RELATIONSHIP AMONG FUNCTIONAL TRAITS OF WETLAND PLANTS AND CLIMATIC VARIABLES ALONG AN ARIDITY GRADIENT ACROSS THE HIGHVELD, SOUTH AFRICA

By

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DECLARATION

I, Seadi Sefora Mofutsanyana, declare that the Masters's Degree research dissertation that I herewith submit for the Master's Degree qualification in Botany at the University of the Free State is my independent work and that I have not previously submitted it for a qualification at another institution of higher education.

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Seadi Sefora Mofutsanyana

DEDICATION

To my loving mother Pontsho Peete

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TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

ABBREVIATIONS

Alt	Altitude
ARC	Agricultural Research Council
Ca	Calcium
CCA	Canonical Correspondence Analysis
CWM	Community Weighted Means
Diam	Stem Diameter
EC	Electrical Conductivity
ENSO	El Niño Southern Oscillation
Evap	A-Pan Evaporation
GIS	Geographic Information System
GPS	Global Positioning System
HCA	Hierarchical Cluster Analysis
HGM	Hydrogeomorphic
Humimax	Maximum Humidity
IPCC	International Panel on Climate Change
K	Potassium
Lat	Latitude
Leaf N	Leaf Nitrogen Content
Lon	Longitude
Maxtemp	Maximum Temperature
MEA	Millennium Environmental Assessment
Mintemp	Minimum Temperature
N	Nitrogen
Na	Sodium
NH_4^+	Ammonium
NO_2^-	Nitrogen dioxide
NO_3^-	Nitrate
P	Phosphorus
PCA	Principal Component Analysis

Precip	Precipitation
R depth	Rooting Depth
R/S Rat	Root/Shoot Ratio
RDA	Redundancy Analysis
RGR	Relative Growth Rate
RIL	Rhizome Internode Length
SH Leng	Shoot Length
SLA	Specific Leaf Area
Weig	Plant Weight

ABSTRACT

Wetlands are among the most threatened ecosystems in South Africa due to human activities such as changing land use. In addition to these threats, wetlands are now faced with the threat of climate change, which may affect their biota in the future. Therefore, South Africa needs locally relevant biological indicators to detect changes in wetland ecosystems that can be used in monitoring programmes for wetland vegetation. Plant functional traits are recognised as an effective tool that can be used to understand community assembly processes that determine the abundance and distribution of plant species and their response to climate change. The aim of the study was to determine whether plant functional traits change along an aridity gradient across the Highveld of South Africa. Functional traits of the dominant plant species were collected in the wetlands of the Highveld along a climatic gradient from dry in the west to mesic in the east. The measured traits include plant weight, rhizome internode length, shoot length, leaf nitrogen content (Leaf N) and specific leaf area (SLA). In the analysis canonical ordination techniques were applied to find the correlation between plant functional composition, non-climatic environmental variables and climatic variables. Community-averaged traits were calculated for all wetland vegetation plots and these were plotted against non-climatic environmental variables and climatic variables using the CANOCO program. Hierarchical Cluster Analysis (HCA) was carried out to delineate plant functional groups using the PC-Ord program. Plant functional groups were plotted against non-climatic environmental variables and climatic variables using CANOCO program. The distribution ranges of each plant functional group were mapped using Geographical Information System (ArcGIS). Principal Component Analysis (PCA) was carried out using the PC-Ord program to find the relationship between non-climatic environmental variables and climatic variables. The RDA results showed that the correlations between climatic variables and plant traits in general are not as strong as expected; plants seem to respond much more strongly to non-climatic environmental variables. This means that plants seem to respond much more directly to local factors that determine the wetland habitat and not directly to the climate itself. Nonetheless, it is still possible that these environmental conditions (wetness, inundation, nutrient content of the soil) may change as well in the scenario of climate change, but that would be considered as an indirect effect. The results revealed that plant weight and rhizome internode length are correlated with maximum temperature and evaporation. Species with high plant weight and long rhizome internode length represents species growing in dry areas on the western side of the study area. SLA, shoot length and leaf N are correlated with precipitation and minimum temperature. Species with high SLA, long shoot length and high leaf N are specifically those species growing in mesic areas on the eastern side of the study area. Wetland plant species in dry areas grow in wetlands that are exposed to high temperatures, high evaporation rates, low rainfall and high salinity. These species are short and have low SLA which they use as an adaptation to water stress. Wetland plant species in mesic areas grow in wetlands that are exposed to high rainfall and low temperatures. These species grow faster and are more productive. The functional classification resulted with six plant functional groups namely: tufted graminoids, leafless graminoids, rhizomatous graminoids, salt tolerant forbs, succulent shrubs and short trailing forbs and grasses. The tufted graminoids, leafless graminoids and rhizomatous graminoids are distributed in mesic areas and the succulent shrubs, salt tolerant forbs and short trailing forbs and grasses are distributed in dry areas. Changes in community composition will show how the wetland is responding to climatic variability and environmental change. This will provide an improved basis for monitoring the impacts of climate change on wetland vegetation.

Keywords: Wetlands, environmental change, climate variability, plant functional traits, plant functional types

Chapter 1

Introduction

1.1 Background of the study

Plant species have been classified according to their taxonomy for many years; however, this has strong limitations when answering important ecological questions such as the response of vegetation to environmental change and climate variability (Cornelissen et al., 2003). Plant taxonomists and ecologists came up with the idea to use basic plant traits to classify plants into functional groups and study their performance in a changing environment. The study of plant functional traits provides an effective tool that can be used to understand community assembly processes that determine the abundance and distribution of plant species and their response to climate change (McGill et al., 2006; Soudzilovskaia et al., 2013). The use of plant traits resulted in the compilation of a global database of plant traits (Kattge et al., 2011).

Plant functional traits carry important information on the physiological adaptations of plants to certain environments (Lavorel and Garnier, 2002; Garnier et al., 2004). They link environmental conditions to species performance and this provides a basis for understanding how traits of individual species scale-up to determine ecosystem processes and functions (McGill et al., 2006). Traits show consistent correlations with non-climatic environmental variables across many taxa and this suggests general functional relationships between traits and the environment.

Plant functional traits vary along environmental gradients due to the environmental filters that constrain which species from a regionally available species pool can persist at a site (De Bello et al., 2006; Díaz et al., 2007). Environmental filters place a direct selection pressure on the functional traits and filter out the species that lack traits that are suitable for that site. They retain species that have specific combinations of traits that allow adaptation to a specific site (Douma et al., 2012). The variation of plant traits makes it possible to predict community structure (composition) to describe factors that influence the geographical ranges of species (Read et al., 2014).

1.2 Significance of the study

Climate change is resulting in significant changes in the historical patterns of temperature and rainfall events in South Africa, and these changes are likely to accelerate (Burke, 2011). Climate modelling predicts that the country's climate will become hotter and drier in the future than it is today (Chishakwe, 2010). Consequently, South Africa is facing a water crisis and the challenge to adapt to the changing climate. This is observed by the drought that hit the country in 2015; this drought was reported to be the worst drought the country has experienced since 1982 (Azad, 2015). South Africa often experiences drought during an El Niño event (a phase in a cycle referred to as ENSO; El Niño Southern Oscillation). Collins et al. (2010) defined El Niño as a natural warming of surface temperatures of the eastern Pacific Ocean and it affects ecosystems, agriculture, freshwater supplies, hurricanes and other severe weather events worldwide but mostly in the Southern Hemisphere.

Wetlands are faced with the threat of climate change which may affect their biota in the future. Therefore, South Africa needs locally relevant biological indicators for change in wetland ecosystems that can be used in monitoring programmes for wetland vegetation. Functional traits used to describe wetland plant species will aid such monitoring system because on their basis plant species will be grouped into morphologically and functionally similar groups. Plant functional traits provide information on the direct physiological adaptations of plants to environmental change and thereby link plants to climatic conditions.

Plant functional traits have proven to be an effective tool in the analyses of the interactions between plant individuals and their environment (Lavorel and Garnier, 2002); particularly in quest for understanding the effects of climate change on community composition of wetlands. They provide information on the direct physiological adaptations of plants to environmental change and thereby link plants to climatic conditions. This information can be used to predict changes in vegetation distribution in response to future climate changes (Meng et al., 2009).

In this context, the study has the aim to determine whether plant functional traits change along an aridity gradient across the Highveld of South Africa. This will provide biological indicators to detect changes in community composition of wetlands due to climate change in the future.

1.3 Objectives of the study

Within the scope of the overarching aim, the current study has several objectives:

- To identify plant traits of predominant species in wetlands along an aridity gradient across the Highveld and draft a plant functional classification of these species using correlated trait complexes;
- To test for associations between plant traits of the predominant species and environmental conditions along the aridity gradient, and
- To see which plant traits correspond strongly with which environmental and climatic variables and whether these traits can be used in monitoring to simplify species identification.

1.4 Structure of the dissertation

The second chapter presents a literature review focusing on an overview of wetlands, the impact of climate change on wetlands and a review on plant functional types and traits. The third chapter provides the description of the study area, while the fourth chapter provides the methods that are used in this study. The fifth chapter concentrates on the results found in this study and the sixth chapter provides a discussion of the main findings in this study. Lastly, the seventh chapter provides a conclusion of the findings from this dissertation and recommendations for future studies.

Chapter 2

Literature review

2.1 General overview of wetlands

The term ‘wetland’ is used to describe the different kinds of habitats where the land is wet for at least some period of the year. The South African National Water Act (1998) defined wetlands as land that is transitional between terrestrial and aquatic systems where the water table is usually at or near the surface, or the land that is periodically covered with shallow water and which under normal circumstances supports or would support vegetation adapted to life in saturated soil. Wetlands occupy an intermediate position between terrestrial and aquatic ecosystems. They comprise swamps, marshes, floodplains, bogs, and other shallow flooded areas (Keddy et al., 2009). Wetlands are mostly located in those places where the topography slows down the movement of water through the catchment or groundwater surfaces causing the surface soil layers in the area to be temporarily, seasonally or permanently wet. There are three major components that together determine the wetland environment, namely hydrology, vegetation and soils. These three components will be discussed in the following sections.

2.1.1 Hydrology

The movement of water is the single most important factor in controlling where wetlands occur, and it determines which specific types of wetlands and wetland processes occur (Craft et al., 2001; Snidvongs et al., 2003; Lemly and Culver, 2013). Clearly, without water there would be no wetland flora and fauna. Wetlands are dynamic environments whereby environmental conditions such as water depth, water velocity, turbidity, and temperature change daily, seasonally, and annually (van der Valk, 2012).

Hydrology is defined as the inflow and outflow of water through a wetland and its interaction with other site factors (van der Valk, 2012). It is characterized by the source of water, hydroperiod (depth, duration, and frequency of inundation) and hydrodynamics (direction and velocity of water movement). The duration and frequency of inundation in a wetland vary according to the wetland's hydrogeomorphic (HGM) setting and they depend on regional differences in climate, especially rainfall and evaporation.

The description of the wetland hydroperiod integrates all aspects of its water budget. The water budget is defined as the balance between the water inputs (surface inflows, precipitation, groundwater discharge) and water outputs (surface evaporation, evapotranspiration, ground-water recharge) in a wetland (Collins, 2006). The water budget provides information on the hydrological functioning of a wetland, including flood control and groundwater recharge. Over any period, the change in water stored in the wetland is equal to the sum of the water inputs, minus the water outputs.

The direction and rates of subsurface water flow in wetland sediments are determined by the hydraulic conductivity of the sediments, surface water evaporation, evapotranspiration by macrophytes, the height of the water table, and the slope of the wetland. The nature of the movement of the water inputs in a wetland is important in distinguishing different wetland types (Ellery, 2004). For instance, wetlands that are closed systems such as depression wetlands receive water from precipitation and wetlands that are open systems such as floodplains receive water from surface flows. Depressions and floodplain wetlands may lose water through surface runoff, evapotranspiration and ground-water recharge (Euliss et al., 2004).

Wetland hydroperiod is defined as the seasonal pattern of the water level of a wetland that results from the combination of the water budget and the storage capacity of a wetland (Mitsch and Gosselink, 2015). Wetland hydroperiods vary in the frequency, depth and duration of their inundation due to hydrogeologic setting, local ground-water conditions, geomorphology, and regional precipitation patterns (Tiner et al., 2015). For instance, some wetlands are permanently wet, others are seasonally wet and for some wetness changes from year to year depending on precipitation. In South Africa, seasonal wetlands in humid regions have high water tables in summer and low water tables during winter. Additionally, what is considered wet in one region such as the arid west of South Africa (Karoo) may be relatively dry for another area such as Mpumalanga. Generally, variation in precipitation causes variation in inundation in wetlands and is often accompanied by shifts in vegetation patterns (Seelig, 2009; Tiner et al., 2015).

2.1.2 Wetland Vegetation

Wetland vegetation is an important component of a wetland environment that plays an important role in the ecological functioning of a wetland (Gage and Cooper, 2010). It is the most visible part of the wetland and a suitable indicator for the early signs of any degradation in wetlands (Cronk and Fennessy, 2001; Adam et al., 2010). As such, the presence of wetlands and their boundaries can often be identified by the presence of characteristic wetland vegetation.

Lemly and Culver (2013) defined wetland plants as plants growing in water or on a substrate that is at least periodically deficient in oxygen as a result of an excessive water content. Wetland plants are distributed according to their tolerances to flooding (Odland and Del Moral, 2002). They may be floating, floating-leaved, submerged, or emergent and complete their life cycle in flowing or still water, or in inundated or saturated hydric soils (Cronk and Fennessy, 2001).

Wetland plants have evolved different morphological, anatomical, and physiological adaptations for life in wet environments. An example of a morphological adaptation for avoiding water stress is a shallow root system (Tiner, 2005). The roots of most wetland plants grow laterally and near to the surface. This is because there is usually no oxygen in wetland soils and therefore it costs energy to transport oxygen below the soils surface, at least seasonally. However, plants growing in wetlands found in dry areas have deep roots, because the wetlands are only seasonally inundated. Wetland plants can also cope with oxygen deficiency physiologically, such as the development of aerenchyma and other internal pathways for oxygen diffusion to the roots (DeLaune et al., 1999; Batzer and Sharitz, 2014) .

The adaptations of wetland plants are the results of an evolutionary process (Tiner, 2005). As all vascular plants originally are terrestrial, wetland plants are basically terrestrial species that have secondary adaptations to life in water. They are similar in their general anatomy, morphology, and physiology to other terrestrial plants and they reproduce both sexually and asexually (van der Valk, 2012). Wetland plants have some adaptations relating to reproduction that are similar to terrestrial plants, for example, most of them have terrestrial pollination syndromes. However, asexual reproduction is very common among wetland plants. They can reproduce by means of plant fragments breaking off and developing roots. The most common clonal strategy among wetland plants is through the growth of rhizomes.

Wetland plants are important for many reasons. They are at the base of the food chain and they are the primary pathway for energy flow in the system (Fennessy, 2002). Through the photosynthetic process, wetland plants link the inorganic environment to the biotic environment. The primary productivity of wetland plant communities is variable; some herbaceous wetlands have extremely high levels of productivity compared to wetlands dominated by shrubs in arid regions (Cronk and Fennessy, 2001). Wetland plants provide a habitat for other taxonomic groups such as epiphytic bacteria, phytoplankton, and some species of algae, periphyton, amphibians and fish, feeding large numbers of migratory birds (Fennessy, 2002).

Furthermore, there is a strong link between vegetation and wetland water chemistry (Fennessy, 2002). The chemistry of water has a major influence on the composition of the wetland vegetation (van der Valk, 2012). A number of important conditions influencing biogeochemical processes occur in wetlands due to the presence of a shallow water column, notably high primary productivity, the presence of both aerobic and anaerobic conditions at close proximity, and the accumulation of litter (Cronk and Fennessy, 2001). These conditions often lead to a natural cleansing of the water that flows into wetlands.

Wetlands are a sink, source and transformer for many nutrients and organic compounds, and they also act as filters of sediments and organic matter (Bonya'Johnson, 2004). They can be a permanent sink of nutrients and organic compounds if these substances become buried in the substrate. Vegetation plays an important role in wetlands as both nutrient sinks through uptake and as nutrient pumps, moving compounds from the sediment to the water column.

Submerged plants also release oxygen to the water column that is then available for respiration by other organisms.

Wetland processes play an important role in the cycling of nitrogen, carbon and sulfur by transforming them and releasing them into the atmosphere. Materials associated with solids such as phosphorus are removed from the soil and water column in wetlands (Cronk and Fennessy, 2001). Plant uptake and plant tissue accumulation can remove nitrogen and phosphorus from the soil. Furthermore, wetlands are driven by biogeochemical processes which involve the exchange of materials between living and non-living components (Reddy et al., 2010).

2.1.3 Wetland Soils

Together with hydrology, soil represents the most important aspect of the physical environment in a wetland. It is an important zone with a lot of biogeochemical activity and where plants, animals and microorganisms interact with the hydrologic and other elemental cycles (Kolka and Thompson, 2006; Jackson et al., 2014). Wetland soils, also termed hydric soils, are defined as soils that have water at or near the surface for most of the growing season and this leads to the development of anaerobic conditions in the upper soil layers (Fennessy, 2004; Keddy, 2010). Anaerobic conditions develop because the rate of oxygen depletion is higher than the rate at which it is replenished. These soils are saturated for long enough to support plants that grow well in anoxic environments and to prevent any competition from other species (Craft et al., 2001).

Wetland soils form anywhere where there is a prolonged saturation of the soils, largely independent of climate and parent material. The volume of every soil consists of solid matter, water and air. When soils are flooded, their pore spaces are filled by water. The hydroperiod and water table fluctuations influence the air-filled pore space of soils, which are important for oxygen diffusion from the atmosphere into the soil. Typically, the volume of mineral soils consists of about 50% solid material (minerals), 25% water and 25% air, and for organic soils this would be 20% minerals plus organic matter and the remaining volume water and air (Reddy and DeLaune, 2008).

Wetland soils are deficient in oxygen because oxygen is soon depleted from flooded soils by respiration of soil micro-organisms and plant roots, and that leads to reduced soil conditions (Keddy, 2010). Wetland soils are identified by their colour characteristics (termed soil hydromorphic indicators) which are associated with reducing conditions in the soil (Vepraskas and Caldwell, 2008). The period of saturation leading to reducing conditions depends on temperature, organic matter, and microbial activity in the soil. During this period the soil microbes deplete free oxygen and begin to use other metabolic pathways involving nitrogen, iron, manganese, and sulfur resulting in a chemical transformation in the soil (Keddy, 2010; Lemly and Culver, 2013). These transformations can then be observed in the form of soil hydromorphic indicators such as mottling, gleying, and a rotten egg (sulfuric) smell.

Flooded soils develop a black, bluish, greyish colour, termed gley as a result of reduced iron. When reduced these soils become colourless and can be leached out leaving the natural grey or black colour of the parent material. The rotten egg smell originates from hydrogen sulphide. The mottling refers to orange patches or streaks in an otherwise greyish soil and it indicates iron to be in an oxidized state. The soil indicators allow us to deduct the hydroperiod of a wetland (i.e. they are the results of the hydroperiod), and to determine how long the wetland has been flooded. For example a soil that has mottles indicates that the wetland is seasonally or temporarily inundated and a soil with a rotten egg smell indicates that the wetland is permanently inundated.

Nutrients play a major role in productivity (Ngai and Jefferies, 2004), and their presence in the soil is of vital importance for wetland plants. Poff et al. (2002) explained that these nutrients are transported into the wetland by runoff and groundwater. Soil organic matter plays an important role in providing nutrient storage and supply. The macronutrients (nitrogen, phosphorus, and potassium) are used in relatively large amounts by plants and they are essential for the plant to complete its lifecycle (Maathuis, 2009). Macronutrients provide vital functions, for example potassium increases vigour and disease resistance of plants and phosphorus helps with energy transfer in the form of the ATP molecule.

Either phosphorus or nitrogen (sometimes potassium) can be limiting for plant growth especially in terrestrial ecosystems (Güsewell, 2005). In freshwater wetlands nitrogen and organic matter accumulate in the soil, therefore, plant growth is often limited by phosphorus or co-limited by both nitrogen and potassium (Batzer and Sharitz, 2014). The N:P ratio (ratio between nitrogen and phosphorus concentration) in plant tissues and soils is used to identify the threshold of nutrient limitation in wetlands. Liebig's Law of the Minimum states that the nutrient that has the lowest supply relative to the plant's requirement will limit the plant's growth (Ågren et al., 2012).

An N:P ratio below 13 suggest nitrogen limitation, whereas an N:P ratio above 16 suggest phosphorus limitation, and N:P ratio between 14 and 16 are co-limited by nitrogen and phosphorus (Koerselman and Meuleman, 1996; Güsewell, 2005; Batzer and Sharitz, 2014). The nature of nitrogen limitation affect species composition, for example addition of phosphorus in the absence of nitrogen encourages the growth of leguminous species that are capable of dinitrogen fixation. In contrast, addition of nitrogen is the absence of phosphorus is reported to stimulate the growth of grass species (Koerselman and Meuleman, 1996).

