerous studies in the region (McCarthy & Hancox, 2000; Tooth *et al.*, 2002; 2004; 2014; McCarthy *et al.*, 2011; Grenfell *et al.,* 2008; 2009a; Grenfell *et al.*, 2009b; 2010; Ellery *et al., 2003a;* 2012; Joubert & Ellery, 2013). While the model is applicable to southern African wetlands integrated into the fluvial network, it is likely to apply beyond this region alone.

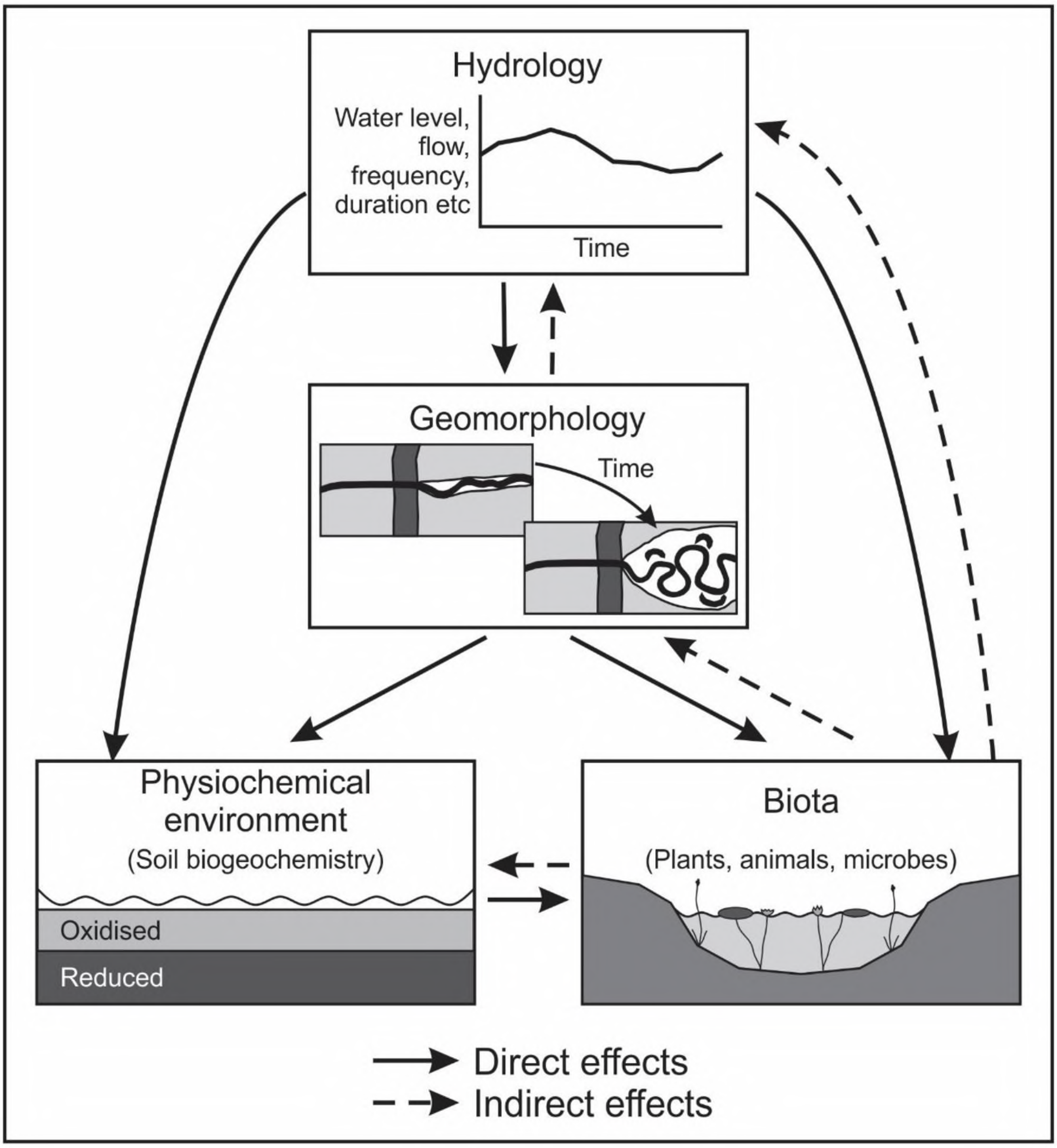

Figure 7.1: A conceptual model of the role of hydrology, geomorphology, soil physiochemistry and vegetation in the structure and functioning of wetlands integrated within the fluvial network.

