THE RESTORATION OF AN ALIEN-INVADED RIPARIAN ZONE IN GRASSY FYNBOS, SOUTH AFRICA

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ABSTRACT

The most recent surveys in South Africa estimate that invasions are still increasing, despite substantial clearing efforts. Riparian systems in South Africa are particularly vulnerable to invasion by woody IAPs. This thesis addresses the restoration of alien-invaded riparian systems, by investigating the factors that facilitate or constrain spontaneous recovery and influence the trajectories of succession. These factors include invasion history and management history, especially the use of fire. A seedling emergence approach was used to test the presence of a viable pre-fire seedbank, and the effect of fire on the seed bank. The efficacy of some active restoration interventions was also tested, with the aim to return invasion-resistant, indigenous vegetation with a structure and function representative of uninvaded sites.

The findings of this study indicated the presence of a viable and persistent riparian soil seed bank, even after 30 years of intermtittent invasion as well as two fire cycles under invasion. It shows that the management practice of fell-and-burn resulted in high soil temperatures, and that this reduced the indigenous soil seed bank density, especially in the upper soil layer. Clear germination sequences and patterns of emergence over time for different species were observed during this study, with many species exhibiting delayed emergence relative to the timing of the fire event. It is proposed that manipulation of the season of fire could be used to selectively optimise the order of arrival and therefore superior recruitment of some species over others in the Eastern Cape fynbos, and thus alter the trajectories of recovery of vegetation towards a more desired state.

Active restoration in the form of indigenous seed and plant additions resulted in a significantly higher indigenous cover after seven months, compared to a control (passive restoration) or restoring with grass. Indigenous cover and composition was also strongly influenced by lateral zonation, and some key guilds and species were missing or present in much lower densities compared to reference sites. Grass restoration significantly suppressed the regeneration of *A. longifolia*, as well as the regeneration of indigenous species. Biotic resistance can thus be achieved through restoration, and it could be a powerful tool in the management of IAPs, although the deliberate introduction of grass after clearing in fynbos also reduces biodiversity and could have unforeseen consequences to riparian function.

DECLARATION

I declare that this thesis is my own work, and that all other sources used or quoted have been fully acknowledged and referenced. It is being submitted for the degree of Doctor of Philosophy at Rhodes University, and has not been submitted for a degree or examination at any other University.

Saskia Fourie

Signature ……………………………………………….

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1 INTRODUCTION

This thesis addresses the restoration of alien-invaded riparian systems in the grassy fynbos of the Eastern Cape. Chapter 1 aims to introduce the context for this research, by providing an overview of existing knowledge and gaps. It starts by describing the extent of alien plant invasions in South Africa, particularly in riparian zones, and the impacts resulting from these invasions. Section 1.2 provides a brief overview of the ecology of riparian systems, and the relationship between riparian dynamics and invasions. Section 1.3 describes the management of invasive alien plants (IAPs) and the impacts resulting from the management process. Section 1.4 provides a broad overview of restoration terms and concepts, while Section 1.5 focusses on the specific role of soil seed banks in the restoration of fynbos. Section 1.6 discusses the challenges of assessing the success of restoration interventions, which lead to the target of biotic resistance, discussed in Section 1.7.

Based on the above overview, Section 1.8 highlights the objectives and key questions that are addressed as part of this study in investigating the restoration of a riparian system, while Section 1.9 describes the structure of the remainder of the thesis. Section 1.10 describes the study area.

1.1 INVASIVE ALIEN PLANTS

The extent of transformation and degradation of ecosystems due to alien invasions is a global ecological and economic problem (Radosevich *et al.* 2003; Brooks *et al.* 2004; Thuiller 2007; Wilson *et al.* 2011a). The spread of invasive alien plants (IAPs) poses the second largest threat to indigenous biodiversity, as well as to other ecosystem services such as water yield (Millennium Ecosystem Assessment 2005; Gaertner *et al.* 2009; van Wilgen *et al.* 2008; Vilà *et al.* 2010; Richardson and Rejmánek 2011).

Various definitions and criteria have been used to classify IAPs, ranging from introduced, alien, weeds, naturalised, problem plants to ecosystem transformers (D'Antonio and Vitousek 1992; Radosevich *et al.* 2003; Brooks *et al.* 2004, 2010; Ortega and Pearson 2005).

Unfortunately, different criteria are used by different authors to categorise alien species (Richardson and Rejmánek 2011). The review by Richardson *et al.* (2000b) and the more recent review by Richardson and Rejmánek (2011) only include plants as IAPs which "have sustained self-replacing populations for at least 10 years without direct intervention by people (or in spite of human intervention) by recruitment from seed or ramets capable of independent growth" and "recruit reproductive offspring at considerable distances from the parent plants and thus have the potential to spread over a large area". The ecological or economic impacts of the IAP were not included as part of their criteria for defining an invasive species; nor were plants which are only naturalised in highly disturbed areas such as heavily human-modified landscapes or roadsides. Transformer species were considered to be a subset of IAPs which "change the character, condition, form or nature of ecosystems over a substantial area relative to the extent of that ecosystem" (Vitousek and Walker 1989; Richardson *et al.* 2000), "a definition which has impact central to its meaning". These impacts can include alterations of fire regimes, hydrological cycles or nutrient cycles.

The extent of transformation and degradation of ecosystems due to alien invasions is a global ecological and economic problem, and in Southern Africa (Versfeld *et al.* (1998) estimated that approximately 10 million hectares in South Africa and Lesotho had been invaded by IAPs by 1996, equating to approximately 1.736 million condensed ha[1] in 1996 (Le Maitre *et al.* 2000). More recent surveys of Kotzé *et al.* (2010) and van den Berg (2010) estimate that the extent of invasion in 2008 was approximately 1.813 million condensed ha, despite substantial clearing efforts. These results indicate that overall invasions have not decreased, and remain a serious threat in most biomes (van Wilgen *et al.* 2012).

The density of some species have been reduced, e.g. Le Maitre *et al.* (2000) estimated that approximately 643 000 ha of South Africa had been invaded by Australian *Acacia* species (commonly referred to as "wattles") in 1996, and more recent estimates (Kotze *et al.* 2010) estimated the alien *Acacia*-invaded area to have declined to 554 000 ha; a decrease which

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[1] The term condensed hectare is commonly used in the management of IAPs in South Africa, and refers to an invaded area with an IAP canopy cover of 100 %. A condensed hectare can thus be calculated as the invaded proportion × the area of the polygon (Marais and Wannenberg 2008). For example, an area of 100 ha with 50 % cover is equivalent mathematically to a condensed area of 50 ha with 100 % cover (Le Maitre *et al.* 2000).

can probably mostly be attributed to the effective biological control of *A. cyclops* and *A. saligna*, as well as to the intensive harvesting of fuel wood (van Wilgen *et al.* 2011). However, *A. mearnsii*, *A. dealbata* and *A. decurrens* invasions are estimated to have increased by an alarming 92 %, from 231 000 to 443 000 ha (Kotze *et al.* 2010).

Riparian systems in South Africa are particularly vulnerable to invasion by woody IAPs (Le Maitre *et al.* 1996, 2000, 2002, 2011; Richardson and van Wilgen 2004; Richardson *et al.* 2007) and if invasion is compressed to a condensed or close-stand (100 % cover) invasion, will comprise 33 % (approximately 51 266 km) of the total river length in South Africa (Cullis *et al.* 2007; Marais and Wannenburgh 2008). *Acacia longifolia*, *A. mearnsii*, *Eucalyptus camaldulensis*, *Paraserianthes lohantha* and the reed *Arundo donax* are the most prolific invader species in fynbos riparian zones (Galatowitsch and Richardson 2005). Higher and more reliable availability of water or moisture makes riparian zones one of the most invaded ecosystems in the world (Planty-Tabacchi *et al.* 1996; Henderson 1998; Richardson 2001).

The invasion of riparian zones by woody IAP species is particularly concerning, as these IAPs transform ecosystems by displacing indigenous vegetation, altering fire regimes and increasing fire hazard, reducing water yield and biodiversity, increasing soil water repellency[2], altering soil chemistry, erosion and siltation, destabilising river banks and degrading many other ecosystem services (Holmes *et al.* 2007; Richardson *et al.* 2007, 2008; Gaertner *et al.* 2009, 2011; Le Maitre *et al.* 2011). Many of the impacts that result from IAPs interact with each other, and abiotic changes and biotic responses occur in a simultaneous manner (Le Maitre *et al.* 2011).

The reductions in water resources due to IAPs are of great concern to South Africa (Dye *et al.* 2001, Dye and Jarmain 2004, Blignaut *et al.* 2007). Average precipitation in South Africa is approximately 500 mm per annum, well below the world average of approximately 860 mm per annum (DWAF 2002); and South Africa has been classified as a country with chronic water scarcity (Ashton 2002). Rainfall is predicted to become more erratic with climate

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[2] Water repellent soils impede infiltration and percolation (Scott 1993), and often develop where hydrophobic organic compounds found in plant litter vaporise during wildfires. These condense at or near the soil surface where they produce a water-repellent layer, varying in thickness and spatial continuity (De Bano 2000).

change, due to increased frequency and intensity of the swings between dry and wet years (Crous *et al.* 2012). Water resource and supply management is therefore becoming more challenging (Blignaut *et al.* 2007) and a national assessment in 2004 (DWAF 2004) estimated a mere surplus of 1.4 % of the total supply. Twelve of the 19 water catchments recorded water deficits, and these have only been offset by engineered inter-basin water transfer schemes (Blignaut and van Heerden 2009). It is predicted that South Africa will experience a national water deficit of 1.7 % by 2025, and the availability of water has been predicted to be the greatest constraint to development in South Africa (Scholes 2001; Aronson *et al.* 2006; Farley and Daly 2006).

Streamflow reduction is the most important concern regarding the invasion of riparian zones and mountain catchment areas (Versfeld *et al.* 1998, Dye *et al.* 2001, Dye and Jarmain 2004). Estimates vary between catchments (Görgens and van Wilgen 2004; Cullis *et al.* 2007; Crous *et al.* 2012), but it has been estimated that over 3 000 million m^3 of surface water runoff (approximately 7 %) is lost annually to IAPs, and most of this from the fynbos and grassland biomes (Le Maitre *et al.* 2000). If IAPs are allowed to spread unchecked and were to reach their full potential, reductions could reach 25 000 million m^3 of surface water runoff (approximately 58 % of the surface water runoff of the country) (van Wilgen *et al.* 2008).

Invasion also reduces biodiversity, with the fynbos biome being most affected (van Wilgen *et al.* 2008), although the prominence of woody invaders in the fynbos biome is unusual compared to other Mediterranean ecosystems. Biodiversity plays an important function in the delivery of ecosystem services (Naeem and Wright 2003; Naeem 2006; Turpie *et al.* 2003; van Wilgen *et al.* 2008) and can also be a service in its own right, e.g. as a basis for ecotourism. In addition to the above, biodiversity plays an important role in ensuring the resilience of ecosystem functions (de Groot *et al.* 2002; Hooper *et al.* 2005) and it is generally accepted that diverse, intact ecosystems are more resistant to invasion (Diaz *et al.* 2006; Naeem *et al.* 2000; Maron and Marler 2007) and other disturbances. The importance of biodiversity in resisting invasion is discussed further in Section 1.7.

These, and other impacts, have cost South Africa billions of rands (van Wilgen *et al.* 2001, 2008), with an estimated annual cost of more than R4 billion due to impacts on biodiversity, water resources and grazing (Turpie *et al.* 2003; van Wilgen *et al.* 2011). More than 70 % of these costs can be attributed to reductions in water resources in the grassland and fynbos biomes (de Lange and van Wilgen 2010) and affect all sectors of society, including the poor (Kull *et al*. 2011).

The Australian *Acacia* species are considered to be some of the worst invaders in South Africa (Richardson *et al.* 2000a; Kotze *et al.* 2010; Le Maitre *et al.* 2011; van Wilgen *et al.* 2011), especially in riparian zones. Most of these *Acacia* species were introduced in the middle of the 19th century for commercial, cultural and horticultural purposes (Richardson and Kluge 2008). A number of key traits give the Australian *Acacia* a competitive advantage over indigenous species (Gallagher *et al*. 2011; Gibson *et al.* 2011; Morris *et al.* 2011); these include a high reproductive output (Milton and Hall 1981), rapid growth rates and the ability to outcompete indigenous plants (Peperkorn 2005), the ability to accumulate high biomass (Witkowski 1991) and large, persistent seed banks, an ability to fix nitrogen (Yelenik *et al.* 2007; Marchante *et al.* 2009), the absence of natural enemies (Keane and Crawley 2002, Impson *et al.* 2008, Le Maitre *et al.* 2008, Moran and Hoffmann 2011, Gibson *et al.* 2011), and phenotypic plasticity (Callaway *et al.* 2003b).

Due to the extent of invasion in riparian zones, coupled with the severe impacts of IAPs on surface run-off, water availability and biodiversity, the focus of this study is on the restoration of *Acacia*-invaded riparian zones in the fynbos biome of South Africa. The vulnerability of riparian zones to invasion is linked to their unique dynamics and ecological processes, and restoration efforts have to take these dynamics into account. A broad overview is presented in Section 1.2 below, which places invasion and restoration into the riparian context.

1.2 RIPARIAN SYSTEMS

Riparian zones fulfil important physical, chemical, biological and socio-economic functions (Richardson *et al.* 2007) and play a significant role as the interface between terrestrial and aquatic systems (Naiman and Décamps 1997). They serve as critical transition zones and conduits for the transfer of energy and material between these systems (Ewel *et al.* 2001), despite forming a proportionally small part of the landscape (Holmes *et al.* 2005).

Riparian zones are strongly influenced by the ecosystems that they link (Naiman and Décamps 1997; Ewel *et al.* 2001; Dwire and Kauffman 2003; Casco *et al.* 2010). They differ from adjacent upland areas in geomorphology, hydrology, vegetation, microclimate and fuel characteristics (Naiman *et al.* 1993; Naiman and Décamps 1997; Dwire and Kauffman 2003, Smith-Adao and Scheepers 2007). They are usually characterised by high levels of species diversity and environmental processes (Naiman and Décamps 1997), which can be attributed to the dynamic, non-equilibrium nature of riparian zones (Richardson *et al.* 2007). Since they form corridors through the landscape, they provide connectivity and can make vital contributions to restoring and maintaining regional diversity (Casco *et al.* 2010).

Defining and delineating the spatial extent of riparian zones is challenging, due to their dynamic nature and heterogeneity. Various definitions exist, the most commonly used being that of Naiman and Décamps (1997), who define the riparian zone as the stream portion between the low and high water mark, including the adjacent areas which are influenced by riparian processes (e.g. flooding or a higher soil moisture content). Gregory *et al.* (1991) define riparian areas as “three-dimensional zones of direct physical and biotic interactions between terrestrial and aquatic ecosystems, with boundaries extending outward to the limits of flooding and upward into the canopy of streamside vegetation”. Areas outside the riparian zone that are not directly influenced by hydrological conditions but that contribute organic matter (e.g. leaves, wood, dissolved materials) to the floodplain or channel, or that influence the physical regime of the floodplain or channel by shading, may be considered part of riparian zones (Brosofske *et al.* 1997; Lowe *et al.* 2008).

Riparian zones exhibit both longitudinal and lateral gradients (Richardson *et al.* 2007; Casco *et al.* 2010). They differ in width depending on the size of the stream, the location of the stream within the catchment, the hydrological regime and the local geomorphology (Rowntree 1991; Naiman and Décamps 1997; Freeman and Rowntree 2005; du Preez and Rowntree 2006). Riparian zones are generally narrowest in the headwaters and widen downstream. Riparian zones of larger rivers often consist of floodplains which may be subject to long periods of annual flooding, with complex geomorphological features such as braiding and lateral channel migration (Kalliola and Puhakka 1988; Hupp and Osterkamp 1996; Kalliola *et al.* 1991; Hughes *et al.* 2008).

Rivers and riparian zones are particularly difficult to manage because they tend to form part of, as well as receive, inputs from large watersheds, over which managers generally have no control (Ewel *et al.* 2001). They have been the focus of intensive human habitation and activity for centuries, and are one of the world's most impacted and degraded ecosystems (Bernhardt *et al.* 2007; Brooks and Lake 2007; Lemons and Victor 2008; Williams *et al.* 2008). Degradation results from a number of activities, including the clearing of land for agriculture or development (Hancock *et al.* 1996; Kentula 1997; White and Greer 2006; White and Stromberg 2011), grazing and trampling (Robertson and Rowling 2000; Meeson *et al.* 2002; Sarr 2002; Krueper *et al.* 2003), pollution from the surrounding catchment (Basnyat *et al.* 2000; Casey and Klaine 2001; Braskerud 2002), water abstraction and the creation of dams which alters hydrological regimes (Meeson *et al.* 2002; Shafroth *et al.* 2002a; Bhattacharjee *et al.* 2006; Stromberg *et al.* 2007), as well as invasion by alien species (Tickner *et al.* 2001; Harms and Hiebert 2006; Richardson *et al.* 2007; Shafroth *et al.* 2008). The preservation and protection of rivers and riparian zones therefore require collaboration among scientists, managers and stakeholders (Ewel *et al.* 2001; Kondolf and Yang 2008).

The freshwater component of South Africa's National Spatial Biodiversity Assessment estimated that some 84 % of South African freshwater ecosystems are threatened, with 54 % critically endangered (Nel *et al.* 2007). Mediterranean-type ecosystems, of which the fynbos biome is part, are particularly threatened as a result of predicted changes in climate and increases in water abstraction (Hobbs 2004; Crous *et al.* 2012).

1.2.1 Riparian vegetation

Riparian vegetation plays a critical function in providing and maintaining ecosystem health and services (Ewel *et al.* 2001), such as ensuring good quality water, moderating stream temperature and light levels, accumulating sediments and organic matter, maintaining stream bank and channel integrity, reducing flood severity, increasing groundwater recharge, regulating nutrients, providing habitat, food, refugia for biodiversity, natural fire breaks as well as corridors for dispersal and movement of plants and animals (Gregory *et al.* 1991; Kemper 2001; Dwire and Kaufmann 2003). Although riparian vegetation differs in structure and function from adjacent terrestrial vegetation, it generally contains components of terrestrial systems (Naiman and Décamps 1997; Dwire and Kauffman 2003; Holmes *et al.* 2005).

Riparian vegetation can vary widely, depending on a variety of factors, such as the regional climate and pool of species, stream order, local topography, substrate and fluvial processes, and the hydrological, geomorphological and disturbance regime (Naiman *et al.* 1993; Shafroth *et al.* 2002b; Richardson *et al.* 2007; Casco *et al.* 2010). The availability of water in particular influences the distribution of riparian plants through controlling the arrival, establishment, growth and survival of species, and is considered a major limiting factor, especially for many woody species (Ellery *et al.* 1993). Flooding regimes, as well as available moisture and oxygen in the riparian zone determine the lateral zonation of the vegetation (Boucher 2002; Sieben and Reinecke 2008; Casco *et al.* 2010). Most riparian plants are adapted to fluctuations in the water-table, possessing suitable morphological adaptations to floods and seasonally waterlogged conditions (Hupp and Osterkamp 1996; Kozlowski 2002). The dynamic nature of active channels makes it difficult for vegetation to establish, but the adjacent riparian zones can be colonised by disturbance-adapted vegetation.

1.2.2 Disturbance in riparian zones

Riparian zones are subject to frequent disturbance, both natural and human-mediated (Sala *et al.* 2000; Dwire and Kaufmann 2003; Richardson *et al.* 2007). Disturbance is an important, often essential, component of many natural ecosystems, and regeneration may depend on disturbance (Hobbs and Huenneke 1992; Le Maitre and Midgley 1992; Walker and del Moral 2008; Thomas *et al.* 2010; Moreno *et al.* 2011). Riparian systems are particularly prone to frequent and intense natural disturbance in the form of floods and often fire (Bisson *et al.* 2003; Dwire and Kaufmann 2003; Stromberg *et al.* 2009). This gives rise to a non-equilibrium, temporally and spatially varying mosaic of riparian communities in different successional phases and ages (Halpern and Spies 1995; Naiman and Décamps 1997; Sieben and Reinecke 2008). As riparian zones form the transition between terrestrial and aquatic systems, the vegetation is influenced by disturbances typical of each of these systems, such as hydrologically-related processes of flooding, sedimentation, erosion and debris flows, as well as terrestrial disturbances caused by fire, wind, grazing, etc. (Richardson *et al.* 2007). However, the distinctive differences in riparian zone vegetation and topography will modify these disturbances (Hupp and Osterkamp 1996; Dwire and Kaufmann 2003; Holmes *et al.* 2005). Recovery of the riparian zone will depend on the type, size and periodicity of the disturbance event (Richardson *et al.* 2007; Moreno *et al.* 2011; van Wilgen *et al.* 2011; White and Stromberg 2011), in combination with the survival strategies of the various component species. Riparian vegetation responds to disturbance by means of various morphological, physiological and reproductive strategies to endure, resist or avoid the extreme conditions imposed by disturbance (Naiman and Décamps 1997; Richardson *et al.* 2007). Disturbance thus acts as an ecological filter to select species that can establish and persist, which gives rise to unique riparian plant communities (White and Stromberg 2011).

Although riparian systems are inherently resilient, the relatively high frequency of disturbance events in riparian zones can compromise the resilience of vegetation communities (Richardson *et al.* 2007; White and Stromberg 2011), especially through cumulative disturbance effects (Sala *et al.* 2000). For example, an untimely fire followed by a medium frequency flood event can delay recovery for much longer than either event in isolation. Frequent disturbances provide many opportunities for the reshuffling of species composition (Stohlgren *et al.* 1998; Richardson 2001; Suding *et al.* 2004), with multiple successional trajectories. The efficient dispersal of propagules (including IAP propagules) in conjunction with frequent disturbance aids the process of invasion in riparian systems compared to terrestrial systems (Thebaud and Debussche 1991; Planty-Tabacchi *et al.* 1996). The dynamic nature of riparian systems also means that some component is almost always in a state of recovery from disturbance (Fierke and Kauffman 2006; Richardson *et al.* 2007). It is therefore difficult to apply the traditional concepts of resilience: "the ability of an ecosystem to return to its former state following a disturbance or stress" (Wali 1999), or "time required to return to its former state" (Mitchell *et al.* 2000). There is increasing recognition that ecosystems are dynamic, with disturbances constantly altering the composition of assemblages and pushing them in various directions that do not necessarily include a return to some hypothetical original, a concept referred to by Hobbs and Norton (2004) as the non-equilibrium paradigm. This is especially the case in riparian systems and makes the setting of targets and goals based on pre-defined or reference community assemblages particularly challenging (Perrow *et al.* 2008) (Section 1.6). Suding and Hobbs (2008) defined resilience as the "capacity of a system to absorb disturbance and reorganise so as to retain essentially the same function, structure, identity and feedbacks", a definition that is more appropriate to riparian systems.

Resilience may be compromised if disturbance causes either abiotic or biotic thresholds to be breached, thus preventing the recovery of an ecosystem (Whisenant 1999; Hobbs *et al.* 2006; Hobbs and Suding 2008). The larger the departure from a natural disturbance regime, the more IAPs will be favoured, whereas regimes closer to natural disturbance regimes will favour indigenous species and diversity (Daehler 2003; Brown and Johnstone 2012; van Wilgen *et al.* 2011). This is an important consideration for restoration, as disturbance can be manipulated to facilitate recovery.

Although disturbance with moderate frequencies and intensities can increase species richness and heterogeneity through the creation of regeneration niches (Naiman and Décamps 1997), the high levels of natural disturbance in riparian zones also make them particularly prone to invasion by disturbance-mediated alien species (Rejmánek 1989; Tickner *et al.* 2001; Pyke and Knick 2003; Holmes *et al.* 2005). Disturbance also creates "invasion windows" through the release of resources (Davis *et al.* 2000; D'Antonio and

Chambers 2006). The duration of this “window” will depend on the type, size and frequency of disturbance event, in combination with community- and species-specific responses. Invaders themselves can create feedback loops which alter naturally-occurring disturbance regimes, at times further promoting invasion (D’Antonio and Vitousek 1992; Mack and D’Antonio 1998). The alteration of disturbance regimes is thus sometimes considered to be the greatest impact that an invader species can have on ecosystem function and structure (Stromberg *et al.* 2007), for example the impact of woody invaders on fire severity in South African riparian zones (van Wilgen and Richardson 1985; Richardson and van Wilgen 2004; Holmes *et al.* 2008; van Wilgen 2009).

1.2.3 Fire

Insufficient attention has been given to the impact of fire on riparian zones in South Africa (Holmes *et al.* 2005). These zones differ from the adjacent upland areas in geomorphology, hydrology, vegetative composition and structure, microclimate and fuel characteristics (Dwire and Kauffman 2003), all of which will influence the fire environment, fire regimes and fire properties like severity, frequency, behaviour and extent in any given riparian area (Reinecke *et al.* 2008; Stromberg *et al.* 2009).

Fire frequency, intensity and season, all of which comprise the fire regime, affect the development, structure and composition of plant populations (Bond and Keeley 2005). Mediterranean ecosystems, including fynbos, are fire-prone and fire-driven systems (van Wilgen and Forsyth 1992; Bond and van Wilgen 1996; De Luis *et al.* 2008b), and fire is therefore a natural and regular disturbance in fynbos, and essential for the regeneration of fynbos plants (Le Maitre and Midgley 1992; van Wilgen and Forsyth 1992; Figueroa *et al.* 2004; Thomas *et al.* 2010). Fire intensity can affect plant survival and resprouting potential, the number of viable seeds in seed banks, seedling production, post-fire vigour, soil properties, and therefore the entire post-fire community (Moreno and Oechel 1991; Scott and van Wyk 1992; DeBano 2000b, c; Holmes 2002). The relationship between fire and alien-invaded ecosystems is complex (Mandle *et al.* 2011), as fire influences and is influenced by the structure and composition of the plant community. Each fire is unique, and the impact of fire can be long-lasting (Bond and van Wilgen 1996; Baker 2009; Moreno *et al.* 2011).

Despite the fact that many fynbos species regenerate after fire, concerns have been raised about the effect of burning as part of the clearing of IAPs on the regeneration of indigenous vegetation, due to its effect on vegetation, its impact on indigenous soil seed banks and soil properties (Yelenik *et al.* 2004; Holmes *et al.* 2008; Tye and Drake 2011). Fuel loads increase dramatically after invasion by woody IAPs (van Wilgen and Richardson 1985), up to 300 % (Versfeld and van Wilgen 1986,) and clearance generates large volumes of biomass, resulting in fires of high severity which can damage ecosystem function. Heavy fuel loads concentrated near the soil surface result in unnaturally intense fires (Richardson and van Wilgen 1986; Holmes and Cowling 1997b), which can eliminate remnant indigenous vegetation by killing resprouters and remaining indigenous seeds (van Wilgen and Richardson 1985; Bond and van Wilgen 1996; Cilliers *et al.* 2004). This could reduce species richness and could also result in soil erosion (Richardson and van Wilgen 1986; Scott and van Wyk 1992) and thereby severely retard or compromise ecosystem rehabilitation.

1.3 MANAGEMENT OF INVASIVE ALIEN PLANTS IN RIPARIAN ZONES

In response to the threats posed by IAPs, the South African government launched an innovative national-level IAP management initiative, Working for Water (WfW), in 1995. WfW has capitalised on the opportunity to combine clearing with job creation and poverty relief (Turpie *et al.* 2008, van Wilgen *et al.* 2011), which has granted it a sustainability and scope that few other IAP management initiatives can match. This programme has become one of the world's largest IAP management initiatives, with the threefold aim of enhancing water security, ecological integrity and social development (van Wilgen *et al.* 1998, 2012). It has been recognised internationally as a major success (Hobbs 2004; Woodworth 2006) and has been used as a model for more recent and related programmes in South Africa (Ntshotsho *et al.* 2011).

The programme has grown immensely, from an annual budget of US$ 2.71 million in 1995 to an annual budget of over US$ 43.32 million in the 2003/2004 financial year (Marais *et al.* 2004) and US$ 45.18 million by 2007 (DWAF 2007). A total of US$ 346.73 million has been spent on control over the last 15 years (van Wilgen *et al.* 2012). The costs of follow-up treatments form a substantial portion of the WfW operational budget, and have steadily increased after the initiation of WfW in 1995, since most areas require at least two (mostly more) follow-up treatments. In the 2002/2003 financial year, US$ 6.35 million was spent on initial clearing and US$ 7.37 million on follow-up. The follow-up of wattle-infested areas, in particular, contributes significantly to the follow-up costs (Marais *et al.* 2004). For example, a recent analysis by Marais and Wannenburgh (2008) found that only 7 % (2.3 % of a total 33 %) of closed-stand riparian invasions have been cleared after 15 years of WfW clearing operations, as much of the effort exerted in these areas is on follow-ups. By 2006, the WfW programme had spent more than US$ 346.73 million and had created temporary employment opportunities for 30 000 people per year. More than 1.6 million ha of land received initial clearing, 42 653 ha of which is riparian (Marais and Wanneburgh 2008). Significant investments in the development of biological control have also been made.

WfW mechanically cleared 135 000 ha of invasive *Acacia* trees between 2000 and 2010, at a cost of US$ 95.35 million (van Wilgen *et al.* 2011). However, this excludes clearing between 1996 and 1999, clearing by other agencies and firewood harvesting, so the clearing effort was definitely greater than the above figure. Prevention, early detection, biological control and eradication through mechanical and chemical means form part of the management strategy (van Wilgen *et al.* 2011). Many IAP species, e.g. pines and wattles, have high commercial value (Dunlop and MacLennan 2002; Le Maitre *et al.* 2004) but are aggressive invaders (Henderson 2001) and some novel approaches, e.g. through the use of select biological control agents, have been adapted to try and resolve the conflict of interest between eradication and commercial use (de Wit *et al.* 2001).

The recovery of riparian systems and their functioning is the implicit core goal in the management of IAPs (Holmes *et al.* 2008; Shafroth *et al.* 2008). Regeneration of fynbos can take place without active intervention (Blanchard and Holmes 2008; Holmes *et al.* 2008) and

WfW have mostly followed this passive approach (Section 1.4.1), although natural recovery and re-establishment of indigenous vegetation is often limited (Le Maitre *et al.* 2011). This usually occurs in long- and densely-invaded areas (where IAP densities exceed 75 %), where areas have experienced more than three fire cycles under invasion, and where the indigenous soil seed bank has been damaged or depleted (Holmes and Cowling 1997a). Legacy effects, such as increased soil nitrogen and large alien soil propagule banks also hinder the re-establishment of indigenous communities (Richardson and Kluge 2008; Marchante *et al.* 2008a, b, 2009; Le Maitre *et al.* 2011). Many of these areas thus remain degraded after clearing, which impacts significantly on the functioning and ability of these riparian systems to deliver ecosystem services such as water, flood attenuation and reduction of siltation (Reid *et al.* 2009; Le Maitre *et al.* 2011). Restoration of these systems to reinstate basic habitat, ecological functioning and services is therefore crucial, especially if South Africa is to meet its target of maintaining 20 % of its freshwater ecosystem types in a natural state, as proposed in the Freshwater Cross-sector Policy (Roux *et al.* 2006, 2008).

Another motivation for the restoration of these long- and densely-invaded riparian systems is that they often require on-going management in the form of numerous follow-ups to eliminate the IAPs, especially where they have deposited large seed banks, or to prevent secondary invasions (Mason and French 2007; Holmes *et al.* 2008; Le Maitre *et al.* 2011; van Wilgen *et al.* 2011), a phenomenon which is echoed from IAP control in other parts of the world (Simmons 2005). Repeated follow-ups reduce the human and financial resources available for the initial clearing, and these higher cumulative costs in densely-invaded areas may make restoration to prevent re-invasion a more viable, cost-effective option (Taylor and McDaniel 2004; Marais and Wannenburgh 2008).

1.4 RESTORATION

1.4.1 Restoration concepts and terminology

The definition of restoration has changed over the past two decades, as the science and practice of restoration has developed into a discipline in its own right, in response to the widespread degradation of ecosystems (D'Antonio and Chambers 2006). The Society for Ecological Restoration (SER) has grappled with defining ecological restoration since its inception, and originally defined restoration as returning a system to its historical state. Most practitioners and scientists now accept that this is not possible, and the current accepted definition defines ecological restoration as the "the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed. It is an intentional activity that initiates or accelerates ecosystem recovery with respect to its health (functional processes), integrity (species composition and community structure), and sustainability (resistance to disturbance and resilience)" (http://www.ser.org, Clewell *et al.* 2005).

Restoration ecology has become a "vibrant economy" over the last two decades (Follstad-Shah *et al.* 2007; Kondolf *et al.* 2007; Sudduth *et al.* 2007; Ntshotsho *et al.* 2011). It is currently estimated to be worth about US $1.6 trillion annually and is predicted to grow (Merritt and Dixon 2011). In many ways, however, it is still considered an emerging science (Hobbs 2006, 2007), although founded upon and informed by many other established ecological disciplines and theories (D'Antonio and Chambers 2006; Suding and Hobbs 2008). It has been argued that the practice of restoration can serve as the "acid test" to inform and improve existing ecological theory (Bradshaw 1987; Clewell and Rieger 1997; Palmer *et al.* 1997; Young *et al.* 2005). Recent research has focused on improving the conceptual, methodological and socio-economic bases for effective ecological restoration (Clewell *et al.* 2005; Hobbs 2007; Ntshotsho *et al.* 2011).

Restoration can be either active or passive, although some confusion exists around the exact meaning and use of these terms. Most authors refer to passive restoration as the process of recovery where no intervention other than the removal of stressors takes place (for example the removal of IAPs, cessation of mining, etc.) (Holmes *et al.* 2008; Řenhounková and Prach 2008; Le Maitre *et al.* 2011; Baasch *et al.* 2012). This is also referred to as spontaneous, unassisted or autogenic recovery, or natural re-establishment as opposed to active or technical restoration. Active restoration relies on active manipulation of either or both the abiotic and biotic environment, e.g. soil additions or the deliberate re-introduction of species

(McLachlan and Bazely 2003; Holmes *et al.* 2008; Le Maitre *et al.* 2011). Whether an active or passive approach is followed depends on a number of factors, the most important being the level of degradation, whether and which biotic or abiotic thresholds may have been exceeded (Section 1.4.2), the target condition and available resources.

Some recent literature (Beschta and Ripple 2010; Ntshotsho *et al.* 2011) have used passive and active restoration in a different context. Ntshotsho *et al.* (2011) included alien plant removal in the category of active restoration, as per the SER's (2004) definition of "Active restoration as the intentional and physical manipulation of the system to kick-start recovery" (Ntshotsho *et al.* 2011), which contradicts the above. Beschta and Ripple (2010) considered the act of "minimizing human interventions" as active restoration, whereas other research considers this to be passive restoration through removal of stressors and allowing unassisted recovery.

For the purpose of this study, the term "passive restoration" will be defined as restoration through the removal of stressors (e.g. IAP removal), while "active restoration" will be used for actions such as deliberate re-introductions of indigenous species, manipulation of soil or geomorphology, etc. (Blumenthal *et al.* 2003; Holmes *et al.* 2008; Pretorius *et al.* 2008; Le Maitre *et al.* 2011). However, categorising the use of prescribed fire is problematic in the above context, as it can form part of IAP control (removal of stressors, i.e. passive restoration), as well as facilitate indigenous plant recovery (Holmes *et al.* 2008; van Wilgen 2009; van Wilgen *et al.* 2010; Marchante *et al.* 2011a).

Unassisted, self-recovery (passive restoration) can take place where resilience is still sufficiently intact (Le Maitre *et al.* 2011), e.g. where a functional soil seed bank is still present (further discussed in Section 1.5), depending on the type, intensity, duration and frequency of disturbance (Section 1.2.2), while recovery to a functional ecosystem can often not take place without active intervention (McLachlan and Bazely 2003; Holmes *et al.* 2008; Marchante *et al.* 2011b; Le Maitre *et al.* 2011). This occurs where thresholds to recovery have been exceeded, and ecosystems no longer have the capacity to recover unaided, but require the modification of either abiotic factors (i.e. the physical environment) or biotic factors (e.g. manipulation of vegetation) or both (Whisenant 1999). Restoration often requires multiple efforts, since in most cases multiple perturbations have disturbed the ecosystem in the first place, pushing it beyond a threshold of spontaneous recovery (Palmer *et al.* 2006).