Micronutrients (calcium and magnesium) are needed only in small amounts and are virtually nowhere limiting growth. They are involved in the entire metabolic enzyme system of plants and the range between toxic and deficient levels is small, thus, proper supply of micronutrients is needed for good plant growth (Brennan and Malabayabas, 2011). In wetlands, the biochemical and electrochemical changes caused by submergence influence the solubility and availability of micronutrients in the soil. Submergence increases the availability of iron, molybdenum and magnesium and decreases the availability of sulfur, zinc, and copper. Micronutrients provide vital functions for wetland plants, for example calcium is important for the growth of new roots and root hairs, and magnesium is a key component of chlorophyll.

Soil pH is a measure of hydrogen ion concentration expressed on a scale from 0 (acid) through 7 neutral to 14 (alkaline). Soil pH plays an important role in determining the availability of soil nutrients. Generally, plant nutrients in soil decreases below pH 6 and this applies to most wetlands (Johnson and Gerbeaux, 2004). The pH of wetland soils and water is different over a wide range of values (Xiong and Wang, 2005). In wetlands organic soils tend to be more acidic (pH < 7) whereas mineral soils tend to be more alkaline (pH > 7) (Epp and Mitsch, 2006).

Wetlands soils in areas with little or no water inflow are acidic than in wetlands with greater amounts of water input. Inland wetland systems fed by rainwater tend to be acidic with peatlands on the extreme (pH < 5), and wetlands in arid or semi-arid regions or wetlands strongly linked to groundwater tend to be basic (alkaline) (Batzer and Sharitz, 2014). The acidity of peaty soils is due to the reduction of iron and manganese oxides, and the mineral soils are alkaline because of the decomposition of soil organic matter**.**

2.1.4 Classification system for wetlands

Wetlands are complex ecological systems; therefore, there is a need for a wetland classification system to simplify our understanding of them. In South Africa, Ollis et al. (2013) developed a classification system for wetlands and other aquatic ecosystems, and it is based on a top-down, hierarchical classification following the functionally oriented hydrogeomorphic (HGM) approach. The HGM approach can provide information about the fundamental processes responsible for the development of different types of aquatic ecosystems and the determinants of ecosystem structure and function (Ollis et al., 2015).

The HGM approach is in contrast to the older classification system suggested by Cowardin et al. (1979), whereby different wetland units were distinguished based on structural features such as size, depth, vegetation cover and the presence of surface water. This classification system consisted of five major wetland categories based on their connectivity with various types of open water bodies, classified as marine, estuarine, riverine, lacustrine or palustrine as the main subdivision.

Ollis et al. (2013) proposed six levels in the hierarchy for the classification system for wetlands and other aquatic ecosystems in South Africa, whereby each level refines the classification further. Level 1: differentiates between inland, estuarine and shallow marine systems using the degree of connectivity to the open ocean as the key discriminator; level 2: groups inland systems according to the most appropriate spatial framework; level 3: distinguishes four primary Landscape Units (valley floor, slope, plain, bench) based on the topographic position within a particular inland aquatic ecosystem where the wetland is situated; level 4: identifies hydrogeomorphic (HGM) units within an inland aquatic system, defined according to landform, hydrological characteristics and hydrodynamics; level 5: applies discriminators to classify the hydrological regime of an HGM unit and level 6: uses descriptors to categorize a range of biophysical attributes (Ollis et al., 2015).

In the current study the emphasis will be on Inland Systems since the ecosystems under study have no existing connection to the ocean. The most important level for the classification is level 4 (HGM unit) as this characterizes a single functional unit of wetland driven by the same hydrological and geomorphological processes.

There are six primary hydrogeomorphic (HGM) wetland types recognized for Inland Systems of the classification system (Ollis et al., 2013), namely:

- **Floodplain wetlands:** wetland areas on the mostly flat or gently-sloping land that is driven by annual flooding when the river water overtops their banks;
- **Channelled valley bottom wetlands:** mostly flat wetland areas located along a valley floor with a river channel running through it. They are characterized by their location on valley floors, the absence of characteristic floodplain features and the presence of a river channel running through the wetland. Water inputs are mainly from adjacent slopes, while the channel itself is not typically a major source of water for the wetland (Ellery, 2004);
- **Unchannelled valley bottom wetlands:** mostly flat wetland areas associated with a drainage line but without a major channel running through it. They are characterized by the prevalence of diffuse flow, and even after high rainfall events no channel

develops. These wetlands are generally formed when a river channel loses confinement and spreads out over a wider area;

- **Depressions:** wetlands with closed elevation contours which increases in depth from a perimeter to a central area of greatest depth, and within which water typically accumulates. Depressions may be flat bottom (often referred to as pans) or round-bottomed (often referred to as pools or lakes), and may have any combination of inlets and outlets or lack any connection completely;
- **Slope seepages:** wetland areas located on gently to steeply sloping land and dominated by colluvial, unidirectional movement of water and material down-slope. Seeps are often located on the side-slopes of a valley but they do not extend on a valley floor. Water inputs are subsurface flows from an up-slope direction; and
- **Wetland flats:** level or near-level wetland areas that are not fed by water from a river channel, and which are situated on a plain or bench. They are characterized by the dominance of vertical water movement associated with precipitation, groundwater inflow, infiltration, and evapotranspiration.

Ollis et al. (2013) proposed that for all wetlands there should be a classification for the hydrological regime according to the hydroperiod. The hydroperiod is defined as the length of time that the wetland surface is inundated. It results from the balance between inflows, outflows, the wetland storage and groundwater conditions (Foster, 2007). Hence, the water budget and the storage capacity of the wetland define the hydroperiod. At level 5A of the classification, five categories have been provided for the hydroperiod, namely:

- **Permanently inundated** – with surface water present throughout the year;
- **Seasonally inundated** – with surface water present for extended periods during the wet season but drying out annually, either to complete dryness or saturation during the dry season;
- **Intermittently inundated** – holding surface water irregularly for changeable time periods of less than one season’s duration, at intervals varying from less than a year to several years; and
- **Never/Rarely inundated** – covered by water for less than few days at a time, but the saturation with water is at least intermittently for one week or more at a time.

2.1.5 Wetland ecosystem services

Wetland ecosystems are recognized as important ecological systems that provide the ecosystem services. Hence, the Ramsar Convention on Wetlands has promoted the wise use of wetlands to maintain their ecological structure and the ecosystem processes which form the basis for the delivery of ecosystem services (Novitski et al., 1996; McInnes, 2007). Wetland ecosystem services are components of wetlands which are directly enjoyed, consumed, or used to enhance human well-being (Boyd and Banzhaf, 2007). The ability of wetlands to provide the goods and services valuable to human communities is associated with their ecological functioning (Desta et al., 2012). It is noteworthy that not all wetland types will perform all the services nor will they be able to perform them equally well (Novitski et al., 1996).

The ability of the wetland to perform the ecosystem services depends on hydrogeomorphic types and the location within the catchment. The factors that determine whether the wetland will be able to perform the ecosystem services are climatic conditions, water quality and quantity entering the wetland, disturbances or alterations within the wetland or the surrounding ecosystem. It is the interactions of physical, biological, and chemical components of a wetland such as soils, water, plants, and animals that enable wetlands to perform an enormous variety of important ecosystem services (Desta et al., 2012). The global value of the goods and services from wetlands has been estimated at US$14 trillion annually (Baral et al., 2016).

The Millennium Environmental Assessment (MEA, 2005) grouped the ecosystem services provided by wetlands into four categories namely:

1) **Regulating services** which are the benefits obtained from the regulation of ecosystem processes such as water quality improvement, climate regulation, flood and erosion control;

2) **Provisioning services** explained as the products that are obtained from wetlands such as food, fresh water, fibre and fuel, and habitat;

3) **Cultural services** explained as the non-material benefits people obtain from wetlands through spiritual enrichment, recreation and education; and

4) **Supporting services** which are necessary for all other ecosystem services, they differ from all the other services because their impacts on people are either indirect or occur over a long time, they include soil formation, biodiversity, nutrient cycling and pollination.

Examples of regulating and provisioning services provided by wetlands are explained in the following sections.

Regulating services

Wetlands are important regulators of water quantity and water quality (Bergkamp and Orlando, 1999). They are often called the kidneys of nature because of their ability to purify water by trapping sediments and storing pollutants and excess nutrients such as nitrates, phosphates, and heavy metals in their soils and vegetation (Turpie et al., 2010; Clarkson et al., 2013). MEA (2005) emphasized that marshes and swamps are the wetlands that play a major role in treating and detoxifying a variety of waste products, including heavy metals mostly depending on the type of vegetation that is present.

Wetlands remove and transform pollutants through a combination of physical, chemical, and biological processes. They have proven to significantly reduce nutrients which are commonly associated with agricultural runoff and sewage effluent. Furthermore, studies by Phillips et al. (2015) showed that fast growing wetland plants such as *Typha capensis* and *Phragmites* species have the ability to accumulate nutrients and heavy metals to extremely high levels. Therefore, they are used effectively to treat sewage effluent and industrial waste water.

Maltby and Acreman (2011) showed the example of the Nakivubo *Papyrus* swamp in Uganda in which semi-treated sewage effluent from Kampala passes through the wetland to purify water. During the passage of the effluent, sewage is absorbed and the concentrations of pollutants are reduced, and afterwards this water can be used for public utility. The function of this swamp has led to its use as a buffer zone, particularly in the prevention of the spread of pollutants from sewage treatment plants.

The rate of nitrogen removal from surface waters depends on the position of the wetland in the catchment. Wetlands that are positioned in the lower parts of catchments, receiving water from large contributing areas, are more efficient in removing excess nitrogen, while wetlands in upper reaches are most effective for removing excess phosphorus (Clarkson et al., 2013). However, water quality improvement services are only considered valuable downstream from places where wastes are generated (Turpie et al., 2010).

Wetlands play a vital role in flood control, as they provide a physical barrier to slow the speed and reduce the height and force of floodwaters. Floodplains, valley bottom wetlands and seepages are often said to "act like a sponge", soaking up water during wet periods and releasing it during dry periods (MEA, 2005; Nyman, 2011). As such, they are the main providers of a reliable base flow in the rivers in inland areas, and the loss of these wetlands could increase the risks of floods occurring because all runoff from rainfall will be released at once (MEA, 2005). Rivers such as the Senegal, Niger, and Zambezi have large floodplains that play an important role in flood control (Maltby and Acreman, 2011).

Flood control occurs due to water storage in the soil as well as vegetative resistance to the water flow (Turpie et al., 2010). In some cases the function of flood control is rather a function of resistance of the wetland, and less a function of its holding capacity (Turpie et al., 2010). Resistance is related to vegetation cover whilst water storage tends to be greater in wetlands with substantial water level fluctuations such as forested wetlands and those with large wet meadow zones, or with intermittent, seasonal, temporary, or semi-permanent hydrologic regimes. A specific South African example is formed by wetlands dominated by the species *Prionium serratum,* a wetland plant which is specially adapted to deal with large flood events which is commonly found in the southern cape River systems (Le Roux, 2013). It is characterized by fibrous, net-like root systems and woody stems which are effective in trapping sediment and reducing the velocity of waters in flood.

The discharge of a river changes overtime depending on rainfall in the catchment. A hydrograph is defined as the graph showing the rate of discharge in a river through time (Brutsaert, 2005). For example, after heavy rainfall the discharge of a river is higher and the water is released in spate-flows (sudden peaks in the hydrograph as large discharges are released at once) and when it settles down water is released gradually and discharges are similar throughout (flat gradual hydrograph). A wetland that control floods effectively therefore results in a broader and flatter peak on the flood hydrograph. Floodplains are known to be critical in mitigating flood damage, as they store large quantities of water, thereby reducing the risk of flooding downstream.

Wetland vegetation along the riparian zones and shorelines of rivers, streams, and lakes plays an important role in preventing soil erosion by reducing stream energy and stabilizing soil, allowing for better recovery of these systems after a damaging flood event. The roots of wetland plants bind the wetland soils to resist erosion. For example, tree roots stabilize the soil and foliage intercepts rainfall thus preventing compaction and erosion of bare soil (De Groot et al., 2002). Plants growing along shorelines contribute greatly to controlling erosion and facilitating sedimentation. In the absence of such vegetation, efforts to control shoreline erosion are usually expensive. Also, these efforts are not always successful and can result in further degradation.

Provisioning services

Wetland ecosystems are home to many living organisms that can be harvested for personal and commercial use. The products derived from wetlands include food, medicinal plants, and materials for clothing and building (Bergkamp and Orlando, 1999; De Groot et al., 2002). In addition, the water that humans use originate from various freshwater systems, including wetlands, lakes, rivers, swamps and shallow groundwater aquifer (MEA, 2005). Wetlands recharge groundwater which plays an important role in the water supply for people who are dependent on it as a source of drinking water and for irrigation purposes.

Wetlands provide a habitat for a large variety of animals including fish, birds, amphibians, and aquatic invertebrates. However, the extent to which each wetland provides habitat for terrestrial and aquatic organisms depends largely upon its location within the landscape, the environmental gradients within the wetland and the connectivity with other ecosystems in the surrounding catchment as well as with the broader drainage network.

Wetlands that are connected to rivers and lakes are important for fish populations because fish depend on certain wetland processes. For example, wetlands provide food for fish species and vegetated areas where fish can reproduce and hide from predators. Wetlands also filter out sediments and pollutants, providing clean water that is required for fish populations. The services that wetlands provide for fish are vital for humans because fish is the main source of protein for one million people worldwide (Clarkson et al., 2013). Fishing contributes to many local and national economies in Africa. Phoenix and Walter (2009) reported that seventy percent of dietary animal protein in Malawi is derived from fish. In addition, people eat small mammals, aquatic snails, arthropods, insects and amphibians that are harvested from wetlands in many parts of the world. For example, in South Africa, people eat bullfrogs and cane rats which provide a rich source of protein (Macaskill, 2010).

Wetlands also provide edible plant species, for example, people in South Africa use the sweet smelling flowers of *Aponogeton distachyos* (Waterblommetjie) in the Waterblommetjie bredie recipe (Macaskill, 2010). The waterblommetjie (*Aponogeton distachyos*) is a plant endemic to the Cape Lowland Freshwater Wetlands. The tuber of *Nymphaea nouchali* (blue water lily) is another indigenous vegetable that can be roasted like a potato. In addition, rice, originally a wetland plant, is one of the most important staple foods in the world, accounting for one fifth of total global calorie consumption and it is presently cultivated in artificial wetlands.

Other wetland plants are collected and used for construction, fencing, clothing, mats, baskets and rope (Egoh et al., 2012). For example, people in Kwa-Zulu Natal in South Africa have the tradition of using wetland plant species such as *Cyperus latifolius, Cyperus marginatus* and *Juncus kraussii* for crafts (Kotze and Traynor, 2011).

Furthermore, wetlands contribute to the maintenance of human health by providing medicinal plants. In Africa, people are often dependent on using plants for health purposes because of a lack of accessible medical facilities (Egoh et al., 2012). Medicinal plants can also be used commercially, for example Cameroon is exporting medicinal plants which are a major foreign exchange earner with annual earnings of 2.9 million dollars. This trade includes many wetland species.

In South Africa, about 19500 tons of medicinal plant materials are provided by wetlands and they are used by 28 million South Africans every year (Macaskill, 2010). For example, in Kwa-Zulu Natal province people use the river pumpkin (*Gunnera perpensa*), a common wetland plant, to ease childbirth, and to treat kidney and bladder infections. Moreover, the medicinal plants derived from wetlands provide chemicals that can be used as drugs and pharmaceuticals or that may be used as models to synthesize these drugs (De Groot et al., 2002). Some animals from wetlands are used to test new medicines or may even serve as medical tools such as medicinal leeches (*Hirundo medicinalis*) which are applied to reduce blood pressure.

The 'indirect use' values provided by wetlands include habitat provided for both resident and migratory animal (bird) species which is essential for the maintenance of the biological and genetic diversity on earth (De Groot et al., 2002). For example, the wetlands that support populations of mosquito-fish and aquatic macroinvetebrates such as water boatman, backswimmers, and dragonfly larvae provide a form of biological pest control to manage mosquito populations (Moore and Hunt, 2012).

2.2 Wetlands and climate change

Wetlands are environments which have been under pressure from humans for many years. As a result, in many areas a large portion of wetlands has been lost. They have been converted to agricultural fields, overgrazed by livestock or drained for commercial development. Most of the remaining wetlands are in a degraded state because of altered flow regimes and deterioration of water quality (Kibria, 2015). On top of all these threats from changing land use, the wetlands are now faced with the threat of climate change, which is one of the most important factors that may affect wetlands in the nearby future as it has a direct impact on the water cycle (Tong et al., 2014).

Climate change occurs naturally over millennial time scales related to cycles in the occurrence of sunspots, the wobble of the earth, the tilt of its axis and the shape of its orbit (Woodward et al., 2010). However, the rates of warming observed in recent years threaten the functioning of natural ecosystems because of the much faster rate in which it occurs, which exceeds the speed in which organisms can adapt. This warming is due to rising concentrations of greenhouse gases (particularly carbon dioxide) in the atmosphere which are caused by human activities such as industrial development and the burning of fossil fuels (Boon and Ahenkan, 2012; Barros and Albernaz, 2014).

The International Panel on Climate Change (IPCC) 2013 reported the average rise of the temperature of all land and ocean surfaces on the planet to be 0.85 ^{o}C from 1880 to 2012 (Stocker et al., 2013). The climate models predict that temperatures are expected to continue rising further. In Africa, predictions show that temperature will have risen by 1-2.6 ^{o}C by 2050 since pre-industrial levels (Junk et al., 2013). The temperature of the Southern African sub-region (i.e. the total geographical area occupied by members of States of Southern Africa Development Community, SADC) has risen by over 0.5 ^{o}C over the last 100 years and will continue to rise as the climate changes (Chishakwe, 2010).

The reported warming will have significant effects on the hydrological cycle and it will increase the frequency of floods, storms, and drought. It will also lead to an overall desiccation of soils (Snidvongs et al., 2003). These changes will cause modifications in biogeochemical processes including carbon dynamics, the structure of food chains, primary and secondary production (Solomon, 2007; Junk et al., 2013). Furthermore, Dawson et al. (2003) explained that changes in climate are likely to affect wetlands in terms of their spatial extent, distribution and ecological functioning.

Wetlands are more vulnerable to climate change because they are isolated and physically fragmented within a large terrestrial landscape. On the other hand, wetlands occupy positions in the landscape that accumulate water from the surrounding catchment; therefore they may still have a reliable water supply even if rainfall decreases. Changes in both the mean and the variability of climatic variables determines the impacts of climate change on wetlands and the goods and services they provide (Erwin, 2009).

It is therefore expected that changes in temperature and precipitation due to climate change will degrade the goods and services provided by wetlands (Conway, 1996). Moreover, the provision of ecosystem services by wetlands will not be altered in the same way across all wetlands because the local effects of climatic change will not be the same across all regions of the world. Some regions will experience more droughts while other regions will receive higher rainfall.

Nonetheless, wetland ecosystems are viewed as resilient to changes in atmospheric temperatures. Resilience is defined as the capacity of a system to absorb disturbance and reorganize while undergoing change in order to retain the same structure and function. According to McKinstry et al. (2004) a wetland can recover from the impacts of climate change several times before being critically damaged. This recovery will depend on the condition of the habitat, and on the ability of species in the wetland to reproduce and disperse (Dodds and Whiles, 2010). Even so, Poff et al. (2002) predicted that rapid climate change may enforce new environmental changes that will exceed the limits of resilience of wetland ecosystems that could have otherwise been absorbed. If this resilience is lost, the effects of climate change on wetlands could lead to irreversible changes in their condition.

2.2.1 Hydrological effects of climate change on wetlands

Wetland functions are closely associated with their hydrology which is determined by the balance of water inputs and outputs. This causes wetlands to be sensitive to alterations in the hydrological cycle, and such alterations are to be expected under the scenario of climate change through changes in air temperature, regional precipitation, surface runoff, groundwater storage, and evaporation (Mortsch, 1998; Kibria, 2015).

It is expected that climate change will affect the quantity of water resources by altering the hydrological regime. A drying climate will impact wetlands that receive a major part of their water from precipitation and the water levels may drop (Kling et al., 2003; Flournoy and Fischman, 2013). Contrasting to this, there are wetlands that are driven by groundwater and these receive water from large volumes of water stored in aquifers which stabilizes the water table around these areas (Brooks, 2009). However, these wetlands are also subject to water table fluctuations in the groundwater recharge areas from which the aquifers receive their water (Pitchford et al., 2012). These recharge areas may be far removed from the wetland and therefore subjected to a completely different climate regime.

