Fynbos Riparian Biogeochemistry and Invasive Australian Acacias

by

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ABSTRACT

Riparian ecotones, transitional areas between upland terrestrial communities and aquatic ecosystems, are very dynamic and complex ecosystems with intrinsic ecological properties differing in spatial structure, function and temporal dynamics. Riparian habitats along rivers of the Mediterranean south-western Cape are sensitive to environmental change and particularly vulnerable to invasion by invasive alien plants (IAPs), especially nitrogen-fixing *Acacia* spp., and yet relatively little work has focused on how riparian ecosystems in this region respond to such stressors. The important roles that intact riparian vegetation play in maintaining ecosystem integrity and services have been increasingly highlighted as we acknowledge the degradation of these habitats. While the Working for Water (WfW) programme has been shown to be very successful in eradicating IAPs in riparian zones in the short-term, the extent to which riparian ecosystems recover following alien clearing activities remains poorly understood. The results presented in this study addressed several different aspects of riparian structure and function and acts as a steppingstone for guiding future research and management in riparian zones by adding to the evaluation of the success of clearing initiatives and restoration thereof.

The aim of this study was to assess plant functional type (PFT) cover, soil physical and chemical properties, and selected biogeochemical processes in natural, *Acacia*- invaded and cleared riparian ecotones and associated non-riparian upland fynbos. Fieldwork was performed in mountain and foothill sections of six perennial river systems within the south-western Cape. Eleven sites of three categories were chosen: four natural sites (uninvaded); four moderate to highly invaded sites (predominantly *A. mearnsii*); and three cleared sites (a formerly invaded site that had been cleared more than 7 years prior to the study). Within each site, four to five replicate plots were established along each of three geomorphological zones (wet bank, dry bank, and upland fynbos). Seasonal soil samples were collected for a period of one year.

Results from this study showed that PFT cover and composition, soil physical and chemical properties and rates of nitrogen (N) and phosphorus (P) mineralization differed amongst invasion status, between geomorphological zones and across seasons. Regarding most soil physical and chemical properties and indices N and P cycling, river floodplains (dry banks) were very similar to terrestrial uplands. *Acacia* spp. changes soil properties and affects plant functional attributes by i) enriching the system with N; ii) enhancing litter inputs; iii) altering soil physical properties; iv) changing the composition and reducing the cover of PFT; and v) enhancing P mineralization rates. Although measured soil physical and chemical properties and N and P mineralization rates were reduced to levels that were similar to or resembled the situation at natural areas, available inorganic N remained two times higher after more than seven years of clearance. Furthermore,

cleared areas were characterized by sparse woody cover and a high cover of alien grasses. Correlations between soil silt and clay content and several soil properties measured in this and other studies indicates important linkages between soil texture and resource availability.

Clearing *Acacia* spp. may initiate restoration of invaded riparian ecosystems, but changes in ecosystem function (e.g. elevated soil N availability) as a result of invasion may necessitate active restoration following the removal of the alien species. Active restoration under such conditions would be required to facilitate the restoration of cleared riparian communities. However, we still lack the mechanistic understanding around fynbos riparian recovery after clearing, as the success of restoration may depend on complex interaction and feedback cycles between plants and their physical environment. A greater comprehensive understanding of fynbos riparian ecological processes will not only improve the effectiveness of restoration initiatives by integrating science and management, but also advance the field of riparian ecology.

SAMEVATTING

Rivier oewerwal-areas, oorgang gebiede tussen aangrensende terrestriële gemeenskappe en akwatiese ekosisteme, is baie dinamiese en komplekse ekosisteme met intrinsieke ekologiese eienskappe wat verskil in struktuur, funksie (bv. biogeochemie siklusse) en temporale dinamika. Oewerhabitatte langs riviere van die Mediterreense suid-wes Kaap is sensitief vir omgewingsveranderinge en kwesbaar vir indringing deur uitheemse plante (bekend as "invasive alien plants" (IAPs)), veral stikstof-fiksering *Acacia* spp., en relatief min werk het nog gefokus op hoe ekosisteme in die streek reageer op sulke veranderinge in die omgewing. Die belangrike rol wat gesonde oewerwal plantegroei speel in die handhawing van ekosisteemdienste- en integriteit, is al hoe meer uitgelig soos ons die agteruitgang van hierdie habitat in ag neem. Terwyl die Werk vir Water (WvW)-program al dat baie suksesvol was in die uitwissing van IAPs in oewersones in die kort termyn, is die mate waarin oewer-ekostelsels herstel na skoonmaakaksies swak verstaan. Fynbos oewerwal-areas is grootliks ingeneem deur houtagtige IAPs, veral stikstof fiksering *Acacia* spp. (soos *Acacia mearnsii*). Die resultate wat in hierdie studie aangebied is, het verskillende aspekte van oewer- struktuur en funksie aangespreek en dien as middel vir toekomstige navorsing en bestuur van oewerwal ekosisteme deur by te dra tot die evaluering van die sukses van skoonmaak inisiatiewe en die herstelproses daarvan.

Die doel van hierdie projek was om die moontlikhede vir herstel van fynbos owerwal-ekostelsels te evalueer deur middel van verskeie grond- fisiese en chemiese eienskappe; plant funksionele groep dekking (genoem 'plant functional types' (PFT)); en geselekteerde grond biogeochemie prosesse in natuurlike, *Acacia*- aangetaste, en skoongemaakte rivierstelsels en nabygeleë terrestriese areas te vergelyk. Veldwerk is gedoen in bergstroom en voetheuwel rivierseksies van ses standhoudende rivierstelsels in Suid-wes Kaap, Suid Afrika. Van uit hierdie geselekteerde rivierstelsels is elf studie areas van drie kategorieë (of indringing status) gekies: vier natuurlike areas (nie aangetas); vier gematig- tot hoogs aangetaste areas (hoofsaaklik *A. meanrsii*); en drie skoongemaakte areas (rivieroewers wat meer as sewe jaar van te vore skoongemaak is). Binne elke studie area was vier tot vyf soortgelyke persele gevestig by elke van drie breë geomorfologiese sones: naamlik nat-, droë en hoogliggende terrestriese fynbos. Seisoenale grondmonsters vir 'n tydperk van een jaar is geneem.

Resultate van hierdie studie het getoon dat PFT dekking en samestelling, grond fisiese- en chemiese eienskappe en N-mineralisasie en suur fosfatase aktiwiteit verskil tussen indringing status, geomorfologiese sones en oor seisoene. Ten opsigte van meeste grond fisiese en chemiese eienskappe en indekse van stikstof (N) en fosfor (P) siklusse kom die rivier vogregimes (droë oewersones) baie ooreen met die terrestriële gebiede. Aan die anderkant is die

natbanksones gekenmerk deur grondeienskappe wat baie verskil van die ander twee geomorfologiese gebiede. Die gegewens ondersteun die hipotese dat indringing deur *Acacia* spp. verskeie grondeienskappe verander en plante se funksionele kenmerke beïnvloed deur i) die sisteem met voedingstowwe te verryk (veral N); ii) verhoog die toevoeging van plantmateriaal; iii) verander grond fisiese eienskappe; iv) verander die samestelling en verminder die dekking van PFT; v) en verhoog P biogeochemie. Hoewel grond fisiese -en chemiese eienskappe, en indekse van N en P mineralisasie verminder is tot vlakke wat soortgelyk aan natuurlike areas, het beskikbare anorganiese N twee keer hoër gebly by skoongemaakte gebiede. Nietemin, voorheen skoongemaakte gebiede is weer-binnegeval deur eksotiese grasse en die regenerasie of hertelling van inheemse fynbos gemeenskappe is taamlik beperk, veral houtagtige oewer struike en bome. Korrelasies tussen grond slik-en klei-inhoud en verskeie grondeienskappe gemeet in hierdie en ander studies dui op belangrike skakeling tussen die grondtekstuur en voedingstof beskikbaarheid.

Die opruiming van *Acacia* spp. mag as aansporing dien vir die herstellingsproses van rivieroewerstelsels, maar veranderinge in die funksie van ekosisteme (bv. verhoogte grond N beskikbaarheid), as gevolg van indringing, mag aktiewe herstel noodsaak nadat die indringer spesies verwyder is. Aktiewe herstel onder sulke omstandighede sal verwag word om die herstel van skoongemaak oewer gemeenskappe te fasiliteer. Ons het wel egter nog 'n gebrek aan die meganistiese begrip in verband met die herstel van fynbos oewerwal areas na opruimings-inisiatiewe, sedert die sukses van herstel kan afhang van komplekse interaksie en terugvoer siklusse tussen die plante en hul fisiese omgewing. 'n Meer omvattende begrip van fynbos rivieroewer ekologiese prosesse sal nie net die doeltreffendheid van opruimings-inisiatiewe deur die integrasie van wetenskaplike navorsing en bestuur verbeter nie, maar ook vooraf die gebied van rivieroewer-ekologie.

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CHAPTER 1

General Information

The work presented in this thesis forms part of a Water Research Commission (WRC) funded research initiative entitled "Identifying relationships between soil processes and biodiversity to improve restoration of riparian ecotones invaded by invasive Acacias". This specific MSc project undertook to investigate soil biogeochemistry and plant functional type diversity across landscape position and the impact of the nitrogen-fixing invasive *A. mearnsii* (sometimes growing in riparian ecotones in combination with *A. longifolia*) and clearing on riparian ecosystem structure and function.

1.1. INTRODUCTION

The structure of ecological boundaries has been shown to play a major role in regulating the movement of energy, materials, and organisms and is of fundamental importance to ecology (Pickett and Cadenasso, 1995). Soil nutrients play an important ecological role and their availability is thought to be a key factor in determining landscape-level community composition and species distributions (Richards et al., 1997). Riparian ecotones, transitional areas between upland terrestrial communities and aquatic ecosystems (Gregory et al., 1991; Naiman and Décamps, 1997; Richardson et al., 2007; Pettit and Naiman, 2007), are well known for their distinctive and intrinsic ecological properties and functions relating to biodiversity, productivity and biogeochemistry (Gregory et al., 1991; Pemberton and Boucher, 2001; Décamps et al., 2004). They are complex and dynamic habitats (Naiman and Décamps, 1997) and are often associated with unique vegetation assemblages in comparison to upland terrestrial vegetation, in terms of species composition and growth forms (Rowntree, 1991; Naiman and Décamps, 1997; Reinecke et al., 2007). Riparian zones and associated vegetation are therefore acknowledged as among our most essential and threatened ecological resources, playing a critical role in mediating terrestrial and aquatic exchanges (Gregory et al., 1991; Bechtold and Naiman, 2006). For example, riparian vegetation slows down turbulent floods, moderates erosion, maintains water quality, consumes water but moderates base flow and adds to species and habitat diversity (Esler et al., 2008; Sieben and Reinecke, 2008).

Worldwide, riparian zones have been degraded on a large scale (Richardson et al., 2007; Holmes et al., 2008). Important categories of impacts to riparian ecosystems are those associated with

plant invasions and hydrological modifications of river systems (Richardson et al., 2007; Esler et al., 2008; Holmes et al., 2008). Many invasive alien plants (IAPs) are able to alter ecosystem processes (Le Maitre et al., 2011), especially those species that change resource regimes, termed "transformer species", pose serious threats to native biodiversity and ecosystem function (Richardson et al., 2000; Funk and Vitousek, 2007). Riparian ecosystems are generally regarded as being highly prone to invasion by alien plants, compared to terrestrial environments, and IAPs easily become established along rivers mainly because they are exposed to natural and human induced disturbances associated with their dynamic hydrological nature and ability to transport propagules (Rowntree, 1991; Galatowitsch and Richardson, 2005; Richardson et al., 2007; Blanchard and Holmes, 2008). There is increasing concern, both worldwide and locally, about the effects of IAPs (Le Maitre et al., 2000; Richardson et al., 2007; Marais and Wannenburgh, 2008). Recently there has been an upsurge in interest in assessing changes in native community composition and structure and changes in ecosystem function (such as biogeochemical processes) that are associated with invasion of alien plant species (Ehrenfeld, 2003; Yelenik et al., 2004; Esler et al., 2008). However, whether invasive species are drivers or passengers of change in degraded ecosystems remains a controversial subject (Esler et al., 2008). Insight into the mechanisms used by invasive species to outperform native species is critical to controlling their spread (Funk and Vitousek, 2007).

Riparian vegetation of the fynbos biome of South Africa, which is distinctly different from the surrounding fynbos vegetation (Blanchard, 2007), has been heavily invaded by woody IAPs, especially *Acacia* spp. (Richardson et al., 1992; Reinecke et al., 2008) and a number of hypotheses have been proposed to explain the susceptibility of these systems to invasion (Pieterse, 1997). Within fynbos riparian and terrestrial ecosystems of the south-western Cape, the influence of woody exotic plant invaders on ecosystem structure and function has been investigated by a number of authors *inter alia* nutrient cycling and soil physical- and chemical properties (e.g. Musil and Midgley, 1990; Witkowski, 1991; Stock et al., 1995; Yelenik et al., 2004, 2007; Cilliers et al., 2005; Jovanovic et al., 2009), hydrology (e.g. Le Maitre et al., 1996; van Wilgen et al., 1996; Dye et al., 2001), fire (e.g. van Wilgen and Richardson, 1985; Versfeld and van Wilgen, 1986; Musil and Midgley, 1990; van Wilgen et al., 1990; Le Maitre et al., 1996; Cilliers et al., 2004; Jayiya et al., 2004); vegetation structure and composition (e.g. van Wilgen and Richardson, 1985; Richardson and van Wilgen, 1986; Richardson et al., 1989; Holmes and Cowling, 1997; Reinecke et al., 2007) and river geomorphology (e.g. Macdonald and Richardson, 1986; Rowntree, 1991). Australian *Acacia* spp. are some of the most productive and successful invasive species worldwide (Richardson and Rejmánek, 2011; Morris et al., 2011) and the most damaging invaders in fynbos riparian ecosystems (Richardson et al., 2007; Reinecke et al., 2008)

with a range of socio-economic and ecological impacts (Le Maitre et al., 2011). These species (e.g. *Acacia mearnsii, A. longifolia, A. saligna*) form dense stands that largely exclude indigenous fynbos riparian vegetation (Boucher, 2002; Holmes et al., 2005; Blanchard and Holmes, 2008) by successfully competing for resources in nonnative environments (Morris et al., 2011). Some of these invasions, in turn, have diminished the capacity for rivers to provide ecosystem services (Galatowitsch and Richardson, 2005; Esler et al., 2008).

Given this context, restoration of these degraded ecosystems is recognised as a fundamental component in reducing impacts of IAPs (Hobbs and Harris, 2001). The susceptibility to invasion of riparian ecosystems also poses challenges for restoring those systems that are already invaded by alien species (Galatowitsch and Richardson, 2005). Clearing stands of IAPs, therefore, is of primary concern when restoring rivers (Jasson, 2005). In some areas of South Africa, particularly the Western Cape Province, clearing headwater reaches has been a major part of the overall removal efforts of exotic species, providing an important opportunity to monitor riparian vegetation dynamics during the post-clearing transition (Galatowitsch and Richardson, 2005). The South African government supports a number of alien plant clearing programmes, the majority of which give priority to riparian areas to reduce the spread of propagules along rivers and into adjacent terrestrial ecosystems (Richardson et al., 1997). The Working for Water Programme (WfW) was initiated by the Department of Water Affairs and Forestry (DWAF) in 1996 with multiple aims of controlling woody invading plants (Le Maitre et al., 1996; van Wilgen et al., 1998; Dye and Jarmain, 2004), conserving biodiversity, seeking to maximize and protect water resources, and thus increasing ecological integrity, while providing employment (van Wilgen et al., 1998). Many IAPs that are being targeted by Working for Water (WfW) are N_2-fixing legumes (Fabaceae family; Jovanovic et al., 2009). The large-scale clearing of symbiotic nitrogen (N_2)-fixing invaders may cause problems for restoration, since changes in nitrogen (N) cycling may hamper efforts to restore native species (Yelenik et al., 2004). Additionally, alien species may dominate during initial succession of communities and modify conditions for the establishment of native species, as these species accumulate large soil-stored seed banks and can rapidly recolonize after a disturbance (Beater et al., 2008; Vosse et al., 2008).

1.1.1. Problem statement

Riparian zones are relatively small components of the landscape, but extremely important in fulfilling many important biological, physical, chemical, and socio-economic roles (Gregory et al., 1991; Esler et al., 2008). There has been much interest recently in the patterns, determinants and function of biodiversity in Mediterranean-climate ecosystems (Cowling et al., 1996). The

introduction of novel traits into an area where it is largely absent, such as high resource use and N_2-fixation (Werner et al., 2010; Morris et al., 2011), may promote *Acacia* invasiveness in fynbos riparian ecotones via alterations in the biophysical environment (for instance nutrient cycling processes). It has been shown that *Acacia* spp. cause simultaneous transformations in vegetation and microbial communities, microclimates, soil nutrient levels (especially N) and moisture regimes (e.g. Yelenik et al., 2004; Blanchard, 2007; Reinecke et al., 2007; Marchante et al., 2008; Werner et al., 2010), each of which may necessitate a different restoration approach following clearing (Reinecke et al., 2008). Changes in ecosystem functions, such as altered soil nutrient levels and cycling processes, as a result of invasion by *Acacia* spp. may require active restoration following the removal of the invader (Gaertner et al., 2011), as these changes may lead to further alterations in community structure by promoting secondary invasions of other problem species (Yelenik et al., 2004; Holmes et al., 2005). The effectiveness of restoration efforts in ecosystems adapted to resource-poor environments, such as fynbos, will depend on how long biogeochemical legacies persist (Yelenik et al., 2007; Marchante et al., 2009; Gaertner et al., 2011). Management initiatives, or resource alterations (as mentioned above), or the combinations of these also often impede or complicate restoration attempts (Galatowitsch and Richardson, 2005; Le Maitre et al., 2011). There is evidence that indigenous riparian species recovery may be exceedingly limited after clearing, with widespread regeneration of woody aliens (Galatowitsch and Richardson, 2005). The failure of re-establishment may be attributed to low densities of native vegetation, a depauperate seed bank, and elevated levels of juvenile mortality associated with clearing or reinvasion by alien species (Reinecke et al., 2008).

Most research on riparian and riverine structure and soil processes is focused in temperate ecosystems. It is uncertain whether riparian soils of fynbos riparian ecosystems are enriched in nutrients relative to terrestrial areas. Soils associated with Table Mountain Sandstones are documented to have low nutrient levels, such as N, carbon (C) and phosphorus (P) (Cowling et al., 1996; Rebelo et al., 2006). Furthermore, a number of studies have found that soil processes, such as N mineralization, are elevated in riparian ecotones compared to adjacent upland areas (Naiman et al., 2005). Several studies have also recognized correlations of particle size distribution and soil physical and chemical properties with organic matter (OM) storage, N mineralization, microbial biomass, and primary productivity (Pinay et al., 1992; Pinay et al., 1995; Bechtold and Naiman, 2006). However little is known about fynbos riparian biogeochemistry. Answers to crucial questions remain regarding relationships between many riparian ecosystem processes and functions and plant functional type diversity (Richardson et al., 2007). Aside from studies that have investigated the effects of woody IAPs on ecosystem structure and function within in fynbos riparian and terrestrial ecosystems (as mentioned above), no studies have

specifically investigated soil processes and ecosystem functioning of fynbos riparian ecotones, and the changes induced by invasion or recovery after clearing. Riparian restoration has become a major ecosystem activity and is supported by funding from government sources (Marais and Wannenburgh, 2008). Limited budget frequently results in inadequate and unsatisfactory results, especially since restoration of riparian function is seldom monitored or achieved (Holmes, 2001). While riparian structure is often seen as the endpoint of repair efforts, riparian function does not necessarily follow. Following the eradication of IAPs, the dynamics of natural succession in the process of riparian vegetation recovery and soil biogeochemistry, therefore necessitate further investigation (Reinecke et al., 2008).

1.1.2. Rationale and motivation

Riparian zones are vulnerable to invasion by IAPs, since they are disturbed by floods and associated hydrological perturbations, and their linear structure facilitate movement of alien propagules. They therefore necessitate active management in areas where problem species occur (Reinecke et al., 2007). Along with many other riparian ecosystems all over the world, habitats along rivers are amongst the most densely invaded features in South African landscapes (Richardson et al., 1992; Richardson and van Wilgen, 2004; Pretorius et al., 2008). Several Australian *Acacia* spp. are widespread along fynbos rivers in the Western Cape Fynbos and form dense stands that mostly exclude indigenous vegetation (Richardson et al., 1992; Boucher, 2002; Holmes et al., 2005). Since riparian ecosystems play a vital role in maintaining ecosystem services and function, understanding the level of invasion and degradation and associated changes in ecosystem function is essential for successful restoration. While the WfW program has been shown to be very successful in eradicating IAPs in riparian zones, the potential biogeochemical legacies that may persist as a result of invasion by N_2-fixing species, on ecosystem structure and functioning are uncertain, and are thus the focus of this study. Legacies may persist in the form of modified soil organic matter levels, soil chemistry, and soil N and P stocks (Corbin and D'Antonio, 2004; Yelenik et al., 2004). Nevertheless, knowledge of these processes is limited, and as a consequence, knowledge on the links between fynbos riparian ecosystem functioning and restoration is currently lacking. The research presented in this thesis provide insights into the important role of soil processes in regulating nutrients in fynbos riparian ecotones, the role of plant functional types (PFTs) in supporting these processes, and how this is affected by N_2-fixing IAPs. This new knowledge adds significantly to a mechanistic understanding of fynbos riparian ecosystem function, offers insight into their restoration and management as well as information of potential barriers for restoration (such as changed soil processes and function). The issues outlined within this paragraph and the preceding two paragraphs, serve as key motivations for the initiation of the study.

1.2. RESEARCH OBJECTIVES, HYPOTHESES, AIMS AND KEY QUESTIONS

1.2.1. General objective

The purpose of this project was to quantify PFTs, soil physical and chemical properties, and selected soil biogeochemical processes in *Acacia*- invaded and cleared riparian ecotones and associated non-riparian upland fynbos. Emphasis is placed on the way in which the relationships between soil properties and PFTs are affected by invasion and clearing of alien invasive *Acacia* spp. (mostly *A. mearnsii*) by elucidating the interrelationships in natural, invaded and cleared riparian ecotones and associated upland fynbos in the south-western Cape.

1.2.2. Hypotheses, aims and key questions

The following research questions and hypotheses were addressed in order to meet the objectives of the study:

1.2.2.1. Aims:

a) To quantify PFT cover and composition, soil physical and chemical properties, total carbon C and N, available N and P concentrations in natural, invaded and cleared riparian ecotones and associated upland fynbos (Chapter 3).

b) To quantify soil potential N and P (acid phosphatase activity) mineralization in natural, invaded and cleared riparian ecotones and associated upland fynbos (Chapter 4).

c) To assess important relationships amongst selected soil physical and chemical properties and process rates (Chapters 3 and 4).

1.2.2.2. Hypotheses:

a) Fynbos riparian soils have higher concentrations of C, N, and P compared to adjacent upland zones.

b) Fynbos riparian soils are associated with higher N and P mineralization rates compared to uplands.

c) *Acacia* invasion enhances soil nutrient availability, changes soil physical and chemical properties, and increases process rates.

1.2.2.3. <u>Key questions:</u>

a) How does the cover of important PFTs and selected ecosystem attributes differ depending on landscape position and invasion status?

b) How do soil physical and chemical properties vary depending on landscape position and invasion status?

c) How do soil nutrient concentrations (C, N and P) differ depending on landscape position and invasion status?

d) What important relationships exist between selected soil physical and chemical properties?

e) How do soil N and P mineralization rates differ in relation to landscape position and invasion status?

f) What interaction exists between soil processes and selected soil physical and chemical properties?

1.3. STUDY AREA

1.3.1. Climate and geology

The western part of the Cape Floristic Region (CFR) experiences a Mediterranean winter rainfall climate, most of which occurs between April and September, with hot, dry summers (Deacon et al., 1992; Sieben, 2003). The Western Cape Rivers rise in mountains that can reach an elevation of about 2000 m. The geomorphology is characterized by the Cape Fold Belt Mountains that dominate the area (Prins et al., 2004). Most mountains in the Western Cape have rainfall between 1000 and 2000 mm per year, but in the wettest areas it might exceed 3000mm (Sieben, 2003). Therefore, the percentage of perennial flow in rivers is greater in headwater or mountain streams for the south-western Cape than elsewhere in the Fynbos Biome (Galatowitch and Richardson, 2005). Riparian zones embedded in these systems are physically, chemically, and biologically shaped by the geomorphology and seasonal and predictable rainfall events (Gasith and Resh, 1999), producing small and narrow streams defined by strong seasonal patterns of flow, with high-flows in winter and spring in response to rainfall, and low-flows in summer (Corbacho et al., 2003). Fynbos ecosystems are adapted to climatic fluctuations, periodic fires, and to soils that are shallow, acidic, sandy in nature and of low nutrient status (Stock and Lewis, 1986; Witkowski and Mitchell, 1987; Deacon et al., 1992; Rebelo et al., 2006; Sieben et al., 2009).

The geological substrate of the catchment is important as it defines how the river network will develop (Reinecke et al., 2007). The geomorphic structure of a valley floor is a consequence of the interaction of hydrology, basin geology, and inputs of organic/inorganic material from the surrounding catchment (Gregory et al., 1991). The high degree of topographical diversity within the CFR has created diverse soils, resulting in a combination of young and ancient soils (Cowling et al., 2009). The geology of the fynbos biome leads to highly constrained river reaches in the headwaters, with a relatively strong bedrock influence on hydrology (Reinecke et al., 2007). Erosion is the dominant geomorphological process in mountain stream zones. The headwater stream sections of the river dominate the landscape, owing to the short distance between mountains and coast (Prins et al., 2004). The dominant lithologies in the Western Cape are sandstone and quartzite that is underlain by granites (Rebelo et al., 2006). Within this area, the upper reaches of rivers change from sandstone and granitic derived soils to calcareous sand and soils associated with shales in the lower reaches of the river systems (Sieben et al., 2009). The soils next to mountain stream sections of rivers are weakly developed, shallow and contain a high percentage of bedrock, boulders and large cobbles. However, deepest soils are found in the dry bank zone further away from the water's edge (Sieben and Reinceke, 2008). Alluvial, sandy or silty soils over Quaternary sediments are largely derived from weathering of Table Mountain Sandstone, Cape Supergroup shale and Cape granite (Rebelo et al., 2006), yielding predominantly nutrient-poor substrate (Prins et al., 2004). Many floodplains of the rivers in the Fynbos Biome with surrounding quartzitic and Sandstone Mountains are covered with deep sandy alluvium (Rebelo et al., 2006).

1.3.2. Site description and experimental design

Fynbos vegetation in the Cape Floristic Region (CFR) of temperate South African ecosystems forms a vital component and has been particularly well studied ecologically (Holmes and Richardson, 1999). The Western Cape region has been recognised as biologically distinct, supporting unique vegetation types rich in endemic species (Rebelo et al., 2006). The vegetation in Mediterranean climates of fynbos and west-Australian kwongan is typically sclerophyllous and evergreen, adapted to water stress during the dry period, and able to grow in infertile soils (Gasith and Resh, 1999; Lambers et al., 2010). Compared to other nutrient-poor Mediterranean-climate regions of the world, fynbos soils are more similar to the soils of the kwongan (Australian heathlands) (Richards et al., 1997). This has been attributed to the low nutrient status of soils found in these regions (Witkowski, 1989). Both fynbos and kwongan plants have specialized strategies for nutrient uptake and internal nutrient cycling (Richards et al., 1997; Cramer, 2010). Community structure and composition is hypothesized to be controlled by site moisture levels,

vulnerability to fires and soil type (particularly pH and texture) (Deacon et al., 1992; Prins et al., 2004; Reinecke et al., 2008).

Fynbos riparian vegetation, Cape Lowland freshwater wetlands and Cape Lowland Alluvial vegetation are the three broad azonal community groups in the fynbos (Mucina et al., 2006). Riparian ecosystems with a fynbos affinity have been described as Closed-Scrub Fynbos dominated by broadleaved woody species, mainly small, perennial trees and shrubs, including characteristic fynbos elements such as species of Ericaceae and Restionaceae (Cowling and Holmes, 1992) in addition to forbs and graminoids in the understory (Reinecke et al., 2008). However, a particularly large turnover of species (i.e. high beta diversity) occurs among different catchments (King and Schael, 2001; Reinecke et al., 2007), although there are some common species with wider distributions across catchments (e.g. *Ischyrolepis subverticillata*; *Brabejum stellatifolium*; *Brachylaena neriifolia*; *Meterosideros angustifolius*) (Reinecke et al., 2008). In steep valleys that are protected from fire, riparian ecosystems give rise to Afromontane forest, where taller tree species (e.g. *Ilex mitis*, *Rapanea melanphloeos*, *Kiggelaria africana*, *Podocarpus* spp.) may establish (Manders, 1990; Mucina et al., 2006; Reinecke et al., 2008).

Boucher (2002) identified three main lateral zones extending outward from the active channel in rivers to the outward end of riparian influence: the aquatic, wet bank, and dry bank zones. Many different microhabitats are found along the banks as well as in the aquatic environment of all lateral zones (Sieben, 2003). A cross-section through a riverbed (Appendix A) illustrates the different habitats, each of which is affected uniquely by different levels of flow. This study concentrated on the latter two zones in addition to associated non-riparian upland vegetation. The wet bank substratum remains moist during most of the year and contains sedge/moss and a shrub subzone. Flooding is seasonal, which results in frequent inundation and would also influence the vegetation on this bank. The dry bank zone occurs mainly on alluvial deposits of accumulated sediments within the 1:20 year floodplain and plants are able to access water via deep root systems. Long-lived vegetation forms the main tree-shrub zone while it can also contain transitional elements when moving from the wet bank to the dry bank (Boucher, 2002; Blanchard, 2007; Vosse, 2007). In the lower reaches, the wet- and dry bank zones are very distinct, but in fast-flowing mountain streams, which are eroding and have not built up any lateral alluvial deposits, they are more likely to blend into each other. As a result, some wet bank zones can be absent or very narrow (Boucher, 2002; Sieben, 2003).
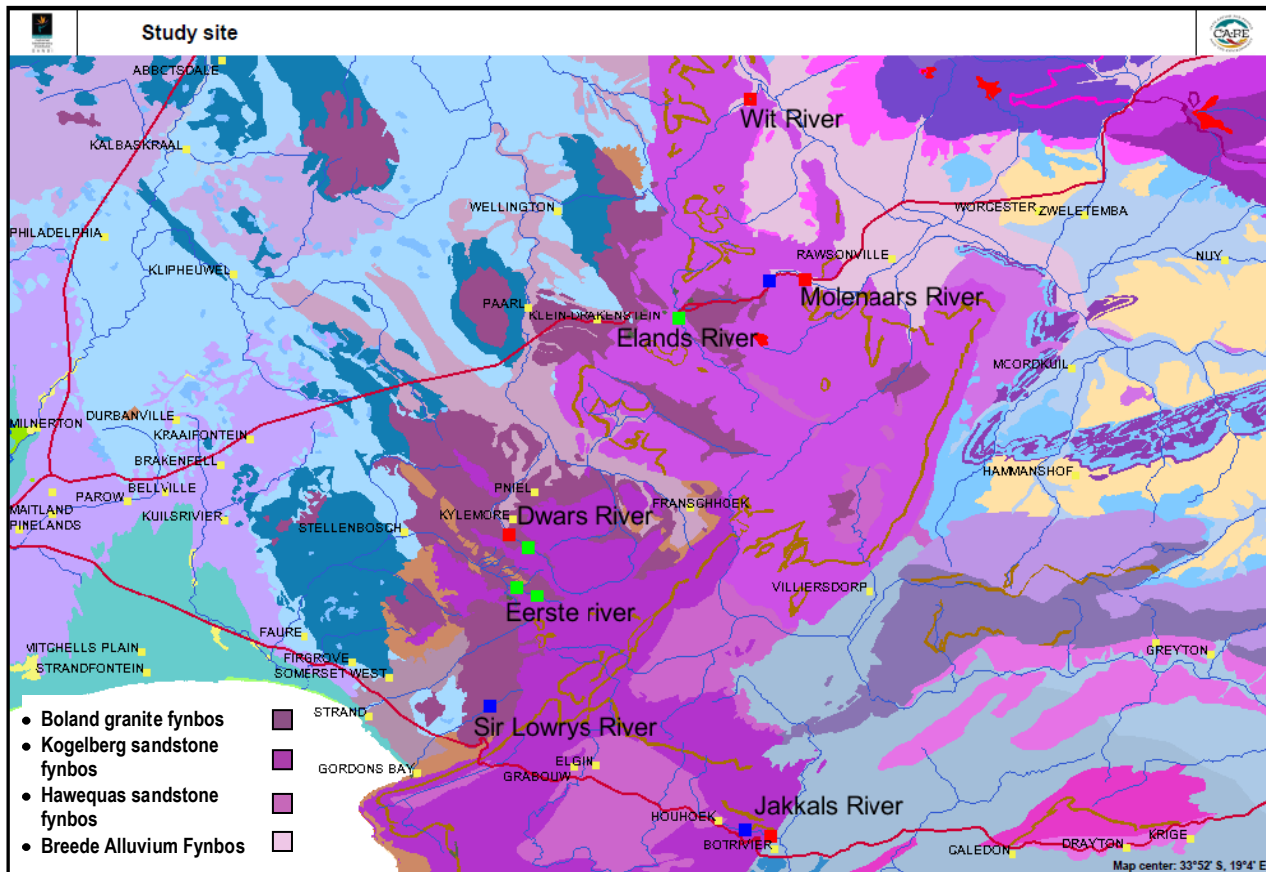
Figure 1.1. Map indicating location of the sites. Natural (reference) sites are indicated with green symbols, invaded sites with red symbols, and cleared sites with blue symbols. Map created with spatial data provided by South African National Biodiversity Institute (SANBI) GBIS. Elands River is a tributary of the Molenaars River and forms part of the Molenaars River system. Layers: National roads; rivers; towns, and colours denote different vegetation types based on South African Vegetation Map (Mucina and Rutherford, 2006). Vegetation types associated with sites are Kogelberg sandstone fynbos (Jakkals; Eerste; Dwars), Hawequas sandstone fynbos (Wit; Molenaars), Boland granite fynbos (Sir Lowry's; Eerste; Dwars), and Breede alluvium fynbos (Molenaars; Wit). Map scale: 1:750 000.

Six perennial river systems within the Western Cape (Jakkals, Sir Lowry's, Eerste, Dwars, Molenaars and Wit; Figure 1.1) were chosen as study sites for their variety of reach types, history of invasion and clearing, and for their relatively close proximity to Stellenbosch University. The focus of the study is the mountain stream and foothill segments of rivers where sites with dense invasion, cleared, and reference sites may be found. The original sampling design called for nine sites, each consisting of three natural (reference), invaded (predominantly *A. mearnsii* or a mixture of *A. mearnsii* and *A. longifolia* invaded for at least more than 10 years) and cleared riparian sites (a prior invaded site that has been cleared more than 7 years ago, with *A. mearnsii* as the dominant invader). One additional invaded and natural site was added, bringing the total to 11 sites and the number of invaded and natural sites to four each. Reference sites are frequently used in restoration and rehabilitation efforts to provide structural information on historical disturbance conditions and direction for restoration goals (Blanchard and Holmes,

2008). To be selected, invaded sites had to have an aerial cover of at least 50% *A. mearnsii* or a mixture of *Acacia* spp.

Where possible, some sites were selected in the same location where previous studies, e.g. that of Reinecke et al. (2007), Blanchard (2007) or Vosse (2007) were carried out. The study of Reinecke et al. (2007) is especially important, as geomorphological zones could be determined (wet bank, dry bank, and upland fynbos), which are the three categories used in this study. At each site, 4-5 replicate plots were selected for each zone (wet bank, dry bank, and upland zones; Appendix B) giving a total of 12-15 plots per site. Wet- and dry banks contain distinctive vegetation types and the border between them can often be quite sharp (Sieben and Reinecke, 2008). The location of the wet banks was determined by within-year flows and dry bank zones by recurrence intervals of floods of more than one year (Reinecke et al., 2007). This is crucial as fynbos riparian areas are characterized by steep environmental gradients and high levels of heterogeneity, requiring careful selection within similar geomorphological zones. It is challenging to separate differences between sites attributed to variations in environmental factors (e.g. geology and climate) that can differ between a number of catchments (Prins et al., 2004; Blanchard 2007). Fire history differs between several sites and is considered an important environmental factor in this study. Maps in combination with Google Earth were used to determine the mean river gradient over five 200m river sections where each of the sites is located; this was used to determine the longitudinal zone (King and Schael, 2001).

1.3.2.1. Eerste River system and sites

The Eerste River is a relatively small perennial river and has its source in the Dwarsberg Mountains, with a maximum altitude of 1320 m above sea level (Rebelo et al., 2006). The mountain stream zone flows into Jonkershoek Nature Reserve and in a north-westerly direction through the town of Stellenbosch, where it becomes highly disturbed by canalization and dominated by woody non-native trees. It then bends southwards towards False Bay. The vegetation in the upper reaches of the river (Jonkershoek Nature Reserve) has a near-pristine status and comprises predominantly indigenous fynbos and riparian communities (Vosse, 2007). The mountain stream longitudinal zone is evident within the Jonkershoek Nature Reserve as it flows through indigenous fynbos and Afromontane forest. The river bed is covered with gravel and boulders and with an initial steep slope from the source. Much of the catchment consists of undulating hills with fertile soils overlying the Table Mountain Group sandstones, Cape Granite, and Malmesbury Group shales. The Table Mountain Group sediments are dominant in the upper reaches of the river (Salie, 2003). The two natural sites are situated approximately 2km from one

another. Both study areas burned during March 2009. The vegetation in the vicinity of the study area is mainly Kogelberg Sandstone fynbos and Boland Granite Fynbos (Rebelo et al., 2006).
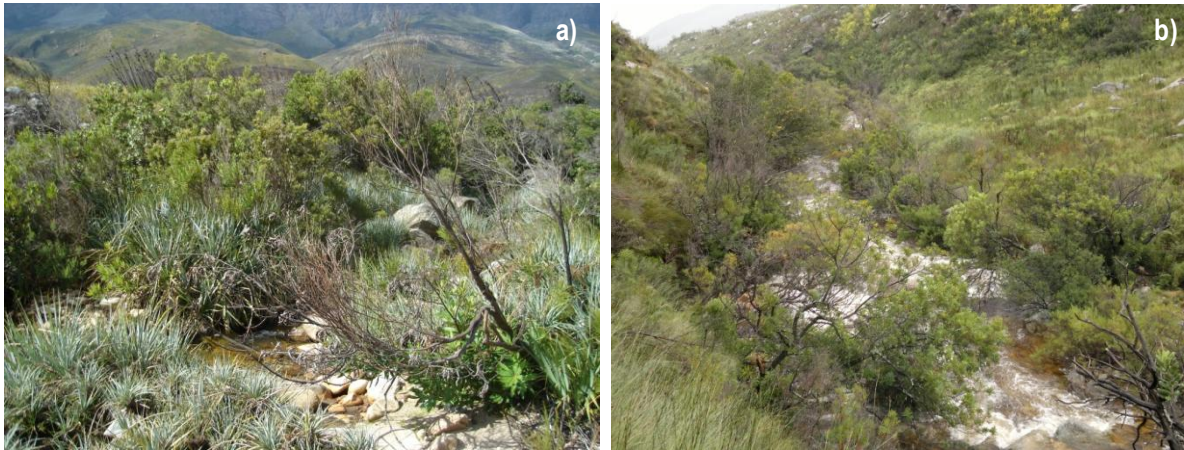
Figure 1.2. (a) Lower and (b) upper Eerste River natural sites

1.3.2.2. Dwars River system and sites

The Dwars River, a tributary to the Berg River, originates in the Dwarsberg mountains and runs past the town of Kylemore in a north-westerly direction. Much of the catchment consists of overlying Table Mountain Group Sandstones, Cape Granite, Malmesbury Group shales, with Table Mountain Sandstones more predominant in the upper reaches of the river. Soils are shallow and rocky in terrestrial areas. The vegetation is classified as a combination of Boland Granite Fynbos and Kogelberg Sandstone Fynbos (Rebelo et al., 2006). A fire swept through the valley in March 2009. The longitudinal zone in the Upper Dwars (natural; Figure 1.3a) and lower Dwars (invaded) is characterized as headwater mountain stream and mountain stream respectively. Due to the rocky nature of the riverbed and extremely shallow soils with steep valleys, wet bank plots could not be established for the Upper Dwars River site. Three kilometres downstream of the natural site, invasive alien plant infestations on the northern side of the river have been controlled by the private landowner. Plots were established on the southern side of the river (CapeNature property) and contain a mixture of both *A. mearnsii* and *A. longifolia* (Figure 1.3b).

Figure 1.3. Dwars River (a) natural and (b) invaded (mixture of *A. longifolia* and *A. mearnsii*) sites; (c) riverbank erosion at invaded site.

1.3.2.3. The Wit River system and site

The Wit River is a large tributary of the Breede River and originates in the Haweques mountain range in Bainskloof Pass. The river drains the south-western slopes of the Slanghoek Mountains and the Obiekwa Mountains (Brown et al., 2004; Reinecke et al., 2007; Vosse, 2007) with an estimated length of 11-12 km. The study site was located in the foothill sections of the river where the channel is particularly wide (5-10 m). The bedrock is deep in many places with cobble/boulder-bottomed pools which are also interspersed with longer riffle/run sections (Brown et al, 2004). The geology of the Wit River catchment consists mainly of the Peninsula formation supporting Hawequas Sandstone Fynbos vegetation type (Rebelo et al., 2006). The site is located on private land and efforts have been made by the landowner to clear areas along the river, but many strips of heavily invaded *A. mearnsii* trees are still evident. On the southern side of the river, where my site is located, both the wet and dry bank lateral zone is heavily invaded by closed-stands of *A. mearnsii* trees (Figure 1.4). Only a few scattered individuals of *A. longifolia* were evident under *A. mearnsii* canopies. The lower wet bank, however, does support Palmiet

(*Prionium serratum*) and includes *B. stellatifolium*, *M. angustifolia* and *Morella serrata* with invasion being more prominent in the dry bank zone. The riparian zone on the opposite northern side was cleared of aliens some time ago (Reinecke et al., 2007). Prior to invasion, species assemblages within these zones would have contained both characteristic riparian genera that do not have a terrestrial affinity, as well as riparian scrub species with a fynbos affiliation (Pretorius et al., 2008). Campbell (1985) described the Wit River riparian community which includes common species: *M. angustifolia*, *B. stellatifolium*, *B. neriifolia*, *Erica caffra* and *Elegia capensis*. This "Witriver" riparian community is common to the west and southern interior of the Cape Fold Belt Mountains (Blanchard, 2007).
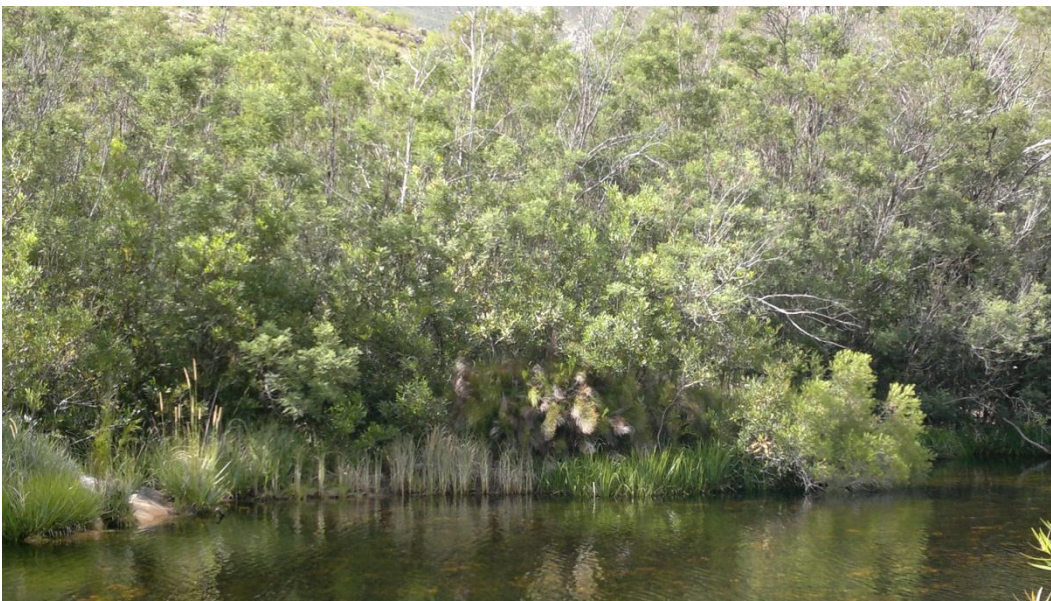
Figure 1.4. Wit River (highly invaded by *A. mearnsii*).