1.4.2 Succession, filters and thresholds

In essence, restoration is the purposeful manipulation of succession to achieve a desired condition (Walker *et al.* 2007; Zedler 2007). Succession, i.e. the predictable sequential change in species composition or structure over time following a severe disturbance, has served as an organizing concept in ecology for more than a century (Hobbs and Norton 2004; Řenhounková and Prach 2008; Walker and del Moral 2009; Prach and Walker 2011). Nevertheless, species assembly rules and successional pathways are still not fully resolved, especially in developing countries (Suding and Hobbs 2008; Pyšek *et al.* 2004a; McClain *et al.* 2011; Schwienbacher *et al.* 2011). Many authors use different terms for the same concepts, which confuses the debate considerably (Hobbs and Norton 2004; McClain *et al.* 2011; Prach and Walker 2011). It is difficult to predict the outcomes of succession and assembly, although these processes form the most important foundations of restoration ecology (Young *et al.* 2001; Hobbs *et al.* 2007; Prach *et al.* 2007; Walker *et al.* 2007). Successional studies provide an understanding of how communities respond to a disturbance and a dynamic physical environment, how they colonise and interact, and how they assemble and change over time (Walker and del Moral 2008). The study of succession therefore provides insight into ecosystem dynamics during as well as beyond the lifespan of plants, and is crucial to the practice of restoration ecology, informing goals and targets (Section 1.6).

Traditionally, ecosystems were viewed as stable, where any disturbance results in a well-ordered, predictable successional progression, proceeding through a sequence of states, back to original climax state (Hobbs and Norton 2004). This is referred to as the equilibrium paradigm, and assumes that it is possible to predict and control succession towards a set endpoint or stable climax state. This concept is also referred to as the deterministic model (Temperton and Hobbs 2004), gradual continuum model (Suding and Hobbs 2008) or the relay floristics (RF) composition model (McClain *et al.* 2011). The RF model predicts that each organism or group of organisms creates conditions favourable for the next colonizing group (Connell and Slatyer 1977), a process also referred to as facilitation. However, Connell and Slatyer (1977) also recognised that preceding organisms could equally inhibit later successional species, or have a neutral effect.

Various other models have also been proposed to explain reassembly; the main ones being the stochastic succession model (Gleason 1917, 1926; in Temperton and Hobbs 2004) and alternative stable state model (Lewontin 1969, in Suding and Hobbs 2008), both subject to non-equilibrium dynamics. These models incorporate various concepts such as threshold dynamics, feedback loops, alternative trajectories and stochasticity (Temperton and Hobbs 2004; Suding and Hobbs 2008). They assume that succession is event-dependent, i.e. controlled by random processes or chance events, such as climatic events or severe fires, which can send the trajectory of succession in various directions (Bond and van Wilgen 1996; Moreno *et al.* 2011). The trajectories will depend on a number of conditions such as ecological legacy, organisms present at the time of disturbance, the pre-disturbance history and current disturbance event, the availability and order of arrival of propagules, etc., with none of the end-states being predictable (Young *et al.* 2001; Suding and Gross 2004; Temperton and Zirr 2004; Le Maitre *et al.* 2011). Multiple stable states, which vary in time and space, are therefore possible (Hobbs and Norton 2004; Suding and Hobbs 2008), but are not likely in many disturbance-prone ecosystems. The initial floristics composition (IFC) model (McClain *et al.* 2011) falls under this paradigm, and predicts that all species establish early or at the same time after disturbance and thus the composition of the mature community will reflect early establishment (Egler 1954). The concept of stable states has largely been superseded by non-equilibrium paradigms, which are now widely accepted in restoration ecology, and mostly incorporate the concepts of thresholds and filters described earlier (Hobbs and Norton 2004), with succession viewed as an unpredictable process (Gibson-Roy *et al.* 2010). However, despite this, restoration plans often still design and plan for orderly succession to an end-point of equilibrium (Sheley and Krueger-Mangold 2003) or pre-determined target (Section 1.6). It may be more appropriate to instead monitor actual trajectories to inform restoration (Suding *et al.* 2004; Palmer *et al.* 2005; Zedler 2007), and examine the mechanistic processes and application of successional theory for ecosystem management, rehabilitation, and restoration (Gibson-Roy *et al.* 2010).

The various ecosystem models, and an understanding of the processes driving these, are crucial decision-making tools in restoration and land management (Suding and Hobbs 2008; McClain *et al.* 2011). For example, the relay floristics approach will assume that pioneer species which are adapted to disturbed and early successional conditions would be reintroduced first after disturbance at the start of a restoration project. This model assumes that they will facilitate (Connell and Slatyer 1977) the establishment of woody or other later successional species over time. A passive RF approach assumes that later successional species will establish in time, but have often been found to result in trajectories toward alternative states dominated by invasive plants (Suding and Hobbs 2008), especially where these species occur in the proximity of restoration sites (Prach and Hobbs 2008; Baasch *et al.* 2012). Where indigenous propagule supply is limiting (as is mostly the case in degraded areas), this model can be adapted to an "active RF" approach, where missing species are introduced over time as conditions become suitable (Holmes *et al.* 2008; McClain *et al.* 2011).

Following the non-equilibrium paradigm or initial floristics composition model, the timing of the introduction of a species will affect filters, succession and trajectories and the ultimate composition of the restored system. For example, it has been shown that species that establish earlier after fire may have a competitive advantage over species that establish later (Quintana *et al.* 2004; De Luis *et al.* 2008b). This can be manipulated to achieve biotic resistance (Chapters 4 and 5). Active re-introduction should ideally take place according to natural community development processes and dynamics (Lockwood and Samuels 2004), but can be manipulated to send reassembly on a different trajectory and result in a different end-state (Suding *et al.* 2004; Walker and del Moral 2009). Even attempting to follow natural patterns may still give unexpected results, as communities do not respond predictably to disturbance (Whisenant 1999; Hobbs and Harris 2001).

The IFC model (Egler 1954; McClain *et al.* 2011) predicts that larger numbers of species will be required at the outset of a project and is seldom used, probably due to prohibitive costs and lack of propagation knowledge. The uncertainty surrounding outcomes, e.g. survival, in the light of costs, is also a deterrent. The RF model is therefore usually adopted in guiding restoration, and although methods following this model are generally sufficient in restoring widespread species, they often do not succeed in restoring entire indigenous assemblages (Bonilla-Moheno and Holl 2010; McClain *et al.* 2011).

The concepts of thresholds and filters are integral to the process of succession (Klimkowska *et al.* 2010). Invasions often cause a breach in abiotic or biotic thresholds, which results in decreased structure and function (Ewel *et al.* 1999; Richardson *et al.* 2007; White and Stromberg 2011). Although the processes of either degradation or restoration are continuous processes, each breach of either a biotic or abiotic threshold can be viewed as a stepwise change (Suding *et al.* 2004). Abiotic thresholds are usually crossed first, followed by changes in abiotic structure, with an accompanying collapse of ecological processes, which are mostly more difficult to correct (Milton 2004; Hobbs *et al.* 2009; Brooks *et al.* 2010). Although biotic thresholds are generally dependent on abiotic factors, this is not always the case, as some biota are ecosystem engineers or keystone species and may be needed to change the abiotic environment. Usually, however, restoration of biotic factors will not be successful unless abiotic thresholds have been restored (Richardson *et al.* 2007), for example, the reduction of soil nitrogen (Blumenthal *et al.* 2003; Corbin and D'Antonio 2004; Yelenik *et al.* 2004) before indigenous vegetation will re-establish. Successful restoration thus requires the identification of abiotic and biotic thresholds (Hobbs *et al.* 2006; Hobbs and Suding 2008).

These biotic and abiotic thresholds are similar to the concept of "filters in ecosystem assembly" (Hobbs and Norton 2004). Restoration can attempt to modify the effects of filters or thresholds to allow desired species to speed up or direct the natural process (Prach *et al.* 2007; Klimkowska *et al.* 2010). This can include reinstating disturbance regimes which are important in riparian systems (Rowntree 1991; Richardson *et al.* 2007; White and Stromberg 2011). A combination of key filters will determine the resistance to restoration in any given situation (Hobbs and Norton 2004). However, as ecosystems and communities are dynamic (Brooks *et al.* 2002; Palmer *et al.* 2005), filters do not remain static over time and different filters may be important at different stages of recovery (Hooper and Dukes 2010). Fattorini and Halle (2004) developed the dynamic filter model to explain how abiotic and biotic filters change and operate temporally. This is especially relevant in disturbance-prone ecosystems such as riparian systems, since each disturbance event affects the abiotic filter, but also changes the biotic filter by shuffling species and resetting succession sequences (Fattorini and Halle 2004). The permeability of the biotic and abiotic filters is therefore dynamic and changes with time, e.g. many of the abiotic and biotic thresholds that result as a consequence from IAPs interact in a simultaneous manner with each other (Le Maitre *et al.* 2011). This has to be taken into account when restoring, as manipulation of one component can cause other unforeseen changes in other ecosystem components and thresholds. Filters generated by each new disturbance depend on the type of disturbance, intensity, duration, frequency and spatial scale affected, the interaction of disturbances and disturbance history, the season during which disturbance occurs, habitat characteristics and the regional and local species pool (Fattorini and Halle 2004).

1.5 SOIL SEED BANKS

An important factor influencing the spontaneous recovery of natural vegetation is the presence of an indigenous soil seed bank, which acts as a reservoir of plant propagules (Auld and Ooi 2008; Bossuyt and Honnay 2008; Pyke *et al.* 2010; Valkó *et al.* 2011). A persistent seed bank remains in the soil for more than one season, and is a common strategy in areas where the probability of adult survival and reproduction may vary temporally (Kalisz and McPeek 1993; Auld and Denham 2006; Penman *et al.* 2008; Thomas *et al.* 2010), e.g. in fire-prone ecosystems such as fynbos. In densely-invaded ecosystems, a rapid reduction in fynbos cover and seed production has been found, and these ecosystems therefore rely heavily on the persistent soil seed bank for recovery (Le Maitre and Midgley 1992; Holmes and Cowling 1997a, b). The loss of the soil seed bank can present a biotic barrier to restoration, while its persistence can play an important role in facilitating the recovery of indigenous vegetation after the clearance of IAPs (Holmes 2001b; Holmes and Newton 2004; Sakai *et al.* 2005).

A number of studies in South Africa have investigated the soil seed bank in fynbos (Manders 1990; Musil 1991; Pierce and Cowling 1991; Holmes and Cowling 1997a, b), including the effect of alien invasion on the indigenous soil seed bank (Vosse *et al.* 2008). However, only the studies of Manders (1990) and Vosse *et al.* (2008) investigated riparian seed banks. Little is known of riparian seed banks worldwide (Goodson *et al.* 2001; Williams *et al.* 2008; Lu *et al.* 2010; White and Stromberg 2011), and no information is available on the soil seed banks of either riparian or non-riparian grassy fynbos, or on the effects of IAPs on the indigenous soil seed banks in the Eastern Cape. A decline in seed bank density has been recorded for invaded areas (Holmes and Cowling 1997a), generally declining with increasing invasion age. Holmes and Foden (2001) found that a viable soil seed bank is present in invaded areas for up to 30 years, but in areas that have been invaded for more than 40 years it is impoverished.

The presence of a viable soil seed bank will enable the passive restoration of a cleared site, allowing recovery to proceed according to natural pathways of succession and assembly. A large portion of this study therefore focusses on the soil seed bank and the impact of management interventions on the recovery potential of invaded riparian fynbos ecosystems.

1.6 ASSESSING RESTORATION SUCCESS

There is general agreement amongst restoration ecologists that it is essential to set a clear and achievable goal (Ehrenfeld 2000; Hobbs 2007). The success of restoration projects is often measured using ecologically-based criteria (Palmer *et al.* 2007; Ntshotsho *et al.* 2011, 2012; Wilson *et al.* 2011b; Guldemond *et al.* 2011). However, socio-economic goals, especially in a developing country such as South Africa, are also critical (van Wilgen *et al.* 1998; Aronson *et al.* 2010; Ntshotsho *et al.* 2012), to ensure sustainability. It is also recognised that defining a target for ecological restoration is as much an ethical issue as a technical one (Higgs 1997), and that present-day limitations have to be incorporated into goals.

Assessing the success of a restoration project is not straightforward (Zedler 2007), often due to the lack of consensus surrounding the use of indicators such as ecological integrity or biodiversity (Tongway and Hindley 2003; UNEP 2003; Scholes and Biggs 2005; Hughes *et al.* 2010). As discussed earlier, it may be appropriate to measure the outcomes of restoration against an undisturbed reference ecosystem (Hughes *et al.* 2001; Skinner *et al.* 2008; Beschta and Ripple 2010), but it is highly unlikely that the exact composition of the reference system can be re-created, due to the dynamic nature of filters acting on species reassembly (Palmer *et al.* 2005). The long history of human impacts means that undisturbed riparian reference systems are often scarce. Fynbos systems also inherently exhibit a high degree of spatial heterogeneity and patchiness (Reinecke *et al.* 2007), which further complicates the use of riparian reference systems in fynbos. The setting of goals is also sometimes considered to contradict ecological theory (Palmer *et al.* 1997), due to the large and variable range of trajectories, especially in systems subject to frequent disturbance as is the case in riparian zones. However, much of the literature refers to the setting of endpoints and targets as an essential component of restoration (Higgs 1997; Hobbs 2007). Clewell *et al.* (2005) suggested that a reference state can be used if it is sufficiently broad to accommodate the amplitude of potential endpoints that could reasonably be expected from restoration (Allen and Holling 2010) and if it also recognises present-day constraints.

In riparian systems, restoring structure and function, rather than a pre-defined species composition, is generally the accepted end-state or goal (Palmer *et al.* 2005; Holmes *et al.* 2008; Skinner *et al.* 2008; Suding and Hobbs 2008). Nonetheless, the dynamic nature of riparian zones still makes it difficult to understand how they function and to predict outcomes of any given event or management activity, resulting in much uncertainty in restoration outcomes (Hobbs and Norton 2004; Gregory and Downs 2008; Lemons and Victor 2008).

Achieving a functional, self-sustaining ecosystem with desired properties or trajectories (D'Antonio and Chambers 2006) is a more acceptable goal. Such an ecosystem will need to retain the desired processes as well as typical biotic and abiotic characteristics through subsequent natural disturbance cycles. It will need to be resilient, by returning to pre-disturbance conditions or a trajectory leading to that within a reasonable time frame after subsequent disturbance (Holling 1973), and without requiring additional large-scale interventions. Implicit in this goal is that a restored system should be resistant to invasion. Thus, in projects concerned with restoration after invasion, this could be considered the most critical focus of restoration interventions and goals (D'Antonio and Meyerson 2002; Funk *et al.* 2008; McGlone *et al.* 2011), and forms one of the main goals of this research.

1.7 BIOTIC RESISTANCE IN INVADED SYSTEMS

An ecosystem can gain resistance to invasion through various biotic and abiotic attributes (Collinge *et al.* 2011). This is referred to as invasion resistance or ecological resistance (D'Antonio and Chambers 2006; Richardson and Pyšek 2006; Funk *et al.* 2008). The term "biotic resistance" is also often used, but this is limited to the "ability of the resident species in a community to reduce the success of exotic invasions" (Levine *et al.* 2004, Maron and Vilà 2001; Levine *et al.* 2004; McGlone *et al.* 2011; Taylor and Duggan 2012). However, it is often very difficult to isolate the resistance offered by biota from the ecosystem context in which it takes place (Lonsdale 1999; von Holle 2005; Richardson and Pyšek 2006; Hooper and Dukes 2010). The inverse of ecological resistance is community invasibility, which has received considerable interest since the 1950s, dating from Elton's (1958) "*The ecology of invasions by animals and plants*". Invasibility has been defined as "the vulnerability of a habitat and the associated biological community to invasion" (Alpert *et al.*, 2000; Von Holle and Simberloff 2004; Davis *et al.* 2000; Catford *et al.* 2012). This is linked to the question of which species become invaders (Rejmánek 1996; Rejmánek and Richardson 1996; Thuiller *et al.* 2006; Richardson and Pyšek 2006), and these questions have preoccupied research into invasion ecology for decades.

Although Elton's book is often considered to be the basis of invasion ecology, the concept really has its origins in Darwin's "*The Origin of Species*" (1859, in Pearson *et al.* 2011), where Darwin recognised that invader traits are best understood in the context of the recipient community, but that various mechanisms may facilitate invasions. His theory has been labelled "Darwin's naturalisation hypothesis", or more accurately, "Darwin's naturalisation conundrum" by Diez *et al.* (2008), which reflects the divergent nature of the hypotheses. The questions of why some communities are more prone to invasion than others (Davis *et al.* 2000; Levine *et al.* 2004; Tilman 2004; Richardson *et al.* 2005) and which traits are more likely to make species successful invaders (Rejmánek 1996; Richardson and Pyšek 2006; Thuiller *et al.* 2006; Castro-Díez *et al.* 2011; Pearson *et al.* 2011) all follow on from these early hypotheses. Many studies have considered these two concepts in isolation (Thuiller *et al.* 2010), but it is increasingly apparent that both invader species characteristics and community properties must be integrated to enable the prediction of future invasion risks (Davis *et al.* 2000; Richardson and Pyšek 2006). It is also imperative that invasion ecology be considered as a community phenomenon, with the invasion of a community being a product of the attributes of both invaders and the recipient community (Shea and Chesson 2002; Richardson and Pyšek 2006; Nuñez and Medley 2011). Attempting to understand or predict invasion success or resistance based on either component in isolation is likely to meet with limited success (Lonsdale 1999; Pyšek *et al.* 2004b; Carrillo-Gavilán and Vilà 2010; Diez *et al.* 2012). Integrating these questions will therefore also provide insight into the mechanisms of invasion or ecological resistance and how to manipulate restoration to provide ecological resistance.

1.7.1 Motivation for biotic resistance in the South African context

The repeated follow-up control and maintenance that is required in areas that have been cleared of Acacias is a major challenge in the management of IAPs in South Africa. Recent research in South Africa (Beater *et al.* 2008; Holmes *et al.* 2008; McConnachie unpubl. data) revealed that many infested areas require repeated follow-up treatments to bring woody IAPs under control, a finding which is echoed from studies on IAP control from other parts of the world (Simmons 2005). For example, McConnachie (unpubl. data) found that there has been a decrease of only 133 ha in the Kouga catchment in South Africa, from 888 ha in 2002 to 755 ha in 2009, despite an investment of R95 643 per condensed hectare. Although this is also due to the rapid spread of IAPs, with new areas continuously being invaded, it also reflects the necessity for repeated follow-ups (often as many as eight times), of cleared areas which have been densely invaded (van der Waal 2009). The analysis by Marais and Wannenburgh (2008) found that only 7 % of closed-stand riparian invasions have been cleared after 15 years of extensive and costly WfW clearing operations, and much of this time has been spent on follow-ups. The most recent assessment of the effectiveness of the WfW programme expresses concern about the overall reduction in the extent of invasion in South Africa, as invasions appeared to have increased in many areas (van Wilgen *et al.* 2012). A post-clearing plant community which is resistant to re-invasion would therefore be a major benefit in the management of IAPs in South Africa. Attempts have been made to achieve this in the WfW programme in the Eastern Cape, with apparent success (Jonathan Prior pers. comm.), although no data were available.

Achieving biotic resistance is one of the greatest challenges in invasion and restoration ecology (Bakker and Wilson 2004; Levine *et al.* 2004; Pokorny *et al.* 2005; Funk *et al.* 2008; Middleton *et al.* 2010). The quest for biotic resistance has to consider the factors which control invasion success, the traits of successful invaders (Richardson and Pyšek 2006; Gallagher *et al.* 2011; Gibson *et al.* 2011; Morris *et al.* 2011) and what makes communities susceptible to invasion (Levine and D'Antonio 1999; Davis *et al.* 2000). As stated in Section 1.7, invasion should be considered as a community phenomenon, with the invasion of a community being a product of the attributes of both invaders and the recipient community (Shea and Chesson 2002; Richardson and Pyšek 2006; Carrillo-Gavilán and Vilà 2010; Nuñez and Medley 2011). Biotic resistance should be viewed in a similar context, as being dependent on the attributes of both the IAP and recipient community. These factors should therefore not be dealt with in isolation. Other variables - e.g. the dispersal of propagules through human activity, which adds to propagule pressure - can also play major roles (Catford *et al.* 2012).

1.7.2 Role of biodiversity and the empty-niche hypothesis

There has been much debate about the role that plant diversity plays in biotic resistance (Moore *et al.* 2001; Levine *et al.* 2004; Richardson and Pyšek 2006; Fridley *et al.* 2007; Eschtruth and Battles 2011). The concept of biotic resistance (and discipline of invasion ecology) dates back to Elton (1958), who first hypothesised that more diverse communities are more stable and therefore resistant to invasion. The underlying theory of this concept is that as communities become more diverse, niche space is saturated, which prevents exotic species establishing in the community (Richardson and Pyšek 2006), a theory which has been supported by numerous theoretical studies (Rejmánek 1989; Grime, 1997; Hooper and Vitousek 1998; Akatov and Akatov 2010), as well as empirical data (Levine and D'Antonio 1999; Lyons and Schwartz 2001). Inter-specific competition increases with diversity, resulting in fewer resources being available for establishment of invaders (Hooper and Vitousek 1998; Tilman 1999; Fargione *et al.* 2003; Hierro *et al.* 2005) and making them less invasible. However, this has also been opposed (Stohlgren *et al.* 1999, 2003, 2006, 2008; Pyšek *et al.* 2002), although many contradictions appear to result from studies at different spatial scales (Espinosa-García *et al.* 2004; Richardson and Pyšek 2006). More recent research suggests that diversity in functional traits is better correlated with resistance to invasion than species diversity *per se* (Tilman 1997; Funk *et al.* 2008; Hooper and Dukes 2010), as invasive species are unlikely to establish if available niches are filled by plants with similar traits. Restored communities may thus be better able to resist re-invasion when they contain species functionally similar to known high-risk invaders (Zavaleta and Hulvey 2007). This is discussed further in Section 5.5.3.

Fynbos is a highly diverse vegetation type, but nevertheless has been found to be highly susceptible to invasion by woody alien species (Kruger *et al.* 1989). Much of the fynbos biome is bioclimatically suited to afromontane forests (Manders 1990; Manders and Richardson 1992; Manders *et al.* 1992), but fire limits expansion of trees and forests, and true, evergreen forests are confined to fire-free zones such as deep kloofs and scarps. However, fire-adapted trees occur in other Mediterranean-climate vegetation types and the absence of indigenous trees in fynbos can thus not easily be explained (Rundel 2004). It has been suggested that tree species adapted to the environmental conditions of the Cape Floristic Region have never evolved, and Campbell *et al.* (1979) and Moll *et al.* (1980) have proposed the “vacant niche” hypothesis, arguing that trees that can cope in the fynbos environment - i.e. survive periodic fires, low nutrient status and summer drought - can become invasive. Richardson and Cowling (1992) argue that woody IAPs in fynbos utilise a surplus of resources (mainly moisture) that is currently not exploited, and have pushed fynbos vegetation closer to the steady-state biomass predicted for the resource (precipitation) level, as occurs in other Mediterranean areas in the world. This has resulted in a higher steady-state biomass of invaded fynbos as compared to non-invaded fynbos, as a result of surplus resources associated with a vacant niche. Invasion facilitated through resource availability has also been found in other parts of the world (Hobbs and Huenneke 1992; Davis *et al.* 2000). Resource availability, in combination with propagule pressure, appears to be one of the most important factors in facilitating invasions (Richardson and Pyšek 2006; Tanentzap and Bazely 2009). The role that these factors play, and possible ways of manipulating these factors to achieve biotic resistance in riparian areas cleared of woody IAPs, is explored further in the following sections.

Fire-protected areas of the fynbos biome do support afromontane trees with high biomass comparable to invader species (Manders 1990; Geldenhuys 1994; Prins *et al.* 2004), and these areas are more resistant to invasion. Riparian fynbos zones contain shrub and smaller tree elements such as *Brabejum stellatifolium*, *Diospyros glabra*, *Brachylaena neriifolia* and *Metrosideros angustifolia* in the Western Cape (Prins *et al.* 2004; Sieben and Reinecke 2008) and *Halleria lucida, Burchellia bubalina* and *Rapanea melanophloeos* in the Eastern Cape, although these are not as fast-growing or large as invasive wattle species. These species are fire-resistant and generally resprout after fire, but do not have the same reproductive ecology as Acacias, where mass germination is triggered by fire. The invasibility of fynbos, or lack of biotic resistance, is therefore considered to hinge on patterns of resource utilisation as well as spatial and temporal disturbance (Richardson and Cowling 1992). Recurrent fires in fynbos can create windows of opportunity for the entry of IAPs by causing large spatial and temporal fluctuations in population sizes (Richardson and Cowling 1992). Flooding in riparian systems has the same effect, with disturbance creating gaps for the entry of woody

IAPs (Richardson *et al.* 2007), which is one of the factors that generally makes riparian communities invasible.

MacDonald (1984) argues that fynbos is not particularly invasible, but that a few invaders possess the traits to successfully invade fynbos and spread over a large area. However, Eschtruth and Battles (2011) found that the extent of invasion is a poor indicator of invasibility, and that higher levels of invasion in riparian forests result from greater propagule pressure rather than higher invasibility, a finding which is supported by Catford *et al. (*2012) and Nuñez and Medley (2011). Boedeltje *et al.* (2003) also found that a higher propagule pressure better explains the distribution of invasive plants in riparian systems than does morphological adaptations. This confirms the findings of other research, e.g. Thomsen *et al.* (2006), who found that more seed results in the higher establishment of unoccupied gaps, and von Holle and Simberloff (2005) who concluded that propagule pressure overwhelmed ecological resistance to invasion.

1.7.3 The role of propagule pressure

High propagule pressure is one of the main factors associated with invasions (Lonsdale 1999; Richardson and Pyšek 2006; Warren *et al.* 2011a), and is related to residence time (Wilson *et al.* 2007). Within intact riparian fynbos, the entry of alien plants will be slow at first, and establishment and density will increase exponentially over time, followed by increasing propagule pressure. *A. longifolia* was the first wattle species to be introduced to South Africa in 1827 (van Wilgen *et al.* 2011), and since the seeds of most wattle species remain viable for decades, large propagule banks have accumulated. In fact, most *Acacia* species were introduced more than 150 years ago and have been widely propagated since (Poynton 2009). For many invasive species, increased extent and intensity of propagation, including multiple introductions and extensive trading, have resulted in increased propagule pressure and invasion (Griffin *et al.* 2011; Wilson *et al.* 2007, 2011a). Castro-Diez *et al.* (2011) have found that including human use as a predictor in modelling invasions is an important factor in explaining invasiveness. This has also been supported by other research (Alpert *et al.* 2000; Carrillo-Gavilán and Vilà 2010; Catford *et al.* 2012). Useful *Acacia* species have better chances of being transported, and this combined with the increasing propagule pressure, is likely to make them more invasive (Castro-Diez *et al.* 2011). Holmes *et al.* (1987) have reported viable soil seed banks of 4 000–46 000 seeds/m^2 in the Western Cape. Where wattles have remained unchecked for decades, the degree of current invasion is a product of residence time, efficient dispersal and propagule pressure (Thuiller *et al.* 2006).

1.7.4 Mechanisms of biotic resistance

Understanding the mechanisms of biotic resistance is essential in achieving successful restoration (Hooper and Dukes 2010) and necessarily has to include the traits of the successful invader as well as the factors that make the community invasible. Although higher diversity results in more complete use of limiting resources, leaving little for IAPs (Tilman 1999, 2004; Fargione *et al.*, 2003), Leffler *et al.* (2011) also found that many IAPs exhibit greater resource acquisition rates and greater plasticity in resource acquisition. This makes invasive species more flexible and opportunistic, and enables them to acquire limited resources to a greater extent than indigenous species, increasing their niche breadth and competitive ability in variable environments. However, Daehler (2003) found that many IAPs are not uniformly more competitive than indigenous species, but that their relative performances were context-dependent. He coined the term “super-invaders” for the few IAPs that have a consistent superior performance over indigenous species, and wattle may be considered one such species.

Generally, although competition is considered the mechanism that governs invasibility, it is not the only one (Richardson and Pyšek 2006). It is important to recognise the importance of species identity, community composition and interaction and mechanisms of co-existence (Levine and D’Antonio, 1999) between species within a community, where keystone species can have an overriding effect (Booth *et al.* 2003; Crawley *et al.* 1999) in explaining invasibility or biotic resistance. Competition at different life stages will differ, e.g. between establishment versus growth phases, and biotic resistance will vary accordingly (Hooper and Dukes 2010).

1.8 OBJECTIVES AND KEY QUESTIONS

1.8.1 Objectives

There are very few studies documenting recovery in grassy fynbos after disturbance, and these have been limited to documenting in-field succession after fire (Martin 1966; Jacot-Guillarmod 1983; Richardson *et al.* 1984). There is no information available on recovery after the clearing of IAPs in grassy fynbos, either riparian or terrestrial. Although some active restoration after clearing has been undertaken as part of WfW activities and small-scale studies in the area, no accurate records were kept and no conclusive evidence exists regarding the efficacy of these activities. This study is the first to investigate the restoration of an alien-invaded riparian site in grassy fynbos and the factors that influence the process of recovery.

This study investigated the restoration of a riparian zone in the fynbos biome of the Eastern Cape, which has been long and densely invaded by an Australian wattle species, *Acacia longifolia* (Jacot-Guillarmod 1983). It set out to investigate the factors that facilitate or constrain spontaneous recovery and influence the trajectories of recovery or succession. These factors include invasion history and management history, especially the use of fire. It tested the efficacy of some active restoration interventions with the aim to return invasion-resistant, indigenous vegetation with a structure and function representative of uninvaded sites.

1.8.2 Key questions

The following key questions were posed to achieve the objectives above:

1. What is the restoration potential of the soil seed bank in a long-and densely-invaded riparian zone in grassy fynbos?
2. How does the use of fire as part of IAP management affect the soil seed bank in riparian grassy fynbos?

3. What are the temporal patterns of emergence of species from the persistent soil seed bank after fire in grassy fynbos?
4. Can alien-invaded riparian zones in grassy fynbos restore passively after clearing?
5. Can active restoration improve indigenous diversity and cover, compared to passive restoration?
6. Does follow-up control of IAP regrowth in the form of foliar herbicide affect indigenous diversity or cover, and how does it compare to a non-herbicide follow-up treatment?
7. Can restoration achieve biotic resistance and if so, how can this be achieved?
8. What are the implications of the results of the above questions for the management of IAPs in riparian grassy fynbos?

1.8.3 Aims and hypotheses of each chapter

1.8.3.1 Chapter 2: Potential for recovery based on the indigenous soil seed bank after the clearing of invasive alien vegetation in a riparian zone in the grassy fynbos of the Eastern Cape.

Aim:

1. Investigate the regeneration potential of riparian grassy fynbos, based on the composition and abundance of the soil seed bank.

Hypothesis:

1. The density of seeds in the soil seed bank will be low, due to the invasion period of 30 years and number of fire cycles under invasion.

1.8.3.2 Chapter 3: The impact of fire as a management tool on a riparian soil seed bank

Aims:

1. Investigate the change in soil temperatures during a controlled fire as part of IAP management.
2. Investigate the effect of a controlled management fire on the soil seed bank in riparian grassy fynbos by comparing the pre- and post-fire soil.
3. Investigate the effect of fire in the soil profile and across lateral zones.

Hypotheses:

1. High (and lethal) soil temperatures will be experienced during a controlled burn of an IAP-infested area cleared of IAPs.
2. Soil temperatures will be higher under higher slash stacks than low stacks.
3. The post-fire density of seeds in the soil seed bank will be lower than the pre-fire seed density in the soil seed bank.
4. The above effects will be more pronounced in the upper soil layer, compared to deeper layers.
5. The composition of the soil seed bank will be altered due to the fire.
6. The percentage contribution to the soil seed bank of various guilds will be altered after the fire, compared to the pre-fire soil seed bank.

1.8.3.3 Chapter 4: The temporal patterns of seedling emergence in grassy fynbos

Aims:

1. Investigate the patterns of emergence of species from the persistent soil seed bank after a simulated fire in grassy fynbos.
2. Determine whether all seedlings recruit in the first year following fire-related cues, following the IFC model (Egler 1954; Kruger 1983; Le Maitre and Midgley 1992; McClain et al. 2011)?
3. Is the timing of germination restricted to the typical fynbos phenological pattern where germination takes place in the rainy autumn to winter season (Kruger 1983; Cowling et al. 2005), or is there a wider germination window, shifting towards spring and summer?
4. Is there potential to manipulate the temporal patterns of emergence to direct succession?

Hypotheses:

1. Seeds in the soil seed bank will exhibit synchronised germination within the first two months after fire, followed by available moisture (as a typical germination response of Mediterranean-type vegetation)

2. Seedling emergence from the 0-4 cm and 4-8 cm soil layers will follow a similar temporal pattern of emergence, but the number of emergents from the 4-8 cm layer will be lower than that from the 0-4 cm layer.
3. Emergents from the same guilds will exhibit a similar temporal pattern of emergence.

1.8.3.4 Chapter 5: Restoration of an alien-invaded riparian zone in grassy fynbos

Aims:

1. Investigate the potential for passive and active restoration of alien-invaded riparian zones in grassy fynbos.
2. Investigate whether active restoration can improve indigenous diversity and cover, compared to passive restoration.
3. Investigate whether follow-up control of IAP regrowth in the form of foliar herbicide affect indigenous diversity or cover compared to a non-herbicide follow-up treatment.
4. Investigate whether restoration can achieve biotic resistance and if so, the probable mechanism of how this is achieved.

Hypotheses:

1. Active restoration, through the sowing and planting of indigenous species, will increase the cover and diversity of indigenous vegetation compared to passive restoration.
2. Follow-up management, using foliar herbicide, will negatively affect indigenous diversity and cover.
3. Biotic resistance can be achieved through the active restoration of indigenous vegetation.
4. Active restoration, through the sowing and planting of grasses, will achieve a higher degree of biotic resistance but will suppress indigenous vegetation.
5. The success of restoration interventions will vary according to the lateral zonation of the riparian zone.

1.9 STRUCTURE OF THE THESIS

This thesis is composed of the introductory review, four chapters with empirical results, each written as independent papers, and a synthesis chapter which integrates and assess the results as a whole.

The restoration potential of invaded fynbos relies heavily on the presence of a soil seed bank. Chapter 2 investigated the regeneration potential of riparian grassy fynbos, based on the composition and abundance of the soil seed bank. Little is known about riparian seed banks worldwide, and this study was the first to investigate the seed banks in grassy fynbos.

Fire is an integral part of fynbos systems, and also has and still plays an important role in the management of IAPs (Roura-Pascual *et al.* 2010). However, the increased fire severities that result from the high volumes of biomass generated by IAPs can result in degradation of the cleared riparian systems, through damage to the soil, soil seed bank and above-ground vegetation, and fire thus has the potential to alter or arrest trajectories of succession. Comparatively little information regarding the impact of fire in alien-invaded riparian fynbos zones is available, especially in the eastern extent of the fynbos biome (Section 1.10). Chapter 3 investigated the impact of fire on soil seed bank composition and abundance, and presents the first results on the impact of fire on the soil seed banks in riparian grassy fynbos.

The emergence of seedlings from the soil seed bank over time is presented in Chapter 4. The timing of seedling emergence after fire affects recruitment success and can influence survival, growth and fecundity of the emergent. Timing of emergence can inform fire management and active restoration, as the timing of the emergence or introduction of a species can affect the successional trajectories and the composition of the restored system after clearing of IAPs and fire (McClain *et al.* 2011). Little information exists on the temporal patterns of emergence worldwide, and of the factors that influence them, especially in fire-prone areas with aseasonal rainfall patterns. No information exists on the temporal emergence patterns of species from the persistent soil seed bank in riparian fynbos and the role that this could play in vegetation development and management of IAPs. This study is the first to document these data.

Chapter 5 assesses the outcomes of two active restoration interventions against spontaneous succession in a cleared riparian zone. It investigates the impact of two follow-up methods on vegetation cover and composition, and compares the outcomes of the restoration interventions against a range of reference and other cleared sites. It is the first record of both passive and active restoration trials after clearing of IAPs in the grassy fynbos biome. One of the most important motivations for the restoration of alien-invaded areas is to achieve a resilient, self-sustainable system that will be able to recover from natural disturbance events. Implicit in this goal is that the restoration of alien-invaded systems should aim to establish a vegetation cover that is resistant to re-invasion, and this should be considered the over-arching goal for alien-invaded systems. Chapter 5 assesses the degree of biotic resistance achieved during this study, and investigates the possible mechanisms that may be utilised to prevent or decrease re-invasion. It is the first record of the development of biotic resistance through the process of active restoration in South Africa.
Chapter 6 provides a synthesis of the findings of this thesis. All species recorded during the study are listed in Appendix A.