Since wetlands are dependent on water levels, changes in climatic conditions that affect water availability will influence the nature and function of wetlands. It is expected that reduced precipitation levels due to climate change will cause a decreased surface water flow, which will isolate wetlands from their primary water sources. A reduction in the high flows that inundate floodplains will isolate them from their adjacent stream or river (Poff et al., 2002; Sheldon et al., 2010). Disconnected floodplains resulting from a drier climate would cause wetland communities and riverine wetland species to become more vulnerable (Flournoy and Fischman, 2013). Changes in the flow regimes and water levels such as prolonged drought may lead to terrestrialisation of wetlands (Kibria, 2015).

Moreover, as the climate changes precipitation will not be equally distributed as some areas will become wetter and while other areas will become drier (Arnell, 1999; Pittock et al., 2008). This will result in changes in the degree of wetness of wetlands, and the distribution of wetland species (Sheldon et al., 2010). However, the colonization of new locations will be constrained by the dispersal abilities of organisms as well as geographical and human barriers. In addition, a reduction in precipitation will affect the arid regions more than the mesic areas, and the effects of prolonged dry periods may have lasting effects due to changes in surface and groundwater levels.

Climate change will lead to alterations of the hydrologic regime which can affect the water quality through salinisation of inland wetland ecosystems in the coming decades. Increased temperatures, the resulting drought and high evaporation will cause areas with slowly discharging ground water to be subjected to extended periods of salinity (McEwan et al., 2006; Skrzypek et al., 2013). Salinity occurs when dissolved salts in the water table rise to the soil surface and accumulate as water evaporates. Extensive evaporation leads to accumulation of salts such as carbonates, gypsum and halite. Salinity is common in wetlands occurring in warm and arid environments because these wetlands are often subjected to prolonged periods of drought and high evaporation.

Salinity alters the physiochemical nature of the soil-water environment, increasing ionic concentrations and altering chemical equilibria and mineral solubility (Herbert et al., 2015). Increased concentrations of solutes can alter the biogeochemical cycling of major elements including carbon, nitrogen and phosphorus. This in turn will alter the water quality, nutrient cycling and functioning of wetland biota.

2.2.2 Effects of climate change on wetland vegetation

Vegetation has continuously changed with climate and this implies that the distribution of species corresponds with the climate according to the environmental tolerances of the species (Skarpe, 1996). Erwin (2009) reported that the potential impact of climate change will vary between regions and among wetland types. Species survive within specific ranges of temperature, water and chemical conditions. If they are exposed to conditions outside of their normal environmental range they must either adapt or migrate; otherwise they will perish (Jin et al., 2009).

The success of a species in adapting or migrating will depend largely on its life history, its dispersal traits, the fragmentation of its habitat and the rate at which its environment changes (Woodward et al., 2010). It is expected that wetland vegetation in different areas will respond differently to climate change, but there are also some general responses to be expected. For example, increased carbon dioxide levels will increase plant growth rates and biomass accumulation (Burkett and Kusler, 2000).

Increased levels of carbon dioxide increase the photosynthetic rate of all species, including emergent macrophytes. These species respond to increased carbon dioxide levels with a decrease in stomatal conductance which reduces transpiration rate (McCarthy, 2001). The different photosynthetic responses to increased carbon dioxide among species could result in changes in plant community structure that have impacts at higher trophic levels (Burkett and Kusler, 2000).

Kibria (2015) reported that the vulnerability of plants results from the balance between the rainfall, temperature and evapotranspiration that governs their physiology. Rising temperatures as a result of climate change are expected to change the distribution of plants especially if those temperatures exceed the physiological tolerance range of a species. The odds of survival for each species of wetland plant in a specific environment depend on the changes in temperature, the availability of suitable habitat and the dispersal ability of each species (Neubauer and Craft, 2009). The shift in species will result in shifting dominant species in communities, and this may lead to the formation of new communities (Walther, 2010).

Moreover, an increase in temperature will extend the poleward shift and ranges of many invasive aquatic plants such as *Eichhornia* species (water hyacinth) and *Salvinia* species (floating fern) (Kibria, 2015). The presence of invasive species will have an impact on native species and the former may start to dominate many communities. In many cases, native species are less competitive and more vulnerable as invasive species have a very wide tolerance range.

Wetland plants may also be threatened by salinity because increased salinity can influence the physiological stress that wetland biota experience and this can result in shifts of wetland communities and their associated wetland functions. Soil salinity can affect plant growth by way of an osmotic effect on water uptake (Sheldon et al., 2004). As salinity increases it becomes difficult for a plant to take-up water because it has to transport water against a gradient in soil water potential (Sheldon et al., 2004; Schagerl, 2016). For plants to maintain water uptake from saline soils they have to adjust osmotically. Halophytes adjust amongst others by taking up salts and storing it in specialized compartments such as vacuoles without affecting cell processes. The plants that cannot tolerate salinity appear affected by drought even at low salt concentrations.

Furthermore, decreased precipitation could lead to water stress and extinction of wetland plants (Kibria, 2015). Reduced soil moisture and increased soil oxidation could lead to the formation of different soils that are more suitable for terrestrial and invasive species, which may become more competitive. It may also result in an altered phenology of plants, changes in community structure and altered food webs (Sheldon et al., 2010). Frequent droughts may result in the acquisition of more species in the community, particularly non-wetland and woody species. Most wetland species are typically clonal with distinct vegetation properties and the rhizomes of these species form a network of roots which help with soil stabilization: terrestrial plants are mostly non-clonal plants.

Moreover, increased precipitation could result in a greater frequency of flooding events, which means the nutrients and organic matter may not be present long enough for efficient decomposition. This will create more reasons for changes in wetland chemistry combined with extended growing seasons that will alter species composition, community structure and productivity. Heino et al. (2009) reported that the effects of climate change on wetland plants promise a dim future for biodiversity in wetlands.

Plant performance under environmental change is determined by characteristics and adaptations in the plants. A study by Soudzilovskaia et al. (2013) demonstrated that plant functional traits may be used as predictors of correlations between plant performance and climate change. For example, plants growing in arid regions have structural traits that are mainly related to an increase in water uptake and storage and reduction of water loss during dry periods (De Micco and Aronne, 2012). These traits can be used to predict relationships between temperature or precipitation trends and plant performance, and therefore, predict changes in plant composition and abundance attributable to climate changes (Soudzilovskaia et al., 2013).

2.3 Plant functional types and traits

Plants have been classified on the basis of functional properties in order to understand the assembly of plant communities, and to interpret their responses to environmental change and climate variability (Grime, 2006). There are several terms that have been used for such classifications and this include ‘life forms’ (Raunkiær, 1937), ‘strategies’ (Grime, 2006), and ‘functional types’ (McIntyre et al., 1999). Plant functional types are defined as groups of plant species sharing similar functional characteristics at the organism level and similar responses to environmental change (Cornelissen et al., 2003). They are obtained by comparing different plant species on the basis of traits based on morphology, physiology and other evolutionary adaptations (Ni, 2003).

Reich et al. (2003) defined a plant functional trait as an attribute that has significant influence on the establishment, survival and fitness of a particular species. It can also be defined as a morphological, anatomical, biochemical, physiological and phenological feature that is measurable at the level of the individual (Kattge et al., 2011). Plant traits are linked to plant functions such as growth (e.g. water use efficiency, nutrient acquisition and light) competition and persistence (e.g. dispersal). They help to explain community shifts along environmental gradients as traits are adaptations to a specific environment (Cornelissen et al., 2003).

There is variation in trait values of species that occupy similar environments and species that occupy contrasting environments because traits arise as a result of evolutionary and ecological adaptation (Reich et al., 2003). Species that have traits best suited to that environment will most likely attain dominance in that community (Shipley, 2010). This is due to variation of traits between plants of different species occurring together at the same site. Trait variation results from environmental drivers that operate at a variety of different scales which makes it difficult to differentiate them.

The species composition of plant communities arises from processes and factors that act on different spatial scales. Environmental factors are seen as filters that constrain which species from the regionally available species pool can persist at a site. Filtering determines the proportion of different species in a community and it determines which traits and functions of species can persist at any particular site (Castro, 2008). The environmental filters include climate, disturbance regime and biotic interactions (Diaz et al., 2007). Additionally, there are trade-offs that exist between different combinations of traits because there is no set of traits that provides optimal fitness in every environment. Therefore, information on how different environments select different trait values can assist us in predicting which species are likely to occur and dominate in different environments.

On the other hand, plant traits affect ecosystem processes directly through changes in abiotic controls. Plant traits that affect ecosystem processes include the traits that modify the availability and use of soil resources such as water and nutrients, traits that affect the trophic structure within a community, and traits that influence the frequency, severity and extent of disturbances (Castro, 2008). For example, a plant community that contains many legumes will be able to fix nitrogen in the soil more and the nitrogen cycle will be accelerated. Plant traits can affect resource availability through differences in litter quality which influences the turnover rate of nutrients in litter and soil organic matter.

Moreover, plants that depend on fire for their continued persistence may be replaced by non-flammable species if fire does not occur. As a result, fire-prone vegetation has evolved flammability traits as part of its competitive strategy to avoid being replaced by non-flammable species (Bond and Midgley, 1995).

Lavorel and Garnier (2002) categorized plant functional traits into response and effect traits based on whether traits are mainly a response to or an effect on the environment. A response trait represents a manner in which a plant responds to certain environmental conditions, and it includes traits such as life span, growth rate or shoot height. An effect trait represent a manner in which a plant has an effect on ecosystem processes, for example by speeding up nutrient cycles, depleting water from the soil and increasing fuel load for fires.

This differentiation of response and effect traits makes it possible to make predictions about community structure to describe factors influencing geographical ranges of species and to find the reason why processes such as nutrient cycling and plant productivity vary among systems (Read et al., 2014). Species with similar responses to environmental changes do not necessarily have the same effects on ecosystem properties (Reich et al., 2003). In order to understand the contribution that a particular species makes on ecosystem processes, it is necessary to determine how species interact with both their biotic and abiotic environment.

It is important to understand functional properties of the dominant plant species, because dominant species are expected to have a strong effect on ecosystem properties. Plant functional traits play an important role in predicting the potential impacts of environmental change and climate variability on plants (Jamil et al., 2012). For example, it is expected that environmental changes and climate variability will affect plant traits such as seed size, leaf thickness, seed shape and mass. Environmental changes such as reduced water availability will lead to reduction in specific leaf area and this in turn will lead to poor nutrient acquisition and reduced primary production by plants thereby affecting ecosystem functioning (Valladares et al., 2015).

Knowledge regarding the functional relationship between species traits and environmental factors assists us in our understanding of changes in species distributions under the changing climate. For example, if a plant species with a specific trait value is successful in a particular existing environmental and climatic condition; this relation can be used to estimate changes in trait distribution under future environmental changes. This led to the use of functional traits in recent years to explain and predict the performance of species in a changing environment (Lavorel and Garnier, 2002; McGill et al., 2006).

Specific traits that are known to be adaptations to the wetland environment include a well-developed aerenchyma in stems and roots, a shallow root system and the prevalence of rhizomes. Development of a functional aerenchyma is the most important adaptation to flooded soil. Aerenchyma is defined as large intercellular spaces that act as a mediator of internal gas exchange between the roots and the shoots (Jung et al., 2008). The presence of aerenchyma allows plants to grow without experiencing the metabolic costs of anaerobic respiration. Wetland plants avoid the stress of inundation by developing a shallow root system so that oxygen does not have to be transported far (Tiner, 2005). Most roots of wetland plants grow laterally or upward because roots near the surface can obtain oxygen.

Most wetland plants are clonal species and as a result they have developed special reproductive adaptations such as rhizomes (stems that spread out under water or underground and are connected to the root system). Rhizomes play an important role as a channel for oxygen, water and nutrient transportation (Hong and Kim, 2014). Rhizomatous plants are competitive; they use rhizomes for population expansion and establishment. Rhizomes guarantee vigorous growth of shoots and high tolerance against environmental stress.

Chapter 3

Study area

3.1 Description of the study area

The study was conducted in the Highveld region of South Africa. The Highveld is situated in the interior of South Africa, and it is defined as the inland plateau that is separated from coastal regions by the Great Escarpment (Figure 3.1; Ritter, 2011). This Great Escarpment ranges between 2000m and 3300m in elevation. The Great Escarpment is the product of the major uplift of the interior in Africa which happened about 180 million years ago during the fragmentation of Gondwana in the late Jurassic up to the early Cretaceous period (Cowling et al., 2004). The cross section on Figure 3.1:**A** illustrates the high elevation of the subcontinent and highlight that the Highveld tilts from east to west.

The Great Escarpment separates the inland plateau from the coast, and is steepest in the southeastern region where the Drakensberg Mountains form this transition (Domingo and Gritzer, 2004). The Great Escarpment lies mainly within the borders of South Africa, but it extends further north: in the east it extends northwards to form the border between Mozambique and Zimbabwe, and in the west it continues northwards into Namibia and Angola. Figure 3.1 shows the Highveld as it is bordered by the Great Escarpment.

The Highveld is divided into several regions with distinct climate and geology as a result of the distribution of rainfall in South Africa. It is relatively wet in the east and becomes increasingly drier and more arid towards the west as illustrated in Figure 3.2. The following provinces are part of the Highveld: the whole of the Free State, Gauteng, and North West, the larger part of Mpumalanga and Northern Cape and portions of the Eastern Cape and Limpopo.

The geology of the Highveld is relatively uniform and a large part of it (i.e. whole of Free State, large parts of Mpumalanga and Northern Cape) comprises of the rocks of Gondwana that lie under the Karoo supergroup (McCarthy and Rubisge, 2005; Grab and Knight, 2015).

The Karoo supergroup was deposited about 300 million years ago and it consists of a number of layers of sedimentary rocks. About 70% of the Highveld consists of sedimentary rocks with significant exposures of dolomite along the northern and western boundaries of some catchments (Hes, 1997; Thieme et al., 2005; Booysen and Tainton, 2012). The very thick layers of sedimentary rock generally form gently undulating or flat plains; river valleys cut through the plains exposing different geological layers in those places that are easily eroded (Grant and Thomas, 2011).

The Highveld is characterised by plains with low to moderate relief, low drainage density and low stream frequency (Walker and Schulze, 2008). The topography is mostly flat and this means that the landscape is crossed by many meandering rivers. Some regions have high concentrations of depression wetlands (pans) for example Panveld near Wesselsbron, Lake Chrissie at Chrissiesmeer and Sak River pans near Brandvlei. The main part of the Highveld is formed by the drainage basin of the Orange Vaal River, with northern sections draining into the Olifants and Limpopo River systems.

The Highveld consists of three biomes: the Nama-Karoo in the west, Grassland in the east and Savanna in the north (Thieme et al., 2005). The current study focuses on the contrast between arid biomes in the west and mesic biomes in the east and does not include wetlands from the Bushveld.

The Nama-Karoo is an arid (semi-desert) region that occurs on the central plateau of the Eastern Cape, Western Cape, Northern Cape provinces and it extends over the Orange River into Namibia in the northwest. The Great Escarpment divides this biome into two parts between 500 and 900m in elevation: the Great Karoo (not part of the Highveld) and between 900 and 1300m, the Upper Karoo (part of the Highveld) (Olson and Dinerstein, 1998). The Nama-Karoo usually experiences droughts, and seasonal and daily temperatures fluctuate.

The Nama-Karoo experiences a high mean maximum temperature (>30 ^{o}C) in mid-summer (January) and very low mean minimum temperatures (<0 ^{o}C) with frequent frost in mid-winter (July) (Cowling et al., 2004). Rainfall in this biome is highly seasonal, and it varies between 100-500mm and decreases from the east to the west with very low precipitation in the rain-shadow of major mountain ranges of the Western Cape. The vegetation of the Nama-Karoo is dominated by dwarf shrubs, leaf-succulents, bulbous monocotyledons, grasses and annuals (Cowling et al., 2004).

The east to west gradient plays an important role in the physiological implications for growth form and species distribution across the Nama-Karoo Biome. Montane grasslands and shrublands predominate in the east of the Nama-Karoo, and drought tolerant grasses and succulent dwarf shrubs are dominant in the west. Tall shrubs are more abundant on cool, wet, southern slopes; contrasting with warm, dry, northern slopes, where plants are shorter and vegetation cover is sparse with dwarf shrubs dominating at lower elevations and C_3 grasses at higher elevations. In most areas, the soils of the Nama-Karoo are rich in lime which is weakly developed over rock (Mucina et al., 2006).

The Grassland biome is centrally located in southern Africa (Cowling et al., 2004). The rainfall of this biome ranges from 400- >1200 mm yr^{-1} (Suttie et al., 2005). Some parts of this biome are free from any frost in winter while some parts are covered by snow every winter. The plant communities correspond with different climatic zones which are associated with altitude. The dominant species in the grasslands include *Themeda triandra, Eragrostis curvula* and *Cynodon dactylon* (Moyo et al., 1993; Cowling et al., 2004; Rafferty, 2010). The east-west gradient plays an important role in the distribution of plant communities of this biome because rainfall increases towards the east. The rainfall gradient in grassland is the main determinant of community composition. Rainfall in semi-arid regions is more variable than in moister regions.

In the central inland plateau, grassland types such as *Themeda triandra-Eragrostis curvula* grassland are common and widespread. In their pristine condition most grasslands are dominated by *Themeda triandra*. Soils can be either one of the clay type or/and sandy type. Moreover, the dry and hot areas in the western part of the biome are dominated by the *Eragrostis obtusa-Eragrostis lehmanniana* plant community. There is also encroachment of Karoo vegetation manifested by communities dominated by dwarf shrubs in the south in an area of Ae land-type west of Bloemfontein (Cowling et al., 2004). This grassland merges with the bordering Kalahari thornveld to the west. This area represents a transition between the Grassland and Nama-Karoo biomes.

Although all grasslands of the Grassland biome comprise of tufted perennials, it is suggested that semi-arid grassland in the western part of the Grassland biome has a faster turnover of individual tufts, because of the increased frequency of drought-related mortality and therefore it has a rapid compositional change (Palmer and Ainslie, 2006). In contrast, in the montane areas of the east, the turnover of tufts is low because of the stable rainfall regime.

Vegetation in the east of the inland central plateau occurs at a higher altitude with the likelihood of frost and it receives a higher rainfall. The variation in vegetation is determined mostly by the position in the landscape within land-types. This is because of the higher rainfall which moderates the variation in the physical environment. The vegetation of the wet, poorly drained floodplains and water courses within the drier western grassland can be regarded as outliers of this grassland (Cowling et al., 2004). These communities are then examples of seasonally moist habitats within the dry western grasslands.

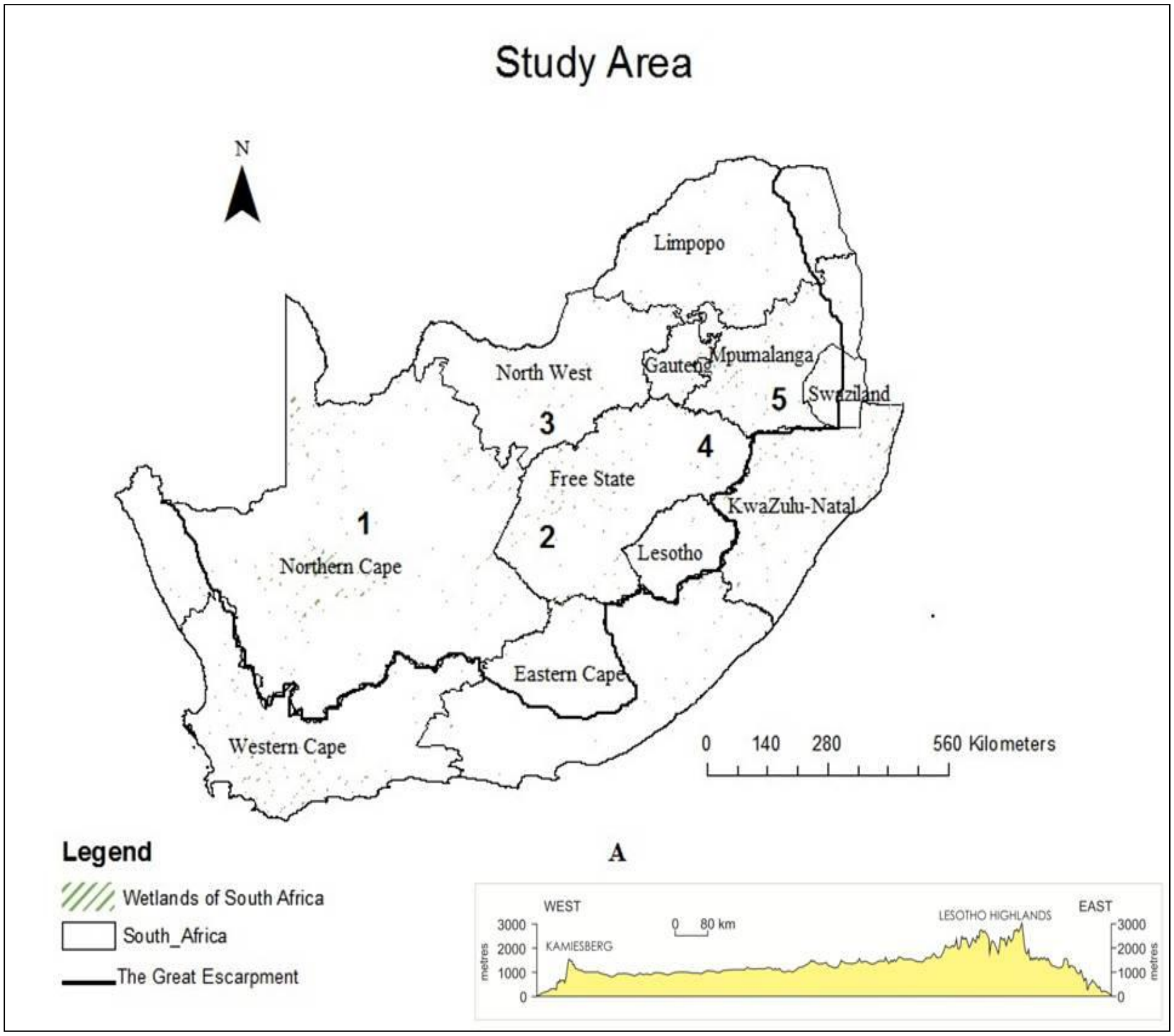

Figure 3.1 Map of the study area showing the Highveld bordered by the Great Escarpment, emphasizing the occurrence of wetlands in the country. The inset at **A** indicates the cross section of the uplifts of the interior in Africa 20 million years ago. The numbers on the map show the locations of the weather stations displayed in Figure 3.2.