1.3.2.4. Sir Lowry's River system and site

The Sir Lowry's River arises near Somerset West in the Hottentots Holland mountain range and flows in a south-easterly direction towards False Bay. This particular site was the most disturbed of all the cleared sites. The site is located on the Wedderwille Estate, which is currently grazed by game under very low stocking density. Closed-stand invasion consisting of 30 year old stands that had supported mixed invasions of *A. mearnsii, A. saligna, A. longifolia* and *Pinus pinaster,* was clear felled in 2000 and 2002 and the alien debris was burnt in stacks (Reinecke et al., 2007) on higher ground away from riparian zone. The scars in the landscape are still evident, as a consequence of burned piles of slash (Figure 1.5c); an indication of extremely high temperatures during burning. Plants did not regenerate on burned patches; therefore plots were carefully selected in terrestrial upland zones so as to avoid these intensely disturbed areas. The study site

is heavily disturbed and invaded by alien grasses in both riparian and terrestrial lateral areas (Figure 1.5b). This site is currently free of infestation by alien trees, as follow-up clearance is continued on a regular basis by the landowner. The geology of the area is made up of Quanternary sediments with granite of the Stellenbosch Batholith occurring upstream. The river itself follows a faultline between shale and granite terraces. The predominant vegetation type of the area is Boland Granite fynbos (Rebelo et al., 2006). Recent flooding after the river has been cleared has scoured the river channel, causing excessive bank erosion (Figure 1.5a). Terraces in the lateral zone, which separate the wet-, dry bank and terrestrial plots, are particularly evident at this site.
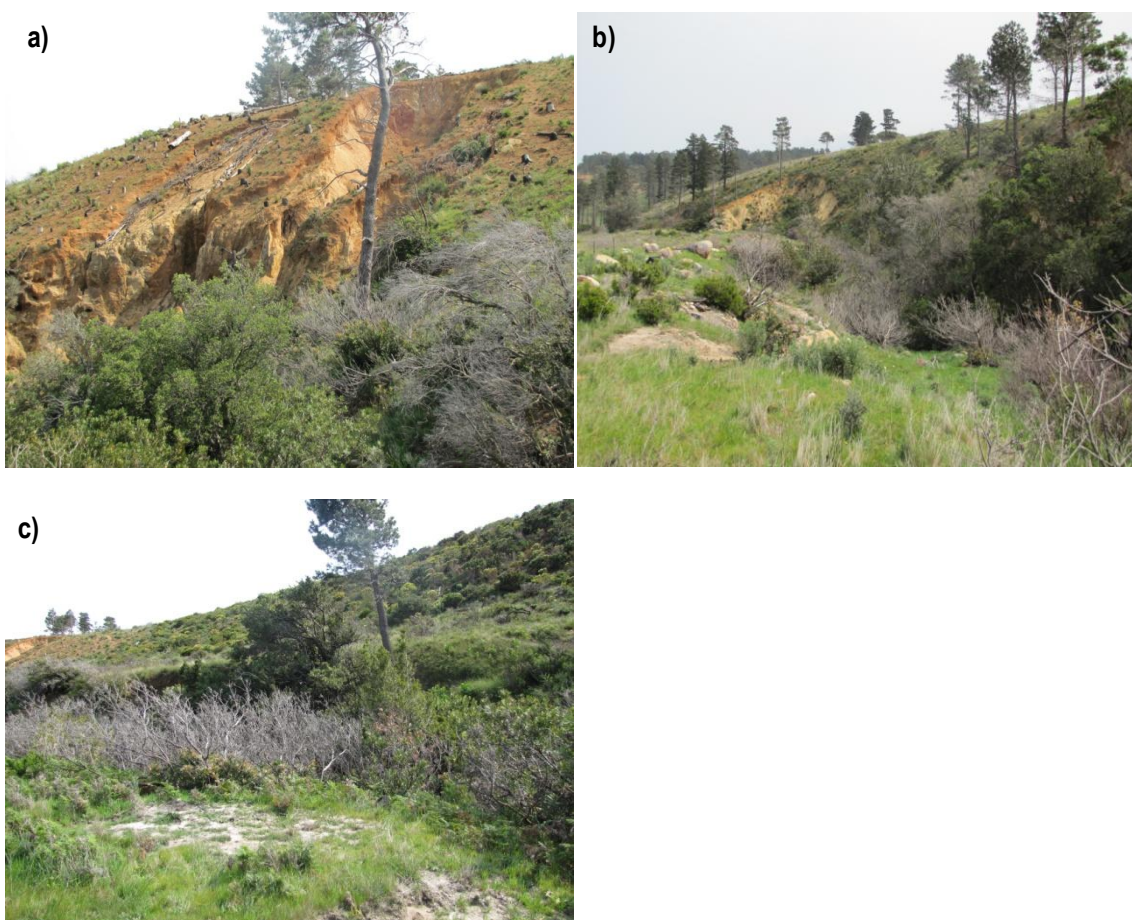
Figure 1.5. Sir Lowry's River cleared site: (a) river bank erosion; (b) riparian zones invaded by grasses and (c) scars present in terrestrial zones caused by slash that was burned in piles.

1.3.2.5. Jakkals River system and sites

The Jakkals River runs along the Houhoek Pass and eventually flows into the Bot River. The geology of the region is complex and consists of the Skurweberg, Goudini, Cederberg, and Rietvlei formations. The vegetation type is mostly Kogelberg Sandstone Fynbos (Rebelo et al.,

2006). The cleared site along the Jakkals River was first cleared in 1996 and 1997 and occurs upstream of the invaded site. Alien species comprised of several *Acacia* spp. although *A. mearnsii* was the dominant species. Alien trees were felled and burned and 2 follow-up treatments were recorded yearly after the initial clearing (Blanchard, 2007). The terrestrial plots along the mountain slope are rocky and soils are particularly very shallow. At the cleared site, a fire swept through the riparian and terrestrial zones during January 2010. Localized erosion with exposed riverbanks was noted at this site (Figure 1.6a, b). Only a few riparian shrubs (partially burned) were observed in the riparian zone with n number of emerging seedlings of *A. longifolia* and *A. meanrsii.*   Both invaded and cleared sites are characterized as mountain stream transitional zones. The invaded site further downstream is heavily invaded by mature stands of *A. mearnsii* trees (Figure 1.6c). There is evidence of tree felling by the surrounding. No sign of a recent fire was evident within the riparian or terrestrial areas.

Figure 1.6. Jakkals River cleared site with (a) exposed riverbanks and (b) localized erosion (indicated by die arrow) and emerging seedlings of *A. mearnsii* and *A. longifolia*; (b) invaded (mostly *A. mearnsii*) site.

1.3.2.6. Molenaars River system and sites

The Molenaars River originates in the Klein Drakenstein Mountains in the Du Toit's Kloof Pass and runs through Rawsonville before joining the larger Breede River. Several tributaries of the Molenaars River originate in the surrounding mountains of which only the Elands River was included as a natural site. The river is fed by streams on the southern slopes of the Witte Mountains. It also drains the northern slopes of the Du Toits Mountains, the north-eastern Klein Drakenstein Mountains, and the south-eastern Slanghoek Mountains (Brown et al., 2004). The main river channel is somewhat braided in certain areas forming islands close to either sides of the river. The geology of the upper reaches of the Molenaars River consists of Peninsula and Wellington pluton granite outcrops and recent Quaternary deposits. Further downstream the alluvial deposits make up most of the riverbanks (Rebelo et al., 2006). The major vegetation types within the catchment valley are Hawequas Sandstone Fynbos with Breede Alluvium Fynbos along the foothill sections of the river (Rebelo et al. 2006).

Figure 1.7. (a) Elands River (natural) and Molenaars River (b) invaded (mostly *Acacia mearnsii*) and (c) cleared sites.

The reference mountain stream site is located on the Elands River. The Elands originates in the Hawequas mountain range and is part of the Breede River system (Reinecke et al., 2007). It flows in a north-westerly direction where it joins the Molenaars River close to the Huguenot Tunnel. The site is characterized by steep mountain slopes and flanks of intermontane valleys. Riparian woody shrubs and trees are relatively sparse compared to the Eerste- and Dwars River natural sites. Vegetation is classified as Hawequas Sandstone Fynbos dominated by restioid, asteraceous and ericoid fynbos (Rebelo et al., 2006). Characteristic Riparian Scrub species were observed, including *B. stellatifnlium, B. neriifolia, M.angustifolia, Isolepis prolifer, P. serration* and *Todea Barbara.* Shrubs, ferns and graminoids are also common in the dry bank zone (*Elegia capensis, Blechnum capense, Pteridium aquilinum* and the restio *Askidiosperma chartaceum*). The site is characterized by a foothill-cobble bed river, with instream habitat being characterised by large cobbles and boulders. The gentle lateral slope distinguishes the wet- and dry bank lateral zones, whereas the river channel on the opposite side is more confined and characterized by steep slopes (Figure 1.7a). The geology of the area consists of acidic lithosol soils derived from Ordovician sandstones of the Table Mountain Group (Rebelo et al., 2006). The site is relatively pristine and undisturbed by human impacts, except for occasional hikers. The terrestrial section of the site burned during March 2011, but there was no evidence of recent fire before or during sampling and vegetation surveys.

The Molenaars cleared site occurs approximately two kilometres upstream from the invaded site. Previous records indicate that *A. mearnsii* was the dominant alien species targeted in the riparian areas. For the initial clearing treatment, alien trees were felled and slash was removed from the riparian zone in 2002-2003. Follow-up records reveal that other alien species were also present, namely: *A. longifolia*, *A. saligna* and *Rubus* spp. (Blanchard, 2007). Woody riparian shrub, *B. stellatifolium* and *M. angustifolia*, are prominent along the riparian corridor (Figure 1.7c). Above the wet bank, the gradient flattens and the substrate is soft sand overlaying cobbles and boulders. No fire has burned this part of the river in the last 10 years. The Lower Molenaars site was moderately to highly infested with *A. mearnsii* (Figure1.7b). The infested site was cleared during February 2011, where *A. mearnsii* were felled and some of the slash removed. The riparian zone and adjacent terrestrial fynbos burned during March 2011. But, this fire had no impact on the overall results, since all soil and vegetation surveys were completed before the site burned. The river is also braided in sections and erosion has scoured the river channel, which was particularly evident between the wet- and dry bank lateral zones. Scattered shrubs of *B. stallatifolium* and *M. angustifolia* occurred in the upper wet- and dry bank zones. Palmiet (*P. serratum*) is abundant along the active channel.

1.4.   THESIS STRUCTURE

The five chapters presented here contribute to the understanding of fynbos riparian biogeochemistry and consequent changes in structure and function induced by *Acacia* spp. invasion. Each chapter includes its own reference list. The data chapters in this thesis have been written in the form of stand-alone chapters for publication, consequently there is some repetition in the material of chapters 3, 4 and 5. Duplication, particularly regarding methods is unavoidable but kept to a minimum.

Chapter 1 – This chapter gives a general introduction to the study and provides a brief overview of the literature surrounding the research objectives. It introduces the rationale and motivation; hypotheses, aims and key research questions to meet the objectives of the study. Furthermore, a detailed overview of the study area is given, which includes the geographical location, climate, geology, experimental design used and descriptions for each river system and site(s).

Chapter 2 – This chapter presents a review of the literature on riparian structure and function and the impacts of invasive alien plant (IAPs) species, with particular focus on Mediterranean-type ecosystems of south-western Cape region and invasive *Acacia* spp., in order to assess the possible impacts of riparian woody IAPs on ecosystem structure and function.

Chapter 3 – This chapter investigates soil physical and chemical properties in natural, invaded and cleared (i.e. post alien plant control) riparian ecotones and associated non-riparian uplands in addition to the cover of plant functional types and other ecosystem attributes. Interrelationships between soil properties are also addressed. The first 4 of the 6 key questions (listed in 1.2.2.3) are addressed in this chapter.

Chapter 4 – Nitrogen cycling rates and P availability (using acid phosphtase as indicator) in fynbos riparian ecotones and associated upland terrestrial fynbos of the south-western Cape are investigated in this chapter. The possible impacts of invasion and clearing by N_2-fixing *Acacia* spp. on soil biogeochemical (N and P) processes are also evaluated. Furthermore, the relationship between phosphatase activities, potential N mineralization rates and selected soil physical and chemical properties are assessed. The last 2 of the 6 key questions (listed in 1.2.2.3), are addressed in this chapter.

Chapter 5 – This concluding chapter summarizes major findings in the entire thesis and reflects on the general problems posed by *Acacia* spp. (specifically *A. mearnsii*) in South African fynbos riparian ecotones. The contribution of this study towards restoration and research in fynbos

riparian ecosystems is also discussed. Here strategies are recommended for management and control of these particular species (practical restoration strategies to be used by land-owners and managers as part of future alien-clearing operations). Furthermore, results from this study revealed gaps in knowledge and provides recommendations for future research needs to address these gaps that may add to our understanding of fynbos riparian function.

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CHAPTER 2

LITERATURE REVIEW:

Riparian Structure and Function and the Impacts of Woody Invasive Alien Plants

2.1. SUMMARY

Riparian ecotones form the interface between aquatic and terrestrial ecosystems. Not only do they have intrinsic conservation value, but intact riparian vegetation communities are important ecological systems for maintaining ecosystem integrity. Geomorphological processes, aquatic biota, and riparian vegetation are intimately linked in the river system and are fundamental in determining nutrient stocks available for river functioning. Owing to geomorphic, hydrologic, and human-induced events, the linkage between the river and its valley is subject to frequent change. One of the main threats to functioning of riparian zones is the invasion of woody alien invasive plant species (IAPs). IAPs out-compete indigenous plants and disrupt ecosystem functioning by altering the fire regime, water quality, soil communities, patterns of sedimentation and erosion, river geomorphology, water availability and nutrient cycling. Acacias are amongst the most prolific, successful and severe plant invaders globally. This chapter presents a review of the literature on riparian structure and function and the impacts of IAPs, with particular focus on Mediterranean-type ecosystems of south-western Cape region and invasive *Acacia* spp., in order to assess the possible biophysical impacts of riparian woody IAPs on ecosystem structure and function. While the impacts of nitrogen (N_2)-fixing IAPs on ecosystem structure and function have been investigated throughout the world. Nevertheless, the implications for invasive N_2-fixing Australian *Acacia* spp. (and clearing thereof) on fynbos riparian ecosystem function have received less attention, especially possible alterations to soil biogeochemical properties.

2.2. RIPARIAN ECOSYSTEMS

2.2.1. Defining riparian ecosystems

Some differences exist in the precise definitions of the boundary of the riparian zone, as the limits vary depending on the nature of the study (Tickner et al., 2001; Blanchard, 2007). Riparian ecotones are three-dimensional transition zones that comprise the interface between aquatic and terrestrial ecosystems (Gregory et al., 1991; Naiman and Décamps, 1997). Within the south-

western Cape, river corridors are relatively linear, narrow features of the landscape, except in broad floodplains (Holmes et al., 2005). Habitats along rivers support vegetation that is distinctive, both structurally and functionally, from adjacent terrestrial and aquatic vegetation (Naiman and Décamps, 1997). Patterns in vegetation distribution beside river floodplains have been shown to be very patchy with regards to the diverse nature of sedimentary processes (van Coller et al., 2000). Riparian ecotones are affected by strong moisture and disturbance gradients and complex interactions among fluvial processes, light, temperature, geomorphology, soil composition, nutrients, and fire, which influence the structure, function and dynamics of riparian zones, including its various cycles (Naiman and Décamps, 1997; van Coller et al., 2000; Naiman et al., 2005; Reinecke et al., 2007; Richardson et al., 2007; Blanchard, 2007). Even though riparian zones occupy only a small area in relation to the greater catchment, their influence on the surrounding landscape is greater than expected (Gregory et al., 1991), because of their intricate linkages between terrestrial and aquatic ecosystems and their central location within watersheds (Pinay et al., 1993).

Microbial composition and plant and animal diversity associated with riparian zones are often enhanced in riparian ecosystems due to their natural disturbance regimes, higher resource availability and intrinsic heterogeneity (Gregory et al., 1991; Décamps et al., 2004; Petit and Naiman, 2007). However, not all riparian systems have higher species richness than associated uplands, with regard to either vegetation or other taxa (Stromberg, 2007). Owing to geomorphic, hydrologic, and human-induced events, the linkage between the river and its valley is subject to frequent change (Naiman and Décamps, 1997). The resilience and stability of the internal structure of a river corridor plays a fundamental role in controlling those changes (Tabacchi et al., 1998). Riparian ecotones are often the first indicator of environmental change (natural or anthropogenic), because they as sensitive to disturbances (Naiman and Décamps, 1997; Tickner et al., 2001). Accordingly, these critical transitions zones have become the focus of much effort concerning restoration, monitoring, and conservation in support of ecosystem services (Bardgett et al., 2001).

2.2.2. Riparian function and ecosystem service provision

Floodplain, riparian, and instream zones are important ecological components of river ecosystems, because of the ecosystem services and ecological functions they provide, including the provision of food, flood control, recreation, stream bank stabilization, and their intrinsic conservation value (Naiman and Décamps, 1997; Bardgett et al., 2001; Corbacho et al., 2003; Richardson et al., 2007; Reinecke et al., 2007). Their vegetation and inherent heterogeneity and

associated surface roughness therein fulfil important geomorphological, ecological and social roles, many of which have been well documented (Strayer et al., 2003; Bardgett et al., 2001; Blanchard, 2007; Richardson et al., 2007; Sieben and Reinecke, 2008). Their ecological nature and functioning are influenced by river size and their position in the catchment's drainage network (Naiman and Décamps, 1997). Not only do riparian zones provide a corridor for the movement of biota, but they are also a habitat for biodiversity (Naiman and Décamps, 1997; Corbacho et al., 2003; Esler et al., 2008). Riparian soils and their associated unique or diverse biota, including invertebrates, soil microbes and soil fungi, are also central to the role of riparian ecotones in regulating material flows (such as water, propagules, nutrients, organic matter, detritus and sediments) between terrestrial and aquatic ecosystems. Plant cover also influences the efficiency of riparian zones in filtering nutrients and pesticides and thus play a fundamental role in maintaining the biotic integrity of streams and rivers (i.e. water quality) (Gregory et al., 1991; Bardgett et al., 2001; Ewel et al., 2001; Corbacho et al., 2003; Strayer et al., 2003; Petit and Naiman, 2007). Furthermore, they stabilize river banks and regulate light inputs, thereby moderating river temperature via evapotranspiration and shading (Gregory et al., 1991; Hood and Naiman, 2000; Reinecke et al., 2007).

2.2.3. Soil biogeochemistry

The flow of materials and energy through the biotic and abiotic environment provides a framework for understanding the functioning of physical and biological processes (Chapin et al., 2002). Hydrological and geomorphological processes in riparian ecotones are primary ecosystem drivers (Tabacchi et al., 1998) and are one of the most essential agents shaping the landscape (Pinay et al., 1992). Temporal and spatial variation in the deposition and erosion of materials creates complex patterns of soil development, and consequently large variations in soil properties (Gregory et al., 1991; Chapin et al., 2002). Riparian soils are therefore characterized by high heterogeneity of process rates and structure (Tabacchi et al., 2000; Hefferman and Sponseller, 2004). Geomorphological processes, aquatic biota, and riparian vegetation are intimately linked in the river system and are fundamental in determining the stocks of nitrogen (N), carbon (C) and phosphorus (P) available for river functioning (Pinay et al., 1992). Soil physical and chemical properties and resource availability are major factors affecting ecosystem nutrient cycling and the structure of plant communities (Gregory et al., 1991; Chapin et al., 2002; Ratnam et al., 2008). The exchange of dissolved and particulate organic- and inorganic nutrients, sediments, and contaminants between habitats, creates a distinctive context for mineral organic matter (OM) interactions (Bechtold and Naiman, 2006). Riparian ecotones are known to be enriched with nutrients compared to adjacent terrestrial ecosystems, since dissolved and particulate organic and inorganic nutrients in sediments are transported and deposited from aquatic, terrestrial,

biotic, and atmospheric sources (Pinay et al., 1993; Naiman and Décamps, 1997; Jacobs et al., 2007).

Most of the N and P necessary for plant growth in natural ecosystems are supplied by the decomposition of soil OM and plant litter (Chapin et al., 2002). N and P in the soil can move from upland to riparian environments as dissolved or particulate forms in surface water flow or as dissolved forms in subsurface flow (Jacobs et al., 2007). Soil humus and OM provide active cation exchange sites that retain several important cations, such as ammonium (NH_4^+), potassium (K^+), calcium (Ca^{2+}), and magnesium (Mg^{2+}), therefore playing a significant role in regulating pH regimes in soils (DeBano, 1990). Soil biogeochemical processes, such as nutrient cycling and decomposition, transfer materials and energy to and from the soil and consequently, important in regulating the movement of nutrients. Nutrient cycling processes is strongly affected by the physical nature of soils, especially soil texture and pH, which in turn is largely dependent on parent material and soil formation (Anderson and Ingram, 1993; Tabatabai, 1994; Chapin et al., 2002; Hefferman and Sponseller, 2004; Bardgett, 2005). Soil-borne micro-, meso and macrofauna play a key role in hydrology and biogeochemical cycling of nutrients (Anderson and Ingram, 1993; Tabatabai, 1994; Bardgett, 2005; Cilliers et al., 2005; Naiman et al., 2005; Jovanovic et al., 2009), in addition to plant roots (Tabatabai, 1994), making nutrients available to higher plants (Cilliers et al., 2005). Materials in the soil are transformed through interactions of biological, physical, and chemical processes (Chapin et al., 2002). The release of organically bound nutrients into plant available, inorganic forms is termed mineralization, and is fundamental to the productivity of ecosystems (Anderson and Ingram, 1993; Šarapatka, 2003).

Plant species composition can affect the physical and chemical properties of soil, rates of litterfall, and net primary productivity and plant growth rates (Ehrenfeld, 2003). Root turnover and root exudates are essential sources of C for soil micro-organisms (Knops et al., 2002). Plant litter is the most important substrate for element recycling and stimulates many biogeochemical processes (Eviner and Chapin, 2003). OM is the primary reservoir for a number of nutrients and, hence, is the source for virtually all available N, and the majority of the available P and sulfur (DeBano, 1990). N and P occur in a variety of chemical forms, depending on the reduction-oxidation potential, which are transformed as cycling reactions proceed (Naiman et al., 2005). In terrestrial systems, N is regarded to be the key limiting element but production can also be influenced by limitation of P (Bengtsson et al., 2010), especially in geologically older areas (Hartshorn et al., 2009; Bengtsson et al., 2010; Vitousek et al., 2010) where P is derived primarily from rock weathering (Vitousek et al., 2010), such as South Africa (Bengtsson et al., 2010). N on

the other hand is rapidly accumulated from the atmosphere via biological N fixation, or more slowly via atmospheric deposition (Vitousek et al., 2010).

2.2.3.1. Nitrogen

The N balance is very complex (Jovanovic et al., 2009) and there are several biological, physical and chemical factors that control N transport and transformation in river catchments, including the rate of *in- situ* decomposition, the state of ecosystem maturation (e.g. time since fire), moisture availability, soil physical and chemical characteristics, and the activity of micro-organisms and their relative demands for N and C (Cirmo and McDonnell, 1997; Chapin et al., 2002; Bengtsson et al., 2003; Bechtold and Naiman, 2006). Physical properties include soil moisture, aeration, texture, structure and temperature, whereas chemical properties are related to soil nutrient characteristics and pH (Chapin et al., 2002; Bardgett, 2005). Nitrogen is available to plants primarily in the form of ammonium (NH_4^+) and nitrates (NO_3^-) (Naiman et al., 2005) through the conversion of organic N by microbially mediated processes occurring above and/or in the soil (Anderson and Ingram, 1993; Chapin et al., 2002; Jovanovic et al., 2008). Available N in soils can originate from many sources such as wet and dry deposition, N mineralization of OM, microbial fixation of atmospheric N_2, lightning, and N fertilizers (Jovanovic et al., 2008).

C and N are bonded together in soil OM, thus N mineralization is coupled to soil respiration activities in the soil (Orlander and Vitousek, 2000). Given the close relationship between N and C, C/N ratios play an essential role in controlling the rate of OM decomposition, thereby regulating the rate at which nutrients, including N, are released and cycled (DeBano, 1990). The quality and quantity of organic material supplied by plants can regulate net N mineralization rates (Knops et al., 2002). Accordingly, soil C/N ratios may be an important controlling factor on whether immobilization or mineralization occurs (Hart et al., 1994). Net rates of N mineralization in the absence of plant assimilation, leaching, NO_3^- reduction and denitrification, is determined from the change in soil inorganic N pool size over time (Hart et al., 1994). N mineralization and microbial immobilization happen simultaneously in the soil (Bardgett, 2005). When net mineralization occurs then microbes are strongly limited by N, consequently, more dissolved organic N is used to meet their C requirements, secreting NH_4^+ as a waste product during respiration (Chapin et al., 2002; Naiman et al., 2005). Riparian ecosystems immobilise N through several processes, mostly by vegetation and microbial uptake of nutrients from river and/or groundwater, trapping sediment and OM (Adair et al., 2004), and via the process of denitrification (Naiman and Décamps, 1997).

N-cycling rates in soils are highly variable in space and time (Chapin et al., 2002; Naiman et al., 2005) and understanding the factors that control the rates of internal N-cycling processes is essential because of the effects that these processes have on ecosystem structure and function (Hart et al., 1994). The effectiveness of internal biogeochemical cycling through soil-plant pathways are influenced by environmental variability. Soils associated with fine textures are inclined be to be less affected by pulsed C and N mineralization that accompanies frequent drying and wetting (Fierer and Schimel, 2002; Austin et al., 2004). Wet and dry cycles may be important in increasing enzyme activities and stimulating denitrification in wet cycles and increasing nitrification in dry cycles (Gutknecht et al., 2006). Many biogeochemical characteristics of riparian zones require that soils be anaerobic or of low oxidation/reduction potential at least part of the year (Naiman et al., 2005). Whereas nitrification requires aerobic conditions, ammonification can occur in both anaerobic and anoxic conditions (Chapin et al., 2002; Bardgett, 2005; Naiman et al., 2005). Changes to fluctuating water levels in riparian soil do not only change oxic and anoxic phases by direct influence on N-cycling, but also indirectly by affecting soil structure and texture through sediment deposition (Pinay et al., 2002). Although riparian ecosystems are less limited by water than the surrounding uplands, N dynamics may ultimately or occasionally be limited by the availability of water, resulting in altered patterns of N-cycling (Adair et al., 2004).

2.2.3.2. Phosphorus

Phosphorus is a critical plant macronutrient (Hartshorn et al., 2009) and its availability is controlled by both biological and soil geochemical reactions (Zou et al., 1995; Šarapatka, 2003; Hartshorn et al., 2009). P is highly immobile and forms strong absorptive reactions with iron, aluminum, manganese, calcium and clay minerals, restricting its uptake by plants (Chapin et al., 2002; Šarapatka, 2003; Naiman et al., 2005; Hartshorn et al., 2009; Vitousek et al., 2010). The adsorption and precipitation of P, which is pH dependent, could compete with organisms for available P in the short-term (Vitousek et al., 2010). Given that P availability for uptake by plants is sensitive to soil pH (Pinay et al., 1992); riparian zones can be either sinks or sources for P (Pinay et al., 1992; Naiman and Décamps, 1997). Incoming particulate P can easily be trapped by physical processes in the riparian zone, acting as a sink; however, riparian ecotones may also augment surface water by releasing P in available forms. Considerable quantities of P may first accumulate in riparian sediments before being transported into aquatic ecosystems in a different form, which are processed during their transport by shallow groundwater flow (Naiman and Décamps, 1997; Tabacchi et al., 2000).

As a biological process, the mineralization and immobilization of organic P is strongly influenced by variations in soil forming factors that determine the physical and chemical nature of soils

(Tabatabai, 1994; Šarapatka, 2003), such as OM (Amador et al., 1999), soil texture (Tabatabai, 1994; Šarapatka, 2003); inorganic phosphorus content (Šarapatka, 2003), soil moisture, edaphic and hydrogeomorphic templates (Cirmo and McDonald, 1997). Dust may also be an important external source of P (Hartshorn et al., 2009). Microbial biomass is an essential reservoir for potentially available P, since it accounts for 20-30% of organic P in soils (Chapin et al., 2002). Hence, organic P is often the dominant form of P the in topsoil (Šarapatka, 2003) and is available to plants in the form of orthophosphates (PO_4^{3-}), which is the only inorganic form where P occurs (Naiman et al., 2005). Rather than being absorbed from the soil solution, P uptake and its availability to vegetation seem to be greatly dependent on the interrelationship between OM and mycorrhizae (DeBano, 1990). P can also be accessed by organisms through the production of charged organic compounds that can free available P from binding sites in the soil (Eviner and Chapin, 2003). Orthophosphate can be removed from soil solution via plant uptake, inorganic fixation, and microbial immobilization (Zou et al., 1995).

The internal cycling of P in ecosystems, as with N, requires the separation of bonds in organic compounds in a form that is water soluble for absorption by both plants and microbes (Chapin et al., 2002). Several enzymes are involved in the decomposition of organic P compounds (Tabatabai, 1994; Šarapatka, 2003). Those that hydrolyse P esters of organic P compounds, thereby releasing phosphates, are called phosphatases (Orlander and Vitousek, 2000; Šarapatka, 2003). Phosphatases are produced by plants, bacteria, and fungi, in forms that can be excreted, or used internally (Orlander and Vitousek, 2000). Low concentrations of P in soils causes microbes and plants to invest N in enzymes to obtain P (Chapin et al., 2002). However, although microbial diversity can enhance decomposition and nutrient cycling, vegetation composition usually has a larger effect on these processes by controlling the substrates available for microbial utilization (Eviner and Chapin, 2003; DeCant, 2008). Nutrient supply, such as N, could not only affect the enzymes mineralizing that particular nutrient, but also those enzymes mineralizing other nutrients, such as phosphatases (Orlander and Vitousek, 2000). Acid phosphatase enzymes are the predominant group of enzymes engaged in P mineralization in acidic soils. Since enzymes serve a number of essential functions in soils and since soil phosphatase activity is ubiquitous in soil, it may serve as an indicator of soil changes in riparian ecosystems (Amador et al., 1999; Dick et al., 2000). Because of the importance of these enzymes in soil organic P mineralization (Tabatabai, 1994; Šarapatka, 2003) and plant nutrition, considerable literature has accumulated on phosphomonoesterases, especially acid phosphatase (Tabatabai, 1994).

2.3.   FYNBOS RIPARIAN ECOTONES

2.3.1. Description

Riparian ecotones often exhibit sharp environmental gradients and ecological succession of communities (Corbacho et al., 2003; Sieben, 2003), which results in a mosaic of environmental patches (Naiman and Décamps, 1997) and a considerable variation in both species richness and composition (Corbacho et al., 2003). The spatial extent of the riparian zone may be difficult to delineate precisely because heterogeneity is expressed in an array of successional patterns and life-history strategies, while functional attributes depend on community composition and the environmental setting (Naiman and Décamps, 1997). Similarly, riparian zones in the Western Cape are not easily delineated, because the valley floors within constrained reaches of the rivers are narrow and include few geomorphic surfaces within the valley floor. Geomorphology and vegetation may be largely considered as the main indicators of riparian habitats. In a mountain stream, the lateral extent of vegetation is more compressed than in the lower reaches (Sieben, 2003; Blanchard, 2007). Within South African fynbos rivers, major components of a riparian zone can be defined on a lateral (distance from the river's edge) and longitudinal scale, such as mountain stream, foothill, transitional and lowland zones (Davies and Day, 1998; Boucher, 2002). Mountain stream zones occur where erosion exceeds sediment accumulation; foothill zones where erosion and accumulation are more or less in balance; and lowland river zones, where accumulation exceeds erosion (Davies and Day, 1998). Identifying gradients in riparian landscapes are vital, since they denote alterations in several important environmental variables including water availability, flooding, geology, substrata, morphology, nutrients and soil composition (van Coller et al., 2000).

Riparian vegetation in the fynbos biome is normally distinctive from the surrounding fynbos vegetation in terms of species and growth from composition, even though it occurs under similar macroclimatic conditions (Prins et al., 2004; Reinecke et al., 2007). Within the Western Cape, riparian vegetation is subject to very complex environmental patterns resulting from a plethora of historical-biogeographical and ecological gradients (Sieben et al., 2009). Fynbos riparian ecotones form narrow and linear features where the development of floodplain is restricted in the landscape (Holmes et al., 2005). Woody plants comprise about one-third of the riparian flora of which 66% are geographically widespread in the Western Cape (Galatowitsch and Richardson, 2005). The scrub vegetation of riparian sites is described as 'Closed-scrub Fynbos' (Campbell, 1985) where the overstorey consists of common species of tall shrubs such as *Brachylaena neriifolia*, *Metrosideros angustifolia* and *Brabejum stellatifolium* (Rebelo et al., 2006; Sieben and Reinecke, 2008) and the understorey comprises of graminoids and forbs with constant

recruitment of woody and perennials species within the sub-canopy (Reinecke et al., 2008). However, this is not the only type of vegetation found in fynbos riparian areas, as riparian vegetation types can range from forest to tall herbland (Rebelo et al., 2006). Afromontane forests may develop in areas of steep topography that receive protection from fires (Prins et al., 2004). Cowling and Holmes (1992) described riparian vegetation as similar to thicket and forest, with a reasonably high cover of broadleaved, non-proteoid mesophyllous woody plant species, but different in that they are characterized by a high cover of Restionaceae and the occurrence of Ericaceae. Herbaceous and low-shrub growth forms dominate the seed bank in both the Western and Eastern Cape, with families such as Poaceae, Cyperaceae and Asteraceae most prominent (Vosse et al., 2008). Riparian species from the families Cyperaceae and Poaceae are prominent in wet bank zones, whereas dry bank zones have a higher diversity and richness which comprise of both wetland-adapted and terrestrial fynbos species (Holmes et al., 2008). The narrow, slightly sloping alluvial flats support a complex of reed beds dominated by tall palmiet (*Prionium serratum*), restios (*Calopsis, Cannomois, Elegia, Ischyrolepis* and *Rhodocoma*), and low shrubs with moisture loving species of *Berzelia*, *Cliffortia*, *Helichrysum* and others (Rebelo et al., 2006). Legumes form only a small component of the native plant cover and do not persist during post-fire succession in fynbos communities (Cocks and Stock, 2001; Power et al., 2010).

2.3.2. Biotic and abiotic factors as drivers in fynbos riparian ecosystems

The geology of the fynbos biome, leads to highly constrained reaches in headwater streams (Reinecke et al., 2007). Rivers in the Western Cape have a large turnover of species among different catchments and therefore catchments have distinctive "catchment signatures" (King and Schael, 2001; Reinecke et al., 2007). A possible explanation is the amount and seasonality of precipitation, which can change sharply across a single mountain range (Cowling and Holmes, 1992; Sieben et al., 2009). Furthermore, vulnerability to fires, site moisture levels and soil type (e.g. soil texture, rockiness, pH, and levels of moisture) are also major abiotic determinants in shaping riparian community structure in the Western Cape, by promoting the establishment of particular growth forms with different resistance to flammability and fire (Brown et al., 2004; Reinecke et al., 2008). The composition of woody species along Fynbos Rivers is likely to regulate ecosystem function by affecting nutrient cycling, various microclimatic conditions, substrate anchoring and establishment of other riparian species (Galatowitch and Richardson, 2005). Over the whole course of a river, riparian vegetation is influenced by seasonal flooding regimes (Sieben, 2003). Hydrological connectivity is critical in maintaining several biogeochemical processes such as N, P, and C release into rivers (Austin et al., 2004). Plant species traits are imperative in determining their distribution along the riparian lateral zone, since species closer to the river channel are capable of surviving the physical stress of regular flooding,

while those at higher elevations further away from the channel tend to be intolerant of disturbances caused by flooding, but necessitate access to the water table (Holmes et al., 2005). Many fynbos riparian plants are adapted to floods and are able to resprout after branch breakage and uprooting of trees (Richardson et al., 2007). After a flood, mountain streams have the capacity to return to base levels more rapidly than lowland rivers so that flooded periods are less influential on plant communities of rivers in the upper reaches (Sieben et al., 2009). In low nutrient ecosystems such as fynbos, the riparian zone plays a critical role in augmenting nutrients for biota in streams and, ultimately, estuaries (King et al., 1987).

Fire is an important natural type of disturbance in various terrestrial landscapes and other ecosystems, especially in Mediterranean-type ecosystems where it plays a central role in plant evolution and community dynamics. It influences the heterogeneity and diversity of ecosystems by altering soil chemical, physical, biological and biochemical properties. These changes, to some extent, will depend on soil type and moisture, climate conditions, plant biomass and on the basis of disturbance regimes of specific frequency, severity and timing of occurrence (Gillon and Rapp., 1989; Hernandez, 1997; Brooks et al., 2004; Bêche et al., 2005; Pettit and Naiman, 2007; Pauchard et al., 2008). Fire is an important process in fynbos, which is both fire-adapted and fire-dependent (Deacon et al., 1992; van Wilgen et al., 1985; van Wilgen, 2009). The natural process is that fynbos burns, usually with frequencies between 12-15 years, in the late summer season. However, human interference can also change the frequency and timing of fires, with potential detrimental consequences for conservation (van Wilgen, 2009). In fynbos, fire and fire temperature influence the nutritional status of soils by indirectly effecting soil N (organic mineralization and volatilization of slowly decomposing litter), soil microbial population, additions of cations and P in ash, and altering other physical and chemical properties of the soil (Stock and Lewis, 1986; Cocks and Stock, 2001; Cilliers et al., 2005).

Fire is often assumed to be an insignificant driver of riparian ecology, however, in Mediterranean and semi-arid environments, fire is considered to be the chief perturbation and a major driver of riparian structure (Gasith and Resh, 1999; Pettit and Naiman, 2007). Mediterranean-type riparian vegetation should be more adapted to fire and show greater rapid recovery after fire than riparian communities along temperate rivers (Gasith and Resh, 1999). However, fynbos riparian ecosystems burn less frequently (<50 year return interval) with lower intensity burns than surrounding terrestrial fynbos ecosystems , as most riparian communities are sheltered from fire by topography (Galatowitch and Richardson, 2005). Different leaf chemistry, higher leaf and soil moisture content, and the structural attributes of riparian communities, such as canopy architecture of dominant tree species associated, makes them less flammable (van Wilgen et al.,

1990; Galatowitch and Richardson, 2005; Holmes et al., 2005). Nevertheless, fire can spread from neighboring environments into riparian areas under very dry conditions, especially in areas with more open canopies and a dense understory (Manders, 1990). Riparian vegetation regenerates after fire by either sprouting, or from canopy/soil-stored seed banks (Galatowitsch and Richardson, 2005). Since nutrients are important in shaping vegetation structure and function in Mediterranean ecosystems (Cowling et al., 1996), understanding changes in nutrient dynamics after fire in fynbos riparian ecosystems is essential to successful management of these ecosystems.

Nutrients stored in living vegetation are released once OM decomposes (Tabacchi et al., 2000). Several studies have found soil processes such as N mineralization, denitrification and soil respiration to be elevated in riparian ecotones compared to upland areas, providing important pathways whereby nutrients are immobilized, thus preventing deterioration of water quality (Mainstone and Parr, 2002; Naiman et al., 2005; Jacobs et al., 2007). Decomposition and mineralization rates in the natural vegetation of the fynbos are a slow process due to high level of lignins and soluble phenolic compounds and low levels of tissue N (Stock et al., 1995; Yelenik et al., 2004). Fynbos in the Cape Floristic Region (CFR) has some of the most nutrient-limited soils of all its Mediterranean counterparts (Musil and Midgley, 1990; Cowling et al., 1996). Soil characteristics within these ecosystems, particularly N and P, are essential in determining community structure, species presence or absence (Stock and Lewis, 1986; Yelenik et al., 2004) and function (Stock and Lewis, 1986). Therefore, given that nutrients play such a significant ecological role, one would anticipate spatial variation in their availability to be a key factor in determining community composition and species distribution in nutrient-poor habitats (Richards et al., 1997). It remains uncertain whether fynbos riparian soils are enriched in nutrients relative to terrestrial areas, which is recognized to have low nutrient concentrations, such as N, C, and P (Cowling et al., 1996).

2.4. PLANT INVASION

2.4.1. Defining invasive alien plants (IAPs)

Degradation of ecosystems is one of the most important and pervasive environmental challenges globally (Gaertner et al., 2011). Human activities are changing ecosystem functioning and biodiversity at a global scale. A fundamental driver of these changes is invasion by alien plant and animal species, several of which are able to effectively reach high abundance to affect biodiversity (Vilà et al., 2011). In recent decades, problems linked with biological invasions have rapidly increased globally (van Wilgen et al., 2011). Richardson et al. (2000) have reviewed the

issues surrounding terminology in plant invasive ecology and the importance of defining the terms 'alien or introduced plants', 'naturalized plants' and 'invasive plants'. Whereas 'alien plants' are plants whose presence in a given area is due to transport by humans, intentionally or accidentally, at a location outside their biogeographical region, 'naturalized plants' are 'alien plants' that have overcome abiotic (geographic, environmental and dispersal) and biotic (reproduction) barriers and reproduce persistently to maintain populations without direct human interference. Invasive plants are 'naturalised plants' which invade and ultimately transform ecosystems by producing reproductive offspring in areas distant from parent plants, often in exceedingly large numbers, consequently becoming more abundant and/or widely distributed (Richardson et al., 2000; Tickner et al., 2001; Heger and Trepl, 2003).

IAPs are frequently ''passengers'' of other environmental change, such as modified disturbance regimes (Gaertner et al., 2011). The most damaging invaders are species that are able to transform ecosystems at the trophic and ecological levels, such as alterations in the physical structure of ecosystems or changes in nutrient dynamics (Richardson et al., 2000; Blanchard, 2007; Le Maitre et al., 2011). These species are termed "transformer" species (Richardson et al., 2000). No species can maximize reproduction, growth, and competitive ability across all environments (Funk and Vitousek, 2007), therefore the success of invasive species is dependent on the environmental conditions and community structure of the habitat which they invade (Tickner et al., 2001; Funk and Vitousek, 2007). Non-indigenous woody plant species, introduced by humans, have become invasive and have spread into native ecosystems and agricultural areas (Jayiya et al., 2004).