1.9.1 Study timeline

Activity	**Start date**
Pre-fire emergent study:	
• Demarcation of plots	Apr 2004
• Collection of soil	Oct-Nov
• Survey of slash and vegetation	Nov - Dec 2004
• Smoke treatment and start of emergent study	Jan 2005
• 2nd survey of slash and vegetation (1 year after clearing)	Oct - Nov 2005
• Placement of Tempilstik samples	Oct 2005
• Collection of fuel samples	Oct 2005
• Prepare site for collection of temperature data	Nov 2005
• Collection of pre-fire soil samples	Nov 2005
• Termination of emergent study	Dec 2005
Post-fire emergent study:	

- Controlled burn of site - Add additional plots for post-fire studies - Collect soil - Start of emergent study - 1st survey of vegetation in restoration trial site - 2nd survey of vegetation in restoration trial site - Termination of emergent study	Nov 2005 Nov - Dec 2005 Jan 2006 Jun 2006 Apr - May 2009 Dec 2006 Dec 2006
Chronosequence study: - Obtain data of cleared sites and associated clearing histories from WfW - Survey of riparian sites: variables	 Jan 2005 Mar –Sep 2005
Restoration trials: - Controlled burn of site - Implement three initial restoration treatments - 1st survey of site - Manual follow-up treatment to selected plots by hand pulling of *Acacia* seedlings - Chemical (foliar herbicide) follow-up treatment to selected plots.	 Nov 2005 Dec 2005 Jun 2006 Jun 2006 Sep 2006

1.10 STUDY AREA

The study area falls within the fynbos biome, which occupies most of the Cape Fold Belt. Fynbos is characterised by poor soils, recurrent wildfires and a Mediterranean to all-year-round rainfall regime (Cowling and Holmes 1992; Deacon *et al.* 1992; Bond and van Wilgen 1996). The fynbos biome is often considered synonymous with the Cape Floristic Region (CFR), which is the world's richest region of plant species diversity and endemism (Goldblatt and Manning 2000). The CFR contains 9 000 plant species, with 69 % of these being endemic to the CFR, making it one of the world's 25 biodiversity hotspots (van Wyk and Smith 2001).

The CFR is one of the Mediterranean-type ecosystems (Ojeda *et al.* 2001) which are found between latitudes 30° and 40° north and south of the equator on the western coasts of continents in five regions of the world; these are the Mediterranean Basin, California, central Chile, South-western Australia, and the Cape Region of South Africa (Rundel 2004). Mild rainy winters and summer drought are the defining factors for Mediterranean-type ecosystems (Rundel 2004; Gaertner *et al.* 2009). However, although the climate is strictly Mediterranean in the west, the eastern half of the CFR also receives a large proportion of its rainfall during other seasons (Goldblatt and Manning 2000). All Mediterranean-type ecosystems are prone to frequent disturbance in the form of fire, with a mean fire return interval of 20 years, and range of 6-40 years in fynbos (Kruger 1983; Ojeda *et al.* 2005). The western portion of the CFR typically experiences spring and autumn fires, while fires can occur during any season in the eastern half (Le Maitre and Midgley 1992; Heelemann *et al.* 2008). Regeneration in fynbos after fire takes place by means of resprouting or from seed banks (canopy or soil-stored) (Kruger and Bigalke 1984).

Fynbos forms the dominant vegetation type (Mucina and Rutherford 2006) and is characterised by the presence of species of the family Restionaceae, in addition to a frequently high cover of shrubs in the following families: Ericaceae, Asteraceae, Rhamnaceae and Thymelaceae, and often members of the Proteaceae. Fynbos mostly occurs on nutrient-poor soils and under a climate ranging from winter to bimodal rainfall (Deacon *et al.* 1992; Le Maitre and Midgley 1992).

The vegetation in the riparian zones of the fynbos biome is often similar to forest and thicket in having a higher cover of broad-leaved woody plants, but dissimilar in the high cover of fynbos elements of the Restionaceae and Ericaceae (Holmes *et al.* 2005). Woody elements increase where riparian zones are protected from fire, and can result in forests (Manders 1990; Cowling and Holmes 1992). Riparian vegetation in the fynbos biome has been described by a number of authors (Prins *et al.* 2004; Sieben and Reinecke 2008; Galatowitsch and Richardson 2005). Galatowitsch and Richardson (2005) estimated scrub forest, consisting of small trees, to comprise approximately 40-100 % of riparian headwater reaches; *Cunonia capensis* being the main indicator species, along with other common species such as *Platylophus trifoliatus* and *Rapanea melanophloeos*. Afromontane forests, consisting of large trees, make up the remaining vegetation type where there is protection from fire. There is an extremely high level of species turnover in riparian fynbos between different catchments (King and Schael 2001; Reinecke *et al.* 2007), whereas forests in different catchments are relatively similar in species composition (Sieben and Reinecke

2008). Plant communities can be stratified by height above the river channel (Boucher 2002; Holmes *et al.* 2005), which is determined by the frequency and severity of flooding. Sieben and Reinecke (2008) have distinguished two zones in riparian zones of the fynbos: the wet bank, which is inundated annually, and the dry bank which is inundated inter-annually.

The study area falls at the eastern limit of fynbos biome, and the vegetation is classified as Suurberg Quartzite Fynbos (Mucina and Rutherford 2006), which is found on nutrient-poor, sandy soils derived from the Witteberg Group quartzite, at altitudes of 350-1 010 m above sea level. Fynbos in this area, the Albany region, is characterised by a higher percentage grass cover, and an associated high cover of non-proteoid nanophylls and forbs. Grassy fynbos typically occurs on south-facing wetter slopes, unless transformed to grassland through overgrazing or burning (Mucina and Rutherford 2006). On north-facing, drier slopes grassy fynbos is replaced by grassland. Fynbos in the Albany region often occur in the form of intricate mosaics with the thicket and grassland biomes (Victor and Dold 2003, Mucina and Rutherford 2006). The study site is located in the headwaters of the Palmiet catchment, a tributary of the Kariega River near Grahamstown (33° 20′ S, 26° 29′ E) (Figure 1.1). Mean annual rainfall is 545 mm with bimodal peaks during October to November and February to March. The mean daily maximum temperature is 27.7 ^{o}C, February being the hottest month, and the mean daily minimum temperature (4.7 ^{o}C) occurs in July (Mucina and Rutherford 2006).

The original vegetation in the area consisted of grassy fynbos on the hill slopes, dominated by *Erica chamissonis* and *E. demissa* (Martin 1966; Richardson *et al.* 1984), with a patch of Afrotemperate forest at the top of the catchment 200 m upstream of the treatment strip (see below). There are no detailed accounts of the pre-invasion riparian vegetation of this catchment, but riparian vegetation in nearby similar catchments is dominated by Restionaceae and Cyperaceae such as *Carpha* spp. and *Eleocharis* spp., interspersed with woody species such as *Halleria lucida*, *Burchellia bubalina*, *Rapanea melanophloeos*, *Erica caffra* and *Cliffortia graminia*. By 1974, the south-facing slopes in the catchment were covered almost entirely by alien species (*Pinus* species, *Hakea sericea*, *Acacia longifolia*, *A. saligna* and *Solanum mauritianum*) (Jacot-Guillarmod 1983).

Figure 1.1: Location of study area (Source: maps-africa.blogspot.com)

The area was cleared, and experienced a hot wildfire in August 1980. After the fire, all woody alien species re-appeared rapidly, except for *H. sericea,* and aerial photographs indicate that by 1990 a closed alien stand, consisting of mostly *A. longifolia*, had re-established. This has also been found in other areas, where *A. longifolia* established after the removal of *Hakea* (Pieterse and Cairns 1986). Another wildfire went through the valley in 1996, with a repeat of the post-fire re-establishment of alien vegetation. The study area has thus experienced two fire cycles resulting in closed-stand IAPs (see Figure 1.2).

A strip approximately 150 m wide and 300 m long, running from the south-west across the stream and upslope towards the north-east, encompassing riparian and terrestrial fynbos communities, was cleared by Working for Water in 2000. Follow-up clearance was not done and regrowth of the invasive vegetation was such that by 2004 a closed-canopy stand of trees of up to 6 m tall had re-established, consisting of mainly *A. longifolia*. The strip was cleared again in June 2004, and used for this study (Plates 1-4). A diagram of the study site and layout of treatments is shown in Figure 1.3. Refer to this diagram for description of methods in the following chapters.

Figure 1.2. The Palmiet catchment, indicating the study area (outlined in white). The darker patches are dominated by the invasive alien tree *Acacia longifolia* (source: <u>www.googleearth.com</u>, 2003).

Plate 1. Cleared study site in 2004, facing north-east

Plate 2. Cleared stream channel, 2004, facing north-west. Note large volumes of biomass

Plate 3. Cleared stream channel, 2004, facing south-east.

Plate 4. Cleared study site, 2004.

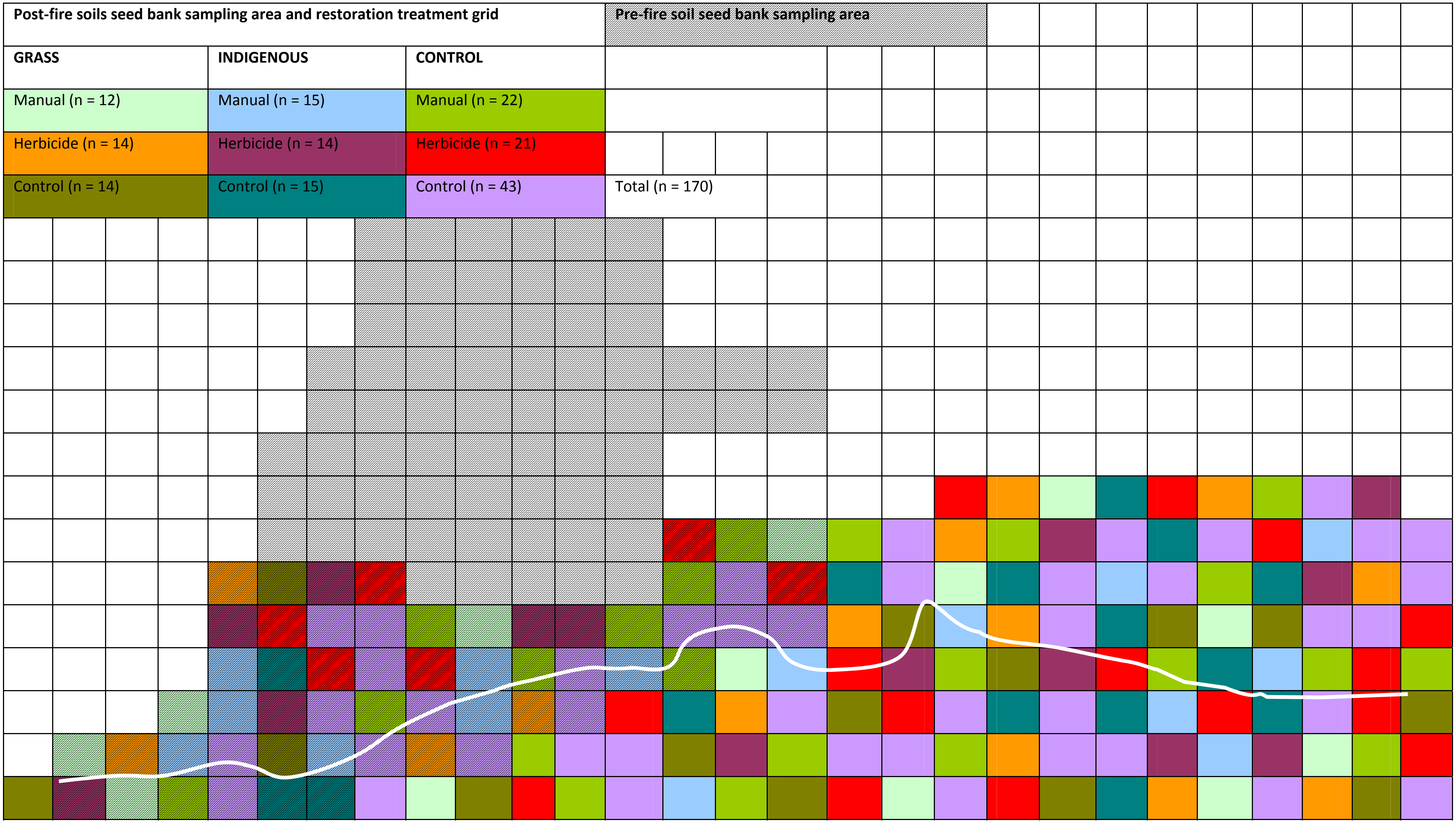


Figure 1.3. A schematic diagram of the study site, indicating the layout of the sampling and treatment blocks. Each block is 6 x 6 m.

2 POTENTIAL FOR RECOVERY BASED ON THE INDIGENOUS SOIL SEED BANK AFTER CLEARING OF INVASIVE ALIEN VEGETATION IN A RIPARIAN ZONE IN THE GRASSY FYNBOS OF THE EASTERN CAPE

2.1 INTRODUCTION

The invasion of indigenous ecosystems by IAPs poses a threat worldwide, with major impacts on ecosystem functioning and biodiversity (Richardson and van Wilgen 2004; Lee *et al.* 2009, Richardson and Rejmánek 2011). In 1998, it was estimated that about 8 % of South Africa had been invaded (Versfeld *et al.* 1998). Riparian ecosystems are especially vulnerable to invasion (Galatowitsch and Richardson 2005; Holmes *et al.* 2005), and in response to the negative impact of invasion on water resources, a government programme, Working for Water, was initiated in 1995 to clear woody alien species from catchment areas.

Implicit in the alien plant removal programme is the assumption that indigenous ecosystems will recover naturally after the removal of invasive species. However, especially in long and heavily invaded systems, vegetation resembling the pre-invasion structure and composition does not recover naturally (Holmes *et al.* 2000, 2005, 2008; Beater *et al.* 2008; Reinecke *et al.* 2008) and these areas are often further degraded through soil erosion and re-invasion (Euston-Brown 2000; Yelenik *et al.* 2004; Beater *et al.* 2008; Witkowski and Garner 2008). One of the factors influencing the recovery of natural vegetation is the nature of the indigenous soil seed bank, as it acts as a reservoir of plant propagules, ensuring persistence, regeneration and recolonisation after disturbance, as well as conserving genetic variability (Bossuyt and Honnay 2008; Auld and Ooi 2008; Wright and Clarke 2009; Li *et al.* 2012). Its persistence can play an important role in facilitating the recovery of indigenous vegetation after the clearance of IAPs (Holmes 2001b; Holmes and Newton 2004; Sakai *et al.* 2005). In densely-invaded ecosystems, there is a rapid reduction in above-ground cover and seed production, and these ecosystems rely heavily on the persistent soil seed bank for recovery (Le Maitre and Midgley 1992; Holmes and Cowling 1997a, b; Keeley 2004). A persistent seed bank remains in the soil for more than one season, and is a phenomenon commonly exhibited by vegetation in areas where the probability of adult survival and reproduction may vary temporally (Kalisz and McPeek 1993), such as in fire-dependent ecosystems.

Fynbos, including riparian fynbos, is adapted to periodic fire events and adaptations for the survival of species during these events also, to a degree, equip fynbos species to survive invasion. During fire events, many individual plants are killed by fire and depend on germination of the seeds stored in the soil or canopy for the regeneration of their populations (Le Maitre and Midgley 1992; van Wilgen and Forsyth 1992; Clemente *et al.* 2007). Species which have life cycles shorter than the fire return interval have persistent soil-stored seeds which are fire-stimulated (van Wilgen and Forsyth 1992). Although most fynbos species are adapted to cope with regular fire, the increased plant biomass in invaded systems can cause extreme temperatures during the fire which can damage the soil and cause soil erosion (Scott 1993). These fires may also kill resprouters and seeds near the soil surface.

A number of studies in South Africa have investigated the soil seed bank in fynbos (Manders 1990; Musil 1991; Pierce and Cowling 1991; Holmes and Cowling 1997a, b), including the effect of alien invasion on the indigenous soil seed bank (Vosse *et al.* 2008). However, only the studies of Manders (1990) and Vosse *et al.* (2008) investigated riparian seed banks. Little is known of riparian seed banks worldwide (Goodson *et al.* 2001; Williams *et al.* 2008; Lu *et al.* 2010; White and Stromberg 2011), and no information is available on the soil seed banks of either riparian or non-riparian grassy fynbos, or on the effects of IAPs on the indigenous soil seed banks in the Eastern Cape. A decline in seed bank density has been recorded for invaded areas (Holmes and Cowling 1997a), generally declining with increasing invasion age. Holmes and Foden (2001) found that a viable soil seed bank is present in invaded areas for up to 30 years, but is impoverished after 40 years under invasion. Thus, there may be an irreversible threshold of good recovery potential for invaded fynbos ecosystems.

2.2 AIMS AND OBJECTIVES

This study aimed to assess the recovery potential of a riparian and adjacent terrestrial fynbos community, based on the soil seed bank composition, in an area that has been densely invaded for approximately 30 years.

2.2.1 Aim

1. Investigate the regeneration potential of riparian grassy fynbos, based on the composition and abundance of the soil seed bank.

2.2.2 Hypothesis

1. The density of seeds in the soil seed bank will be low, due to the invasion period of 30 years and the number of fire cycles (more than two) under invasion.

2.3 MATERIALS AND METHODS

2.3.1 Sampling

In spring 2004 the cleared strip (Section 1.10) was divided into a grid of 6×6 m blocks within different landscape zones, with the corner of each block marked with a 10 mm diameter round bar rod. The blocks were grouped into the following lateral zones: wet bank (WB, n = 21), north-east facing (NF, n = 14) dry bank, south-west facing (SF, n = 9) dry bank, lower hill (LH, n = 28) slope and upper hill (UH, n = 46) slope. Delineation of the zones was based on their distance from the river channel, slope and aspect. The lower and upper hill zones also influence riparian zones, and have therefore been included in this study. For ease of reading the above abbreviations are used to refer to these zones.

In the centre of each block a soil sample was taken during October and November 2004, using a 15×15 cm square metal frame (Holmes 2002). The metal frame was hammered into the soil to a depth of 4 cm after which the soil was carefully removed and placed in paper bags. The frame was then hammered in to a depth of 8 cm and the process repeated. Each sampling point therefore had soil excavated at two layers of 4 cm each.

2.3.2 Soil processing and emergence monitoring

The soil was air dried and sieved though a 2 mm sieve to remove stones and pieces of root and wood, as well as invasive *Acacia* seeds. Any seeds, other than *Acacia* seeds, were returned to the sieved samples. The *Acacia* seeds from each sample were counted and viability tested using the standard tetrazolium chloride test (Association of Official Seed Analysts 1998).

The seedling emergence approach was used to determine the composition and density of the soil-stored propagules. In January 2005, the sieved soil was spread to a depth of 1.5 cm on top of a 7 cm layer of a mix of Hygromix and sterile compost (to prevent the loss of sample soil) in 20 x 15 cm seedling trays and placed randomly in a small nursery. Twenty control trays containing the sterile growth medium were also placed in the nursery to test for seed contamination. The nursery was completely covered in shade cloth (60 % density, green, knitted) and open to ambient weather conditions.

As smoke is a vital germination cue for many fynbos species (Brown 1993; Moreira *et al.* 2010), the samples were exposed to a smoke treatment by covering the nursery with a large PVC plastic sheet, and making a fire in a metal drum in a wheelbarrow. Once the fire was burning strongly, green fynbos branches were placed on the fire, and the wheelbarrow was wheeled inside the nursery. This was maintained for an hour.

The seedling trays were watered by hand every second day during summer, except during very hot berg-wind days, when they were watered every day, and every three days in winter, other than during rain events. Emerging seedlings were identified, recorded and removed from the trays. Date of germination was also recorded. Seedlings which could not be identified were potted into black bags and grown on until a positive identification could take place. Nomenclature followed Goldblatt and Manning (2000). Monitoring continued for 12 months, by which time germination had ceased.

2.3.3 Estimation of soil seed bank

Data were analysed according to species, genus and family to assess floristic composition of emergent species. Species densities and distribution as well as densities of species per habitat type (zone) were calculated. In this chapter data were not analysed according to the two depths, but only total seed density per sample (up to 8 cm depth).

Multivariate analysis was undertaken using the community analysis package, PRIMER (Clarke and Warwick 2001), to assess habitat groupings, by means of non-metric multi-dimensional scaling (MDS). An analysis of similarity (ANOSIM) was undertaken to establish differences between the zones, and a SIMPER analysis was undertaken to assess the contribution of individual species in defining the differences between the zones, using PRIMER (Clarke and Warwick 2001).

2.4 RESULTS

A total of 5 294 seedlings emerged in the nursery, representing 48 species (Appendix A), of which five were alien species (contributing 1 093 seedlings to the overall number).

2.4.1 IAP soil seed bank

Alien species represented three families: Fabaceae (*A. longifolia*), Asteraceae (*Conyza canadensis* and *Pseudognaphalium luteoalbum*) and Solanaceae (*Solanum nigrum* and *S. mauritianum*) (Appendix A). *A. longifolia* seeds within the soil seed bank were most abundant in the WB zone (3 912 ± 1 217 seeds/m^2) and NF dry bank immediately adjacent to the WB zone (4 528 ± 1 075 seeds/m^2). *Acacia* seed densities were lower on the SF dry bank and reduced moving upslope (Figure 2.1). Almost all (99 %) of the *Acacia* seeds were viable.

Two other alien species exhibited densities comparable to the commonest indigenous species, i.e. *S. nigrum* (181 ± 70 seeds/m^2) and *C. canadensis* (98 ± 9 seeds/m^2).

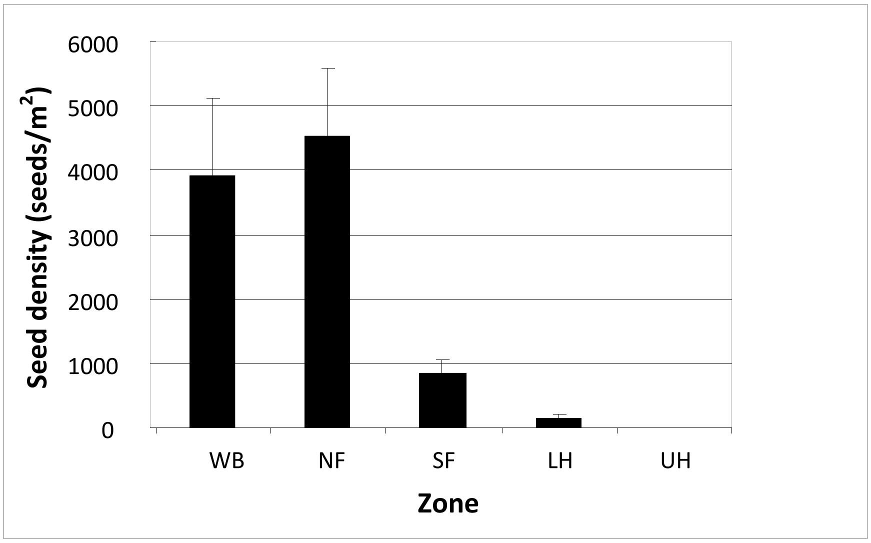


Figure 2.1. Density of *Acacia longifolia* seeds within soil seed bank (mean ± SE) (WB, n = 21; NF, n = 14; SF, n = 9; LH, n = 28; UH, n = 46).

2.4.2 Indigenous soil seed bank

A total of 30 indigenous genera were distributed over 18 families, the families Asteraceae (13 species), Cyperaceae (6 species) and Poaceae (4 species) being the most species-rich (Table 2.1 and Appendix A).

Table 2.1. Percentage proportion of soil seed bank per family

Family	% of indigenous soil seed bank	Family	% of indigenous soil seed bank
Dryopteridaceae	2	Droseraceae	2
Pteridaceae	5	Ericaceae	5
Cyperaceae	14	Fabaceae	2
Hypoxidaceae	2	Gentianaceae	5
Iridaceae	2	Geraniaceae	5
Poaceae	10	Polygalaceae	2
Araliaceae	2	Rosaceae	2
Asteraceae	31	Scrophulariaceae	5
Campanulaceae	2	Thymelaceae	2

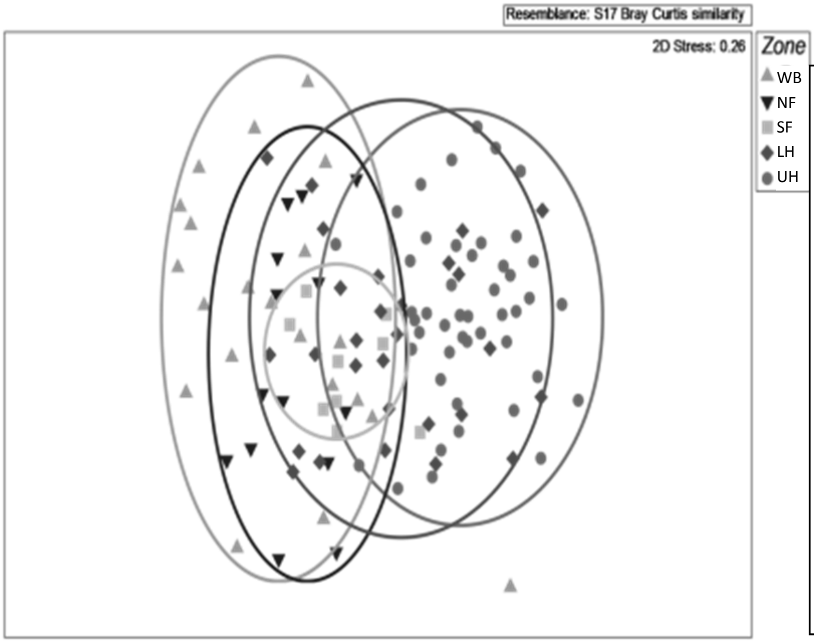
The mean density of indigenous seeds in the persistent soil seed bank, as inferred by the emergence of seedlings, was 1 582 ± 129 seeds/m^2 for the study area. The species exhibiting the highest density was *Senecio rigidus* (Asteraceae), with a mean density of 274 ± 51 seeds/m^2, followed by *Chironia baccifera* (151 ± 22 seeds/m^2) and *Rumohra adiantiformis* (136 ± 70 seeds/m^2). Most of the species identified were forbs (Appendix A). Seed densities for the dominant indigenous species in each zone are given in Table 2.2. Although there is a gradual shift in community composition upslope from the WB zone, *S. rigidus* and *Conyza pinnata* remained dominants within all the zones. The propagule densities ranged between 567 ± 379 propagules/m^2 (*R. adiantiformis*) in the WB zone and 20 ± 13 seeds/m^2 (*Hypoxis argentea*) in the SF dry bank, for the 10 most abundant species. The highest species richness was found in the WB zone and UH slope (both 34), while the lowest species richness was found in the SF dry bank (26).

The highest indigenous seed density was found in the WB zone (2 753 ± 533 seeds/m^2), followed by the NF dry bank (1 435 ± 392 seeds/m^2) and the UH slope (1 400 ± 102 seeds/m^2). Patchiness was greatest in the WB zone and NF dry bank, as evidenced by the high variance, with some samples exhibiting densities of up to 7 688 seeds (sporophytes)/m^2 (*R. adiantiformis*), 4 666 seeds/m^2 (*S. rigidus*) and 3 910 seeds/m^2 (*C. pinnata*). Some alien species also exhibited high densities in patches, e.g. S. *nigrum*, with up to 7 021 seeds/m^2.

The multi-dimensional scaling analysis of species data (excluding alien species) for combined depths (Figure 2.2) indicated that although zones tended to cluster, there is considerable overlap in community composition for some zones. The highest dissimilarity was found between the NF dry bank and UH slope with an r value of 0.659 ($P < 0.005$) and the WB zone and UH slope, with an r value of 0.655 ($P < 0.005$). This pattern remains similar if alien species are included.

Table 2.2. Seed density of the ten most dominant indigenous species for each zone. n = number of samples, D = seed density (mean ± std. error); R = ranking within the zone, F = % frequency (percentage of samples where species was recorded)

SPECIES	WET BANK (n = 21)			NORTH-FACING DRY BANK (n = 14)			SOUTH-FACING DRY BANK (n = 9)			LOWER HILLSLOPE (n = 28)			UPPER HILLSLOPE (n = 46)		
	D	R	F	D	R	F	D	R	F	D	R	F	D	R	F
Rumohra adiantiformis	567±379	1	38	143±99	2	29									
Senecio rigidus	559±237	2	81	321±181	1	93	410±102	1	100	248±43	1	93	120±25	3	70
Conyza pinnata	290±184	3	57	124±58	4	50	173±80	2	78	111±32	4	46	66±11	7	28
Ficinia oligantha	241±112	4	52				35±24	6	33						
Cyperus esculentis	121±48	5	57	76±35	8	43									
Halleria lucida	119±104	6	14	83±55	7	29	25±15	9	33						
Erica caffra	116±53	7	52	48±21	9	50									
Helichrysum sp.	104±35	8	57	111±40	5	79	25±15	8	44						
Helichrysum epapposum	102±37	9	38												
Isolepis cernua	93±27	10	52	89±69	6	29									
Cheilanthes viridis				140±58	3	43	104±62	4	33	162±65	2	36			
Helichrysum petiolare				44±13	10	57	138±47	3	100	52±18	7	43			
Chironia baccifera							44±22	5	44	143±34	3	64	278±44	1	78
Anthospermum herbaceum							35±16	7	44	73±36	6	39	62±15	8	50
Hypoxis argentea							20±13	10	22	41±30	8	18	60±20	9	41
Selago corymbosa										83±35	5	39	160±28	2	72
Erica chamissonis										38±19	9	32	96±28	4	52
Eragrostis obtusa										37±14	10	36	57±18	10	43
Lobelia tomentosa													91±27	5	41
Helichrysum cymosum													80±16	6	61
Total density of zone	**2 753±553**			**1 435±392**			**1 146±163**			**1 217±141**			**1 400±102**		



Zone	r	p
WB & NF	0.016	0.35
WB & SF	0.069	0.77
WB & LH	0.278	0.001
WB & UH	0.655	0.001
NF & SF	0.062	0.18
NF & LH	0.279	0.001
NF & UH	0.659	0.001
SF & LH	0.129	0.92
SF & UH	0.353	0.002
LH & UH	0.195	0.001

Figure 2.2. Multi-dimensional scaling plot of the soil seed bank species for different zones. Analysis of similarity between zones is given on the right of the figure (WB, n = 21; NF, n = 14; SF, n = 9; LH, n = 28; UH, n = 46)

The analysis of dissimilarity indicated that *S. rigidus* and *R. adiantiformis* contribute most in defining the dissimilarity between zones (Table 2.3). In the upslope zones, *C. baccifera* becomes more important in defining the different zones, and *S. nigrum* also influences zone boundaries when aliens are included in analysis.

Table 2.3. Analysis of dissimilarity between different zones, with main indicator species of dissimilarity

Zone	% Dissimilarity (excl. alien)	Indicator Species	% Contri-bution	% Dissimilarity (incl. alien)	Indicator Species	% Contri-bution
R & NF	83	*S. rigidus*	16	78	*S. nigrum**	14
		R. adiantiformis	13		*S. rigidus*	12
R & SF	79	*S. rigidus*	20	78	*S. rigidus*	16
		R. adiantiformis	11			
		C. pinnata	10			
NF & SF	76	*S. rigidus*	22	77	*S. nigrum**	15
		C. viridis	10		*S. rigidus*	15
R & LH	85	*S. rigidus*	15	84	*S. rigidus*	12
		R. adiantiformis	11			
NF & LH	83	*S. rigidus*	15	83	*s. nigrum**	14
		C. viridis	26		*s. rigidus*	10
SF & LH	72	*S. rigidus*	19	71	*S. rigidus*	16

		C. viridis	12		*C. viridis*	10
		C. pinnata	11			
R & UH	89	*S. rigidus*	12	87	*S. rigidus*	10
		R. adiantiformis	10		*R. adiantiformis*	
				87	*S. rigidus*	10
NF & UH	87	*C. baccifera*	12	85	*S. nigrum**	12
SF & UH	79	*S. rigidus*	18	78	*S rigidus*	15
		C. baccifera	12		*C. baccifera*	11
LH & UH	78	*C. baccifera*	13	76	*C. baccifera*	12

* alien species

2.5 DISCUSSION

There is much debate about whether alien-invaded systems can restore successfully from seed banks alone (Bossuyt and Honnay 2008; Marchante *et al.* 2011b). Seed bank densities vary greatly between different ecosystems, making comparisons difficult. Persistent seed banks are generally found in invaded systems, but with reduced seed densities (Holmes and Cowling 1997a; Holmes 2002; Sternberg *et al.* 2003), and these can therefore facilitate recovery in cleared areas. A recent review by Bossuyt and Honnay (2008) concluded that spontaneous restoration was not possible at sites which have been degraded for more than five years, except in heathlands, where long-lived persistent seed banks are found, although they did not distinguish between Mediterranean and other types of heathlands. Comparison of soil seed bank densities between different ecosystems can be problematic, due to different vegetation dynamics.

For example, Alvarez *et al.* (2006) found very high seed densities of 286 886 seeds/m^2 in mesic grasslands in Chile, which can mostly be attributed to one species of sedge. Diggory and Parker (2011) found seed densities of up to 151 696 seeds/m^2 in restored tidal marshes, but with great variance between sites. Fagan *et al.* (2010), in a survey of chronosequences in calcareous grasslands, found an average density of 13 606 seeds/m^2 in restored sites and 7 319/m^2 reference sites.

2.5.1 Assessment of the soil seed bank

The assessment of soil seed banks is complicated by shortcomings in the methodology that is used. The seedling emergence method is generally the preferred method because of easy identification of emerging seedlings and presumes that the number of seedlings detected equals the number of viable seeds (Baskin and Baskin 1998; Sakai *et al.* 2005). However, this method can underestimate the true seed bank, as vital germination cues, e.g. a heat pulse and fluctuation of soil temperatures may be absent or seeds may be dormant (Fenner and Thompson 2005; Kulkarni *et al.* 2007; Penfield and King, 2009; Wright and Clarke 2009), as could have been the case in this study. However, some of the larger-seeded species such as *Psoralea pinnata* which need a heat pulse, would probably have been found during the sieving process (only two *P. pinnata* seeds were found). Small-seeded species, e.g. *Metalasia,* may also require a fire-related germination cue other than smoke and may be underrepresented (Holmes and Cowling 1997a). The issues of dormancy and germination cues are further addressed in Chapter 3. Some studies have also found a higher recruitment from soil samples germinated in the nursery compared to field conditions (Holmes and Cowling 1997a; Holmes and Foden 2001). For the purposes of this study, seedlings or emergents are used as the indicators of the viable soil seed bank.

Soil seed banks reflect the composition of past vegetation, but at any given time present a snapshot of a dynamic situation. The balance and variability of seed production, dispersal, predation, mortality and germination will affect the spatial distribution and size of the seed bank of a species at a local scale (Sakai *et al.* 2005; Clemente *et al.* 2007; Williams *et al.* 2008). Seasonal variability may be responsible for differences in the soil seed bank between different years (Martin 1966; Holmes and Cowling 1997b). In riparian zones soil seed bank dynamics are also affected by fluvial processes such as scouring and hydrochory, which varies according to the lateral gradients (Williams *et al.* 2008). Lateral zonation of density and composition was very evident in this study. The spatial distribution of seeds in the soil is notoriously patchy, as was also evidenced during this study, in common with the findings of Strydom *et al.* (2012) in *Acacia* invaded systems in the Western Cape. White and Stromberg (2011) also found uneven distributions of seed in the soil seed bank, and concluded that local-scale dispersal processes shape the soil seed bank, rather than regional processes such as longitudinal dispersal along the river.

2.5.2 Seed bank composition

The viable invasive *Acacia* soil seed bank in the study area is much lower (max. 4 500 seeds/m^2) than that reported in studies in the Western Cape, where between 4 000–46 000 seeds/m^2 were measured (Holmes *et al.* 1987). This is probably due to the successful introduction of a biological control agent in 1982 (the gall wasp *Trichilogaster acaciaelongifolia*) (Dennil 1985, Impson *et al.* 2008, van Wilgen *et al.* 2012).

Nonetheless, this alien plant seed density is still far higher than that of any of the indigenous species in this area, and presents management challenges to the eradication of *Acacia* species (Milton and Hall 1981; Richardson and Kluge 2008; Le Maitre *et al.* 2011; Strydom *et al.* 2012), as seeds will germinate after clearing or fire, requiring timeous follow-up treatments to eliminate the invasive regrowth.

Forty-three indigenous species were represented in the soil seed bank of the study area (Appendix A). A comparison with a previous vegetation study in the region (Richardson *et al.* 1984), reveals that this represents approximately 30 % of the full post-fire species complement (which should correlate better with the soil seed bank than mature vegetation). Thus, many taxa are not represented in the soil seed bank. Although the soil seed bank will not represent the full species complement of the above-ground vegetation, it has been found that long-invaded fynbos (two or more fire cycles of dense invasion) in the Western Cape experiences a loss of about 70 % of species from the standing vegetation (Holmes and Cowling 1997b), comparable to the balance of this figure. This is also commonly found in other systems (Bossuyt and Honnay 2008; Wright and Clarke 2009; Fagan *et al.* 2010). Holmes (2002) found a significant decrease in seed bank species richness with increasing age of invasion in the Western Cape.