Figure 3.2 Graphs showing average temperature and rainfall at the four provinces included in the study area from 2007-2014. These graphs emphasize the distribution of rainfall across the Highveld (wet: east and dry: west).

Chapter 4

Methodology

4.1 Data collection

The data needed to address the research questions in this study exists largely in the literature, but part of it was additionally collected in the field. In this study, I mostly utilized data on vegetation, soil and environmental data from the National Wetland Vegetation Database compiled by Sieben et al. (2014). Functional trait data was collected by making field collections of a number of wetland plant species. Additionally, climatic data was obtained by requesting it from the Agricultural Research Council (ARC).

4.1.1 Selection of plots and species

The criterion that was used to select the plots from Sieben et al. (2014) for this study was that they should be located on the Highveld, and they should have vegetation data as well as complete soil data. The resulting selection contained 167 plots from four provinces namely Northern Cape, Free State, North West, and Mpumalanga. Figure 4.1 shows the localities plots that were selected for this study. The dominant plant species in these plots were selected from the vegetation data table. The criterion for selecting these species was that the species should have at least an average of 20% cover abundance in the plots where it occurs. The dominant plant species were selected in order to obtain a good representation of the wetlands under study.

4.1.2 Vegetation sampling

The vegetation data in the Sieben et al. (2014) study was collected by sampling representative homogenous vegetation plots, mostly 3x3 meters in size, but sometimes larger, in wetlands of all the provinces in South Africa. Vegetation plots were chosen in the field in such a way that the plot was large enough to contain all representative species belonging to the plant community, the habitat was uniform within the plot, and plant cover and vegetation structure were homogenous (Ellenberg and Mueller-Dombois, 1974). Plant cover is an estimate of the space covered by a vertical projection of all the above-ground parts of the plant onto the ground level and therefore it takes the size of individuals into account (Damgaard, 2014). It is used to describe plant-environmental interactions within plant communities and to monitor the effects of changes on plant species within these communities (Bonham et al., 2004).

The vegetation data was collected using the Braun-Blanquet method (Westhoff and Van Der Maarel, 1978). The Braun-Blanquet method is a standardized protocol for sampling vegetation and it is used to provide rapid, floristically complete descriptions of vegetation (McAuliffe, 1990). This method involves setting out quadrats of representative homogenous vegetation where the species composition is recorded by noting all the species present in the plot together with an estimate of their cover abundances (combination of cover and abundance). Quadrats are used to sample the frequency and cover of the species making up the vegetation by using spatial delimitation of a plot. The Braun-Blanquet method is useful because it has been used for a long time and current data can be compared with historically collected data.

The Braun-Blanquet cover abundance scale was used to describe vegetation composition including dominant species, average height, and total cover of the vegetation. The cover abundance scales that were used are listed in Table 4.1 (Ellenberg and Mueller-Dombois, 1974). The species that were not readily identified in the field where collected were identified at one of the national herbaria.

The vegetation data and explanatory variables were entered in a database using the programme Turboveg (Hennekens and Schaminée, 2001). Explanatory variables explain the potential reasons for variation in a dataset. Vegetation data in the database includes plant species, cover abundance scale, total cover (%) and vegetation structure. The explanatory variables that were included were standardized in the database and they are discussed in Sieben et al. (2014) in detail. They include wetland type, topography, wetness, inundation, soil form, soil texture and soil nutrients.

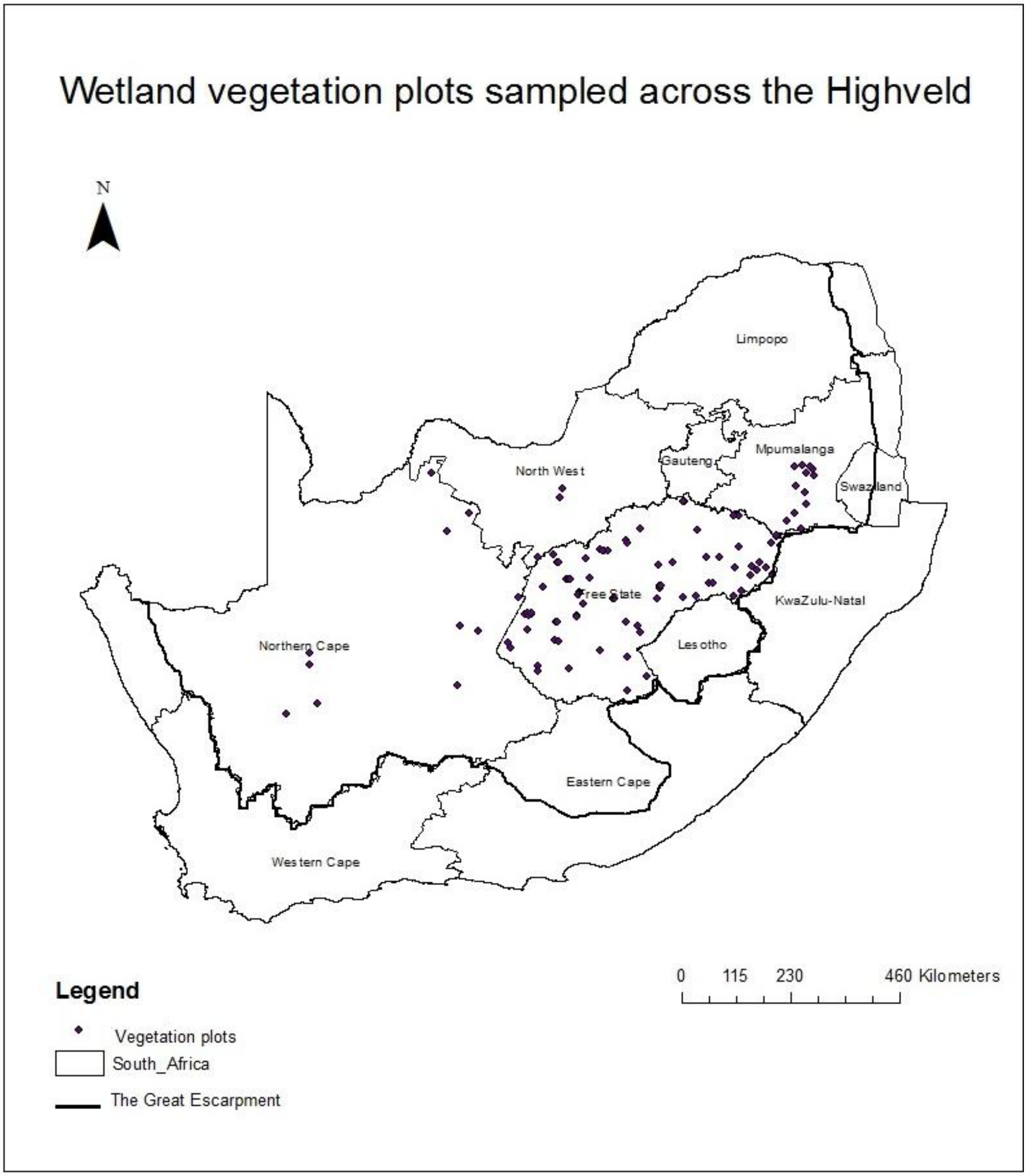

Figure 4.1 Map of the study area showing the 167 plots selected from the National Wetland Vegetation Database (Sieben et al., 2014) for this study.

Table 4.1 Braun-Blanquet plant cover abundance scales and descriptions

Cover abundance scale	Percentage value %	Description
R	1	1-2 specimens
+	2	2-10 specimens
1	3	10-100 specimens
2m	4	>5%, >100 specimens.
2a	8	>5-12.5% cover of the total sample plot area
2b	18	>12.5-25% cover of the total sample plot area
3	38	>25-50% cover of total sample plot area
4	68	>50-75% cover of total sample plot area
5	88	>75% cover of total sample plot area

4.1.3 Environmental data

Non-climatic environmental variables in the Sieben et al. (2014) study were collected following a sampling protocol which includes the collection of standardized environmental data relevant for wetland habitats. The non-climatic environmental variables that were collected include the hydrogeomorphic (HGM) unit, topography, and the degree of wetness. Table 4.2 summarises the non-climatic environmental variables that are available for each wetland vegetation plot in the database of Sieben et al. (2014).

The degree of wetness was determined using a soil auger to observe hydromorphic features in the soil profile. The soil was cored with the soil auger and inspected for the presence of mottles and gleying. A soil that has mottles indicate that the wetland is temporary or seasonally inundated and the soil that has no mottles (but a generally grey colour from gleying) indicates that the wetland is permanently inundated (Kotze et al., 1996). Altitude, longitude and latitude readings were recorded for each plot using a Global Positioning System (GPS). In those cases where the wetland was subjected to a specific type of disturbance, for example grazing or pollution, this was also reported.

Table 4.2 Non-climatic environmental variables (Sieben et al., 2014)

Variable	Measurement /Assessment
Hydrogeomorphic unit	Categorized as the following:
	Depression
	Valley bottom with a channel
	Valley bottom without a channel
	Seepage
Wetness	Categorised as the following:
	Permanent
	Seasonal
	Temporary
Topography	Categorised as the following:
	Floor
	Slope
	Foot

4.1.4 Soil samples

The soil samples in the Sieben et al. (2014) study were collected from the top soil (top 20cm) where the plants are rooted, more or less at the centre of the plot. The soil samples were collected with clean plastic bags and they were dried before they were sent to Agricultural Research Council (ARC) in Pretoria for further analysis. The laboratory analysis included particle size analysis (fractions of sand, silt and clay) for each sample. The soil samples were also analyzed for pH, electrical conductivity (EC), organic matter content, and nutrient content (N, P, and the major cations Ca, Mg, Na, K). Table 4.3 summarises these soil variables and the methods used for their measurement.

Table 4.3 Soil variables measured at Agricultural Research Council (ARC-ISCW) (Sieben et al., 2014)

Variable	Measurement
Electrical conductivity	Measured in mS/m
pH	Water extraction
Nitrogen	Sum of (NO_3^-+NO_2^-+NH_4^+) converted into mass percentage
Phosphorus	P-Bray I method, in mg/Kg
Sodium, Potassium, Calcium Magnesium	1:10 water extraction measured in mg/Kg
Soil particle distribution	In mass percentages for three categories: clay (<0.002mm), silt (0.05-0.002 mm), sand (2-0.05 mm)
Organic matter	Using the Walkley-Black method, expressed in mass %

4.1.5 Climatic variables

Basic climatic data constructed from records of weather stations in South Africa was requested from the Agricultural Research Council (ARC). A Geographic Information System (ArcGIS) was used to map the stations in order to choose the weather stations located in the four provinces (Free State, Mpumalanga, Northern Cape and North West). The ARC sent the climatic data for the time period from the date when the station started operating until the first six months of 2015.

The climatic variables obtained from ARC include precipitation, minimum and maximum temperature, A-pan evaporation, minimum and maximum relative humidity and windspeed. The ARC used the daily records of data to generate monthly data for each station. From this data average annual precipitation, average annual minimum and maximum temperature, average annual A-pan evaporation, average annual maximum relative humidity, and average annual windspeed were calculated for each weather station. The years that had incomplete data were excluded from the study as averages on a yearly basis had to be calculated. The climatic variables were calculated from the time the weather station started operating up to the first six months of 2015 in order to obtain an average expected value for climatic measurements. The climatic data provided by ARC and the calculations used to obtain climatic metrics are summarized in Table 4.4. The values of climatic variables for each weather station are shown in Appendix A.

Furthermore, an interpolation method was used to obtain the climatic variables for all the sampled plots. This was necessary because the weather stations are far apart and most of the sampled plots are in between these weather stations. Interpolation is a method used in GIS to predict the values of cells at locations that fall in between the weather stations, where the data was gathered. Interpolation is based on the principle of spatial autocorrelation which measures the degree of relationship between near and distant objects (Childs, 2004). There are different kinds of tools used in interpolation; for this study the method of kriging was applied using GIS. Kriging focuses on a specified number of points or all points within a specified radius to determine the output value for each location. After kriging, the climatic data for each vegetation plot could be extracted from a grid of climatic variables using an extraction tool that finds the coordinates of the locality on the grid.

Table 4.4 Climatic variables

Climatic variable	Calculations	Abbreviation	Units
Precipitation	Average annual rainfall	Precip	mm
Minimum temperature	Average annual minimum temperature	Mintemp	^oC
Maximum temperature	Average annual maximum temperature	Maxtemp	^oC
A-pan evaporation	Average evaporation per year	Evap	mm
Windspeed	Average windspeed per year	Windspeed	m/s
Maximum humidity	Average maximum humidity per year	Humimax	%

4.1.6 Plant collection and trait measurements

Plant functional traits are used to predict the performance of a species in a changing environment (Lavorel and Garnier, 2002; McGill et al., 2006; Cordlandwehr et al., 2013). The adaptive traits of the dominant plant species are expected to show a correlation with the environmental and climatic variables. For this reason, specimens of these dominant plant species were collected to carry out trait measurements. The dominant plant species were collected from various wetlands across the Highveld.

Ten reproductively mature, healthy looking specimens for each species of the selected dominant species were collected and washed before the traits were measured. The traits were measured in replicates in order to calculate average values, and because trait values are used comparatively to classify species into different functional groups (Pérez-Harguindeguy et al., 2013). Each species was collected from a single location so geographical variation is not accounted for in this study. It is noteworthy that the dataset was supplemented with trait data of nine species collected at Wakkerstroom wetland from the study of Sieben (2012).

The functional traits that were collected fall into several categories, namely whole plant traits, leaf traits and clonal traits. Shoot length, rooting depth, stem diameter, and rhizome internode length were measured on fresh specimens, whereas plant weight and root/shoot ratio were measured on oven-dried plants. Table 4.5 shows the traits that were measured in this study. The values of the measured plant traits are shown in Appendix B.

Table 4.5 Measured plant traits (Pérez-Harguindeguy et al., 2013)

Traits	Method of measurement	Units	Equipment used
Shoot length	Average shoot length of 10 mature plants	cm	Measuring tape/ruler
Plant weight	Average value of total biomass divided by number of mature shoots	g	Weighing balance
Rooting depth	Average maximum rooting depth of 10 mature plants	cm	Measuring tape/ruler
Stem diameter	Average diameter of 10 stems	mm	Vernier caliper
Root/shoot ratio	Average ratio of biomass of roots and shoots for 10 plants	g/g	Weighing balance
Rhizome internode length	Average length between 10 internodes on a rhizome or stolon	cm	Measuring tape/ruler
Specific leaf area	Leaf surface area divided by dry weight based on average of 10 leaves	cm^2/g	CI-202 area meter and weighing balance
Leaf chemical content	Nitrogen	%	Nitrogen in ash after combustion

4.1.7 Description of the measured traits

4.1.7.1 Whole plant traits

- **Shoot length**

Shoot length is defined as the shortest distance between the upper boundary of the main photosynthetic tissues (excluding inflorescence) on a plant and ground level measured in centimeters (Cornelissen et al., 2003). Shoot length is associated with growth form and position of the canopy in the vertical light gradient of the vegetation.

- **Rooting depth**

Rooting depth is the measure of how the root is distributed vertically through the soil. The distribution of the root in the soil provides information about the soil layer in which different species obtain water and nutrients, and the likelihood of below ground competition between species (Cornelissen et al., 2003). The roots were collected using an auger or a spade, a hole was dug close to the base of the ramet in order to obtain the roots. The soil was removed from the roots by washing carefully with water. The roots were placed in a bucket filled with water, and after the soil aggregates dissolve in water, fingers were used to gently squeeze the aggregates apart. Once the soil was removed from the roots, the plants were air dried and the longest root was measured with the measuring tape or ruler (attempts were made not to break the roots).

- **Plant weight**

Plant weight is the total biomass of the plant. The whole plants (above and below ground biomass) were oven dried for 48 hours at 60 ^{o}C (if the plant was still not dry the drying period was extended to 72 hours) and weighed by means of a weighing balance. If one root system is shared by several shoots, the total biomass of the plant was divided by the number of shoots in order to obtain the total mass of the ‘single’ functional unit or ramet.

- **Root /shoot ratio**

Root/shoot ratio is the ratio between below ground biomass and above ground biomass. After weighing the total dry biomass of a single plant or group of connected clones, the above ground biomass was separated from the below ground biomass by cutting at the point where the shoot system separates from the root system, and these two sections were weighed separately. If one root system is shared by several shoots, then all the shoots were weighed together to represent above ground biomass

4.1.7.2 Clonal traits

Cornelissen et al. (2003) defined clonality as the ability of the plant species to reproduce vegetatively, produce new ramets (aboveground units) and expand horizontally. Plants use clonality to migrate short distances and to colonize an area once they are established in a suitable location (Perez-Harguindeguy et al., 2013).

- **Rhizome internode length**

For the clonal traits, the rhizome internode length (cm) was measured using a ruler and a measuring tape. Rhizome internode length is the distance between shoots on the rhizome; it was measured to determine how the species uses clonal growth to advance itself in the wetland. Clonal plants can be classified into main growth forms: phalanx and guerrilla. In the phalanx growth form, ramets are closely packed and have very few or short internodes termed clumping ramets (Ye et al., 2006). Plants with phalanx growth form are very dense, they tolerate more stressful conditions and make better use of local resources and out-compete other species in a favourable site. In contrast, the ramets in the guerrilla growth form have many and/or long internodes which result in spaced ramets termed spreading ramets. The plants with this growth form can spread spatially much more and can penetrate already existing vegetation; they have the ability to escape from stressful sites and find favourable ones.

4.1.7.3 Leaf traits

The leaf is a very important organ of the plant because it is where photosynthesis and primary production takes place. Specific leaf area and leaf nitrogen content are proxies for the rate of photosynthesis and primary productivity.

- **Specific leaf area**

Ten fresh mature leaves from ten different plants were collected in the field for each species and were stored in an acetaldehyde solution for analysis in the laboratory. The acetaldehyde solution was used in order to prevent the leaves from wilting and drying before measurements were made in the laboratory. The leaf area of a fresh leaf removed from the solution was measured using a leaf area meter (CI-202 area meter, CID Inc.; USA), and the leaves were labelled 1-10 on a paper and oven dried at 60^0 C for 24 hours prior to the measurements of dry weight per leaf. Petioles were not included under the leaf area. In the case of leafless species, an estimate of specific leaf area was made by taking the surface area of the leafless stem divided by the dry mass of that leafless stem. The Leaf Area Meter had limitations for narrow leaves due to its resolution, and as a result, the leaf area for narrow leaves was often corrected by measuring the width and length of the leaf.

The leaf area and the leaf dry mass were used to calculate the specific leaf area. Specific leaf area is the one-sided area of fresh leaf divided by its oven dry mass measured in cm^2 g^{-1} (Cornelissen et al., 2003). Specific leaf area is an important trait in plant ecology because it is strongly linked to important aspects of plant growth specifically relative growth rate (RGR; Yulin et al., 2005).

- **Chemical composition of the leaves**

The chemical composition of leaves is the measurement of essential nutrient content of plant leaves in the laboratory. The chemical analysis of plant material is used in order to determine the relationship between growth rate of plants and nutrient content in the entire plant or plant structures such as leaves and stems (Kalra, 1997; Marschner, 2011). However, the nutritional status of the plant is mostly reflected in the mineral element content of the leaves than in other organs of the plants because there is most biological activity in the leaves by enzymes.

Vegetative photosynthetic material excluding woody stems, but including green stems and petioles were measured for chemical composition in this study. The chemical contents of the plants that were measured include nitrogen, phosphorus and potassium as these are the most important nutrients utilized by the plants as they are most likely to limit plant growth and these nutrients were also measured in the soil samples. However, in the end only nitrogen was used in order to keep the data comparable with the data that was utilized from the study of Sieben (2012).