2.4.2. Factors promoting invasion in riparian ecosystems

Human activities have long been associated with riparian zones and have several negative impacts related to land use management, resulting in degradation (both direct and indirect) of their ecological integrity (Holmes et al., 2005; Blanchard, 2007). Even tough riparian ecotones are naturally affected by disturbances (Esler et al., 2008), they are sensitive to environmental changes and especially prone to alien plant invasion, both woody and herbaceous (Hood and Naiman, 2000; Tickner et al., 2001; Décamps et al., 2004; Blanchard, 2007). The same factors that support high biological diversity in these systems are therefore also considered to increase their susceptibility to invasion (Hood and Naiman, 2000; Naiman et al., 2005). Degradation and both natural and human-induced disturbances (e.g. floods), in addition to their dynamic nutrient patterns and close proximity to water, have been found to promote invasion by IAPs in riparian habitats, as disturbances trigger the dispersal and proliferation of alien plant species (Rowntree,

1991; Richardson et al., 1997; Galatowitch and Richardson, 2005; Holmes et al., 2005; Naiman et al., 2005; Blanchard, 2007; Richardson et al., 2007; Pretorius et al., 2008). Fluvial processes (erosion and deposition of sediment) are also instrumental in providing new habitats for the establishment of exotic species (Tickner et al., 2001). Many fynbos riparian invasions came about through the introduction of invading species into upper catchments (Le Maitre et al., 2000). These species have subsequently spread rapidly downstream as habitat disturbances by periodic flooding have been found to promote invasion by exotic plant species (Le Maitre et al., 2000; Pretorius et al., 2008). Along riparian corridors and within specific sites, effective dispersal of propagules makes the most diverse and richest communities the most liable to invasion, due to their considerable environmental heterogeneity (Levine, 2000; Esler et al., 2008). It is therefore not surprising that riparian habitats are regarded worldwide as amongst the most degraded ecosystems (Esler et al., 2008).

The ability of IAPs to establish and successfully invade and proliferate in a native environment, is their ability to acquire and compete with native species for limiting resources (e.g. light and nutrients) for growth and survival (Funk and Virousek, 2007; Werner et al., 2010; Morris et al., 2011). Studies have suggested that invasion by exotic plants create conditions that promote its own growth and it also seems likely that exotic plants enhance their invasiveness by creating positive feedback loops (Erhenfeld, 2003). Nutrient-poor fynbos ecosystems are highly susceptible to soil nutrient enrichment from biological fixation of N by leguminous species. According to Dassonville et al. (2008), large positive impacts of invasion are particularly found in areas with lower pools of topsoil nutrients. Many studies have shown that high resource environments often experience greater invasion than resource-poor habitats; however, invasive species may succeed in nutrient-poor ecosystems due to mechanisms that actively use resource conservation traits, such as high resource-use efficiency (Funk and Vitousek, 2007). However, the mechanisms that direct the successful invasion of resource demanding plant species are still poorly known (Funk and Vitousek, 2007; Werner et al., 2010). Even though there are increasing numbers of studies on the impacts of AIPs, we still require a broader quantitative synthesis on how impacts differ depending on the characteristics of receiver ecosystems and of the invader species themselves (Levine et al., 2003; Vilà et al., 2011).

2.4.3. Woody invasive plants in the Fynbos Biome

Riparian zones are amongst the most densely invaded features in South African landscapes (Dye and Jarmain, 2004; Richardson and van Wilgen, 2004; Pretorius et al., 2008). Poor management and the ability of some of these species to spread rapidly, has lead to commercial forestry

species (*A. mearnsii*, *A. longifolia* and *P. pinaster*) being among the main invaders (Blanchard, 2007). Fynbos Riparian vegetation in the south-western Cape is mainly impacted by Australian *Acacia* spp. (e.g. *Acacia mearnsii*, *A. longifolia, and A. saligna*), *Eucalyptus* spp. (e.g. *E. camuldulensis*) and *Sesbania punicea* (Sieben, 2003; Richardsonn and van Wilgen, 2004). Several Australian Acacias are widespread along Western Cape rivers and form dense impenetrable stands which dominate the canopy and exclude indigenous vegetation (van Wilgen et al., 1985; Boucher, 2002; Holmes et al., 2005; Blanchard and Holmes, 2008). Alien trees invade both the wet and dry bank lateral riparian zones, with the dry bank riparian scrub zone being more susceptible to woody alien species (Boucher, 2002). It is only in the higher reaches of the mountain streams in the Western Cape that riparian vegetation is found in a more or less natural state (Sieben and Reinecke, 2008).

2.4.4. Invasive Australian Acacias

Australian *Acacia* spp. are well-known for their ability to fix atmospheric N (Levine et al., 2003; Tye and Drake, 2011), and N_2-fixation appears to be essential during early life stages (Schortemeyer et al., 2002). Acacias are amongst the most prolific, successful and severe plant invaders globally (Morris et al., 2011; Racher, et al., 2011), especially in disturbed environments (for instance post-fire and riparian areas; Morris et al., 2011), and nutrient limited Mediterranean-type ecosystems, such as Portuguese dune (Marchante et al., 2009; Hellman et al., 2011) and fynbos ecosystems of the Cape Floristic Region (CFR) in South Africa (Witkowski, 1991; Stock et al., 1995; Brown et al., 2004). They support a relatively small but essential plantation industry; however several species are aggressive invaders including those that are grown for commercial use (van Wilgen et al., 2011). *Acacia* spp. are fast-growing small trees or shrubs and successfully out-compete indigenous species for light, enabling them to potentially grow larger and overtop indigenous vegetation (Witkowski, 1991). Furthermore, higher rates of growth are reinforced by their ability to obtain limited resources, such as nutrients and water (Marchante et al., 2008; Werner et al., 2010; Morris et al., 2011). Invasive *Acacia* seedlings have a greater investment in roots that penetrate deeper into the soil and at significantly faster growth rates than native species (Morris et al., 2011) enhancing their ability to access a greater pool of P (Cramer, 2010).

Acacia spp., as in other legumes, are able to persist in invaded ecosystems (Richardson and Kluge, 2008) through their capacity to accumulate excessive biomass and production of prolific quantities of viable, hard-coated and nutrient-rich seeds with physical dormancy that is stimulated by fire (Richardson et al., 1992; Pieterse and Boucher, 1997; Yelenik et al., 2007; Van Wilgen,

2009; Marchante et al., 2010). These are key factors underlying their successful invasion and persistence (Morris et al., 2011). *Acacia* seeds, which can persist for more than 50 years in the soil (Brown et al., 2004), are dispersed by ants, birds, movement of water along rivers, or by moving soil, resulting in slow lateral spread of stands (Holmes and Cowling, 1997; Pieterse and Boucher, 1997). *Acacia* spp. are well adapted to sandy soils that are poor in trace elements and, like most legumes; they have N_2-fixing bacteria on their roots that allow them to cope with the low nutrient levels found in the Fynbos Biome (Sieben, 2003; Jasson, 2005). It is therefore not surprising that Australian *Acacia* spp. have the ability to successfully compete for nutrients and become notorious invasive plants in different regions of the world, considering that they themselves are largely derived from nutrient-poor soils (Marchante et al., 2010; Morris et al., 2011).

2.4.5. Study species

2.4.5.1. *Acacia mearnsii*

Invasive aliens, such as *Acacia mearnsii* (black wattle), have replaced indigenous riparian vegetation along many watercourses in the South Western Cape; this invasion has been in progress for many decades (Richardson et al., 1992; Galatowitch and Richardson, 2005). In comparison to other highly invasive *Acacia* spp. in the Fynbos Biome (*Acacia saligna*, *A. longifolia*, and *A. cyclops*), which are phyllodinous and sclerophyllous, *A. mearnsii* have particularly long-lived bipinnate leaves, which may turn brown during drought conditions, but recover after the arrival of the first rains. These species are more dependent on water than phyllodinous *Acacia* spp. and invade river systems as well as more mesic regions (Morris et al., 2011). Not only is *A. mearnsii* a fire-adapted pioneer species (Pieterse and Boucher, 1997), but it is also the most widespread invasive alien tree in South Africa and serious infestations occur in higher rainfall regions of the country (Le Maitre et al., 2000; Dye and Jarmain, 2004). This species obtain resources though mechanisms of extensive root production, both shallow and deep root systems, and symbiotic N_2-fixation (Pretorius et al., 2008; Morris et al., 2011). Their formation of large, persistent seed banks coupled to water dispersal enables them to disperse rapidly downstream. Germination is initiated by disturbances, especially fire (Galatowitsch and Richardson, 2005; Pretorius et al., 2008).

2.4.5.2. *Acacia longifolia*

Acacia longifolia (long-leaved wattle) is an evergreen shrub or spreading tree growing 2-6 meters in length (Henderson, 2001). *A. longifolia*, along with *A. mearnsii*, has become invasive in fynbos mountain slopes and watercourses in the southern and south-western Cape (Holmes et al., 2005;

Jasson, 2005). The survival and spread of *A. longifolia* is due to its high seed set throughout its life cycle (Jasson, 2005; Marchante et al., 2010). Seeds germinate *en masse* after post-control fire events, creating problems for management (Marchante et al., 2010). Seeds accumulate beneath the canopies of the parent plants and are buried and dispersed by ants over moderate distances and can remain viable in the soil for many years (Marchante et al., 2010; Hellmann et al., 2011). Similar to *A. mearnsii*, *A. longifolia* has competitive features that promote its invasiveness even in environments associated with limited resources (Hellmann et al., 2011).

2.5. EFFECTS OF IAPs ON ECOSYSTEMS

2.5.1. Introduction

IAPs have detrimental effects on forestry, agriculture, and human health, and are regarded as the second largest threat to the Earth's biodiversity after habitat destruction and modification (Hood and Naiman, 2000; Richardson and van Wilgen, 2004; Pretorius et al., 2008; Richardson et al., 2007; Gaertner et al., 2009; Hellmann et al., 2011). They are known to have multiple effects on both ecosystem structure and function of the invaded community (Erhenfeld, 2003; Gaertner, et al., 2009; Hellmann et al., 2011), particularly invasive N_2-fixing plants (Yelenik et al., 2004; Erhenfeld, 2003). These changes have severe consequences for native populations and community dynamics, including rare and endangered species (Mack and D'Antonio, 1998; Erhenfeld, 2004; Marchante et al., 2010; Le Maitre et al., 2011), thus reducing the ability of ecosystems to provide corresponding services and the benefits they provide (Vilà et al., 2011; Le Maitre et al., 2011). In general, biological invasions are likely to alter ecosystems where they add a new biological process (for instance, N_2-fixation) to a specific environment, or where they maintain such processes in a new area (Vitousek et al., 1987). Many IAPs are capable of transforming ecosystems (Le Maitre et al., 2011) by altering disturbance regimes in both intact and altered systems and may also be agents of disturbance themselves (Mack and D'Antonio, 1998). The impacts of Australian *Acacia* spp. in natural ecosystems have been widely documented with various recorded impacts (Le Maitre et al., 2011). Once established, Australian Acacias cause simultaneous biotic and abiotic changes in ecosystem structure and function of below- and above-ground communities, such as fire regime, microclimates, nutrient cycling, river geomorphology, soil moisture regimes, community structure, and reduce local biodiversity, consequently threatening several taxa with extinction (Rowntree, 1991; Richardson et al. 1992; Stock et al., 1995; Holmes and Cowling, 1997; Yelenik et al., 2004; Marachante et al., 2008; Reinecke et al., 2008; Le Maitre et al., 2011) and forming one of the major threats to biodiversity in the Cape Floristic Region (Holmes and Cowling, 1997). Similar impacts have also been attributed to riparian invaders in other parts of the world (e.g. *Tamarax* spp.; Shafroth and Briggs.

2008). Other impacts which have not been assessed over large areas, include recreational and aesthetic aspects, modifications to river-bank stability and erosion, and increased soil N (Yelenik et al., 2004; Gaertner et al., 2011; van Wilgen et al., 2011).

2.5.2. Vegetation structure and function

Mediterranean-type ecosystems comprise specific plant communities with high endemism. These ecosystems are especially endangered by IAPs, and accordingly, anticipated to experience great loss of biodiversity in the future (Hellmann et al., 2011). Changes in structure result from alterations in patterns of species dominance within the plant community, since the effects of a given species on ecosystem processes are modulated in relation to its abundance within the community (Grime, 1998). Since IAPs grow faster and larger than native species, they are able to reduce light penetrability and change litterfall, fuel properties and nutrient cycling patterns (Holmes et al., 2000). Many *Acacia* spp. are major or emerging invaders in many parts of the world (Le Maitre et al., 2011) and have a variety of ecological impacts (Marchante et al., 2008; Gaertner et al., 2009; Racher et al., 2011). Habitat modifications have been one of the major attributes resulting in displacement of indigenous fynbos species by Acacias (Jasson, 2005).

N-limited terrestrial ecosystems are sensitive to alterations in N and additions of N through biological N_2-fixation are known to affect community composition (Tye and Drake, 2011). Nutrient enrichment, as well as their ability to recruit prolifically, Acacias in the Western Cape compromise resilience by altering the competitive relationships in favour of these species, thereby outcompeting indigenous species and replacing diverse communities by low diversity, homogenous communities (Musil, 1993; Richardson et al., 1997; Holmes et al., 2005; Esler et al., 2008; Gaertner et al., 2011). Some of the other native N_2-fixing genera and species of the Fabaceae are rare in mature stands of fynbos (>6 years) and often occur in low abundance, however, these species are able to take advantage of the post-fire environments because of altered soil nutrient conditions (Cocks and Stock, 2001). Furthermore, under stressful conditions, N-demanding IAPs can particularly benefit from low resource-use of native species (Werner et al., 2010; Hellmann et al., 2011) affecting the performance of indigenous species well adapted to N-limited ecosystems (Hellmann et al., 2011).

2.5.3. Soil biogeochemistry

Research has shown strong feedbacks between plant species and soil nutrient dynamics (Stock et al., 1995). Invasive N_2-fixing species threaten native ecosystems not only by replacing native plants but also through their potential for altering ecosystem N inputs though biological N_2-fixation

(Ehrenfeld, 2003; Rice et al., 2004; Marchante et al., 2008; Hellmann et al., 2011; Tye and Drake, 2011). There is evidence that biological N_2-fixation, often in association with a single plant species, can facilitate the input of significant amounts of N (Vitousek et al. 1987; Knops et al., 2002). Amongst the best studied impacts of alien plant invasions are those concerning ecosystem processes (Yelenik et al., 2007). Due to their abundance and differing resource requirements, N_2-fixing invaders have the potential to disrupt ecosystem dynamics and alter the collective properties of ecosystems. They enrich soils by means of excessive production of N and P rich litter with long-term effects on soil nutrient cycling, rate of litter decomposition, soil microbial communities, and primary productivity, making the soil progressively more unsuitable for indigenous fynbos plants (Musil and Midgley, 1990; Witkowski, 1991; Stock et al., 1995; Pieterse, 1997; Yelenik, 2004; Jovanovic et al, 2009). Several studies have shown that IAPs can change the physical and chemical properties of soils in invaded ecosystems including; OM, nutrient stocks, nutrient cycling rates, soil moisture content, pH and cation distribution, with suggested negative impacts on soil and indigenous plant biodiversity (Stock and Allsopp, 1992; Mack and D'Antonio, 1998; Ehrenfeld, 2003; Corbin and D'Antonio 2004; Yelenik et al., 2004; Reinecke et al., 2007; Marchante et al., 2008; Jovanovic et al., 2009; Werner et al., 2010). These changes may induce profound and often irreversible changes to ecosystems (Mack and D'Antonio, 1998).

Long-lasting biogeochemical changes (legacy effects) are a major problem (Le Maitre et al., 2011) as they affect ecosystem structure, for example, by enhancing soil nutrient concentrations that persist even following the removal of the invader (Yelenik et al., 2004; Marchante et al., 2009). Furthermore, higher soil N may aid establishment and growth of *Acacia* spp. as well as other nitrophilous weedy species through secondary plant invasions (Yelenik et al., 2007). An overabundance of available N of naturally N-limited ecosystems my also increase soil acidity, enhance losses of nitrate and nutrient base cations to receiving waters, and cause imbalances in plant tissue nutrient:N ratios (Gress et al., 2007; Hellmann et al., 2011). Even though several studies have found changes in soil and ecosystem properties in response to the introduction of new functional groups and new traits, other studies have not found such effects (Ehrenfeld, 2003). The magnitude of impacts on ecosystem function are probably determined by the composition of the invaded community and soil properties, which often appear to be species- and site-specific (Ehrenfeld, 2003; Dassonville et al., 2008).

2.5.4. Fire dynamics

Plants also modify disturbance regime by affecting flammability (Chapin et al., 2002). Many invasive alien species are capable of rapid dispersal into modified environments and can persist

under altered disturbance regimes (Corbin and D'Antonio, 2004). Fires are known as a major disturbance factor, creating "invasion windows" by promoting the spread of invasive trees (Richardson et al., 1992; Pieterse and Boucher, 1997). Invasive species can result in fires that have important consequences for communities and ecosystems, reducing the diversity and abundance of native species and generating long-term effects on biogeochemical cycling (Pauchard et al., 2008; Esque et al., 2010). Invasion can either promote or suppress fire (Mack and D'Antonio, 1998; Brooks et al., 2004). As already mentioned, fire is an important ecosystem process in the fynbos biome to which many alien invasives are extremely tolerant. The superior fire resilience of *Acacia* populations buffers them from local extinctions and damage under hot fires (Pemberton and Boucher, 2001). After fire, growth of *Acacia* seedbanks are stimulated with concurrent germinating fynbos species being rapidly out-competed (Holmes and Cowling, 1997; Pemberton and Boucher, 2001; Le Maitre et al., 2011). With each successive wildfire, Acacias increases in density (Brown et al., 2004), thereby playing a critical role in driving alien plant invasions (Richardson et al., 1997). By changing fire regimes, IAPs also thrive under the new conditions they create (Brooks et al., 2004). Indigenous riparian shrubs and trees do not readily burn and are able to withstand natural fires (Boucher, 2002), but with increased invasion by woody species in riparian zones, the resultant higher fuel loads, in comparison to native ecosystems, cause higher intensity burns that can instigate mortality of indigenous trees and lead to a change in vegetation composition after fires (Jayiya et al., 2004; Jasson, 2005; Blanchard, 2007). Even in non fire-adapted ecosystems, IAPs promote frequent fires and out-compete indigenous vegetation (Milton, 2004).

Studies from fire-prone fynbos ecosystems have shown that fire in invaded ecosystems not only affect native species re-establishment and vegetation composition, but also alter several physical and chemical properties of soils (for instance soil structure, water repellency and available nutrients), in addition to the activity and development of belowground organisms (van Wilgen and Richardson, 1985; Brown and Mitchel, 1986; Scott et al., 2000; Cilliers et al., 2005, Jasson, 2005; Le Maitre et al., 2011). Enhanced fuel loads (van Wilgen and Richardson, 1985) elevate fire temperatures and severity of fires to such an extent that the soil may be sterilized during regular fires and subsequently increase periods of post-fire soil exposure (Cilliers et al., 2004). This in turn negatively affects the stability of soils by leaving the soil surface loose and more exposed to erosion, which could lead to enhanced rates of sedimentation processes in rivers and dams (Euston-Brown, 2000; Le Maitre et al., 2011). The mechanism whereby alien vegetation may enhance post fire soil erosion is usually related to the severity of fires and high fuel loads associated with the invader (Euston-Brown, 2000).

2.5.5. Water resources and hydrogeomorphology

In South Africa, it has been shown through experimental evidence that IAPs use more water than native vegetation, particularly Australian Acacias (Le Maitre et al., 1996; Le Maitre et al., 2000; Calder and Dye, 2001; Dye et al., 2001; Dye and Jarman, 2004). Excessive use of water by IAPs results in diminished water supplies for human needs, with considerable implications for water security and detrimental effects for river environments (Görgens and van Wilgen, 2004; Jasson, 2005). For this reason, riparian ecosystems and their subcatchments invaded by water demanding IAPs are targeted by the national Working for Water programme (WfW) (more detail on clearing initiatives in section 2.6; van Wilgen et al., 1998). The influence of alien clearing operations on the economics of hydrological planning appears to be beneficial (Görgens and van Wilgen, 2004), since the removal of woody invasive trees in close proximity to stream channels where they form dense stands is believed to strongly enhance streamflow (Dye et al., 2001). Besides the gains in terms of water resources through clearing initiatives, there are many other advantages including biodiversity conservation, improved catchment stability and fire management, and employment opportunities (Le Maitre et al., 1996). Much less work has been done on the effects of IAPs on groundwater resources, which are a critical component of the hydrological cycle (Görgens and van Wilgen, 2004).

In riparian ecosystems, invasions have the potential to affect the physical processes that are essential to maintain ecosystem integrity (Rowntree, 1991). Woody IAPs in riparian systems can quickly dominate an area if left uncontrolled (Blanchard, 2007); eventually leading to altered channel geomorphology by affecting the stability of soils (Rowntree, 1991; Blanchard, 2007). Dense alien stands of *A. mearnsii* causes several undesirable outcomes, such as obstruction in the flow of water during flooding, resulting in profound changes to channel morphology. This in turn leads to the erosion of water courses, soil loss and the conversion of rivers into diffuse ecosystems of shallow channels (Pieterse, 1997; Boucher, 2002; Prins et al., 2004; Blanchard, 2007). *Acacia mearnsii, A. longifolia, A. saligna,* and *P. pinaster* have been shown to accelerate bank erosion and reduce bank stability (Versfeld and van Wilgen, 1986; Macdonald and Richardson, 1986). In addition, the accumulation of woody debris within the river channel can have a significant impact on geomorphological and hydraulic processes (Tickner et al., 2001).

2.6. MANAGEMENT AND IMPLICATIONS FOR RESTORATION

Ecological restoration is known to be a vital response for undertaking current degradation of ecological systems (Gaertner et al., 2011). Over the past two decades, the potential for non-native species to dramatically alter ecosystem structure and function has become broadly

recognized (Levine et al., 2003) and this is now receiving considerable attention as we try to manage them and their associated negative impacts (Esler et al., 2008). Management interventions are also ongoing in other parts of the world to address these impacts (Le Maitre et al., 2011). The need to respond successfully to invasion by alien species has guided research in order to address the practical requirements of policymakers and conservation managers (Roura-Pascual et al., 2009). The restoration and control of invasives is recognised as a fundamental component in reducing the global loss of biodiversity and an important task of restoration ecologists (Hobbs and Harris, 2001; Reinecke et al., 2008). Naturalized or species that have become invasive (*sensu* Richardson et al., 2000) have required some form of management and need to be assessed for their potential to cause ecological impact (Richardson et al., 2000; Brooks et al., 2004; Jayiya et al., 2004). Differentiating between the terms 'restoration' and 'rehabilitation' is important in prioritizing clearing programmes. The re-establishment of some fully-functional, pre-invasion state (restoration) may be a suitable target in areas that are relatively lightly invaded or have only recently become densely invaded. However, in areas where invasion has been ongoing for a long time, such a goal may be unachievable without very costly interventions, and a more desirable and realistic approach be used to re-establish former function (rehabilitation) and not necessarily biodiversity (Holmes and Cowling, 1997; Holmes et al., 2008; Sieben and Reinecke, 2008). Rehabilitation, for example, may be sufficient to bring an ecosystem towards a trajectory of recovery through active intervention in a particular ecosystem, whereas restoration will not be feasible at all (Reinecke et al., 2007; Holmes et al., 2008).

The government of South Africa supports a number of alien-plant clearing programmes, the majority of which give priority to river systems to decrease the spread of propagules along rivers and into adjacent terrestrial areas (Richardson et al., 1997). The Working for Water (WfW) Programme was initiated by the Department of Water Affairs and Forestry in 1996 with the aim of controlling woody invading plants (Le Maitre et al., 1996; van Wilgen et al., 1998; Dye and Jarmain, 2004) and enhancing ecological integrity under the assumption that control of AIPs alone will improve ecosystem function and structure (Holmes et al., 2008). The primary objectives are linked to water resource management including water security and sustainable runoff from catchments, conservation of biological diversity, reduction in intensity and frequency of fires and floods and to empower impoverished communities (van Wilgen et al., 1998). It provides government and non government organization (NGO) partners with necessary resources to embark on the clearing of IAPs (Roura-Pascual et al., 2009). Extensive areas of land are currently being cleared under this programme (Jovanovic et al., 2008). Important long-lasting success of the WfW Program is the extent to which native vegetation recovers and withstands re-invasion by woody IAPs (Holmes et al., 2005). It remains unclear whether large investments on

control operations are significantly reducing the extent of the problem (Roura-Pascual et al., 2009). The management of woody IAPs, particularly *Acacia* spp. (with the exception of *Pinus* spp.) is difficult due to problems associated with conflicts of interest that develop when species have both positive benefits and negative impacts (van Wilgen et al., 2011).

A range of methods are available to control invasive alien plants, including chemical, mechanical, and biological control (Holmes et al., 2000; Jasson, 2005), but the latter provides a more sustainable solution. Nevertheless, in fynbos, biological control is only available for some of the invasive plant species (van Wilgen, 2009). A combination of felling and herbicidal treatment of stumps is used as methods in areas invaded by Australian Acacias to prevent resprouting (van Wilgen et al., 2011). In riparian zones, removal of invasive woody plants (e.g., *A. longifolia, A. mearnsii*) involves felling, generally combined with prescribed burning and herbicide application (Galatowitsch and Richardson, 2005). The efforts directed at clearing them often results in further disturbances, depending on the duration and intensity of the invasion (Holmes et al., 2005). Whether these clearing operations initiate recovery of native riparian vegetation is uncertain and dependent on suitable propagule supply and/or suitable microsites for the establishment of species (Galatowitsch and Richardson, 2005) and possibly.

Some researchers are of the opinion that a changed nutrient status can negatively influence the re-establishment of indigenous species following clearing, particularly as nutrients can, in some cases, remain in the soil for prolonged periods of time (Brown et al., 2004; Yelenik et al., 2007; Marchante et al., 2009). The persistence of biogeochemical legacies at cleared sites may also have consequences for riparian foodwebs. Soil changes may be an important factor in invasion success, since positive-feedback mechanisms favour re-invasion, thus complicating and hampering restoration of native environments (Marchante et al., 2008). The effects of exotic species can be very dramatic, however, it is less well understood how long the legacies of N_2-fixing invaders on soil N pools prevail after a species has been removed (Corbin and D'Antonio, 2004), especially in fynbos riparian ecosystems, and how they might affect the likelihood of succession and restoration of post-removal vegetation. These changes in ecosystem function, such as increases in available N following the invasion of N_2-fixing species might be an important pathway by which invaders favour secondary invasion of other exotic species (Davis et al., 2000; Levine et al, 2003; Galatowitsch and Richardson, 2005; Yelenik et al., 2007; Shafroth and Briggs. 2008) even after removal of the N_2-fixers (Corbin and D'Antonio, 2004; Galatowitsch and Richardson, 2005; Le Maitre et al., 2011). Already increases in alien grass abundance have been noted after the clearing of Acacias in the Western Cape (e.g. Holmes and Cowling, 1997; Yelenik et al., 2004; Reinecke et al., 2007). Other practical problems that may prevent the success of

restoration goals is the inadequate recovery of riparian vegetation, which can result in soil erosion, loss of indigenous soil-stored propagules (Vosse et al., 2008) and poor water quality (Jovanovic et al., 2009). This poses a daunting challenge for efforts to restore invaded habitats (Corbin and D'Antonio, 2004). Changes in community composition have significant consequences for conservation and utilization of ecosystem services (Ehrenfeld, 2003).

To facilitate restoration of degraded environments and to know whether either restoration or rehabilitation should be used as a particular aim in clearing operations, depends on the clearing treatment used, the alien plant species concerned, soil and vegetation types and fire cycles prior to and after clearing. It is also essential to identify the duration, extent, and current impacts of the invader (Esler et al., 2008; Pretorius et al., 2008; Gaertner et al., 2011). According to a study by Sieben and Reinecke (2008) the success of a restoration strategy may depend on the clearing and control method used. They concluded that "Fell and Remove" treatments to be the most successful treatment in adding passive recovery of indigenous species. Bare riverbanks that have to rely on natural or spontaneous succession following alien clearing are unstable and prone to severe erosion and riverbank collapse, and over the long-term, alien plants returns to the place it previously occupied (Sieben and Reinecke et al., 2008).

Whenever degradation, caused by invasion, has reached a particular threshold where ecosystems are unable to recover naturally without active restoration (Marchante et al., 2009), the introduction of native species through planting or sowing and the removal of biomass and litter may improve restoration problems to some extent and reduce a site's susceptibility to new invasions (Sieben and Reinecke, 2008; Marchante et al., 2009). Le Maitre et al. (2011) emphasized the need for active restoration following prolonged invasion in order to restore ecosystems, as they are unlikely to recover passively. A great deal of emphasis on follow-up control treatments have also been highlighted in the literature (e.g. Holmes et al., 2005; Reinecke et al., 2007; Marchante et al., 2009, 2010; Le Maitre et al., 2011). Since *Acacia* spp. have long-lived seeds that lie dormant in the soil for long periods of time, biological control and follow-up programmes, especially after fire, are important for long-term restoration and management of Acacias and in maintaining recovery of native ecosystems. The situation will worsen if no action is taken (Marchante et al., 2010; Le Maitre et al., 2011).

In fynbos ecosystems, controlled burning has been adopted as a management tool to eradicate alien invasive species and maintain ecosystem structure and function (Stock and Lewis, 1986). There is an urgent need to integrate prescribed burning and invasive alien control operations after fire, or by careful selection of rehabilitation treatments, to elude either increased control costs, or

else suffer increased impacts (DeBano, 1990; van Wilgen, 2009). Widespread unplanned fires will lead to the need for additional effort in the form of 'follow-up' treatments (van Wilgen, 2009).

For various riparian systems, guidelines for extensive ecological- and economical appropriate restoration practices are still lacking (Esler et al., 2008). In order to save operational costs many management interventions and alien clearing initiatives take up a passive approach to restoration, by merely aiming to remove the existing invasive species and prevent or control their regeneration, with no active intervention to assist the recovery of indigenous species (Holmes et al., 2005; Reinecke et al., 2008; Vosse et al., 2008; Le Maitre et al., 2011). However, these methods often fall short in achieving the preferred outcome of ecosystem function (for instance a community dominated by native species; Le Maitre et al., 2011). Appropriate restoration strategies are necessary if unaided recovery is ineffective (Gaertner et al., 2011). Knowing which situations are prone to a long-lasting transition phase is essential for planning alien-clearing programs (Galatowitsch and Richardson, 2005). It is suggested that the probability of successful restoration, where no active restoration is applied, decreases rapidly as the duration and/or intensity of the perturbation is enhanced (Le Maitre et al., 2011). Given that removal of IAPs is expensive, the likelihood of success should first and foremost be assessed before embarking on major restoration control programme. In order to design and perform broad-scale clearing and restoration operations trial clearings ought to consider the range of conditions that might have an effect on the outcome of control programmes (Marchante et al., 2011).

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CHAPTER 3

Soil Properties and Plant Functional Type Cover in Natural, *Acacia*- Invaded and Cleared Fynbos Riparian Ecotones and Associated Uplands

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3.1. ABSTRACT

Riparian corridors are dynamic and complex biophysical systems, but also important linkages between aquatic and terrestrial ecosystems where essential ecological, hydrological and geomorphological processes occur. Invasive nitrogen (N_2)-fixing plant species have been shown to affect carbon (C) and nitrogen (N) inputs, and plant growth and community dynamics. *Acacia mearnsii* is the primary invader in fynbos riparian zones of the Western Cape, South Africa. No studies have specifically investigated soil properties and ecosystem functioning of fynbos riparian ecotones, and the changes caused by invasion or recovery after clearing. The aim of this chapter was to quantify soil physical and chemical properties and assess the cover of selected plant functional types (PFTs) and other ecosystem attributes in natural, invaded and cleared (i.e. post alien plant control) riparian ecotones and associated non-riparian uplands. We hypothesized that invasion of fynbos riparian ecotones by *Acacia* spp. changes soil properties and significantly alter functional type composition and cover. Additionally, fynbos riparian ecotones differ from upland zones with regard to above mentioned properties. Fieldwork was performed in mountain and foothill sections of six perennial river systems within the south-western Cape, South Africa. Eleven sites of three categories were chosen: four natural (uninvaded), four moderate to highly invaded (mainly *A. mearnsii*) and three cleared (a previously invaded site that has been cleared more than 7 years ago) sites. Within each site, three geomorphological zones (wet bank, dry bank, and upland fynbos) were sampled, and four to five replicate plots were established along each zone. Seasonal soil samples were taken, a survey of the aboveground vegetation was carried out, and comparisons made. The results showed that exotic *Acacia* spp. affect fynbos riparian ecosystem by i) enriching the system with nutrients; ii) altering litter inputs and soil physical properties and iii) changing the composition and reducing the cover of growth form types. Furthermore, *A. mearnsii* forms a novel structural layer in both the wet- and dry bank lateral zones. A legacy effect with respect to N availability persists in cleared riparian ecotones while no apparent discrepancies were detected for other soil properties. Areas cleared of *Acacia* spp. are re-invaded with exotic grasses, in addition to low cover of native riparian woody species and other growth form types. Active restoration under such conditions would be required to facilitate the

restoration of cleared riparian communities. Growth form composition and cover differed between landscape positions. Wet bank zones are very different from both dry bank and terrestrial zones with regard to soil physical and chemical properties. Soil texture was shown to be an important factor affecting soil physical and chemical properties.

KEYWORDS: riparian structure and function; invasive alien plants; Nitrogen-fixing plants; Plant functional types; landscape position, invasion status; soil physical and chemical properties

3.2. INTRODUCTION

Riparian corridors are are dynamic complex biophysical systems in terrestrial areas, but also one of the most essential landscape elements for maintaining ecosystem integrity (Naiman and Décamps, 1997; Hood and Naiman, 2000; Décamps et al., 2004). Together with other freshwater and marine ecosystems, riparian corridors are considered as "critical transition zones (CTZ)" (Ewel et al., 2001) which are defined as hybrid ecosystems or interfaces that link ecosystems and function as conduits of materials and energy between these ecosystems. In the case of riparian zones, two clearly defined ecosystems are the river and surrounding uplands (Bardgett et al., 2001; Ewel et al., 2001). Although these systems are highly dynamic in the short term, if left in their natural state, they demonstrate substantial stability over the longer term (Ewel et al., 2001). Riparian corridors possess specific biotic properties, hydrological processes and physical and chemical characteristics, but are very distinctive in their interactions with surrounding ecological systems (Tickner et al., 2001; Décamps et al., 2004). Even though active river channels normally are hostile to vegetation establishment, riparian ecotones support specialized disturbance-adapted plant communities (Naiman and Décamps, 1997).

Riparian ecosystems have well-defined ecological functions related to their position along the river continuum (Vannote et al., 1980). Not only do they have intrinsic conservation value, but intact riparian vegetation communities are important ecological systems in maintaining ecosystem health and services (Bardgett et al., 2001; Ewel et al., 2001). Within riparian zones, the modification, mobilization and accumulation of materials and nutrient fluxes from the aquatic environment and adjacent upland areas is strongly linked to several ecosystem services (Naiman et al., 2005; Esler et al., 2008), among other things, modulation of hydrological changes, buffering against floods and maintaining bank integrity by preventing erosion, maintaining water quality (sink for pollutants), cycling of nutrients, and serving as a refuge and source of nourishment for biota (Hood and Naiman, 2000; Bardgett et al., 2001; Naiman et al., 2005; Esler et al., 2008). It is

because of significant interactions between these processes that management practices involving riparian corridors or of their adjacent ecosystems must take the whole complex of ecosystems into consideration (Ewel et al., 2001).

Natural disturbances are essential mechanisms maintaining spatial and temporal heterogeneity in riparian zones and generating conditions under which niche overlap can occur (Ward et al., 2002). Riparian vegetation composition and structure is determined by several factors including: hydrological (i.e. flood discharge); geomorphological (i.e. channel morphology) (Naiman and Décamps, 1997; Naiman et al., 2005; Richardson et al., 2007); substrate type (Naiman, et al., 2005); the intensity and frequency of fires (Sieben, 2003; Reinecke et al., 2008); and the development of post disturbance successional phases (Ward et al., 2002; Holmes et al., 2005; Reinecke et al., 2007). Nevertheless, riparian vegetation structure and composition are susceptible to frequent change, due to hydrologic, geomorphic, and human-related disturbances. The structure and integrity of the riparian zone plays a critical role in controlling these changes (Tabacchi et al., 1998).

Rivers in Mediterranean-type ecosystems are biologically, chemically, and physically shaped by predictable, seasonal cycles of flooding and drying (Gasith and Resh, 1999). Vegetation structure of riparian zones varies considerably depending on the context. In fynbos mountain streams the vegetation zones are narrow and floodplain development more restricted compared to lower reaches, but differences in vegetation are just as prominent (Sieben, 2003). It has been hypothesized that water availability and susceptibility to fires are the main environmental determinants of fynbos riparian vegetation structure in the Western Cape (Sieben, 2003; Reinecke et al., 2008), but soil physical and chemical properties (such as soil pH and texture), likely promotes the establishment of different types of growth form that differ in their flammability and resistance to fire (Cowling and Holmes, 1992).

The invasion of natural ecosystems by invasive alien plants (IAPs) contribute significantly to global environmental change, are regarded as a serious threat to the earth's biodiversity (Scherer-Lorenzen et al., 2007; Liao et al., 2008) and are also considered as one of the most important elements of impacts to riparian systems (Esler et al., 2008). Moreover, riparian ecosystems have been invaded disproportionately more than other ecosystems world-wide (Hood and Naiman, 2000). Since biodiversity is an essential feature of ecological communities, the threat posed by IAPs to community composition is significant (Boucher, 2002). They threaten the stability of native ecosystems and potentially affect the structure, function and processes of the

invaded system (Richardson, et al., 2007; Liao et al., 2008; Gaertner et al., 2009; Marchante et al., 2010; Hellmann, et al., 2011), especially Mediterranean ecosystems which often consist of highly endemic and specialized communities (Hellmann et al., 2011). Riparian corridors are sensitive to environmental change and invasion by alien plant species across landscape types, because of the complexity of interactions on which they depend (Ewel et al., 2001; Richardson et al., 1997; Décamps et al., 2004; Reinecke et al., 2007) including; periodic disturbances that creates new microhabitats and niches, dynamic nutrient levels, access to water, water dispersal of propagules, and the role of river banks as a reservoir for seeds for both indigenous and exotic species (Hood and Naiman, 2000; Boucher, 2002; Brown et al., 2004; Vosse, 2007). Accordingly, river corridors require constant management in areas where IAPs occur (Reinecke et al., 2007).

Given the body of evidence of elevated invasibility of riparian ecosystems (Hood and Naiman, 2000), and that exotic plant species are known to have several dramatic effects on ecosystems, most commonly assessed through changes in composition of native communities (Ehrenfeld, 2004, Holmes and Cowling, 1997; Reinecke et al., 2007) and changes in the physical environment, such as soil de-stabilisation and erosion (Rowntree, 1991), and soil properties and ecosystem fluxes (Witkowski, 1991; Stock et al., 1995; Hood and Naiman, 2000; Ehrenfeld 2003, 2004; Yelenik et al., 2004, 2007; Liao et al., 2008), there is cause for great concern about the effects and extent of IAPs on riparian ecosystems (Hood and Naiman, 2000). Documented impacts of invasion by exotic species on soil properties have been investigated throughout the world, with some mixed results (Dassonville et al., 2008). When comparing uninvaded systems with those invaded by N_2-fixing IAPs, most studies have found considerable alterations in nitrogen (N) and carbon (C) pools as well as other soil nutrients (such as phosphorus) at the ecosystem level (Table 3.1). The extent of impacts can most likely be determined by soil properties and the community composition of the invaded system (Ehrenfeld, 2003). However, the diversity of outcomes among experimental studies shows that a more complete understanding of entire ecosystem response to invasion remains elusive (Liao et al., 2008).

Table 3.1. The effects of invasive N_2-fixing species on litter production and soil nutrients in different ecosystems around the world. Relative to native ecosystems and where applicable, (+), (-) and (0) indicates an increase, decrease or no difference in litter production or soil nutrients in invaded ecosystems respectively. ND: no data was available on litter production.

N-fixing species	Country	Ecosystems	Litter production	Soil nutrients	Reference
Acacia cyclops	South Africa	Coastal strandveld	ND	Available N (+); Available P (+)	Stock et al., 1995
			+	Total N (0); Available N (+); Available P (+)	Witkowski, 1991
A. longifolia	Portugal	Coastal dune	+	Organic C (+); Total N (+); Available N (+)	Marchante et al., 2008
A. saligna	South Africa	Sandplain and lowland fynbos	ND	Available N (0); Available P (0)	Stock et al., 1995
			+	Available P (+); Available N (0); Total N (+)	Witkowski, 1991
			ND	Available N (+)	Musil, 1993
			+	Total N (+); Available P (+)	Yelenik et al., 2004, 2007
Alnus crispa	Alaska	Agashashok river valley	+	Total N (+); Available P (+); Available P (+)	Rhoades et al., 2001
A. rubra	Oregon, Canada	Douglas-fir forests	ND	Available P (+)	Giardina et al., 1995
Cytisus scoparius	California, USA	Coastal prairie	ND	Total N and C (+)	Caldwell, 2006
Elaeagnus angustifolia	New Mexico, USA	Riparian	ND	Available N (+)	DeCant, 2008
			+	Total N (+)	Follstad Shah et al., 2010
Falcataria moluccana	Hawaii	Lowland forests	+	Soil nutrients (+)	Allison et al., 2006
			+	Total N (+); Available P (+)	Hughes and Denslow, 2005
Lupinus arboreus	Califorina, USA	Coastal dune	ND	Available N (+)	Pickart et al., 1998
			ND	Total N (+); Available N (+)	Maron and Jefferies, 1999
Myrica faya	Hawaii	Young volcanic ecosystems	ND	Total N (+); Available N (+)	Vitousek and Walker, 1989 Vitousek et al., 1987
Robinia pseudoacacia	New York, USA, Central Japan	Pine-oak Riparian	+	Total N (+)	Rice et al., 2004
			+	Available N (+)	Akamatsu et al., 2011

It has frequently been suggested that nutrient-limited soils inhibit the establishment and limits the productivity of invasive resource-demanding species; but this perception has recently been challenged (Funk and Vitousek, 2007; Hellmann et al., 2011), since these species have mechanisms to enhance availability of resources in resource-poor environments, e.g., N_2-fixing species (Wolf et al., 2004; Funk and Vitousek, 2007; Dassonville et al., 2008; Hellmann et al., 2011). Through biological fixation, N_2-fixing invasives not only threaten indigenous ecosystems and affect community dynamics, but have been shown to influence microbial processes and C and N inputs as well, thereby altering ecosystem-level characteristics (Yelenik et al., 2007; Malcolm et al., 2008; Marchante et al., 2008; Follstad Shah et al., 2010; Tye and Drake, 2011). Riparian ecotones that are associated with N_2-fixing trees can become a source of additional N to streams, such as nitrates and dissolved organic N (Mineau et al., 2011). In comparison to non-N_2-fixing or herbaceous species, N_2-fixers have a larger influence on species richness (Gaertner et al., 2009) and ecosystem N dynamics (Liao et al., 2008, Hellmann et al., 2011). It is postulated that ecological impacts associated with invasive exotic species diminish instantly after eradication or control, but this is not always the case (Marchante et al., 2009). Limited success in ecosystem recovery has been reported after restoration efforts in areas previously invaded by N_2-fixing species (Yelenik et al., 2004; Galatowitch and Richardson, 2005; Malcolm et al., 2008). After invasion by these species, enhanced N availability may favour the proliferation of other exotic species even after removal of the invader (Corbin and D'Antonio, 2004; Yelenik et al., 2007; Malcolm et al., 2008).