Although viable persistent seed banks have been found in long-invaded sites (two or more fire cycles; more than 25 years), with representatives of all major fynbos growth forms, alien invasion results in a decrease in species richness, diversity and abundance (Holmes and Cowling 1997a, b). The shift in community composition and loss of some taxa becomes more noticeable with an increase in invasion time. Non-sprouting serotinous and ericoid shrubs are readily outcompeted under a closed *Acacia* canopy, while shrubs with bird-dispersed seeds are favoured (Holmes and Cowling 1997a, b). One bird-dispersed species, *H. lucida*, which is common in both fynbos and forests, was found in this study and it is likely that this species persisted under the closed *Acacia* canopy.

At this study site, the family Asteraceae dominated the soil seed bank, with six genera and 13 species (Table 2.1 and Appendix A). This is similar to the findings of Marchante *et al.* (2011b) of *A. longifolia*-invaded dunes in Portugal. The genus *Helichrysum* was the best represented, and the species *S. rigidus* most abundant, while *C. pinnata* also exhibited a high abundance. This is similar to the findings of Holmes and Cowling (1997a), where annuals and short-lived perennials dominate the soil seed banks at long-invaded fynbos sites on the Cape Peninsula. Holmes and Cowling (1997a) also found that long-lived obligate seeders, especially ericoid shrubs, dominate the soil seed bank in long-invaded sites (Holmes 2002), and in this study, the two *Erica* species were also found within the top 10 dominant species within the soil seed bank.

There was only one indigenous species (*P. pinnata*) represented in the family Fabaceae (Appendix A). This family generally has long-lived and persistent seed in the soil seed bank, and more species and higher densities would have been expected. It is likely that members of the Fabaceae germinated during the last heat pulse (1996), and then became suppressed under the alien canopy, preventing further seed set. This is discussed further in Chapter 3.

2.5.3 Seed bank density

The total indigenous seed density (1 582 seeds/m^2) is comparable to those found in winter rainfall areas of the fynbos biome, e.g. Holmes and Cowling (1997a) who found a range of 1

100-1 900 seeds/m^2 in uninvaded areas and Holmes (2002) with a range of <400 to >1 200 seeds/m^2. This also compares well with the seed density values of 1 754 seeds/m^2 from cleared conifer plantations in Japan (Sakai *et al.* 2005) and species seed densities of obligate seeders of 640–4 388 seeds/m^2 and 102–3 061 seeds/m^2 (Clemente *et al.* 2007) and 1 050- 1 802 seeds/m^2 in the Mediterranean basin (Valbuena and Trabaud 2001). Miller and Cummins (2003) have found seed densities of 600-64 000 seeds/m^2 in Scottish heathlands far exceeding the densities found in this study. However, seed densities are problematic to compare, as methodology differs (e.g. sampling depth). The timing of sampling and application of germination cues can also yield different results (Ooi 2010; Thomas *et al.* 2010; Moreno *et al.* 2011) (Chapter 3).

The highest species density in any zone was for *R. adiantiformis* with 567 spores/m^2, followed by *S. rigidus* (a bi-annual) with 559 seeds/m^2, both in the WB zone. The production of high volumes of seeds of annual species is common in Mediterranean climate vegetation (Marchante *et al.* 2011b). However, there is a high spatial heterogeneity and typically high variance (Clemente *et al.* 2007), with some samples (*S. rigidus*) exhibiting densities of up to 4 666 seeds/m^2. Although a high variance is common in soil seed bank studies, a larger spread of smaller samples throughout the area may have resulted in a smaller variance, as a relatively low number (118) of samples were taken. *S. rigidus* and *C. pinnata* were the only species, within the ten most dominant species, which occurred in all the zones (Table 2.2). Frequencies of occurrence were highest for *S. rigidus*, ranging from 70–100 %.

These relatively high densities are surprising, given the length of invasion, and compared to the work undertaken by Holmes and Cowling (1997a), where significant reductions in the soil seed bank were found under invasion. This suggests that either species have very long-lived seeds, managed to set seed between fire cycles or propagules were dispersed into the site during invasion; either by floods, wind or animals. Long-distance dispersal of propagules in Mediterranean systems is rare (Brits 1987; Le Maitre and Midgley 1992; Morzaria-Luna and Zedler 2007), especially of obligate seeding species (Keeley 1992). Wind is not likely to disperse seeds within a dense adult stand of wattle, although it is possible for the very small Asteraceous wind-dispersed seeds or fern spores, and riparian corridors can act as conduits for small wind-dispersed seeds (Nathan *et al.* 2002, Richardson *et al.* 2007). In ferns the highest density of spores usually occurs near mother plants (Penrod and McCormick 1996, Flinn 2007), but long-distance dispersal is considered an important component of fern demography (Karst *et al.* 2005)and spores have been recorded to be wind-dispersed up to 30 km from mother populations (Ramirez-Trejo *et al.* 2004). Ferns produce vast numbers of spores and Flinn (2007) recorded up to 60 000 spores deposited at 10 m distance from mother plants and more than 4 000 spores/m^2 in the spore bank (seeds/m^2). It is unlikely that the heavier seeds of some species, e.g. *Chironia* and *Halleria*, which occurred in relatively higher densities, were brought in by wind. The seeds of these species were also found above the flood line, and therefore could not have been introduced through flooding, although the seeds of *Halleria* could have been introduced by birds.

The possibility of seed set in between invasions cycles will depend on the particular life history of the species (Corbin and D'Antonio 2010). Van Wilgen and Forsyth (1992), in a study in the Swartboskloof, found that 70 % of sprouting species matured within one year, enabling seed set. This is possible for a species such as *Halleria*, which resprouts rapidly after fire, but assumes that it survived the invasion cycle as well as fire under invasion. Van Wilgen and Forsyth (1992) also found that 86 % of all species flowered within the first year, and perhaps the species found in the seed bank managed to set seed between fire cycles and after the 2000 clearance. This is therefore a possibility, although regrowth of alien plants is fast and there was unlikely to have been a long period before a closed alien canopy re-established. Many of the species, e.g. *Helichrysum* spp. and the sedges, are relatively fast-growing and mature quickly. Slowly maturing species, including obligate seeders such as Ericaceae, would be unlikely to set seed before being suppressed by invading *Acacia*. Their presence in the soil seed bank, especially in the deeper layers, therefore indicates long-term persistence (Chapter 3). The last explanation is that the seeds of these species are very persistent and retain viability for more than 30 years. Longevity is reflected in vertical distribution of seeds in the soil (Holmes and Newton 2004) and evidence indicates that more deeply buried seeds are older than seeds closer to the surface. Very little is known about the longevity of most seeds, and no information was available for seeds of these species, although Holmes and Newton (2004) have investigated the longevity of the seeds of selected species in Western Cape fynbos. They found that the Fabaceae, *Pelargonium*, and the nut-fruited Proteaceae have long-term persistent seed banks, as well as the nut-fruited Restionaceae. *Pseudopentameris*, *Passerina*, *Elegia* and *Restio, Erica baccans*, *Metalasia muricata* and *Roella ciliata* also have potentially long-term persistent seed (Holmes and Cowling 1997a; Holmes 2002; Holmes and Newton 2004).

There are no data available on the soil seed bank of uninvaded fynbos areas in grassy fynbos, which presents a shortcoming in assessing whether the post-clearing recovery potential based on the soil seed bank of these invaded areas is sufficient to initiate recovery towards a functional system. The review by Turnbull *et al.* (2000) and other studies (Moles and Westoby 2002; Seabloom *et al.* 2003; Valkó *et al.* 2011) also suggests that early successional communities are often seed-limited and therefore contain unoccupied microsites which are available for the establishment of IAPs. Moles and Westoby (2002) also found that seed addition is often required for large seeded rather than small seeded species, as small seeds are more likely to be dispersed to establishment sites, which appeared to be the case in this study, e.g. Asteraceae and Cyperaceae.

Other studies indicate that seed availability is not the limiting factor after severe fires in Mediterranean systems, but that changes in soil properties could substantially retard establishment of seedlings (Pausas *et al.* 2008). The post-fire and/or management conditions in the field are thus likely to affect establishment and survival of seedlings, e.g. changes in soil structure and chemistry after a severe fire may be unfavourable to the establishment of some indigenous species (Madrigal *et al.* 2010). In-field post-management recovery should therefore also be monitored to assess the true potential of the soil seed bank in restoring an alien-invaded riparian system (Chapter 5).

2.6 CONCLUSION

This study revealed that the soil seed bank of a WB and adjacent hill slope area of grassy fynbos which had been invaded for approximately 30 years, interspersed with brief periods of clearing, still has a diverse and apparently viable soil seed bank with relatively high seed densities. Species from the family Asteraceae such as *Senecio* sp., *Conyza* sp. and *Helichrysum* spp. are well represented, as well as graminoids in the WB zone. Species representing some guilds are missing, e.g. serotinous species from the genera *Leucadendron* and *Protea*, and few geophytes are present in the soil seed bank, although ericoid shrubs are well represented. It would appear from this that the soil seed bank would be adequate to enable indigenous vegetation to re-establish after clearing, possibly with the addition of some missing guilds and species to enhance vegetation structure, provided that post-clearing follow-up treatments do not prevent or hinder the establishment of these indigenous species. These data need to be compared with the soil seed bank of uninvaded areas, as well as with the recovery in the field, especially after further management interventions (Chapter 4), to evaluate the factors affecting actual in-field recovery.

3 THE IMPACT OF FIRE AS A MANAGEMENT TOOL ON A RIPARIAN SOIL SEED BANK

3.1 INTRODUCTION

3.1.1 Invasion in South Africa

The spread of IAPs is a global concern (Vitousek *et al.* 1997; Thuiller 2007; Richardson and Rejmánek 2011), and poses a serious threat to ecosystem functioning (Lee *et al.* 2009; Vilá *et al.* 2010; Crous *et al.* 2012). Alien invasive species represent the second most important threat to biodiversity after direct habitat destruction (Holmes *et al.* 2000). Approximately 10 million ha of South Africa and Lesotho's land surface area has been invaded (Versfeld *et al.* 1998). Riparian zones are particularly prone to invasion by woody alien species, in part because they are naturally disturbance-mediated ecosystems. Cullis *et al.* (2007) estimated that riparian invasions in South Africa, if compressed to close-stand invasions, will comprise 33 % of the total river length.

In South Africa the most problematic riparian woody plant invaders are from the Australian genera *Acacia* and *Eucalyptus*, as well as the Mexican *Prosopis.* These have significantly degraded and transformed ecosystem functioning, integrity and services (Richardson and van Wilgen 2004; Holmes *et al.* 2005). One of the most severe impacts of invasion by woody IAPs in South Africa is the reduction of water yield (Versfeld *et al.* 1998; Le Maitre *et al.* 2000). Other impacts include altered soil nutrients (Yelenik *et al.* 2004; Marchante *et al.* 2008a, b, 2009; Drake 2011; Tye and Drake 2011), erosion and loss of top-soil, siltation of dams, increased fire risks and damage and altered fire regimes, all of which intensify as invasions spread and densify with time (Holmes and Cowling 1997b; Galatowitsch and Richardson 2005; Richardson *et al.* 2007). These, and other impacts, have cost South Africa billions of rands (van Wilgen *et al.* 1997, 2001) and continue to do so.

3.1.2 Management of invasive alien plants

In response to the threats caused by IAPs, the South African government launched a countrywide alien plant clearing programme, Working for Water, in 1995. This programme was funded through poverty relief money to create employment, as well as increasing water security and maintaining biodiversity. Initially, it was expected that areas would self-restore after clearing, but in old- or densely-infested areas this is not always the case (CSIR 2000; Holmes *et al.* 2005, 2008; Blanchard and Holmes 2008; Reinecke *et al.* 2008), and many of these areas have remained degraded or have required numerous follow-ups to eliminate the IAPs. A recent analysis by Marais and Wannenburgh (2008) found that only 7 % of closed-stand riparian invasions have been cleared after 15 years of WfW clearing operations. The degree of recovery of cleared systems is critical to the long-term success of WfW (Holmes *et al.* 2005), and the establishment of functional vegetation cover after clearing is one of the most important factors which will prevent re-invasion or secondary invasions and prevent or decrease the need for follow-ups (D'Antonio and Chambers 2006; Holmes *et al.* 2008).

The success of IAP clearance projects are mostly measured by the hectares of IAPs removed and not by the recovery of indigenous vegetation and a functional ecosystem (CSIR 2000; Holmes *et al.* 2008). This has resulted in clearing often being implemented with little emphasis on minimising the impacts on the residual indigenous vegetation and ecosystem. It is imperative that IAP control and restoration be integrated (CSIR 2000) and that IAP clearing methods do not compromise, but rather facilitate the recovery of natural vegetation and restore ecosystem functions (CSIR 2000). This is especially so in riparian systems, which are sensitive and include many critically threatened habitats (Nel *et al.* 2008), and the management of which have significant bearing on water yield and quality.

Recovery, and hence the need for restoration, depends to a large degree on the method of clearing and follow-up (Simmons 2005; Blanchard and Holmes 2008; Reid *et al.* 2009; te Beest *et al.* 2011). The three options for clearing woody IAPs are the following:

1. to kill standing (with or without the use of fire)
2. felling and removing the biomass, and

3. felling and burning the biomass. Felled trees are often stacked to provide access for follow-up treatments, especially when burning is not an option.

Burning has formed an integral part of WfW control strategies (CSIR 2000; van Wilgen *et al.* 2011) for the following reasons:

- Burning can kill seedlings and seeds of IAPs, especially in the case of *Pinus* or *Hakea* (Holmes *et al.* 1987; van Wilgen *et al.* 1992; Pieterse and Boucher 1997; CSIR 2000).
- Burning can trigger the mass germination of *Acacia* seeds, which can then be eliminated during follow-ups (Milton and Hall 1981; Richardson and Kluge 2008).
- Leaf litter and nutrients which constrain recovery can be removed through the use of fire (Richardson and Kluge 2008; Marchante *et al.* 2011b).
- Follow-up operations are easier when the vast volumes of biomass generated through the felling of invasive species (see plates 1-4) are removed through burning (Blanchard and Holmes 2008).
- The regeneration of many indigenous species in fynbos is stimulated through fires (Le Maitre and Midgley 1992; van Wilgen and Forsyth 1992) and is necessary for maintaining diversity, as a large proportion of species are fire-dependent and only germinates after fire (Keeley *et al.* 1985; Bond and van Wilgen 1996; Keeley and Fotheringham 2001).
- Felled trees and biomass pose a risk if left in the flood-line (see plates 1-4), as the debris can cause log jams (Pretorius *et al.* 2008) or scour the rivers and cause damage to downstream infrastructure. These should be removed to above the flood-line, but many invaded tributaries, especially in upper water catchment areas, are narrow, steep-sided or inaccessible, and it is impossible to remove the felled biomass. Often the only solution is therefore to burn (CSIR 2000; Holmes *et al.* 2000).
- Less time is spent stacking wood outside the flood-line when it is burnt, and is therefore less costly (Clearing norms, Malan, pers. comm.; WIMS and APO norms and standards, http://sites.google.com/site/wfwplanning/implementation).

Despite the fact that many fynbos species regenerate after fire, concerns have been raised about the effect of burning as part of the clearing strategy on the regeneration of indigenous vegetation, its impact on indigenous soil seed banks as well as impacts on soil properties (Yelenik *et al.* 2004; Holmes *et al.* 2008; Tye and Drake 2011). Fynbos is a fire-prone and fire-driven system (van Wilgen and Forsyth 1992; Bond and van Wilgen 1996), and fire is therefore a natural and regular disturbance in fynbos. However, fuel loads increase dramatically after invasion by woody IAPs (van Wilgen and Richardson 1985), up to 300 % (Versfeld and van Wilgen 1986) and clearance generates large volumes of biomass resulting in fires of high severity which can damage ecosystem function (see Plates 1-8). Heavy fuel loads concentrated near the soil surface result in unnaturally intense fires (see Plates 5-8) (Richardson and van Wilgen 1986; Holmes and Cowling 1997b), which can eliminate remnant indigenous vegetation by killing resprouters and remaining indigenous seeds (van Wilgen and Richardson 1985; Bond and van Wilgen 1996; Cilliers *et al.* 2004). This could reduce species richness and could also result in soil erosion (Richardson and van Wilgen 1986; Scott and van Wyk 1992) and thereby severely retard or compromise ecosystem rehabilitation.

3.1.3 Fire in riparian systems

Not much attention has been given to the impact of fire on riparian zones in South Africa (Holmes *et al.* 2005). These zones differ from the adjacent upland areas in geomorphology, hydrology, vegetative composition and structure, microclimate and fuel characteristics (Dwire and Kauffman 2003), all of which will influence the fire environment, fire regimes and fire properties like severity, frequency, behaviour and extent in any given riparian area (Reinecke *et al.* 2008). There is evidence that fires occur less frequently in riparian areas than adjacent upland sites (Dwire and Kauffmann 2003; White and Stromberg 2011). However, due to the higher productivity of riparian areas compared to upland sites as well as longer fire return intervals, higher fuel loads accumulate which increases the vulnerability of riparian areas to severe and intense fires during dry conditions (Dwire and Kaufmann 2003). The channels and wet banks in riparian areas can also limit the continuity of fires.

Riparian vegetation that is exposed to fires often consists of a mosaic of plant communities in different successional stages, displaying varying ages, structures and compositions (Naiman *et al.* 1993). Fires will therefore burn in a patchy manner preventing large areas burning at the same time and limiting large-scale fire impacts, such as the loss of soil propagules, at any given time.

3.1.4 Soil propagules

Soil propagules are important for initiating recovery after disturbance as long-distance dispersal of propagules in fynbos is rare (Brits 1987; Le Maitre and Midgley 1992) and regeneration from persistent soil-stored seed banks is an important adaptation enabling fynbos species to survive fires (Holmes and Newton 2004; Auld and Denham 2006; Penman *et al.* 2008; Thomas *et al.* 2010). In fynbos, soil seed banks can persist for decades after dense alien invasion (Holmes 2002), and Holmes and Cowling (1997a) have found over 75 % of fynbos species with dormant soil-stored seed banks persisting at long-invaded (30 years) *Acacia saligna* sites even after two fire cycles. The burning component of the clearing process, however, can irreversibly damage the soil seed bank by reducing seed densities and eliminating some species (Richardson and Kluge 2008).The loss of a soil seed bank may present a barrier to recovery, but it is still not known how important seeds are compared to other vegetative propagules in the colonisation of disturbed sites in fynbos, specifically in grassy fynbos, which has a smaller component of obligate seeders and a higher component of resprouting species (Le Maitre and Midgley 1992; Bond and Keeley 2005). The importance of soil-stored seed banks in the regeneration and vegetation dynamics of riparian zones is also not well understood (Holmes *et al.* 2005). Only two other studies have focussed on riparian soil seed banks in South African fynbos (Manders 1990; Vosse *et al.* 2008), and none in grassy fynbos.

Although there is evidence that slash and burn retards re-establishment of indigenous riparian species, the degree to which this takes place and the impact of fire on the soil seed bank is unclear (Holmes *et al.* 2005; Richardson and Kluge 2008). The presence of a viable soil seed bank confers recovery potential on an alien-invaded system, but an understanding of the impacts of the clearing treatment, i.e. fell-and-burn, is needed to ascertain whether riparian zones can return to functional systems after clearing without additional intervention. Knowledge of the impact of fire on riparian soil seed banks will also aid decision makers on whether the higher costs of felling and removing is justified in terms of improved recovery of riparian systems.

This study is the first to assess the impact of fell-and-burn on the soil seed banks of riparian systems in the grassy fynbos, with the aim of providing recommendations to managers.

3.1.5 Fire and assessing fire impacts

To assess the impact of fell-and-burn on the soil seed bank, the fire intensity or severity has to be quantified, or more specifically, the extent to which this affects the soil seed bank. Fire intensity is defined as the heat released per unit time per unit area (Trollope 1984; Keeley 2009), while fire severity: "refers to the magnitude of fire effects on biological and physical components of ecosystems (Baker 2009), or "the degree of environmental change caused by fire" (Key and Benson 2006). It is notoriously difficult to measure or quantify fire intensity in a non-homogenous landscape, as it is affected by micro site and climatic variables. The most common measure of fire intensity is Byram's fire-line intensity equation (Byram 1959), which uses the parameters heat yield, fuel mass and rate of spread. Fire intensities can vary from 10 to more than 1 000 kW/m (Baker 2009).

Fire intensity equations and models have been found to yield inaccurate results when simulating high-intensity fires (van Wilgen and Richardson 1985) and Breytenbach (1989) suggests that models may underestimate fire intensity from felled stands as well as their biological impacts. Other authors (Bond *et al.* 1990; Moreno and Oechel 1991; Bradstock and Auld 1995) have reported both positive and negative relationships between Byram's fire intensity or other indices of fire intensity and field responses, such as germination. Many fire models and equations deal with above-ground fire behaviour and ecological responses such as topkill of stems and branches (Trollope *et al.* 2002), while the effect of the fire on the soil (and soil propagules) at any given location is dependent on many variables and is difficult to predict, especially with so few studies. Remote sensing has also been used in more recent studies to assess fire severity and predict post-fire recovery (Lentile *et al.* 2006; Roy *et al.* 2010).

3.1.6 Fire and soil heating

Bradstock and Auld (1995) found no relationship between Byram's measure of fire intensity and the maximum temperature change or duration of heating at the soil surface or in the upper soil layer. Nor was there a significant relationship between rate of spread and maximum temperature change in the upper soil profile. There was a relationship between fine fuel consumption on the ground and an increase in temperature. Below five cm depth, they found a relationship between a combination of rate of spread and fuel in predicting temperature change in the soil. In all cases temperatures increased with increased fuel consumption, with the duration of temperature change in the upper layer related to fine fuel consumption and to coarse fuel consumption in the deeper layers of soil (Bradstock and Auld 1995).

Soil temperatures are related to duration of heating at the soil surface (Bradstock and Auld 1995) which depends on the residence time of flaming combustion. They found that higher soil temperatures were reached under slow-moving fires with rates of spread less than 0.03 m/s and that variability in maximum temperature change in the soil was highest under fast moving fires. This is in contrast with Byram's fire-line intensity equation, which predicts increased intensity with faster-moving fires. Van Wilgen and Richardson (1985) also found that the rate of spread as an indicator of fire severity not to be reliable and found lower rates of spread in alien-invaded, densely packed fuel beds with higher fire severities, compared to uninvaded fynbos. Trollope *et al.* (2002) also found that slower burning back fires generated higher temperatures at ground level than faster moving front fires. Clark (2001) and Moreno and Oechel (1991) found higher heat penetration with longer duration into the soil under coarse fuels or slow moving fires.

While ecosystem response is related to the fire intensity (Keeley and Bond 1997; Bárcenas-Moreno and Bååth 2009), it is very difficult to relate fire intensity directly to its ecological effects (Bond and van Wilgen 1996). Highly variable localised severity effects are often observed (Pietikäinen *et al.* 2000) due to variable distribution of the fuel as well as inherent landscape heterogeneity. Variations in fire events can completely override fire frequency or fire intervals with less predictable ecosystem responses, especially in woody vegetation with heterogeneous fuels (Bond and van Wilgen 1996).

Determining how much heat is transmitted into the soil for a given fire intensity is equally difficult (Hartford and Frandsen 1992; Choromanska and DeLuca 2002). Heat generated during a fire has significant effects on the soil as well as post-fire recovery, depending on the temperature reached in the soil and the duration thereof (Doerr *et al.* 2004). The knowledge of what soil temperature is reached is important in evaluating post-fire fertility and physical properties as well as seed bank status as, ultimately, the temperature experienced by the seeds in the soil during a fire event determines whether these seeds survive and germinate (Moreno and Oechel 1991; Bradstock and Auld 1995). Biological disruptions normally start in the 40-70 ^{o}C range while microbes are affected between 50-120 ^{o}C (Neary *et al.* 1999; Korb *et al.* 2004). Dormancy of some seeds may only be broken if temperatures exceed 90 ^{o}C (Bradstock and Auld 1995) while other seeds are killed at lower temperatures. Retrospective methods of determining soil temperatures often have a large margin of error (Doerr *et al.* 2004). Some methods, for example using ash colour as an indicator or the remains of ground fuel (Moreno and Oechel 1989), have not proved that successful.

3.1.7 Heat and soil moisture

Soil properties affect the transmission of heat through the soil column as well as the maximum temperature. Temperature impacts depend on soil type, moisture and oxygen availability during the heating process in combination with the actual temperature reached during the heating process (Pietikäinen *et al.* 2000). The role that soil moisture plays in ameliorating the impact of severe fires is not that clear-cut. Heat conducts better in moist soils and heat can therefore penetrate deeper (deBano *et al.* 2000b). However, soil temperatures will remain at a maximum of 100 ^{o}C while there is still moisture in the soil (Pietikäinen *et al.* 2000; Behenna *et al.* 2008), thus creating a heat buffer, but the moist heat or “steam” that is created can have a more severe impact at lower temperatures than dry heat. After the soil moisture evaporates, temperatures rise rapidly. The duration of exposure to high temperatures is also very important and the interaction between temperature and duration is complex. Heating also has a greater effect on moist soils than dry soils, due to the action of peroxides (Pietikäinen *et al.* 2000). It is difficult to extrapolate results from one study to another due to the variability of ecosystems and their response to fire intensity and severity (Bárcenas-Moreno and Bååth 2009). In addition to this it is often difficult to distinguish the real cause of changes in the soil from several interacting, potentially confounding effects.

3.2 AIMS AND OBJECTIVES

This study sought to quantify the impact of the burning of slash piles on the soil seed bank in a riparian zone in grassy fynbos. The extremely patchy distribution of fuels with high volumes concentrated in some areas and other areas being devoid of fuel due to the stacking of the slash, will result in small-scale but extreme variations in fire severity and heat transmitted into the soil, especially where coarser fuels, i.e. logs, smoulder for a long time and the soils are exposed to glowing combustion, which can have severe effects on the establishment of plants (Madrigal *et al.* 2010). As a result the approach was to attempt to quantify temperatures reached at various depths in the soil under different fuel loads and the impacts that this would have, rather than trying to determine fire intensity at the landscape scale, which would not yield accurate data on highly varied and localised impacts.

3.2.1 Aims

1. Investigate the change in soil temperatures during a controlled fire as part of IAP management.
2. Investigate the effect of a controlled management fire on the soil seed bank in riparian grassy fynbos by comparing the pre- and post-fire soil.
3. Investigate the effect of fire in the soil profile and across lateral zones.

3.2.2 Hypotheses

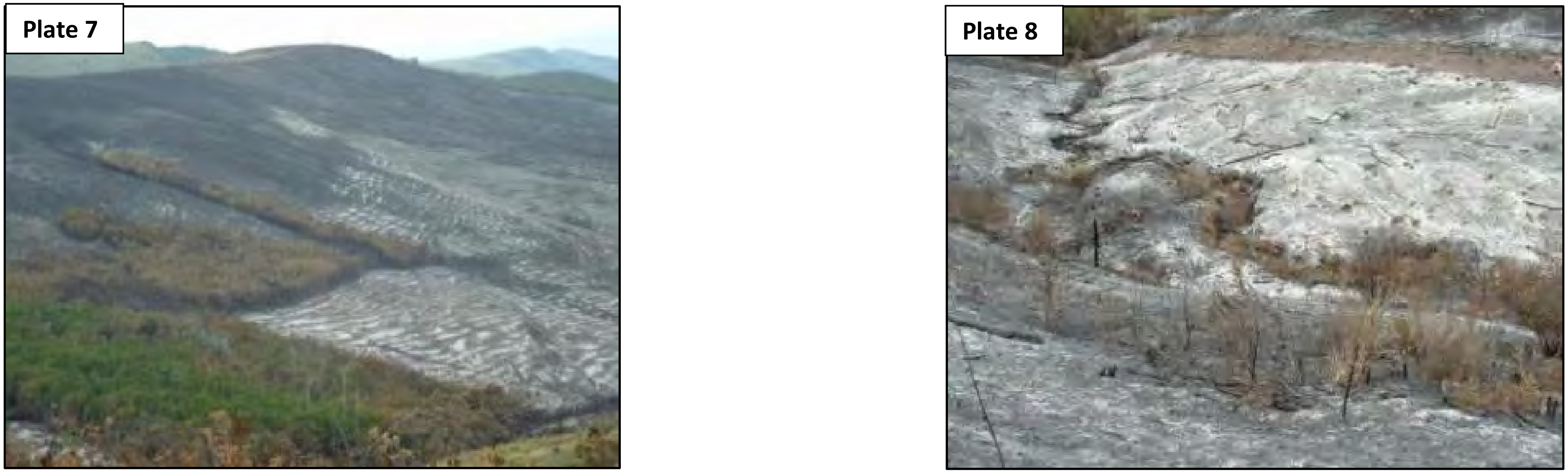
1. High (and lethal) soil temperatures will be experienced during a controlled burn of an IAP-infested area cleared of IAPs.
2. Soil temperatures will be higher under higher slash stacks than low stacks.
3. The post-fire density of seeds in the soil seed bank will be lower than the pre-fire seed density in the soil seed bank.
4. The above effects will be more pronounced in the upper soil layer, compared to deeper layers.
5. The composition of the soil seed bank will be altered due to the fire.
6. The percentage contribution to the soil seed bank of various guilds will be altered after the fire, compared to the pre-fire soil seed bank.

3.3 METHODS

3.3.1 Fire treatment

On 23 November 2005 a prescribed burn was implemented on the site (see Plates 5-8). A five metre wide firebreak was created around the perimeter of the site and the local municipality and WfW teams assisted with the burn. The site was burned ten days after a heavy rainfall event (58.4 mm). The fire was started at 10h54 at the top of the site and burned steadily downhill until 13h34 when it jumped the fire break. The research team had to evacuate the monitoring site and had to abandon some of the environmental monitoring equipment (see below). This meant a loss of data for the time between 13h34 and 18h00, when we could return to the site.

Plates 5-6. Fire treatment on 23 November 2005



Plates 7-8. Study site shortly after fire, 24 November 2005

3.3.2 Environmental variables during fire

Wind speed, temperature and relative humidity were monitored before and during the fire, until 13h30, when the site had to abandoned.

3.3.3 Fire intensity and impacts on soil

Thirty-nine randomly distributed soil samples, ranging between 140 and 190 g, were taken on the morning before the fire from the upper 5 cm layer, and sealed in polyethylene ziplock bags. These were then taken to the laboratory, weighed, and oven-dried at 105^{o} C for 48 hours and re-weighed to obtain soil moisture.

Slash piles (of IAP felled wood stacks) were classified into three categories according to height: low (< 0.5 m high), medium (0.5-1 m in height) and high (> 1 m). The location and size of brush in each plot was also recorded. Pre-fire fuel samples were taken at five locations, by cutting a 50 cm x 50 cm block into a slash pile of known dimensions, bagging the wood and returning this to the laboratory to determine the fuel load. However, the personnel at the storage facility discarded these, and fuel properties could not be quantified or correlated with slash pile classes. However, Holmes (2001a) has quantified the fuel load for sites with felled *Acacia* trees with a known fuel bed depth, and this value (6 326 g/m^2 for fuel bed depth of 0.53 m) was used for the purposes of this study.

An attempt was made to measure the rate of spread and flame height by using fixed standards, consisting of 12 mm roundbar rods. However, the monitoring of these had to be abandoned when the fire jumped the firebreak, but a chronosequence of photographs was taken during the fire, and since the dimensions of the burned area was known, these were used to determine rate of spread.

Fire intensity was calculated using Byram's formula (1959) for fire-line intensity:

$$I = Hwr$$

where I is the fire-line intensity (kW/m), H is the heat yield of the fuel, w is the mass of fuel consumed (kg/m^2) and r is the rate of spread of the fire (m/s). The heat yield of the fuel, 18 700 kJ/kg, varies little among different woody fuels (Trollope 1984, van Wilgen and Richardson 1985, Holmes, 2001a, Baker 2009), and was used for the calculation of fire intensity.

Two methods were used to quantify the fire intensity and degree of soil heating:

1. Nine thermocouples (Type K) were placed under a large slash pile on the site. Two were placed 20 cm below the soil surface, two at 15 cm depth, three at 10 cm depth and two at 5 cm depth. These were connected to a switchboard, with readings being recorded by a digital thermometer (MT630 Thermometer, Major Tech, K-Type). Measurements started at 10h54, and continued until evacuation of the site at 13h30. At this time the fire had not yet reached the thermocouple location, and there had been no change in the baseline soil temperature. The thermocouples were left in place and were re-connected to the digital thermometer at 17h50, when we could access the site again, and readings were taken until 19h33, and continued the next morning at 04h55. Some thermocouple readings were also taken under smouldering logs the next morning after the fire, between 05h00 and 08h00.
2. Shavings from Tempilstik (Tempil suppliers) crayons were wrapped in a small piece of aluminium foil and placed under the slash piles at 54 locations (Table 3.1). The range of Tempilstik crayons used was the following: 107 ^{o}C, 204 ^{o}C, 302 ^{o}C, 399 ^{o}C, 510 ^{o}C, 704 ^{o}C and 927 ^{o}C, and at each location these were placed at the surface, 5 cm and 10 cm below the soil surface. The difficulty of placing the samples under the large volumes of biomass limited the placement of samples underneath the slash piles.
3. Each depth therefore contained seven packets, each with a Tempilstik shaving measuring a different melting point (total of 1 134 packets). These shavings melt when their respective melting point is reached, thus measuring the maximum temperature reached during the fire at these locations. The packets were collected after the fire, and the melted shavings recorded.

3.3.4 Post-fire soil sampling of seed bank

After the fire, soil collection for the soil seed bank study was repeated in the same manner as for the pre-fire study. This took place in the first 10 days after the fire, on a total of 104 blocks. Care was taken not to select soil from the spot where the pre-fire samples were collected.

Table 3.1. Tempilstik measuring points

Slash classification	Number of crayon locations
High	10
In between high slash	17
Medium	8
In between medium slash	7
Low	6
In between low slash	6
TOTAL	**54**

3.3.5 Soil processing and emergence monitoring

The post-fire samples were treated in exactly the same manner as the pre-fire samples (Section 2.3), except that they received no smoke treatment, as they had already been exposed to fire-related germination cues in the field. These trays were placed in the nursery in January 2006. Monitoring of both samples continued for 12 months, when germination of any new species had ceased.

3.3.6 Estimation of soil seed bank

Data were analysed according to species, genus and family to assess floristic composition. Species densities and distribution for the study area as well as densities of species per habitat type or zone (as described in Section 1.10; i.e. WB, NF dry bank, SF dry bank, LH slope and UH slope) were calculated.

Indigenous seedlings were categorised into functional guilds according to growth form and functional groups (geophytes, forb, graminoid, shrub, riparian, annuals and short-lived perennials, and alien) following Holmes *et al.* (2000), since it is postulated that ecosystem functions are driven by the various biotic guilds, and changes in ecosystem function would therefore be reflected by changes in in these guilds.

Multivariate analysis was undertaken using the community analysis package, PRIMER (Clarke and Warwick, 2001), to assess guilds and habitat groupings, by means of non-metric multi-dimensional scaling (MDS), and assess changes in pre- and post-fire emergence. A SIMPER analysis was undertaken to assess the percentage differences between the pre- and post-fire communities, and the contribution of individual species in defining the differences between the zones, using PRIMER (Clarke and Warwick, 2001).

Normality could not be achieved with any transformations and non-parametric analyses were therefore used. Mann-Whitney U tests, using the statistical software package STATISTICA, were undertaken to test for significant differences between overall pre- and post-fire emergence per depth, as well as differences in emergence between different guilds per habitat type.

3.4 RESULTS

3.4.1 Environmental data

Soil moisture on the day of the fire was 14 % (±0.03) under the slash piles and 12 % (±0.04) at exposed sites. Wind speed, air temperature and relative humidity on the day of the fire are presented in Table 3.2. Flame lengths of over 3 m were recorded in the slash piles. In some locations the 12 mm round bar rods bent from the heat.

Table 3.2. Environmental conditions at time of fire

Time	**Ambient temp (^{o}C)**	**Relative humidity (%)**	**Wind speed (m/s)**
10h53	32.9	31.2	0-1.2, with occasional gusts of 1.4 m/s
12h15	31.1	25.0	2, with occasional gusts of 4 m/s
13h22	29.0	16.4	0.4-1, with few gusts of 2.4 m/s

3.4.2 Fire intensity

Rate of spread differed between the upstream, middle and downstream sections of the burned block; being 0.0088 m/s, 0.0064 m/s and 0.0057 m/s respectively. The mass of the fuel, adapted from Holmes (2001a), was 6 326 g/m^2 for low slash piles, 12 652 g/m^2 for medium slash piles and 18 978 g/m^2 for high slash piles.

Fire intensity values for the upstream, middle and downstream location under respective slash pile columns are presented in Table 3.3. This indicates that the highest fire intensity (3 124 kW/m) was reached under high slash at the upstream end of the burned block, and the lowest fire intensity was at downstream, under low slash conditions.