4.2 Data analysis

A constrained ordination method was used for data analysis in this study. Ordination is a method used for ordering species and/ or samples along an environmental gradient (Palmer, 2004). It summarizes variation in the dataset by organising vegetation plots in multidimensional space, and it projects that ordering onto a limited number of dimensions that can be projected and visualised in a two dimensional graph (Sieben et al., 2014). Ordination can be in the form of direct (constrained) and indirect (unconstrained) ordination. In direct ordination, species abundance distributions and collective properties are only displayed after being correlated to non-climatic environmental variables, whereas in indirect ordination, the variation in the vegetation data itself is shown directly (without the constraint of known environmental gradients) (Borcard et al., 2011). Ordination methods display the results in the form of ordination diagrams, which are scatter-plots of the sample objects (e.g. species, functional groups, plots) on two axes (more than two cannot be visualised properly) according to the values taken by the objects along these axes (Legendre and Birks, 2012).

In this study we chose three ordination methods namely Principal Component Analysis (PCA), Redundancy Analysis (RDA) and Canonical Correspondence Analysis (CCA). PCA and RDA were used in this study because we expect linear correlations between variables. Since traits are direct responses to environmental factors we do not expect a 'hump'-shaped correlation when dealing with traits and therefore we used RDA in this study. 'Hump'-shaped curves are the natural way of how we expect species to be distributed along environmental gradients. CCA was used because we expect unimodal correlations because it deals with species which have an optimum in their occurrence along an environmental gradient.

Principal Component Analysis is a statistical technique that linearly transforms an original set of variables into a smaller set of uncorrelated variables that represent most of the information in the original set of variables (Dunteman, 1989). PCA assists in identifying patterns in data and expressing the data in such a way that it shows the trends that exist among correlated variables (Smith, 2002). Therefore, once the patterns are identified, PCA reduces the dimensions of a data set which consists of a large number of interrelated variables while retaining as much as possible variation present in the dataset (Jolliffe, 2002).

This is made possible by transforming the explanatory variables into a new set of variables, termed the principal components. These principal components are composed from the original explanatory variables, but they are completely uncorrelated (in vector terminology: orthogonal) to each other. The principal components are ordered in decreasing importance in terms of the amount of variation they explain; this often results in that the first three or four components explain more than 95% of the variation of the dataset. A small set of uncorrelated (orthogonal) variables is much easier to understand and to use in further analysis than a larger set of correlated variables. PCA aims at explaining part of variation in a set of observed variables and summarizing that variation in the form of principal components, which are linear combinations of existing explanatory variables (Dunteman, 1989). Principal component analysis is based on eigenvectors and eigenvalues.

Redundancy analysis is a method used to relate a data table (Y) of response variables (e.g. species abundances) to a secondary data table (X) of explanatory variables (e.g. non-climatic environmental variables) using multiple regression (Makarenkov and Legendre, 2002). It is therefore a direct ordination making use of multiple regressions, whereas PCA is an indirect ordination. Redundancy analysis is an extension of Principal component analysis (Zuur et al., 2007), whereby not just the general correlation structure is revealed but where some variables are recognized as response and others as explanatory variables. It uses a linear model of multiple regression between the variables in X and Y. It is suitable for sets of explanatory and response variables where it can be assumed that the response variables correlate in a linear manner to the explanatory variables.

Canonical Correspondence analysis is a multivariate method that approximates the unimodal response of the species to environmental gradients (ter Braak and Verdonschot, 1995). Canonical Correspondence Analysis does the chi-square transformation of the species abundances, but the relationship between the transformed response data and the explanatory variables is assumed to be linear. This means that here the response variables (mostly species abundances) can be regarded as having a unimodal response to explanatory variables.

Another method that was used for data analysis in this study is Hierarchical Cluster Analysis (HCA). This method was used because the study wanted to identify and group traits that share common properties. Hierarchical Cluster Analysis (HCA) is an algorithmic approach used to find discrete groups with varying degrees of (dis)-similarity in a data set represented by a (dis)-similarity index (Buttigieg and Ramette, 2014). The groups are organised hierarchically as algorithms proceed and they may be presented in the dendrogram. The position of the branch points along a similarity axis on the dendrogram indicate the level of shared similarity between clusters.

Hierarchical clustering method starts with individual objects, the most similar objects are first grouped, and these initial groups are merged according to their similarities. The merging of clusters can be performed under different linking criteria, for example 1) in single-linkage when a new cluster is formed the similarity between it and the other clusters and/or individual entities present are computed based on similarity between the nearest two members of each group; 2) in complete-linkage when a new cluster is formed the similarity between it and the other clusters and/or individual entities present are computed based on the similarity between the farthest two members of each group; 3) whereas in average-linkage when a new cluster is formed the similarity between it and the other clusters and/ or individual entities present are computed based on the average similarity between all members; 4) and the Ward's method determines which clusters and/or individual entities to merge by evaluating the 'cost' of such a merge against an objective function (Buttigieg and Ramette, 2014). Merges with the minimum cost are performed at each stage of the algorithm and this is implemented by evaluating the sum of squared deviations from cluster centroids.

Furthermore, HCA follows a set of steps and the main ones are 1) a data matrix with columns for the objects to be cluster-analysed and rows are attributes that describe the objects; 2) standardise the data matrix; 3) compute the values of a resemblance coefficient to measure the similarities among all pairs of objects; 4) use a clustering method to process the values of the resemblance coefficient which results in a diagram called a dendrogram, that shows the hierarchy of similarities among all pairs of objects (Romesburg, 2004).

As it was noted by Wold et al. (1987) the first step in all multivariate data analysis is creating a data matrix. In the current study, the data was organized into three data matrices, namely X (plots x non-climatic environmental variables including climatic variables and soil variables), Y (plot x species) and Z (species x traits). In Y, the plant species were recorded with a Braun-Blanquet cover abundance value converted into a percentage value. Furthermore, the plots that had only a small amount of cover by the collected species were left out, and the proportion of each species in a plot was calculated by dividing the cover of the species that had functional traits measured by the total cover of all the species present in the plot. In the case where the total cover of the species in the plot added up to more than 100, the proportion of the species was calculated by dividing the cover of the species in the plot by the total cover value that was arrived at so that each species cover is measured as a fraction of the whole.

Then matrix multiplication was used to calculate the Community Weighted Means (CWM) of the different traits. CWM refers to a weighted average of each trait over an entire community and it is therefore very suitable to indicate how traits respond to the environment. The CWM were calculated by importing matrices Y and Z into PC-Ord program, and then the function of matrix multiplication (calculating YZ as it would be written in matrix algebra) was chosen to calculate the community weighted means; this resulted in the fourth matrix P (plots x traits), this means YZ=P, and this process is illustrated in Figure 4.2. The matrix multiplication function basically calculates the eigenvalues and eigenvectors of the data covariance matrix, and the calculation of this matrix is referred to as the 'fourth corner' problem by Legendre and Legendre (1998).

The program that was used for PCA, matrix multiplication and HCA was the PC-Ord program. PC-Ord program is a software package that is used for analysis of multivariate data (Grandin, 2006). It offers tools such as principal component analysis and cluster analysis. Furthermore, the program that was used for RDA and CCA was the CANOCO program which is used for multivariate statistical analysis using ordination methods in the field of ecology (ter Braak, 1989).

Furthermore, matrix X was imported into the PC-Ord program to carry out the Principal Component Analysis. PCA was carried out to find the relationship among non-climatic environmental variables, soil variables and climatic variables. It was also carried out to find the relationship between the climatic variables. Then, matrix P and matrix X were imported to the CANOCO program to carry out Redundancy Analysis. Three RDAs were carried out, the first RDA was to find the relationship between non-climatic environmental variables (including climatic variables and soil variables) and the community weighted mean plant traits. The second RDA was to find the relationship between non-climatic environmental variables (including soil variables) only (excluding the climatic variables) and the community weighted mean plant traits. The third RDA was to find the relationship between climatic variables alone and community weighted mean plant traits.

Moreover, matrix Z was imported into PC-Ord program to carry out Hierarchical Cluster Analysis (HCA). From this matrix a similarity matrix based on Euclidian distance and Ward's linkage method between species were calculated. A dendrogram was derived from this similarity matrix and this helped to delineate the functional groups. This procedure groups plants according to their functional traits into groups of plants with comparable trait complexes. The cut-off level used to define the functional groups from the dendrogram was set at 90. After determining the functional groups of species, matrix Y was imported to CANOCO program to carry out a CCA.

In the CCA ordination diagram the species of different functional groups were illustrated by means of different symbols. Three CCAs were carried out; the first was to find the relationship between plant functional groups, environmental, soil and climatic variables. The second CCA was to find the relationship between plant functional groups and climatic variables only. The third CCA was to find the relationship between plant functional groups and non-climatic environmental variables (including soil variables) only.

Furthermore, the functional compositions of species per plot were calculated from matrix Y, based on the classification produced by HCA. This was done by adding the abundances of the species if the species fall in the same functional group. Each plot can therefore be characterized by the abundance of each of the functional groups. Then a distribution map of plant functional groups was created using GIS to show the distribution of the functional groups and their total cover per plot.

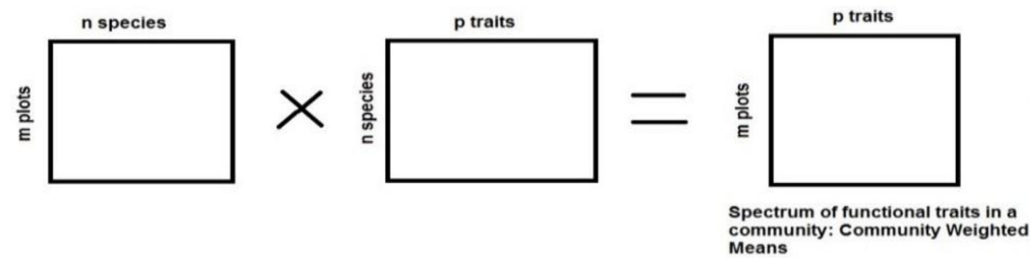

Figure 4.2: Process of matrix multiplication used to obtain the fourth matrix (plots x traits) containing community weighted means (Fourth-corner problem following Legendre and Legendre, 2012).

Chapter 5

Results

5.1 Results for vegetation data used in the current study

Table 5.1 show the selected species used in the current study based on average cover abundance. The species that grow in wetlands in dry areas had the lowest average cover abundance compared to species in mesic areas.

Table 5.1 Species that were selected from the National Wetland Vegetation Database

Species	Frequency	Average cover abundance (%)
Arundinella nepalensis	8	17.75
Atriplex lindleyi	2	23.00
Carex acutiformis	6	47.67
Chenopodium glaucum	1	18.00
Cynodon dactylon	57	36.60
Cynodon transvaalensis	36	41.39
Cyperus fastigiatus	18	42.33
Cyperus laevigatus	3	59.33
Cyperus longus	18	30.00
Cyperus marginatus	14	37.86
Echinochloa holubii	11	24.55
Eleocharis dregeana	87	45.54
Eragrostis bicolor	19	45.79
Eragrostis lehmanniana	10	26.60
Eragrostis plana	59	33.29
Eragrostis planiculmis	37	32.70
Falkia oblonga	8	21.50
Helichrysum aureonitens	17	27.41
Hemarthria altissima	29	31.31
Juncus rigidus	9	59.11
Leersia hexandra	77	31.17
Leptochloa fusca	44	44.91
Lycium cinereum	3	26.00
Mariscus congestus	13	20.31

Table 5.1 continued

Species	Frequency	Average cover abundance (%)
Panicum coloratum	46	21.70
Paspalum dilatatum	25	21.12
Paspalum distichum	20	33.60
Phragmites australis	11	40.55
Pycreus nitidus	16	35.13
Ranunculus meyeri	5	24.80
Ranunculus multifidus	28	24.07
Salsola aphylla	12	23.83
Schoenoplectus brachyceras	9	34.00
Schoenoplectus decipiens	52	27.12
Scirpoides dioecus	8	30.75
Sporobolus albicans	7	28.00
Sporobolus ioclados	19	32.00
Sporobolus ludwigii	1	68.00
Typha capensis	11	43.45

5.2 Results for Principal Component Analysis

The PCA ordination diagram in Figure 5.1 shows the relationship among the climatic variables used in the current study. This figure assists in explaining the general patterns in the parameters that make up the climate. The results from Figure 5.1 show that maximum temperature is strongly correlated with evaporation. This is quite evident as evaporation rate increases with increasing temperature. Higher temperatures are mostly found in dry areas and the evaporation rate increases as a result of hot dry winds. Precipitation is strongly correlated with humidity; this is also well known because increased humidity combined with a decrease in temperature leads to a higher precipitation. Furthermore, precipitation and maximum temperature are negatively correlated; this implies that as temperature increases precipitation decreases. Windspeed does not show correlation with the other climatic variables. The correlations on Figure 5.1 reflect general patterns in climatology; therefore they are not discussed in further detail.

The PCA ordination diagram on Figure 5.2 shows the relationship among the non-climatic environmental variables, soil variables and climatic variables. Figure 5.2 assists in explaining how wetland conditions change along environmental gradients. The first axis of the ordination diagram in Figure 5.2 is positively associated with nitrogen content, wetness and altitude and negatively associated with salinity, phosphorus, magnesium and pH. The second axis is strongly associated with maximum humidity, precipitation, minimum temperature, evaporation and maximum temperature. Furthermore, Figure 5.2 shows that nitrogen is strongly correlated with wetness, this shows that the wetlands in mesic areas have higher nitrogen content.

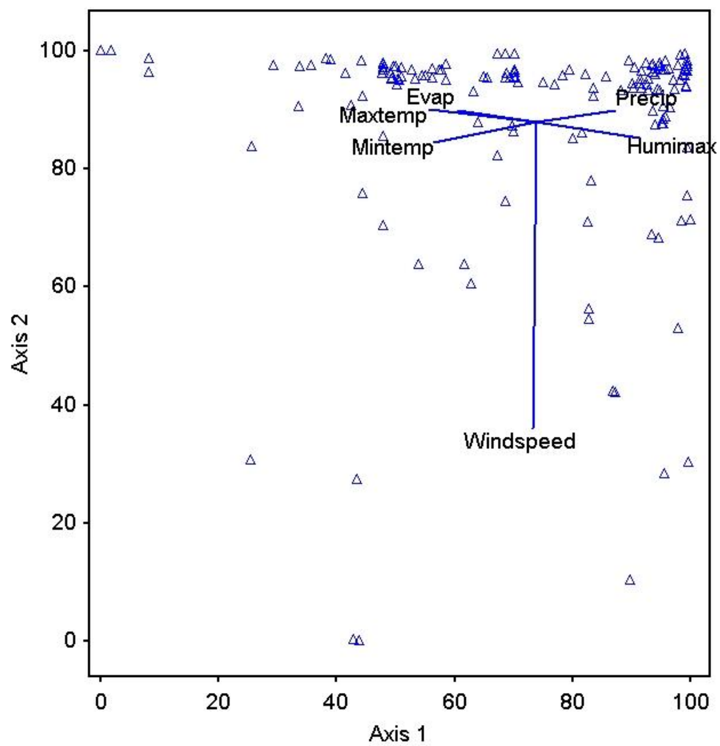

Figure 5.1 PCA showing the relationship between the climatic variables.

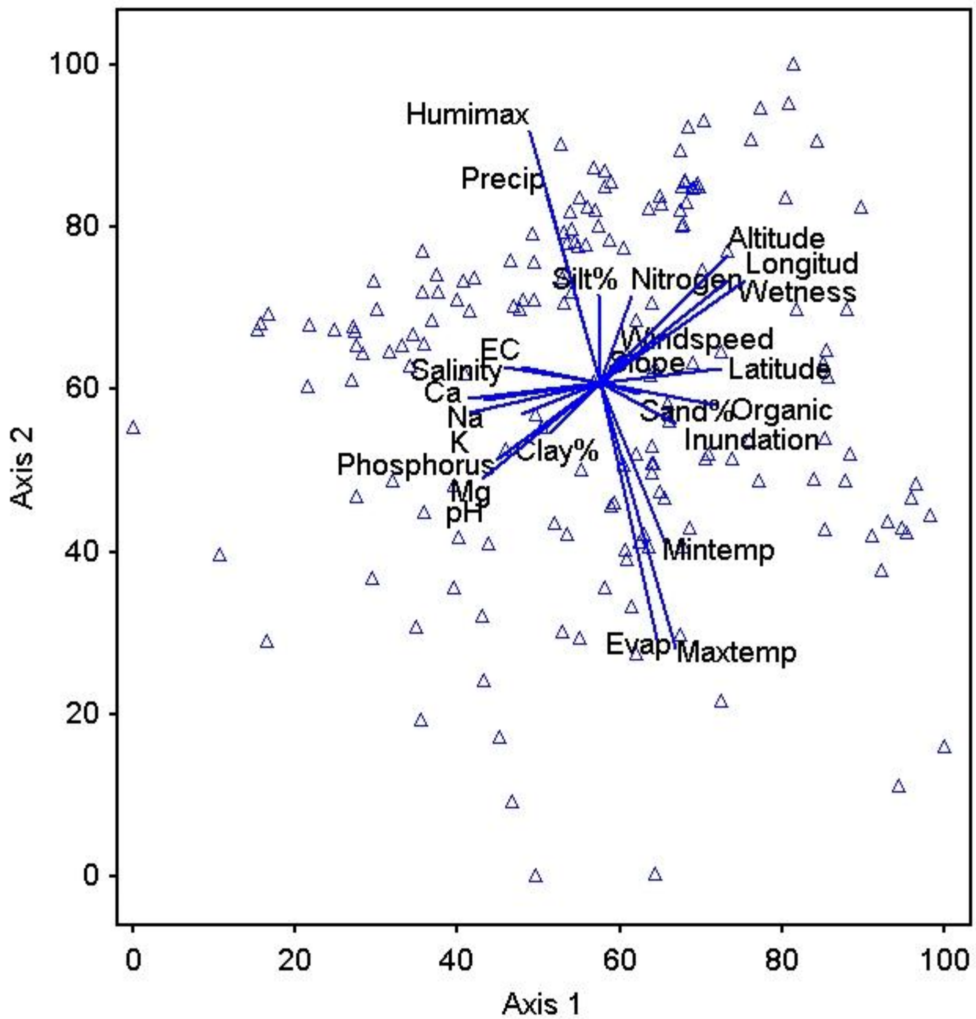

Figure 5.2 PCA showing the relationship between the climatic variables and non-climatic environmental variables (including soil variables).

5.3 Results for Redundancy Analysis (RDA)

The RDA ordination diagram in Figure 5.3 shows the relationship among community weighted mean (CWM) plant traits, environmental, soil and climatic variables; Figure 5.4 shows the relationship among CWM plant traits and climatic variables only; and Figure 5.5 shows the relationship among CWM plant traits, environmental and soil variables. These RDA ordination diagrams assist in explaining how plants mediate the different environments they grow in by evolving specific traits. The relationship among CWM plant traits and climatic variables is important as plants need to develop characteristics to adapt to a particular climate regime.

Redundancy analysis represents the relationship among CWM plant traits, soil, environmental and climatic variables along the first and second axis of the RDA ordination diagram. In Figure 5.3 and Figure 5.4 the correlations between climatic variables and plant traits in general are not as strong as expected; plants seem to respond much more strongly to non-climatic environmental variables. This means that plants seem to respond much more directly to local factors that determine the wetland habitat and not directly to the climate itself. Nonetheless, it is still possible that these environmental conditions (wetness, inundation, nutrient content of the soil) may change as well in the scenario of climate change, but that would be considered as an indirect effect.

In Figure 5.3 the Total Inertia is 1.0 and the Sum of all Canonical Eigenvalues is 0.568. This means that the Total Variation Explained can be calculated as 56.8%. The first axis of the ordination diagram is positively associated with clay content, nitrogen, inundation, wetness and organic matter content, and it is negatively associated with pH, electrical conductivity, salinity, and windspeed. The second axis is positively associated with maximum temperature and evaporation and negatively associated with maximum humidity.

In Figure 5.4 the Total Inertia is 1.0 and the Sum of all Canonical Eigenvalues is 0.032. This means that the Total Variation Explained can be calculated as 3.2%. The first axis of the ordination diagram is strongly correlated with minimum temperature and maximum humidity. The second axis is strongly correlated with maximum temperature, evaporation, windspeed and precipitation. In Figure 5.5 the Total Inertia is 1.0 and the Sum of all Canonical Eigenvalues is 0.548. This means that the Total Variation Explained can be calculated as 54.8%. The first axis in Figure 5.5 is positively correlated with clay content, nitrogen, wetness and organic matter content and negatively correlated with slope, electrical conductivity, pH and salinity and the second axis is not correlated with the explanatory variables.