Several Australian *Acacia* spp. have become successful invaders around the world (Morris et al., 2011). In South African ecosystems, invasive *Acacia* spp. have been intensively investigated (Scherer-Lorenzen et al., 2007). Not only do Acacias successfully out-compete indigenous species for light and limited resources (water and nutrients), which enables it to potentially grow larger and overtop indigenous vegetation (Witkowski, 1991; Werner et al., 2010), but seed production also facilitates the formation of persistent seed banks (Holmes et al., 2005; Marchante et al., 2010; Morris et al., 2011). These species do invade resource-poor environments, such as those characteristic of Mediterranean-type ecosystems (Witkowski, 1991; Stock et al., 1995; Werner et al., 2010; Morris et al., 2011), as well as disturbed environments, e.g. post- fire and riparian environments (Richardson et al., 2007; Morris et al., 2011). In the Cape Floristic Region (CFR) indigenous fynbos riparian vegetation along several watercourses have been suppressed and replaced by invasive alien trees and shrubs. These species have changed ecosystem functions (Galatowitch and Richardson, 2005; Richardson et al., 2007; Blanchard and Holmes, 2008; Vosse et al., 2008). Particularly problematic are the fast-growing *Acacia* (*Acacia mearnsii,*

A. longifolia, A. saligna) and *Eucalyptus* spp. from Australia (especially *E. camaldulensis)*, in addition to *Pinus* spp. from America (Holmes et al., 2005; Richardson et al., 2007); *Acacia* spp. are ranked as some of the most severe invasive species in the fynbos biome (Reinecke et al., 2007).

Pre-adaptation to nutrient-poor soils, extreme tolerance to fires, and Mediterranean climate, largely enables Acacias to successfully invade and persist at the Cape (Witkowski, 1991; Brown et al., 2004; Galatowitch and Richardson, 2005; Morris et al., 2011). Nevertheless, the above mentioned mechanisms that control the successful invasion of resource demanding species, such Australian Acacias, into resource-limited environments, such as fynbos, are still poorly understood (Werner et al., 2010). *A. mearnsii* is a fast growing, fire-adapted, evergreen leguminous tree native to Tasmania and south-east Australia (Pieterse and Boucher, 1997; Tye and Drake, 2011). This species can either resprout or regenerate from seedbank and tends to form dense canopies and monospecific stands that threaten fynbos riparian vegetation (Richardson et al., 1992; Vosse, 2007; Blanchard and Holmes, 2008). Alien trees in fynbos riparian ecotones invade both wet- and dry bank lateral zones, with dry banks being more susceptible to woody IAPs (Boucher, 2002). Whereas all lowland sections of rivers in the CFR have been transformed to a greater or lesser extent, many foothill and some mountain-stream river segments higher up in the catchment have pristine riparian vegetation, but in some areas, also been densely invaded by IAPs (Reinecke et al., 2007).

National- or regional scale aquatic restoration programs (such as South Africa's Working for Water program) have adopted the strategy of clearing exotic species in riparian ecotones since 1995, with multiple aims of increasing water production, improving water quality, providing employment; and conserving biodiversity (Le Maitre et al., 1996; van Wilgen et al., 1998; Galatowitch and Richardson, 2005). However limited finances frequently results in inadequate and unsatisfactory outcomes following removal of IAPs (Holmes, 2001), as clearing operations have depended on spontaneous succession of riparian communities (Reinecke et al., 2008). The result is that many restoration and control efforts have unexpected and detrimental outcomes and do not attain sustainable mitigation of ecosystem impacts induced by IAPs (Le Maitre et al., 2011).

Clearing stands of exotic plants is increasingly of major concern when restoring rivers (Galatowitch and Richardson, 2005). Restoration efforts have been conducted in a number of areas within the fynbos biome, with some mixed results (Holmes and Cowling, 1997; Yelenik et

al., 2004; Galatowitch and Richardson, 2005; Holmes et al., 2008; Reinecke et al., 2008). Areas cleared of dense stands of aliens have been found to recover more slowly compared to those cleared of less dense infestations (Richardson et al., 1989; Holmes and Cowling, 1997). Riparian vegetation that has been invaded for several decades may not rapidly recover following alien clearing operations and inadequate restoration may result in profound changes to river channel morphology. Furthermore, soil erosion, poor water quality, depletion of propagule bank, re-invasion by alien plant species, or secondary invasion by other nitrophilous species poses serious threats (Holmes, 2001; Boucher, 2002; Yelenik et al., 2004; Galatowitch and Richardson, 2005). The question of how long the legacies of altered soil properties persist after the eradication of N_2-fixing invaders, and how this influences restoration, is less well understood.

Much of our knowledge of riparian biogeochemistry and relationships between aquatic and terrestrial ecosystems has been gained from agricultural and afforested humid-temperate regions (Jacobs et al., 2007). Since riparian ecosystems play an integral role in maintaining ecosystem services and function, understanding the level of invasion and degradation and associated changes in ecosystem function is essential for successful restoration. Some studies in terrestrial fynbos ecosystems in the Western Cape have specifically examined the effects of invasive *Acacia* spp. on fynbos communities (e.g. Holmes and Cowling, 1997), nutrient cycling and mineralization (Witkowski, 1991; Stock et al., 1995; Yelenik et al., 2004); and confirmed that soil nutrient enrichment hindered the survival of native species (Musil and Midgley, 1990; Reinecke et al., 2007). It is possible for soil N availability to remain elevated in several ecosystems and this is regarded as a significant factor in re-invasion success (Corbin and D'Antonio, 2004; Yelenik et al., 2007; Marchante et al., 2009).

However, little attention has been paid to fynbos riparian communities, which are azonal systems and generally consist of structurally distinct tree dominated communities in the natural state (Brown et al., 2004). Efforts to clear IAPs from fynbos ecosystems have forced managers to consider the possible impacts of invasion by N_2-fixing species on changed ecosystem processes and the effects of these alterations for community development (Yelenik et al., 2004). Even though an extensive body of research into the ecology and management of alien vegetation already exist in riparian zones (Tickner et al., 2001), and aside from studies that have investigated the effects of woody IAPs on ecosystem structure and function within the Fynbos Biome, no studies have specifically investigated soil processes and ecosystem functioning of fynbos riparian ecotones, and the changes caused by invasion or recovery after clearing

(Reinecke et al., 2007). This research is amongst the first to investigate whether widely colonizing *Acacia* spp. do in fact alter fynbos riparian biogeochemistry.

In this study, I compared soil properties and plant functional type (PFT) cover in fynbos riparian zones with associated non-riparian upland fynbos (lateral zone comparison) and those invaded by- and cleared of *Acacia* spp. (invasion status comparison). The aims of the study were to quantify plant growth form cover and composition; soil physical and chemical properties; total carbon (C), nitrogen (N); available N and phosphorus (P) concentrations in natural, invaded and cleared riparian ecotones and associated upland fynbos, by addressing the following questions:

1. How does the cover of important PFTs (or plant growth forms) and selected ecosystem attributes vary depending on landscape position (wet bank, dry bank, and uplands) and invasion status (natural, invaded, and cleared)?

2. How do soil physical and chemical properties vary depending on landscape position and invasion status?

3. How do soil nutrients (C, N and available P_i) differ depending on landscape position and invasion status?

4. What important relationships exist between selected soil physical and chemical properties?

3.3. MATERIALS AND METHODS

3.3.1. Description of study sites

Due to the lack of reference riparian systems in lowland river systems, and the large scale transformations in these areas, fieldwork was performed in mountain stream and foothill sections of several riparian areas within the south-western Cape, South Africa. The area is characterized by a seasonal Mediterranean climate with cool wet winters and hot dry summers (Deacon et al., 1992; Appendix D). Average monthly rainfall and average minimum and maximum temperatures are depicted in Appendix D. Fynbos riparian ecosystems (also called closed-scrub fynbos; Cowling and Holmes, 1992) are dominated by broadleaved evergreen woody species, mainly perennial small trees and shrubs including other characteristic fynbos elements such as species of Ericaceae and Restionaceae (Cowling and Holmes, 1992; Galatowitch and Richardson, 2005), in addition to forbs and graminoids in the understory (Reinecke et al., 2008).

The high degree of topographical diversity within the CFR has created diverse soils, resulting in a combination of young and ancient soils (Cowling et al., 2009; Cramer, 2010). Within the upper river catchments where sites are located, a short lateral transition occurs through wet bank, dry bank to adjacent upland fynbos (Pretorius et al., 2008). The rocks (mainly sandstone) of the Table Mountain Group series in the Western Cape, which is the dominant lithology, yield largely coarse-grained soil and nutrient-poor substrata that is deficient in N, available P_i and exchangeable bases (Stock and Lewis, 1986; Witkowski and Mitchell, 1987; Prins et al., 2004). Soils in riparian zones are coarsely-textured and mostly derived from alluvial material from sedimentary Table Mountain Group sandstones; however, riparian soils in the upper reaches of Dwars and Eerste River can also be derived from weathered Cape Granite or a mixture of the two (Heydorn and Grindley, 1982). It is challenging to separate differences between sites attributed to treatments from natural variation (Blanchard, 2007), such as climatic and geological differences between various catchments. For this reason, several perennial river systems within this region were selected for this study, due to their variety of reach types and for their relative close proximity to Stellenbosch University. Fire is also considered a significant environmental factor. Geomorphological characteristics, site history and detailed descriptions of each river system and sites have been described in detail (see Chapter 1) and summarized in Appendix C.

3.3.2. Study design

Field measurements (March 2010 to February 2011) were performed at eleven sites in six different river systems within the south-western Cape region (Jakkals, Sir Lowry's, Eerste, Dwars, Molenaars, and Wit; see Chapter 1 for site locations). Sample sites were located based on invasion intensities, previous management and where possible, some sites were selected in the same location where previous studies were carried out. Within this context, the study of Reinecke et al. (2007) is particularly important, as the three broad geomorphological zones that were used in this study could be determined (Appendix A). Wet- and dry banks contain distinctive vegetation types and the border between them can often be quite sharp (Sieben and Reinecke, 2008). The location of wet bank zones were determined by within-year flows whereas dry banks were determined by recurrence intervals of floods of more than one year (Reinecke et al., 2007). At least three sites of each invasion status were located on different river systems to minimize the effects of catchment differences (geology, time since last fire, species composition, and precipitation).

The eleven selected sites were divided into three different categories (invasion statuses) including four reference or natural sites that are relatively pristine and uninvaded, four moderate to highly invaded riparian sites (mainly *A. mearnsii* or a mixture of *A. mearnsii* and *A. longifolia* invaded for at least more than 10 years) and three cleared riparian sites (a prior invaded site that has been cleared more than 7 years ago, with the specific IAPs listed above necessary for selection). At each site, 4-5 replicate plots were selected for each zone (wet bank, dry bank, and upland zones; Appendix B) giving a total of 12-15 sampling plots per site. Terrestrial zones were located at least 15m from the outer boundary of the dry bank zones and 10m from each other. Each sampling location was permanently marked and the coordinates of sites located with a differential GPS. Precipitation data for the past 2 years were obtained from several weather stations located near and/or within the study area (Institute for Soil, Climate and Water - Agricultural Research Council).

3.3.3. Soil physical and chemical analysis

Six composite soil samples were collected with a stainless-steel core-type sampler (5 cm diameter) from the upper 10cm (top soil or A horizon) of the soil profile after litter was discarded. A hand trowel was used in places where soils were too rocky and/or shallow. The following parameters were assessed on each sample: seasonally: pH, gravimetric soil water content (GSWC), Electric Conductivity (EC), available inorganic N (nitrate and ammonium), available P_i; biannually: particle size distribution, soil total C (TC) and total N (TN); and on a single occasion litter mass and bulk density. The determination of exchangeable nitrate (NO_3^-) and ammonium (NH_4^+) in field soils is complicated considerably by extensive variability and subjected to microbial transformations, which can lead to rapid changes in soil inorganic N content (Mulvaney, 1996). To minimize these changes, field moist samples were kept cool and transported back to the laboratory within 2 hours of collection where samples was stored at 4°C. In the laboratory, samples were sieved (2 mm) to remove roots and organic debris. NO_3-N, NH_4-N and moisture content were determined on fresh soils whereas TN and TC, pH, and EC were determined on air-dried soil. Bray-2 extractable inorganic P (P_i) is a measure of plant available P_i (Witkowski and Mitchell, 1987) and was determined on fresh soil (collected within 2-3 days) by a method similar to that of Bray and Kurtz (1945). Concentrations of Bray-2 P_i, NO_3-N, and NH_4-N were determined colorimetrically with a spectrophotometer (Genesys 20). NO_3-N and NH_4-N were extracted with 0.5M K_2SO_4 within 48 hours of collection to measure standing pools of soil inorganic N. For concentrations of NO_3-N and NH_4-N, 10g of soil (<2mm) were placed in 50ml plastic vials together with 25ml of the extractant. The vials were shaken at medium speed for one hour and filtered. NH_4-N was analysed based on the Berthelot reaction involving phenol (Keeney

and Nelson, 1982) and NO_3-N by nitration of salicylic acid (Catado et al., 1975). Soil TN and TC were analyzed by the dry combustion elemental analyzer method (Soil Science Department, Stellenbosch University) from which soil C:N ratios were computed. For GSWC, approximately 20g of soil were weighed; oven dried at 105°C for 12 hours and reweighed to obtain percent soil moisture.

Soil particle size distribution was determined, because soil texture influences a variety of soil physical, chemical and biological properties, such as the rates of microbiological processes, accumulation of materials and water dynamics (Pinay et al., 1995; Chapin et al., 2002). Particle size for each of the bulked samples was quantified on a biannual basis using a modified version of the rapid method by Kettler et al. (2001). Sand fractions were divided in 2 classes: medium and fine sand (0.053-0.425 mm) and coarse sand (0.425-2.0 mm). Silt and clay fractions (<0.053 mm) were analyzed together. Soil pH was measured electrometrically (Hanna 211 Microprocessor) in a 1:2 (w/v, soil:deionised water) slurry (Robertson et al., 1999). Electrical Conductivity, which is the measure of dissolved materials in aqueous solution, was determined on 10g of air dried soil material. Samples were shaken in 40ml deionized water for approximately 60 minutes and allowed to stand for ions to settle before measurements were taken (Corning Conductivity meter 441). Bulk density was determined during spring as oven-dry mass per volume (based on core volume). Aboveground biomass (litter, twigs and seeds) were sampled during spring using a steel frame ($0.0625m^2$) that was randomly located within each plot. Dead stems were discarded and samples were dried at 60°C for 48 hours and weighed.

3.3.4. Plant Functional Types (PFT) and ecosystem components

Plant density is a more sensitive measure to monitor change in plant communities, however, ecosystem function is most likely to be driven by changes in vegetation cover, and can be used as a surrogate measure for biomass (Holmes et al., 2000). Categorizing species with similar life history or physiological traits into functional groups and the associated changes in plant cover for a particular growth form may indicate a possible change or difference in ecosystem function (Holmes et al., 2000; Yelenik et al., 2004) amongst invasion statuses and between landscape positions respectively. Vegetation structure also provides an essential measure of community recovery (Reinecke et al., 2008).

Table 3.2. Growth forms classes and other ecosystem components with their respective descriptions. Growth form descriptions (1-5) follow Goldblatt and Manning (2000).

Growth form classes	Description
1. Forb	A broad-leaved herbaceous plant other than graminoids.
2. Grasses (graminoid)	Plants in the family Poaceae.
3. Other Graminoids	Plants in the family Juncaceae, Cyperaceae, and Restionaceae.
4. Shrub (<2m)	A low or medium sized woody perennial plant often with multiple of stems.
5. Adult shrub/tree (>2 m)	A large woody perennial plant usually with multiple stems or with a main trunk.
6. Tree seedling (<1 m)	Seedlings of the above mentioned growth form class 5
7. Tree juvenile (1-2 m)	Juveniles of the above mentioned growth form class 5
8. Ferns	Both woody and herbaceous
9. Moss	Both on hard soil surfaces or rocks/stones.
Additional classes	**Description (where applicable)**
10. Stones and/or rocks	Either loose or fixed
11. Bare ground	Surface area not covered by any other class
12. Litter	Twigs, leaves, seeds, and small branches
13. Dead standing	Any standing senesced vegetation
14. Tree basal cover	GC of the base of juvenile and adult indigenous and *Acacia* shrubs and trees

The PFT approach that was used embraces broad morphological life-form characteristics (i.e. growth form types). In order to determine differences between invasion statuses (natural, invaded, and cleared) and landscape positions (wet, dry bank, and uplands), I measured the cover of a number of growth form types and other ecosystem attributes (Table 3.2). The four broad growth form classes are forbs (herbaceous dicotyledonous plants), graminoids, shrubs and trees. Plants were assigned to growth forms based on morphology and maximum height reached, as described by Goldblatt and Manning (2000). The narrow growth form classes comprises forbs, graminoids (restioids, sedges, rushes and grasses), shrubs and trees (Goldblatt and Manning, 2000; Table 3.2). Trees (native and invasive) were divided into 3 height classes: seedlings (<1m); juveniles (1-2 m) and adults (>2 m). Ferns were assigned to their own class, since they are very common in riparian as well as terrestrial communities. Restiods, sedges and rushes were separated from grasses, since secondary invasion by weedy grass species has been reported after clearing operations.
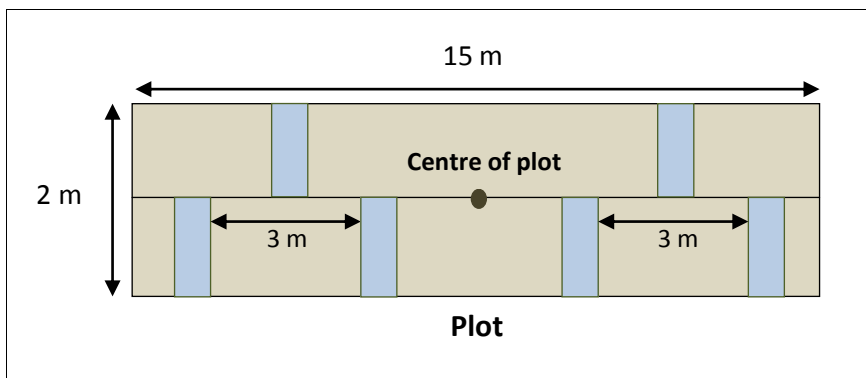
Figure 3.1. Plot layout for vegetation surveys.

For phytosociological studies in fynbos vegetation, 10 X 5 m sized plots are generally used (Reinecke et al., 2007), but, due to the narrow band that wet bank zones usually form in mountain and upper foothill segments of rivers, vegetation survey plots measuring 10 x 2 m (similar to plots used for soil sample collection) were set up in the riparian (wet- and dry bank) and terrestrial zone with the long edge parallel to the river. Canopy cover is a common, easily measured parameter for various analyses. It provides the researcher with information of relative dominance in addition to the influence of plants on soil temperature and rainfall interception (Hanley, 1978). Both Ground Cover (GC) and Canopy Cover (CC) were used in this study for defining the level of influence of the different growth form classes in addition to other classes. CC generally involves a visual estimation of the percentage cover of ground included (i.e. area of influence) in the natural spread of foliage of the specific species (or growth form in this case) (Hanley, 1978). GC within this study is the estimated percentage cover for a number of classes (litter, rocks and/or stones, bare ground, smaller plants, and moss) that cover the soil surface. Within each of the plots, a wooden frame (20 X 50 cm; 0.1 m^2) was placed at six fixed intervals (every 1.5 meters) along the tape and the cover of classes present within or overhanging the frame was recorded (see Figure 3.1), similar as to a study by Daubenmire (1959). Percentage CC (>2 m) of larger shrubs and trees were estimated from a photo taken at a fixed distance from the ground at an angle of 90°. For any given area, total ground- and/or canopy cover classes almost always exceeds 100%, due to vegetation overlap, except for areas that have a very simple structure (i.e. only GC).

3.3.5. Statistical analysis

For each soil parameter, a repeated measures analysis of variance (RMANOVA) was applied to test for significant interactive effects between invasion statuses across seasons and landscape positions across seasons. When seasons were compared, one-way ANOVAs were computed on

all data collected, irrespective of invasion status or position in the landscape. When significant differences between the main (landscape position) and interaction effects (landscape position X seasons) were tested, only data from the four natural sites were applied to exclude the possible effect of invasion and clearing on soil properties. It is important to note that plots selected in terrestrial upland areas at invaded sites are in fact not invaded by *Acacia* spp. and for this reason, excluded from statistical analyses for the purpose of comparing different effects between invasion statuses. Similarly, only measurements from dry bank zones of each site were used to indicate significant differences between invasion status and interaction (invasion status X season) effects, since invasion is most prominent in the dry bank zone. Furthermore, in terms of area, dry bank zones have a larger influence on riparian function. With regard to litter mass and bulk density, the response between both invasion status and landscape position were tested with a one-way ANOVA. Log transformation was applied when necessary to meet the assumptions of ANOVA. Tukey's HSD test was used for post-hoc means separations. Non-normal distributions of data for plant growth forms and other ecosystem attributes, justified the use of non-parametric tests. For each particular class, a Kruskal–Wallis test was used to test for differences between invasion statuses and landscape positions. Similarly, as with soil properties, data from natural sites were used to test for differences between landscape positions and dry banks for effects between invasion statuses. Analyses were performed using Statistica programme (StatSoft, Inc; version 10.0.228.2).

3.4. RESULTS

3.4.1. Soil physical and chemical properties

No significant seasonal interactions were observed for any of the soil particle size distribution classes (Table 3.3). Medium to fine sand particles were significantly greater ($p < 0.001$) and coarse sand significantly reduced ($p < 0.05$) under invaded stands than that of natural riparian fynbos respectively. Although not significant, there was a general trend towards higher silt and clay content in invaded sites relative to natural and cleared sites. Riparian soils were strongly dominated by medium to fine sand (Table 3.3). Silt and clay content differed significantly between landscape positions ($F_{[2, 46]} = 36.90$; $p < 0.001$; Table 3.3) with lowest mean contents in wet banks (3.93%), followed by higher contents in dry bank (7.1%) and upland (13.7%) zones. Furthermore, wet bank soils were characterized by high contents of coarse sand fragments (36.0%), which also differed significantly from upland areas (28.3%; $p < 0.05$).

Table 3.3. Distribution of soil particle size classes between invasion statuses and landscape positions. No significant seasonal interactions were observed for any of the particle size distribution classes (both invasion statuses and landscape positions [#]), therefore data were combined and mean ± SE are based on pooled data for autumn and spring. For each class, letters (distributed horizontally) denote significant differences based on a one-way ANOVA with Tukey post-hoc test (p<0.05): invasion status ([a,b,c]) and landscape position ([x,y,z]).

Particle size distribution classes	INVASION STATUS			LANDSCAPE POSITION		
	NATURAL	INVADED	CLEARED	WET BANK	DRY BANK	UPLANDS
Coarse sand (0.425-2.0 mm)	29.88±1.76 [a]	20.09±2.19 [b]	29.78±2.32 [a]	36.00 ±2.09 [x]	29.88±1.76 [y]	28.29±1.56 [y]
Medium to fine sand (0.053-0.425 mm)	63.00±2.00 [b]	69.99±2.81 [a]	63.06±2.72 [ab]	60.07±2.07 [xy]	63.00±2.00 [x]	57.98±1.33 [y]
Silt and clay (<0.053mm)	7.13±0.63 [a]	9.92±1.37 [a]	7.15±1.06 [a]	3.92±0.30 [z]	7.13±0.63 [y]	13.73±0.68 [x]

[#]Interactions between invasion statuses X season: coarse sand ($F_{[2, 46]}$ =0.101, p=0.905), medium to fine sand ($F_{[2, 46]}$ =0.334, p =0.714) and silt and clay ($F_{[2, 46]}$ =2.156, p =0.127). Interactions among landscape positions X season: coarse sand ($F_{[2, 46]}$ =0.298, p =0.743), medium to fine sand ($F_{[2, 46]}$ =0.236, p =0.791) and silt and clay ($F_{[2, 46]}$ =2.113, p =0.133).

Table 3.4. F-values for selected physical and chemical properties ([#]). Three different ANOVAs were computed as indicated by the different colours. Invasion status and invasion status X season (and the same for landscape position) indicate significant differences for main and interaction effects based on ANOVA, F-value and significance levels indicated by asterisks (*p<0.05, **p<0.01, ***p<0.001). Overall differences between seasons were tested with a one-way ANOVA, based on all data, irrespective of invasion status and landscape position.

ANOVA	df	GSWC	pH	EC
Landscape position	2	32.82***	07.29***	01.10
Landscape position X Season	6	01.62	02.24*	00.64
Invasion status	2	01.89	01.98	20.31***
Invasion status X Season	6	00.22	03.07**	02.23*
Season (all data)	3	35.42***	50.98***	13.23***

[#] See Appendix E for actual values across seasons

Percentage soil moisture content (GSWC) varied significantly throughout the year (One-way ANOVA; $F_{[3, 555]}$ =35.421, p<0.001; Table 3.4), with a peak in winter (mean: 12.49%) and significant declines in summer (mean: 5.03%). Soil moisture content amongst invasion status or its interactions with seasons were insignificant (Table 3.4). Averaged over the year, GSWC showed highly significant differences between landscape positions ($F_{[2, 193]}$ =32.817, p<0.001;

Table 3.4). Soils associated with wet banks had significantly higher moisture content compared to dry bank and upland zones across seasons, with exception to winter (Figure 3.2a). Differences in GSWC between dry banks and terrestrial areas were less apparent, as dry banks were only significantly different from upland terrestrial zones during winter (p<0.01). Soil moisture averaged around 14.9% for wet banks, 8.9% for dry banks and 6.6% for upland areas. Electrical conductivity of soils differed significantly between seasons ($F_{[3, 554]}$ =13.230, p<0.001; Table 3.4) with highest mean values observed during summer (46.98 µs/cm). Concentration of dissolved materials in soils showed significant interactions between invasion statuses and season ($F_{[6, 138]}$ =2.234, p<0.05; Figure 3.2b). The highest mean concentrations of dissolved materials were observed in invaded sites (51.05 µs/cm), followed by the cleared sites (40.57 µs/cm) and natural sites (21.45 µs/cm). No differences were observed between landscape positions; however wet bank zones had the lowest mean EC values of 19.63 µs/cm.

Dry litter mass differed between invasion statuses ($F_{[2, 43]}$ =10.024, p<0.001) and was more than double in *Acacia*-invaded stands (1436.8 g/m^2) relative to natural (553.6 g/m^2; p<0.001) and cleared (500.8 g/m$^{2;}$ p<0.001; Figure 3.2c) riparian areas; natural sites did not differ from cleared areas (p=0.313; Figure 3.2c). Additionally, litter mass also differed between landscape positions (one-way ANOVA: $F_{[2, 35]}$ =3.542, p<0.05; results not shown), with dry banks (553.6 g/m^2) significantly different from wet banks (275.2g/m^2; p<0.05) and upland (284.8 g/m^2; p<0.05; Appendix E) lateral zones. Soil bulk densities differed significantly between invasion status ($F_{2, 43}$ =3.773, p<0.05; Figure 3.2c) and landscape positions ($F_{2, 42}$ =5.228, p<0.01; results not shown). Compared to both natural (p<0.05) and cleared (p<0.05) sites, soils underneath *Acacia* stands had significantly lower bulk densities (0.93g/cm^3), whereas no differences were apparent between natural and cleared sites (p=0.876; Figure 3.2c). Wet bank zones (1.24 g/cm^3) were associated with significantly higher bulk densities (heavier soils) compared to both dry bank (1.11 g/cm^3; p<0.05) and upland (1.06 g/cm^3; p<0.01) zones (statistics not shown; Appendix E).

Typical of fynbos soils, pH is acidic (Figure 3.2d). Soil pH decreased significantly as the dry season progressed (one-way ANOVA: $F_{[3, 555]}$ =50.983, p<0.001; Table 3.4). Soils were significantly more acidic in spring (pH: 4.90) and summer (pH: 4.82) compared to autumn (pH: 5.29) and winter (pH: 5.25). pH showed no statistical significances between invasion statuses (Table 3.4) but invaded sites showed trends towards lower soil acidity compared to natural sites. There was a significant interaction between seasons and landscape position for pH ($F_{[6, 138]}$ =2.242, p<0.05; Table 3.4). Soils associated with wet- (pH: 4.92; p<0.001) and dry bank (pH:

5.00; p<0.01) zones were significantly more acidic than terrestrial areas (pH: 5.20) when seasons were pooled (Figure 3.2d).
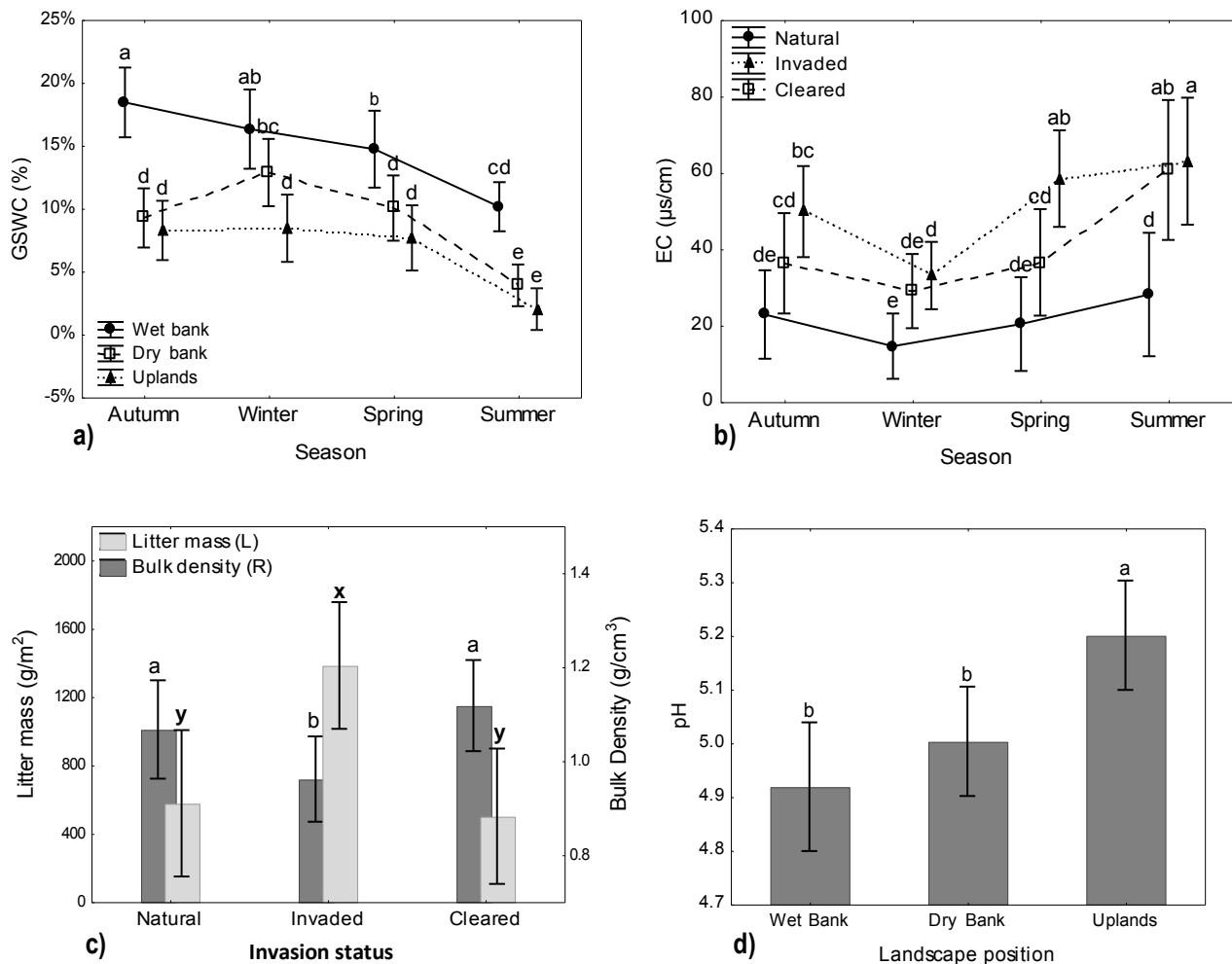
Figure 3.2. Soil physical, chemical and biological (litter mass) properties. (**a**) Gravimetric soil water content (GSWC) for landscape positions across seasons; (**b**) Electric Conductivity (EC) for invasion statuses across seasons; (**c**) litter dry mass and bulk density for invasion statuses; and (**d**) soil pH for landscape positions. Point symbols (Fig 3.2 **a**, **b**) and bars (Fig 3.2 **c**, **d**) indicate means and whiskers indicate ± 95% confidence interval. (Fig 3.2**a**) Landscape positions X seasons ($F_{[6, 138]}$ =1.618, p =0.147) and (Fig 3.2**b**) invasion status X season ($F_{[6, 138]}$ = 2.234, p =0.049) indicate significant differences (Tukey tests; p<0.05) for interaction effects based on repeated measures ANOVAs. Different letters represent significant differences (Tukey tests, p<0.05) based on one-way ANOVAs: Fig 3.2**c** [litter mass (^{x,y}) and bulk density (^{a,b})] and Fig 3.2**d** [soil pH (^{a,b})]. Statistics for litter mass was computed on log transformed data to meet normality assumptions.
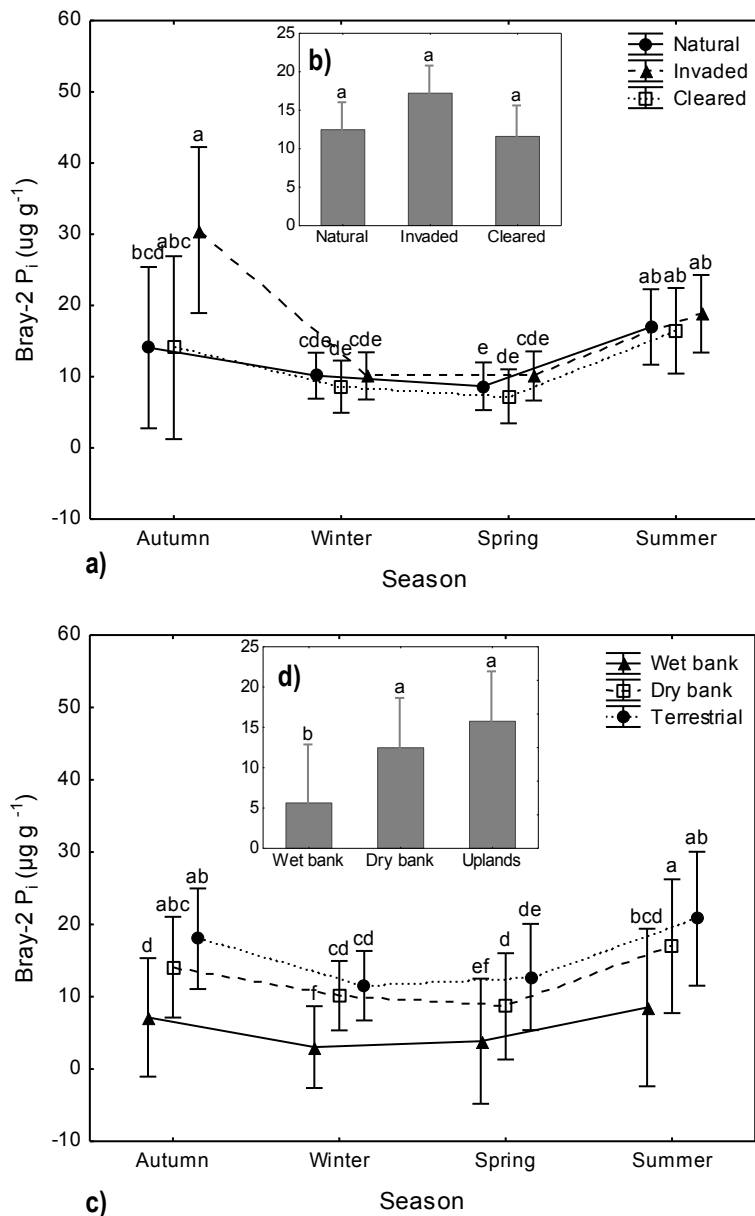
Figure 3.3. (**a**) Bray-2 available P_i for invasion statuses and (**c**) landscape positions across seasons. Mean values are indicated by different point symbols and whiskers indicate ± 95% confidence interval. Letters indicate significant differences (Tukey tests, p<0.05) for interaction effects based on repeated measures ANOVAs: Invasion statuses X seasons (Fig 3.3**a**: $F_{[6,\ 138]}$ =0.897, p =0.499) and landscape position X season (Fig 3.3**c**: $F_{[6,\ 138]}$ =1.030, p =0.409). Mean seasonal measurements for Bray-2 P_i are depicted in embedded bar graphs for (Fig 3.3**b**) invasion statuses and (Fig 3.3**d**) landscape positions. In the embedded graphs letters represent significant differences (Tukey tests, p<0.05) based on one-way ANOVAs: invasion statuses ($F_{[2,\ 196]}$ =1.327, p =0.268) and landscape positions ($F_{[2,\ 193]}$ =12.701, p<0.001). All statistics were computed on log transformed data to meet the assumptions of ANOVA.

Significant overall seasonal trends were noted for available P_i ($F_{[3,\ 564]}$ =31.073, p<0.001) with higher overall concentrations in summer (15.9 µg g^{-1}) and autumn (16.3 µg g^{-1}). Phosphorus did not differ between invasion statuses (one-way ANOVA: $F_{[2,\ 196]}$ =1.327, p =0.268) and its

interactions with seasons ($F_{[6, 138]}$ =0.897, p =0.499; Figure 3.3a, b). Nevertheless, there was a general trend towards enhanced available P_i concentrations under *Acacia* canopies (mean: 17.42 µg g^{-1}; Figure 3.3a, b). Interactions amongst landscape positions and season were insignificant ($F_{[6, 138]}$ =1.030, p =0.409; Figure 3.3c), however, averaged over the year, available P_i showed significant differences between landscape positions (one-way ANOVA: $F_{[2, 193]}$ =12.701, p<0.001; Figure 3.3d). Mean Bray-2 P_i concentrations associated with wet bank zones (5.63 µg g^{-1}) were significantly lower compared to both dry banks (12.47 µg g^{-1}; p<0.001) and upland (15.76 µg g^{-1}; p<0.001) areas, whereas no differences were observed between dry banks and upland terrestrial zones (p =0.947; Figure 3.4d) and both followed similar trends across seasons (Figure 3.3c).

Significant interaction between available N (NH_4^+ and NO_3^-) and seasons were noted (two-way ANOVA: $F_{[3, 792]}$ =29.969, p<0.001; Figure 3.4a). NH_4^+ had significantly higher concentrations in summer (4.03 µg g^{-1}) relative to autumn (1.43 µg g^{-1}), winter (0.94 µg g^{-1}) and spring (1.36 µg g^{-1}), and also differ significantly from NO_3^- (across all seasons). On the other hand, NO_3^- concentrations showed a peak in autumn (2.99 µg g^{-1}) with significantly lower concentrations in winter (1.93 µg g^{-1}) relative to other seasons (Figure 3.4a). Significant overall interaction ($F_{[1, 264]}$ =9.522, p<0.01) showed that NO_3^- (mean: 2.49 µg g^{-1}) is the dominant form of available inorganic N in the topsoil.