Table 3.3. Fire intensity (in kW/m)

Location	Low slash	Medium slash	High slash
Upstream	1 041	2 083	3 124
Middle	753	1 506	2 258
Downstream	670	1 341	2 011

3.4.3 Soil temperatures

3.4.3.1 Thermocouples

The thermocouple readings (Figure 3.1) indicated a baseline temperature of 14-15 ^{o}C before the fire, with an increase at 5 cm to over 80 ^{o}C before the site had to be evacuated. The maximum temperatures could therefore not be measured. The temperature at 05h00 the next morning was still 10-15 ^{o}C higher than the baseline temperature. Some of the readings under smouldering logs the next morning still registered high temperatures, with temperatures of over 300 ^{o}C at the soil surface, over 100 ^{o}C at 5 cm depth and up to 74 ^{o}C at 10 cm. In these locations the ash layer was up to 6 cm deep, and the soil had burned to an orange-coloured, sandy consistency.

3.4.3.2 Tempilstiks

Table 3.4 indicates that under the high brush piles 90 % of the Tempilstiks registered a temperature exceeding 900 ^{o}C at soil surface level, 63 % under medium brush and 17 %

under low brush. At 5 cm depth, only 20 % of the Tempilstiks registered an increase in temperature above 100 °C under the high brush, and no increase was recorded at 5 cm depth under medium and low brush, or at the 10 cm depths. However, the lowest indicator was 107 °C, and any temperatures below this could not be recorded. Only 2 out of the 30 samples in between the slash piles registered temperatures of more than 900 °C at the soil surface level.

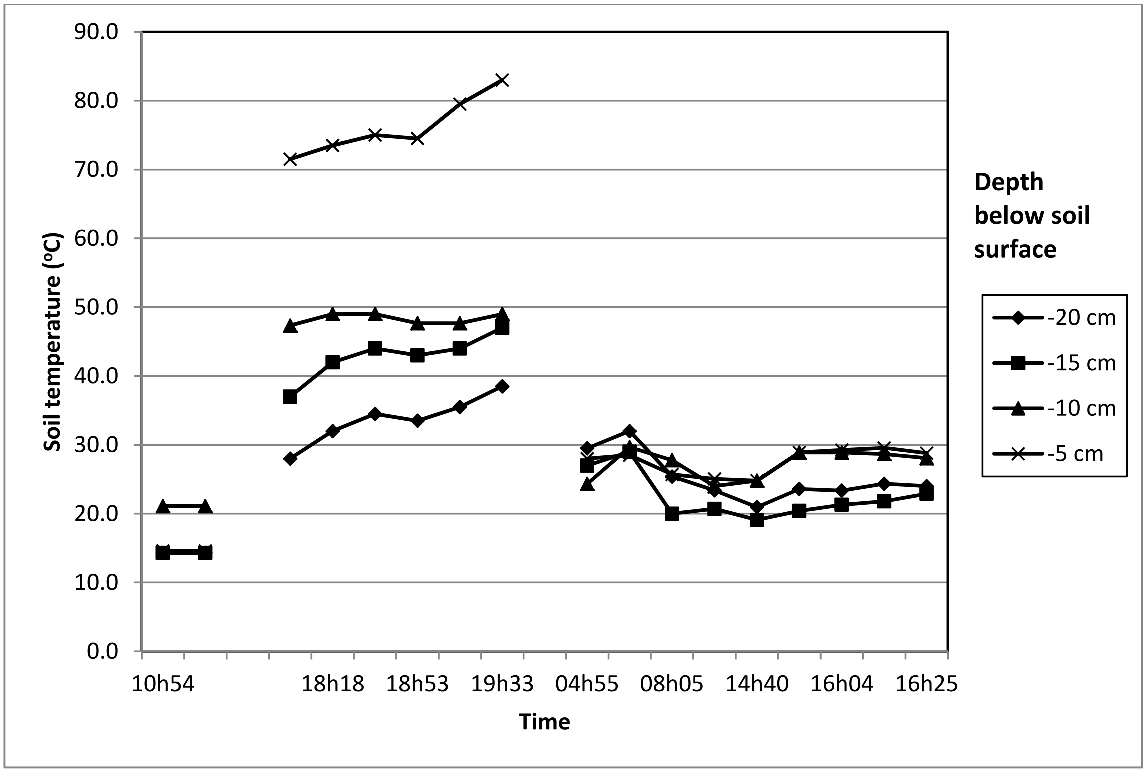


Figure 3.1. Soil temperatures at different depths before and after the fire taken from thermocouple readings

Table 3.4. Soil heating estimates from Tempilstiks

Slash category	% exceeding 900 °C at surface	% exceeding 107 °C at 5 cm depth	% exceeding 107 °C at 10 cm depth
High (10)	90 (9)	20 (2)	0
Medium (8)	63 (5)	0	0
Low (6)	17 (1)	0	0
In between slash (30)	7 (2)	0	0

3.4.4 Soil seed bank

3.4.4.1 **Acacia** *seeds in soil seed bank*

The highest *Acacia* soil seed bank densities were recorded in the NF dry bank, at the pre-fire 0-4 cm depth (2 970 ± 875 seeds/m^2). *Acacia* soil seed bank densities were lower at the 4-8 cm depth for all zones, and densities also decreased upslope (Figure 3.2). The fire reduced *Acacia* seed bank densities at both depths in all zones, with a significant decrease after fire for combined depths (pre-fire n = 115, post-fire n = 64, U = 2 737, Z = 2.837, $p < 0.005$).

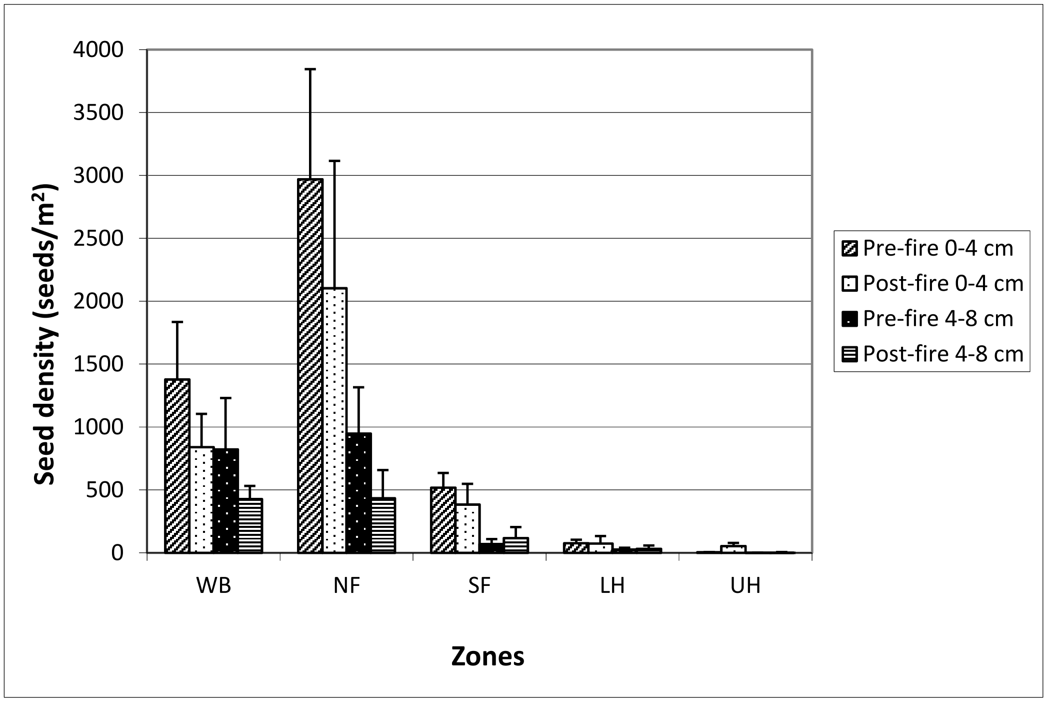


Figure 3.2. Effect of fire on *Acacia* soil seed bank density at two depths

3.4.4.2 Total emergence over landscape

A total of 5 294 seedlings emerged from the pre-fire samples (n = 115) (4 201 indigenous and 1 093 alien), and 3 332 from the post-fire samples (n = 104) (2 770 indigenous and 562 alien). The mean pre-fire indigenous seed density was 1 582 ± 129 seeds/m^2 and the mean post-fire indigenous seed density 1 014 ± 99 seeds/m^2.

Fire had the most pronounced effect at the 0-4 cm depth, with significant differences in pre-fire and post-fire density of seeds, from 999 ± 96 seeds/m^2 pre-fire to 597 ± 51 seeds/m^2 post-fire (U = 4 268, Z = 3.656, p = 0.0003).The reduction in seed density after fire at the 4-8 cm layer was much less; from 667 ± 66 seeds/m^2 pre-fire to 532 ± 51 seeds/m^2 seeds post-fire (U = 5 704, Z = 0.589, p = 0.556). Where larger volumes of slash were concentrated, the highest reductions in soil seed densities post-fire compared to pre-fire occurred, with values of up to 76 % and 73 % in two of the high-slash volume plots.

3.4.4.3 Total emergence per zone

The highest density per zone occurred in the pre-fire WB zone (2 754 ± 553 seeds/m^2), which was significantly reduced to 898 ± 159 seeds/m^2 post-fire (U = 60.0, Z = 3.15, p = 0.002) at combined depths. Seed densities were also significantly reduced in the LH slope, from 1 217 ± 141 seeds/m^2 to 765 ± 102 seeds/m^2 (U = 118.0, Z = 2.32, p = 0.02) after the fire. Although there was a significant reduction in seed density across the landscape at 0-4 cm depth after the fire, the effect was more pronounced in some zones (Figure 3.3). Seed densities declined after the fire at 0-4 cm depth in all zones (except the NF dry bank, due to an increase in annuals and short-lived perennial species), but the most pronounced reductions were in the WB zone from 1 677 ± 379 to 340 ± 87 seeds/m^2 (U = 58.0, Z = 3.210, p = 0.001) and LH slope from 774 ± 101 to 405 ± 76 seeds/m^2 (U = 109.0, Z = 2.561, p = 0.010). The only significant reduction in seed density at the deeper 4-8 cm layer was in the WB zone from 939 ± 195 to 559 ± 102 seeds/m^2 (U = 98.0, Z = 1.957, p = 0.050).

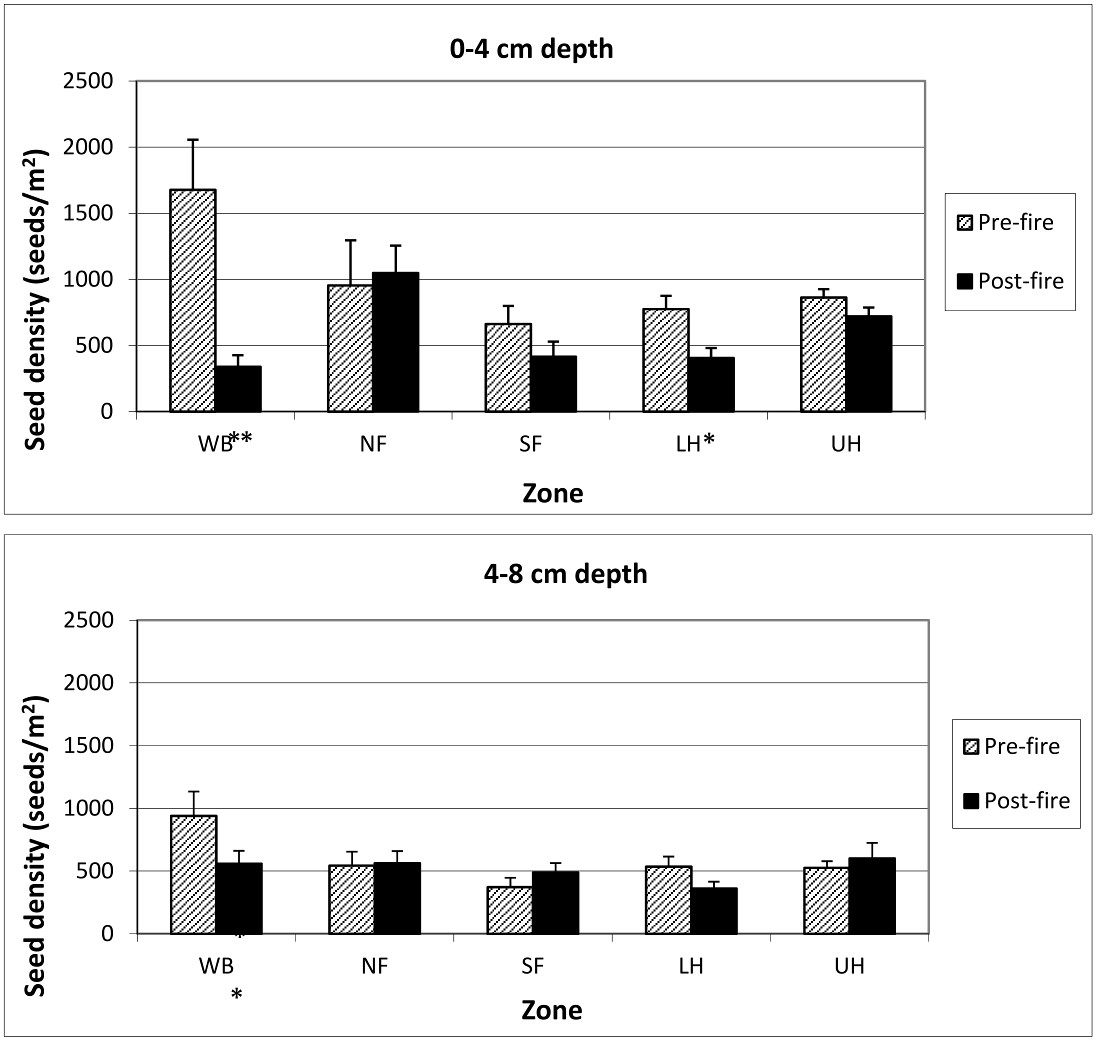


Figure 3.3. Difference in pre- and post-fire seed densities at 0-4 cm and 4-8 cm (* $p < 0.05$, ** $p < 0.01$)

3.4.4.4 Emergence per guild

Although there was an overall decline in seed densities at 0-4 cm after the fire, there is wide variation in effect across the guilds at the respective depths (Figures 3.4 – 3.8). Graminoids and geophytes are not indicated in Figure 3.4, as densities were very low, and Figure 3.4 b-e present data only indigenous emergents only.

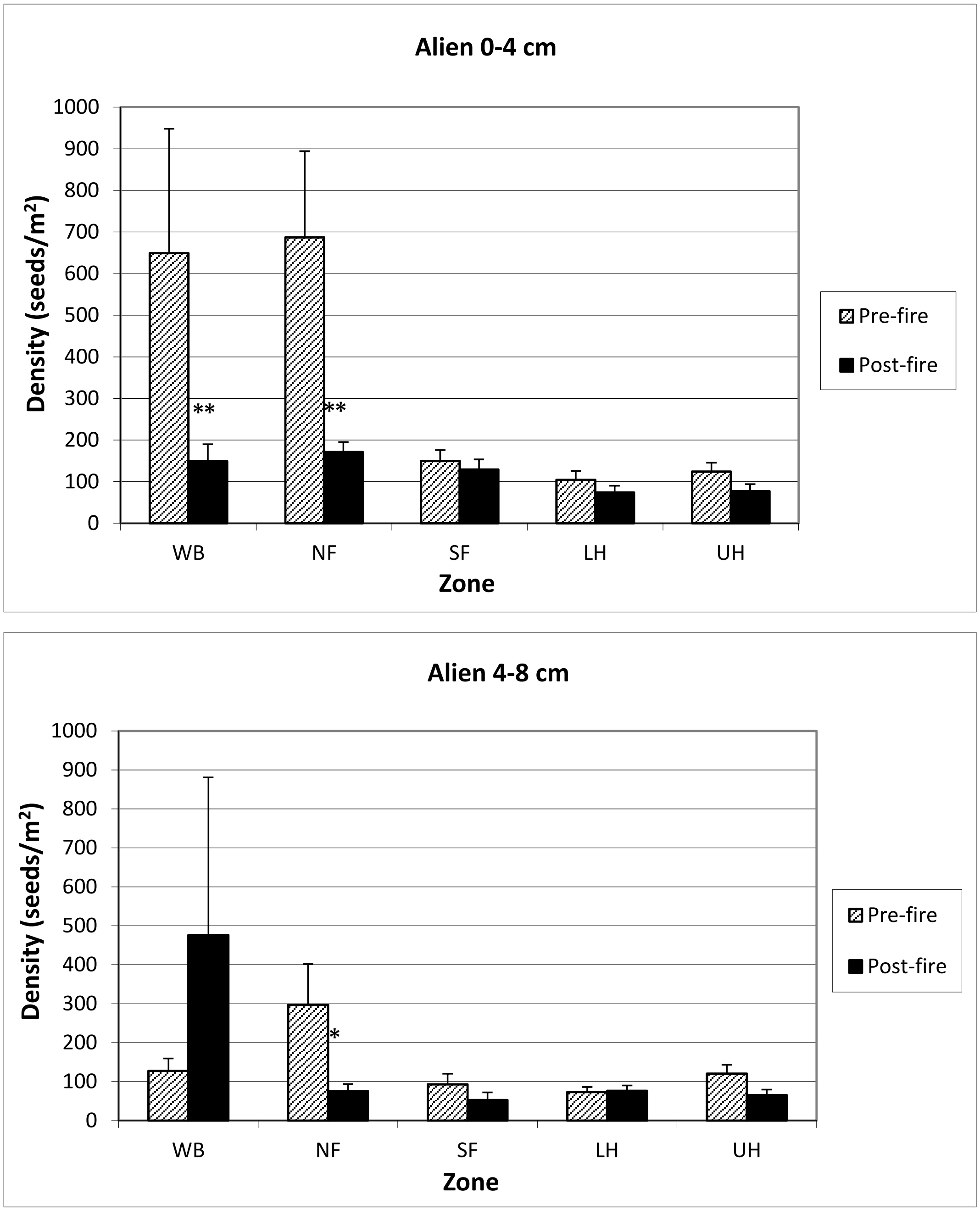
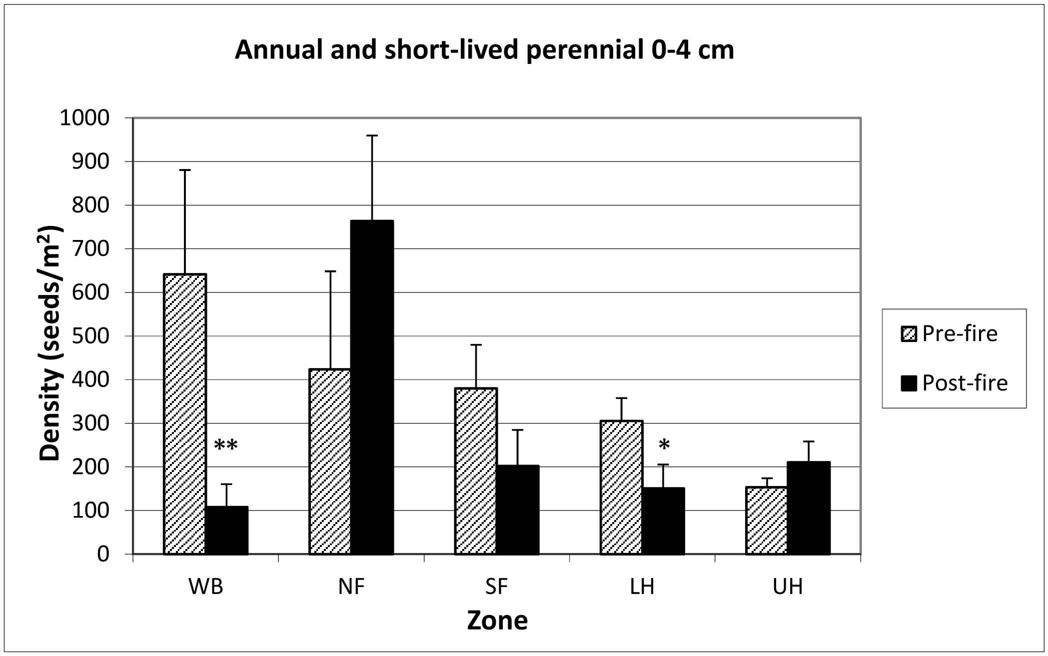


Figure 3.4. Difference in pre- and post-fire emergence of alien guild across lateral zones, at 0-4 cm and 4-8 cm. (* $p < 0.05$, ** $p < 0.01$)



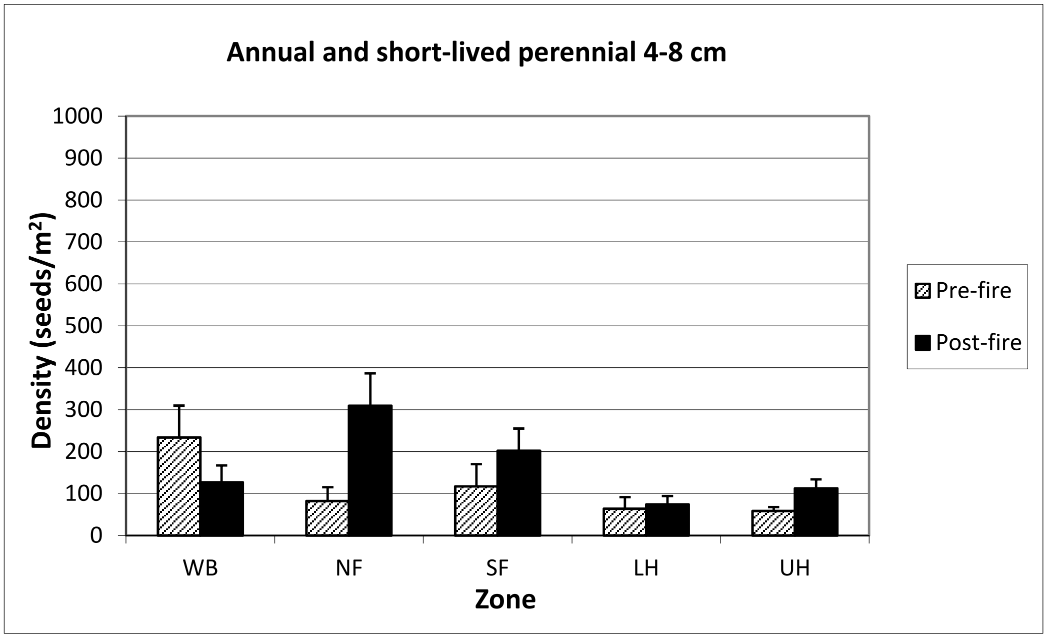


Figure 3.5. Difference in pre- and post-fire emergence of annual and short-lived perennial guild across lateral zones, at 0-4 cm and 4-8 cm. (* $p < 0.05$, ** $p < 0.01$)

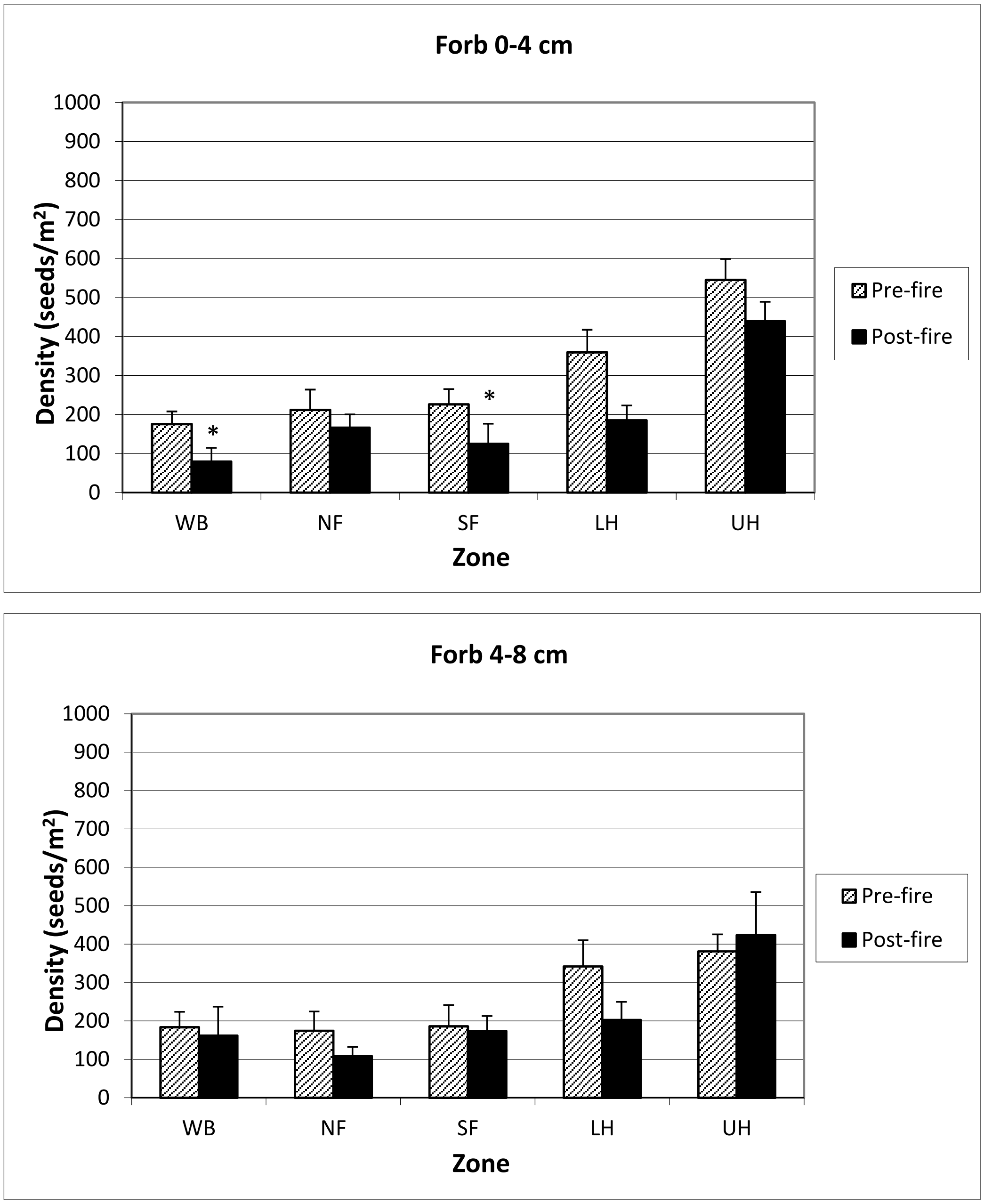
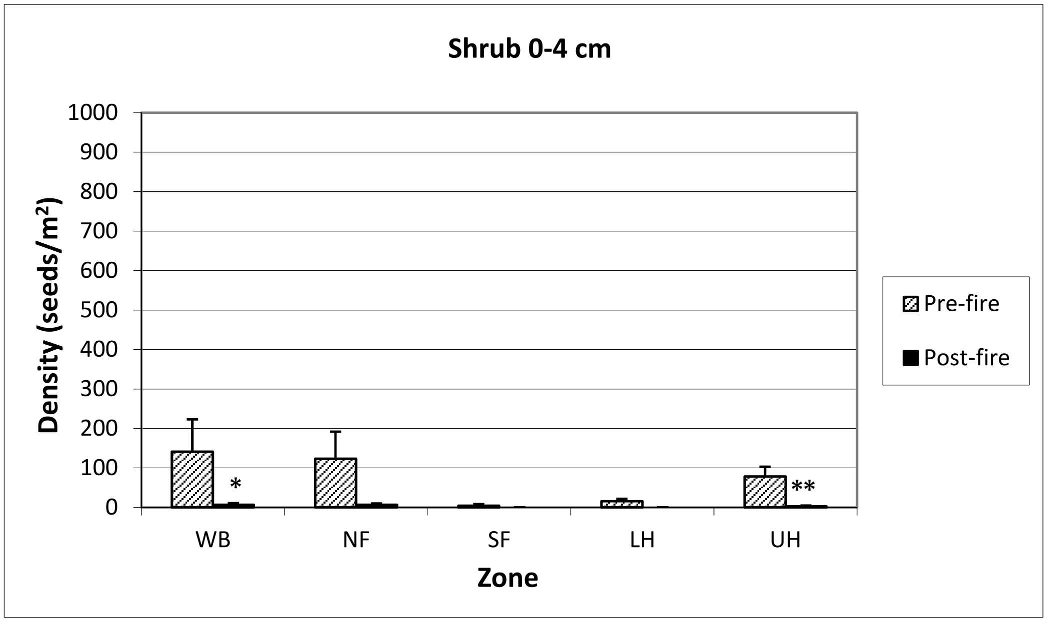


Figure 3.6. Difference in pre- and post-fire emergence of forb guild across lateral zones, at 0-4 cm and 4-8 cm. (* $p < 0.05$, ** $p < 0.01$)



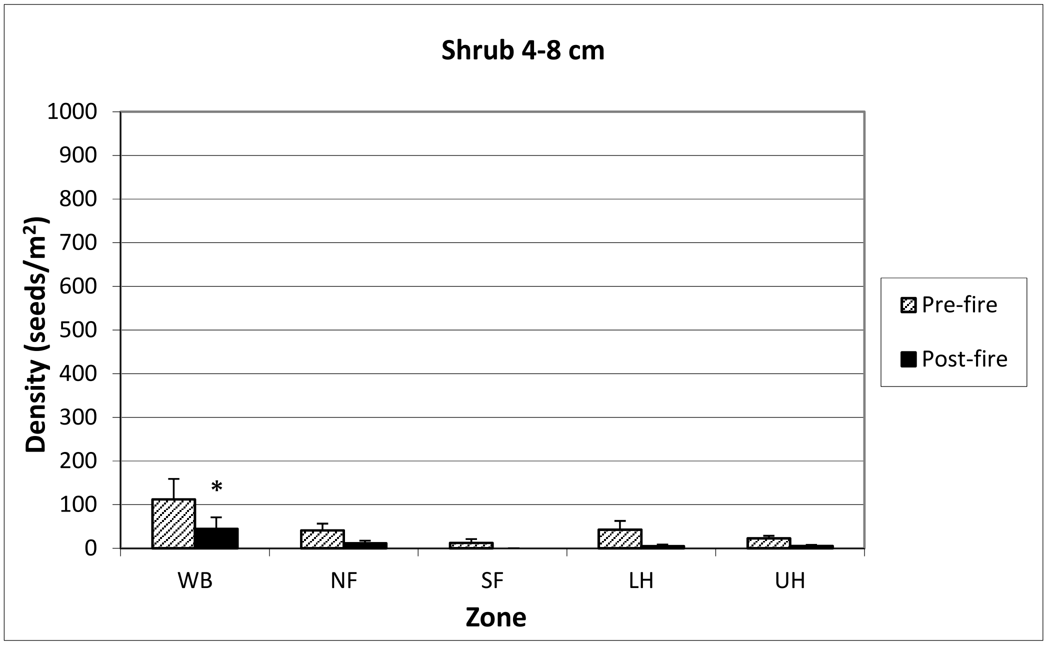
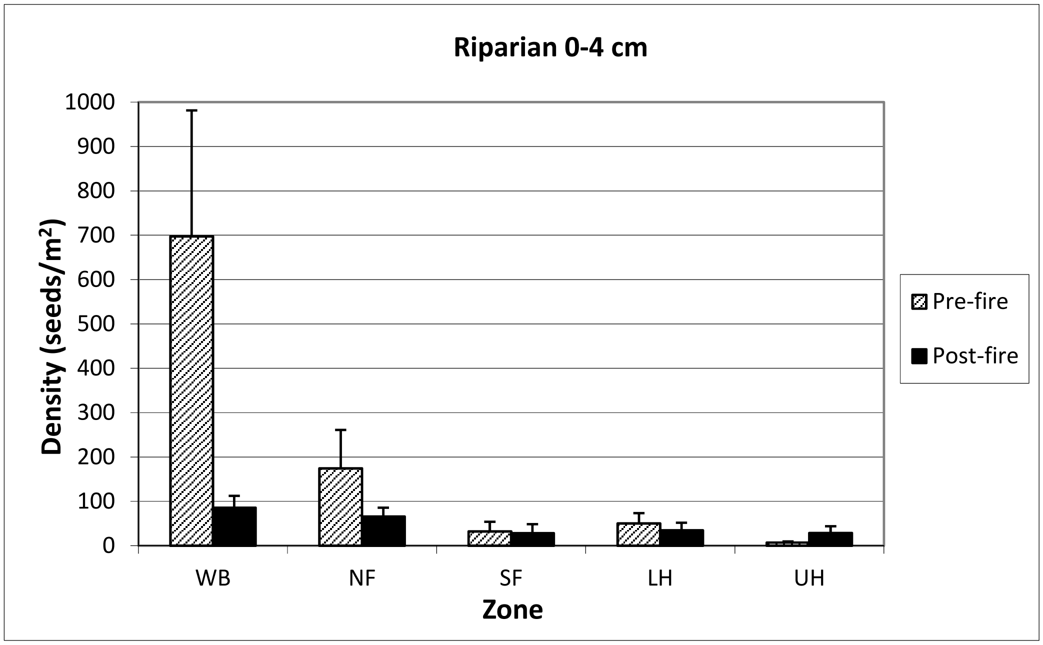


Figure 3.7. Difference in pre- and post-fire emergence of shrub guild across lateral zones, at 0-4 cm and 4-8 cm. (* $p < 0.05$, ** $p < 0.01$)



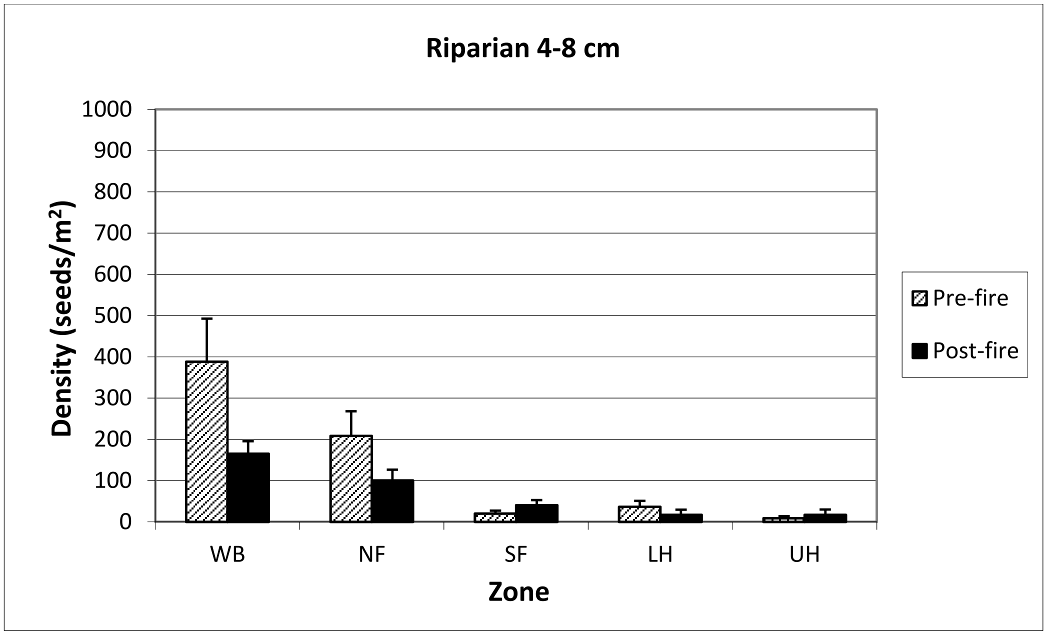


Figure 3.8. Difference in pre- and post-fire emergence of riparian guild across lateral zones, at 0-4 cm and 4-8 cm. (* $p < 0.05$, ** $p < 0.01$)

The alien seed density (Figure 3.4) was significantly decreased from 649 ± 299 seeds/m^2 to 149 ± 41 seeds/m^2 (U = 75.5, Z = 2.66, p = 0.008) after the fire at the 0-4 cm depth in the WB zone, and at both depths in the NF dry bank, from 687 ± 207 seeds/m^2 to 171 ± 24 seeds/m^2 at 0-4 cm (U = 67.5, Z = 3.10, p = 0.002) and 297± 104 seeds/m^2 to 76 ± 18 seeds/m^2 at 4-

8cm zone (U = 100.5, Z = 2.15, p = 0.031). There were also significant decreases in annual and short-lived perennial seed densities (Figure 3.5) at 0-4 cm, from 641 ± 239 seeds/m^2 to 108 ± 53 seeds/m^2 (U = 82.0, Z = 2.46, p = 0.014) in the WB zone, as well as the LH slope, from 305 ± 53 seeds/m^2 to 151 ± 55 seeds/m^2 (U = 110.0, Z = 2.54, p = 0.0112).