Furthermore, the results from Figure 5.3 revealed that plant weight and rhizome internode length are correlated with maximum temperature and evaporation. Root/shoot ratio is strongly correlated with sodium, magnesium, potassium and salinity. These represent plants from saline wetlands in dry regions on the western side of the study area. Wetlands in dry regions experience increases in salinity as a result of high evaporative conditions and the variability in annual seasonal precipitation. The plants in dry areas are generally short; they have increased plant weight and long rhizome internode lengths. These plants include short grasses and woody plants such as shrubs.

Specific leaf area shows a positive correlation with a minimum temperature in Figure 5.3 and in Figure 5.4 it shows a correlation with windspeed and precipitation, however, the correlation is not strong. Shoot length is strongly correlated with wetness and organic matter content on Figure 5.5 and it is also correlated with windspeed and precipitation on Figure 5.5. Furthermore, Figure 5.3 shows that leaf nitrogen content, rooting depth and stem diameter are strongly correlated with soil nitrogen, inundation and clay soils. These traits are also correlated with windspeed and precipitation in Figure 5.4. These traits are the characteristic for the graminoids growing in mesic areas in the eastern part of the study area. The graminoids have long shoot lengths and rooting depths and this indicate that these plants are competitive. Increased SLA and leaf nitrogen content shows that these species have high nutrient acquisition and are more productive. The RDA results show that climatic variables did not have a large effect on CWM traits as initially anticipated.

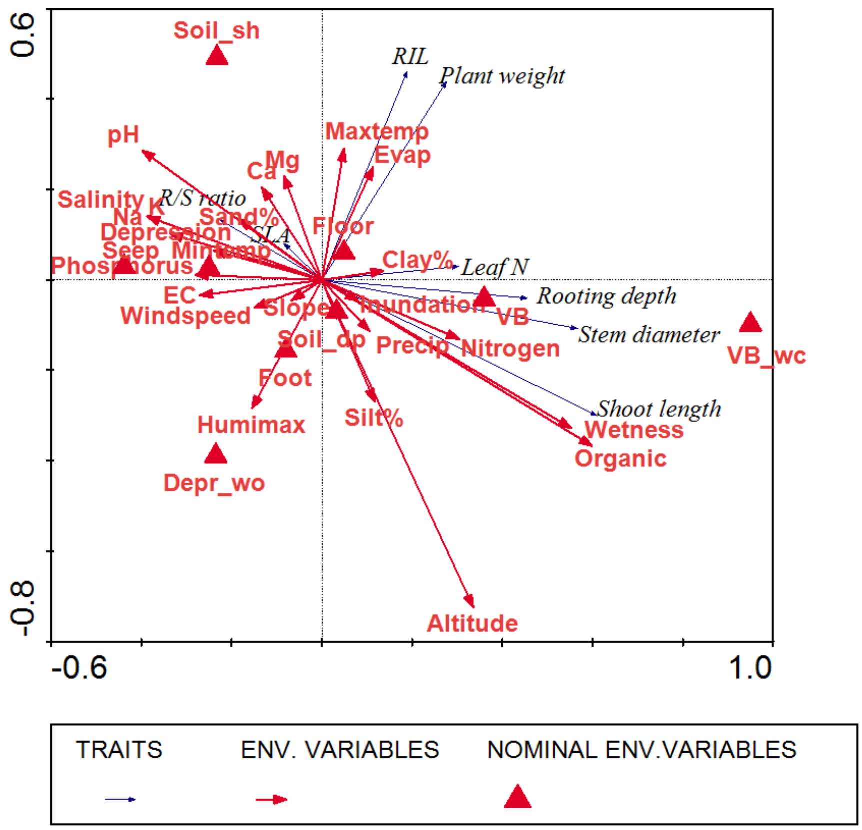

Figure 5.3 RDA showing the relationship between the CWM traits, soil, climatic and non-climatic environmental variables.

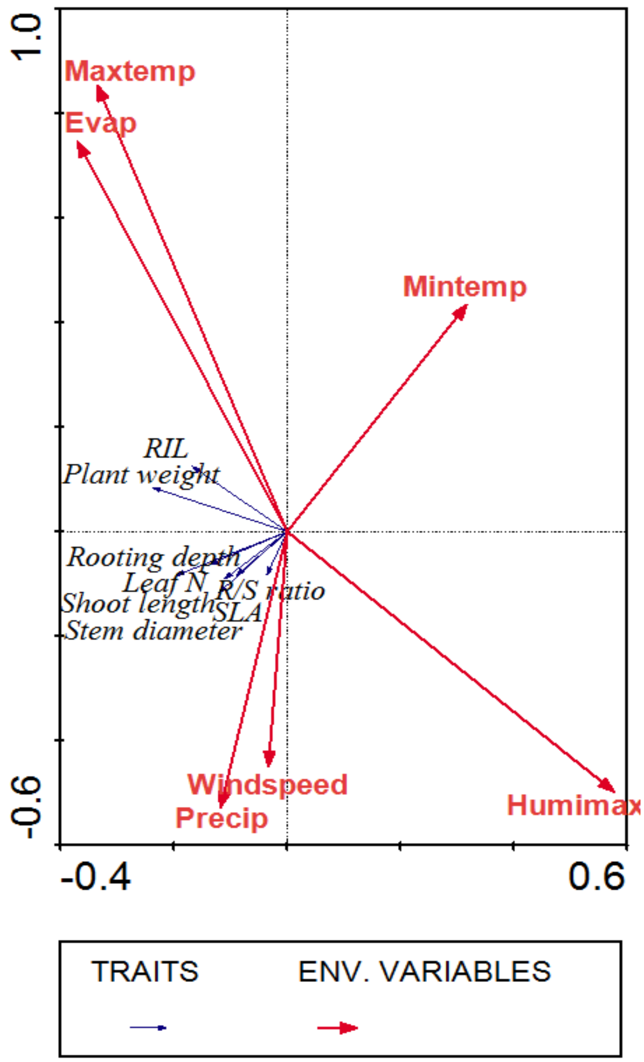

Figure 5.4 RDA showing the relationship between the CWM traits and the climatic variables.

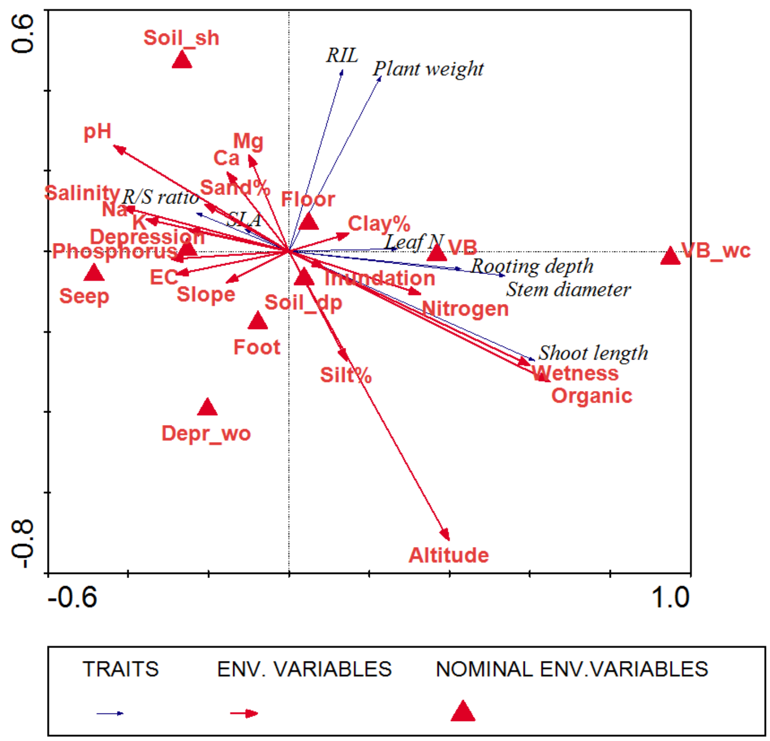

Figure 5.5 RDA showing the relationship between the CWM traits, non-climatic environmental variables and soil variables.

5.4 Functional classification of the species

The functional classification of all the species with the cut-off at 90 indicates the presence of six functional groups as illustrated in Figure 5.6. These functional groups are explained below.

Tufted graminoids

The functional group of tufted graminoids consists of species that have tufts, and they belong mostly to the families Poaceae and Cyperaceae. This group has eight species and they include *Arundinella nepalensis*, *Eragrostis planiculmis*, *Cyperus marginatus* and *Schoenoplectus decipiens*.

Leafless graminoids

The leafless graminoids functional group consists of seven species that are from the families Poaceae, Juncaceae and mostly Cyperaceae. Many species in this functional group are leafless. They include *Cyperus longus, Eleocharis dregeana, Scirpoides dioecus* and *Juncus rigidus*. Only three species namely *Echinohloa holubii, Cyperus longus* and *Hemarthria altissima* have leaves.

Salt tolerant forbs

The salt tolerant forbs functional group consists of eleven species which include species that grow in saline wetlands in dry areas on the western side of the study area. Most of the species in this group grow well in saline wetlands because they can tolerate salinity. They include *Atriplex lindleyi, Lycium cinereum, Cyperus laevigatus*, and *Eragrostis lehmanniana*. However, there are also species that usually do not grow in saline environments such as *Ranunculus meyeri, Ranunculus multifidus, Helichrysum aureonitens* and *Paspalum distichum.* Therefore, the name salt tolerant forbs is a bit ambigious.

Short trailing forbs and grasses

This functional group consists of seven species from the families Poaceae, Chenopodioideae and Convolvulaceae. The species in this group are generally short and form a mat. They include *Cynadon transvaalensis, Cynodon dactylon, Chenopodium glaucum* and *Falkia oblonga.*

Succulent shrubs

This functional group has only one species, *Salsola aphylla,* which is a succulent shrub. This species grows in wetlands in dry areas and has small succulent leaves as an adaptation to deal with drought and salinity.

Rhizomatous graminoids

The functional group of rhizomatous graminoids is divided into two groups on the dendrogram but they were merged together because the differences were only minimal whereas the whole group is very distinct. These species include *Carex acutiformis, Schoenoplectus brachycerus,* and *Typha capensis.*

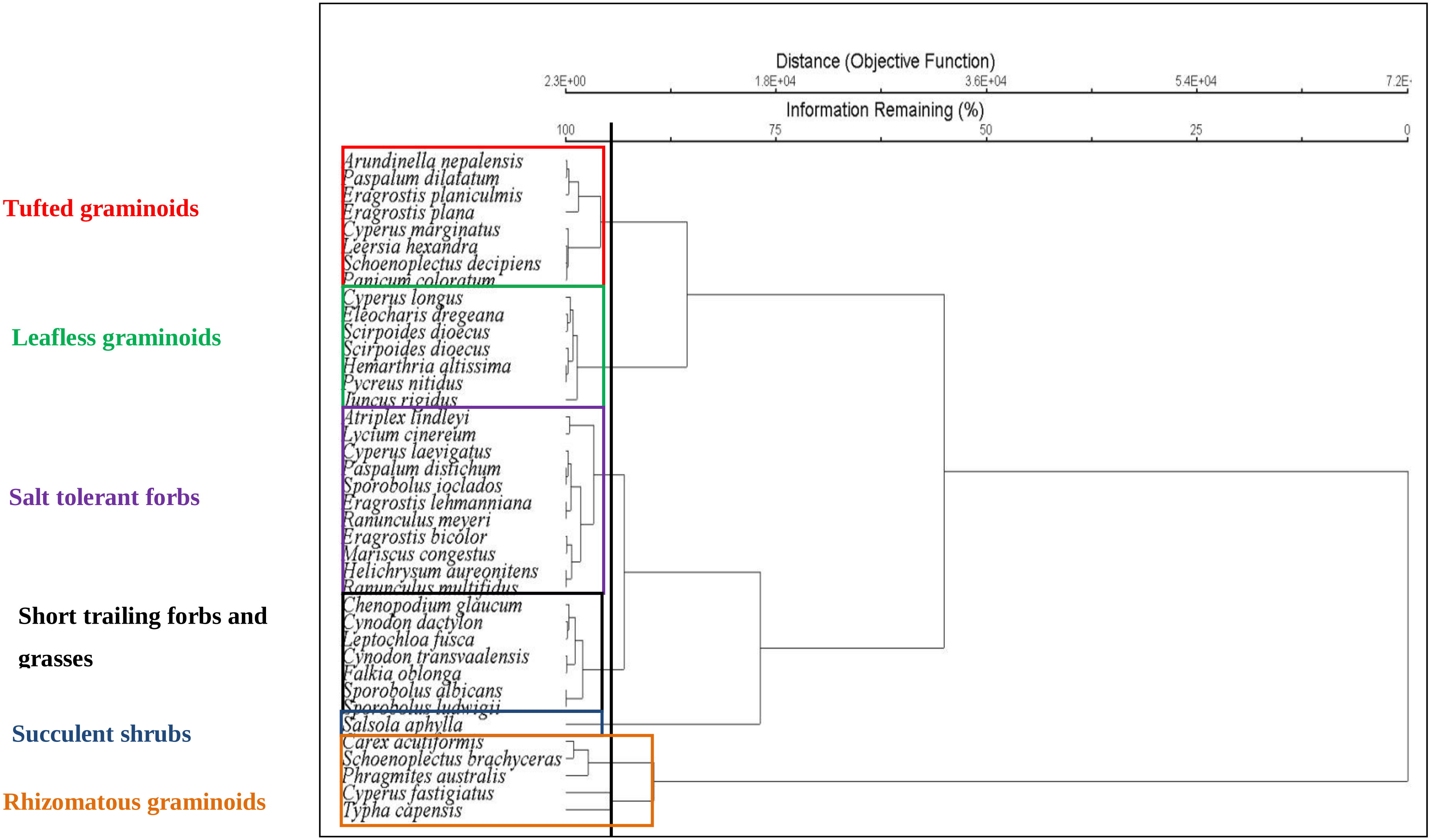

Figure 5.6 Dendrogram indicating functional classification of the species.

5.5 Results for Canonical Correspondence Analysis (CCA)

The CCA ordination diagram in Figure 5.7 shows the relationship between the plant functional types, climatic variables, soil variables and non-climatic environmental variables; Figure 5.8 shows the relationship between plant functional types and climatic variables; and Figure 5.9 shows the relationship between plant functional types, non-climatic environmental variables and soil variables.

Canonical correspondence analysis represents the relationship among plant functional types, soil, environmental and climatic variables along the first and second axis of the CCA ordination diagram. In Figure 5.7 the Total Inertia is 0.112 and the Sum of all Canonical Eigenvalues is 0.034. This means that the Total Variation Explained can be calculated as 30.4%. The first axis of the ordination diagram is positively associated with salinity, cations, phosphorus and pH and negatively associated with wetness, nitrogen, inundation and organic matter content. The second axis is strongly correlated with maximum humidity, precipitation, maximum temperature and evaporation.

In Figure 5.8 the Total Inertia is 0.112 and the Sum of all Canonical Eigenvalues is 0.004. This means that the Total Variation Explained can be calculated as 3.6%. The first axis of the ordination diagram is positively associated with maximum temperature and evaporation, and negatively associated with precipitation and maximum humidity. The second axis is strongly correlated with minimum temperature. Furthermore, in Figure 5.9 the Total Inertia is 0.112 and the Sum of all Canonical Eigenvalues is 0.03. This means that the Total Variation Explained can be calculated as 26.8%. The first axis of the ordination diagram is positively associated with salinity, cations, phosphorus and pH and negatively associated with nitrogen, wetness, and organic matter content. The second axis is strongly correlated with clay and sand content.

The CCA ordination diagrams show that the functional groups that are best segregated are rhizomatous graminoids and tufted graminoids, Figure 5.7, 5.8 and 5.9. The results from Figure 5.7, 5.8 and 5.9 showed that tufted graminoids, leafless graminoids and rhizomatous graminoids are dominant in mesic areas on the eastern side of the study area. These three groups are found in areas with high wetness, nitrogen, inundation, and precipitation. The short trailing forbs and grasses, succulent shrubs and salt tolerant forbs are dominant in the dry areas on the western side of the study area. They are correlated with salinity, phosphorus, maximum temperature and evaporation.

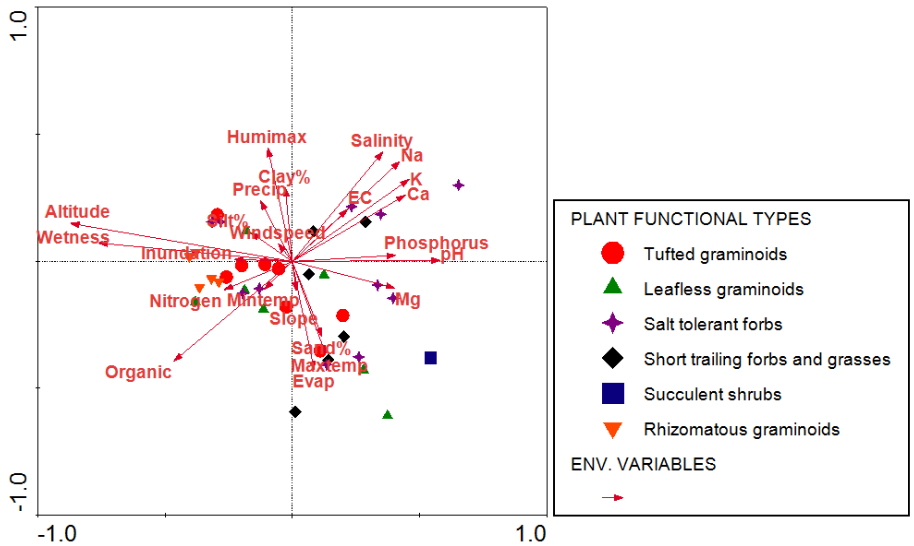

Figure 5.7 CCA showing the relationship between the plant functional types, climatic, soil and non-climatic environmental variables.

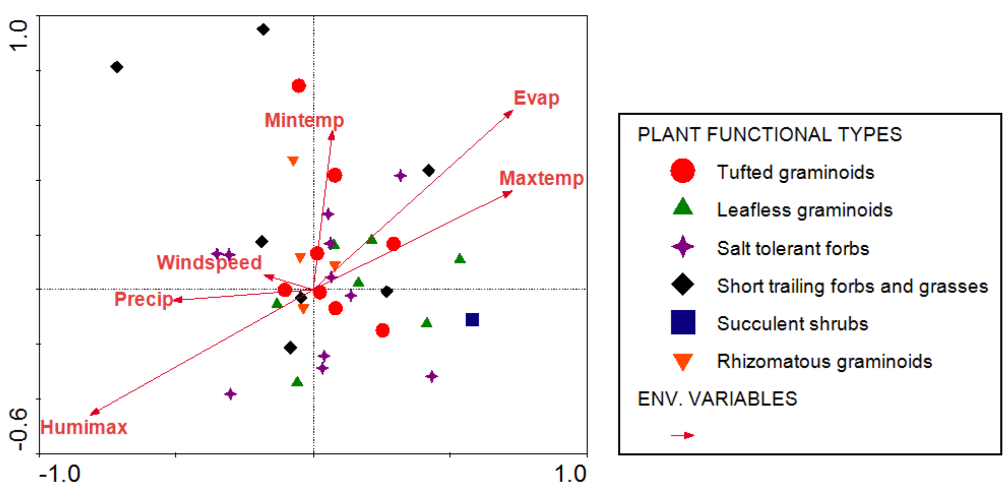

Figure 5.8 CCA showing the relationship between the plant functional types and the climatic variables.

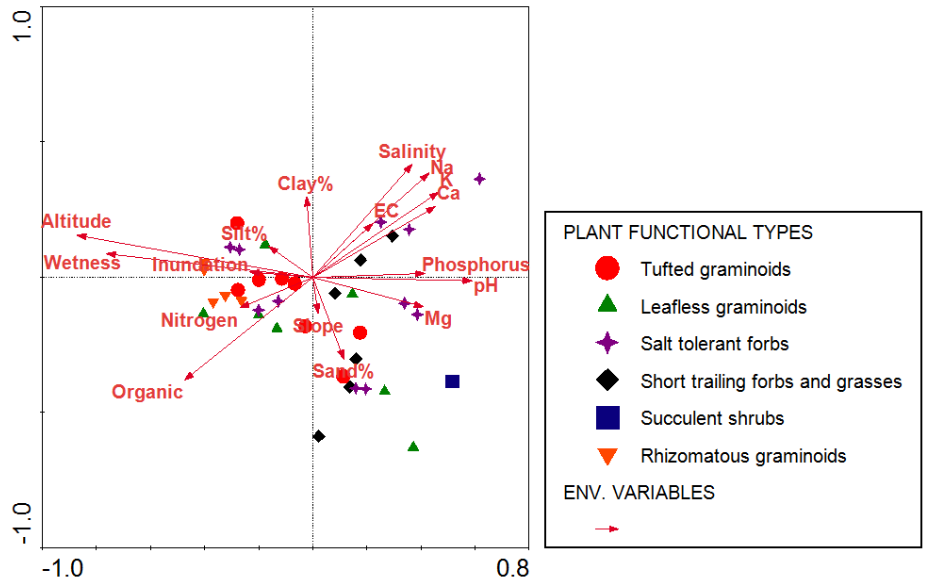

Figure 5.9: CCA showing the relationship between the plant functional types, soil and non-climatic environmental variables.