Averaged over the course of the year, *Acacia*- invaded and cleared plots had 1.7 and 2 times as much NO_3^- and 2.2 and 1.8 times as much NH_4^+ as natural riparian areas respectively (Figure 3.4b). Average annual total available N (NO_3^- and NH_4^+) was significantly greater in both *Acacia*-invaded (5.9 µg g^{-1}; p<0.001) and cleared riparian sites (6.1 µg g^{-1}; p<0.001) than in natural fynbos (3.62 µg g^{-1}), with no difference between invaded and cleared (Figure 3.4b). Mean concentrations for both NH_4^+ and NO_3^- differed significantly between landscape positions when seasons were pooled (Figure 3.4c). In general, NH_4^+ concentrations in wet banks differed from both dry banks (p<0.001) and terrestrial (p<0.001) areas, whereas NO_3^- concentration did not differ amongst riparian wet- and dry bank zones (p =0.453), but both were significantly different from terrestrial upland areas (Figure 3.4c). Furthermore, total available N (NO_3^- and NH_4^+) showed significant differences between landscape positions ($F_{[2, 92]}$ =7.195, p<0.01; Figure 3.4c) with dry banks (3.63 µg g^{-1}; p<0.01) and associated uplands (3.96 µg g^{-1}; p<0.001) characterized by considerably greater concentrations of available N compared to wet banks (2.49 µg g^{-1}), with no differences between dry bank and uplands (p =0.358).
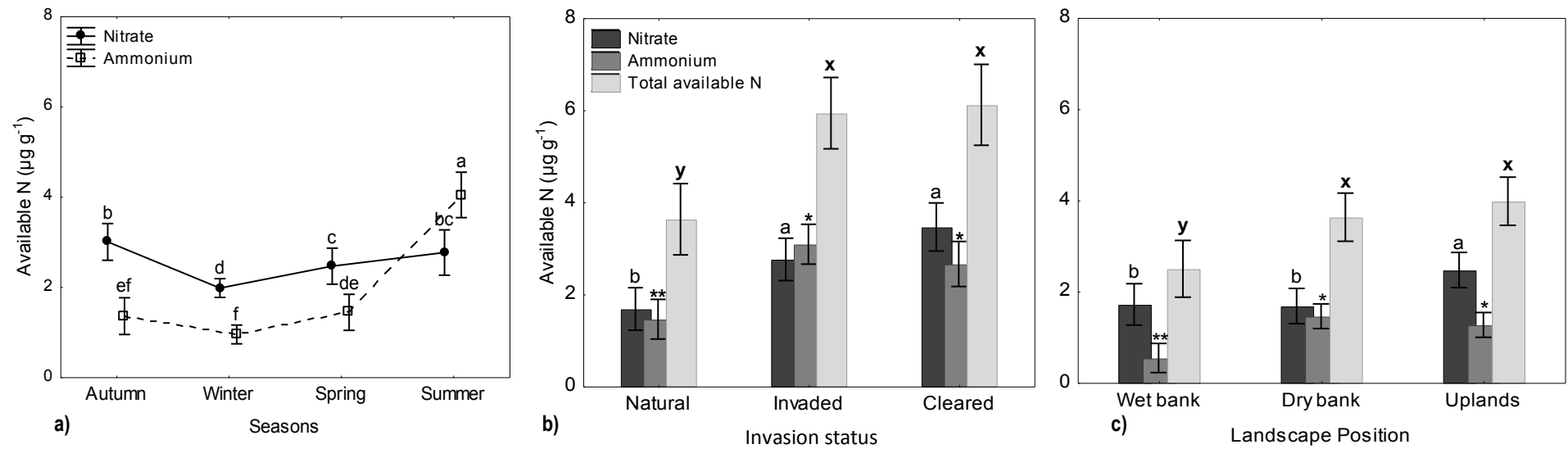
Figure 3.4. (**a**) Ammonium (NH_4^+) and nitrate (NO_3^-) concentrations in soils across seasons. Letters denote significant differences (Tukey tests, $p<0.05$) based on a two-way repeated measures ANOVA ($F_{[3, 792]}=29.969$, $p<0.001$) using all the data collected over the year, and irrespective of invasion status or position in the landscape. Mean values are indicated by solid symbols (NO_3^-) and squares (NH_4^+), and whiskers represent the 95% confidence interval. Available inorganic N in the form of ammonium (NH_4^+), nitrate (NO_3^-), and total available inorganic N ($NH_4^+ + NO_3^-$) for (Figure 3.4b) natural, invaded and cleared sites (invasion statuses), and (Figure 3.4c) wet- and dry bank and uplands lateral zones (landscape position). Mean values are indicated by bars and whiskers represent ± 95% confidence interval. Different letters and symbols [NO_3^- ($^{a;b}$); NH_4^+ (*;**); and total available N($^{x;y}$)] represent significant differences (Tukey tests, $p<0.05$) based on one-way ANOVAs: invasion statuses (NH_4^+: $F_{[2, 197]}=7.180$, $p<0.001$; NO_3^-: $F_{[2, 197]}=12.158$, $p<0.001$; total available N: $F_{[2, 197]}=8.405$, $p<0.001$) and landscape positions (NH_4^+: $F_{[2, 193]}=9.932$, $p<0.001$; NO_3^-: $F_{[2, 193]}=4.970$, $p<0.01$; total available N: $F_{[2, 193]}=6.729$, $p<0.01$).
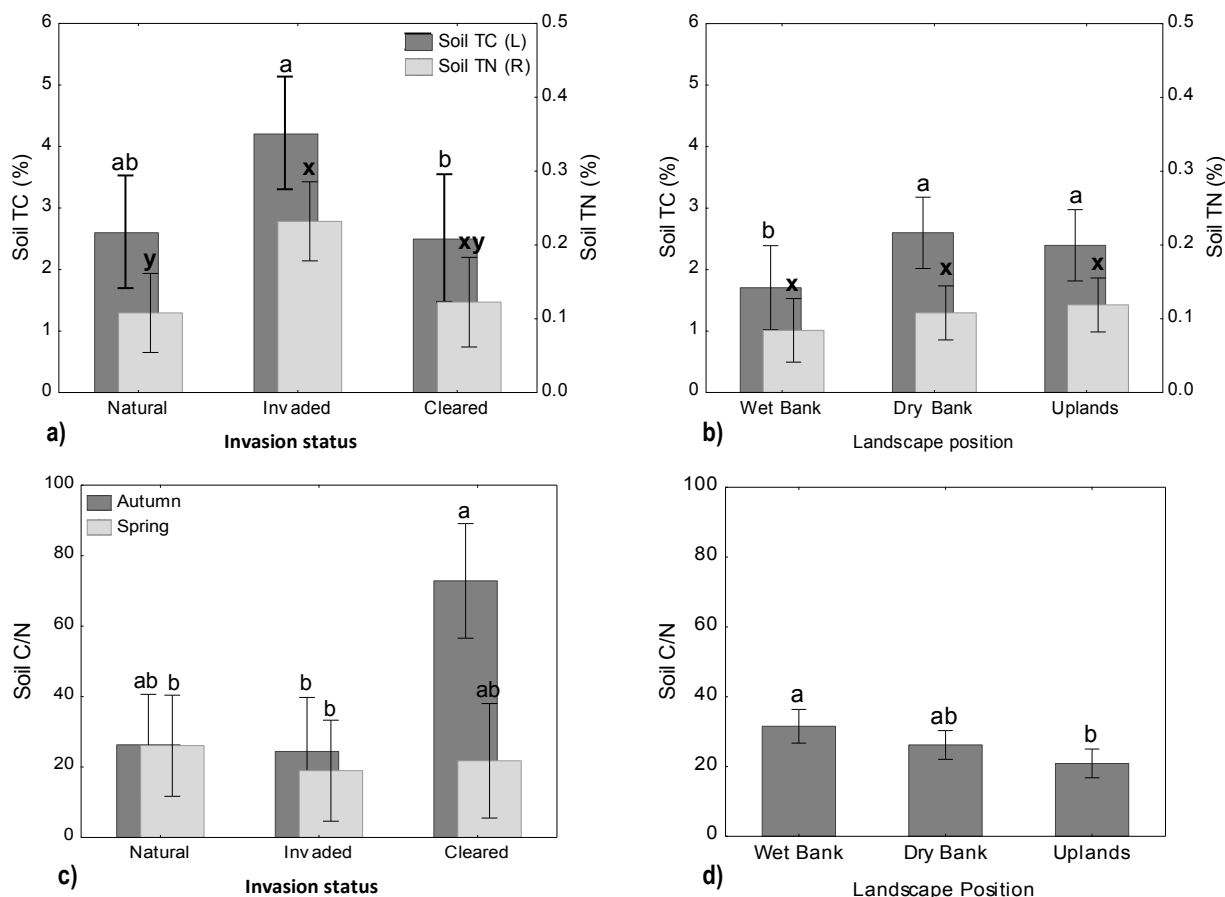
Figure 3.5. Soil total N and C for (**a**) invasion statuses and (**b**) landscape positions. Soil C/N for (**c**) invasion status across seasons and (**c**) landscape positions. Bars represent means and whiskers represent ± 95% confidence intervals for percentages (soil TN and TC) and ratios (C/N). Significance levels (Tukey post hoc test; p<0.05) are indicated by different letters for one-way ANOVAs: [TC ([a]; [b]) and TN ([x]; [y]) for invasion statuses and landscape positions] and [C/N ([a]; [b]) for landscape positions] and repeated measures ANOVA [C/N ([a]; [b]) for invasion statuses X seasons]. All statistical analyses were computed on log transformed data to meet the assumptions for ANOVA. .

Interactions between invasion statuses and seasons were not significant for soil total N ($F_{[2,\ 47]}$ =1.051, p =0.358), and soil total C ($F_{[2,\ 47]}$ =0.409, p =0.667), however significant differences between invasion statuses for TN (one-way ANOVA: $F_{[2,\ 97]}$ = 5.951, p<0.01) and TC (one-way ANOVA: $F_{[2,\ 97]}$ = 4.191, p<0.05) were found when seasons were pooled (Figure 3.5a). TN content was significantly higher under *Acacia* stands than in both natural (p<0.01) and cleared (p<0.01) areas, with no differences between natural and cleared sites (p =0.773). Natural sites were not different from invaded sites (p =0.093) with regard to TC content, but cleared areas had a significantly lower TC content (p<0.01) relative to invaded sites. The effect of season on soil C/N was only apparent at cleared sites (p<0.001); Figure 3.5c). Soil mean C/N was 6.4% lower under Acacias than under native stands, but this was not significant. Cleared sites had high soil C/N ratios (mean: 1:47) and differed significantly from invaded (p<0.05), but not from natural (p

=0.224) sites. Soil TC differed significantly between landscape positions and showed higher concentrations in upland and dry bank soils compared to wet banks, however, TN did not differ between landscape positions (Figure 3.5b). Significant differences between landscape positions were observed for soil C/N (one-way ANOVA: $F_{[2, 95]}$ =4.029, p<0.05). Wet bank zones were characterized by high mean C/N ratios (31.5) and differed significantly from upland (25.8; p <0.01), but not dry bank (20.7; Figure 3.5d) zones.

Table 3.5. Spearman's correlation coefficient ρ (rho) for selected soil physical and chemical properties. Significant relationships (p<0.05) are indicated by an asterisk (*). Correlations were calculated from all available data irrespective of invasion status or landscape position, however, different variables differed in the regularity of sampling: seasonally (Bray-2 P_i, NO_3^-, NH_4^+, EC and pH); biannually (Soil TN, TC and C/N) and once of during spring (bulk density). Correlation values represent only instances where comparisons could be made. For example, bulk density was determined during spring and Bray-2 P_i, seasonally, so that the ρ-value (-0.037) is based on a single season (spring) where data was available for both factors. N/A: not applicable.

Soil Properties	GSWC (%)	Silt and clay (%)	Bray-2 P_i ($\mu g\ g^{-1}$)	NO_3^- ($\mu g\ g^{-1}$)	NH_4^+ ($\mu g\ g^{-1}$)	Soil TN (%)	Soil TC (%)
Bray-2 P_i ($\mu g\ g^{-1}$)	-0.426*	0.416*					
NO_3^- ($\mu g\ g^{-1}$)	-0.258*	0.501*	0.380*				
NH_4^+ ($\mu g\ g^{-1}$)	-0.486*	0.559*	0.442*	0.535*			
Soil TN (%)	0.110	0.663*	0.345*	0.419*	0.565*		
Soil TC (%)	0.102	0.714*	0.349*	0.477*	0.603*	0.922*	
Soil C/N	N/A	-0.302*	N/A	-0.197	-0.341*	N/A	N/A
EC (µs/cm)	-0.208*	0.404*	N/A	0.395*	0.661*	0.439*	0.467*
Bulk density (g/cm^3)	N/A	-0.355*	-0.037	-0.355*	-0.435*	-0.494*	-0.509*
pH (H$_2$0)	N/A	0.379*	-0.043	-0.162	0.091	N/A	N/A

Silt and clay content was significantly correlated with soil nutrients (N, P and C), bulk density and other chemical properties (pH and EC), regardless of invasion status or landscape position. Soil bulk density showed a significant inverse relationship with available N (NO_3^- and NH_4^+) concentrations and soil TN and TC (Table 3.5). Bray-2 P_i concentrations showed a significant positive relationship with soil total and available N (NO_3^- and NH_4^+). A significant negative correlation occurred between soil moisture content (GSWC) and available nutrient (N and P) concentrations (Table 3.5). Soil pH had no effect on Bray-2 available P_i (ρ =-0.043). Soil total C (TC) and total N (TN) are highly correlated with one another. Furthermore, available N concentrations, particularly NH_4^+, were strongly related to soil total N and C (Table 3.5).

3.4.1. Plant functional types (PFTs) and other ecosystem components

Results from the Kruskal-Wallis test indicates that there are significant differences in the cover of selected plant growth form types and other ecosystem attributes between invasion statuses and landscape positions (Table 3.6). Natural sites were characterized by the most complex structural composition with a good combination and cover of different plant growth form types. The four prominent functional types in natural sites, which also differed significantly from both invaded and cleared sites, were: trees/shrubs (>2m); grasses; graminoids (excluding grasses); and shrubs. With exception to litter cover, invaded sites had the lowest cover for all functional types and other ecosystem components presented in Table 3.6. The cover of grasses, shrubs, bare ground, rocks/stones, forbs, ferns, and graminoids were significantly different from natural sites (Table 3.6). Invaded riparian dry bank zones were structurally and compositionally the least complex, as litter- and *Acacia* tree/shrub (>2m) cover dominated the understorey (74.7%; Table 3.6) and overstorey (61.3%; Figure 3.6) respectively. Compared to both natural ($p<0.001$) and cleared ($p<0.001$) sites, litter cover was significantly higher in invaded areas. Grasses (36.52%) and other ecosystem attributes, such as bare ground (39.6%) were dominant features associated with cleared sites. Mostly alien grass species, such as *Briza maxima, Paspalatum dilatatum,* and *Pennisetum clandestinum* were detected at the cleared sites.

Table 3.6. Percentage canopy- and ground cover for plant functional types and other ecosystem attributes. The data reflect means ± SE based on percentage cover for all classes. For each class, letters (distributed horizontally) denote significant differences based on a Kruskal–Wallis multiple comparisons test ($p<0.05$): invasion status (^{a,b,c}) and landscape position (^{x,y,z}). Invasion statuses are based on dry bank data and landscape position on natural site data only. GC: ground cover; and CC: canopy cover.

Cover classes	INVASION STATUS			LANDSCAPE POSITION		
	Natural	Invaded	Cleared	Wet Bank	Dry Bank	Uplands
Litter (GC)	23.58±2.62 [b]	74.75±5.49 [a]	7.29±1.43 [c]	8.24±2.2 [y]	23.58±2.6 [x]	18.21±2.5 [x]
Bare ground (GC)	27.92±2.81 [a]	20.11±5.24 [a]	39.61±8.08 [a]	37.63±4.7 [x]	27.92±2.8 [x]	39.66±4.2 [x]
Rocks/stones	9.11±1.74 [a]	1.52±1.07 [b]	4.15±2.42 [b]	22.31±5.4 [x]	9.10±1.7 [x]	14.28±2.7 [x]
Moss (GC)	0.71±0.26 [a]	0.05±0.04 [a]	0.24±0.24 [a]	8.08±1.6 [x]	0.71±0.3 [y]	0.59±0.3 [y]
Grasses (GC+CC)	14.70±2.77 [b]	0.41±0.37 [c]	36.52±8.07 [a]	4.68±1.5 [y]	14.70±2.8 [x]	8.28±1.9 [xy]
Graminoids	18.65±2.83 [a]	1.39±0.80 [b]	3.03±1.35 [b]	8.51±2.2 [x]	18.65±2.8 [x]	8.73±2.3 [y]
Geophytes (GC+CC)	0.71±0.26 [a]	0.00±0.00 [a]	0.04±0.04 [a]	1.40±0.4 [x]	0.71±0.3 [x]	2.33±0.7 [x]
Shrubs (CC)	9.25±1.74 [a]	0.62±0.30 [b]	1.87±0.77 [b]	2.89±1.3 [y]	9.25±1.7 [xy]	18.18±2.9 [x]
Forbs (GC+CC)	3.74±1.10 [a]	0.01±0.01 [b]	1.77±0.44 [a]	1.56±1.0 [y]	3.74±1.1 [xy]	4.71±1.1 [x]
Ferns (CC)	7.25±1.44 [a]	0.23±0.15 [b]	0.57±0.31 [b]	13.86±4.4 [x]	7.25±1.4 [x]	9.59±3.5 [x]

The cover of PFTs and other components also reflects landscape position (Table 3.6) and significant differences were found for a number of classes: grasses, moss, litter, graminoids, shrubs and forbs (see Table 3.6 for significance values). The cover of grasses (8.3%), graminoids (18.7%) and litter (23.6%) were higher in dry banks relative to wet bank and upland zones. Moss cover ($p < 0.001$) was significantly reduced in dry bank and terrestrial zones, whereas shrubs were more prominent in uplands areas (18.2%; $p < 0.01$).
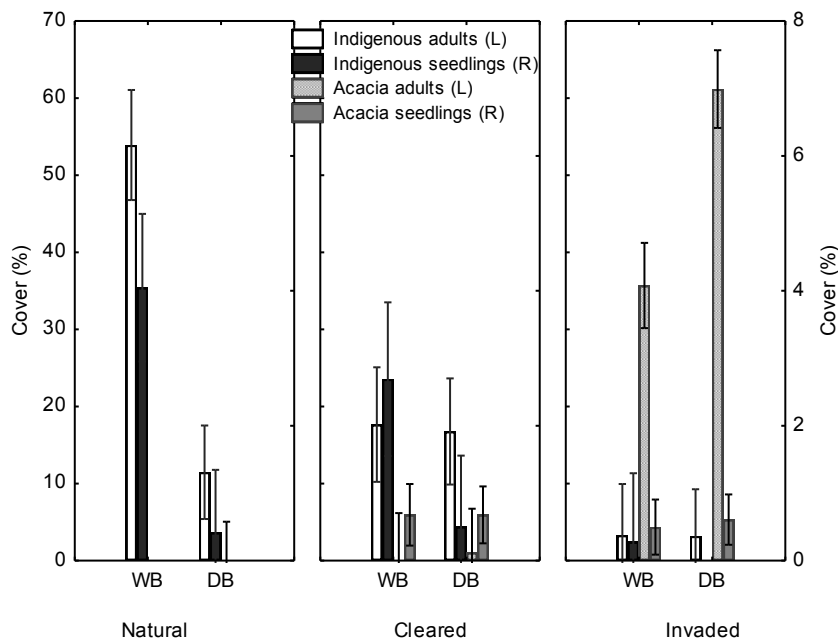
Figure 3.6. Canopy cover (%) of indigenous- versus invasive *Acacia* adult (>2m) trees/shrubs and seedlings (<1m) between invasion statuses (natural, cleared, invaded) and landscape positions (wet- and dry banks). Bars indicate means ± SE. Only data for dry- and wet bank are shown since *Acacia* spp. were absent in upland terrestrial plots. Wherever data are not shown, cover is 0%. WB: wet bank; and DB: dry bank.

In natural sites, mean indigenous- tree/shrub and seedling cover was considerably higher in wet bank compared to dry bank zones, whereas no *Acacia* individuals were present (Figure 3.6). As opposed to indigenous tree/shrub species in natural sites, which were more prominent in wet bank areas, mean cover of *Acacia* spp. in invaded sites were much higher in dry bank (61.3%) compared to wet bank (35.7%) zones. Indigenous adults and seedlings of both indigenous- and invasive woody plants were largely non-existent in *Acacia*-invaded riparian zones (Figure 3.6). Compared to natural sites (53.9%), indigenous tree/shrub cover observed at cleared sites was considerably lower in wet bank (17.7%) zones.

3.5. DISCUSSION

Invasive N_2-fixing species affect vegetation communities and soil properties in a variety of ecosystems. Based on results from previous studies (e.g. Musil, 1993; Yelenik et al., 2004; Marchante et al., 2008; Hellmann et al., 2011) we expected higher nutrient levels and litter cover under *Acacia* stands. As hypothesized, invasion by *Acacia* spp. (mostly *A. mearnsii*) do affect fynbos riparian structure and function by i) enriching the system with N (total and available N) and C; ii) altering litter inputs and soil physical properties and iii) decreasing the cover and changing the composition of PFTs. There is evidence for a legacy effect with respect to N availability persisted at the cleared sites while no apparent differences were detected for other soil properties. This legacy effect may explain why cleared riparian ecotones are invaded by exotic grasses. In intact systems, the cover of PFTs and other ecosystem components differed between landscape positions. Differences in soil physical and chemical properties were also apparent. Wet banks zones, in particular, were associated with distinctive soil properties that differed from both dry bank and upland lateral zones with regard to soil nutrient concentrations (low total available N and P_i), soil physical (high moisture and low silt and clay content) and chemical properties (low EC values). Soil texture was an important factor controlling soil nutrient characteristics, regardless of invasion status or position in the landscape.

3.5.1. Soil physical and chemical properties

Table Mountain Sandstone, which is the dominant lithology observed at sites, weathers to sandy soils, and is manifested by the coarsely textured nature of stream sediment observed in these systems, although hydraulic and geomorphic factors also have an important influence on sediment sorting (Heydorn and Grindley, 1982; Pinay et al., 1995). Soils associated with high silt and clay contents were found on higher topographic positions in the landscape (such as upland areas). Silt and clay contents progressively increase away from the river channel, whereas coarsely textured materials (0.425-2.0 mm) decline. Wet banks had particularly low concentrations (<4%) of fine materials, whereas dry banks were intermediate between wet bank and upland lateral zones. Vegetation decreases water velocity further away from the active channel so that lighter finer, binding material is deposited further away, whereas the heavier coarser sand fractions settle closer to the channel (Brown et al., 2004; Adair et al., 2004). Since erosion exceeds deposition in fynbos riparian ecosystems, one would expect these systems to have lower contents of finer materials. Therefore, being regularly eroded and inundated, wet bank soils are differentiated from adjacent dry banks and uplands by their higher percentage of coarse sand fractions and significantly lower proportions of finer materials, such as silt and clay.

Fluvial dynamics therefore play an important role in the differences observed between landscape positions with regards to soil textural classes.

Fine-textured soils have the capacity to preserve or protect OM and microbial biomass, which may allow greater nutrient retention (Austin et al., 2004). Differences in soil particle size distribution in riparian zones versus uplands may also give rise to patterns of resource distribution, such as N (Bechtold and Naiman, 2006). The low silt and clay content of wet bank soils, which were also coupled to lower concentrations of nutrients (soil available P_i and N; total N and C) may explain why soils closely associated with the river channel have a lower capacity to store nutrients. Available inorganic N, TN, TC, and electric conductivity were significantly positively correlated to soil silt and clay contents. This is supported by a study of Bechtold and Naiman (2006) that reported positive correlations between silt and clay concentrations and soil TN and total organic C along the Phugwane River, South Africa. By controlling several soil physical and chemical properties and nutrient concentrations (N, C, P), as detected in this study, soil texture, soil moisture content and bulk density can be a particularly good predictor of many ecosystem properties (Chapin et al., 2002). This study confirms that soil texture has a strong influence in mediating the retention of nutrients in both riparian and upland ecosystems.

Invaded sites had significantly lower contents of coarse sand fractions and higher contents of finer binding materials, such as silt and clay, compared to natural sites. Similarly, DeCant (2008) found comparatively finer textured soils under cottonwood trees in riparian zones with subcanopy N_2-fixer, *Elaeagnus angustifolia,* compared to native cottonwood trees alone, whereas Rice et al. (2004) did not find any differences in particle size distribution between native pine oak ecosystems and N_2-fixing *Robinia pseudoacacia* (black locust) stands. Do Acacias tend to recruit more effectively on finer textured soils (i.e. are they passengers of change) or does invasion change soil particle size distribution by trapping finer particles (are they drivers of change)? Compared to natural sites at the same landscape position; *Acacia* stands lead to a widening the river channels. These species may create a damming effect by slowing down the velocity of water, consequently trapping finer sediments in these systems (Rowntree, 1991; Boucher, 2002). Hoffmann and Moran (1988) found that stands of *Sesbania punicea* trap sediments in riparian zones, creating a more favorable habitat for further expansion of this species. It is important to note that differences in soil types (geology) between different catchments may also complicate overall findings, as Brown et al. (2004) found soils under both invaded and natural vegetation to differ significantly between rivers in different catchments with regard to soil texture and pH.

Soil moisture strongly affects the flux of nutrients in the soil (Chapin et al., 2002; Morris et al., 2011), and therefore plays an essential role in the cycling and storage of nutrients. Differences amongst areas that remains moist throughout the year, associated with proximity to perennial fynbos rivers, compared to areas that are dependent upon seasonal precipitation events (non-riparian uplands), might be very different in microbial composition and soil physical and chemical properties. In Mediterranean-type ecosystems, the seasonal pattern of cool temperatures coinciding with high discharge, followed by hot temperatures and low discharges, greatly differs from that of most other temperate systems (Gasith and Resh, 1999). Soil nutrient concentrations (NO_3^-, NH_4^-, and available P_i) increase significantly as soil moisture levels decline, as anticipated with rainfall/ enrichment factor relationships (Booi, 2011). Heffernan and Sponseller (2004) found that available nutrient pools were negatively correlated with soil moisture in Sonoran desert riparian soils. Soil water dynamics, which change across lateral zones (i.e. distance away from the river channel), may therefore play an essential role in explaining differences observed for several soil properties between landscape positions. The higher moisture content and low soil pH, EC and nutrient concentrations together with the coarsely-textured nature of wet bank zones may be indicative of leached soils. Changes in soil moisture contents under IAPs have been reported in other studies with some mixed results. Gaertner et al. (2011) reported a decline in soil moisture contents during late winter and early spring in the *Acacia*-invaded relative to reference fynbos sites. Conversely, Yelenik et al. (2004) and Marchante et al. (2008) found higher water contents under *Acacia* stands compared to non-invaded areas, whereas no difference was observed between invasion statuses in this study.

Based on results from previous studies in *Acacia*-invaded ecosystems (e.g. Yelenik et al., 2004; Marchante et al., 2008), higher litter mass and higher nutrient levels was expected under *Acacia* stands. Litter mass was substantially greater under *Acacia* spp., largely consisting of *Acacia* seed pods and leaves. These species have also been shown to markedly increase aboveground biomass and add to the litter layer in other invaded ecosystems (Witkowski and Mitchell, 1987; Witkowski, 1991; Gaertner et al., 2011; Hellmann et al., 2011). The significantly higher litter concentrations in invaded sites relative to natural and cleared sites may likely play an important role in enhancing nutrient concentrations (especially N), as observed in surface soils of this study, because litter provides the C and N substrates that can sustain enzyme production (see Chapter 4) and enhances microbial growth (Allison et al., 2006). Bulk density of soils is closely related to soil OM content (Robertson et al., 1999; Chapin et al., 2002) and this relationship has been verified many times in the literature. Soils associated with invaded areas were characterized by low bulk densities (<1g/cm^3) and with higher percentage total C and N. Soil bulk density varies with soil OM content and texture, and may therefore be a good indicator of OM distribution in

soils. Furthermore, silt and clay content of soils, which was inversely correlated with bulk density, may be an important factor explaining the differences in bulk densities observed between landscape positions. Finer textured soils associated with terrestrial uplands have higher internal surface area and their bulk densities lower than coarsely textured wet bank areas (Chapin et al., 2002).

Enhanced evaporation rates during dry summer months may result in increased concentrations of minerals in the soil (Gasith and Resh, 1999) which likely explains the significantly higher EC values observed in summer. Both soil moisture and silt and clay contents (which showed a significant inverse and positive relationship with EC respectively) are physical properties that strongly affect the concentration of dissolved materials in the soil. Various biophysical factors, such as soil moisture, OM distribution and acid and base-forming ions in soils (Chapin et al., 2002), influence temporal changes in soil pH and therefore possibly explain the decline in pH observed in spring and summer. Opposed to the study by Cramer (2010), soil pH was significantly lower in fynbos riparian zones (both wet- and dry banks) compared to upland terrestrial fynbos. Soil chemistry under *Acacia* spp*.* differed from those under indigenous species in that they had significantly higher concentrations of dissolved minerals in soil solution. Changes in soil pH with invasion have been reported in other ecosystems. Similar to my findings, Marchante et al. (2008) and Malcolm et al. (2008) found that soil pH in sites invaded *A. longifolia* (>20 years) and *Robinia pseudoacacia* respectively did not differ from non-invaded sites. Similar findings were reported by Witkowski (1991) in south-western Cape ecosystems invaded by *A. saligna* and *A. longifolia* in sand fynbos and strandveld ecosystems respectively. Contrary, Caldwell (2006) reported increases in soil pH with invasion by *Cytisus scoparius* It is important to note that differences in soil chemical properties detected in this study, such as pH, which is a property mostly influenced by the underlying substrate, may regulate soil enrichment by *Acacia* spp. (Stock and Allsopp, 1992), because pH strongly affects the availability of nutrients through its effects on solubility of phosphate compounds and exchange of cations, such as NH_4^+, K^+, Ca^{2+} (Chapin et al., 2002). In this study, no correlation was found between soil pH and nutrient concentrations (available P and N). Accordingly, pH was probably not a significant factor controlling nutrient availability; however more research is needed to further clarify these relationships.

Low levels of available P_i observed in this study are well documented for fynbos soils (Cramer, 2010), as most of the sites are derived from nutrient-poor sandstones. A significant inverse relationship between patterns in soil moisture and available P_i was noted, regardless of landscape

position or invasion status and this has been supported by other studies (e.g. Grierson and Adams, 2000). P_i concentrations may not only be ascribed to microbial P turnover rates, but may also be related to root growth in response to seasonal changes in temperature and soil moisture (e.g. Grierson and Adams, 2000). The accumulation of available P_i during summer may be attributable to dry and hot conditions that limit plant growth (reducing the demand for nutrients), (Fabre et al., 1996); or the supply of available P_i from organic P pools may be driven by the activities of phosphatase enzymes, which are temperature dependent (Binkley et al., 2000; Dassonville et al., 2008). The higher concentrations of available P_i during summer may also be due to the release of organic P from dying microbial biomass during this time of the year (Jacobs et al., 2007). The lowest available P_i concentrations were observed during the season of optimal growth (spring), consequently increasing the demand for available P_i, and are in accordance with other studies (e.g. Fabre et al., 1996; Grierson and Adams, 2000). The depletion of available P_i concentrations during the wet season (winter) may be a consequence of leaching or direct uptake by plant roots and microbes.

Although overall soil available P_i concentration was enhanced under invasive *Acacia* spp., relative to indigenous fynbos riparian ecosystems, the data taken together are equivocal. Due to their higher growth rates, Australian Acacias may necessitate reasonably high sources of soil P, consequently increasing the rate at which inorganic P enters soil pools (see Chapter 4). But trends for soil available P in response to invasion vary substantially in the literature. Some studies have reported increases (Giardina, et al., 1995; Rice et al., 2004; Hughes and Denslow, 2005; Malcolm et al., 2008), no differences (Marchante et al., 2008) and decreases (Caldwell, 2006) in soil available P in invaded ecosystems compared to their indigenous counterparts (Morris et al., 2011). Binkley et al. (2000) found different effects on different inorganic and organic fractions of P under N_2-fixing *Albizia facalteria*. Contrary to my findings, infestation by N_2-fixing *A. cyclops* (Witkowski and Mitchell, 1987; Witkowski, 1991) and *A. saligna* (Witkowski and Mitchell, 1987) significantly increased available P_i in in coastal lowland strandveld fynbos.

Soil P_i concentrations were strongly associated with fine particle concentrations. A lateral gradient (from river to uplands) of soil texture and phosphorus status occurred, both increasing away from the river channel. Since environmental factors that drive riparian ecosystems processes are very different from adjacent uplands, soil available P is transported into and out of riparian ecotones mainly through adhering to silt and clay particles from lateral and longitudinal vectors, and much of the riparian soil nutrient stocks are transferred to the river through seasonal high flows (Naiman et al., 2005; Jacobs et al., 2007). Cramer (2010) reported significantly higher

concentrations of available P and other soil nutrients, such as K^+, Ca^{2+} and Mg^{2+} and total N, in afromontane forests associated with a fynbos river compared to neighboring open-canopied terrestrial fynbos. Higher nutrient concentrations are thought to enhance the growth of native trees and successional forest development (Manders, 1990; Cramer, 2010). On the contrary, both wet- and dry bank soils had overall lower extractable P_i concentrations compared to upland terrestrial fynbos. Wet bank soils are more acidic and highly leached, and for these reasons, also low in available P_i.

Significant seasonal variations were noted for NO_3^- and NH_4^+ concentrations. Environmental factors, such as seasonality in precipitation and temperature (warm and dry summers, and cold, wet winters), may play an essential role in the seasonal variability in available N concentrations found in this study. The significantly higher concentrations of NH_4^+ observed in summer may be ascribed to ceased nitrification during this time of the year (when water availability is limited), resulting in the accumulation of NH_4^+ in soils. Accumulation of inorganic N usually occurs during dry periods because diffusion of ions is severely restricted in thin water films of dry soil and because sinks of inorganic N are limited by reduced microbial growth and limited plant uptake (Austin et al., 2004; Bardgett, 2005). In addition, N may also be released from a portion of the microbial biomass which is killed under dry conditions in summer (Austin et al., 2004).

In summer, low soil moisture content may limit denitrification, whereas in winter, anaerobic conditions in the soil are more favourable for denitrification (Pinay et al., 1993; Bernal et al., 2007) resulting in a significant drop in soil NO_3^- concentrations relative to other seasons. The peak in NO_3^- concentrations during autumn sampling coincided with the first seasonal rains (Figure 4.1; Chapter 4). Nitrification, which tends to be low in dry soils where low soil moisture content restrict the diffusion of NH_4^+ to nitrifying microbes (Bardgett, 2005), is often stimulated by rainfall after dry cycles (Chapin et al., 2002). Re-wetting of soils after a dry cycle stimulate microbial processes including nitrification (Heffernan and Sponseller, 2004), thereby enhancing soil NO_3^- concentrations. A combination of nutrient leaching (e.g. labile organic N), as a result of seasonal precipitation, and low temperatures (which restricts microbial activity) may account for the significantly lower concentrations of both NH_4^+ and NO_3^- observed in winter relative to other seasons (Follstad Shah et al., 2010). Follstad Shah et al. (2010) and Pinay et al. (1995) also reported significant variation in pools of soil inorganic N in riparian ecosystems through time. Relative to non-invaded terrestrial fynbos, Yelenik et al. (2004) found that both forms of inorganic N (NO_3^- and NH_4^+) in *Acacia*- invaded and cleared terrestrial fynbos ecosystems significantly pulsed during the first winter rains (May and June) and then declined back to lower levels. These

results suggest that fynbos riparian soils may act as sinks or sources of dissolved available inorganic N, depending on the time of the year (Bernal et al., 2007).

The impact of IAPs, particularly *Acacia* spp., on terrestrial soil N stocks have been well documented in the south-western Cape (e.g. Musil, 1993; Witkowski, 1991; Stock et al., 1995; Yelenik et al., 2004, 2007). Soil N availability was significantly enhanced in *Acacia*- invaded and cleared riparian areas relative to natural ecosystems. Increases in soil N were expected, as *A. mearnsii* is a nitrogen fixer (Forrester et al., 2007; Tye and Drake, 2011) and N_2-fixing *Acacia* spp. add to soil N stocks (Yelenik et al., 2004). These findings concur with other studies that investigated the impacts of N_2-fixers on soil N dynamics. Compared to native lowland acid sand fynbos, total annual available N (NH_4^+ and NO_3^-) was greater in both *A. saligna* invaded (Yelenik et al., 2004, 2007) and cleared (Yelenik et al., 2004) areas. Meta-analyses by Ehrenfeld (2003) and Liao et al. (2008) reported relatively consistent increases in soil total- and available N with invasion by N_2-fixers. There is also evidence elsewhere that N_2-fixing species, such as invasion by *A. longifolia* in Portugal dune sand ecosystems (Marchante et al., 2008; Hellmann et al., 2011); *Elaeagnus angustifolia* in New Mexico, USA (DeCant, 2008) and *Robinia pseudoacacia* in pine-oak ecosystems (Rice et al., 2004) increased available inorganic N relative to their respective non-invaded native environments. Hughes and Denslow (2005) reported profound increases in total available inorganic N between *Falcataria*-invaded stands and native forests in Hawaii by factors greater than 100-fold. Nevertheless, exceptions have been recorded locally, such as the study by Stock et al. (1995). Relative to adjacent native ecosystems, they found that available N was significantly higher in *A. cyclops*- invaded strandveld ecosystems, but not in *A. saligna* invaded low nutrient, acid sand fynbos. They suggested that differences in these effects may be attributed to differences in soil properties between sites or leaf chemistry between invasive and native species. The opposite was found in a Europe-wide study, which showed that IAPs increased site nutrient pools only in sites with initially low soil nutrient levels (Dassonville et al., 2008). Even if nutrient availability can promote invasion by plant species, abiotic soil factors may also likely be a driving mechanism for invasion (Wolf et al., 2004). Due to site-specific effects, as mentioned above, each particular ecosystem should be considered and investigated and managed independently (Ehrenfeld, 2003).

Changes in ecosystem nutrient stocks (N and C) after invasion may be associated with the physiological and physical characteristic of the invasive species (Ehrenfeld, 2004). Accordingly, a possible explanation for the significantly greater total- and available N observed under *Acacia* stands may be attributed to key biological traits which are different from native riparian

communities (Morris et al., 2011) including higher growth and photosynthetic rates, larger size (Ehrenfeld, 2004; Liao et al., 2008; Marchante et al., 2011; Morris et al., 2011) and higher inputs of N-enriched litter with rapid turnover rates, resulting in more N returned to the soil (Musil and Midgley, 1990; Witkowskii, 1991; Ehrenfeld, 2004; Yelenik et al., 2004; Marchante et al., 2008). Increases in soil TN and TC content associated with *Acacia*-invaded fynbos riparian ecotones are consistent with those reported for N_2-fixing plants in the fynbos (e.g. Stock et al., 1995; Yelenik et al., 2004, 2007) and other ecosystems around the world (e.g. Rice et al., 2004; Allison et al., 2006; Caldwell, 2006; DeCant, 2008; Marchante et al., 2008; Follstad Shah et al., 2010). Slow decomposition of fynbos litter, which is ascribed to high concentrations of recalcitrant compounds (Stock and Allsopp, 1992; Witkowskii, 1991), reinforces the low nutrient availability found in natural riparian zones.

Stock et al. (1995) and Witkowski (1991) found that the increase in soil N, in response to invasion by Acacias, were very different between two invaded ecosystems (higher fertility strandveld versus lower fertility acid sand fynbos ecosystems) under similar climatic conditions. Compared to soils that contain higher contents of finer binding material (such as silt and clay), sandy soils in riparian zones (particularly wet banks) are subjected to rapid leaching and incapable of storing large quantities of N (Vitousek and Walker 1989; Chapin et al., 2002). Riparian ecosystems have higher sand fractions relative to associated terrestrial uplands, and combined with suspension and leaching of OM and available nutrients during seasonal floods (including the loss of N through denitrification etc) in riparian habitats, may explain the less dramatic effect of *Acacia* invasion on these systems compared to those reported in terrestrial fynbos ecosystems invaded by other *Acacia* spp. (e.g. Yelenik et al., 2004). Additionally, denitrification is a processes often associated with riparian environments (Naiman and Décamps, 1997; Naiman et al., 2005; Jacobs et al., 2007). Denitrification by soil- and sediment-bound microbes will quickly reduce soil NO_3^- concentrations, given the right conditions.

Available inorganic N (NH_4^+ and NO_3^-) concentrations were significantly positively correlated with soil TN and TC. High soil total N in *Acacia*-invaded sites may subsequently lead to elevated levels of NH_4^+ and NO_3^- relative to native fynbos riparian zones. Higher levels of soil TN may lead to consistently higher levels of NH_4^+ and NO_3^- (Yelenik et al., 2004). The process of nitrification is influenced by NH_4^+ availability (Bardgett, 2005). The positive association between NH_4^+ and NO_3^- concentrations may be as a result of high NH_4^+ availability driving the rate of nitrification and enhancing NO_3^- production (Hart et al., 1994). The highly significant correlation between soil total N and C, irrespective of invasion status or landscape position was expected, because N is directly

bonded to C in soil OM and therefore, mineralization of N is coupled to soil respiration by soil organisms (Orlander and Vitousek, 2000; Chapin et al., 2002). Enhanced soil N under N_2-fixing trees is linked to the addition of soil C, but high variation may depend on the difference in C and N biogeochemistry and landscape position (i.e. wet and dry bank zones), such that C added to soils may easily be lost through soil respiration, whereas N may remain fixed or lost through the process of denitrification (Binkley, 2005). Soil TN accumulation in invaded sites was very similar to accumulation of TC, resulting in slightly lower, but no significant net change in soil C/N and is in accordance with results reported by Caldwell (2006) in coastal prairies ecosystems invaded by *Cytisus scoparius*. Similar to my findings and compared to non-invaded areas, Marchante et al. (2008) and Maron and Jefferies (1999) reported no significant change in soil C/N at sites invaded by *A. longifolia* and *Lupinus arboreus* respectively.

It is possible for soil N availability to remain elevated for at least a number of years and perhaps longer following alien clearing, and this is regarded as a significant factor in re-invasion success (Brown et al., 2004; Corbin and D'Antonio, 2004; Yelenik et al., 2007; Marchante et al., 2009). Even though no discernible differences were observed between natural and cleared sites with regard to soil physical and chemical properties investigated, available N was significantly higher at cleared sites. Several factors may explain enhanced N availability at cleared sites. Areas cleared of invaders are more exposed to light (low cover of woody perennials; Section 3.5.2) with associated changes in microclimates. Higher soil temperatures and the combination of seasonal fluctuations in moisture may stimulate N mineralization by a changed community of microbes, resulting in high available N concentrations (Yelenik et al., 2004). An overabundance of available N may result in a number of undesired effects on ecosystems including imbalances in plant tissue nutrient:N ratios, increased production of nitrous oxide and enhanced leaching of soil cations to receiving waters (Rice et al., 2004; Gress et al., 2007). In contrast to available N, TN and TC contents did not differ between natural and cleared sites. Legacies related to soil N and C, as a result of invasion by N_2-fixing *Acacia* spp., have previously been reported (e.g. Yelenik et al., 2004; Marchante et al., 2009). Malcolm et al. (2008) found that restoration of formerly (2-4 years after clearance) invaded sites occupied by N_2-fixing black locust (*Robinia pseudoacacia*) trees, resulted in significant reductions in soil N contents, returning them to levels closer to natural pine–oak stands. After the death of the invasive N_2-fixing species, *Lupinus arboreus,* from a coastal prairie ecosystem, available N (both NH_4^+ and NO_3^-) concentrations remained elevated in the soil (Maron and Connors, 1996). The high soil C/N observed in autumn at the cleared sites may be attributable to the fire that occurred during January 2010 (4 months prior to sampling), since fire volatizes soil N, whereas C remains in the soil, resulting in significant net changes in soil C:N ratio.

Soil inorganic nitrogen (NH_4^+ and NO_3^-) concentrations and TN and TC content differed significantly between lateral zones. Wet banks were characterized by lower TN and TC concentrations compared to dry bank and upland areas, however, only TN was statistically significant. Topographical differences and associated spatial heterogeneity of anaerobic/aerobic interfaces (by influencing mineralization rates) control the spatial distribution of soil NH_4^+ and NO_3^- (Grimm et al., 2003). Overall, wet banks had significantly lower total available N levels, whereas dry banks were not different from terrestrial uplands. The geomorphic pattern through the process of erosion from inter-annual flooding hinders the accumulation of litter and OM in wet bank zones (Pinay et al., 1992), and ultimately TN and TC content. The movement and continual supply of water in wet bank zones of perennial streams may release a number of monovalent cations (Na^+, NH_4^+, K^+) and anions (NO_3^-, Cl^-) from the exchange complex into solution, making these minerals particularly prone to leaching (Chapin et al., 2002). As finely-textured soils tend to have greater N pools than coarsely-textured soils (Bechtold and Naiman, 2006; Jacobs et al., 2007), the coarsely textured nature (low clay contents) of the wet bank zones and the constant hydrological influences provides an environment for the leaching of NH_4^+ and NO_3^-.

3.5.2. Plant functional types (PFTs) and ecosystem components

In this study, invasion by Australian Acacias cause significant changes to functional type cover and composition in invaded fynbos riparian ecotones. *Acacia* spp. invade both wet- and dry bank lateral zones; however invasion is more prominent in dry bank zones, confirming observations by Boucher (2002). A possible reason for these findings is that physical stress of frequent flooding, which causes erosion and periodic inundation, is limited in this part of the channel (Gregory et al., 1991). *A. mearnsii* forms a novel structural layer in both wet- and dry bank lateral zones, as they are able to grow to a height of 10 m or more (higher than that of fynbos riparian tree species). The results clearly show that invasion by Acacias in fynbos riparian ecotones result in low structural complexity by replacing indigenous riparian vegetation and leaving the understorey bare. The significant decline in native plant cover under N_2-fixing *Acacia* stands could be ascribed to the competitive advantage of these species in nutrient-poor soils (Yelenik et al., 2004; Marchante et al., 2008; Werner et al., 2010) by competing directly with indigenous vegetation for limited resources including nutrients, moisture, light and space (Funk and Vitousek, 2007; Werner et al., 2010; Gaertner et al., 2011; Morris et al., 2011).

By dominating the canopy, Acacias reduce light penetrability and suppress the growth and cover of indigenous trees/shrubs, in addition to many other understorey plants (including both indigenous- and *Acacia* seedlings). These findings are consistent with other studies that reported

a decrease in total number of species and vegetation cover beneath woody invasive canopies as a result of canopy-level changes in fynbos terrestrial (Richardson et al., 1989; Musil, 1993; Holmes and Cowling, 1997; Gaertner et al., 2011) and riparian (Blanchard and Holmes, 2008; Reinecke et al., 2008) ecosystems in the Western Cape and elsewhere, such as Portuguese dune ecosystems (Hellmann et al., 2011; Racher et al., 2011). Similar findings have been reported in ecosystems invaded by other N_2-fixing trees; for instance, Vitousek and Walker (1989) found that introduced *Myrica faya* rapidly invades native Hawaiian forest ecosystems and successfully competes with dominant native trees for nutrients and light. Native woody vegetation that was able to persist in *Acacia*-invaded ecosystems mostly occurred along the edge of the canopy at wet bank zones, where invasion was less prominent and substantially lower cover under *Acacia* canopies.

No studies have explicitly investigated the impacts of IAPs on shade tolerances of plant species in fynbos riparian ecosystems. However, in terrestrial fynbos communities, where the overstorey shrubs/trees forms a dense canopy, understorey plant species richness is considerably reduced, which suggest that certain fynbos species are shade intolerant (Holmes and Cowling, 1997; Brown et al., 2004). Because of the high cover of shrubs and trees (>50% in wet bank zones) in intact riparian ecotones, it is expected that riparian understorey species should be more shade tolerant than those found in terrestrial fynbos ecosystems. Nevertheless, under natural conditions, the cover of vegetation in riparian areas is quite patchy and also consists of different layers. This structural complexity (canopy architecture) of plant communities associated with intact riparian systems allows some light to penetrate to the riparian floor. In *Acacia*-invaded riparian ecotones, the leaf layer is generally quite solid and mono-layered, allowing less light penetrability. For these reasons, decreases in solar radiation and alterations to a number of properties associated with soils (as discussed in section 3.5.1) are preventing indigenous species from growing and/or persisting in *Acacia*-invaded ecosystem.