The findings in this study enhance understanding of the formation and dynamics of freshwater valley-bottom wetland systems within southern African landscapes. Additionally, the study highlights the importance of understanding the complex primary and secondary controls on the formation and dynamics of wetlands. While the traditional view of wetland ecology implies that hydrology is the main controlling factor, this study suggests that geomorphology has to be considered as one of the primary controls of wetland formation, structure, function and dynamics. If wetlands are to be managed wisely, they need to incorporate geomorphic processes, as neglecting this important subject may lead to unsustainable wetland management outcomes.

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Appendix A

Species List of all 75 species, along with their number used in the TWINSPAN analysis.

No.	Species Name	Code	No.	Species Name	Code
1	*Prionium serratum*	PRIOSERR	39	*Rumex sp.*	RUMEXRUM
2	*Miscanthus capensis*	MISCCAPE	40	*Leucadendron salignum*	LEAUALIG
3	*Acacia mearnsii*	ACACMEAR	41	*Lepidium africanum*	LEPIAFRI
4	*Centella asiatica*	CENTASIA	42	*Gymnosporia* heterophylla	GYMNHETE
5	*Trifolium burchellianum*	TRIFBURC	43	*Plantago lanceolata*	PLANLANC
6	*Zantedeschia aethiopica*	ZANTAETH	44	*Chamaesyce inaequilatera*	CHAMINAE
7	*Hydrocotyle bonariensis*	HYDRBONA	45	*Cliffortia ferruginea*	CLIFFERR
8	*Restio paniculatus*	RESTPANI	46	*Metalasia densa*	METADENS
9	*Rhus rehmanniana*	RHUSREHM	47	*Euryops munitus*	EURYMUNI
10	*Clifortia strobilifera*	CLIFSTRO	48	*Stenotaphrum secundatum*	STENSECU
11	*Conyza scabrida*	CONYSCAB	49	*Brachiaria serrata*	BRACSERR
12	*Helichrysum odoratissimum*	HELIODOR	50	*Leersia hexandra*	LEERSIAA
13	*Pteris dentata*	PTERDENT	51	*Virgilia oroboides*	VIRGOROB
14	*Juncus kraussii*	JUNCKRAU	52	*Cynodon dactylon*	CYNODACT
15	*Psoralea latifolia*	PSORLATI	53	*Osteospermum herbaceum*	OSTEHERB
16	*Cyperaceae fimbriscylis*	CYPEFIMB	54	Oplismenus burmanni	OPLIBURM
17	*Juncus oxycorpus*	JUNCOXYC	55	*Blechnum capense*	BLECCAPE
18	*Rubus affinis*	RUBUAFFI	56	*Hakea gibbosa*	HAKEGIBB
19	*Helichrysum rosum*	HELIROSU	57	*Fimbristylis complanata*	FIMBCOMP
20	*Nesaea radicans*	NESARADI	58	*Plecostachys serpyllifolia*	PLECSERP
21	*Wachendorfia thyrsiflora*	WACHTHYR	59	*Leonotis leonurus*	LEONLEON
22	*Elegia capensis*	ELEGCAPE	60	*Dombeya tiliacea*	DOMBTILI
23	*Cuscuta cassytoides*	CUSCASSY	61	*Spermacoce natalensis*	SPERNATA
24	*Mentha aquatica*	MENTAQUA	62	*Bidens formosa*	BIDEFORM
25	*Searsia rehmanniana*	SEARREHM	63	*Conyza bonariensis*	CONYBONA
26	*Persicaria attenuata*	PERSATEN	64	*Drosera capensis*	DROSCAPE
27	*Arctotis arctotoides*	ARCTARCT	65	*Phragmites australis*	PHRAAUST
28	*Athanasia trifurcata*	ATHATRIF	66	*Anagallis arvensis*	ANAGARVE
29	*Pennisetum clandestinum*	PENNCLAN	67	*Persicaria limbata*	PERSLIMB
30	*Oxalis sp.*	OXALSPAA	68	*Medicago polymorpha*	MEDIPOLY
31	*Selago corymbosa*	SELACORY	69	*Senecio macrocephalus*	SENEMACR
32	*Pentzia dentata*	PENTDENT	70	*Rumex acetosella*	RUMEACET
33	*Eriocephalus africanus*	ERIOAFRI	71	*Helichrysum cooperi*	HELICOOP
34	*Eragrostis curvula*	ERAGCURV	72	*Helichrysum petiolare*	HELIPETI
35	*Seriphium plumosum*	SERIPLUM	73	Juncus lomatophyllus	JUNCLOMA
36	*Dipogon lignosus*	DIPOLIGN	74	*Pycreus polystachyos*	PYCRPOLY
37	*Chenopodium mucronatum*	CHENMUCR	75	*Eregrotis curvula*	EREGCURV
38	*Asparagus africanus*	ASPAAFRI			