5.6 Cover abundance and distribution maps of plant functional types across the Highveld

Figure 10 shows the distribution of the six functional groups across the plots on the Highveld. The map from Figure 5.10A shows that the tufted graminoids are distributed across four provinces, but they are dominant at the eastern Free State with the cover between 80-100% and they are less abundant at North West with the cover between 1-20%. The leafless graminoids are distributed in four provinces, but they are more dominant in the Free State with a cover between 80 and 100%. They have less cover abundance (5-20%) at the border between Northern Cape and North West (Figure 5.10B).

The salt tolerant forbs are distributed across the four provinces, but they are more dominant in the western Free State with cover between 80 and 100% (Figure 5.10C). Figure 5.10D shows that short trailing forbs and grasses are distributed across the four provinces but they are dominant at Free State with the cover between 80 and 100%. The succulent shrubs are distributed at the western Free State and Northern Cape, however, they are dominant at Northern Cape with the cover between 60 and 80% and they are less abundant in the Free State with the cover between 1 and 20% (Figure 5.10E).

Moreover, the rhizomatous graminoids are distributed at Free State and Mpumalanga, they are dominant at Free State towards the border between Free State and KwaZulu-Natal with cover between 80 and 100% (Figure 5.10F). Rhizomatous graminoids are also found at Northern Cape towards the border between the Northern Cape and North West with cover between 1 and 20%.

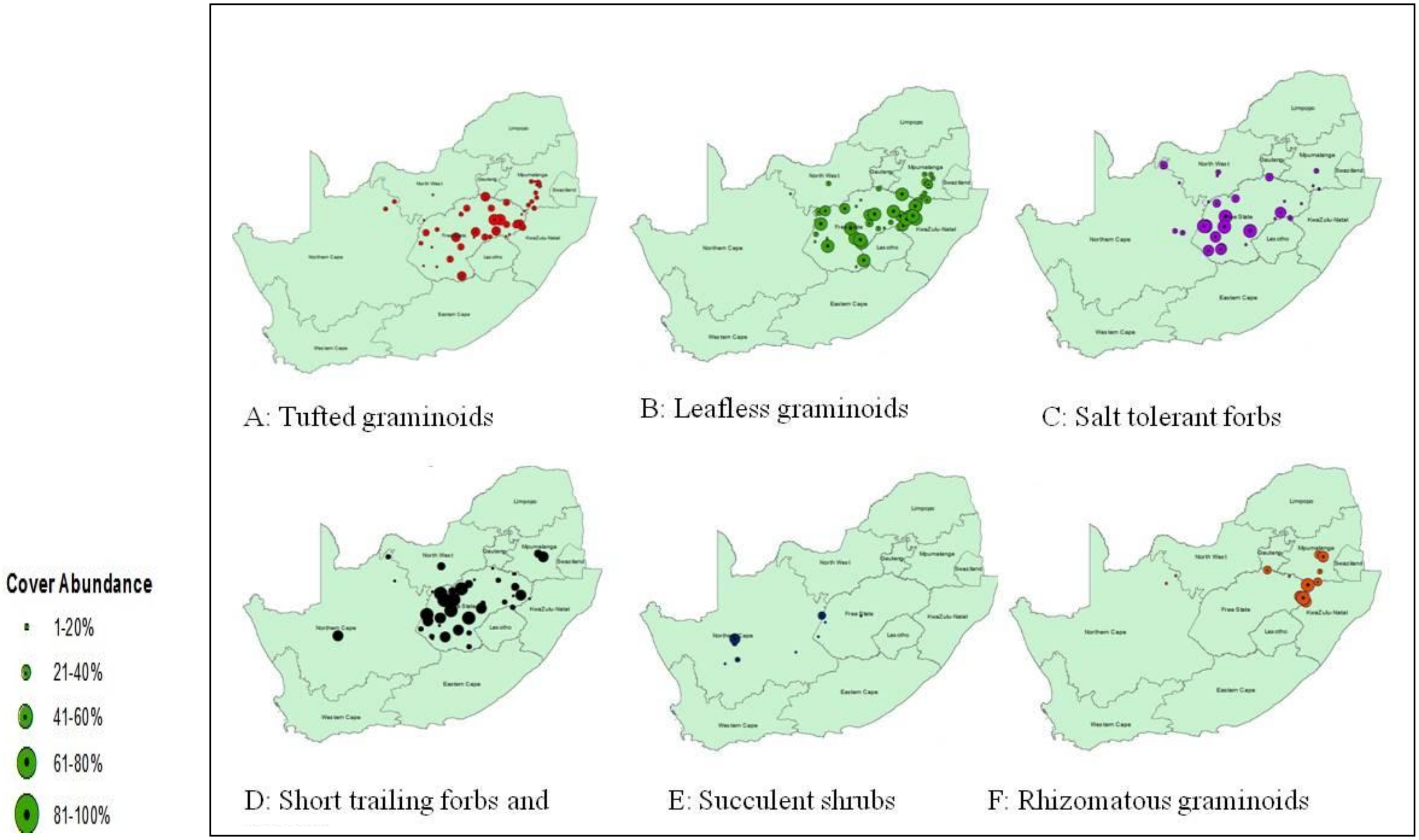

Figure 5.10: Cover abundance and distribution maps of plant functional types across the Highveld.

Chapter 6

Discussion

6.1 Distribution of plant traits along aridity gradient

The results presented in chapter 5 revealed that there is variation in species traits in different sites that correspond with the position along the aridity gradient. This variation is due to the environmental and climatic filters on species composition. The results revealed that both environmental and climatic variables play an important role in the distribution of plant functional types, because they both had a strong correlation with the measured traits.

Rainfall is the main driving factor of the distribution of plant traits along the aridity gradient. Wetland species from mesic areas on the eastern part of the study area grow in wetlands that are exposed to lower temperatures, low evaporation rates and high rainfall; as a result these wetlands are often inundated. The wetlands on this side of the study area are rich in nitrogen. The high nitrogen content in these wetlands is because these wetlands are open to hydrological fluxes; they constantly get more nutrients as water flows through the system.

Wetlands in mesic areas receive nutrient-rich sediments from sediment deposition during river flooding, surface water and groundwater inflows. Nitrogen is one of the major inorganic nutrients that attach to sediments that enter the wetland. By holding water during floods, wetlands in mesic areas allow sediments to settle down on the wetland floor. Additionally, flooding provides adequate water supplies for these wetlands and with the additional inputs of nutrients this creates conditions which are favourable for soil chemistry and plant growth.

Wetland species in mesic areas tend to have a high leaf nitrogen content and high specific leaf area (SLA). This means that these species are characterized by a high rate of photosynthesis, suitable for productive environments. Wang et al. (2015) explained that species with higher SLA adapt better to resource rich environments as they have high growth rates thereby effectively competing for resources. The high SLA of these species is regarded as a strategy for the rapid production of new leaves during the early life stages. This will also have an impact on competitive ability because a fast growth rate implies that these species can effectively outcompete their neighbours.

Specific leaf area (SLA) is strongly correlated with relative growth rate (RGR); hence a high SLA indicates that these species have an ability to respond to opportunities for rapid growth (Westoby, 1998). This is the reason why species in mesic areas tend to have long shoot lengths. Species with long shoot lengths tend to acquire available resources fast and are found in productive areas where competition for those resources is high. The species in mesic areas also have deep rooting which indicates the potential for a high water and nutrient uptake. Deep rooting shows that some of the productivity is also invested to increase competitive ability belowground as plants have to compete both below-ground as well as above ground.

In contrast, wetland species from dry areas in the western part of the study area grow in wetlands that are exposed to high temperatures, high evaporation rates and low rainfall. These wetlands have an increased salinity due to the high evaporative conditions and the variability in seasonal precipitation. The wetlands on the western side of the study area are rich in phosphorus, which is commonly high under conditions of low soil moisture and high temperature, which lead to high evaporation. Additionally, wetlands in dry areas are nitrate limited whereas wetlands in mesic areas are phosphorus limited; this is because phosphorus binds to the rock whereas nitrates dissolve in water more easily. He and Dijkstra (2014) showed that as the aridity increases the nitrogen and phosphorus cycles become decoupled, and while nitrogen concentrations are reduced, phosphorus concentrations increase in the soil.

The plant species growing in these wetlands have low leaf nitrogen content and low specific leaf area (SLA). The low soil moisture in wetlands in dry areas leads to a decrease in soil nitrogen availability and this results in a decrease in the uptake of nitrogen by plants (He and Dijkstra, 2014). In the wetlands of dry areas, plant nitrogen fixation rates are low, because the low soil moisture and high temperatures result in nitrogen limitation (He et al., 2014).

Furthermore, SLA decreases when water is limiting (Ordonez et al., 2010). Therefore, low SLA of these species can be thought as an adaptation to water stress that the plants have developed. Low SLA of species in dry and warm areas assist leaves to avoid overheating when wind speeds fall and allow continued leaf function under dry conditions (Wright et al., 2005; Meng et al., 2015).

Moreover, the low SLA is associated with increased leaf life span in a habitat where rapid growth is not possible, therefore plants need to use their resources sparingly (Reich et al., 2003). In addition to the low SLA, species growing in wetlands in arid areas have thick leaves with sclerophyllous structures and increased epicuticular waxes to reduce transpiration. Parolin et al. (2010) explained that such leaves protect plants against excess evaporation and heat. Often these species also develop thorns and succulent stems which perform photosynthesis (Salvador, 2013).

Wetland species growing in dry areas have traits that are associated with conservative growth strategies such as slow growth rates (Sandel et al., 2010). These species have short shoot lengths and this assists them to tolerate low soil moisture availability because less energy is required to transport water through the plant. Additionally, they have short shoot lengths because competition for light is not necessary if there are no taller species around in an otherwise unproductive environment.

The species growing in wetlands in dry areas have increased plant weight and rhizome internode length. The increased plant weight is due to the fact that some species that grow in dry areas are woody plants such as the shrubs *Lycium cinereum* and *Salsola aphylla*. The shrub species *Lycium cinereum* stands out in that it uses clonality to spread and it has a long rhizome internode length. The abundance of shrubs in dry areas can be explained by the fact that they can grow in areas of high environmental stress as they are tolerant to saline soils, high temperatures and variable seasonal rainfall (De Micco and Aronne, 2012).

The results revealed that three functional groups – namely tufted graminoids, leafless graminoids and rhizomatous graminoids – are dominant in mesic areas whereas the other three functional groups – short trailing forbs and grasses, salt tolerant forbs and succulent shrubs – are dominant in the dry areas. However, only two of the six functional groups are good indicator groups in that they occur strictly in their respective areas. The rhizomatous graminoids are abundant mostly in mesic areas on the eastern part of the study area and the succulent shrubs are abundant in the dry areas in the western part of the study area.

6.2 Response of wetland plant traits to climate change

The predicted changes in mean annual temperature and distribution of precipitation are expected to influence the community structure and composition of vegetation and the species interactions within the community. In order to monitor these changes there is a possibility to use local indicators such as plant traits that can be easily interpreted in terms of environmental changes. Monitoring changes in wetlands will provide important information that can be used to enhance the management of the wetlands of the Highveld.

Such monitoring can be achieved by classifying plants into functional types. This will serve as an effective tool that can be used to analyse and monitor the long term effects of climate change on wetland vegetation (Kernan et al., 2010; Middleton et al., 2015). Plant functional types can play an important role in monitoring of wetland vegetation because they can be generalized to similar habitats (Kennedy et al., 2006; Vandewalle et al., 2010). The results of this study revealed that plant traits vary over environmental and climatic gradients, and therefore they may also change over time if the climate changes. It is expected that some plant species will persist, grow, and reproduce better in a drier climate than other species, depending on their specific trait values (Frenette-Dussault et al., 2013).

A decrease in precipitation combined with an increase in evaporation is likely to increase droughts in South Africa and this will increase aridity in most parts of the study area. As a result of climate-induced altered hydrologic regimes and the more frequent occurrence of droughts, the distribution of plant functional groups in wetland ecosystems will be altered. Species will adjust to the changed environmental conditions through phenotypic plasticity or migrate to follow suitable conditions where they are adapted. Consequently, as the climate changes either there will be a different species composition or species will use phenotypic plasticity to adapt to the new environment.

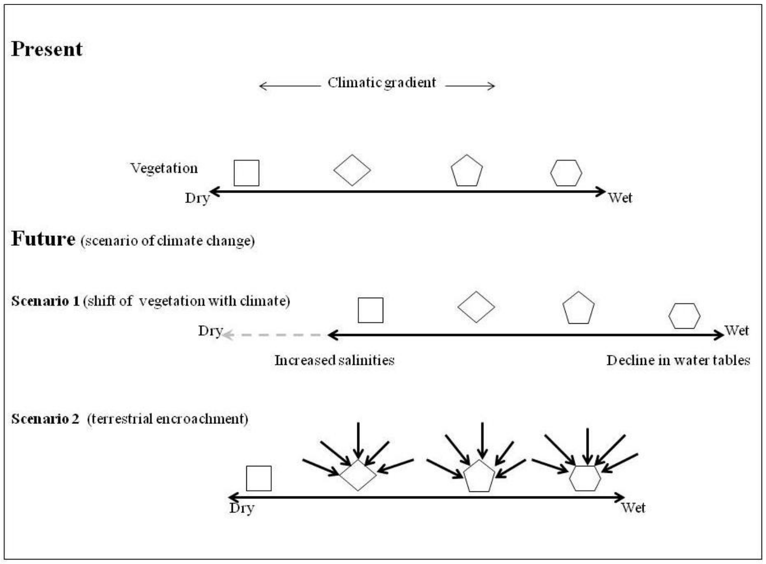

Figure 6.1: Illustration of the outcome of climate change in wetlands of the Highveld with two possible scenarios for future development given a drier climate.

In the future, we expect that as the climate changes an overall rainfall will decrease and two things may happen, as illustrated in Figure 6.1. Firstly, the aridity gradient may shift towards the east of the Highveld. As the aridity gradient shifts towards the east, the wetlands in mesic areas will be subjected to conditions that are currently prevailing further to the west and therefore wetland communities will move towards the east. Wetlands in dry areas on the western side of the study area will experience increased salinities which could result in loss of species or in the increased occurrence of unvegetated pans, due to extreme conditions. This scenario is illustrated in Figure 6.1 (scenario 1). According to this scenario, and following the results of the current study we can assume that a drier climate will lead to an increase in the number and abundance of the functional group of short trailing forbs and grasses as well as an increase in woody species such as the succulent shrubs functional group.

Secondly, reduced water levels in wetlands would reduce the extent of wetland areas and convert them to terrestrial vegetation. A decrease in water supply may cause plant mortality among the true wetland species and a shift in species composition, resulting in the establishment of terrestrial species (Figure 6.1, scenario 2). It is noteworthy that both scenarios presented in Figure 6.1 (scenario 1 and scenario 2) are not mutually exclusive and they could occur simultaneously in various combinations.

Terrestrial encroachment can result in an opportunity for exotic species to increase in abundance under drier wetland conditions (Catford et al., 2011). Invaders disperse quickly because of their strong competitive abilities and their ability to exploit new opportunities; as a result there will be an increase of both terrestrial and invasive species in wetlands in mesic areas. The characteristic wetland species that currently contribute most to ecosystem services are likely to decrease in abundance.

The changes in community composition may affect ecosystem services directly due to the decline in abundance of valuable wetland plants such as those that play important roles in water purification and flood and erosion control. Terrestrial species and wetland species are fundamentally different with regards to some traits, particularly the rhizomatous graminoids, and their replacement with terrestrial species will have important consequences for ecosystem services. Terrestrial species lack the potential to control erosion because most of them are non-clonal species and they lack the interconnected web of rhizomes that can effectively hold the soil together in fully functioning wetlands.

However, the structure of the vegetation is one of the factors that influence the susceptibility of plant communities to invasion by non-wetland plant species. Mulhouse et al. (2005) found that vegetation dominated by species small in stature such as *Leersia hexandra* are more susceptible to invasion by terrestrial species than vegetation that is dominated by robust clonal species such as *Typha capensis*. This suggests that the wetlands dominated by the functional group of the rhizomatous graminoids will provide fewer opportunities for the establishment and expansion of terrestrial and invasive plant species. Therefore, the wetland ecosystems that contain most robust rhizomatous graminoids are expected to be more resilient towards terrestrial encroachment.

Moreover, the lower water tables in mesic areas will result in habitat changes and this will create new habitat conditions for many plant species. As a result, species growing in these wetlands will have to adapt to the new habitat conditions or migrate to suitable habitats. Only those species with suitable traits will be selected to thrive in those newly created habitats. If the species in mesic areas lack traits that allow them to survive conditions of increased aridity, they are likely to migrate to other mesic areas outside of the Highveld if they are still available.

Additionally, it is quite possible that rhizomatous graminoids will go extinct on the Highveld as they are currently restricted to the eastern edge and are unable to migrate further east as the wetland habitat changes due to climate change. However, studies by Driver et al. (2011) found that the rhizomatous species notably *Phragmites* sp. and *Typha* sp. are resilient to drought. During drought periods *Typha* sp. continue to increase in abundance, whereas the abundance of *Phragmites* sp. only decrease slowly after prolonged drought and it recovers quickly after conditions improve, this indicates that these two species have a great resistance and resilience to drought.

Generally, wetland plants are equipped for long distance dispersal and the light weight and small seed size of many species in mesic areas gives these species the ability to disperse over long distances to reach suitable habitats. Seed dispersal is very important for wetland plant species because they occur in spatially isolated habitats. The small seed size of the species allows them to disperse to suitable habitats by water, wind and animals moving over long distances.

The most common dispersal mechanisms in wetland plants are water dispersal and dispersal by water fowl, as these mechanisms ensure that seeds will be dispersed towards suitable environments. Additionally, there is wind dispersal, which can transport seeds to a wide variety of sites in all directions, but wind is not directed specifically to a suitable habitat. Water dispersal transports seeds to other wet sites within the same drainage network, which are likely suitable sites for establishment. However, water dispersal is limited to areas that are connected by surface water to the source of the seed and limit seeds from crossing over into other catchments (Soons et al., 2008). As a result, waterfowl proves to be most suitable method to disperse seeds of these plants as the wetland habitats will face the consequences of climate change.

Ducks are particularly effective dispersers of seed because they are common in wetlands throughout the year and they also undertake long migrations between breeding and wintering areas (Wongsriphuek et al., 2008). Soons et al. (2008) explained that the droppings of ducks have been shown to contain intact seeds as the birds travel between wetlands in large numbers. The current study did not include seed traits, however, studies by Boutin and Keddy (1993) and Gordon (1998) did include seed characteristics of wetland plants and other studies looked at seed characteristics of terrestrial plants (Díaz and Cabido, 1997; Díaz et al., 2016). These studies reported that wetland plant species produce numerous small light weight seeds; as a result these species have a high probability of being dispersed to new environments.

The eventual loss of rhizomatous graminoids due to habitat changes will cause wetlands in mesic areas to become more susceptible to erosion. This would be a problem as the eastern edge of the Highveld is marked by a very steep topography and erosion in wetlands is a common problem in this area because many wetlands are located on slopes as they are connected to the drainage network. Rhizomatous graminoids in mesic areas play an important part in the provision of ecosystem services by holding the soil together and preventing erosion by means of an entangled web of interconnected rhizomes.

6.3 Response of wetland plant functional types to salinity

In the long term as the climatic conditions change towards more aridity in the eastern part of the study area, conditions of wetlands in mesic areas will become similar to conditions as they are currently in wetlands in the dry areas on the western part of the study area. Reduced rainfall and a higher evaporation potential will lead to an increase in the concentration of salts in wetlands. Salinisation in wetlands can occur on many time scales; it can be gradual, prolonged and irreversible, or alternatively salinisation can occur in short periodic pulses due to recurring droughts (Herbert et al., 2015).

Salinity results in reduced plant growth, reproduction and competitive ability, and if it is persistent, it will ultimately alter species dominance, biomass and diversity. Nonetheless, species in mesic areas may be resilient to periodic pulses of salinity. According to Herbert et al. (2015), the exposure of vegetation to low levels of salinity cannot alter species composition, but prolonged exposure of vegetation to salinity can alter plant communities. Therefore, plant species can tolerate slight increases in salinity but abrupt increases in salinity could cause species dieback.

Moreover, if wetlands in mesic areas experience prolonged salinities due to climate change there will be a shift in plant composition of graminoid functional groups (rhizomatous graminoids, leafless graminoids and tufted graminoids) to salt tolerant functional groups (salt tolerant forbs and succulent shrubs) resulting in lower diversity and productivity. However, it is not possible to guarantee the recruitment of salt tolerant functional groups because these species will only grow in wetlands in mesic areas if they are present in local seedbanks, unless the plants find a way to migrate from adjacent saline wetlands in arid regions to wetland in mesic areas.