It is generally recognized that nutrient inputs from invasive species influence native community successional patterns and structure, mainly by affecting growth and competitive interactions (Malcolm et al., 2008). Changes in soil physical and chemical properties (current chapter) and nutrient cycling (Chapter 4) associated with invasion by Acacias (Marchante et al., 2008, 2009; Racher et al., 2011) may restrict growth of indigenous species, since plants adapted to nutrient-poor conditions may not compete successfully on nutrient enriched soils, making the environment less suitable for native plants (Witkowskii and Mitchell, 1987). N_2-fixing invasive plants in other habitats have been shown to change vegetation community composition by enhancing available

soil N in the invaded community (Maron and Connors, 1996; Hughes and Denslow, 2005). In addition to other factors, the dense stand cover and litter layer under *Acacia* stands may form a physical barrier that hamper the influx, germination and sprouting of native seedlings (Witkowski, 1991; Richardson et al., 1992; Hellmann, et al., 2011; Racher et al., 2011). Invasion by Acacias may therefore decrease functional heterogeneity by changing growth form composition and dominating the canopy in fynbos riparian ecotones, thereby limiting the establishment and growth of native species. Clearly, no one specific factor is responsible for ecosystem changes relating to invasion, as multiple and interactive ecosystem effects (resulting from *Acacia* invasion) may cause changes in community composition (Eviner and Chapin, 2003).

After more than seven years following clearing of invasive *Acacia* spp. in riparian zones, regeneration of several fynbos growth form types were fairly limited. Cleared areas were characterized by sparse woody cover and a high cover of alien grasses. Limited regeneration of woody riparian shrubs and trees observed after the removal of closed-stand invasions in fynbos riparian ecosystems is supported by other studies (Galatowitsch and Richardson, 2005; Reinecke et al., 2008; Blanchard and Holmes, 2008). In fynbos terrestrial ecosystems, Musil (1993) and Holmes and Cowling (1997) found similar trends with poor recovery of fynbos elements after clearances. Blanchard and Holmes (2008) reported a general trend towards increased vegetation cover and recovery over time when sites cleared less than 5 years prior were compared to those cleared more than 5 years prior. Galatowitch and Richardson (2005) concluded that following the removal of *Acacia* spp., some riparian sites returned to pre-invasion state without any associated management interventions, whilst other sites have failed to recover naturally. As opposed to sites cleared of *Acacia* spp., Reinecke et al. (2008) found that fynbos riparian vegetation growth form composition and cover rapidly recovered in areas where *Pinus pinaster* was cleared, and stated that the specific invasive species concerned plays a fundamental role in whether the riparian community recovers naturally after clearing activities. Limited resilience and poor regeneration of riparian indigenous shrubs/trees at cleared sites may indicate that either they were intensely disturbed and suppressed during clearing operations, absent from seed banks attributed to prolonged invasion, or that mature trees simply did not survive invasion (Galatowitch and Richardson, 2005; Reinecke et al., 2008). It has been suggested that changes to microclimatic conditions after alien clearing and soil properties (as a result of invasion) might also impede germination or establishment of native seedling (Yelenik et al., 2004; Rascher et al., 2011; Hellmann et al., 2011).

Low PFT cover and exposed soils associated with cleared sites may alter soil conditions (high solar radiation and elevated soil temperatures). This, in addition to the high availability of inorganic N, may be a contributing factor in promoting germination and increasing the abundance of weedy grass species after *Acacia* removal (Yelenik et al., 2004; Reinecke et al., 2008; Hellmann et al., 2011) and simultaneously reducing the competitiveness of many native fynbos riparian species (Holmes and Cowling, 1997). Witkowski (1989) revealed significant increases in the cover of annual, graminoid and restiod species following additions of only 5g N and 0.5g P per m^2 to sand fynbos ecosystems. Re-invasion by the same species or secondary invasion by nitrophilic species, such as alien grasses, associated with cleared sites have also been observed in other studies (Milton and Hall, 1981; Milton, 2004; Yelenik, 2004; Holmes et al., 2005; Reinecke et al., 2008) and these species may also capitalize on disturbances caused by control operations (Le Maitre et al., 2011).

Other than high availability of N or changes in microclimate, the growth and spread of alien grasses can also be facilitated by long-distance transport and other disturbances (Milton, 2004) or simply by the absence of riparian shrubs and trees (Reinecke et al., 2008). Gaertner et al. (2011) found that high abundances of *Pennisetum clandestinum* (one of the alien grasses reported in this study) did not trigger any significant alterations in soil nutrient concentrations compared to native fynbos areas. They suggested that the low native cover and species richness in the kikuyu field could indicate a competitive advantage of this grass species over fynbos species. Given that cleared areas differed significantly from natural areas with regard to plant functional type cover, and that areas previously invaded by *Acacia* spp. had been cleared more than seven years ago, it is likely that these areas may not recover as time progresses or that recovery may take a few decades. However, we still lack the mechanistic understanding of fynbos riparian recovery after clearing, as the success of re-establishment may depend on complex interaction and feedback cycles between plants and their physical environment.

In indigenous riparian systems, plant composition and cover differed significantly across landscape position (i.e. distance away from the river channel), which may correspond to a lateral gradient of declining riparian influence on vegetation, reflecting differences in stream power, intensity of flooding disturbance, and inundation frequencies of rivers (Hood and Naiman, 2000; Sieben et al., 2009). Apart from water dynamics, differences in soil particle size distribution, soil pH and vulnerability to fire across geomorphological zones also likely plays an essential role in the structure and composition of riparian and upland plant communities (Prins et al., 2004; Bechtold and Naiman, 2006; Reinecke et al., 2008). Shrubs, forbs, grasses and other graminoids

were more prominent in dry bank compared to wet bank areas. The presence of moss and shade-loving ferns at wet bank zones indicates that microclimatic conditions are very different from dry banks, as more light is intercepted by trees/shrubs (>2m). Dry bank zones were located just beyond riparian tree/shrub line, which explains the lower cover of indigenous trees/shrubs observed. Furthermore, the higher cover of indigenous trees in wet bank zones, relative to that of invasive *Acacia* spp. in wet bank zones, suggests that fynbos riparian shrubs and trees are better adapted to withstand hydrological fluxes connected to these systems.

3.6. CONCLUSION

This study offered a number of insights into fynbos riparian dynamics and the extent to which *Acacia* spp. alter the structure and function of these ecosystems. The data supports the hypothesis that invasion by *Acacia* spp. changes soil properties and affects plant functional attributes. Invasion by *Acacia* spp. (mostly *A. mearnsii*) has markedly affected vegetation structural complexity by decreasing important plant functional type cover and preventing establishment of other important riparian classes; whereas sites that have been cleared 7+ years ago had limited recovery with high cover of alien grass species. The most pronounced effects of Acacias are changes to growth form composition, soil physical (bulk density, particle size distribution), chemical (greater concentrations of dissolved salts), biological (litter inputs), and nutrient characteristics (total and available N). Alterations in plant functional attributes and soil properties have potential implications for restoration, as riparian function and integrity may be compromised. *Acacia* spp. have different resource use strategies and ecophysiological traits relative to indigenous species (Morris et al., 2011; Werner et al., 2010). These changes and feedbacks in system may mostly explain why invasion by Acacias could expand so quickly in novel ecosystems and alter biogeochemical cycles there (Werner et al., 2010; Racher et al., 2011).

Soil physical and chemical properties and litter mass at cleared sites resembled the situation in natural areas, but N availability was significantly higher and likely aided the establishment and growth of weedy grasses. Clearing Acacias will initiate restoration of invaded riparian ecosystems, but higher N availability may hamper long-term success of restoration initiatives (Marchante et al., 2009). The lack of *Acacia* spp. observed at cleared sites was attributed to several follow-up clearances by WfW and private landowners. After clearing, the time needed for N pools to reach conditions more or less similar to pre-invasion conditions will depend on community composition of re-colonising fynbos and rain water percolating down the soil profile as

a major leaching agent, with temperature and soil moisture as important factors for N mineralisation. Nitrogen concentrations will also depend on environmental conditions contributing to denitrification (Jovanovic et al., 2009). Fynbos riparian overstorey shrubs/trees maintain understorey species and their lasting absence from these systems may threaten vegetation communities and affect ecosystem function (Holmes et al., 2000). Despite all of these implications, it remains uncertain whether the sites cleared of IAPs in this study will recover with regards to function type composition and cover as time progresses.

It has previously been hypothesized that higher nutrient concentrations in fynbos riparian forest ecosystems play an essential role in the development of forest species. However, the outcomes from this study reject the hypothesis which states that fynbos riparian soils are richer in nutrients relative to adjacent non-riparian uplands. A possible explanation for these findings is that nutrient retention in constrained river reaches, such as in the upper reaches of fynbos rivers, is lower than unconstrained reaches (Gregory et al., 1991), since erosion exceeds deposition in these systems. *Acacia* spp. therefore do invade low-resource environments, and do not only favour high resource environments as previously thought (Marchante et al., 2008). Compared to wet bank zones, river floodplains (dry banks) were more similar to terrestrial uplands when a number of soil properties (GSWC, bulk density; available N and P) were compared. In riparian lateral zones fluvial processes such as sediment erosion and deposition influence several soil properties by controlling variations soil texture and redox condition (Grimm et al., 2003). Correlations between soil particle size distribution and several soil properties measured in this and other studies indicates important linkages between soil texture and resource availability.

Additional studies are being conducted so as to determine whether changes to soil processes, such as soil respiration and denitrification, may be problematic for restoration of indigenous plants adapted to nutrient-poor soils. Long-term impacts of IAPs are only seldom assessed and experimental studies evaluating the possible changes in soil conditions that prevail after the removal of the invader are scarce (Vosse, 2007). The duration of invasion has not been reflected on in this study; even if this issue has in recent times been acknowledged as an important aspect that needs to be considered to adequately evaluate the effects of many invaders on ecosystems (Marchante et al., 2009). Riparian areas with limited potential of recovery following Acacia removal necessitates further investigation to evaluate the best possible way of promoting community recovery (Vosse, 2007).

3.7. REFERENCES

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CHAPTER 4

Selected Soil Processes in Natural; *Acacia*- Invaded and Cleared Fynbos Riparian Ecotones, and Associated Uplands

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4.1. ABSTRACT

Riparian ecosystems are linear features of the landscape, which comprise a dynamic mosaic of ecological processes, and possess specific biotic properties and physical and chemical characteristics. In nitrogen (N)-limited ecosystems, nitrogen (N_2)-fixing plant species have been the focal point of studies assessing the potential impact on structure and function of indigenous plant communities. No studies have explicitly addressed the question of nutrient processes, such as N and phosphorus (P) cycling, in fynbos riparian ecotones and the possible impacts of *Acacia* invasion and clearing on these processes, but this is of potential importance given Acacia's ability to fix atmospheric N via root symbionts. The research was aimed at answering the following questions: How do selected soil processes vary depending on landscape position and invasion status?   What interaction exists between soil processes and soil physical and chemical properties? I hypothesized that rates of N and P mineralization are elevated in riparian zones and that invasion by *Acacia* spp. further enhance these processes. Furthermore, I expected process rates to decline in cleared riparian ecotones. Fieldwork was performed in mountain and foothill sections of six perennial river systems within the south-western Cape, South Africa. Eleven sites of three categories were chosen: four reference sites that are relatively pristine and uninvaded, four moderate to highly invaded sites (mainly *Acacia mearnsii*) and three cleared riparian sites (prior invaded sites cleared more than 7 years ago). Within each site, four to five replicate plots were sampled for each of three geomorphological zones (wet bank, dry bank, and upland fynbos). Soil samples were collected seasonally for one year and analyzed for N mineralization potential (NMP), acid phosphatase (APME) activity and selected soil properties. The geomorphological zone (which ultimately controls particle size distribution, soil nutrient retention and soil moisture content); invasion status; and seasonal fluctuations in temperature and precipitation explained much of the trends in N and P mineralization rates. NMP rates and APME activity differed significantly between landscape positions. NMP rates in invaded sites did not differ from natural areas. APME activity, on the other hand, was significantly higher in soils under *Acacia* stands. Both N and P mineralization rates at cleared sites were similar to those in natural areas.

4.2. INTRODUCTION

The functioning of ecosystems not only depends on their existing environment and structure, but also on historical events and disturbances and the rate at which ecosystems respond to these events (Chapin et al., 2002). Ecologists increasingly regard ecosystems as having permeable boundaries that enable the exchange of energy and nutrients with adjacent systems (Ballenger and Lake, 2006). Exchange of materials, nutrients, organisms and energy between the river channel, riparian zone and the surrounding catchment through linked ecosystem processes are integral to the function of river-riparian systems (Naiman and Décamps, 1997; Wall et al., 2001; Ballenger and Lake, 2006). For this reason, riparian ecotones are considered as "critical transition zones" (Ewel et al., 2001). They are linear features of the landscape, which comprise a dynamic mosaic of ecological processes (Ward et al., 2002), and possess specific biotic properties, and physical and chemical characteristics, which are very distinctive in their interactions with the surrounding ecological systems (Grimm et al., 2003; Décamps et al., 2004). Their functions and roles in ecosystems, from an ecological perspective, and their application for river management have been researched extensively (Pinay et al., 1992), although less so in Mediterranean-type environments.

In riparian landscapes, lateral (horizontal distance away from the river channel), vertical (elevation above the channel), and longitudinal (along the river length) gradients are vital, since they correspond to changes in several important environmental variables including water availability, flooding, soil composition and nutrients, morphology and geology (Davis and Day, 1998; van Coller et al., 2000). Ecosystem processes are defined by Ehrenfeld (2004) as "the change in the sizes of pools of elements and materials and the rates of material flux and transformation among pools". Zones where aquatic and terrestrial ecosystems meet have been known to enhance soil fluxes and reaction rates (e.g. Gregory et al., 1991, Pinay et al., 1995), because seasonal flooding events bring nutrients and water from the surrounding catchment (Pinay et al., 1995). However, not all riparian ecotones are hot spots of biogeochemical cycling (McClain et al., 2003). In riparian ecosystems, fluvial processes such as sediment erosion, sorting, and deposition influence soil biogeochemical processes through variations in sediment or soil texture and redox condition (Grimm et al., 2003). Although these systems are less limited by water than the

surrounding terrestrial uplands, mineralization may be limited periodically by water availability, and may cause alterations in the patterns of N and P cycling (Adair et al., 2004).

Soils are highly complex and dynamic ecosystems (Bardgett, 2005). They contain a variety of nutrient elements, in addition to effective mechanisms of nutrient recycling and retention (Grimm et al., 2003). The physical and chemical nature of soils is determined by variations in soil-forming factors, which in turn influences soil organisms and ultimately the decomposition of organic matter (OM) and water and nutrient cycling (Chapin et al., 2002; Bardgett, 2005). In most terrestrial and aquatic ecosystems, either N or P may limit productivity, and riparian zones often play an essential role in augmenting stream N, P, and carbon (C) stocks through litterfall and release of nutrients (Naiman and Décamps, 1997). Biogeochemical cycles are essential ecosystem processes that regulate the transformation and movement of nutrients (Anderson and Ingram, 1993) via interactions of chemical, physical, and biological processes (Chapin et al., 2002). Knops et al. (2002) suggested that microbes control N-cycling, but that plants (which consume N and produce biomass) ultimately regulate the quantity and quality of OM inputs, which in turn control microbial activity. Variation in the quantity and quality of litter originating from different plant species influence rates of soil biogeochemical cycling and fluxes of elements such as N and C (Chapin et al., 2002; McClain et al., 2003).

Models predicting changes in soil N turnover and retention frequently include soil C/N as an essential factor in determining mineralization and immobilization rates (Bengtsson et al., 2003; Grimm et al., 2003; Bardgett, 2005). Soil micro-organisms, through the process of decomposition, mineralization, and transformation of organic compounds and inorganic nutrients, are fundamental role-players in several physiological processes and important to many biogeochemical reactions necessary for plant survival (Anderson and Ingram, 1993; Chapin et al., 2002; Bardgett, 2005; Cilliers et al., 2005). Mineralization of nutrients is that part of the biogeochemical cycle where soil soluble and insoluble OM is converted by soil microbes to biologically available, inorganic nutrients (Anderson and Ingram, 1993; Bardgett, 2005). The soil's capacity to transform organic N to inorganic forms (potential N mineralization) is often used as an index of plant available N (Robertson et al., 1999). During mineralization of N, ammonium (NH_4^+) released from the decomposition of proteins, chitins and nucleic acids, is readily absorbed by plant from the soil solution (Chapin et al., 2002; Bardgett, 2005). Mineralization of soil N depends on several factors which are reflected by changes in biological substrates and microbial communities being used and temporal variations in substrate quality (Bengtsson et al., 2003).

Soil enzymes serve several important functions as they are closely involved in nutrient cycling (Dick et al., 2000). Factors that influence soil microbial activity exercise control over enzyme production (Dick et al., 2000; Grierson and Adams, 2000; Chapin et al., 2002; Sardans et al., 2006), so that their activity relate well with soil fertility and nutrient availability (Sardans et al., 2006). Soil enzyme activity responds not only to changes in climate (Kramer and Green, 2000), but also depends on the plant root type (Grierson and Adams, 2000) and the composition of the soil matrix (which are subsequently regulated by temperature, soil moisture and substrate quality; Grierson and Adams, 2000; Chapin et al., 2002). Soil phosphatase enzymes (phosphomonoesterases) produced by plant roots, soil fungi and micro-organisms, cleave ester bonds that bind C to P in organic phosphorus compounds to release ortho-phosphate. Their activities play a vital role in controlling and maintaining the rate of P-cycling through soils (Amador et al., 1999; Šarapatka, 2003; Bardgett, 2005). Soil phosphatases have been extensively studied and not only constitute an important association between mineral and biologically unavailable P pools in soils (Amador et al., 1999; Kramer and Green, 2000; Orlander and Vitousek, 2000; Vance et al., 2003; Bardgett, 2005), but may be a good indicator of change in the soil environment, such as organic P mineralization potential and biological activity of soils (Dick et al., 2000; Kramer and Green, 2000).

Plants and microbes under P limitation, may allocate more resources to acquire P, especially the synthesis of phosphatase enzymes (Olander and Vitousek, 2000; Cramer, 2010; Vitousek et al., 2010). Along with N, P availability may be the most limiting nutrient to plant growth in many ecosystems (Chapin et al., 2002; Vance et al., 2003; Kramer and Green, 2000; Cramer, 2010), especially in Mediterranean ecosystems (Kramer and Green, 2000), such as the fynbos (Cramer, 2010). A general response to P-deficiency by plants is the production of acid phosphatase enzymes and their activities have frequently been used as indicators for P-deficiency (Vance et al., 2003). Development of an indicator of soil quality in fynbos riparian ecosystems invaded by *Acacia* spp. may not only enable scientists to better understand P-cycling and its relationship with plant available P_i, but also to aid management/restoration of *Acacia*-invaded and previously infested catchments. Thus, management decisions must be designed with these processes in mind.

Most ecosystem processes respond in complex ways to alterations in community composition by changing pathways of material and energy flow (Chapin et al., 2002). Soil processes are mediated by soil microbes (Bardgett et al., 2001; Cilliers et al., 2005; Naiman et al., 2005); however, invasion by alien plant species in riparian zones can substantially alter soil microbial community composition (Corbin and D'Antonio, 2004). Many invasive alien plants (IAPs)

transform ecosystems (Richardson et al., 2000) and are widely acknowledged as one of the most important threats to ecosystem stability by affecting water production from catchments, soil maintenance and several other components related to C and nutrient cycles and consequently, the ability of ecosystems to provide services (Ehrenfeld, 2003; Corbin and D'Antonio, 2004; Richardson and van Wilgen, 2004). Invasive plants may affect ecosystems dynamics (e.g. soil nutrients) through various mechanisms such as N_2-fixation, different photosynthetic pathways and plant structure (Ehrenfeld, 2003). These mechanisms affect how plants interact with the biological and physical components of soil.

In N-limited ecosystems, N_2-fixing plant species have thus been the focal point of studies assessing for changes in ecosystem function, since these species can impact the structure and function of indigenous plant communities by enhancing soil N pools (Vitousek and Walker, 1989; Ehrenfeld, 2003; Levine et al., 2003; Yelenik et al., 2004) and cycling rates by means of higher inputs of N-rich litter that mineralizes rapidly (Yelenik et al., 2004; Malcolm et al., 2008; Akamatsu et al., 2011). All of these changes imply that IAPs profoundly affects ecosystem processes (Liao et al., 2008). Among the best studied impacts of N_2-fixing invasive species are those involving ecosystem processes, such as N-cycling (Vitousek and Walker, 1989; Witkowski, 1991; Stock et al., 1995; Yelenik et al., 2004; Marchante et al., 2008) and P biogeochemistry (Giardina et al., 1995; Zou et al., 1995; Allison et al., 2006; Caldwell, 2006; Houlton et al., 2008). With exception to Australia, native N_2-fixing trees are seldom found in Mediterranean systems (Ehrenfeld, 2003; Racher et al., 2011), and differ from non-leguminous trees not only by their ability to obtain N through biological N_2-fixation, but also in its litter chemistry and litter production. These differences may affect ecosystem functioning (Allison et al., 2006; Racher et al., 2011; Morris et al., 2011).

Acacias are N_2-fixing leguminous species and are remarkably successful invaders in Mediterranean climate, low-fertility ecosystems, such as the fynbos (Werner et al., 2010; Morris et al., 2011). Studies in *Acacia*-invaded Cape ecosystems have shown increased soil OM and nutrient pools relative to non-invaded fynbos (e.g. Witkowski, 1991; Stock et al., 1995; Yelenik et al., 2004, 2007), which suggests that the decomposition of organic material and nutrient cycling processes are affected and that N_2-fixing *Acacia* spp. are able to exert profound impacts on ecosystem dynamics (Corbin and D'Antonio, 2004; Stock et al., 1995). Many Australian *Acacia* spp. can be strong engineers in several ecosystems (Richardson et al., 2000; Morris et al., 2011), such as terrestrial fynbos, however this may not necessarily hold true for fynbos riparian ecosystems invaded by *Acacia meanrsii*.

Native N_2-fixing plants, however, are rare in post-successional fynbos communities (Cocks and Stock, 2001; Cramer, 2010). A possible explanation for this is that most legumes are deficient in highly effective root adaptations essential for acquisition of P in low-P ecosystems (Power et al., 2010). This suggest that Australian Acacia's ability to establish, grow, proliferate and survive in nutrient-poor fynbos ecosystems is highly dependent on specific life-history traits including; symbiotic N_2-fixation by bacteria in root nodules, high seed set, extensive root production, adaptations to fire cycles, and high growth rates and biomass production. These specific traits may be essential mechanisms through which *Acacia* spp. obtain and compete effectively with native species for nutrients, water and light (Richardson et al., 1992; Pieterse and Boucher, 1997; Yelenik et al., 2007, van Wilgen, 2009; Pretorius et al., 2008; Werner et al., 2010; Morris et al., 2011), consequently enabling Acacias to dominate competitive interactions with indigenous species (Le Maitre et al., 2011).

Apart from the effect on water resources (Le Maitre et al., 2000; Dye et al., 2001), current knowledge of the effects of *Acacia* spp. on ecosystem processes in fynbos ecosystems comes from a limited number of studies (e.g. Witkowski, 1991; Stock et al., 1995; Yelenik et al., 2004, 2007). *A. mearnsii* and *A. longifolia* are important invaders within fynbos riparian ecosystems (Pieterse and Boucher, 1997; Holmes et al., 2005). Because of a wide-ranging concern on the effects of IAPs on nutrient cycles (Caldwell, 2006; Richardson et al., 2007; Gaertner et al., 2011), and given that soil enzymes play fundamental roles in regulating nutrient cycling processes (Tabatabai, 1994; Dick et al., 2000; Chapin et al., 2002; Naiman et al., 2005), understanding the factors that control the rates of internal cycling processes is essential and may help predict possible impacts of IAPs on ecosystem structure and function (Hart et al., 1994). N-cycling is a slow process in natural vegetation of fynbos ecosystems due to the sclerophyllous nature of their leaves (Stock and Allsopp, 1992; Witkowski, 1991) and acceleration of the N-cycling poses a particularly large threat to fynbos vegetation due to their adaptations to low N, and the nitrophilous nature of many of its invaders (Witkowski, 1991; Yelenik et al., 2004). High N inputs may hinder efforts to restore indigenous plant community and ecosystem function in areas previously occupied by invasive N_2-fixers (Holmes et al., 2005).

To date no studies have explicitly addressed the question of N and P mineralization in fynbos riparian ecotones and the possible effects of *Acacia* invasion on these processes, but this is of particular importance given its ability to fix atmospheric N_2 via root symbionts (Tye and Drake, 2011). Given the specific gaps in our knowledge regarding the ability of Acacias to alter several components of fynbos riparian ecosystem nutrient cycles; there is a need to understand how soil processes respond to plant invasion. Nevertheless, based on previous findings of the impacts of

invasion by N_2-fixers (e.g. Vitousek and Walker, 1989, Zou et al., 1995; Yelenik et al., 2004, Allison et al., 2006; Caldwell, 2006; DeCant, 2008; Marchante et al., 2008, Racher et al., 2011), higher inputs of biomass (e.g. litter) associated with *Acacia* invasion in riparian environments are expected to enhance N and P cycles. Although fynbos riparian ecotones lack significant inputs from symbiotic N_2-fixers, N and P may still accumulate in these areas, but the extent of accumulation and transformation rates remain elusive.

The Working for Water (WfW) Programme was initiated by the Department of Water Affairs and Forestry in 1996 with the aim of controlling woody invading plants (Le Maitre et al., 1996; van Wilgen et al., 1998; Dye and Jarmain, 2004) and enhancing ecological integrity (Holmes et al., 2008). However, many management interventions and alien clearing initiatives take up a passive approach to restoration, by merely aiming to remove existing IAPs and prevent or control their regeneration (Le Maitre et al., 2011). It is often postulated that impacts on an ecological level will diminish immediately after the control or eradication of invasive species, however IAPs that cause ecological changes leave a legacy of altered soil biogeochemical processes, and removal of these species may not be sufficient to allow the ecosystem to return to its original pre-invasion state (Yelenik et al., 2004; Marchante et al., 2009). Even though much has been accomplished though the WfW programme, the impact of *Acacia* invasion on riparian soil processes, and the biogeochemical legacy that may prevail in these ecosystems after removal, has not received attention. Knowledge on the links between fynbos riparian ecosystem functioning and restoration is currently lacking (Esler et al., 2008).

The objectives of this study were to assess seasonal changes in N (potential N mineralization rates) and P (phosphatase activities) mineralization in natural, *Acacia*-invaded and cleared fynbos riparian ecotones and associated upland terrestrial fynbos of the south-western Cape. Interactions between selected soil physical and chemical properties and processes (N and P mineralization) were also quantified. The research was aimed at answering the following questions: How do N and P mineralization rates vary depending on landscape position and invasion status? What interaction exists between these processes and soil physical and chemical properties? Understanding variability along different geomorphological zones and the effects of *Acacia* invasion on soil physical and chemical properties, which in turn affect N and P mineralization, may help clarify the factors driving soil process rates. Fynbos riparian ecotones are noted for their relatively fertile soils compared to adjacent nutrient-limited terrestrial fynbos (Manders, 1990; Cramer, 2010), though these studies were carried out in an Afromontane riparian ecotone (Jonkershoek Nature Reserve), and not necessarily representative of all fynbos riparian ecotones. Cramer (2010) suggested that fynbos riparian ecotones collect nutrients by

trapping ash and dust and taking up water and nutrients from deep in the soil. For this reason and assuming that fynbos riparian zones are more productive than adjacent upland terrestrial fynbos, I hypothesized that rates of N and P mineralization are elevated in riparian corridors. Considering that *A. mearnsii* is a leguminous tree (Tye and Drake, 2011), which grows faster than most fynbos riparian native species, I hypothesized that invasion by *Acacia* spp. (mostly *A. mearnsii*) promotes changes in the rates of N and P mineralization by affecting properties related to N- and P cycling. *Acacia* spp*.* increase litter inputs (Chapter 3), and litter provides resources for microbes to increase the synthesis of enzymes that degrade organic C compounds, further enhancing soil biogeochemical cycling. By removing large quantities of biomass after clearing, I expected N and P mineralization rates to decline in cleared riparian ecotones. If soil biogeochemical legacies persist, it may create obstacles for management and restoration of fynbos riparian ecosystems, by preventing recovery and re-establishment of native species, and/or facilitate re-invasion of the same or other exotic species (Yelenik et al., 2007; Marchante et al., 2009).

4.3. MATERIALS AND METHODS

4.3.1. Study area

Eleven study sites were selected in the upper reaches of six river systems in the south-western Cape, South Africa: Molenaars, Wit, Eerste, Dwars, Jakkals, and Sir Lowry's Rivers (see Chapter 1: Figure 1.1). Field experiments were conducted seasonally for one year (Mar-2010 to Feb-2011). The study area has a typical Mediterranean-type climate characterised by cool moist winters, and hot and dry summers (Figure 4.1). More than 70% of the annual precipitation occurred between April and September 2010, which is typical of the western part of the Cape Floristic Region (CFR) experiencing Mediterranean winter rainfall climate (Deacon et al., 1992; Sieben, 2003). Fynbos soils are derived mainly from Table Mountain Group Sandstone and are highly leached, coarsely-grained and shallow, low in exchangeable bases, and deficient in essential nutrients, such as N and P (Stock and Lewis, 1986; Witkowski and Mitchell, 1987; Deacon et al., 1992; Rebelo et al., 2006; Cramer, 2010). However, soils developing on granite and shales are richer in nutrients and contain higher concentrations of fine particles (Deacon et al., 1992; Sieben, 2003; Prins et al., 2004). Riparian soils in the upper reaches of fynbos rivers are coarsely-textured and are mostly derived from alluvial material from sedimentary sandstones; however, certain catchment areas may also be derived from weathered Cape Granite or a mixture of the two (Appendix C).
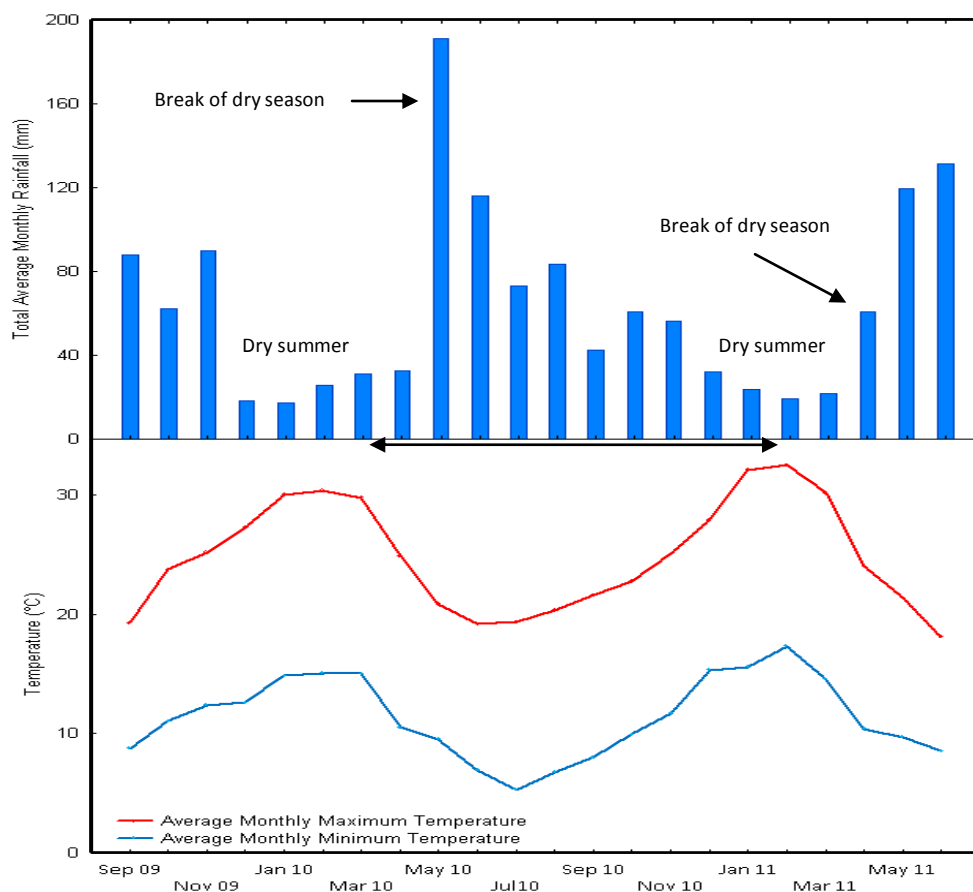
Figure 4.1. Minimum and maximum temperatures (°C) and total monthly rainfall (mm) calculated from averages of 6 weather stations located near and/or within the study area (Sep-09 to Jun-2011; Institute for Soil, Climate and Water - Agricultural Research Council). Arrow below bars indicate the time and duration of the study during which sampling occurred.

Important riparian vegetation classes observed at the study sites are shrubs and trees, particularly *Brabejum stellatifolium, Metrosideros angustifolia* and *Brachylaena neriifolia*, in addition to grasses, restiods and other graminoids, such as palmiet (*Prionium serratum*) in wet bank zones. Invasive *Acacia* spp. (*A. mearnsii* and *A. longifolia*) dominate riparian communities in invaded sites and in most cases, form high density monospecific stands, which not only exclude indigenous shrubs and trees, but also exclude important understorey riparian plant species. *Acacia* spp., predominantly *A. mearnsii*, forms an enclosed canopy cover of more than 60% (Chapter 3). Areas cleared of *Acacia* spp. (as well as other woody species; Appendix C) more than seven years ago have shown limited recovery and low cover of essential growth form elements. Other than the sparse cover of woody elements, which are an important attribute of fynbos riparian vegetation communities, a prominent feature was the high cover of alien grass species at cleared sites (Chapter 3). Geomorphological characteristics and site history are shown in Appendix C and detailed descriptions for each river system and site have been covered in Chapter 1.

4.3.2. Sampling layout

To investigate the effects of invasion by, and clearing of Acacias (mainly *A. mearnsii*) on fynbos riparian biogeochemistry, we selected sites representing natural, invaded and cleared areas. I chose: four reference sites that are relatively pristine and uninvaded, four moderate to highly invaded riparian sites (mainly *A. mearnsii* or a mixture of *A. mearnsii* and *A. longifolia* invaded for more than 10 years) and three cleared riparian sites (a former invaded site that has been cleared more than 7 years ago, with *Acacia mearnsii* as the dominant invader). Within each site, riparian ecotones were divided into two broad geomorphological zones according to Boucher (2002), namely wet- and dry bank zones (Appendix A). To examine differences in soil biogeochemistry between riparian and adjacent terrestrial fynbos (landscape position comparison), upland zones were also selected and located at least 15m from the outer boundary of the dry bank zones. Four to five replicate plots were selected for each of the three zones; giving a total of 12-15 sampling plots per site (see Appendix B). Transects, 15 m in length and parallel to the river channel, were located at least 10m apart. The location of riparian wet- and dry bank zones were determined by within-year flows and recurrence intervals of floods of more than one year respectively (Reinecke et al., 2007). The coordinates of each study sites are shown in Appendix C.

4.3.3. Soil sampling

4.3.3.1. Soil physical and chemical analysis

Soils were collected once every season. Within each plot, six composite samples from the upper 10cm of the soil profile were collected (after litter was discarded) with a stainless steel soil corer (5 cm in diameter; 10 cm in length) and placed in tightly sealed plastic bags, kept cool, and transported to the laboratory where they were stored at 4°C until analysis. Soils were manually sampled with a hand trowel in places where it was not possible to use a core sampler. In the laboratory, subsamples were pooled to represent 1 sample for each plot to avoid pseudo-replication. Samples were carefully mixed and sieved through a mesh (2 mm) to remove rocks and organic debris. Soil physical and chemical parameters assessed and their respective analytic methods are given in Table 4.1. Total nitrogen (TN) and total carbon (TC), pH, and electric conductivity (EC) were determined on air-dried soil. Bray-2 extractable inorganic phosphorus (P_i), which is a measure of plant available P (Witkowski and Mitchell, 1987), was determined on fresh soil within 2-3 days of collection. Nitrate (NO_3^-) and ammonium (NH_4^+) were extracted and analyzed from fresh soil samples within 48 hours and concentrations were determined colorimetrically (Table 1). Soil TN and TC were analyzed biannually by dry combustion elemental analyzer (Soil Science Department, Stellenbosch University). Approximately 20g of soil were weighed; oven dried at 105°C for 12 hours and reweighed to

obtain gravimetric soil water content (GSWC). Soil available inorganic nutrient concentrations (N and P) and TN and TC were expressed as µg g^{-1} dry soil and percentages respectively.

Table 4.1. Soil properties and analytical methods.

Soil properties	Methods	Laboratory instruments	Reference
NH$_4$-N (µg g^{-1})	Extracted with 0.5M K$_2$SO$_4$. 10g of soil (<2mm) was placed in 50ml plastic vials together with 20 ml of the extractant. The vials were shaken at medium speed for an hour and filtered. Concentrations were analysed based on the Berthelot reaction involving phenol.	Spectrophotometer (Genesys 20)	Keeney and Nelson, 1982
NO$_3$-N (µg g^{-1})	Same extraction method as for NH$_4$-N. Concentrations were analysed based on nitration of salicylic acid.	Similar to above	Catado et al., 1975
Available inorganic P (µg g^{-1})	Dilute acid fluoride-extractable P$_i$ (Bray-2 P$_i$). Phosphorus was analysed colorimetrically using a modified ascorbic acid method	Similar to above	Bray and Kurtz, 1945
pH (H$_2$0)	Soil pH was measured electrometrically in 1:2 (w/v, soil:deionised water) slurry.	Hanna 211 Microprocessor	Robertson et al., 1999
Electric conductivity (µs/cm)	10g of air dried soil were placed in 40 ml deionized water. Soil slurry was shaken for approximately 60min and allowed to stand for ions to settle before measurement was taken	Corning Conductivity meter 441	-
Particle Size Distribution	Modified rapid method: Sand content was divided in 2 classes: medium and fine sand (0.053-0.425 mm) and coarse sand (0.425-2.0 mm). Silt and clay content (<0.053 mm) was analyzed together.	Stainless-steel mesh sieves	Kettler et al., 2001
Bulk density (g/cm^3)	Bulk density was determined as oven-dry mass per volume (based on core volume)	Sharp-edged tins	-

Soil properties were analyzed seasonally, except for particle size distribution (autumn and spring) and bulk density (spring).

4.3.3.2. Potential N mineralization rates

The 7-day anaerobic incubation method is a widely adopted approach and a very good biological indicator for potentially available N (Schomberg et al., 2009) and for detecting differences between sites (Binkley and Vitousek, 1989; Anderson and Ingrim, 1993). This procedure measures NH$_4$-N released from soil microbes killed by anoxic conditions, thus preventing the oxidation of NH$_4^+$ to NO$_3^-$. Therefore only NH$_4^+$ needs to be analysed, as the concentration of NO$_3$-N is always insignificant after anaerobic incubation and lost through denitrification (Binkley and Vitousek, 1989; Anderson and Ingrim, 1993; Schomberg et al., 2009). Even though the anaerobic incubation conditions do not mimic environmental conditions, the values frequently

correlate well with plant uptake and foliar nutrient concentrations (Binkley and Vitousek, 1989). This method yields potential anaerobic N mineralization rates (Anderson and Ingrim, 1993; Chapin et al., 2002).

Seasonal measurements of potential anaerobic N mineralization (NMP) rates for each sample were determined by adding 20ml of distilled water to 10g of a field moist subsample and incubated for 7 days (T_7) at 27°C, following the method by Keeney and Bremmer (1966). Caps were tightly fastened to prevent the exchange of gases, such as oxygen. To measure initial concentrations (T_0) of NH_4–N for each sample (plot), a 10g subsample of fresh soil was measured and extracted with 25 ml of 0.5M K_2SO_4, shaken at medium speed for 1 hour, and filtered (Table 4.1). The concentrations for each sample was determined colorimetrically (Page et al., 1992) and calculated form a standard equation after which the volume of the solution, the mass of the soil, and soil moisture content were considered. After 7 days of incubation, 2M K_2SO_4 were added to bring the solution to a concentration of 0.5M K_2SO_4. Concentrations of NH_4-N (T_7) underwent similar invasion status as for the determination of for NH_4-N (T_0) (Table 4.1). Net anaerobic N mineralization was calculated from the difference in the final incubated (T_7) concentration minus the initial (T_0) concentration ($\mu g\ g^{-1}$ dry $soil^{-1}$ day^{-1}) for each soil sample divided by the incubation interval.

4.3.3.3. Acid phosphatase activity

The activity of extracellular P-releasing enzyme was assayed each sampling season except to winter, using field-moist soil samples (2-3 days after collection). Field-moist soils were used, because it is assumed to be more representative of enzyme activity under field conditions, as air-dried soils has been shown to markedly change phosphatase activity (Amador et al., 1999). Studies have shown that acid phosphatase predominates in acidic soils. Since fynbos soils are typically acidic, only acid phosphatases were analysed using the method of Tabatabai (1982). Optimal conditions for soil enzyme studies may possibly give information about the potential activity of enzymes or the quantity of active enzyme (Tabatabai, 1982). However, since the enzyme activities in the field are under the influence of environmental conditions, the actual activity could be different from the potential activity (Tabatabai, 1994).

The procedure described for the assay of acid phosphomonoesterase (PME) activities is based on colorimetric estimation of the p-nitrophenylphosphate (p-NPP) released by phosphatase activity when soil is incubated at constant temperature with buffered pH 6.5 sodium p-nitrophenylphosphate solution and toluene (Tabatabai, 1994). The compound p-NPP acts as an

artificial substrate for acid PME, which releases the colored compound p-nitrophenol (p-NP) (Gress et al., 2007). Four milliliters of 0.1M maleate buffer (pH 6.5) and 1.0ml 0.115M p-nitrophenylphosphate (PNP) were added to 2g soil sample. After stoppering the flask, it was placed in an incubator at 37°C. After one hour, the reaction was terminated by the addition of 4.0mL of 0.5M NaOH and 1.0ml 0.5M CaCl$_2$ were added to allow the dispersion of clay particles. Controls were prepared as ascribed for the assay procedure, although the substrate (p-NPP) was added before the addition of CaCl$_2$ and NaOH in order to assess the colour precipitation not coming from the enzymes (Tabatabai, 1982). All samples were filtered and the yellow colour intensity of calibration standards, samples and controls were measured with a spectrophotometer Spectronic Genesys 20 at 402nm against the reagent blank. Enzyme activities are expressed as µg p-NP g^{-1} dry soil h^{-1}. It is not possible to differentiate among extracellular, abiontic, or released intracellular enzymes using this method. Although, for enzyme activity to be accounted for in this assessment, the enzymes must cleave ester bonds that are too large to pass through the cell membranes, so that all activity measured took place outside microbial cells (Orlander and Vitousek, 2000).