At the 0-4 cm layer, there was a significant decrease in the forb guild (Figure 3.6) in the WB zone, from 176 ± 32 seeds/m^2 79 to ± 35 seeds/m^2 (U = 84.5, Z = 2.38, p = 0.017) and SF zone from 226 ± 40 seeds/m^2 to 125 ± 51 seeds/m^2 (U = 28.0, Z = 2.10, p = 0.036). Shrub seed densities (Figure 3.7) declined in the WB zone at both depths, from 141 ± 82 seeds/m^2 to 6 ± 4 seeds/m^2 at 0-4cm (U = 84.0, Z = 2.40, p = 0.017) and from 112 ± 47 seeds/m^2 to 44 ± 26 seeds/m^2 at 4-8 cm (U = 92.0, Z = 2.15, p = 0.032), as well as in the UH slope at 0-4 cm depth, from 78 ± 25 seeds/m^2 to 3 ± 2 seeds/m^2 (U = 492.0, Z = 2.70, p = 0.007). Overall, the effect of fire was most pronounced in the shrub guild (Figure 3.7), with significant reductions in densities from 76 ± 21 seeds/m^2 to 3 ± 1 seeds/m^2 (U = 4044.0, Z = 4.13, p = 0.00004) at the 0-4 cm depth, and 46 ± 11 seeds/m^2 to 12 ± 4 seeds/m^2 (U = 4 466.5, Z = 3.23, p = 0.001) at 4-8 cm layer.

Geophyte densities increased from the WB upslope, but were very low, ranging from zero seeds/m^2 for geophytes in the 0-4 cm post-fire NF and SF dry banks to 32 ± 14 seeds/m^2 in the 0-4, pre-fire UH slope, and generally exhibiting a decrease in post-fire density. Grass densities were also very low, with the only significant change an increase from 12 ± 6 seeds/m^2 pre-fire to 60 ± 15 seeds/m^2 post fire at the 0-4 cm depth in the SF dry bank (U = 23.0, Z = -2.43, p = 0.015). There were no significant changes in seed density in the riparian guild, although there was a pronounced decline in both the WB zone and NF dry bank.

3.4.4.5 Changes in community composition

Analysis of the ten most dominant species in each zone at combined depths (Table 3.5) of both pre- and post-fire seed densities, revealed a general shift in floristic post-fire composition moving upslope; e.g. *Rumohra adiantiformis* and *Isolepis cernua* are only dominant in the WB zone and NF dry bank, *Helichrysum eppaposum* only in the WB zone, whereas species such as *Selago corymbosa, Erica chammisonis* and *H. cymosum* are only dominant in the LH and UH slopes, and *Hypoxis argentea* in the SF zone and further upslope. However, some species like *Senecio rigidus* and *Conyza pinnata* were found across all zones, although in decreasing densities moving upslope.

S. rigidus exhibited the highest seed density of all species, peaking in the post-fire NF zone (576 ± 139 seeds/m^2) and pre-fire WB zone (559 ± 237 seeds/m^2). *R. adiantiformis* exhibited the second highest density, with 567 ± 379 seed/m^2 in the pre-fire WB zone, followed by *C. pinnata* (472 ± 136 seeds/m^2) in the post-fire NF zone. Some pre-fire dominants (e.g. *S. rigidus* and *C. pinnata*) remained dominant in the post-fire seed bank, although generally in decreased densities throughout all zones, other than in the NF dry bank, where there was an post-fire increase in both *S. rigidus* (from 321 ± 181 to 576 ± 139 seeds/m^2) and *C. pinnata* (from 124 ± 58 to 472 ± 136 seeds/m^2). Other pre-fire dominant species such as *Rumohra adiantiformis, H. epapposum* and *Hypoxis argentea* decreased in density after the fire, e.g. *R. adiantiformis* decreased from 576 ± 379 to 35 ± 35 seeds/m^2.

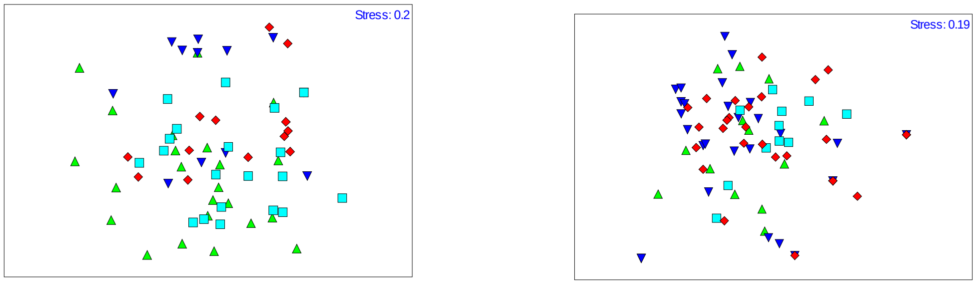
Of the dominant species, the fire appeared to have negatively affected the seed densities of the species in the shrub guild the most, i.e. *Halleria lucida* (119 ± 104 to 38 ± 26 seeds/m^2 in the WB zone), *Erica caffra* (116 ± 53 to zero in WB zone, and 48 ± 21 to zero seeds/m^2 in the NF zone) and *Erica chamissonis* (38 ± 19 to zero in the LH slope and 96 ± 28 to zero seeds/m^2 in the UH slope) (Table 3.5). Some species exhibited an increase in density in the WB zone after the fire, e.g. *Chironia baccifera* (e.g. zero to 67 ± 50 seeds/m^2)*, H. petiolare* (e.g. zero to 76 ± 39 seeds/m^2)*, Ficinia trichodes (*e.g. zero to 29 ± 13 seeds/m^2). *Carpha glomerata* increased from zero to 28 ± 17 seeds/m^2 in the NF zone, and *H. umbraculigerum* from zero to 36 ± 17 in the SF zone and 29 ± 12 seeds/m^2 in the UH slope. The last three species were absent in the pre-fire dominant species.

Table 3.5. Seed density (seeds/m^2) of the ten most dominant indigenous species for each zone, pre- and post-fire (combined depths). Absence of a value indicates zero seedlings emerged

SPECIES	RIPARIAN				NORTH-FACING				SOUTH-FACING				LOWER HILL SLOPE				UPPER HILL SLOPE			
	PreF (n=21)		PostF (n=14)		PreF (n=14)		PostF (n=27)		PreF (n=9)		PostF (n=11)		PreF (n=28)		PostF (n=18)		PreF (n=46)		PostF (n=34)	
	D	F	D	F	D	F	D	F	D	F	D	F	D	F	D	F	D	F	D	F
Rumohra adiantiformis	567±379	38	35±35	7	143±99	29														
Senecio rigidus	559±237	81	194±80	57	321±181	93	576±139	67	410±102	100	319±92	82	248±43	93	136±45	83	120±25	70	84±50	62
Conyza pinnata	290±184*	57			124±58	50	472±136	44	173±80	78	28±14	45	111±32	46	69±19	61	66±11	28	103±23	76
Ficinia filiformis	241±112	52	60±29	50			31±11	37	35±24	33					40±21	22				
Cyperus esculentis	121±48	57	63±19	64	76±35	43	41±14	37			16±11	18								
Halleria lucida	119±104	14	38±26	21	83±55	29			25±15	33										
Erica caffra	116±53**	52			48±21**	50														
Helichrysum sp.	104±35	57			111±40*	79	26±8	41	25±15	44	16±7	27							112±40**	50
Helichrysum epapposum	102±37	38																		
Isolepis cernua	93±27**	52			89±69	29	38±22	22												
Cheilanthes viridis			41±32	21	140±58	43			104±62	33	16±12	18	162±65	36	42±30	11			64±25	35
Helichrysum petiolare			76±39	50	44±13	57	104±25	70	138±47	100	93±24	91	52±18	43	27±14	28			66±16	50
Chironia baccifera			67±50	14			76±24	52	44±22	44	76±31	36	143±34	64	128±46	44	278±44	78	316±105	88
Anthospermum herbaceum							43±30	11	35±16	44	20±9	36	73±36	39	27±11	28	62±15	50	37±14	29
Hypoxis argentea									20±13	22			41±30	18	17±13	11	60±20	41		
Selago corymbosa													83±35	39	79±29	50	160±28	72	103±30	44
Erica chamissonis													38±19	32			96±28**	52		
Eragrostis obtusa			32±22	14									37±14	36			57±18**	43		
Lobelia tomentosa																	91±27	41		
Helichrysum cymosum															30±11	39	80±16	61	54±14	41
Carpha glomerata							28±17	15												
Ficinia trichodes			29±13	36							40±21	27								
Helichrysum umbraculigerum											36±17	36							29±12	26
Average density of zone	2 753±553**		898±159		1 435±392		1 661±266		1 146±163		828±163		1 217±141*		765±102		1 400±102		1 298±153	

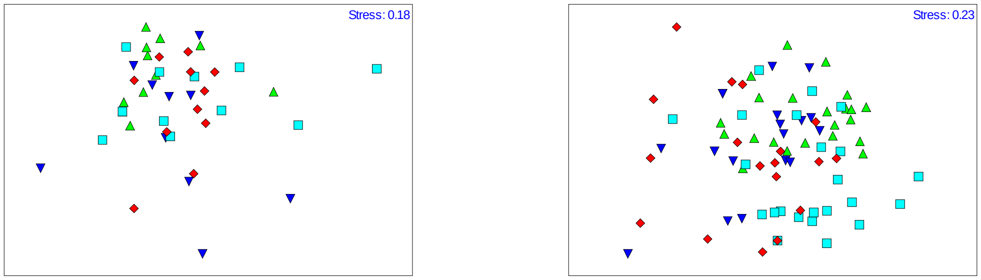
PreF = pre-fire, postF = post-fire, D = density, F = % frequency

± standard error, significant difference between pre- and post-fire densities * $p < 0.05$, ** $p < 0.01$



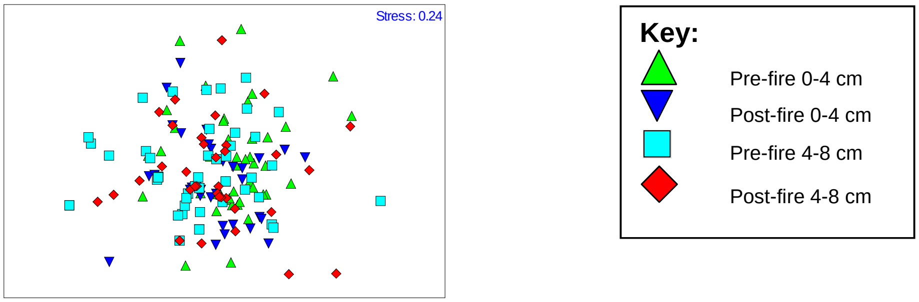
(a) Wet bank; 0-4 cm: 76 %, 4-8 cm: 65 %

(b) North-facing dry bank; 0-4 cm: 72 %, 4-8 cm: 67 %



(c) South-facing dry bank; 0-4 cm: 66 %, 4-8 cm: 59 %

(d) Lower hill slope; 0-4 cm: 60 %, 4-8 cm: 62 %



(e) Upper hill slope; 0-4 cm: 51 %, 4-8 cm: 55 %

Figure 3.9 (a-e). Multi-dimensional scaling plots of pre- and post-fire emergence per zone per functional group

Figure 3.9 (a-e) indicates that all zones exhibited a shift in functional group composition (with seed density as dependent variable) of the seed banks between pre- and post-fire vegetation, but the greatest dissimilarities were found in the WB zone and adjacent NF and SF dry banks. In these zones there were greater dissimilarities in the upper depths (66-76 %), and lower dissimilarities (59-67 %) at the 4-8 cm layer. Smaller dissimilarities were found in the LH and UH slope pre- and post-fire communities. The degree of dissimilarity between guilds which contribute most to dissimilarity in the pre-fire and post-fire soil seed bank are listed in Table 3.6 below.

Table 3.6: Results of the analysis of dissimilarity between guilds in the pre-fire and post-fire soil seed bank per zone (only contributions of >20 % are listed) (A&P = annual and short-lived perennials, R = riparian, F = forb)

Wet Bank 0-4 cm				
Guild	**Avg. Abund (pre-fire)**	**Avg. Abund (post-fire)**	**Avg. Diss**	**Contribution%**
A&P	641.48	125.91	26.61	35.23
R	697.51	99.99	24.73	32.75
Wet Bank 4-8 cm				
R	446.62	153.83	21.04	32.57
A&P	268.86	123.06	16.78	25.98
F	211.09	174.34	14.04	21.73
North-facing dry bank 0-4 cm				
A&P	423.89	763.71	35.39	49.48
F	211.94	166.24	14.43	20.18
North-facing dry bank 4-8 cm				
A&P	96.96	309.43	20.60	30.98
R	246.44	100.40	19.57	29.43
F	206.04	108.63	15.53	23.36
South-facing dry bank 0-4 cm				
A&P	379.76	202.09	32.44	49.13
Forb	226.24	125.24	20.48	31.02
South-facing dry bank 4-8 cm				
A&P	117.16	202.00	21.41	36.52
F	185.84	173.72	20.04	34.18
Upper Hill slope 0-4 cm				
F	545.13	439.17	23.87	47.21
A&P	153.07	210.44	13.08	25.88
Upper Hill slope 4-8 cm				
F	389.86	423.49	31.87	58.03
Lower Hill slope 0-4 cm				
F	375.72	185.17	24.15	39.95
A&P	319.16	150.60	1.36	38.40
Lower Hill slope 4-8 cm				
F	341.99	202.45	30.82	49.36

3.5 DISCUSSION

3.5.1 Fire intensity and soil temperatures

The rate of spread recorded during this fire was low (less than 0.01 m/s), which is lower than that rates of spread (approximately 0.1 m/s) modelled by van Wilgen and Richardson (1985) under low and moderate fire hazard conditions. It is also much lower than that found by Holmes (2001a), of 3 m/s for a winter fire and 6 m/s for a summer wildfire. However, rate of spread is often lower in densely packed fuel beds and is not always a reliable indicator of fire severity (van Wilgen and Richardson 1985). Van Wilgen and Richardson (1985) argued that the rate of spread, as an indicator of fire severity, was unreliable and found lower rates of spread in alien-invaded, densely packed fuel beds with higher fire severities (see Plates 5-8), compared to uninvaded fynbos. This has also been found in other studies (Clarke 2001). During this study, the upper 2-3 cm of soil was burnt away under the high fuel loads in the WB and NF zones; this layer was high in organic matter and duff, which often results in glowing combustion (Hungerford *et al.* 1991, in Baker 2009). This has also been found in other studies (Madrigal *et al.* 2010), and the loss of this layer alters the micro-environmental conditions, e.g. moisture and nutrient availability, and affects the post-fire recruitment and successful establishment of seedlings. The rate of spread of glowing combustion is typically two orders of magnitude lower than flaming combustion and temperatures half or less, but lasts longer. This can result in much higher heating of the soil (Hungerford *et al.* 1991, in Baker 2009).

The estimated fire intensities for this study were comparable to those of Holmes (2001a), of 2 017 kW/m for a winter burn under comparable environmental conditions, and an estimated 7 150 kW/m for a summer wildfire. Le Maitre (1981, in Trollope 1984) found fire intensities ranging from 3 614 – 8 644 kJ/m in fynbos, while Le Maitre (1980, in Kruger and Bigalke 1984), found fire intensities of 5 130 kJ/m under fuel loads of 1 204 g/m^2. The fire intensities were lower than those of van Wilgen and Richardson (1985) of 11 000 kW/m for *Acacia*-invaded (not felled) fynbos. However, although there is a fairly wide range of fire intensities recorded under similar conditions, the fire temperatures on the ground are the most important factor influencing plant responses, and in this case, the soil seed bank.

The amount of fuel is one of the factors determining fire intensity (Neary *et al.* 1999) and therefore maximum ground temperature. Maximum ground temperatures under fires are typically in the range of 200–300 °C, but areas with high fuel loads can reach temperatures over 500 °C, and soil surface temperatures of up to 800 °C have been found during forest fires in Finland (Doerr *et al.* 2004), which is similar to the upper range of temperatures (i.e. > 900 °C) found under large slash piles during this study. Rundel (1983) has reported soil surface temperatures of up to 500-700 °C during heavy slash fires in chaparral, while Martin (1966) found temperatures of 550 °C at surface under natural fynbos of 0.6 m height, but of short duration (10 seconds), with little change in sub-surface temperatures.

There is also a gradient of soil temperature according to depth, with soil surface temperatures exceeding 900 °C and decreasing to 107 °C at 5 cm depth, with lower temperatures deeper in the soil profile. The much higher than average monthly rain in November 2005 (137 mm as opposed to the average 66 mm), of which 124 mm fell before the controlled burn, meant that soils were much wetter than normal, especially under the brush piles. The soil moisture of 12-14 % registered during this study could have ameliorated the heating effects of the fire, with slightly wetter soils under the slash piles which would lower the upper temperatures values. The decrease in soil temperature with depth has also been found by other studies (Bradstock *et al.* 1992; Behenna *et al.* 2008). Roberts (1965) found temperatures of up to 250 °C and 100 °C at 10 cm and 20 cm depth, respectively, in pine slash fires (in Korb *et al.* 2004). Under felled IAP biomass Holmes (1989) found temperatures exceeding the range of the thermo-indicators used; 160 °C at 1 cm depth, and 71 °C at 4 cm depths. Behenna *et al.* (2008) found temperatures of up to 300 °C at 2 cm depth under high fuel loads in dry soils, while Diaz-Gonzalez (2009) found temperatures of 927 °C, and 399 °C and 143 °C at the soil surface, 2 cm and 5 cm depths respectively, under 2 m high slash piles. Busse *et al.* (2005) found lethal temperatures to be transmitted up to at least 10 cm deep under fine woody fuels, and although Richardson and Kluge (2008) and Marchante *et al.* (2011b) recommended fire to remove *Acacia* leaf litter, this is also likely to result in smouldering and damage.

3.5.2 Soil seed bank densities

The soil seed bank densities found in this study compare to seed bank densities of 1 100-2 000 seeds/m^2 in uninvaded fynbos found by Holmes and Cowling (1997a) and Holmes (2002), and Meney *et al.* (1994) in kwongan, although a considerable range in indigenous soil seed bank densities in Mediterranean-type vegetation has been reported. The process of invasion results in a reduced seed rain which depletes the soil seed bank over time (Holmes and Cowling 1997a; Holmes 2002). This process is also aggravated by fire events in between generations of invaders (CSIR 2000). Soil seed bank densities between 800 and 1 300 seeds/m^2 for recently- and long-invaded sites have also been reported (Holmes and Cowling 1997a), and the mean pre-fire and post-fire soil indigenous soil seed bank densities found in this study (1 582 seeds/m^2 pre-fire and 1 014 seeds/m^2 post-fire) are comparable to these densities. This could indicate that soil seed bank densities have declined as a result of the invasion process. Manders (1990) found no significant difference between the pre- and post-fire soil seed bank after a natural fire event across a fynbos-forest ecotone, in which the forest did not burn. He recorded the seed densities of up to 1 777 seeds/m^2 in the forest, with lower densities in the transitional zone (1 066 seeds/m^2) and fynbos (530-822 seeds/m^2). Velbuena and Trabaud (2001) found an average of 1 050 seeds/m^2 in the soil seed bank before fire and 1 050 seeds/m^2 after a natural fire in a Mediterranean shrubland in Spain. In this study the increase in seedlings after fire appears to reflect the lack of germination cues for the pre-fire seeds.

Upper individual species seed densities of 576 seeds/m^2 (*S. rigidus*) are also comparable to those of Holmes (2002) of 516 seeds/m^2 for mountain fynbos. Similarly, Holmes (2002) also found alien seed bank densities in a long-invaded *Acacia* site of 6 897 seeds/m^2, comparable to this study (3 918 seeds/m^2). Both pre- and post-fire variance is high, which is an inherent characteristic of soil seed bank studies (Pierce and Cowling 1991), but post-fire variance is also a result of the extreme variation in exposure to fire, with some plots being covered by more than 2 m high slash piles, and other plots in between slash piles not displaying a fire effect at all.

Pierce and Cowling (1991) found seed bank densities in dune fynbos ranging from 1 833 seeds/m^2 (north-facing slopes) to high densities of 9 514 seeds/m^2 on south-facing slopes. They also reported high variance values, similar to this study and others (Manders 1990; Clemente *et al.* 2007; Fourie 2008; White and Stromberg 2011), supporting the patchiness and heterogeneity of soil seed banks across the landscape or between reaches. However, Vosse *et al.* (2008) reported seed densities in orders of magnitude less than the findings of this study and other fynbos soil seed bank studies with the highest indigenous seed density being 19.5 seeds/m^2 along a reference riparian zone in the Western Cape. It is possible that these relatively low values are a reflection of the dynamic nature of these riparian areas, where new sediment is continually being deposited (and requires time to build up soil-stored seed) and older banks with accumulated soil seed bank densities being washed away. Even at these low densities, they reported decreased abundance after invasion, especially for shrubs and herbaceous perennials. They concluded that the soil seed bank was diverse enough to initiate successful recovery, although dominated by indigenous graminoid and herbaceous species, but missing some key riparian species. The area that was used during this current study is less subject to disturbance by floods, other than the wet bank channel, so it is likely that seed banks would have had a greater chance of accumulating seed in the soil.

The total indigenous seedling density (1 582 seedlings/m^2) is comparable to those found in winter rainfall areas of the fynbos biome, e.g. Holmes and Cowling (1997a) who found a range of 1 100–1 900 seedlings/m^2 in uninvaded areas and Holmes (2002) with a range of <400 to >1 200 seedlings/m^2. This also compares well with the seed density values of 1 754 seeds/m^2 from cleared conifer plantations in Japan (Sakai *et al.* 2005) and seed densities of obligate seeders of 640–4 388 seeds/m^2 and 102–3 061 seeds/m^2 (Clemente *et al.* 2007). Miller and Cummins (2003) have found seed densities of 600–64 000 seeds/m^2 in (Scottish) heathlands far exceeding the densities found in this study. However, seed densities are problematic to compare, as methodology differs (e.g. sampling depth).

The fire reduced *Acacia* seed bank densities at both depths in all zones, with a significant decrease after fire for the combined depths, but is still high enough at approximately 2 500 seeds/m^2 in the NF dry bank zone to pose a significant challenge to post-clearing and -fire management.

3.5.3 Zonation and guilds

Seedling emergence generally reflects the above-ground lateral zonation of plant species, although some species emerged from soil outside their zone of occurrence, e.g. *R. adiantiformis* and *F. filiformis* emerged from soil from the LH and UH hill slopes, but in lower densities. These species have small, wind-dispersed seeds which may land in areas where they will not be able to establish. Soil seed bank densities in this study will thus be an over-estimate of what will germinate and survive in field conditions (Holmes and Cowling 1997a, b). This is discussed later in more detail (Sections 3.5.5. and 5.5.2.3).

The highest soil seed bank densities, both pre- and post-fire, were found in the annual and short-lived perennial, as well as the forb guild. This has been found in other studies as well, e.g. Vosse *et al.* (2008) found a shift towards herbaceous forms with a few common woody species. It appears that herbaceous species are able to persist during invasion and fire, and even though there was a significant decrease in annual and short-lived perennials, as well as forb densities in some zones after the fire during this study, these guilds can recover without active intervention.

The invasion appeared to affect woody species most severely, with overall low pre-and post-fire densities and significant decreases in densities of woody shrubs after the fire. Resprouters are virtually absent in long-invaded sites, and in grassy fynbos most of the shrub guild consists of resprouting shrubs (Le Maitre and Midgley 1992), and the decline of abundance and cover in this guild can threaten catchment stability in the immediate post-fire phase (Holmes *et al.* 2000). Le Maitre and Midgley (1992) also found that resprouters make up less than half of fynbos flora after fire, especially in the first year (Kruger 1979, 1987). Vosse *et al.* (2008) also found that woody species are most affected by invasion.

3.5.4 Effect of fire and depth

The higher soil seed bank densities in the upper 0-4 cm layer compared to the deeper 4-8 cm layer corresponded to findings from Pieterse and Cairns (1986), Holmes (2002), Cilliers *et al.* (2004) and Vosse *et al.* (2008), where the soil-stored seed banks of fynbos were found to be concentrated in the upper 3-5 cm of the soil profile. However, significant densities were still found in the deeper layer, but these seeds at lower profiles may not be able to germinate (Bond *et al.* 1999), unless they are brought closer to the surface through some disturbance. Deeply buried seeds are insulated from germination cues (Brits 1986; Pierce and Moll 1994) and thus the density of viable seed banks in deeper layers may be relatively high due to conditions conducive to persistence (Baskin and Baskin 1998).

The upper 2-3 cm of soil was burnt away during the fire under the high fuel loads, effectively lowering the soil surface. The loss of the top layer indicated that glowing combustion took place, with a higher heat loading of the soil (Madrigal *et al.* 2010). Madrigal *et al.* (2010) found a severe reduction in the litter and humus layer after glowing combustion, relative to a control (unburnt) soil, with a significantly reduced percentage of accumulated germination (29 % in the burnt soil compared with 71 % in the control soil). Loss of the organic layer changes the soil conditions and can severely retard the recruitment and successful establishment of seedlings. In this study the highest reductions in soil seed densities post-fire compared to pre-fire occurred (e.g. 76 % and 73 % in two of the plots), where the larger slash piles were located, indicating that the loss of the top layer of soil to high fire intensities had a severe negative impact on the soil seed bank. Reyes and Trabaud (2009) have also observed decreased germination under high or prolonged exposure to fire and Holmes (1989) found that few *A. cyclops* seeds survived in the upper 3 cm of the soil after a slash fire, with reduced seed viability at 4 cm depth.

This study indicates that there was a significant reduction of alien and indigenous seed densities in the upper soil layer as a result of the fire, but less in the deeper soil layer. Auld and Denham (2006) also found significantly lower densities of viable seeds in the upper 0-5 cm layer of soil compared to deeper 5-10 cm or 10-15 cm after a natural, low to moderate intensity fire. They attributed the reduction in seed density to loss either due to germination or seeds killed in fire. Whether recovery would be retarded by this decrease is not certain, as representatives of all the guilds are still present, although at reduced densities, and the soil seed bank, even at these lower densities, may still be sufficient to initiate recovery towards a functional system. However, some guilds such as shrubs were more affected than others, and since this also reflected in post-fire above-ground surveys, it indicates that the decreased densities resulting from fire do compromise the establishment of at least some guilds.

Other authors (Odion and Davis 2000, Holmes 2001a, Behenna *et al.* 2008) have reported the loss of soil seed banks as a result of burning slash piles. Korb *et al.* (2004) found pre-fire densities of 1 176 seeds/m^2 in forest, and virtually none afterwards. Pierce and Cowling (1991) also found a large reduction in soil seed banks in dune fynbos after fire, with post–fire values (after 33 months) of 753 seeds/m^2 on north-facing slopes and 5 052 seeds m^2 on south-facing slopes. This reduction, however, could also be due to post-fire germination. Although there was a significant reduction in the soil seed bank of *A. longifolia* after the fire, seed bank densities of over 2 000 seeds were still found in some of the lateral zones, enough to still maintain high levels of recruitment and thus present a serious challenge for management after clearing and fire (Richardson and Kluge 2008; Strydom *et al.* 2012). This will be discussed further in Chapter 5. The fire also resulted in a general decline in diversity, but with a lesser effect at the deeper layer. This corresponds to the general decline in density, which also had a more significant response at the upper 0-4 cm layer.

One of the difficulties in interpreting the results of this study and other soil seed bank studies is that new inputs into the soil seed bank will constantly increase the soil seed bank densities at any given time (Fenner and Thompson 2005; Wright and Clarke 2009), while germination, predation or pathogens can decrease densities (Knox and Clarke 2006). This effect will be more pronounced for small, wind-dispersed seeds, which also tend to be more numerous and therefore have a larger influence on abundance. However, dormancy may affect the contribution of recent seed releases to regeneration after fire, and this is discussed in Chapter 4. The increase in seedling emergence at a deeper layer could not have resulted from a post-fire influx of seed, and it is probable that the heat of the fire broke the dormancy of the seeds of some species and triggered a germination response, resulting in a higher post-fire germination response than pre-fire. Musil (1991) concluded that all species are inhibited by temperatures above 120 ^{o}C, which is similar to studies of seeds of many Mediterranean-type species (Keeley *et al.* 1985), but that the individual seed response to heat and duration of heat exposure is extremely varied. This makes the interpretation of a community response very difficult. It is also probable, since germination cues are so varied between species, that the actual pre-fire soil seed bank densities were higher than reflected in this study, since many germination cues were not met or seeds had some inherent dormancy which delayed germination (Fenner and Thompson 2005). However, the effects of repeated fell-and-burn treatments are of concern, as they are likely to result in cumulative reductions in soil seed bank densities.

In this study, *Chironia baccifera* also showed an increase in post-fire seed density. This species is not wind-dispersed and could not have been widely distributed post-fire, and it is likely germination was stimulated by heat, or that seed set between clearing and the fire had increased the soil seed bank substantially. Musil (1991) also found an increase in non-dormant soil-stored seed reserves after fire, which would result in increased germination. This contrasts with other studies (e.g. Manders 1990), where no stimulatory effect was found. Few legumes were found in this study, although the above-ground community included legumes such as *Otholobium*. However, there was often little overlap between species in the soil seed bank and above-ground vegetation (Vosse *et al.* 2008). Many legumes are heat-stimulated, and need a minimum temperature to break dormancy and initiate germination (Bradstock and Auld 1995), and seedlings were expected in the post-fire samples. It is possible that these seeds, and other larger seeds like *Polygala* seeds were removed through sieving. However, *Polygala* species are myrmocochorous (Le Maitre and Midgley 1992), and may have been present deeper in the soil profile.

In addition to the soil seed bank, post-fire seedling recruitment levels will depend to a large extent on post-fire factors affecting germination, seed and seedling survival (Bond 1984; Le Maitre 1988). Post-fire factors will vary seasonally and annually, resulting in different recruitment outcomes. For example, post-fire recruitment followed by an unseasonal dry period will negatively affect seedling survival. This is discussed further in Chapter 5.

3.5.5 Landscape responses to fire

Landscape responses to invasion and clearing, including fell-and-burn; have been studied, with most of the work having taken place in the Western Cape (Holmes *et al.* 2000; Blanchard and Holmes 2008). Their research indicates that fell-and-burn treatments have a much higher impact on community richness, cover and guild structure, than (i) fell, remove and burn, (ii) fell alone, or (iii) burn standing treatments. The respective effects of long, dense invasions and fires are not easy to distinguish from each other, as most long, dense invasions would have experienced more than two fire cycles with high fire intensities.

Richardson and van Wilgen (1986) found much lower indigenous plant cover (13.3 %) under a fell-and-burn treatment 18 months post-fire, compared to a fell, remove and burn treatment (40.8 %) and burn standing (43.3 %). Holmes *et al.* (2000) found that fell-and-burn resulted in a decrease of most functional guilds, except for non-mycorrhizal graminoids, which increased, although Blanchard and Holmes (2008) found a lower restioid cover in fell-and-burn treatments than reference or fell-and-remove treatments. Fell-and-burn had the greatest impact on shrub cover, which decreased dramatically. Obligate mycorrhizal species, like *Erica*, failed to establish after extreme fire and geophytes (although relatively persistent under invasion) are susceptible to lethal temperatures (Holmes *et al.* 2000). Serotinous species are also quickly eliminated during invasion and fire (Vlok 1996).

In long-invaded sites ephemeral forbs and grasses are first to recover (Le Maitre and Midgley 1992), and Holmes and Cowling (1997b) found that ephemeral forbs remained an important growth form in long-invaded stands. Forb cover increased in unburnt stands, and graminoids in fell-and-burn treatments (Blanchard and Holmes 2008). However, Holmes and Cowling (1997b) found that resprouters were severely reduced by invasion, making up only 2 % of cover in long-invaded stands as opposed to 42 % of uninvaded stands. Blanchard and Holmes (2008) also found the greatest decrease in resprouters under fell-and-burn treatments (half of reference site cover). Highly variable responses of resprouters to fire have been found (Bond and van Wilgen 1996), depending on fire intensity and season, with some species being strongly affected by intensity and others by season, and some species by neither. In-species response is often linked to size of plant, and high-intensity fires can also result in secondary effects through weakening of the plant, making it more susceptible to death e.g. from herbivory.

Riparian trees have a limited resilience to prolonged invasion and clearing, which appears to be largely due to their absence from soil seed banks (Galatowitsch and Richardson 2005; Reinecke *et al.* 2008), as well as a large mortality of juvenile riparian trees due to clearing (Reinecke *et al.* 2008). Blanchard and Holmes (2008) also found a decrease in small trees (3-10 m) after fell-and-burn. The decrease in shrub and trees after clearing will result in a lack of structural complexity, which will attract fewer birds and possibly inhibit recovery due to lower influx of frugivorous seed dispersal.

Although not the focus of this study, fire frequency and season also play significant roles in structuring plant communities. Short fire intervals can eliminate species, especially serotinous and overstorey species, which were not able to grow to maturity between fires (van Wilgen *et al.* 2011; Brown and Johnstone 2012). Increased fire intensities resulting from invasions will aggravate this impact. The effects of fire season are discussed in Chapter 4.

Fell-and-remove treatments thus generally best promote indigenous recovery, resulting in community compositions closest to uninvaded reference sites (Blanchard and Holmes 2008), and fell-and-burn treatments have the largest negative impact. Although the soil seed bank represents the potential for recovery, other invasion and fire impacts will also influence the post-fire environment and affect the successful establishment of a viable, functional post-fire community. Post-germination conditions are a vital determinant of the success of post-clearing recovery (see Chapter 5).

3.6 CONCLUSION

It is clear that soil seed bank densities are decreased by a fell-and-burn treatment, and that some guilds, like resprouting shrubs, are more affected than others. Seeds in the upper layer are also more affected than the deeper layer, with a significant decrease in overall density.

Whether the recovery of this system is compromised by the decrease is not certain – representatives of all guilds are still present, although in lower densities, and the soil seed bank, even at these lower densities, may still be sufficient to initiate recovery towards a functional system. It is however probable that the lowered seed densities would infer greater risk of failure should post-fire conditions be adverse. Overall biodiversity could also be diminished, making the community less resistant against disturbance (Holmes *et al.* 2000) and decreasing the inherent buffering capacity against disturbance (Richardson *et al.* 2007). This will have to be verified by in-field monitoring. Defining an acceptable structural and functional reference level of either the soil seed bank or standing vegetation in riparian systems is difficult due to their inherently dynamic nature (Richardson *et al.* 2007), and the lack of data on reference uninvaded riparian grassy fynbos soil seed banks makes it even more problematic. This question can only be answered through in-field monitoring over time.

A frequent recommendation in cases where the soil seed bank is depleted is to create seed sources to restock the degraded site (Holmes *et al.* 2005; Vosse *et al.* 2008) especially where surrounding sources of propagules are not present. However, high-intensity fires may render the post-fire environment unreceptive for the establishment of seedlings, even where seed sources are available (Madrigal *et al.* 2010). Korb *et al.* (2004), implementing seeding trials after fell-and-burn, doubled their success by using seeds and living soil (soil from intact vegetation).

Ultimately, managers have to weigh up constraints and costs of slash removal against environmental impacts, or attempting to rather burn standing, which has other risks attached. This study also underscores the importance of clearing light invasions or preventing the accumulation of biomass, to avoid repeated high-severity fires and associated damage to soil seed banks. It also recommends that serious attention be given to attempting to find other solutions to controlled burning to get rid of biomass. New avenues for this could be explored, e.g. in the carbon-market, where removal of biomass may gain carbon credits and subsidise the removal process.

4 THE TEMPORAL PATTERNS OF SEEDLING EMERGENCE IN GRASSY FYNBOS

4.1 INTRODUCTION

The freshwater component of South Africa's National Spatial Biodiversity Assessment highlights that some 84 % of South African freshwater ecosystems are threatened, with some 54 % critically endangered (Nel *et al.* 2007). One of the main threats to freshwater ecosystems is the invasion by woody alien species, which replace indigenous vegetation and alter ecosystem functioning. Mediterranean-type ecosystems, including fynbos, are particularly threatened (Hobbs 2004). Riparian systems have been shown to be fairly resilient, and regeneration of fynbos usually takes place without active intervention after IAPs have been removed (Blanchard and Holmes 2008; Holmes *et al.* 2005, 2008; Reinecke *et al.* 2008). However, in some situations this is not the case, especially in long- and densely-invaded areas (where IAP densities exceed 75 %), where areas have experienced more than three fire cycles under invasion, and where the indigenous soil seed bank has been depleted (Holmes and Cowling 1997a). This significantly impacts on the functioning and ability of these riparian systems to deliver ecosystem services such as water yield, flood attenuation and reduction of siltation. Restoration of these systems to re-instate basic ecological functioning and habitats is therefore crucial, especially if South Africa is to meet its target of maintaining 20 % of its freshwater ecosystem types in a natural state, as proposed in the freshwater cross-sector policy (Roux *et al.* 2006).

In these cases the riparian systems will require active restoration to recover (CSIR 2000; Holmes *et al.* 2005, 2008; Blanchard and Holmes 2008; Reinecke *et al.* 2008), and understanding the reproductive regeneration strategies is thus an important component of active restoration.