In addition, salt tolerant functional groups will be able to replace the graminoid functional groups if a wetland in a mesic area has a historical pattern of salinity that shapes the current community composition and if the salt tolerant functional groups are present in the local seed banks. The chance that wetlands will have a shift of species from various functional groups consisting of graminoids to the salt tolerant functional groups is high in cases where salinity fluctuations have been common throughout the wetland's history. However, it will be low in geographically isolated wetlands which are exposed to salinity for the first time.

Under natural conditions wetlands in arid regions in the western part of the Highveld experience salinity as a consequence of rainfall variability and increased evaporation. As the aridity gradient shifts towards the east increasingly arid conditions on the west could lead to extended periods of increased salinity and high evaporation rates in wetlands on this side. Increased salinities in wetlands in arid regions can alter the biogeochemical cycling of major elements, including carbon, nitrogen and phosphorus (Herbert et al., 2015). The alterations of the biogeochemistry of the wetland will include decreased inorganic nitrogen removal with negative effects on water quality and climate regulation.

Moreover, increased salinities can cause physiological stresses on plants such as osmotic stress, ion toxicity stress, oxidative stress and disturbance of photosynthesis, thereby affecting plant growth and overall plant productivity (Nielsen and Brock, 2009; Wang et al., 2015). Increased concentration of salts can lead to toxic Na^+ and Cl^- accumulation in cells and this may result in disruption in the uptake of other essential ions and water. This will lead to mortality of the plant species as their environment will become toxic (Herbert et al., 2015).

Because of their effect on individual plant performance, increased salt concentrations can results in reduction of wetland communities and their associated wetland ecosystem functions. This is supported by the fact that most saline pans in the western side of the study area are completely unvegetated at the centre due to extreme saline conditions. Saline pans are also unvegetated because the clay that is deposited in the pans is not a suitable substrate for plant growth as the plants cannot penetrate through it during drought (Sieben et al., 2016). Furthermore, years of better rains in dry areas for successful recruitment of shrubs can be scarce, leading to the loss of species in these wetlands.

Alien invasive species are known to have traits that can tolerate a wide range of stresses and in most environments this gives them a competitive advantage over the native wetland species. However, the extreme conditions in saline pans results in difficulties for plants to absorb water. As a result, plant growth and productivity declines. The unproductive conditions in wetlands in dry areas show that these wetlands are unlikely to be invaded by exotic species as salinity increases. The wetland plant communities in stressful environments such as those with increased salinities and increased drier conditions are less susceptible to invasion by non-native species, as compared to the wetlands in mesic areas (He et al., 2012; Zefferman et al., 2015). This also means that as salinity increases there will be loss of species rather than just replacement in these wetlands.

Species growing in wetlands in arid regions on the west have adaptation mechanisms to both water and salt stress as these are the stresses they will experience as the wetland habitat changes due to climate change. The species that are tolerant to water stress could also be tolerant to salinity and generally the adaptations to both stresses are similar. The species growing in these wetlands from the functional groups of salt tolerant forbs and succulent shrubs survive water stress by having adaptations in their morphology in order to minimise transpiration.

The tolerance mechanisms that these species use during the dry period include dormancy, reduced body size and a prostrate growth form. Additionally they shed their leaves and decrease their leaf number and branching. Wetland grasses such as *Sporobolous* sp. in dry areas reduce water loss by leaf curling; this reduces the transpirational surface area and it shields the stomata from wind induced transpiration (Batzer and Sharitz, 2014). Wetland plants in these areas can also source water from succulent storage organs such as rhizomes, leaves and stems (that were filled in times when there was excess water) to other parts of the plant where water is needed.

Wetlands in arid regions (dry pans) are often regarded as dead or degraded systems because they are subjected to a complete desiccation during the dry season and this drought can sometimes last for decades. However, when it rains enough for pans to hold water, dormant wetland species respond: these are the species that survive the water stress by escaping it in time. These plants complete their life cycles while there is rain. Annuals such as *Chenopodium glaucum* remain dormant in the form of seeds in the seedbank during the period of drought and after they germinate they have very short life cycles in which they set seed again in a very short time (this means that their seeds are long-lived). Such plants produce seeds when it is raining in order to ensure their long-term persistence (Salvador, 2013).

Species that grow in saline wetlands have three potential mechanisms that they use to deal with salinity, namely salt dilution (succulence), salt exclusion and salt excretion. Many plants employing either of these strategies are found in the family Chenopodiaceae (mostly the genera *Salsola*, *Suaeda* and *Atriplex*), and the family Poaceae (grasses) they are common in the genus *Sporobolus.*

The species employing these mechanisms grow in inland salt pans and coastal salt marshes. The difference between these two environments is that inland salt pans are subjected to an annual cycle of water level fluctuations, primarily driven by rainfall. Inland salt pans are inundated for a short time period in a year, as a result these wetlands lack water for most part of the year and sometimes they can be dry for many years. Salinity in these wetlands results when salts from surrounding landscape as well as rain water become concentrated in the wetland, once water collects in a wetland and evaporates. The water in coastal salt marshes originates from marine input, these wetlands are subjected to daily fluctuating water levels, and as a result the soils always have the presence of water with salinity.

Most inland halophytes use the strategy of salt dilution (succulence) in order to deal with salt stress. Succulence is defined as the thickening of the leaves, stems and roots of plants that are exposed to salinity (Ashraf et al., 2010). Succulent plants store large amounts of water in their body to dilute absorbed salt ions, thereby minimising the effect of salt toxicity. They use this mechanism to avoid high salt concentrations in plant organs. Species such as *Salsola aphylla* which are found in inland salt pans are highly succulent.

The second strategy involves species that can survive high salt concentrations in the rooting zone by excluding the salt from entering the plant through the roots (Aslamsup et al., 2011).The lower permeability of the roots assists in the exclusion of salts under excessively high salinities for example in mangroves (Hasanuzzaman et al., 2014).

The third strategy involves species that have specialized salt glands on the leaf surface that are responsible for secreting excess salt from the plant. These halophytes eliminate the salt by either transferring it to the vacuoles of glands or by secreting it to the outside of secretory cells: in that case salt crystals can be seen visible on the plant leaf surface (Leksungnoen, 2012). Some halophytes release excess salt by shedding old leaves which are grown under high salt concentrations in order to avoid toxic effects of sodium salts which are accumulated in leaves. Salt exclusion and excretion do occur in inland salt marshes but are mostly found in coastal salt marshes.

6.4 Role of community-weighted plant traits along aridity gradient on ecosystem functions and services

Different plant functional groups vary in their ability to contribute towards ecosystem functions and services. Therefore, combinations of community-weighted plant traits of the dominant plant species in communities are good indicators of ecosystem functioning and, hence of the delivery of ecosystem services (Grime, 1998; Lundholm et al., 2015; Moor et al., 2015). Traits such as SLA and plant height determine the response of plants to resource availability and affect functions such as biomass production (Lavorel, 2013).

Mesic areas are dominated by species with long shoot lengths and deep rooting and this result in high above and belowground biomass production. Long shoot lengths of species in the mesic areas have a greater contribution to carbon storage. Species with long shoot lengths also provide a habitat for a variety of animals, as many species of birds and mammal species can hide or nest under the foliage. Additionally, the high specific leaf area of these species assists in controlling ecosystem functions such as primary productivity and nutrient cycling. Traits such as SLA of species from both dry and mesic areas play an important role in soil fertility, climate regulation (including carbon sequestration) and water regulation.

Moreover, mesic areas are dominated by clonal plants that have high rooting depth and a relatively high belowground biomass. The rhizomes of these plants assist in holding the soil together. They also have important effects on water and sediment retention, controlling floods particularly in mesic areas (Díaz and Cabido, 2001). Clonal growth in both mesic and dry areas may also lead to nutrient enrichment and associated soil functions (Cornelissen et al., 2014).

The study of plant species traits can assist in determining how climate change impacts on ecosystem structure and function, because the shift in dominance within the plants can cause shifts in weighted averages of trait values and this will result in ecosystem changes that are large in magnitude. Climate change can affect wetland ecosystem processes indirectly through the effects on the physiology and morphology of individual species and the composition of communities.

Chapter 7

Conclusion and Recommendations

7.1 Conclusion

The current study shows that the approach of functional ecology has a good potential to improve our understanding of the impacts of environmental change and climate variability on species composition in wetlands along the aridity gradient. This shows that plant functional traits and plant functional types are suitable tools that can be used in monitoring changes of wetland vegetation under future climate changes.

The strong relationship between the measured plant functional traits and non-climatic environmental variables including climatic variables provide a convincing evidence that easy measurable traits such as specific leaf area can be used as predictors of species distribution under environmental and climate change. Species that grow on the eastern part of the study area tend to acquire available resources fast and are found in productive areas where competition is assumed to be high. As a result, these species are fast growing and are able to outcompete their neighbours. Species that grow on the western part of the aridity gradient are slow growing and have traits that are associated with conservative growth strategy.

Furthermore, there are two plant functional types described in this study that can serve as specific indicators, namely: the rhizomatous graminoids that occur only in the mesic areas on the eastern side of the study area and the succulent shrubs which occur only in dry areas on the western side of the study area. These indicator plant functional types can serve as flagship warning entities as the climate changes. They can also be chosen to reveal the effects of climate change in different aspects of the physical environment of the wetland such as drought sensitivity.

Wetlands are sensitive to climate changes since they lie between terrestrial and aquatic ecosystems. Therefore, a decrease in the amount of water in the wetland can cause it to become more terrestrial. This study shows that as the climate changes there will be a shift in wetland species composition along the aridity gradient across the Highveld. The wetlands on the western side of the study area will be subjected to increased salinities and this will result in loss of species. The wetlands on the eastern side will be subjected to decline in water tables and this might result in terrestrial encroachment.

The findings of this study are important because they can allow management and conservation of wetland areas as data on the dynamics of wetlands in the changing environment is scarce. These findings can be used for the long-term monitoring programme for wetlands of the Highveld, because such a monitoring programme can benefit from intensive knowledge of the species that make up communities in wetlands. Monitoring wetland vegetation is important in the management of wetlands because it can detect long-term ecosystem changes; it provides insight to the potential ecological consequences of the change and it helps decision makers to determine how management practices should be implemented.

7.2 Recommendations

It is important that the efforts to study and understand the impact of environmental change and climate variability on wetlands should be continued because change can only be quantified where baseline data are available. This can be done by prioritizing wetlands that are likely to experience the greatest impacts of climate change such as those that receive water from precipitation. These are the wetlands that are expected to experience drop in water tables and terrestrial encroachment, which might result in invasive species colonizing these wetlands and further threaten native biodiversity.

More research can still be done on the impacts of drought on wetland ecosystems because drought is a key disturbance influencing changes in species composition in wetland ecosystems. Drought is associated with extreme hot dry weather conditions such as those during El Nino, and such conditions are expected to be more frequent in future climates and this may have significant impacts on wetland vegetation in the long term.

Future studies can use a combination of remote sensing and field sampling including Global Positioning System Satellite technology to study the impacts of climate change on species composition and to see how the vegetation will change over the years as the climate changes. Wetland vegetation is an important indicator of any changes in the wetland because it can also be observed from space and different plant functional types can have different emission spectra and structure on satellite images. The use of remote sensing can assist in the long-term monitoring because it will give conservationists the possibility to monitor wetlands without spending much effort for going into the field.

The National Wetland Vegetation Database can be used as a reference to see how species composition has changed in wetlands over the years as the climate changes. The data collected in the future can also be compared with the findings of this study and changes overtime can be quantified.

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Appendix A

Climatic data calculated for each weather station

Province	Station name	Lat	Lon	Alt	Years with complete data	Precip	MaxTemp	MinTemp	Evap	HumiMax	Windspeed
Free State	Koppies	-27.21	27.43	1358	13	609.99	14.20	8.07	1509.07	92.35	2.22
Free State	Qwaqwa; uniqwa	-28.48	28.83	1699	11	552.62	23.33	8.45	1440.27	89.72	2.42
Free State	Gladdedrift: klippoort	-27.00	28.96	1522	11	718.78	23.95	6.78	1280.42	93.71	1.81
Free State	Reitz; silos	-27.80	28.44	1623	10	4474.28	23.97	6.81	1270.21	88.01	1.76
Free State	Lonetree farm: aws	-28.51	28.10	1714	9	484.64	22.66	5.97	1298.32	88.44	1.89
Free State	Verkykerskop: van koppe	-27.95	29.43	1782	8	528.09	22.57	6.71	1393.05	87.33	2.98
Free State	Koffiefontein: aws	-29.36	25.13	1238	9	480.05	27.11	8.5	1569.21	78.62	2.57
Free State	Zastron: camelot	-30.11	27.03	1475	7	685.88	25.47	4.61	1379.26	90.59	1.36
Free State	Koranna	-28.90	27.33	1540	3	579.19	24.01	7.14	1445.57	81.35	2.37
Gauteng	Tarlton; deodar	-26.14	27.57	1581	10	659.95	23.98	10.04	1416.53	80.69	2.03
Kwazulu-Natal	Baynesfield estate	-29.75	30.33	914	29	799.25	24.06	11.12	1430.83	86.98	91.46

Climatic data calculated for each weather station continued

Province	Station name	Lat	Lon	Alt	Years with complete data	Precip	MaxTemp	MinTemp	Evap	HumiMax	Windspeed
Kwazulu-Natal	Pmburg:ukulinga res.sta.	-29.67	30.40	775	28	742.45	23.82	13.07	1565.7	82.94	124.7
Kwazulu-Natal	Fountainhill: wartburg	-29.45	30.53	850	24	767.29	24.77	11.66		91.53	
Kwazulu-Natal	Umbumbulu	-29.99	30.64	632	12	875.92	25.90	12.74	899.31	94.28	1.69
Kwazulu-Natal	Hoopstad: vryheid	-27.94	25.71	1313	9	462.69	26.87	8.8	1621.17	83.69	2.55
Mpumalanga	Amsterdam; athole	-26.57	30.48	1550	14	670.09	23.02	10.01	1158.94	91.44	1.41
Mpumalanga	Marble hall moosrivier	-25.03	29.37	846	11	506.26		12.45	1549.74	86.27	1.4
Mpumalanga	Morgenzon	-26.88	29.72	1612	13	665.07	23.92	6.89	1275.44	96.56	2.21
Mpumalanga	Piet retief; sulfur springs	-27.18	31.09	946	10	617.38	25.07	11.3	1217.01	90.82	1.34

Climatic data calculated for each weather station continued

Province	Station name	Lat	Lon	Alt	Years with complete data	Precip	MaxTemp	MinTemp	Evap	HumiMax	Windspeed
Mpumalanga	Highlands: verlorenvalei_natpark	-25.30	30.13	2134	8	946.63	20.46	5.28	1076.85	94.97	2.79
Mpumalanga	Kwa mhlanga: loopspruit	-25.55	28.74	1405	9	598.08	25.19	10.78	1464.06	83.84	1.25
Mpumalanga	Belfast: driefontein	-25.75	30.16	1775	7	969.53	22.23	8.87	1225.94	91.22	2
Mpumalanga	Thaba chweu: blyderivier_natpark	-24.84	30.89	1628	7	1396.60	20.95	10.25	1007.58	93.18	2.39
North West	Petit - monsanto	-26.08	28.40	1635	12	712.61	23.55	9.1	100.1	87.68	1.56
North West	Louwna: aws	-26.86	24.23	1327	10	422.22	27.05	9.76	1665.02	79.72	2.89
North West	Tosca: aws	-25.87	23.93	661	8	508.91	27.95	10.18	1609.77	75.29	2.07

Climatic data calculated for each weather station continued

Province	Station name	Lat	Lon	Alt	Years with complete data	Precip	MaxTemp	MinTemp	Evap	HumiMax	Windspeed
North West	Schweizer reneke: boskop	-27.17	25.45	1348	10	499.70	25.93	8.95	1600.06	81.28	2.33
North West	Ventersdorp; buffelsvlei	-26.48	26.62	1383	8	584.43	25.62	8.2	1721.55	87	2.12
North West	Skuinsdrift	-25.36	26.40	1000	4	492.70	30.01	8.86	1434.11	91.21	0.84
Northern Cape	Colesberg	-30.70	25.10	1328	19	397.99	24.17	13.74	2016.62	80.3	123.04
Northern Cape	Stoeifontein	-31.52	22.85	1379	8	338.38					
Northern Cape	Jakkalskuil/venterd	-30.07	24.35	1212	5	321.64					
Northern Cape	Kgalakgadi: nossob	-25.42	20.60	964	5	238.51	33.16	11.02	1791.85	65.97	1.43
Northern Cape	Kenhardt: driekop	-29.28	21.13	815	7	167.41	29.12	12.16	1867.69	63.63	2.54

Appendix B

Trait values of the species

Species	SLA	SH_Leng	R_depth	Diam	R/S_Rat	Weig	RIL	Leaf N
Arundinella nepalensis	2.11	77.00	12.90	1.70	0.69	1.37	0.27	1.26
Atriplex lindleyi	2.24	18.40	21.90	2.60	0.06	9.12	3.00	2.71
Carex acutiformis	1.65	125.50	21.67	4.86	1.04	10.36	2.56	1.36
Chenopodium glaucum	2.08	11.40	9.20	2.40	0.25	1.36	3.00	3.25
Cynodon dactylon	3.50	14.29	4.57	0.01	0.89	0.13	0.36	1.19
Cynodon transvaalensis	0.78	2.50	4.70	0.80	0.25	0.22	0.48	1.21
Cyperus fastigiatus	1.36	171.00	18.63	6.20	0.38	9.99	1.80	1.26
Cyperus laevigatus	1.12	16.30	14.20	1.20	4.45	0.22	0.13	1.21
Cyperus longus	2.05	53.50	8.60	1.50	2.08	2.16	0.41	0.98
Cyperus marginatus	1.15	65.90	10.65	1.50	6.67	1.70	0.22	1.15
Echinochloa holubii	2.35	45.43	7.86	0.05	4.87	2.05	0.48	1.29
Eleocharis dregeana	2.00	47.80	13.35	1.97	0.65	0.25	1.35	0.74
Eragrostis bicolor	1.71	34.43	11.71	1.00	1.05	0.42	0.04	0.80
Eragrostis lehmanniana	0.96	25.20	16.20	1.00	0.48	0.39	0.04	1.18
Eragrostis plana	1.32	79.70	18.80	1.40	1.57	1.71	0.04	1.00
Eragrostis planiculmis	1.88	92.10	14.40	2.20	0.72	5.42	0.04	1.00
Falkia oblonga	3.04	4.80	1.45	0.01	1.73	0.53	0.42	1.90
Helichrysum aureonitens	3.04	25.90	9.90	0.02	1.13	3.90	0.85	1.34
Hemarthria altissima	2.22	43.60	11.30	1.30	2.01	2.82	0.78	1.43
Juncus rigidus	1.16	39.80	21.90	2.10	1.85	2.20	0.49	1.06

Trait values of the species continued

Species	SLA	SH_Leng	R_depth	Diam	R/S_Rat	Weig	RIL	Leaf N
Leersia hexandra	1.95	64.44	11.14	1.40	0.92	0.65	1.98	0.96
Leptochloa fusca	0.39	12.15	6.20	0.80	5.59	0.77	0.04	0.95
Lycium cinereum	1.76	15.20	29.10	2.10	0.27	11.25	1.49	3.01
Mariscus congestus	2.21	30.50	13.40	2.60	2.01	1.32	0.38	0.82
Panicum coloratum	2.07	68.10	13.00	1.90	1.06	0.66	0.04	1.21
Paspalum dilatatum	1.94	77.50	13.90	2.10	1.22	6.02	0.30	1.10
Paspalum distichum	2.51	19.00	10.50	1.20	0.29	0.41	0.13	1.80
Phragmites australis	2.03	100.88	13.63	6.63	2.12	22.83	0.83	2.00
Pycreus nitidus	1.41	42.40	12.36	2.13	1.88	2.83	1.66	1.41
Ranunculus meyeri	1.98	23.10	17.50	1.37	0.35	0.16	2.12	1.31
Ranunculus multifidus	2.28	24.40	8.00	0.90	0.74	2.68	2.15	1.66
Salsola aphylla	1.71	31.70	34.10	5.30	0.09	79.05	3.00	2.27
Schoenoplectus brachyceras	2.01	113.00	24.62	8.80	0.65	5.11	1.16	2.00
Schoenoplectus decipiens	1.49	65.50	7.80	1.30	1.17	0.48	0.30	1.46
Scirpoides dioecus	0.47	52.60	17.10	1.50	1.69	0.88	0.48	0.67
Sporobolus albicans	1.85	3.58	14.20	1.00	2.95	0.16	0.04	2.04
Sporobolus ioclados	3.27	20.90	11.80	1.00	3.01	0.94	0.04	0.97
Sporobolus ludwigii	2.28	6.00	16.70	0.75	3.61	0.92	0.04	0.97
Typha capensis	0.99	144.20	25.30	24.80	0.67	33.32	2.25	1.09