4.3.4. Statistical analysis

To test the effect of soil biogeochemical processes (APME activity and NMP rate) between invasion statuses (natural, invaded, cleared) and landscape positions (wet- and dry bank, uplands) across seasons, a repeated measures analysis of variance (RMANOVA) was applied. When significant differences between the main (landscape position) and interaction effects (landscape position X seasons) were tested, only data from the four natural sites were applied with the intention of excluding possible effect of invasion and clearing on soil properties. It is important to note that plots selected in terrestrial upland areas at invaded sites are in fact not invaded by *Acacia* spp. and for this reason, excluded from statistical analyses for the purpose of comparing different effects between invasion statuses. Since invasion is most prominent in dry bank lateral zones, data from all sites within this landscape position were used when invasion status and interaction effects were tested. Mean differences were separated with post hoc Tukey's HSD test at 5% level of significance. Relationships between soil properties and processes were examined using Spearman's Correlation Coefficient from all the data collected during the year, irrespective of invasion status or position in the landscape. Analyses were performed using Statistica software (StatSoft, Inc; version 10.0.228.2). Interactions between soil biogeochemical processes and other important soil properties and their grouping according to invasion status and landscape position were investigated with PCA Biplots (autumn and spring data only). The statistical biplot GUI package was used to construct biplots in R statistical package.

4.4.   RESULTS

4.4.1.   Potential N mineralization rates

NMP rates did not show significant seasonal interactions with landscape positions ($F_{[6, 138]}$ =1.614, p =0.148; Figure 4.2a) or invasion statuses ($F_{[6, 141]}$ =1.267, p =0.277; Figure 4.2c), however NMP rates differed significantly amongst seasons (one-way ANOVA: $F_{[3, 556]}$ =25.517, p<0.001), and between landscape positions (one-way ANOVA: $F_{[2, 193]}$ =10.517, p<0.001; Figure 4.2b) and invasion statuses (one-way ANOVA: $F_{[2, 197]}$ =3.404, p<0.05; Figure 4.2d). Mean NMP rates were 195% and 199% greater in dry bank and terrestrial soils compared wet bank soils respectively. The seasonal course of mineralization rates presented similar patterns amongst landscape positions and invasion statuses with a maximum rate in spring (apart from invaded sites, where NMP rates were highest in summer), and low but measurable rates in autumn and winter. NMP rates under *Acacia* stands were significantly higher (p<0.05) when compared with cleared areas, but did not differ from natural sites (p>0.05). Mineralization occurred throughout the year, but microbial immobilization was evident in certain areas, particularly wet bank zones (Figure 4.2a; c).
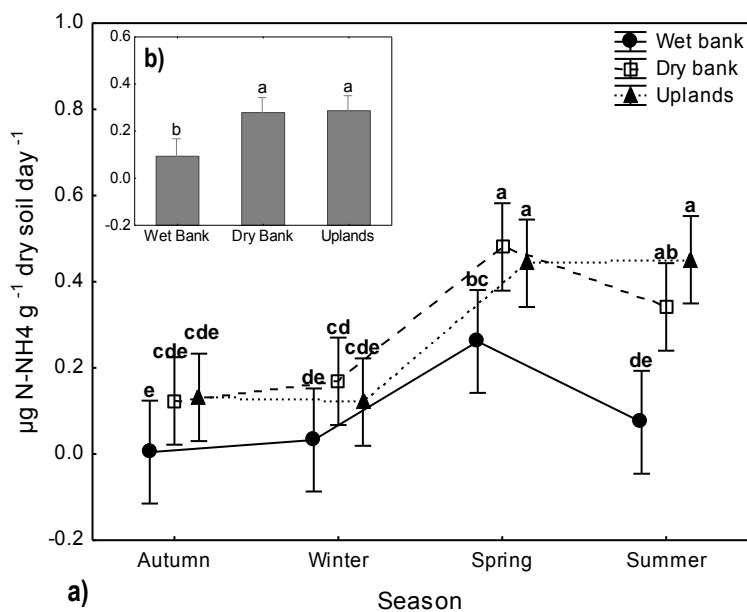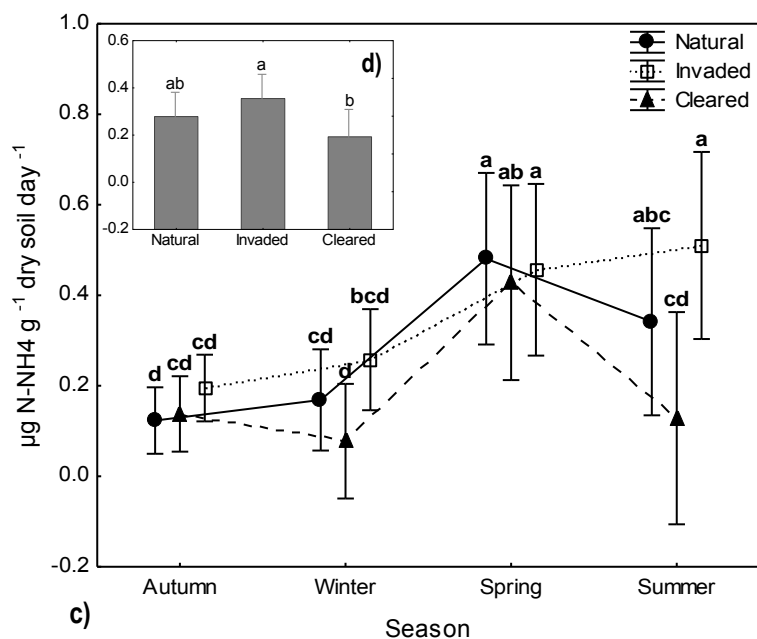
Figure 4.2. (**a**) Potential anaerobic N mineralization (NMP) rates for landscape positions (wet bank, dry bank, and uplands) and (**c**) invasion statuses (natural, invaded and cleared) across seasons. Mean values indicated by different symbols, and whiskers represent ± 95% confidence interval. Letters denote significant differences using repeated measures ANOVAs: landscape position X seasons ($F_{[6, 138]}$ =1.614, p =0.148) and invasion status X seasons ($F_{[6, 141]}$ =1.267, p =0.277), with post hoc Tukey tests (p<0.05). Average seasonal measurements for NMP rates taken over 1 year are depicted in the embedded bar graph for (**b**) landscape position and (**d**) invasion status. Mean values indicated by bars, and whiskers ± 95% confidence interval. Different letters indicate statistical differences using one-way ANOVAs followed by Tukey post hoc tests (p<0.05): landscape position ($F_{[2, 193]}$ =10.517, p<0.001) and invasion status ($F_{[2, 197]}$ =3.404, p<0.05).

4.4.2. Acid phosphatase activity

Acid phosphatases, which release inorganic phosphate from organic monophosphate esters, showed significant interactive effects between landscape positions and seasons and the same was also true for invasion statuses (Figure 4.3a; b). Enzyme activity was highest in summer at each lateral zone and invasion status (Figure 4.3a, c). APME was significantly lower at wet bank zones during spring and summer compared to both dry bank and uplands (Figure 4.3a). Upland areas, on the other hand, were significantly different from both wet- and dry banks during autumn and spring. Overall mean acid phosphatases showed low activity in wet bank soils (196 µg p-NP g^{-1} h^{-1}), intermediate in dry banks (265 µg p-NP g^{-1} h^{-1}) and high upland zones (337 µg p-NP g^{-1} h^{-1}; Figure 4.3b). Soils under *Acacia* spp. exhibited significantly greater enzyme activity across all seasons, compared to both natural and cleared, whereas natural sites showed APME activities similar to cleared riparian zones across all seasons (Figure 4.3c). Acid phosphatases were on average 2.3 and 2.4 times higher in *Acacia*-invaded riparian zones than natural and cleared ones respectively.
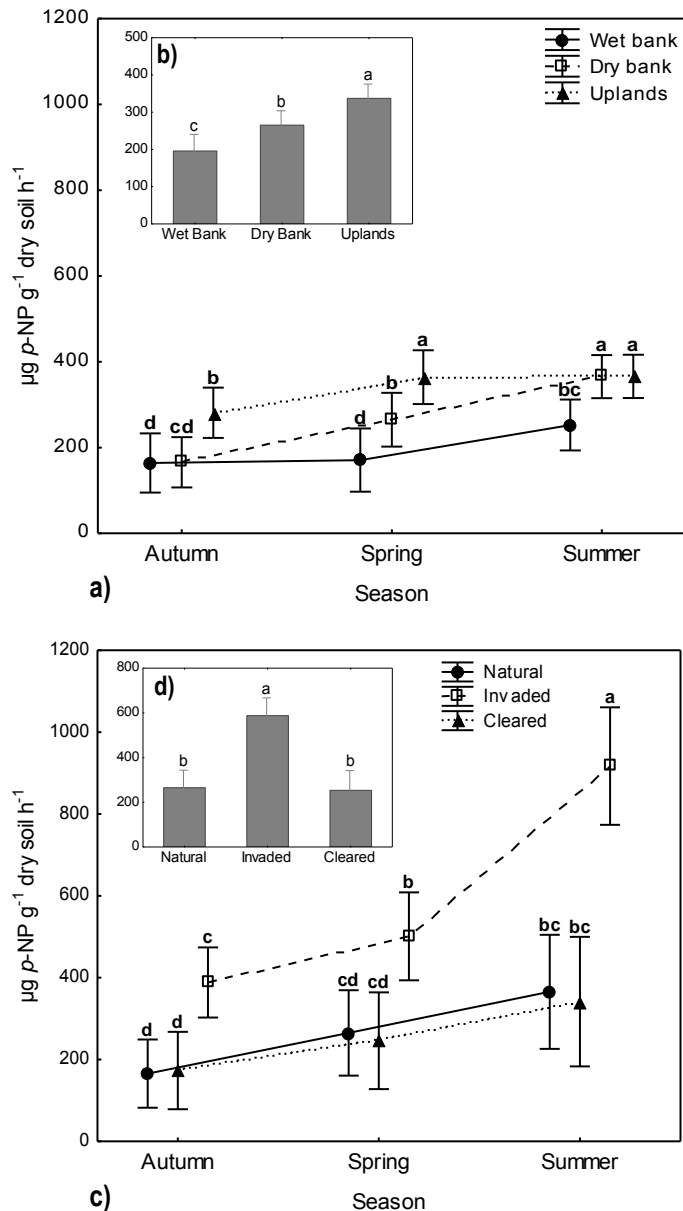
Figure 4.3. (**a**) Acid phosphatase monoesterase (APME) activity across seasons for landscape positions (wet bank, dry bank, and uplands) and (**c**) invasion statuses (natural, invaded and cleared). Mean values indicated by different symbols, and whiskers represent ± 95% confidence interval. Letters represent significant differences ($p<0.05$; Tukey tests) for repeated measures ANOVAs: landscape positions X seasons ($F_{[4, 92]} = 4.853$, $p<0.01$) and invasion status X season ($F_{[4, 92]} = 8.249$, $p<0.001$). Mean APME activity averaged across seasons are depicted in the embedded graph for (b) landscape positions and (d) invasion statuses. Mean values indicated by bars, and whiskers ± 95% confidence interval. Letters denote significant differences ($p<0.05$; Tukey tests) between one-way ANOVAs: landscape position ($F_{[2, 144]} = 13.013$, $p<0.001$) and invasion status ($F_{[2, 146]} = 24.034$, $p<0.001$).

4.4.3. Interactions

Acid phosphatases and NMP rate showed significant correlations with soil physical and chemical properties (Table 4.2). A negative correlation ($r^2 = -0.204$; $p<0.05$) was exhibited between phosphatase activity and soil moisture content, whereas soil pH and Bray-2 available P_i was not

correlated with enzyme activity (Table 4.2). Soil bulk density showed a significant inverse relationship with APME activity and NMP rate. Net N mineralization was negatively correlated with soil C/N (r^2 = -0.408; $p<0.05$; Table 4.2).

SOIL PROPERTIES	APME activity	NMP rate
pH	-0.129	N/A
GSWC	-0.204*	-0.104
Bray-2 P_i	-0.039	N/A
Bulk density	-0.433*	-0.354*
Soil C/N	-0.262*	-0.408*

Table 4.2. Spearman's correlation coefficient ρ (rho) for process rates and selected soil physical and chemical properties. Significant relationships ($p<0.05$) are indicated by an asterisk (*). Correlations were calculated from all available data irrespective of invasion status or landscape position, however, different variables differed in the regularity of sampling: seasonally (pH; GSWC; Bray-2 P_i); biannually (Soil C/N) and once of during spring (bulk density). Correlation values represent only instances where comparisons could be made. For example, Soil C/N was determined during autumn and spring, and NMP rate seasonally, so that the ρ value (-0.408) is only for the seasons (autumn and spring) where data was available for both factors. N/A: not applicable; GSWC (gravimetric soil water content).

Positive correlations between selected soil physical and chemical properties and process rates were exhibited (Figure 4.4a, b), with particularly strong associations between NMP, APME, available N and silt and clay content. Wet banks showed a distinctive clustering of variables, which differed from both dry banks and neighbouring uplands. Wet banks were associated with significantly lower fractions of silt and clay, low concentrations of total available inorganic N (see Chapter 3 for significant values), and low N and P mineralization rates (Section 4.4.1; 4.4.2), compared to dry bank and uplands (Figure 4.4a). Only trends towards enhanced soil TN and TC were evident, but the increases were not as strong as those observed in dry bank and upland zones. Dry banks and uplands were fairly similar with regard their grouping of variables, nevertheless, uplands showed tendencies towards higher rates of NMP and phosphatase activities, silt and clay content and available N. NMP and phosphatase activities and soil silt and clay content were particularly well correlated when landscape positions were compared.
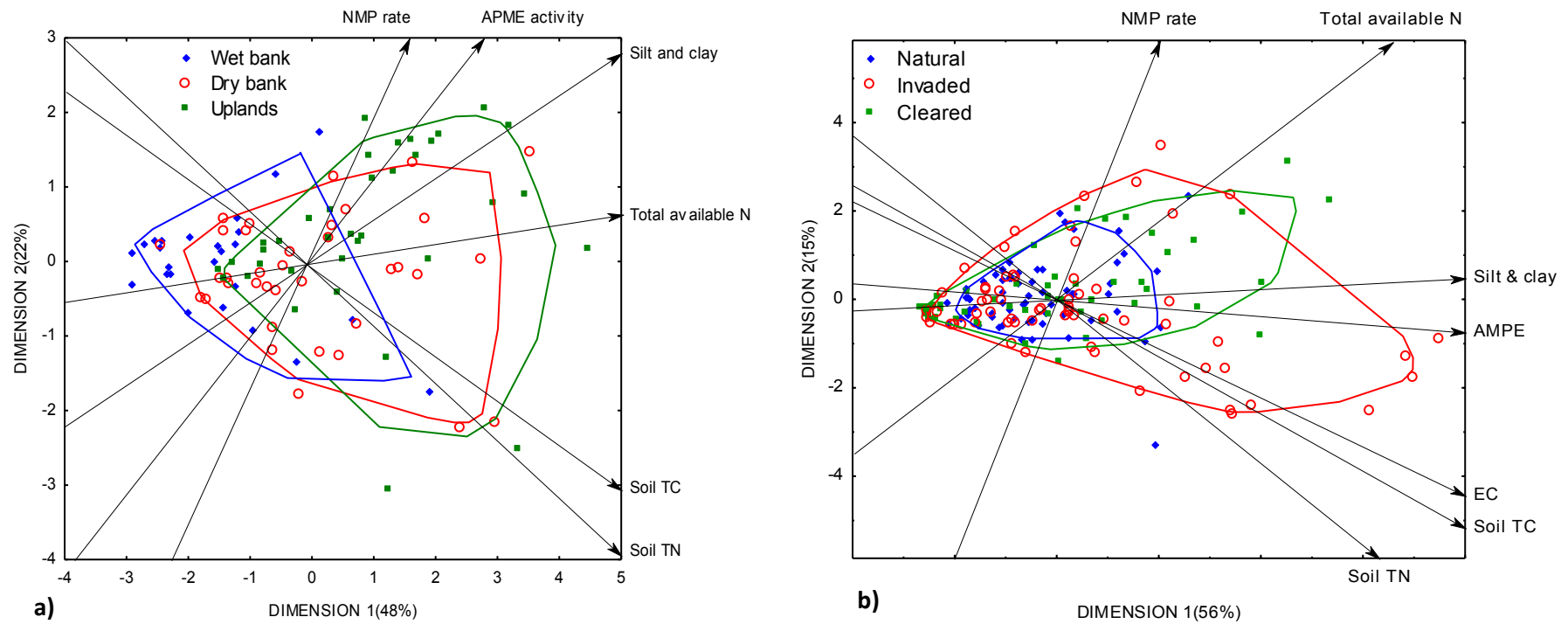
Figure 4.4. PCA Biplots indicating the relationship amongst soil properties according to (a) landscape positions and (b) invasion statuses. Alpha-bags enclose the areas that contain approximately the inner 90% of cases. Certain variables (TN; TC and particle size distribution) were conducted biannually during autumn and spring; therefore results are based on data for these seasons only. Invasion statuses are based on data from dry banks only and landscape positions, natural sites only.

Natural, invaded and cleared sites had their own distinctive grouping regarding soil physical and chemical properties and biogeochemical processes (Figure 4.4b). The clustering of variables was more confined at natural areas compared to invaded sites. Thus, there was no specific trend towards increases in any one specific soil property. Compared to natural sites, invaded sites showed trends towards enhanced silt and clay fractions and TC (see Chapter 3), with significantly higher rates of phosphatase activity, total available inorganic N concentrations, TN and dissolved materials (EC)(Figure 4.4b; Chapter 3). Cleared sites only showed tendencies towards significantly enhanced available inorganic N concentrations (Figure 4.4b; Chapter 3). N mineralization rates were most strongly associated with soil total available N when invasion statuses were compared.

4.5. DISCUSSION

4.5.1. Potential N mineralization rates

Temporal variability in plant productivity, which may vary inter-seasonally and inter-annually, between adjacent habitats, may affect nutrient fluxes, such as N-cycling (Chapin et al 2002; Ballinger and Lake, 2006). As found in other studies (e.g. Maron and Jefferies, 1999), seasonal variation in N mineralization rates was high. The temporal course of mineralization rates presented the same seasonal pattern regardless of invasion status or position in the landscape with a peak in spring and lower, but measurable rates in winter. Competition for resources between plants and microbes are expected to be greatest during optimal growing conditions (spring) and may likely be a possible explanation for higher NMP rates observed during this time of the year. A combination of soil moisture (after seasonal flooding events) and favourable temperature stimulates mineralization by microbes from the soil organic N pool (Bardgett, 2005). N mineralization generally occurs at higher rates under moist than dry conditions, and has been shown to slow down significantly at low temperatures (Chapin et al., 2002), as was observed in this study. Similarly, Rice et al. (2004) found that mean net N mineralization and nitrification rates were enhanced during the growing season, and declined in winter.

River hydrogeomorphological conditions controls the categorization of sediments on the basis of particle size in a riparian floodplain (Pinay et al., 1995). Low-lying wet bank zones are exposed to high energy and current velocity during flooding so that coarsely textured suspended matter, low in its capacity to retain and sequester OM inputs (Rhoades et al., 2001) is deposited. On very coarsely-textured wet bank soils, the accumulation of C, N and OM is slower, and is further limited by slower N-cycling in litter (Prescott et al., 2000). Different microclimatic conditions and fluvial processes associated with wet banks may slow decomposition rates, such that

mineralization rates measured throughout the year remained consistently lower than that of dry bank and upland areas. In addition, pools of labile soil organic N in wet bank zones become depleted (i.e. leached) under conditions of high rainfall events, and as a consequence, reduce the substrate (soil OM) necessary for N transformations (Chapin et al., 2002). Dry bank zones, on the other hand, are not influenced by within-year flooding events and, accordingly, enhance OM accretion. Mean NMP rates between landscape positions and amongst invasion statuses were all above zero, indicating net mineralization. This suggests that microbial immobilization was lower than mineralization.

Litter produced by native species adapted to low-nutrient ecosystems of the fynbos decomposes relatively slowly, because low P and N concentrations and high contents of lignin, tannins and other toxic or recalcitrant compounds (Yelenik et al., 2004; Chapin et al., 2002). Various studies have shown that N_2-fixing species strongly influence available N pools and enhance N mineralization rates (e.g. Stock et al., 1995; Yelenik et al., 2004, 2007; Rice et al., 2004; Malcolm et al., 2008). However, NMP rates under *Acacia* stands did not differ from natural sites, as was hypothesized. Higher litter inputs and N pools (e.g. TN in this study) in invaded sites does not necessarily lead to higher mineralization rates, but interactions between plants' requirements for N and available soil resources (e.g. dissolved organic and inorganic N) may limit the rate of N mineralization. It is also possible that *Acacia* spp. and their mycorrhizal fungi that absorb amino acids may also not greatly depend on N mineralization to meet their N needs in infertile ecosystems due to absorption of dissolved organic matter (DOM). Since there are several environmental factors (temperature, soil moisture), biological (microbial activity and substrate quality), and soil physical and chemical properties that affect N mineralization rates, it is difficult to draw conclusions from this study. Thus, future research should address the link between N-cycling and soil physical, chemical and biological factors affecting these processes.

Overall NMP rates in cleared riparian ecotones were not different from natural sites, suggesting that N-cycling has approached background levels. When plants are removed from ecosystems after clearing, N that otherwise would have been absorbed by plants is immobilized by soil microbes or leached from the soil, consequently resulting in low or negative net-mineralization values (Schmidt et al., 1999). Furthermore, being frequently inundated and more susceptible to leaching, riparian ecotones may recover more rapidly by enhancing the rate at which available- and organic nutrient pools that accumulated as a result of invasion is lost. However, it still remains unclear how long the biogeochemical legacies in the soil may have persisted after alien clearing activities, and it is suggested that long-term research be undertaken to monitor N, C and P concentration and cycles directly after the eradication of *Acacia* spp. from riparian zones.

Biogeochemical legacies in areas cleared of N_2-fixing invaders have recently been investigated. The removal N_2-fixing *Robinia pseudoacacia* trees eliminated a rapidly mineralizable supply of N to soils (Malcolm et al., 2008). Marchante et al. (2009) reported decreases in microbial parameters related to N-cycling four and half years after removal of *A. longifolia*. They concluded that declines were faster than for soil chemical pools, such as N and C. Conversely, N mineralization rates in areas cleared from *A. saligna* stands in terrestrial fynbos ecosystems (Yelenik et al., 2004) and *Lupinus arboreus* in coastal prairies (Maron and Jefferies., 1999) did not differ from rates under invaded stands. However, these experiments were conducted after a few (1-4 years) of clearing. Long-term success of restoration may be inhibited by high rates of N availability that affect plant community interactions and alter successional trajectories (Rice et al., 2004).

4.5.2. Acid phosphatase activity

Plant roots are major producers of acid phosphatases in the soil (Amador et al., 1999; Kramer and Green, 2000), but microbes can also produce and release large quantities of extracellular phosphatases due to their high metabolic activity, large combined biomass, and short lifecycles (Tabatabai, 1994; Kramer and Green 2000). Acid phosphatases showed a significant seasonal pattern with maximum activity during the hot and dry summer season. Soil samples collected from the upper 10cm of the soil profile reflect changes in ambient temperatures, and likely explain some of the significant seasonal differences observed for both enzymatic activity and NMP rate. Seasonal variations in enzyme activity were less discernible in wet banks compared to dry bank and upland zones. The more open-canopied dry bank and upland areas (Chapter 3) receive more solar radiation, and accordingly experience greater fluctuations in temperature and soil moisture than wet bank zones. The activities of phosphatases are related to the response of plant and soil communities to seasonal changes in soil moisture and temperature (Grierson and Adams, 2000; Kramer and Green, 2000). Accordingly, spatial and seasonal heterogeneity in AMPE in soils may be affected by plant species composition, which in turn influences root and microbial activity (Grierson and Adams, 2000).

Higher temperatures can promote microbial activity and metabolism, enhancing the turnover of nutrients and their availability (Sardans et al., 2006; Chapin et al., 2002). The increase in acid phosphatases observed in spring and summer coincides with warmer temperatures. Similarly, Sardans et al. (2006) reported that warming significantly enhanced the activities of acid phosphatases in a Mediterranean shrubland during summer. In addition, the growth response of plants and microbes during this time of the year stimulates mining for P, which may become more deficient as a result of competition for resources. Temperature and soil moisture are important

factors that govern the rate of chemical reactions and the activity and growth of organisms in the soil (Bardgett, 2005). The buildup of phosphatases released into the soil from dying soil micro-organisms may also explain the peak activity found in summer (Kramer and Green, 2000). Seasonal variation in APME activity and NMP rate, emphasize the importance of careful sampling across seasons for ecological studies on biogeochemical cycling (Grierson and Adams, 2000).

McClain et al. (2003) suggested that several landscape features, such as riparian zones and topographical depressions are hotspots for biogeochemical activity; however, this did not apply for fynbos riparian ecotones. Contrary to my hypothesis and compared to terrestrial uplands, biogeochemical cycles were not enhanced within riparian zones, but actually revealed lower process rates in many instances. Wet bank zones had significantly lower NMP and APME rates compared to those higher up in the landscape, whereas dry banks only differed from uplands with regard to phosphatase activity.

As hypothesized, *Acacia* invasion significantly enhanced the activity of APME compared to both natural and cleared sites. The mechanism by which N_2-fixing invasive species affect P biogeochemistry may include changing the components and chemical nature of soil OM and soil enzyme activity in addition to the dynamics of soil geochemical reactions through litter inputs (Zou et al., 1995). By significantly increasing the supply of soil C and N and litter inputs (Chapter 3; Appendix E), in addition to possible changes in litter quality (Yelenik et al., 2004; Marchante et al., 2008), *Acacia* spp. may stimulate P demand and provide raw materials for the synthesis of extracellular acid phosphatases. A similar situation has been reported by Allison et al. (2006). They found that higher inputs of litter and enhanced C and N pools in *Falcataria*-invaded Hawaiian ecosystems, supported high enzyme activity with significant increases in acid phosphatases relative to native forests (Allison et al., 2006). This suggests that enhanced N availability in *Acacia* invaded fynbos riparian zones will increase the demand for P by *Acacia* spp. The substantial increases in APME activity observed under Acacias and other N_2-fixing species has been reported by other studies elsewhere (e.g. Giardina et al., 1995; Zou et al., 1995; Caldwell, 2006; Houlton et al., 2008), allow soil microbes and plant roots to gain access to organic forms of P more effectively; consequently providing a mechanism for increasing the supply of P (Allison et al., 2006). Houlton et al. (2008) reported that the release of available P_i by phosphatase activity appears to be of direct benefit to N_2-fixing plants species, which produced that activity.

Acacia invaded fynbos riparian ecotones support higher fine-root biomass compared to natural ones (Kambol Kambaj, O., unpublished data, 2011), suggesting that root activity likely played a

significant role in enhanced enzymatic activity observed at invaded sites. Furthermore, APME activity may also be enhanced due to increased fungal activity associated with invaded sites (Grierson and Adams, 2000; Slabbert, E.; unpublished data, 2011). The activity of extracellular enzymes, such as phosphatases, associated with different plant species (e.g. natural versus invasive N_2-fixers), is a function of the morphological and physiological attributes of root type (Grierson and Adams, 2000). Molecular studies have showed that the production of extracellular APME is closely related to the P status of plants so that the production of these enzymes might to be a specific response to P deficiency (Gress et al., 2007). Greater release of these enzymes provides a mechanism for scavenging P from organic material (McGill and Cole, 1981).

4.5.3. Interactions

The supply of a nutrient, such as N, may not only affect the enzymes mineralizing that particular nutrient, but also enzymes mineralizing other nutrients (Orlander and Vitousek, 2000), supporting the causality of the association between APME activity and N availability observed in this study. In places where the supply of N is low, such as in fynbos ecosystems, additions of N, through biological fixation by *Acacia* spp. (as mentioned in section 5.5.2) may stimulate production of phosphatases (Giardina et al., 1995; Orlander and Vitousek 2000). Witkowski and Mitchell (1987) and Stock et al. (1995) showed that *Acacia* spp. increase soil N mineralization rates only at sites rich in nutrients, whereas P mineralization was enhanced in *Acacia* stands of both nutrient-limited and nutrient-rich ecosystems. Soil N availability and soil phosphatases are often positively related due to plant and microbial demand for P, which should be higher in N-rich soils. The reason for this is that N is vital for enzyme production, and enhanced productivity of these species increases the demand for P in response to mitigation of N deficiency (Orlander and Vitousek, 2000; Vitousek et al., 2010).

From an ecological perspective, it is thought that a negative association exists between soil inorganic nutrient availability and enzyme activity, but contradictory results have been found (Kang and Freeman, 1998). Studies have suggested that the relation between enzyme activity and P availability does not always apply (Bengstsson et al., 2003; Giardina et al., 2001). According to the outcomes of the study, higher phosphatase activity did not lead to an increase in available P_i. A possible explanation is that the range of P supply was not high enough to activate inhibition through negative feedback systems (Orlander and Vitousek, 2000), since mean P_i availability between landscape positions and invasion statuses across all seasons was less than 20 µg g^{-1} (Chapter 3; Appendix E).

Even though APME activity was significantly higher in *Acacia*-invaded stands, compared to natural ones, available P_i did not differ between sites (Chapter 3). A possible explanation for this finding is that extractable P_i, which is made available through enhanced enzyme activities in invaded sites, is immediately absorbed by plants to meet their growth requirements. This suggests that *Acacia* spp. must therefore use greater quantities of available P_i than natural riparian vegetation by releasing greater quantities of phosphatase enzymes to meet their greater P requirement (Giardina et al., 1995). These results are also consistent with Zou et al.'s (1995) finding in Hawaiian soils where comparisons were made between native *E. saligna* and invasive N_2-fixing *A. falcataria* stands. Rates of P-cycling in litterfall are generally higher under N_2-fixing species, whereas the effects on P pools in soils sometimes increase or decrease (Compton and Cole, 1998; Binkley, 2005). Furthermore, the greater percent increase in phosphatases, relative to that of NMP rate in invaded stands, suggests greater emphasis on P acquisition under *Acacia* spp., probably in response to higher P demands (Caldwell, 2006).

The C:N ratio of substrates, microbial growth- and N-use efficiency all regulate N mineralization and immobilization rates (Hart et al., 1994; Austin et al., 2004). Given the close relationship between total N and C (Chapter 3; Figure 4.4), soil C/N ratios plays an essential role in controlling the rate of OM decomposition and consequentially, regulating the rate at which nutrients are released and cycled (DeBano, 1990). The significant inverse relationship between NMP rate and soil C/N shows that soils with low C/N ratios have higher potential mineralization rates (slower N immobilization) with subsequent production of available NH_4^+ resulting from deamination of OM sources (Bengtsson et al., 2003). Numerous studies have shown that litter C/N correlates with decomposition and N mineralization rates (e.g. Yelenik et al., 2007). In many ecosystems, rates of microbial decomposition can be predicted fairly well from soil TN content and soil C/N (Stock et al., 1995). Soil C/N below which net N mineralization occurs is in the range of 25-30 (Prescott et al., 2000). However, soil C/N which controls the threshold between N mineralization versus immobilization is variable and often differs between species (Eviner and Chapin, 2003). Even if soil C/N ratio and soil available N are predictors of site specific variations of N transformations, temporal variation in soil moisture and temperature influences N decomposition and mineralization more than the spatial variation of the soil C/N (Bengtsson et al., 2003; Erhenfeld, 2003).

This study uncovered a positive relationship between soil silt and clay contents and soil biogeochemical processes (NMP rate and APME activity). The mineralization of organic P has been shown to be strongly influenced by variations in soil forming factors that determine the physical and chemical nature of soils (Tabatabai, 1994; Šarapatka, 2003) such as OM (Amador et

al., 1999), soil texture (Tabatabai, 1994; Šarapatka, 2003); and soil moisture (Cirmo and McDonald, 1997). Even if the complexity of interactions involved renders it challenging to quantify the importance of particular mechanisms that mediate nutrient transport and internal cycling, soil moisture (which is regulated by concentrations in soil fine particles) and OM distribution, likely plays an integrate role (Bechtold and Naiman, 2006). Soils that have high contents of fine materials have the ability to protect or preserve microbial biomass and organic matter, allowing greater retention of nutrient (Austin et al., 2004). It is therefore realistic to assume that soil particle size influences the rates of microbiological processes involved in nutrient cycling (Pinay et al., 1995). Furthermore, soil bulk density, which is a good indicator of OM content (Robertson et al., 1999; Chapin et al., 2002), was significantly correlated with enzyme activity, suggesting that it influences APME activity and NMP rates by controlling soil water and nutrient characteristics.

In general, relationships found here differed between landscape positions and invasion statuses. The position within the landscape, as denoted by different geomorphological zones, appears to control the activity of APME and NMP rates in fynbos riparian soils due to different soil properties and edaphic factors related to each lateral zone. Similarly, Amador et al. (1999) showed acid phosphatase activity in riparian zones to be partly controlled by position in the landscape with soil moisture and OM as essential factors in determining enzyme activity.

Correlations between fine soil particles (silt and clay) and NMP rates measured in this and other studies point to important linkages between soil particle size and resource availability (Bechtold and Naiman, 2006). Fine-textured soils have been shown to be correlated with soil N mineralization rates, soil fertility, and soil microbial biomass (Pinay et al., 1992; Chapin et al., 2002; Eviner and Chapin, 2003; Naiman et al., 2005). Fine-textured soils are not only characterized by higher labile pools of N and C and water-holding capacity than coarsely-textured soils, but also frequently show a much higher flush of N mineralization (Austin et al., 2004). Differences in NMP rates observed between invasion statuses and landscape positions could also be due to microbial utilization of organic N compounds, which may vary in concentration (quantity), and in ease of utilization by, or accessibility to microorganisms (quality) (Fyles et al., 1990). Erosion in wet bank zones during floods hampers the accumulation of OM, explaining their low TC, TN and available inorganic N and process rates compared to dry bank zones. Well-defined soil differences at short distances between lateral (wet and dry bank) zones are typical for steep, river-influenced (confined channel) (Gregory et al., 1991; Ettema et al., 1999), such the upper reaches of fynbos riparian ecotones. This spatial difference may strongly influence the

effectiveness of nutrient removal (Ettema et al., 1999). The gradient of soil moisture and soil particle distributions from riparian to upland exerts some control over nutrient cycling.

4.6. CONCLUSION

My results show that soil phosphatase activity and NMP rate in fynbos riparian ecotones vary seasonally and as a function of position in the landscape. Both seasonal fluctuations in temperature and soil moisture played an important role in regulating N and P mineralization. The composition of woody species in fynbos riparian ecosystems, which differ between dry and wet bank zones and also over invasion status (Chapter 3), affect soil properties and nutrient cycling. Temperature affects the decomposition of OM directly by enhancing microbial activity and indirectly by changing soil moisture content and the quality and quantity of OM inputs to the soil (Chapin et al., 2002). Wet bank zones were associated with relatively low APME activity and N mineralization rates. Geomorphic processes between the floodplain and river channel in fynbos riparian ecotones accordingly have a directly control over nutrient cycling processes. Changes to fluctuating water concentrations in fynbos riparian soils do not only change oxic and anoxic phases by direct influence on N-cycling, but also indirectly by affecting soil structure and texture through sediment deposition. This lateral gradient (landscape position) accounts for differences in soil properties because the environmental disturbance regimes next to a river channel are very specific.

My results show significant correlations between phosphatase activity and NMP rates and a number of soil physical and chemical properties including, silt and clay content, soil moisture, N (total and available) and total C. Many soil properties such as water-holding capacity, bulk density, redox potential and soil nutrient content are related to soil particle size, so texture can be a particularly good predictor for several ecosystem properties (Eviner and Chapin, 2003). Soil texture played a pivotal role in controlling the rate of N mineralization, APME activity and mediating the retention of nutrients in both riparian and upland ecosystems. The sensitivity of phosphatase activity to various soil properties, temporal (environmental) and spatial (landscape position) changes, renders it a potential indicator of changes in soil quality.

Invasion by *Acacia* spp. (mostly *A. mearnsii*) is changing P-cycling in fynbos riparian ecosystems in the south-western Cape. This is not surprising considering that the native fynbos ecosystems with low productivity are now dominated by a highly productive N_2-fixing trees. Invasive Acacias may have the ability to change microbial community composition and ultimately the synthesis of extracellular enzymes, especially phosphatase. These mechanisms allow invasive N_2-fixers to

enhance P availability and facilitate further invasion even in areas where availability of P is expected to constrain invader productivity (Allison et al., 2006). It is important to note that N$_2$-fixing species may result in different impacts depending on the environment (e.g. soil texture; soil nutrient status; temperature) and the particular characteristics of the invader (Ehrenfeld, 2003, Jovanovic et al., 2009), since nodulation and fixation is dependent on environmental factors, of which soil P and N availabilities are the most important (Scherer-Lorenzen et al., 2007). The rates of N and P mineralization of *Acacia*-cleared sites were similar to natural riparian systems, indicating the potential of cleared sites to return to pre-invasion levels; however, it may take several more years for nutrient processes to be restored.

4.7. REFERENCES

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CHAPTER 5

General Conclusions, Recommendations and Future Research

5.1.   KEY FINDINGS, RESEARCH CONTRIBUTION AND MANAGEMENT IMPLICATIONS

The results presented in this thesis addressed several different aspects of riparian structure and function. This research is amongst the first to investigate whether widely colonizing *Acacia* spp. (especially *Acacia mearnsii*) do in fact alter fynbos riparian biogeochemistry. This chapter presents, on the basis of my findings, a number of implications for management and practical guidelines for restoration of *Acacia*-invaded or previously infested catchments. Furthermore, results from this study revealed gaps in knowledge and provides recommendations for future research needs to address these gaps that may add to our understanding of fynbos riparian function. The rationale for this study was to gain a mechanistic understanding of riparian ecosystem function in the south-western Cape and changes brought about by *Acacia* invasion and clearing thereof, with implications for their restoration and management. The purpose of this study was to quantify plant functional type (PFT) cover, soil physical and chemical properties, and selected biogeochemical processes in natural, *Acacia*- invaded and cleared riparian ecotones (invasion status comparison) and associated non-riparian upland fynbos (landscape position comparison). Analyzing seasonal patterns of selected soil properties, nitrogen (N) and phosphorus (P) biogeochemical processes, the factors affecting these processes in fynbos riparian ecotones, and the possible changes as a result of invasion by, and clearing of *Acacia* spp., provided many insights into the dynamics of fynbos riparian ecotones. The results presented in this thesis acts as a stepping stone for guiding future research and management in riparian zones, and add to the evaluation of the success of clearing initiatives and restoration of riparian ecotones.

Results from this study showed that PFT cover and composition, soil physical and chemical properties and soil process rates (N mineralization potential and acid phosphatase activity) differed amongst invasion statuses (natural, invaded and cleared), spatially within the landscape (i.e. distance from the river channel) and across seasons. Regarding most soil properties and indices of nutrient (N and P) cycling, river floodplains (dry banks) were very similar to terrestrial uplands. Wet banks, on the other hand, have different soil characteristics. Fluvial processes, including hydrology, (which affect soil chemistry and physical characteristics) are stronger

ecosystem drivers in wet bank zones, relative to adjacent dry banks. Furthermore, compared to wet bank zones, more opened-canopied dry bank and upland areas (see Chapter 3) differ in microclimatic conditions, which ultimately control soil process rates. Higher temperatures and favourable soil moisture conditions govern the rate at which soil chemical reactions proceed, and can promote microbial activity, enhancing the turnover of nutrients and their availability. Compared to geomorphological zones higher up in the landscape, high moisture content (through inter-annual flooding), together with the coarsely-textured nature of wet bank zones, results in the leaching of various ions, consequently lowering soil pH, electric conductivity (EC), soil nutrient concentrations and organic substrates from which N and P is mineralized. This inter-site soil variability can make a reliable evaluation of biogeochemical properties and nutrient cycling more complex. These results imply that the underlying local heterogeneity (such as micro-topography) and the effect of an environmental lateral gradient related to flooding plays an important role in influencing the spatial distribution of soil properties that are under different geomorphological and biological (litter inputs and microbial activity) control.

This research sheds light on soil nutrient cycling processes in riparian ecosystems and adjacent upland areas and its inter-relationships with specific soil physical and chemical characteristics and other environmental variables controlling process rates or enzyme activity as well as alterations as a consequence of invasion by Australian Acacias and clearing thereof. Furthermore, these results add to previous knowledge on soil phosphatases and N mineralization in other ecosystems. The data presented in this thesis highlight the importance of soil texture as a vital factor controlling soil physical and chemical characteristics and the rate of N and P mineralization, by regulating the factors affecting soil properties and processes (e.g. soil temperatures, water cycling, chemical reactivity, and organic matter and nutrient retention; Pinay et al., 1992; Pinay et al., 1995; Chapin et al., 2002; Adair et al., 2004; Bechtold and Naiman, 2006). Nevertheless, the importance of these observations in terms of nutrient cycling, from a restoration perspective necessitates further investigation (see section 5.3). By relating soil particle size distribution to N mineralization rates and soil acid phosphatases, I highlight the significant functional roles hydrogeomorphlogical processes play that may help elucidate landscape patterns in ecological properties within fynbos riparian zones. This understanding can provide valuable insights into the use of several soil related properties as tools in prioritizing restoration initiatives.

Tye and Drake (2011) underlined the potential for enhanced N inputs by *A. mearnsii* through contributions of biological N_2-fixation. The data supports the hypotheses that invasion by *Acacia* spp. changes soil properties and affects plant functional attributes. N_2-fixing invasive *Acacia* spp.

altered nutrient cycling regimes (both N and P) and physical and chemical properties within mountain- and foothill sections of fynbos riparian ecotones. Compared to other studies of N_2-fixing woody invasive plants and their impact on soils, the results from this thesis demonstrate significant increases in TN, available inorganic N and P cycling rates. However, increases in soil N were not as strong as what was found in other terrestrial ecosystems invaded by N_2-fixing *Acacia* spp. (e.g. Witkowski, 1991; Stock et al., 1995; Yelenik et al., 2004, 2007; Marchante et al., 2008; Hellmann et al., 2011). This may be related to the ability of riparian zones to process nutrients such as N and P through denitrification, organic matter removal and immobilization in standing plants. Another noticeable effect is the dampening impact of *Acacia* invasion on PFT cover and composition, converting diverse plant communities into low diversity, homogenous communities (Holmes et al., 2005; Gaertner et al., 2011). *Acacia* spp. (mostly *A. mearnsii*) in fynbos riparian ecosystems is a transformer species (*sensu* Richardson et al., 2000) and may consequently compromise resilience of riparian ecotones by altering abiotic (e.g. several soil properties) and other biotic components (e.g. high litter inputs). The impacts of exotic tree removal on native plant growth and soil transformations in fynbos riparian ecosystems formerly occupied by N_2-fixing Acacias (in addition to other woody IAPs; Appendix C) were evaluated. Although most selected soil physical (particle size distribution and bulk density), chemical (available P_i, total N and carbon) and biological (litter mass) properties and N and P mineralization rates at cleared sites were reduced to levels that were similar to or resembled the situation at natural areas, available inorganic N remained 2 times higher after several years of clearance (7+ years). But, regeneration of post-clearance indigenous fynbos communities was fairly limited, particularly woody riparian taxa (see also Blanchard and Holmes, 2008) and their absence from these systems may threaten vegetation communities and affect ecosystem function (Holmes et al., 2000). The low plant functional type cover (e.g. the area of cover by different growth from types) and high abundance of alien grasses, indicates that certain fynbos riparian zones will need a long time to return to their initial states, if ever. However, we still lack the mechanistic understanding around fynbos riparian recovery after clearing, as the success of re-establishment may depend on complex interaction and feedback cycles between plants and their physical environment. The significantly higher concentrations of available inorganic N, relative to natural areas, may be attributed to N enrichment of soils (from previously *Acacia*-infested sites) and may be one of the underlying factors in promoting the growth and persistence of alien grass species observed at cleared sites. Clearing *Acacia* spp. may initiate restoration of invaded riparian ecosystems, but legacies in the form of available N hamper long-term success by altering plant community interactions (Yelenik et al., 2004; Marchante et al., 2009). This can lead to long-term problems for restoration of indigenous vegetation and ecosystem function, which may not recover without some form of active intervention.