4.1.1 Reproductive ecology

Fynbos, which comprises most of the Cape Floristic Region (Mucina and Rutherford 2006), is a Mediterranean-climate vegetation type, sharing many reproductive traits with other

Mediterranean shrublands (Ojeda *et al.* 2001; Rundel 2004; Gómez-González 2011, Keeley *et al.* 2011), although it also has many species with unusual reproductive traits (Le Maitre and Midgley 1992). It is a fire-prone vegetation, and fire regimes have largely shaped the demography and life-history traits of the vegetation, such as resprouting and regeneration from persistent canopy- and soil-stored seed banks as the main strategies to survive frequent fires and persist in the landscape (Bond and van Wilgen 1996). The majority of species have soil-stored seed banks, and their survival mechanisms and regeneration strategies, especially vital attributes like seed longevity, specific dormancy mechanisms and germination cues, are largely unknown (Brown and Botha 2004; Figueroa *et al.* 2004; Moreira *et al.* 2010; Thomas *et al.* 2010).

Although a significant proportion of species can recruit in the absence of fire (Keeley 1991), many species in Mediterranean climates, including fynbos, need fire-related cues to recruit (Kruger 1983; Le Maitre and Midgley 1992; Ojeda *et al.* 2005; Moreira *et al.* 2010). Fire is therefore necessary to maintain diversity, as many species (at least 70 %) recruit from persistent seed banks after fire (van Wilgen and Forsyth 1992). Germination is triggered directly by fire-related cues such as heat, smoke or charred wood (Keeley and Fotheringham 2001; Thomas *et al.* 2003, 2010; Figueroa *et al.* 2004, 2009; Moreira *et al.* 2010) or indirect fire cues such as post-fire alterations in soil micro-climate, especially greater fluctuations in temperature (Brits 1986).

It is generally accepted that germination is restricted to a short time period following fire and with the first rains (Quintana *et al.* 2004; Moreno *et al.* 2011). The advantages of this response is that it allows seedlings to establish in conditions of reduced competition for resources such as light and moisture, and to benefit from a post-fire flush of nutrients (Kruger and Bigalke 1984; Keeley 1986; Stubbs and Pyke 2005; Buhk *et al.* 2007). Seedling survival and growth is therefore favoured by rapid seedling emergence (Verdú and Traveset 2005), reduced competition and increased availability of resources (Moles and Westoby 2004; Thanos 2004). Where rainfall is seasonal, the probability of suitable conditions at the onset of moisture availability (rain) is high, and Mediterranean species have therefore developed a favourable germination response to low autumn temperatures, which signals the onset of winter rains (Keeley 1991; Knox and Clarke 2006). This temperature envelope often has a very narrow range (Baskin and Baskin 1998). Germination therefore generally takes place during the first rainy season after fire, from early autumn to late spring, and thus often occurs with the first significant rainfall event (De Luis *et al.* 2008b; Céspedes *et al.* 2012; Moreno *et al.* 2011). The interaction of fire and the reliable rainfall patterns which distinguish Mediterranean climates have therefore selected for particular plant reproductive traits (Kruger 1983; Baker *et al.* 2005), defined by synchronous post-fire germination and rapid post-fire growth of most seedlings as soon as moisture becomes available (Cowling *et al.* 2005; Traba *et al.* 2006). Although germination in Mediterranean climates is normally triggered by the first rains (Quintana *et al.* 2004), the optimum temperature for germination varies between species (Baskin and Baskin 1998). Post-fire germination is therefore not synchronous for all species in Mediterranean climates, and the timing of germination after fire and once exposed to moisture varies between species, depending on their specific germination requirements (Baker *et al.* 2005; Reyes and Trabaud 2009; Moreno *et al.* 2011). This can result in a variation in timing of germination of several months.

De Luis *et al.* (2008a, b) have found that germination can even be delayed into the second and third year. However, survival of seedlings germinating during the first year is much higher than germination in subsequent years (Quintana *et al.* 2004; De Luis *et al.* 2008b). This varies between species and guilds; for example, the survival benefit of early emergence is greater in perennial than in annual species (Verdú and Traveset 2005). Delayed or phased emergence has the advantage of spreading the risk of failure in the event of unfavourable post-fire conditions (Verdú and Traveset 2005), but seedlings face increased competition from co-occurring seedlings and resprouters (Knox and Clarke 2006). Delayed emergence has been shown to reduce the growth and survival of plants (Quintana *et al.* 2004; Verdú and Traveset 2005; Ooi 2010; Moreno *et al.* 2011). Later emergence also means seedlings are smaller and have fewer reserves by the following dry season, and time to maturity is increased as well. Recovery of seed banks will therefore also be slower.

Not much is known about germination controlled by seasonal variations in temperature in fire-prone regions with aseaonal rainfall (Thomas *et al.* 2010), such as South-east Australia (Ooi *et al.* 2006; Ooi 2010), Eastern Australia (Knox and Clarke 2006) and Florida (Carrington and Keeley 1999). In these environments, evidence exists that some species can germinate immediately after fire, while others delay until additional germination requirements are fulfilled (Baskin and Baskin 1998; Ooi *et al.* 2004; Auld and Ooi 2008; Ooi 2010, Thomas *et al.* 2010). The variation in timing of germination can be attributed to ambient temperature and rainfall patterns as well as seed dormancy mechanisms (Ooi 2010). Delayed seedling emergence appears to occur in species with enforced dormancy mechanisms and innate seasonal germination requirements (Ooi 2010; Thomas *et al.* 2010; Moreno *et al.* 2011). The eastern extent of the fynbos biome is similar to the environments described above, in exhibiting a more variable and aseasonal rainfall pattern, with bimodal spring and autumn peaks (Kruger 1979). Little is known about the temporal germination patterns of fynbos species in this area.

Seedling emergence is one of the most crucial stages in the life-history of plants, and survival can be critically dependent on the timing of germination (Quintana *et al.* 2004; De Luis *et al.* 2008b). Soil moisture is probably the most important factor determining survival (Moreno *et al.* 2011), and under dry conditions mortality of seedlings can be very high during the first few months of germination (Quintana *et al.*, 2004). Climatic conditions after fire thus play a significant role in triggering germination and regulating mortality in seedlings, although this response is species-specific. The differential sensitivity of species to drought during the post-fire climate can determine the structure and composition of post-fire plant communities (Moreno *et al.* 2011). As the timing of emergence affects the recruitment success of individual species and cohorts, this in turn will determine successional trajectories and the composition of subsequent populations (Pyke *et al.* 2010). An understanding of temporal patterns of recruitment after fire, and the various biotic and abiotic variables that influence these patterns, are thus crucial in understanding community development (Céspedes *et al.* 2012) and should be a prerequisite for restoration. For example, reintroductions may be confounded by introducing seeds with different rates of germination, as slower-germinating species may be disadvantaged. Also, successful seed germination depends on suitable microsite requirements, which may influence the availability of appropriate germination cues at the right time (Satterthwaite 2007; Uriarte *et al.* 2010; Frei *et al.* 2012).

Since fire plays such an important role in the regeneration of fynbos, an understanding of all the components of a fire regime and its impacts and interaction on biotic components is required for fire management (Auld and Ooi 2008). This often results in a series of complex decisions and trade-offs, to achieve the desired outcomes (van Wilgen *et al.* 2011). Although strong fire-cued germination in many taxa has been found, there is a still a limited knowledge of fire response and the fire-related dynamics of soil seed banks. A knowledge of the timing of germination is important for fire management (Auld and Ooi 2008; Heelemann *et al.* 2008; Pyke *et al.* 2010), and little is known about the seasonal timing of emergence from soil seed banks (Ooi *et al.* 2004).

4.1.2 Persistence, dormancy and germination

Seed dormancy is defined as "an innate seed property that defines the environmental conditions in which the seed is able to germinate" (Finch-Savage and Leubner-Metzger 2006). Seeds of many fynbos species are dormant when shed, and require specific dormancy-breaking mechanisms and germination cues before they will germinate (Brown 1993), making propagation from fynbos seeds often difficult (Brown and Botha 2004). Seed dormancy is one of the most important adaptive traits in plants (Penfield and King, 2009), by timing receptiveness to germination stimuli during the most favourable conditions (Fenner and Thompson 2005). Dormancy mechanisms can diminish over time (Baskin and Baskin 1998) and a wider range of conditions become suitable for germination (Hilhorst 1998).

Applying the right germination cues at the right times can make the difference between success and failure (Thompson and Ooi 2010) in restoration. Dormancy is often incorrectly equated with lack of germination (Fenner and Thompson 2005), and understanding the difference between dormancy release and germination cues is critical in restoration ecology (Vleeshouwers *et al.* 1995; Thompson and Ooi 2010). Failing to do so may result in germination cues applied to dormant seeds and therefore not achieving germination, which in turn results in erroneous conclusions about germination cues, as well as wasting efforts and resources such as seeds, and possibly resulting in failure during active restoration. Dormancy is usually defined as failure of a viable seed to germinate under favourable conditions (e.g. with enough water and light) (Vleeshouwers *et al.* 1995). According to

Vleeshouwers *et al.* (1995) only temperature, and according to Merritt *et al.* (2007) only time, temperature and moisture have been conclusively proven to alter the degree of dormancy, and factors like light, smoke and nitrate in fact only serve to promote germination once a release of dormancy has taken place. However, there appears to be a long-standing and entertaining debate around this issue; in the words of Vleeshouwers *et al.* (1995) "it is surprising that dormancy is not seen as a controversial subject" and this issue obviously remains a source of controversy and confusion (Finch-Savage and Leubner-Metzger 2006). As late as 2010, Thompson and Ooi (2010) still made the following statement: "How could anything so simple be misunderstood…?". Many authors (Keeley and Bond 1995; Figueroa *et al.* 2004; Bond and Keeley 2005; Kulkarni *et al.* 2007) still appear to use the concepts "dormancy release" and "germination cues" interchangeably, which complicates the interpretation of their results, and could compromise the application of their findings in conservation and restoration management.

Dormancy and persistence are also sometimes confused, but dormancy is not a predictor or necessary condition of persistence or the accumulation of a persistent seed bank (Thompson *et al.* 2003). Seeds in persistent soil seed banks may exhibit cyclical dormancy, with increased and decreased dormancy for years or decades without germination, until they experience a favourable cue that the environment is suitable during a (relatively) non-dormant stage (Thompson and Ooi 2010). For example, cycling of physiological dormancy can result in deeper dormancy during winter and no dormancy during summer (Thomas *et al.* 2010). Germination can occur when fire cues are received during a time when dormancy is not present (Baker *et al.* 2005; Merritt *et al.* 2007), which will restrict post-fire germination to cool wet seasons.

The above concepts and definitions are very relevant for interpreting the dynamics of soil seed banks and have implications for management and restoration. Timing of germination and the factors controlling germination affects recruitment success (Céspedes *et al.* 2012), which has been identified as one of the most important components regulating the development of plant communities.

4.1.3 Dormancy, germination cues and the timing of germination

The type of dormancy will determine germination responses to fire cues and the temporal emergence patterns (Ooi et al. 2004; Ooi 2010). Little information is available on the full range of germination responses for most species and Auld and Ooi (2008), in the aseasonal climate of South-eastern Australia, group species into three main germination response categories. The first, consisting of Fabaceae and some other species such as *Dodonea* (Ooi 2010), have physically dormant seeds. These seeds require heat to break dormancy, and will then germinate with the first rain. Physically dormant seeds are stimulated directly by the heat from fire, although the optimum range of temperatures varies between species (Penman et al. 2008). This is mostly the case for hard-coated species (Keeley and Bond 1997; Jeffery et al. 1988; Kulkarni et al. 2007), for example species in the Fabaceae family like *Otholobium* and *Psoralea*, *Phylica* and *Searsia* (Killian and Cowling 1992), as well as *Agathosma* and other Rutaceae, *Hermannia* and some *Leucadendron* and *Erica* species. Some Restionaceae species may also require a heat cue (Keeley and Bond 1997). This process is irreversible once dormancy is broken (Baskin and Baskin 1998).

The second group possess physiological dormancy or water-permeable seeds, and germination is often enhanced by smoke or a combination of smoke and heat. Fire-linked cues such as smoke and heat are common germination cues for many fynbos species (de Lange and Boucher 1990; Keeley and Bond 1997; Penman et al. 2008). Brown and Botha (2004) tested the response of a wide range of fynbos species to smoke, and found a positive response in 161 species out of the 283. These include representatives in all the major fynbos families of Ericaceae, Asteraceae, Boragniaceae, Fabaceae, Lobeliaceae, Loganiaceae, Polygalaceae, Campanulaceae, Scrophulariaceae, Apiaceae, Thymelaceae, Geraniaceae and Poaceae.

In the last group, the mechanisms controlling germination are not known, and seeds from this group exhibit variable responses to smoke or heat. Many of the Ericaceae and Rutaceae occur in both the above groups. It is estimated that physically and physiologically dormant shrub species co-exist in approximately equal proportions in many fire-prone regions (Baskin and Baskin 1998; Ooi 2010), and that both types of dormancy can result in the formation of long-lived seed banks. A consistently greater survival of co-occurring physically dormant species has been found (Auld and Ooi 2008), where seedlings can emerge quickly and timing of emergence is independent of the fire season, although numbers can be lower in winter. This may be related to the findings of De Luis et al. (2008b), where early emergence of species results in higher survival, growth rates and fecundity.

Physiologically dormant seeds have immature embryos when shed, and require time to develop (Ooi et al. 2006). This physiological dormancy is overcome through seasonal temperature changes and this controls the timing of germination. Germination of physiologically dormant seeds will occur if fire cues are received during a non-dormant phase, but not when seeds are in a dormant phase (Baker et al. 2005; Merritt et al. 2007). Fires occurring at different times in the year may therefore affect a different proportion of non-dormant seeds than fires at other times, depending on the physiological dormancy status of the seeds (Céspedes et al. 2012), which will influence successional trajectories. Physiological dormancy is not broken by fire cues, but germination is enhanced through smoke once this dormancy is overcome. In these species the time of emergence or delay since the fire will depend on the season of fire (Ooi et al. 2004; Céspedes et al. 2012), and the delay is therefore not a constant time-since-fire response.

With more than 9 000 plant species in the Cape flora, it is an almost impossible task to determine dormancy traits and germination requirements of all species, and little information is available on the species recorded during this study. The timing of germination, as investigated during this study, gives clues to the germination ecology of species, including dormancy and germination requirements, succession and community development. This in turn will allow better predictions of vegetation dynamics (Bond 1984) and inform the process of active restoration. The active re-introduction of species should take place according to natural community development processes and dynamics (Lockwood and Samuels 2004). An understanding of system-specific steps in community recovery can inform management decisions regarding active restoration, as the timing of the introduction of a species can affect the succession and composition of the restored system (McClain *et al.* 2011). Knowledge of phenology can therefore also aid the design of an invasion-resistant community (D'Antonio and Chambers 2006).

4.2 AIMS AND OBJECTIVES

This study sought to investigate the temporal patterns of post-fire germination of the persistent soil seed bank of grassy fynbos in a riparian zone, as well as the factors which determine the timing of germination.

4.2.1 Aims

1. Investigate the patterns of emergence of species from the persistent soil seed bank after a simulated fire in grassy fynbos.
2. Determine whether all seedlings recruit in the first year following fire-related cues, following the IFC model (Egler 1954; Kruger 1983; Le Maitre and Midgley 1992; McClain et al. 2011)?
3. Is the timing of germination restricted to the typical fynbos phenological pattern where germination takes place in the rainy autumn to winter season (Kruger 1983; Cowling et al. 2005), or is there a wider germination window, shifting towards spring and summer?
4. Is there potential to manipulate the temporal patterns of emergence to direct succession?

4.2.2 Hypotheses

1. Seeds in the soil seed bank will exhibit synchronised germination within the first two months after fire, followed by available moisture (as a typical germination response of Mediterranean-type vegetation)
2. Seedling emergence from the 0-4 cm and 4-8 cm soil layers will follow a similar temporal pattern of emergence, but the number of emergents from the 4-8 cm layer will be lower than that from the 0-4 cm layer.
3. Emergents from the same guilds will exhibit a similar temporal pattern of emergence.

4.3 MATERIALS AND METHODS

The field methods described in Section 2.3 were applied.

4.3.1 Analysis

The data collected as described in Chapter 2 were analysed from a phenological perspective. Seedlings were categorised into guilds according to growth form and functional groups (geophytes, forb, graminoid, shrub, riparian, annual and short-lived perennial, and alien; following Holmes *et al.* 2000). Since there was considerable interspecific variation within guilds, the herbaceous, shrub and riparian guild were also analysed to species level.

An information theoretical approach (Burnham and Anderson 2002, 2004; Johnson and Omland 2004) was used to evaluate the fit of alternative models to explain seed germination relative to time (with month being a proxy variable for environmental differences over time) and quadrat. Model selection was based on Akaike's Information Criteria (AIC) (Burnham and Anderson 2004; Johnson and Omland 2004).

Analyses of individual variables used means for all quadrats per depth, guild and month. This mitigated the effects of the many statistical outliers and zero counts thereby reducing the very large amount of variation in the data. Even then, normality could not be achieved with any transformations so non-parametric analyses were used. For all analyses, seedling count was the dependent variable and depth, guild and month were analysed separately with data collapsed across all independent variables except the one of interest. Depth was analysed using Wilcoxon matched pairs test and Friedman tests were used for month and guild.

4.4 RESULTS

Germination was significantly higher in some months compared to others (Friedman: χ^2 = 253.391, n = 70, df = 10, p < 0.00001), with the highest emergence in March (1 306 seedlings) followed by December (1 227 seedlings) and the lowest in November (16 seedlings) and August (45 seedlings) (Figure 4.1).

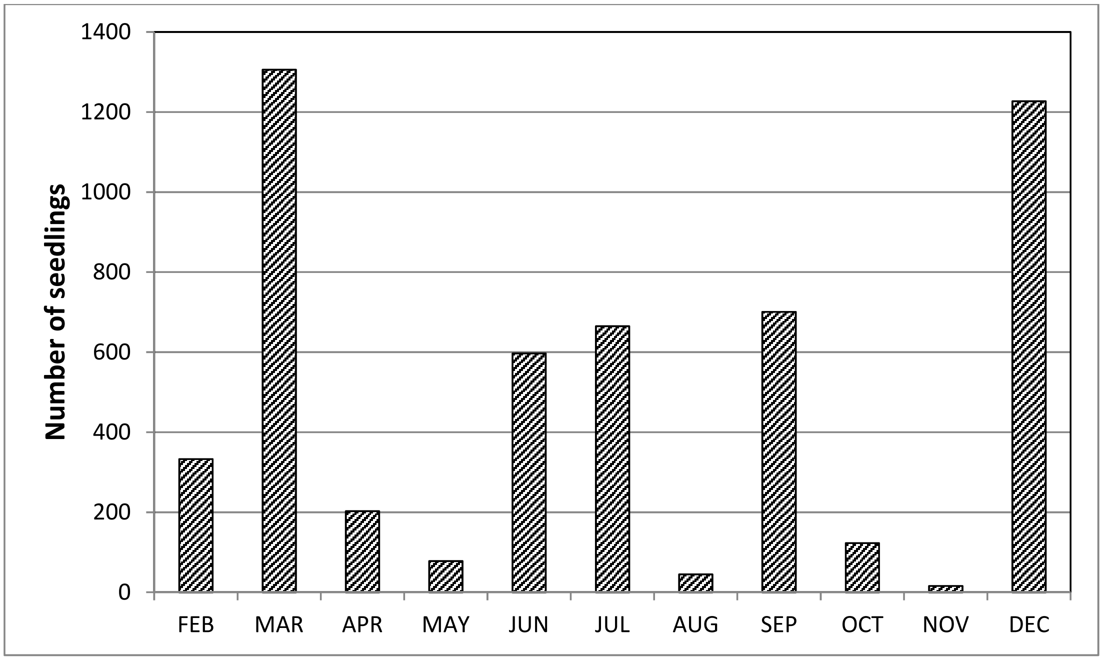


Figure 4.1. Emergence of seedlings in all guilds during 2005

There was a significant difference in germination of alien species over time ($p < 0.001$), with an emergence peak of 333 seedlings (mainly *Solanum nigrum*) in February and declining in March (209 seedlings) (*S. nigrum* and *Conyza canadensis*). Reduced emergence (< 100 seedlings) was recorded for the rest of the year, except for another peak in September (225 seedlings). Emergence of annual and short-lived perennial species were significantly higher in the early months of the year with a peak of 920 seedlings in March, mainly due to the emergence of *Conyza pinnata* and *Senecio rigidus* seedlings, and less than 70 seedlings per month for the rest of the year. There was a significant difference between emergence over time ($p < 0.001$).

Very few geophyte species were recorded, although the main emerging geophyte (*Hypoxis argentea*) contributed considerably to the total seedling count. It emerged mainly in the winter months (56 seedlings), and into early spring (29 seedlings). Herbaceous species also showed a significant difference in germination in time ($p < 0.001$) (Table 4.2). Since individual species numbers were low, seedling emergence in time was grouped according to seasons. Although some emergents were almost completely confined to one season, e.g. *Lobelia tomentosa* and *Helichrysum cymosum* (winter), and *Cheilanthes viridis* (summer), most others had germination spread over two seasons, e.g. *Chironia baccifera* (spring and summer) and *Selago corymbosa* (autumn and winter). Most of the germination of the herbaceous species occurred in winter (490 seedlings) and summer (545 seedlings), although the summer germination is reduced to 292 seedlings if *C. viridis* is removed (being a fern). Only one annual, *Sebaea micracantha*, was recorded, with the remainder being perennial species. The greatest range, with a reasonably high germination rate, was exhibited during winter.

Emergence from the upper 0-4 cm layer was much higher for some species, e.g. *Selago corymbosa*, *Helichrysum petiolare*, *H. cymosum* and *L. tomentosa*, than from the deeper 4-8 cm layer (Table 4.1). In the case of *S. corymbosa*, this was pronounced in the autumn season, with 131 seedlings in the 0-4 cm zone, as opposed to 15 seedlings from the deeper 4-8 cm layer.

Table 4.1. Number of herbaceous seedlings emerging per depth per season

Species	Depth (cm)	Autumn	Winter	Spring	Summer	Totals
H. petiolare	0-4	8	65	9	4	86
	4-8	20	40	7	2	69
C. baccifera	0-4	3	2	85	107	197
	4-8	8	4	76	115	203
S. corymbosa	0-4	131	38	4	1	174
	4-8	15	28	4	1	48
S. micracantha	0-4	0	3	11	20	34
	4-8	0	2	21	22	45
H. cymosum	0-4	0	55	0	2	57
	4-8	6	36	2	6	50
H. epapposum	0-4	0	14	5	4	23
	4-8	0	21	3	1	25
A. herbaceum	0-4	7	42	3	4	56
	4-8	18	42	1	2	63
L. tomentosa	0-4	0	66	6	1	73
	4-8	0	32	2	0	34
C. viridis	0-4	0	0	0	132	132
	4-8	0	0	2	121	123

Other species, such as *C baccifera* and *C. viridis,* had a similar emergence from both the shallow and deeper layer, whereas species like *S. micracantha* and *H. epapposum* had a slightly higher emergence from the deeper layers (Table 4.1).

Significant differences in germination were also exhibited in the shrub guild ($p < 0.001$) (Table 4.2). The two Erica species, *Erica caffra* and *E. chamissonis*, and *Halleria lucida* contributed most to the shrub guild. However, more *E. caffra* seedlings germinated from soil taken from the deeper 4-8 cm (45) layer than the upper 0-4 cm layer (29) (Table 4.2). In contrast, *H. lucida* had more seedlings emerging from soil from the upper 0-4 cm layer (75) compared to the deeper 4-8 cm layer (14). *H. lucida* mainly germinated in winter and spring, while the two *Erica* species mainly germinated in spring and summer. Very few *Chrysanthemoides monilifera* and *Psoralea pinnata* seedlings emerged.

In the riparian guild, emergence was almost entirely confined to the winter months of June and July (Cyperaceae) and December (mostly due to the germination of Rumohra adiantiformis spores, with 257 sporophytes from the 0-4 cm layer and 85 sporophytes from the 4-8 cm layer in summer).

Table 4.2. The number of shrub seedlings emerging per depth per season

Species	Depth (cm)	Autumn	Winter	Spring	Summer	Totals
E. caffra	0-4	0	2	8	19	29
	4-8	0	0	7	38	45
E. chamissonis	0-4	0	0	38	48	86
	4-8	0	2	29	26	57
H. lucida	0-4	0	36	39	2	77
	4-8	0	9	4	1	14
C. monilifera	0-4	0	1	0	0	1
	4-8	0	1	0	0	1
P. pinnata	0-4	0	0	1	0	1
	4-8	1	0	1	0	2

Figure 4.2. Timing of emergence of dominant indigenous soil seed bank species (a = annual and short-lived perennial, h = herbaceous, se = sedge, sh = shrub, g = grass, f = fern)

Species	**Jan**	**Feb**	**Mar**	**Apr**	**May**	**Jun**	**Jul**	**Aug**	**Sep**	**Oct**	**Nov**	**Dec**
Senecio rigidus (a)			▨									
Conyza pinnata (a)			▨									
Selago corymbosa (h)			▨		▨	▨						
Anthospermum herbaceum (h)			▨		▨							
Helichrysum petiolare (h)				▨	▨	▨	▨					
Helichrysum sp .(h)				▨	▨	▨	▨					▨
Helichrysum cymosum (h)						▨	▨					
Ficinia oligantha (se)						▨	▨	▨				
Cyperus esculentis (se)						▨	▨	▨				
Isolepis prolifer (se)							▨					
Isolepis cernua (se)							▨					
Hypoxis argentea (h)							▨	▨	▨			
Helichrysum epapposum (h)							▨	▨	▨			
Lobelia tomentosa (h)							▨	▨	▨			
Halleria lucida (sh)							▨	▨	▨	▨		
Eragrostis obtuse (g)									▨			
Chironia baccifera (h)									▨	▨	▨	▨
Sebaea micracantha (h)									▨	▨	▨	▨
Erica chamissonis (sh)									▨	▨	▨	▨
Erica caffra (sh)									▨	▨	▨	▨
Cheilanthes viridis (f)												▨
Rumohra adiantiformis (f)								▨				▨

Overall, there was a clear sequence in the pattern of emergence over time between guilds (Figure 4.2). Alien species emerged first, peaking during the months of February and March. Annual and short-lived perennial species followed, peaking during March. Most herbaceous species germinated during the winter months of June and July, spring, and with a high emergence in December, mostly due to the emergence of fern sporophytes. Geophytes (mainly *Hypoxis argentea*) mainly emerged in winter and spring, and the highest number of shrub seedlings emerged during July, the spring months of September and October, as well as in December.

4.5 DISCUSSION

4.5.1 Temporal pattern of emergence

The study revealed very distinct patterns of emergence for different species and guilds after a simulated fire (smoke treatment) and rainfall. Although there is an initial flush of germination soon after the smoke treatment, this flush consists of ruderal, weedy and invasive species. This is followed by a species-specific sequence of germination which is spread throughout the year, with cohorts of emergents germinating during a few months of the year. Emergence of some species, guilds and growth forms is confined to certain seasons, i.e. Cyperaceae in winter and ferns in summer, whereas forbs and shrubs do not appear to conform to specific seasons, but exhibit species-specific germination patterns. Other authors have found similar patterns of timing of emergence; e.g. Reyes and Trabaud (2009) found that four out of 14 species germinated within ten days after fire, while the other ten species germinated over the next 18 to 38 days. However, they found that the slower-germinating species consisted mainly of trees or shrubs.

It can thus be inferred that the timing of germination of most of the species found during this study is not limited to an immediate post-fire flush of germination after fire, but is restricted to certain seasons, and is thus probably controlled by ambient temperatures. This has been found in other fire-prone areas with aseasonal or summer rainfall/winter drought patterns, which have physiognomically similar vegetation to Mediterranean-type climates (Carrington and Keeley 1999; Ooi *et al.* 2004; Ooi 2010; Thomas *et al.* 2010). In South-eastern Australia, which has an aseasonal rainfall, many species germinate in any season after exposure to fire cues as long as adequate soil moisture is available, while others have strong seasonal germination requirements and exhibit delayed emergence irrespective of rainfall (Ooi *et al.* 2004, 2006; Merritt *et al.* 2007; Auld and Ooi 2008; Ooi 2010). Thomas *et al.* (2010) found germination after fire in South-eastern Australia cued by ambient temperature and to take place mainly in the wet season. However, they also found some germination to take place in the warm season, to take advantage of early establishment and to spread the risk of failure. Carrington and Keeley (1999) have had similar results in a summer-peak rainfall area in Florida. Here, germination was cued to spring, just before summer rains, even though Florida does not experience a drought season. The time of germination was independent of the fire event, and in some species a delayed emergence of up to 10 months after the fire was recorded (Carrington and Keeley 1999). Knox and Clarke

(2006), in a temperate summer rainfall habitat, found increased seedling emergence after spring fires and reduced emergence after autumn fires, as a result of colder temperatures.

As the period of germination and early establishment is the time when a plant is probably most vulnerable, the timing of germination is a critical aspect for survival (Fenner and Thompson 2005). In early succession, physical stress is an important factor (Walker and del Moral 2008). There is a trade-off between germinating too early (and possibly being killed by drought) or too late (and entering an environment already crowded by seedlings that germinated earlier). Cowling *et al.* (2005) hypothesised that the phenomenon of post-fire germination cued with reliable rainfall will be less advantageous under a non-seasonal, unpredictable rainfall regime, as prolonged dry spells could result in high seedling mortality and a high risk of extinction. One of the strategies to deal with the above dilemma is to spread germination over time to avoid the risk of total failure, even if some early- or late-germinating offspring have a low probability of success, and it appears that some species in this study, e.g. *H. petiolare* and *H. lucida*, have adopted this strategy by spreading germination over up to four months. This may be a safer regeneration strategy in the eastern part of the fynbos biome where rainfall and fire events are unpredictable. The work of Heelemann *et al.* (2008) on recruitment of Proteaceae in the Eastern Cape confirms this, where recruitment patterns of Proteaceae after fire differ significantly from those observed in the western and central Fynbos biome. No optimal fire season was identified, but the most favourable recruitment period was during late summer to autumn and late winter to early summer. These periods coincide with the bimodal rainfall peaks. It also appears that the pattern of germination observed in this study is an expression of the transitional nature of the climate and vegetation; between the winter rainfall of the Western Cape and true Mediterranean vegetation, and the bimodal to summer rainfall regime of the Eastern Cape.

Although competitive interactions can determine the successful establishment of seedlings, facilitation can also play a significant role (Li *et al.* 2012). Nothing is known about specific facilitation effects of the species recorded during this study, and the role that the timing of germination of different species plays in successful recruitment and community development, and will require more research. Competition and facilitation may vary with life-history stage within successional communities (Walker and del Moral 2008); for example, the presence of woody vegetation can favour seed germination but inhibit seedling growth. It is also likely that guilds such as the ferns would only recruit successfully once more favourable microsite conditions (Karst *et al.* 2005) have developed through the establishment of other species. Galatowitsch and Richardson (2005) hypothesise that riparian scrub seeds will not establish in open environments, but can only establish successfully after an initial pioneer layer, consisting of forbs and shrubs, has established. This pioneer layer will stabilise the soil and protect subsequent plants from exposed and extreme conditions. Annual and short-lived perennial (pioneer) species were early emergents during this study, but it is not certain that the same sequence would have been followed after a differently timed fire.

The timing of emergence from seed is also important in terms of interaction with other modes of recruitment, as resprouters are less at risk of failure of recruitment, and also do not relinquish occupied space to competitors after fire, while seeders do (Moreno and Oechel 1991). Later emergence will increase competition from resprouters and influence the survival of seeders and therefore the post-fire plant community (Céspedes *et al.* 2012). In Mediterranean climates, rainfall is strongly seasonal and dormancy-induced seasonal emergence is closely synchronised with moisture availability. Post-fire emergence and resprouting therefore occur more or less concurrently (Carrington and Keeley 1999) and interactions between resprouters, emergents and moisture availability are difficult to separate. Bond (1984) did not find reduced survival of several *Protea* species as a result of earlier resprouter emergence during aseasonal fires, but the earlier emergence of resprouters took place during the dry season, and it is possible that the lack of moisture would have reduced the competitive effect of the resprouters during that period. It is hypothesised that by manipulating the fire season, competitive interactions between various species can also be manipulated to direct succession towards a desired plant community (Section 4.5 and Chapter 5).

A fire in a different season will therefore probably result in a completely different order of emergence with different competitive interactions, successional trajectories and community composition. For example, after a fire in July, *Erica* spp. may be one of the first instead of last species to germinate. The significance and possible application of this principle is discussed further in Chapter 5, and requires further research, either through controlled experiments or in-field observations of emergence after fires (see Section 5.5).

4.5.2 Dormancy, germination cues and the timing of germination

The results from this study indicate that physically dormant indigenous seeds, mainly Fabaceae, are absent or occur in very low densities in the soil seed banks under long-invaded wattle stands. It is probable that these seeds have largely been eliminated from the soil seed bank, since they have fairly straightforward germination responses, germinating after heat cues with the availability of moisture. This process is irreversible once set in motion, and indigenous Fabaceae would have responded in a similar manner to *A. longifolia* during previous fire cycles. Since they are not as vigorous as *A. longifolia*, they would be outcompeted, would not set seed and thus be eliminated from the soil seed bank if follow-up of *A. longifolia* did not take place in time. Physiologically dormant seeds have more exacting germination requirements, and it is likely that only part of the physiologically dormant soil seed bank germinated during previous fire cycles since not all dormancy-breaking and germination cues were present at the receptive time. Seeds would have therefore persisted in the residual soil seed bank. It can be assumed that the remainder of the species that were recorded during this study belong to the remaining two groups of physiologically dormant seeds and seeds with unknown dormancy and germination cues.

The germination requirements of many species in riparian fynbos will also be linked to disturbance events of either flood or fire, for example many riparian species require wet, bare surfaces for germination; these are generally available after floods or channel migration (Kalliola *et al.* 1991). The timing of germination must therefore correspond to the flooding season if seeds want to recruit successfully in the post-flood environment (Leck 1989). The interaction of the hydrological regime with timing of seed release and transport is thus important (Merritt and Wohl 2002). Alterations to either factor can affect whether propagules reach safe sites for establishment (Temperton and Zirr 2004), and species with more specific habitat requirements for establishment will be least resilient to changes in hydrology or geomorphology. It is not known how the reproductive ecology and regeneration dynamics of the species recorded during this study interact with the hydrological regime.

I propose that the type of seed dormancy and germination response displayed by different species in the soil seed bank could also play an important role in recovery and achieving biotic resistance, and this will be discussed further in and Chapter 5.

4.5.3 Fern soil spore banks

The two dominant fern species, *Cheilanthes viridis* and *Rumohra adiantiformis*, had very clear emergence peaks, with almost all of their development into sporophytes taking place in December. There are very few studies on the germination of fern spores and these mostly concentrate on spores in vitro. No information could be found on fern soil spore banks in South Africa. Although more information is available from other parts of the world, data on the fern soil spore banks are still poor, especially regarding the natural patterns of germination of spores (Ramirez-Trejo *et al.* 2004; Hock *et al.* 2006). Spore dispersal occurs mostly in the summer months (Hock *et al.* 2006). Most studies have reported light and high minimum temperatures as requirements for germination of spores (During and ter Horst 1983; Hock *et al.* 2006). This is assumed to impose dormancy until late spring or summer, following spore dispersal (Pangua *et al.* 1994; Hock *et al.* 2006). Other factors such as microbial activity and possible degradation of inhibitory substances can also play a role in dormancy and germination cues.

Dormancy may also influence variation in germination patterns of soil spore banks as increased emergence has been found in soil after one year of storage as compared to samples stored for six months (Hock *et al.* 2006), similar to many soil-stored seeds. It appears that cold induces dormancy (Dyer and Lindsay 1992).

4.5.4 Longevity and persistence

Longevity is reflected in the vertical distribution of seeds in soil (Holmes and Newton 2004) and evidence indicates that more deeply buried seeds are older than seeds closer to the surface. The ratio of seeds or spores in upper and lower layers can therefore be used as an indicator of longevity (Bekker *et al.* 1998), although soil may be disturbed and not remain in the same sequence as it was deposited, thus making this assumption suspect. Little data is available in the literature on the longevity of the seeds of most fynbos species, and none on the species recorded during this study. High emergence from the deeper layer was found for the wind-dispersed *S. rigidus* and *C. pinnata*, indicating persistence rather than recent arrival. No information could be found on the longevity of either *Rumohra* or *Cheilanthes* in other areas; however, large numbers of sporophytes of both species emerged from the deeper layers, e.g. 53 % of *Rumohra* sporophytes from the lateral zones outside the WB (see Chapter 2), which indicates that these were therefore not recently deposited through floods and are therefore persistent. Studies from other parts of the world have reported the longevity of fern soil spore banks, with spores remaining viable for decades and spores only germinating when exposed to light (Dyer and Lindsay 1992; Herrero *et al.* 2002; Ramirez-Trejo *et al.* 2004). Hock *et al.* (2006) found increased germination of fern spores with storage, although Dyer (1979) found decreased viability with increasing age. In addition, little is known about the vertical distribution of spore banks, but Ramirez-Trejo *et al.* (2004) reported viable spores up to depths of 20-30 cm, although spore densities declined rapidly with depth.