In the current study, soils across sampling sites differed significantly (see Appendix F1 and F2) from each other in terms of soil properties (especially those that are directly influenced by the underlying geology) including pH and soil particle size distribution (silt-clay, fine sand and coarse sand). Each river system has a unique soil fingerprint, a result of a combination of factors that differ between catchments, such as parent materials, site history, rainfall and plant communities (Deacon et al., 1992; Brown et al., 2004), called 'catchment signatures' (King and Schael, 2001). Soil pH largely reflects the underlying geology, with high values associated with soils derived from granite parent material and lowest values associated with sandstone-derived parent material (Prins et al., 2004). Similarly, one might expect that differences may exist in soil biogeochemistry, especially as soil particle size is related to indices of N and P cycling in fynbos riparian environments. However, it is important to consider that invasion may result in changes in the above mentioned soil physical and chemical properties. Investigating the impacts of *Acacia* spp. (or clearing thereof) on geomorphological changes was beyond the reach of this study. Nevertheless, incidents of geomorphological alterations were noted, such as localized erosion (see Chapter 1; Section 1.3.2) at cleared sites.

5.2.   RECOMMENDATIONS FOR MAINTAINING FYNBOS RIPARIAN STRUCTURE AND FUNCTION IN RESTORATION

Because of the complex interactions between biotic factors and the physical environment in riparian zones, it is critical to define thresholds that delineate options for intervention (Richardson et al., 2007). Active restoration is necessary in areas where dense alien stands have existed for decades in riparian zones and where native species re-establishment is expected to be slow or undesirable to promote the recovery of indigenous vegetation after alien clearance. Accordingly, several different aspects vital for ecosystem repair needs to be addressed when planning restoration projects including biotic- and abiotic-level restoration, such as mechanisms to mitigate N enrichment and erosion or alteration of river geomorphology (Holmes, 2007; Richardson et al., 2007; Reinecke et al., 2008; Esler et al., 2008).

Changes in ecosystem function (e.g., elevated soil N availability) as a result of invasion, as was found in this study, may necessitate active restoration following the removal of the alien species (Maron and Jefferies, 1999; Malcolm et al., 2008; Gaertner et al., 2011), since nutrient enrichment in N-limited ecosystems may preclude the establishment and the abundance of native species (Yelenik et al., 2004; Marchante et al., 2009). Indeed, higher grass cover was evident from most of the sites cleared from *Acacia* spp. in this study. Mitigation strategies as a means of accelerating the recovery by reducing N availability may improve this situation (Malcolm et al.,

2008). In my study, residual soil N in cleared plots, may have likely altered growth rates of plants and community dynamics and enhanced the abundance of grasses. The efficiency of restoration that involve the removal of transformer alien species (e.g. *Acacia mearnsii*) in low N adapted systems requires managers to deal with the task of returning soil nutrients to pre-invasion levels after clearing efforts (Yelenik et al., 2007; Gaertner et al., 2011). Previous restoration initiatives have used soil amendments to reduce N pools and promote the abundance of native species. To reduce readily plant-available inorganic forms of N and potentially limiting the invasion of forb and grasses species, a short-term solution to immobilize excess N in the soil and microbial biomass is to add sawdust or mulch with a high C:N ratios (Maron and Jefferies, 2001; Rice et al., 2004; Yelenik et al., 2004; Holmes, 2008; Gaertner et al., 2011).

Nitrogen loss in riparian environments can either be facilitated naturally through suspension and removal of organic- and inorganic materials in soils and sediments during predicable seasonal flooding or through denitrification during peak rainfall events. As riparian zones are known to support relatively large microbial communities able to denitrify excess N, an alternative strategy may be to provide a source of labile C, such as sucrose, during a period close to the peak wet period or immediately after when soils are still wet, but temperatures are amenable, such as during early spring in the fynbos biome. Nevertheless, dry bank zones, where invasion is more prominent, are not influenced by interannual flooding (reoccurrence interval of 1:20 years), making this natural process a less reliable mechanism to reduce nutrient enrichment, and topsoils are also less likely to be hotspots for denitrification due to aerobic conditions. Natural processes alone may therefore be insufficient to re-establish former function. I therefore suggest that this natural process be facilitated by combining active restoration strategies (e.g. soil amendments; removal of biomass; burning practices; native species re-establishment) after clearing efforts as discussed above and in the paragraphs to follow.

Another aspect that needs to be explicitly addressed and considered in restoration plans is the particular characteristics of the invader and the notion that different species (even of the same genus) may result in different impacts on ecosystem function depending on the environment (e.g. sandy/low temperature vs. clay loam/high temperature) (Stock et al., 1995; Ehrenfeld, 2003, Jovanovic et al., 2009). It is therefore essential to consider the nature of the soils when planning restoration strategies, as soils in riparian habitats derived from alluvial material of sandstones and quartzites (which are particularly coarsely textured) may recover more rapidly (faster rates of labile N leaching) than those derived from granite or shale parent materials (Brown et al., 2004; Prins et al., 2004). Hence, restoration projects need to account for variations in abiotic and biotic processes across catchments ('catchment signatures'). For restoration or rehabilitation efforts, it

is also essential to distinguish between specific lateral riparian zones that are shaped by different flooding regimes (i.e. wet- and dry bank zones; Sieben and Reinecke, 2008), since each particular zone is characterized by unique plant functional types and soil properties.

Burning an area after aliens have been eradicated is a common practice in fynbos ecosystems (Holmes, 2008; Gaertner et al., 2011). Even if fire may substantially increase available N pools (DeBano 1990), it is an essential management tool in reducing large quantities of organic N pools through the process of volatilization (Stock and Lewis, 1986), though the effects of fire in fynbos riparian environments on soil processes has not been extensively and explicitly studied. As fire can severely affect soil properties and biogeochemical cycles, thorough planning is required to ensure that long-term productivity of ecosystems is not negatively affected by fire-related alterations in soils (DeBano, 1990). Ideally, fire should only be used to reduce *Acacia* seed banks and facilitate litter removal and stimulate indigenous species recovery (Le Maitre et al., 2011), and not as a restoration strategy to remove excessive biomass after clearing operations (according to the outcomes by Sieben and Reinecke, 2008).

Since disturbance regimes within riparian corridors are critical drivers for biodiversity and vegetation succession, the first step of restoration should be to re-establish and then sustain natural disturbance patterns (e.g. removal of sediments) after clearing to allow the river to return to a more natural geomorphology for riparian vegetation colonization and secure long-term restoration (Naiman and Decamps, 1997; Holmes et al., 2005; Richardson et al., 2007). This is especially important in situations when river-bank erosion intensifies after clearing efforts, especially during high flooding events, delivering more sediment downstream (Richardson et al., 2007; Sieben and Reinecke, 2008). Indigenous species adapted to stable environments may be slow to colonize newly post-cleared sites (Galatowitch and Richardson, 2005). Bare riverbanks that have to rely on natural spontaneous succession following alien clearing are unstable and prone to severe erosion and riverbank collapse, and over the long-term alien plants returns to the place it previously occupied (Sieben and Reinecke, 2008). Build-up of coarse and finer sediments in soils under Acacias may only be taken away by the following rainfall event after clearing, before any regeneration has taken place. This process should be actively encouraged so that the river can return to a more natural profile sooner (Prins et al., 2004). However, river-bank stabilization should not be implemented in areas where it is suspected that the *Acacia* stands have caused enhanced channel aggradation (sediment deposition).

In order to suppress re-invasion, prevent proliferation of exotic grasses and promote recovery, the literature strongly recommends that in highly transformed river catchments where degradation

caused by invasion has reached a particular threshold where ecosystems are unable to recover naturally, indigenous riparian species should be actively re- introduced, preferably from areas that most closely resemble the environmental conditions of the community being restored. This can be attained through planting or sowing indigenous species (Prins et al., 2004; Galatowitsch and Richardson, 2005; Holmes et al., 2005; Sieben and Reinecke, 2008; Marchante et al., 2009; Maitre et al., 2011). However, Galatowitsch and Richardson (2005) argued that reseeding will likely not be successful after clearances, because native seedlings have slower growth rates than re-invading aliens and that the dispersal and germination of seeds may be restricted by hydrological impairment normally associated with invaded rivers. Promoting indigenous species by transplanting saplings will likely be most successful in suppressing invasive seedlings and suppressing grasses (native and exotic), as natives will have a height advantage over germinating *Acacia* seedlings (Galatowitsch and Richardson, 2005; Holmes et al., 2005). These efforts should take place in addition to previously mentioned proposed approaches to reduce excess N by addition of C sources, as native seedlings may be unable to survive in N enriched soils either through changes in mycorrhizal inoculants, or could simply be outcompeted by exotic or native grasses (Holmes et al., 2005).

It is, nevertheless, important to note that plant re-introduction techniques are extremely expensive (and unrealistic in some situations), which may necessitate a more appropriate and minimal set of interventions for achieving restoration trajectories or goals (Richardson et al., 2007). Due to low cover of woody shrubs and trees at cleared sites relative to native riparian areas, emphasis should be directed at re-introducing fire-adapted generalists and wide-spread riparian woody species (i.e., *B. stellatifolium*, *M. angustifolia, B. neriifolia* and *E. caffra*), as they are almost certain to rapidly re-establish resilient plant cover and appropriate vegetation structure (Prins et al., 2004). The first two of these are also relatively drought-resistant compared to the invasive species (Swift et al., 2008; Crous et al., 2011). Removing thick litter layers after an area is cleared is desirable and will speed up the recovery process (Marchante et al., 2008), since litter may be allelopathic or support soil organisms not generally associated with the specific area of invasion (Marchante et al., 2011).

Even though not explicitly addressed in this study, clearing treatments used have implications for the success of restoration (Holmes and Cowling, 1997; Holmes et al., 2000). Since *Acacia* spp. have long-lived seeds that can lie dormant in the soil for long periods of time, biological control and follow-up action and can play essential roles in the management of Acacias and long-term restoration success (Le Maitre et al., 2011). Follow-up programmes of *Acacia* spp. and other alien invasive species are critical to maintain recovery of native ecosystems (Marchante et al.,

2010). Monitoring, at least annually, is needed to determine the best time interval for follow-up control, which needs to be repeated (Marchante et al., 2011). The removal of only a few indigenous individuals may affect future vegetation recovery. Ensuring that Working for Water (WfW) teams are adequately trained in the removal of IAPs must be a priority and would greatly improve restoration success, as this will not only reduce the need for active restoration interventions, but also reduce operational costs (Vosse, 2007; Reinecke et al., 2008).

5.3. FUTURE RESEARCH

Alien clearing operations can succeed or fail to facilitate indigenous vegetation recovery and these complexities in the response to restoration activities necessitates the need for improved understanding of the impacts of clearance on target ecosystems in order guide scientifically based strategies and improve operational efficiency and effectiveness (Blanchard and Holmes, 2008; Le Maitre et al., 2011). Given that riparian ecosystems are dynamic through time (Gregory et al., 1991; Naiman et al., 2005; Richardson et al., 2007), prioritizing medium to long-term studies on fynbos riparian biogeochemistry and monitoring programs following removal and control of invasive plants can provide important ecological information, which in turn, would significantly improve current restoration strategies and aid management decisions (Holmes et al., 2005; Marchante et al., 2011). Results from this study revealed essential gaps that need to be addressed to enhance our understanding of fynbos riparian biogeochemistry and the impacts of invasion by N_2-fixing Acacias and removal thereof. Many unanswered questions remain for riparian zones invaded by and cleared of *Acacia* spp., such as how do changes in litter quality and quantity influence N-cycling and mineralization rates? What are the implications for added residual N through N_2-fixation to ground- and freshwater quality? How do soil N pools (in addition to other nutrients) respond to *Acacia* densities? How do microclimatic conditions and geomorphological changes alter riparian structure and function after the removal of *Acacia* spp. and what are the associated implications for restoration of these ecotones?

As mentioned in section 5.1, interactions between soil properties and processes, invasion statuses, and position in the landscape may be very complex. Because of this, and given that research on riparian function and impacts of invasion by woody plant species is still a fairly new field of study, especially in the fynbos biome, a number of these interactions have yet to be fully investigated. Physical soil properties (silt and clay content and soil moisture) played a vital role in controlling rates of soil biogeochemical cycles and nutrient concentration in this study, but soil texture is particularly important in mediating the retention of nutrients. However, little is still known about how fluvial dynamics (which strongly conditions the spatial distribution of different

mineral particle sizes; Bechtold and Naiman, 2006) influence the sorting of sediments in fynbos riparian soils. This necessitates further evaluation, since hydrogeomorphological processes play a vital role in the composition of riparian plant and soil communities (Naiman et al., 2005). Nevertheless, it can be assumed that predictable differences in particle size classes across geomorphological zones in riparian ecosystems contribute to equivalent contrasts in soil conditions.

Soil phosphatases constitute an important association between mineral and biologically unavailable P pools in soils (Amador et al., 1999; Kramer and Green, 2000; Orlander and Vitousek, 2000; Vance et al., 2003. Changes in plant community composition (which influences biomass and productivity) as a result of invasion by and clearing of *Acacia* spp. in fynbos riparian sites, play a critical role in soil P biogeochemistry, which is important from an environmental pollution perspective. Soil phosphatases may be a particularly good indicator for changes in soil conditions and processes, because its activity is not only regulated by changes in plant (e.g. invasion by Acacias) and microbial community composition, but is also sensitive to environmental changes and strongly correlated with a number of soil physical (e.g. soil moisture and silt and clay content) and chemical (e.g. total and available N) properties. Development of an indicator of soil quality in fynbos riparian ecosystems may not only enable us to better understand P biogeochemistry and its relationship with plant available P, but also to aid management decisions regarding these important landscape features. Additions of N through N_2-fixation can increase P mineralization and availability, possibly enhancing short-term productivity in N-limited ecosystems (Orlander and Vitousek 2000). Nevertheless, future research should elaborate more on the specific contribution of plant root type (especially species with root symbiotic associations) and microbial activity in stimulating enzyme production in order to assess the importance of each in driving P biogeochemistry in these systems (Grierson and Adams, 2000). Production of phosphatases may not only increase in response to P limitation (Allison et al., 2006), but additions of C and N sources through enhance productivity and N_2-fixation by *Acacia* spp. may also enhance enzyme activity. Accordingly, long-term studies should investigate biophysical factors (which was not assessed in this study) likely to be important in controlling enzyme production, including litter quality and quantity, soil organic matter distribution and microbial P.

Several studies only address specific effects of plant species on ecosystems, but integrated ecosystem research that investigate all components and their interactions are required (Knops et al., 2002; Eviner and Chapin, 2003; Ehrenfeld, 2004; Werner et al., 2010). Depending on the species and the invaded ecosystem, the effects of different N_2-fixing invasive species can be idiosyncratic (Stock et al., 1995; Yelenik et al., 2007) and this needs to be explicitly addressed in

restoration programs. The interaction between topography, the underlying substratum and fire regimes are fundamental in determining riparian community composition in addition to its lateral extent (Prins et al., 2004). A combination of management interventions may be necessary to reinstate indigenous communities after invasion by N_2-fixing species (Malcolm et al., 2008), because a number of variables can affect the outcome of clearing efforts. Given that vegetation composition and abiotic factors (climate and geological templates) change across different catchments, I suggest that a follow-up studies investigate the relationships between belowground processes and the impacts of invasion by- and clearing of *Acacia* spp. Ecosystem feedback cycles are important in restoration ecology as alterations in soil N may change community dynamics even after alien clearing efforts (Yelenik et al., 2004), particularly in nutrient-poor ecosystems, which have been shown to favour invasion by weedy species (Maron and Connors, 1996; Yelenik et al., 2004). Understanding these issues is vital for long-term solutions to restoration of post-cleared riparian zones by improving the ability to assess the performances of restored riparian ecotones through better knowledge on the effect of *Acacia* spp. on soil biogeochemistry in fynbos riparian ecotones and its interrelationships with biotic and abiotic factors.

The focus on clearing methods is largely at the biotic level, and no emphasis is placed on abiotic-level restoration techniques, such as alteration of geohydrology, control of erosion (Richardson et al., 2007; Esler et al., 2008) or changes to soil biogeochemistry. In order to address geomorphological changes associated with invaded and cleared sites, it is recommended that further research need to assess the impacts of *Acacia* invasion and (and clearing thereof) on fynbos riparian geomorphological processes (Holmes, 2007), as the geomorphological template of a river channel is essential for the successful re-establishment of indigenous riparian communities (Naiman et al., 2005).

Additions of N to soils through biological fixation may augment N flux rates and enhance the loss of soluble nitrate to receiving waters (Follstad Shah et al., 2010). Acacias may therefore potentially be an important new source of bioactive N in rivers and ecosystems further downstream (Tye and Drake, 2011). There is also a risk that clearing woody invasives may lead to eutrophication of surface water bodies and nitrate contamination of groundwater (Jovanovic et al., 2009). Further research is needed to resolve this question and address these issues.

In conclusion, a more comprehensive understanding of fynbos riparian ecological processes will not only improve the effectiveness of restoration and conservation initiatives, but also advance the field of riparian ecology. Success would be more attainable if a holistic and adaptive

approach to restoration of riparian ecosystems is used (Vosse, 2007). Other studies part of a Water Research Commission (WRC) funded research initiative are addressing several other aspects of fynbos riparian function (i.e. soil respiration, denitrification and soil biodiversity) and the changes brought about by *Acacia* invasion and clearing. Integration of each of these aspects may lead to a greater general understanding of system restoration processes. Further research on *Acacia* invasion in fynbos riparian ecotones and their associated impacts could possibly provide managers with more information and contribute to ecological theory concerning processes and patterns of biogeochemistry and plant community composition. Implicit in this is a requirement for improved understanding of the natural recovery processes of riparian areas and nutrient cycling processes after different methods of woody alien invasive clearing to acknowledge elements and processes essential for ecosystem resilience. Improving restoration initiatives are of great value for protecting the integrity of fynbos riparian ecosystems in the south-western Cape. The protection of fynbos riparian ecotones depends on improved scientific understanding, which is likely to be achieved by integrating science and management of these critical transitional zones.

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APPENDICES
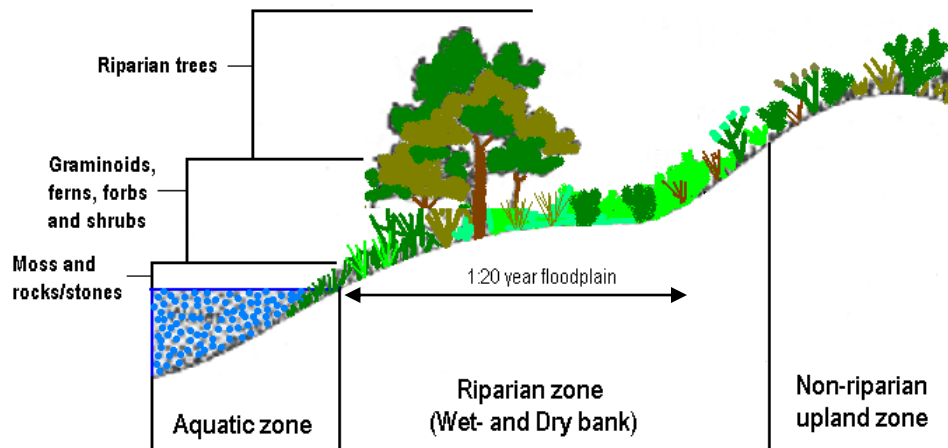
Appendix A Conceptual diagram of zonation patterns in fynbos riparian ecosystems. Modified from Sieben (2003).
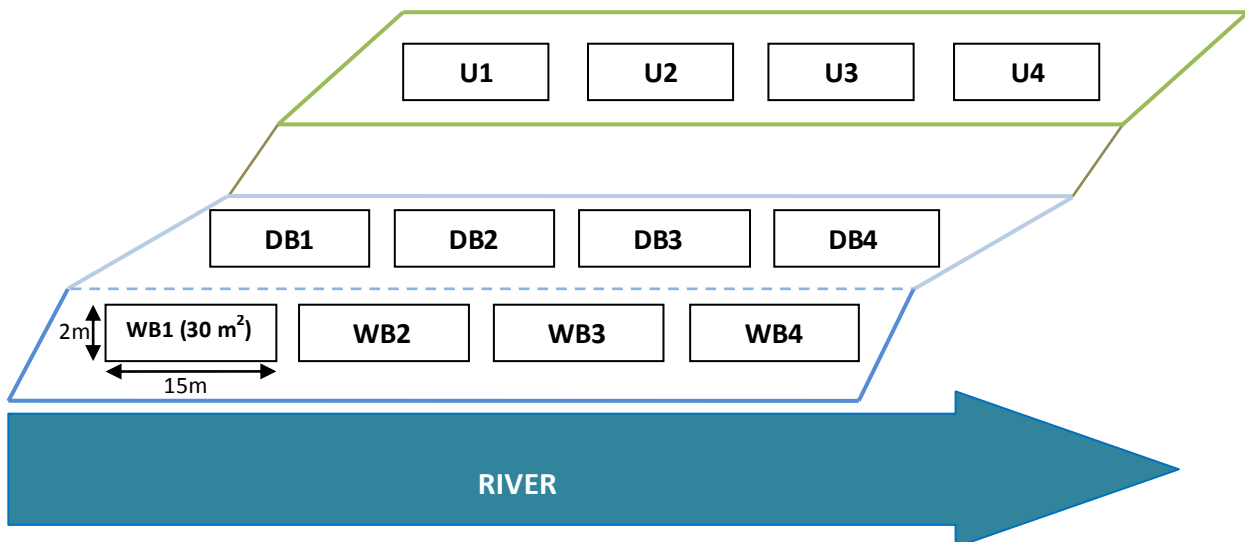
Appendix B Schematic representation of transect plots sampled in each of the landscape positions or geomorphological zones. The three zones are indicated as WB (Wet bank), DB (Dry bank), and U (Uplands). All plots are similar in size (30m^2).

Appendix C Geomorphological characteristics and site history. Invasion status are indicated as natural (NA), invaded (IN) and cleared (CL)

Sites	Geology	Coordinates	Landowners	History of invasion	History of clearance	Fire History	Longitudinal zone
Eerste (NA)	Sandstone and/or Granite	33°57'13.6"S; 18°58'43.8"E	CapeNature	None	None	March 2009	Mountain Stream
Eerste (NA)	Sandstone and/or Granite	33°59'22.28"S; 18°58'03.17"E	CapeNature	None	None	March 2009	Mountain Stream
Dwars (NA)	Sandstone and/or Granite	33°57'16.04"S; 18°58'47.78"E	CapeNature	None	None	March 2009	Mountain Headwater Stream
Elands (NA)	Sandstone	33 44'23.46"S; 19 06'47.29"E	CapeNature	None	None	March 2011#	Mountain Stream transitional
Dwars (IN)	Sandstone and/or Granite	33°56'53.36"S; 19°58'11.25"E	CapeNature	Invaded for >10 years (*A. mearnsii* and *A. longifolia*)	No clear evidence	No evidence of recent fire	Mountain Stream
Wit (IN)	Sandstone	33°32'18.5"S; 19° 0'55.6"E	Mount Bain Development	Invaded for >15 years (A. mearnsii)	No clear evidence	No evidence of recent fire	Foothill
Molenaars (IN)	Sandstone	33 42'16.95"S; 19 13'59.42"E	CapeNature	Invaded for >10 years (moderately invaded with *A. mearnsii*)	Cleared Jan/Feb 2011.	March 2011#	Upper Foothill
Jakkals (IN)	Sandstone	33°13'01.10"S; 19°12'25.84"E	Beaumont Wine Farm, Bot River	Invaded for >15 years (*A. mearnsii* and some *A. longifolia*)	Some evidence of clearing, with piles on site	No evidence of recent fire	Mountain Stream transitional
Jakkalsriver (CL)	Sandstone	33°12'31.81"S; 19°10'38.75"E	CapeNature	Invasion with mostly *Acacia spp.* >10 years ago	Initial clearance: 1996-1997. 2 follow-up treatments. Clearing treatment: Fell and burn	January 2010	Mountain Stream transitional
Sir Lowry's (CL)	Sandstone and/or Granite	34°05'41.5"S; 18°56'39.7"E	Wedderville Estate, Sir Lowry's Village	Mixed invasions: mostly *Acacia spp.* (also *Pinus spp.*) >8 years ago	Initial clearance: 2002 followed up annually by landowner. Clearing treatment: fell and burn	No evidence of recent fire	Mountain Stream
Molenaars (CL)	Sandstone	33°42'38.56"S; 19°11'49.24"E	Boundary of CapeNature and Rainbow's End Farm	Invasion with *Acacia mearnsii* dominant species >7 years ago	Initial treatment: 2002-2003. 2 follow-up treatments. Clearing treatment: fell and remove	No evidence of recent fire	Upper foothill
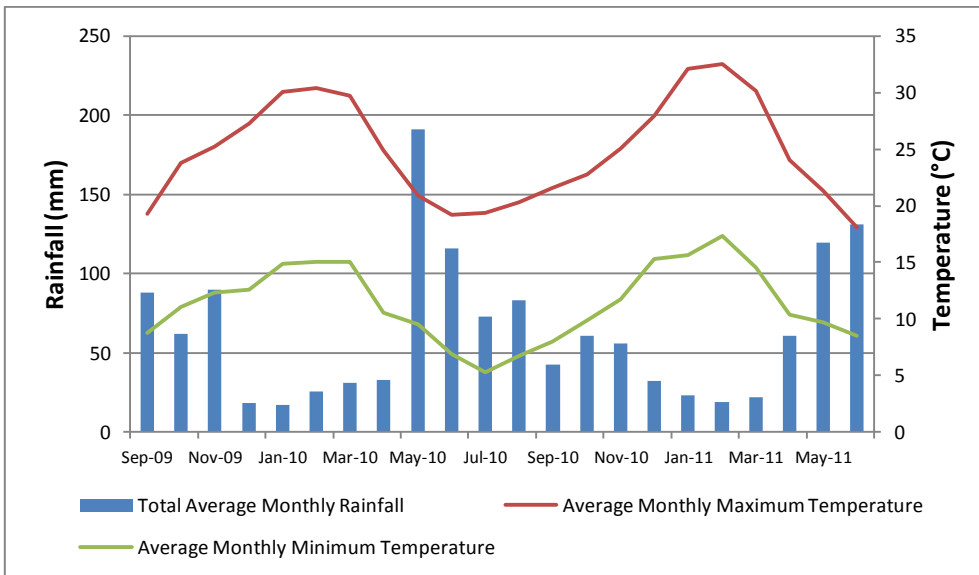
Appendix D Climate diagram (Sept-09 to Jun-11) based on averages for the six selected river systems (Credit: Agricultural Research Council).

Appendix B: Soil physical, chemical and biological properties for invasion status (natural, invaded and cleared) and landscape position (wet bank, dry bank, and uplands) across seasons. The data reflect means ± SE.

SOIL PROPERTIES	SEASON	NATURAL			INVADED			CLEARED		
		Wet bank	Dry bank	Uplands	Wet bank	Dry bank	Uplands	Wet bank	Dry bank	Uplands
pH (H$_2$0)	Autumn	5.08±0.05	5.38±0.11	5.42±0.10	5.48±0.14	5.31±0.13	5.60±0.14	5.12±0.09	5.22±0.08	5.29±0.12
	Winter	5.36±0.12	5.27±0.08	5.43±0.06	5.24±0.13	4.92±0.08	5.23±0.08	5.87±0.09	5.20±0.08	5.28±0.11
	Spring	4.61±0.07	4.67±0.06	4.96±0.06	4.62±0.11	4.52±0.07	5.06±0.11	5.07±0.16	4.81±0.13	5.11±0.10
	Summer	4.62±0.08	4.68±0.08	4.99±0.04	4.83±0.10	4.72±0.06	5.07±0.11	5.45±0.08	4.79±0.13	5.04±0.09
EC (µs/cm)	Autumn	20.2±1.5	22.8±2.5	21.4±2.1	25.4±4.4	48.1±7.9	22.8±1.2	42.5±7.47	36.2±6.1	58.9±15.0
	Winter	15.0±1.6	14.6±0.7	14.2±0.6	17.9±1.9	33.0±6.4	16.9±1.2	33.9±8.9	29.0±4.4	48.9±13.9
	Spring	19.1±0.5	20.3±0.7	20.6±0.7	24.3±1.3	56.7±8.4	30.3±8.8	45.2±10.7	36.5±7.29	47.5±10.5
	Summer	24.2±1.2	28.1±1.6	25.1±1.3	52.7±14.2	61.8±7.2	34.6±2.7	60.2±9.8	60.7±14.2	93.1±20.4
GSWC (%)	Autumn	18.4±1.80	9.2±1.09	8.2±0.93	10.5±0.96	9.6±1.37	10.6±0.74	12.5±1.39	7.7±1.43	8.2±0.98
	Winter	16.3±1.86	12.8±1.50	8.4±0.87	13.9±2.30	12.5±2.33	11.8±0.76	18.4±2.01	9.2±1.60	13.6±1.39
	Spring	14.7±2.11	10.0±1.32	7.7±0.70	10.5±1.86	9.2±2.31	6.1±1.05	18.1±1.30	8.5±1.76	7.5±0.72
	Summer	10.1±1.62	3.9±0.69	2.0±0.15	9.4±1.96	3.6±0.45	1.3±0.19	15.5±1.88	1.8±0.34	1.5±0.21
Bulk Density (g/cm^3)	Spring	1.24±0.05	1.11±0.04	1.06±0.03	1.2±0.03	0.89±0.04	1.17±0.03	1.21±0.05	1.12±0.05	1.13±0.04
Litter (g/m^2)	Spring	276±98	554±129	285±67	1039±229	1437±217	612±128	265±72	500±153	616±222
Silt and clay (%)	Autumn	4.5±0.47	7.7±1.03	13.6±0.91	3.2±0.59	9.6±1.50	18.6±2.29	4.4±0.92	6.5±1.38	18.2±2.72
	Spring	3.4±0.32	6.6±0.73	13.9±1.03	3.0±0.42	10.2±2.30	17.8±2.15	4.5±0.89	7.8±1.63	15.6±2.14
Coarse sand (%)	Autumn	36.2±2.80	31.0±2.74	29.5±2.51	18.6±2.32	21.1±3.37	28.2±2.60	33.7±2.41	31.5±3.39	29.1±2.57
	Spring	35.8±3.22	28.7±2.27	27.1±1.90	22.4±2.71	19.2±2.92	26.7±2.42	30.9±2.73	28.1±3.23	26.1±2.13
Medium and fine sand (%)	Autumn	59.3±2.86	61.3±3.09	57.0±2.09	78.2±2.18	69.4±4.03	53.1±2.71	61.9±2.12	62.0±3.92	52.7±3.82
	Spring	60.8±3.11	64.7±2.58	59.0±1.66	74.5±2.54	70.5±4.06	55.4±2.69	64.7±2.66	64.1±3.92	58.3±3.36
Available P	Autumn	7.1±1.65	14.1±2.59	18.0±4.93	6.8±0.80	30.68±9.32	18.6±4.41	14.49±4.00	14.08±1.69	22.12±2.93
	Winter	3.03±0.33	10.08±2.02	11.48±3.35	2.84±0.28	10.17±1.44	8.31±1.62	5.27±1.58	8.60±1.16	15.36±3.28
	Spring	3.85±0.51	8.67±1.95	12.73±5.67	4.56±1.02	9.91±1.82	8.12±1.92	8.76±2.41	7.25±0.84	13.38±2.42
	Summer	8.51±0.79	16.99±2.91	20.78±6.96	8.67±1.56	18.87±2.91	17.86±3.67	9.36±1.62	16.46±1.73	22.53±4.10

Ammonium (µg g^{-1})	Autumn	0.44±0.16	1.54±0.28	1.35±0.25	1.34±0.45	1.63±0.45	1.20±0.16	0.65±0.16	1.54±0.37	1.77±0.24
	Winter	0.55±0.25	0.75±0.20	0.76±0.11	0.64±0.11	1.26±0.26	0.76±0.15	0.58±0.11	1.16±0.36	1.87±0.39
	Spring	0.46±0.04	0.98±0.11	1.06±0.10	1.16±0.14	1.81±0.17	0.92±0.08	0.66±0.17	1.98±0.41	3.50±0.82
	Summer	0.70±0.18	2.55±0.62	1.88±0.20	4.15±0.66	7.65±0.65	2.91±0.33	1.74±0.48	5.94±1.04	7.67±0.85
Nitrate (µg g^{-1})	Autumn	2.72±0.90	1.83±0.33	2.23±0.32	1.31±0.28	2.19±0.31	1.93±0.27	3.16±0.53	5.37±1.22	6.41±1.48
	Winter	1.92±0.19	1.91±0.13	1.88±0.11	1.78±0.27	2.19±0.22	1.42±0.17	0.65±0.09	2.68±0.80	2.73±0.58
	Spring	0.89±0.14	1.42±0.17	2.17±0.27	2.18±0.24	2.78±0.27	2.25±0.18	1.48±0.18	2.95±0.57	5.53±2.15
	Summer	1.32±0.17	1.54±0.15	3.58±0.85	1.78±0.23	3.84±0.60	2.77±0.32	1.23±0.22	2.83±0.57	4.94±0.84
Total available N (µg g^{-1})	Autumn	3.17±0.98	3.38±0.50	3.58±0.48	2.65±0.68	3.84±0.63	3.13±0.33	3.59±0.64	6.91±1.46	8.18±1.64
	Winter	2.47±0.40	2.66±0.27	2.65±0.16	2.42±0.33	3.45±0.26	2.18±0.21	1.23±0.18	3.84±1.00	4.60±0.90
	Spring	2.32±0.41	4.38±0.40	4.22±0.33	2.80±0.41	4.95±0.62	2.32±0.42	2.460.84	4.93±1.13	6.80±0.76
	Summer	2.01±0.28	4.09±0.63	5.46±0.97	5.93±0.71	11.4±81.18	5.68±0.46	2.97±0.67	8.77±1.33	12.61±1.05
Total Soil N (%)	Autumn	.127±.069	.109±.019	.115±.020	.066±.021	.257±.062	.106±.020	.041±.014	.118±.043	.242±.036
	Spring	.044±.006	.106±.015	.123±.016	.068±.017	.209±.042	.114±.014	.075±.028	.130±.036	.212±.025
Total Soil N (%)	Autumn	2.50±0.92	2.73±0.45	2.53±0.38	1.71±0.47	4.67±0.97	2.69±0.28	0.89±0.29	2.62±0.72	4.12±0.58
	Spring	0.91±0.10	2.46±0.27	2.26±0.26	1.37±0.33	3.74±0.76	2.59±0.27	1.53±0.51	2.41±0.65	3.49±0.40
Soil C:N	Autumn	33.2±3.89	26.3±1.16	23.0±0.53	47.1±12.70	25.4±3.07	32.4±3.91	38.1±10.53	72.8±21.00	17.6±0.75
	Spring	29.8±87.37	26.05±3.15	18.8±0.49	22.6±3.03	17.0±0.99	23.5±0.74	32.1±5.95	21.8±2.64	17.3±1.02
Potential N mineralization rate (µg g^{-1} soil day^{-1})	Autumn	0.00±0.03	0.12±0.04	0.13±0.04	0.00±0.03	0.19±0.03	0.14±0.04	0.04±0.02	0.14±0.05	0.12±0.05
	Winter	0.03±0.01	0.17±0.05	0.12±0.03	0.22±0.07	0.26±0.07	0.14±0.03	0.09±0.09	0.08±0.05	0.21±0.06
	Spring	0.26±0.06	0.48±0.06	0.44±0.04	0.24±0.06	0.46±0.09	0.21±0.06	0.26±0.10	0.43±0.15	0.48±0.08
	Summer	0.07±0.03	0.34±0.12	0.45±0.04	0.22±0.06	0.51±0.09	0.44±0.07	0.14±0.11	0.13±0.11	0.21±0.17
Acid Phosphatase (µg p- NP g^{-1} h^{-1})	Autumn	164±17.3	165±113.6	281±144.3	184±27.6	388±61.1	213±19.8	201±38.6	173±43.8	369±54.5
	Spring	171±25.4	265±26.5	364±39.9	247±36.7	478±74.9	353±41.2	213±32.7	246±50.1	467±79.3
	Summer	253±21.6	365±28.8	366±24.9	588±113.3	886±109.0	324±227.2	227±35.1	341±46.1	399±49.6

Appendix C Percentage canopy- and ground cover of plant functional types and other ecosystem components. The data reflect mean cover for invasion statuses and landscape positions.

CLASSES	NATURAL			INVADED			CLEARED		
	Wet bank	Dry bank	Upland	Wet bank	Dry bank	Upland	Wet bank	Dry bank	Upland
Grasses	2.33	14.70	9.97	4.70	0.41	4.67	19.44	36.52	38.17
Other graminoids	6.51	18.65	10.17	10.82	1.39	8.78	13.03	3.03	2.07
Forbs	0.36	3.74	5.57	0.10	0.01	3.37	4.38	1.77	6.17
Geophyte	1.40	0.71	2.33	0.00	0.00	0.71	0.21	0.04	0.38
Moss	8.08	0.72	0.59	0.00	0.05	1.07	0.07	0.00	0.00
Bare ground	37.63	27.92	39.66	31.37	20.11	28.57	18.83	39.61	22.13
Stones/rocks	22.31	09.11	14.28	1.37	1.52	15.09	17.05	4.15	10.11
Litter	8.24	23.58	18.21	46.04	74.75	24.29	12.76	7.29	12.69
Dead standing	6.02	11.60	11.54	10.08	6.99	18.14	17.24	11.09	9.34
Ferns	13.86	7.25	9.59	0.14	0.23	0.69	1.25	0.57	0.00
Shrubs	2.89	9.25	18.18	0.70	0.62	19.70	3.96	1.87	5.60
Indigenous tree CC	53.92	11.47	0.00	3.51	3.19	1.36	17.65	16.76	2.00
Indigenous seedling	3.88	0.46	0.00	0.34	0.00	0.18	2.69	0.50	0.00
Indigenous basal cover	1.84	0.00	0.00	0.00	0.00	0.00	0.14	0.00	0.00
Alien adult CC	0.00	0.00	0.00	39.60	61.08	0.00	0.00	1.03	0.00
Alien tree seedling	0.00	0.00	0.00	0.50	0.61	0.17	0.68	0.68	0.32
Alien tree juvenile CC	0.00	0.00	0.00	0.97	0.88	0.00	0.74	0.00	0.00

i)

ii)
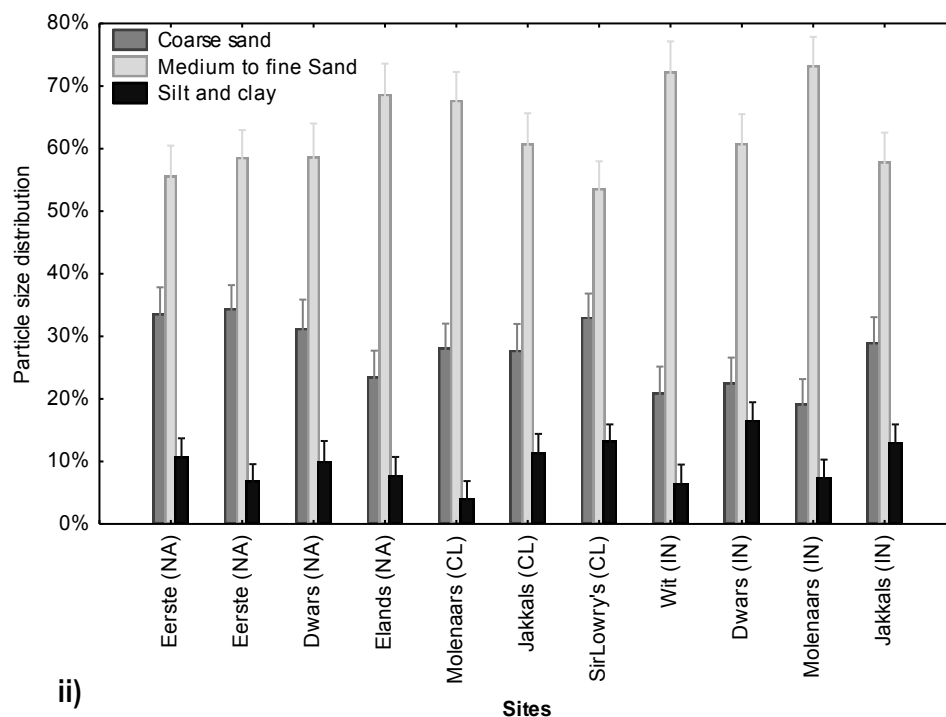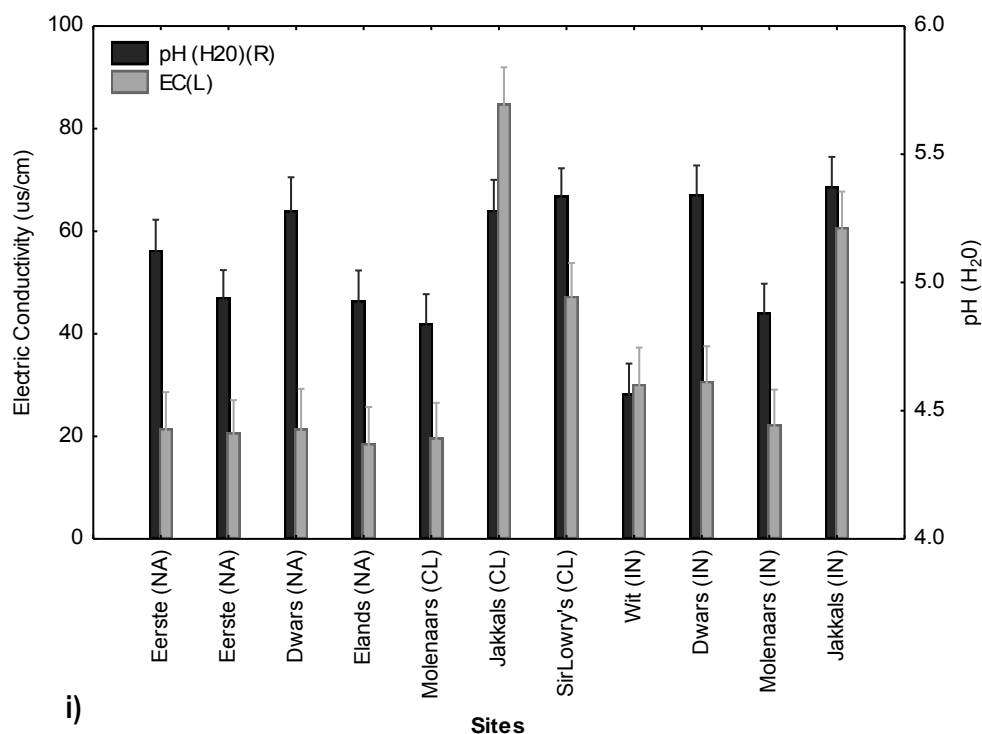
Appendix D Soil electric conductivity and pH (i) and particle size distribution (ii) for each of the study sites. Mean values indicated by bars, and whiskers ± 95% confidence interval. Letters denote significant differences between sites based on a one-way ANOVA for pH ($F_{[10, 548]}$ =20.354, p<0.001); EC ($F_{[10, 547]}$ =35.829, p<0.001); and each size class distribution: silt and clay ($F_{[10, 272]}$ =6.627, p<0.001); medium to fine sand ($F_{[10, 272]}$ =8.2231, p =.00000); and coarse sand ($F_{[10, 272]}$ =6.901, p<0.001). Abbreviations for invasion statuses: natural (NA), invaded (IN), and cleared (CL).