The emergence, during this study, of the bird-dispersed *Halleria lucida* from deeper soil layers, which indicated indicates a long-lived soil seed bank, is an anomaly, since bird-dispersed species found in Mediterranean climates generally do not have persistent seed banks (Manders 1990). However, Teketay and Granström (1997) have found high levels of dormancy and persistence of bird-dispersed tree species in Ethiopia, which seems to be an adaptation to a climate of seasonal drought and unreliable rainfall. It is quite possible that *Halleria* has adapted in a similar fashion, given its wide distribution.

4.5.5 Burial, dormancy, germination, persistence and seed densities

The interaction of length or requirement of burial with germination responses also confounds assumptions about the distribution and density of seeds and spores in the vertical profile. Many seeds in Mediterranean climates require a period of soil burial, which alters dormancy status and the conditions necessary for germination (Holmes and Newton

2004; Baker *et al.* 2005), e.g. *Passerina* and some Restionaceae. In these species, germination is enhanced after a period of soil burial, and it can take years for the dormancy in some species to be broken (Ooi 2010). Merritt *et al.* (2006) found increased germination response in seeds that have been buried and then exposed to light, especially light with high red or far-red ratio which is typical of an open environment, especially in the Asteraceae and Cyperaceae. Holmes and Newton (2004) hypothesised that light and light quality may play an important role as potential germination cues for small-seeded species in the Ericaceae, Campanulaceae and Asteraceae. For these species, the periodicity of light in combination with temperature was therefore important to stimulate germination, e.g. alternating diurnal temperature and light-enhanced germination in *Metalasia* (Pierce and Moll 1994). It is possible that this mechanism controlled the germination of some Asteraceae during this study, e.g. *S. rigidus* and *C. pinnata*. This is supported by the fact that *S. rigidus* increased from 0.2 % immediately after clearing to 5.6 % cover in the field in the space of a year, without any fire-related cues. Removal of the closed wattle canopy may have provided a sufficient light cue for germination.

Since dormancy status alters and germination may be enhanced after a period of soil burial (Baker *et al.* 2005) - and dormancy mechanisms can diminish over time, increasing the range of suitable conditions for germination (Baskin and Baskin 1998; Hilhorst 1998; Céspedes *et al.* 2012) - it is logical to assume that seeds from deeper soil layers will germinate more readily. This could lead to a relatively greater germination percentage from deeper layers compared to the upper soil layer, which does not give a true reflection of the actual soil seed bank densities. In invaded situations, this may be more relevant to more recent invasions, as it is likely that the majority of seeds (and spores) recorded during this study have been persistent in the soil for at least 14 years (last seed set pre-invasion). Most of these have therefore probably lost their dormancy mechanisms, and would be more receptive to germination cues.

The dormancy status of various seeds also complicates the interpretation of the contribution that younger seeds, or the most recent seed rain, will make to the regeneration potential of an area, and how the season of fire will interact with seed age and affect germination response. Moreno *et al.* (2011) state that the "number of seedlings emerging after fire is a function of the size and dormancy state of the soil seed bank in interaction with fire intensity". The size of the seed bank will vary throughout the year in Mediterranean systems, being highest in late summer after seed dispersal and lowest in late spring (Knox and Clarke 2006; Traba *et al.* 2006; Céspedes *et al.* 2012; Moreno *et al.* 2001). Newly released seeds, i.e. from the most recent seed rain, will be most susceptible to predation, and the seed bank will therefore decline after the release of seeds until the next season and seed maturation and dispersal event. It has been argued that recruitment and number of germinants would therefore vary according to the season and delay since seed release, and germination from the seed bank highest just after seed dispersal, before predation and attrition (Moreno *et al.* 2011). However, Céspedes *et al.* (2012) speculates that the most recent seed rain, i.e. seeds on or near the surface which have not been incorporated into the soil, is most vulnerable to exposure to lethal fire temperatures (depending on fire intensity and species-specific fire resistance). The interpretation of the above is that the most recent seed rain contributes less to regeneration potential after fire than seeds that are protected in the soil. The seeds from the recent seed rain which have physiological dormancy mechanisms are also likely to be still dormant, as opposed to older seeds (Baskin and Baskin 1998). For example, some species may only show a germination response to light after a period of burial (Holmes and Newton 2004; Baker *et al.* 2005). These seeds which survive will not germinate or contribute towards regeneration after a fire event, but will be incorporated into the persistent soil seed bank and provide regeneration potential after the next fire event.

The seed regenerating *Erica* species had not reappeared more than a year after the fire, and Richardson *et al.* (1984), as did Martin (1966) before them, concluded that these species have to re-establish from seed brought in by wind from nearby sources. This varies from the findings of this study, where high numbers of *Erica chamissonis* and *E. caffra* seedlings emerged within a year. It also varies from the hypotheses of Kruger (1983) and Le Maitre and Midgley (1992) that all species will establish immediately after fire.

4.5.6 Interaction of fire season with recruitment from canopy- and soil-stored seed banks

The season of fire has been shown to influence regeneration from seed banks in a variety of ways. Kruger and Bigalke (1984) identified the importance of phenology in understanding the influence of different fire seasons in fynbos. However, there are some contradictions in the literature, as most interpretations of recruitment dynamics are based on the germination, fire-response and management of serotinous overstorey species in the Proteaceae and Bruniaceae (Bond *et al.* 1984, 1990; Enright *et al.* 1998; Heelemann *et al.* 2008). The fire response and recruitment of these species has received much attention, as they are highly vulnerable to recruitment failure resulting from aseasonal fires, e.g. spring or winter fires, which result in an increased risk of exposure to predation (Bond 1984; Cowling and Lamont 1987; Knox and Clarke 2006). Fire season has been shown to influence subsequent patterns of serotinous species abundance, since it determines the length of time that seeds have to survive at the soil surface before receiving suitable germination cues (Enright *et al.* 1998). Seeds can also be lost to prolonged high soil temperatures over summer after spring fires, as opposed to autumn fires (Cowling and Lamont 1987). In the Western Cape, the highest recruitment of *Protea* and *Leucadendron* has been found after fire in the late summer or early autumn (Bond 1984; Bond *et al.* 1984). Fire management has thus largely been targeted for optimal regeneration of these species (van Wilgen 2008; van Wilgen *et al.* 2010).

However, there is little empirical evidence of the effect of season of fire on recruitment from the soil seed bank. The majority of Mediterranean plant species have soil-stored seed banks (van Wilgen and Forsyth 1992; Figueroa *et al.* 2009; Thomas *et al.* 2010; Moreno *et al.* 2011) and the same dynamics do not necessarily apply. Although the effects of predation are less for soil-stored seeds, Clarke and Davison (2001) have shown that ants can predate seeds from soil-stored seed banks, and Knox and Clarke (2006) hypothesise that predators can explain reduced emergence from soil seed banks after an aseasonal fire, but little other empirical information is available on predation from soil seed banks. Ojeda *et al.* (2005) state that due to the synchronous nature of the germination response in Mediterranean vegetation, a single recruitment failure from the soil seed bank could jeopardise the viability of a population. They apparently failed to distinguish the mode of seed bank storage, i.e. soil-stored seed banks vs. canopy-stored seed banks, which are indeed at risk from single extensive failure of recruitment, as these species do not have soil-stored seed banks.

Although germination from the latter is fire-stimulated and often synchronous, not all seeds from the soil seed bank germinate during a single fire event, and they are therefore buffered against recruitment failure (Moreno *et al.* 2011). There is little known about the proportion of seed that emerges compared to the portion that persists, and some residual seeds are expected to remain in the soil seed bank after fire (Auld and Denham 2006), which acts as a risk-spreading mechanism.

The season of fire also influences and interacts with fire characteristics to influence patterns of germination and the post-fire population composition (Moreno and Oechel 1991). The fire season affects fuel characteristics and soil moisture, and thus fire severity and the impact on the vegetation and soil seed bank. Fire intensities are often lower during the wet season, and heat does not penetrate as deeply into the soil, due to high soil moisture, which may result in reduced emergence (Bradstock and Auld 1995; Moreno *et al.* 2011), especially in hard-seeded species (Knox and Clarke 2006). This obviously has to be offset against higher fire intensities that are generated by IAP biomass. A variation in fire intensity has been found to create greater diversity, due to different heat requirements for germination (Auld and Ooi 2008).

4.6 CONCLUSION AND IMPLICATIONS FOR RESTORATION

This study presents the first detailed account of temporal germination patterns of the soil-stored seeds in grassy fynbos. Knowledge of seed germination responses, including timing of emergence, is important for plant conservation, management of diversity and the restoration of fynbos. It can also assist restoration practitioners in understanding the processes and sequences of recovery, which will result in more efficient restoration practices (French *et al.* 2011).

Since fire is central to the process of regeneration of fynbos, an understanding of the reproductive ecology and germination responses after fire is crucial, to inform fire management (Pyke *et al.* 2010) and restoration. However, there is still a considerable lack of knowledge regarding the processes that control the fire-response for many species (Ooi *et al.* 2004), and this is certainly the case for the species recorded during this study. Much of the fire management policies in fynbos have been informed by the recruitment responses of serotinous overstorey species such as Proteaceae, Bruniaceae and others in the Western Cape, especially the effect of the season of fire. Very little is known about the impact of the season of fire on the regeneration of the soil seed bank in either the typically Mediterranean-climate Western Cape fynbos or the eastern extent of the fynbos, which experiences more aseasonal and unpredictable rainfall. Also, little is known about the timing of germination of the soil seed bank from this area, and how the timing of emergence will affect the trajectories of post-fire succession and plant community development. The findings of this study go some way towards addressing these gaps. It appears that all growth forms establish within a year, following Egler's (1954) model of initial floristics composition, although the fine time-scale of this current study does show that emergence is not synchronous after fire and appears uncoupled to the availability of moisture. This study has indicated clear germination sequences and patterns of emergence over time for different species, with many species exhibiting delayed emergence relative to the timing of the fire event. Literature suggests that early emergence as opposed to delayed emergence can increase the success of recruitment and afford increased vigour, which can last throughout the life cycle of the plant. Timing of emergence will therefore also alter successional trajectories and the composition of subsequent populations (De Luis *et al.* 2008b; Verdú and Traveset 2005). Some species also exhibited a wider window of emergence, which may be a risk-spreading mechanism in response to more unpredictable rainfall patterns (Moreno *et al.* 2011), or a reflection of linkages to both the predominantly winter-germinating Cape flora and the more tropical spring and summer-germinating flora.

It is proposed that the manipulation of the season of fire can be used to selectively optimise the order of arrival (Temperton and Zirr 2004) and therefore superior recruitment of some species over others in the Eastern Cape fynbos. This will influence trajectories of recovery and direct the succession of the vegetation towards a more desired state. A species with no seasonal requirements will have competitive advantage under certain fire regimes, while a delayed germination response until a particular season can result in a competitive disadvantage, especially if co-occurring species have faster post-fire response. For example, a fire in April or May may result in *H. lucida* being one of the first species to germinate in the July to October period, whereas a fire in November or December could result in a delay of six months before it germinates. During this time, competition from other species that have established will have increased, both from seed and through resprouting. However, the interaction of facilitation and competition between different species and the effect that season of fire has on establishment and succession is not known, and remains to be tested.

As the period of germination and early establishment is the time when a plant is probably most vulnerable (Vilà and Weiner 2004; Fenner and Thompson 2005; Akasaka and Tsuyuzaki 2009), I hypothesise that this is the stage in the life history of an IAP during which biotic resistance could have the greatest effect. This is also discussed further in Chapter 5. *A. longifolia* seeds are physically dormant and dormancy is broken by heat, where after germination can take place as soon as moisture becomes available, irrespective of season. The rapid emergence of invasive species, before the emergence of any of the indigenous species, is obviously one of the strategies that enable these IAPs to establish and gain a competitive advantage. Although rapid growth rates are one of the traits commonly associated with IAPs (Castro-Díez *et al.* 2011; Gallagher *et al*. 2011; Morris *et al.* 2011), the ability to germinate first after disturbance, before indigenous species establish, has not been recorded as such. Rapid germination after fire allows *A. longifolia* to take advantage of the increased resources immediately after fire. This, in combination with the relatively high remaining seed bank (Chapter 2), presents challenges to the management of this species (Strydom *et al.* 2012). Fire could thus be timed to coincide with the seasonal germination of an indigenous species, which can germinate at the same time and offer sufficient competition to reduce the successful establishment and/or vigour of *A. longifolia*. Alternatively, sufficient numbers of physically dormant seeds with the same germination response of another competitive indigenous species, e.g. from the Fabaceae family, must be present or be introduced into the system before fire occurs. Although this method may not be able to fully suppress the regrowth of *A. longifolia*, it may reduce the successful establishment of *A. longifolia* seedlings, therefore reducing post-fire densities, follow-up costs and negative impacts from follow-up treatments. This is discussed further in Chapter 5 and Section 6.5.

5 RESTORATION OF AN ALIEN-INVADED RIPARIAN ZONE IN GRASSY FYNBOS

5.1 INTRODUCTION

The ability of IAPs to colonise, transform and degrade ecosystems is a global ecological and economic problem (D'Antonio and Vitousek 1992; van Wilgen *et al.* 2001; Brooks *et al.* 2004). In South Africa, the invasion of riparian zones by woody IAP species is a serious concern, as these IAPs transform ecosystems by displacing indigenous vegetation, altering fire regimes, reducing water yield and biodiversity, increasing soil erosion and siltation and degrading many other ecosystem services (Le Maitre *et al.* 1996, 1997; Versfeld *et al.* 1998; Richardson and van Wilgen 2004; Richardson *et al.* 2007).

One of the main challenges is how to manage these invasions (CSIR 2000; Holmes *et al.* 2005, 2008; Simmons 2005; Blanchard and Holmes 2008; te Beest *et al.* 2011) as mechanical, chemical and biological management of IAPs can be expensive, have negative ecological impacts and is often unsuccessful (Holmes *et al.* 2000; Simmons 2005). Many standard control methods are detrimental to residual indigenous plant communities, which in turn can accelerate or further aggravate the process of invasion (Zavaleta *et al.* 2001; Sheley and Krueger-Mangold 2003; Parker-Allie *et al.* 2004; te Beest *et al.* 2011). Biological, mechanical and chemical management of woody IAPs have formed part of the IAP control programmes in South Africa. Although riparian systems have been shown to be fairly resilient with the regeneration of fynbos usually taking place without active intervention (Blanchard and Holmes 2008; Holmes *et al.* 2008), in some situations natural recovery and re-establishment of indigenous vegetation is limited. This usually occurs in long- and densely-invaded areas (where IAP densities exceed 75 %), where areas have experienced more than three fire cycles under invasion, and where the indigenous soil seed bank has been damaged or depleted (Holmes and Cowling 1997a). These will require active restoration to reinstate a vegetation cover and basic ecological functioning.

Apart from restoring to reinstate the ecological functioning of riparian systems, there has been a shift towards viewing restoration as an ecologically-based, longer-term solution (McLachlan and Bazely 2003; Sheley and Krueger-Mangold 2003; Svejcar 2003; Simmons 2005) which can form an integral part of the management and control of IAPs. Implicit in this objective is the reassembly of a plant community that is resistant to re-invasion (Davis *et al.* 2000; D'Antonio and Chambers 2006; Funk *et al.* 2008), i.e. offers biotic resistance (see Section 1.7).

5.2 AIMS AND HYPOTHESES

This study implemented passive and active restoration to address the following aims.

5.2.1 Aims

1. Investigate the potential for passive and active restoration of alien-invaded riparian zones in grassy fynbos.
2. Investigate whether active restoration can improve indigenous diversity and cover, compared to passive restoration.
3. Investigate whether restoration using indigenous grass species is more successful in suppressing regrowth of IAPs than restoration using a mix of indigenous guilds.
4. Investigate whether follow-up control of IAP regrowth in the form of foliar herbicide affect indigenous diversity or cover compared to a non-herbicide follow-up treatment.
5. Investigate whether restoration can achieve biotic resistance and if so, the probable mechanism of how this is achieved.

5.2.2 Hypotheses

1. Active restoration, through the sowing and planting of indigenous species, will increase the cover and diversity of indigenous vegetation compared to passive restoration.
2. Follow-up management, using foliar herbicide, will negatively affect indigenous diversity and cover.

3. Biotic resistance can be achieved through the active restoration of indigenous vegetation.
4. Active restoration, through the sowing and planting of grasses, will achieve a higher degree of biotic resistance but will suppress indigenous vegetation.
5. The success of restoration interventions will vary according to the lateral zonation of the riparian zone.

5.3 MATERIALS AND METHODS

The field methods described in Sections 2.3 and 3.3 were applied. In addition to this, a survey of the above-ground vegetation was undertaken in October and November 2004, and again in October and November of 2005 shortly before the controlled fire. The following treatments were implemented after the controlled burn.

5.3.1 Post-fire restoration

Shortly after the controlled burn, in December 2005, two restoration treatments (grass and indigenous) and a control were implemented in a randomised block design, with 151 five by five metre plots with a one metre wide buffer strip between blocks.

5.3.1.1 Grass rehabilitation

The plots (n = 42), were lightly raked, and a mix of *D. eriantha* and *Eragrostis tef* seeds was sown at an application rate of 8 kg/ha. *Digitaria eriantha* plugs were planted at 30 cm intervals (approximately 90 000 plugs/ha).

5.3.1.2 Indigenous rehabilitation

These plots (n – 44), were hoed, and 65 g of a pre-mix of indigenous seed was broadcast per plot (Table 7.1) and the soil lightly raked, equating to an application of 26 kg/ha. Seeds used in the treatment were harvested locally (handpicked) during 2005. Eleven indigenous species (in propagation bags), ranging between 15 and 23 cm in height, were also planted (evenly spaced) in each plot.

Plate 9

Plate 10

Plates 9 and 10. Study site in December 2005, during active restoration. Plate 9 has the same view as Plate 1.

Plate 11

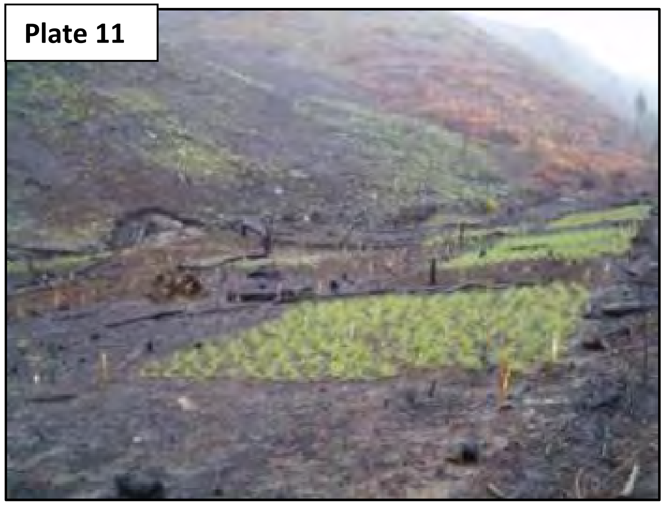


Plate 11. Newly planted restoration plots in December 2005

Plate 12

Plate 12. High mortality of *Acacia* emergents observed during the dry January month of 2006.

Plate 13

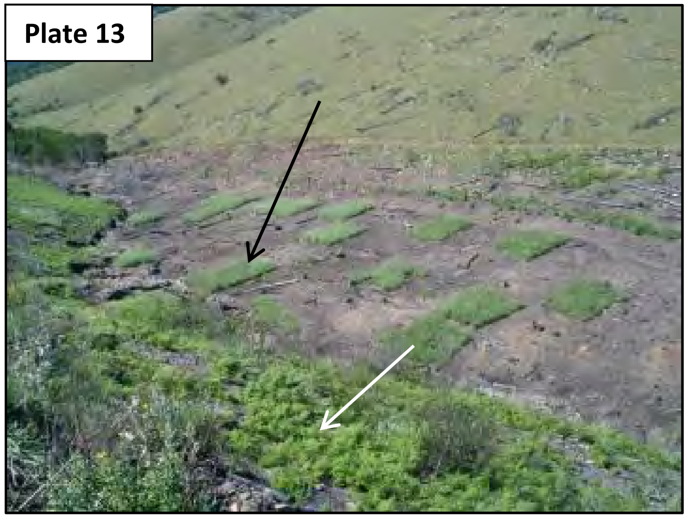
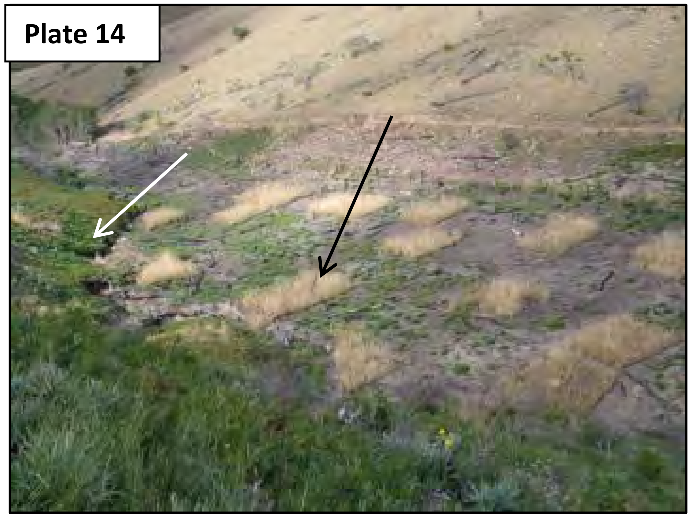


Plate 14



Plates 13 and 14. Plate 13 shows the study site in March 2006 and Plate 14 in June 2006. The black arrows indicate the grass restored plots. The high cover of *Pteridium aquilinum* on the SF wet bank is indicated by the white arrows

Plate 15

Plate 16

Plates 15-16. Restoration treatments in August 2006, eight months after implementation. Note the contrasts between the control plots (indicated by the solid white arrows), the grass restored plots (indicated by the solid black arrows) and the indigenous restored plots (indicated by white dashed arrow)

One of each of the following species was used per plot, unless otherwise indicated in brackets: *Chironia baccifera* (2), *Helichrysum petiolare*, *Halleria lucida*, *Burchellia bubalina*, *Chrysanthemoides monilifera*, *Leonotis leonurus* (2), *Ochna serrulata*, *Pappea capensis* and *Searsia dentata* (see Appendix A for details of species). In addition to the above, some bare root species e.g. *Cymbopogon plurinodis,* were lifted from the adjacent areas and transplanted directly. Most of the plants had been grown from the seeds that germinated during the soil seed bank study the preceding year (Chapter 2) and a few were obtained from the local WfW office, and had also been grown from locally harvested seeds. In April 2006, three plants of the following species were added to each landscape plot: *Hypoxis argentea, Helichrysum cymosum* and *Chironia baccifera*.

Table 7.1. Indigenous seeds used in the seed mix for the indigenous treatment

Species	Amount (g)	Species	Amount (g)
Anthospermum spp.	191	*Metalasia muricata*	81
Blechnum spp.	41	*Montinia caryophyllaceae*	24
Carpha spp.	397	*Otholobium caffrum*	93
Cheilanthes viridis	71	*Pelargonium* spp.	19
Cyperaceae	71	*Protea cynaroides*	43
Disparago ericoides	340	*Psoralea oligophylla*	45
Erica caffra	394	Restionaceae	148
Erica demissa	928	*Rumohra adiantiformis*	21
Halleria lucida	127	*Selago ramulosa*	61
Helichrysum foetidum	18	*Senecio rigidus*	227
Helichrysum spp.	22	*Senecio speciosus*	73
Hermannia flammea	68	**Total mix per plot**	65

5.3.1.3 Control

These plots (n = 85), did not receive any restoration treatment.

Each of the above three treatments were randomly subdivided into the following follow-up treatments:

- Hand pulling of re-emerging *Acacia longifolia* seedlings (undertaken in June 2006)
- Standard foliar herbicide (Garlon) application to kill re-emerging alien regrowth (September 2006)
- No additional follow-up (controls)

5.3.2 Assessments

In June 2006, the number of *Acacia longifolia* seedlings removed from all the manual follow-up treatment blocks was recorded, as well as the time that this took. The aerial cover estimates of bare ground, indigenous vegetation cover, *A. longifolia* and *D. eriantha* cover in each plot was also obtained. Survival of the indigenous species which were planted as part of the indigenous restoration treatment was recorded by counting the number of each species still living.

In October 2006, soil cores to 10 cm depth were taken in 19 control and 18 randomly selected grass plots. The soil was sieved through a 1 mm mesh to remove the *A. longifolia* seeds, and these were counted to determine the density of remaining *A. longifolia* seeds.
A final survey of the vegetation was undertaken in autumn 2009, during which the presence and aerial cover of all species were recorded. Species cover was sampled as ecosystem function is more likely to be driven by changes in the cover of a particular guild (Holmes et al 2000).

5.3.3 Reference sites and chronosequences

A survey of riparian zones in nine tributaries in the vicinity of the project area was also undertaken during 2005. These tributaries in the surrounding areas were mapped in ArcView (Esri 2003) and a 5 x 5 m grid was superimposed over the tributaries. Numbers were allocated to the blocks, and random numbers generated in Excel, and these were used to select sites randomly. The co-ordinates of these blocks were then calculated, and these sites were located in the field using a handheld GPS (Garmin, GPS 12 CX), where the surveys were implemented. A total of 78 plots were sampled over the nine tributaries. During the survey the following variables were recorded:

- species cover
- average species height
- site slope, aspect and percentage rockiness

Five soil samples were taken in each plot, one from each corner, and one in the middle – these were then mixed together, and a subsample sent for analysis. The historical management data for these tributaries were obtained from WfW, and sites were divided into reference sites, where IAPs were absent or present in very low numbers, and sites which had been invaded and cleared. The invaded and cleared sites represented chronosequences, with various times since clearing and number of follow-up treatments. The purpose of this survey was two-fold: (1) to establish reference conditions, against which to measure the outcomes of the restoration interventions and (2), to assess the recovery of various chronosequences of previously invaded and cleared riparian sites.

5.3.4 Analysis

Normality could not be achieved with Arcsine transformations and non-parametric analyses were used. The 2006 data were analysed using Statistica (Statsoft.Inc, 2011) to obtain the descriptive statistics for each treatment, and Kruskal-Wallis tests were used to determine significant differences between the treatments. The relationships between lateral zonation, treatment and vegetation cover were also explored by means of a non-parametric Spearman Rank correlation analysis.

The species from the 2009 survey were categorised into guilds according to growth form and functional groups (geophytes, forb, graminoid, shrub, riparian, annual and short-lived perennial, and alien) following Holmes *et al.* (2000), with percentage cover of guild as the dependent variable. These data were analysed using Statistica (Statsoft.Inc, 2011) to obtain the descriptive statistics of results of each treatment, and Kruskal-Wallis tests were used to determine significant differences between the treatments. As the aerial cover of each species was used and the vegetation has different structural layers, the total cover, made up of the sum of the individual species components, often exceeded 100 %. *E. curvula* was included as an introduced grass in some of the analyses; although it is indigenous, it does not usually occur in high densities in intact fynbos and becomes invasive in disturbed fynbos. For these reasons, as well as its invasive behaviour in other parts of the world, it was included with *D. eriantha* as an introduced species (Appendix A).

Multivariate analysis was undertaken using the community analysis package, PRIMER (Clarke and Warwick 2001), to assess vegetation groupings according to treatment, by means of non-metric multi-dimensional scaling (MDS). Percentage cover of the various guilds described above, were used in the analyses. Analyses of similarity (ANOSIM) were undertaken to establish differences between the zones, as well as treatment within zones, and SIMPER analyses were undertaken to assess the contribution of individual species in defining the differences between the zones, using PRIMER (Clarke and Warwick 2001). The results from the restoration treatments were also compared against the reference sites and cleared chronosequence sites.

5.3.5 Rainfall during restoration period

Annual rainfall varied during the study period; 483 mm was recorded in 2005, 706 mm in 2006, 441 in 2007 and 349 mm in 2008, compared to the average annual rainfall of 545 mm (SA Weather Services). The year 2006 therefore experienced a 30 % higher (161 mm) than average rainfall (Figure 5.1), with the other three years being 11 %, 19 % and 35 % below average, respectively.

Rainfall data obtained from the South African Weather Services reveals that the rainfall for November 2005, when the controlled burn took place, was much higher (137 mm) than the average monthly rainfall for November (66 mm). Most of this (124 mm) fell before the controlled burn, but was followed by a much lower than average rainfall (5.4 mm as opposed to the monthly average of 35 mm) during December after planting had taken place.

The remainder of the first summer months after the restoration trials were implemented had higher than average rainfall: 60 mm in January as opposed to the average 43 mm and 67 mm in February as opposed to the average of 36 mm. The extraordinarily total high rainfall of 2006 was mainly due to high rainfall in August (218 mm as opposed to the average of 58 mm for August).

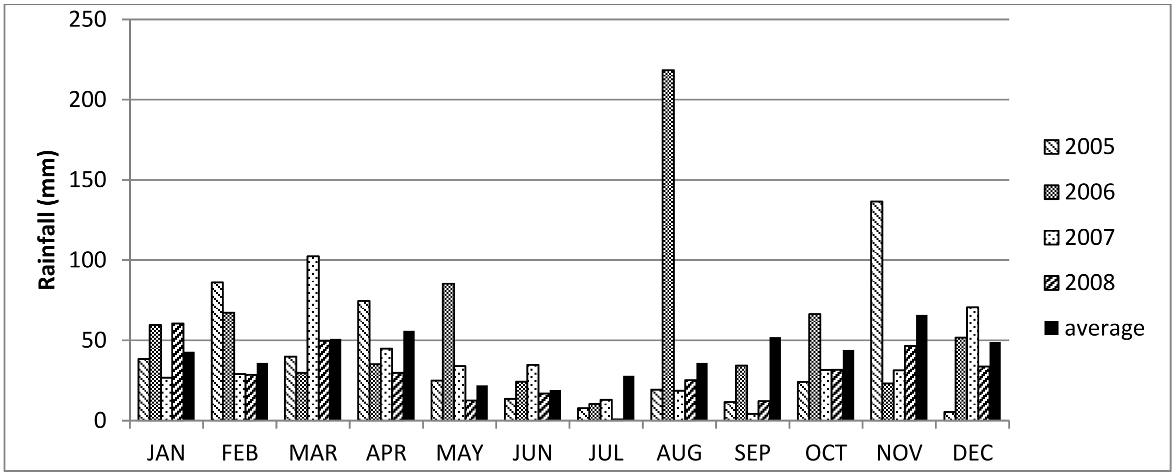


Figure 5.1. Rainfall recorded in the year before the restoration trials and the following three years (source: South African Weather Services)

5.3.6 Treatments: abbreviations

For ease of reading the following abbreviations are used in this paper:

- Grass restoration treatment and herbicide follow-up, foliar spraying of seedlings: GH
- Grass restoration treatment and manual follow-up, hand pulling of seedlings: GM
- Indigenous restoration treatment and herbicide follow-up, foliar spraying of seedlings: IH
- Indigenous restoration treatment and manual follow-up, hand pulling of seedlings: IM
- Control; no restoration with herbicide follow-up, foliar spraying of seedlings: CH
- Control; no restoration and manual follow-up, hand pulling of seedlings: CM

5.4 RESULTS

5.4.1 Short-term effects (2006)

The initial survey (June 2006) revealed significant differences between the restoration treatments and the other two treatments, with significantly reduced numbers of *A. longfolia* seedlings in the grass restoration treatments (25 ± 18) as opposed to the indigenous (246 ± 72) and control (219 ± 52) (Table 5.1). However, the effect of the treatment also interacted with lateral zoning and the most pronounced treatment effect was observed in the NF bank, with a mean of 0.7 ± 0.4 *A. longifolia* seedlings in the grass-restored plots, as opposed to 243 ± 40 seedlings in the indigenous restored plots and 373 ± 77 in the control plots. A similar, but less pronounced trend was found in the SF dry bank with a mean of 3 ± 2 seedlings in the grass restoration treatment, as opposed to 25 ± 11 seedlings in the control and 118 ± 95 seedlings in the indigenous restoration plots. However, differences were not significant, probably because there were too few indigenous plots in this zone. Treatment effects were not significant in the WB zone.

The post-fire sampling of IAP seed in October 2006 revealed no significant difference between the remaining mean number of *Acacia* seeds in control plots (272 ± 78 seeds/m^2) and grass plots (288 ± 89 seeds/m^2).

Table 5.1. Number of *Acacia longifolia* seedlings (per 25m^2) per zone

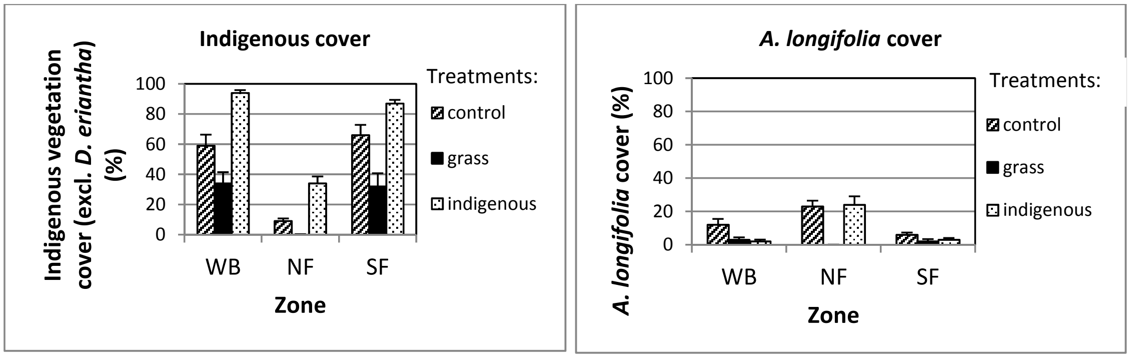
	Control (n=22)	Grass treatment(n=14)	Indigenous treatment (n=15)
All zones	219±52**	25±18	246±72**
NF dry bank	373±77**	0.7±0.5	243±40*
WB	86±29	83±58	286±152
SF dry bank	25±11	3±2.5	118±95

*p < 0.05, ** p < 0.001 between grass treatment and either control or indigenous treatments, as indicated

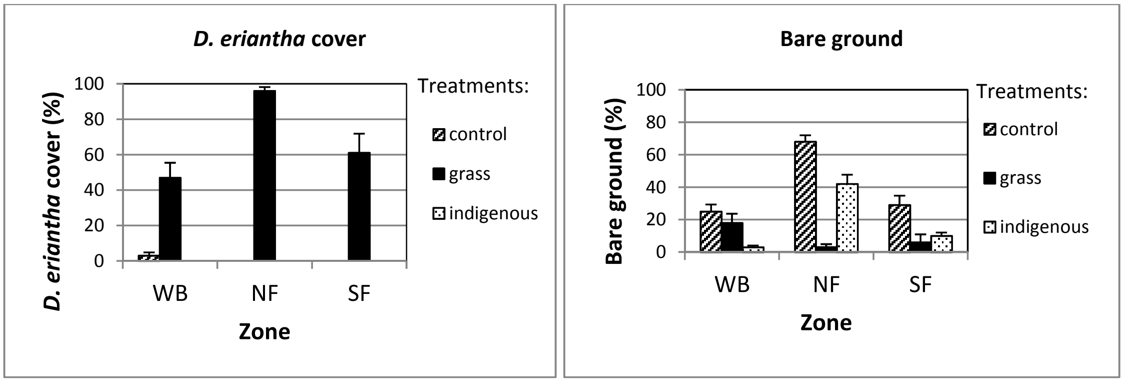
The initial 2006 survey of vegetation cover revealed significant treatment effects, varying across lateral zones and aspect. Treatment effects were most pronounced in the NF dry bank. There were no significant differences in the WB zone and the SF dry bank, but very significant differences between the NF dry bank and both WB zone and SF dry bank (Figure 5.2 a-d).

5.4.1.1 Indigenous cover

In the NF dry bank, there were significant differences in indigenous cover between the indigenous treatments plots (34 ± 5 % cover) with no indigenous cover (0 ± 0 %) in the grass plots and 9 ± 2 % cover in the control plots (Figure 5.2a). Differences were all significant ($p < 0.001$) between grass and control plots, between grass and indigenous plots ($p < 0.00001$) and between control and indigenous plots ($p < 0.01$) ($H = 41.54$).



(a) Indigenous cover **(b) *A. longifolia* cover**



(c) *D. eriantha* cover **(d) Bare ground**

Figure 5.2 (a-d). Vegetation response to restoration treatments seven months after implementation (2006)

Indigenous cover in the SF dry bank was also lower (though not significantly) in the grass plots (32 ± 8 %) as opposed to the indigenous plots (87 ± 10 %) ($p < 0.01$) ($H = 11.93$) and the control plots (66 ± 7 %). In the WB zone indigenous cover exhibited the same pattern: the indigenous cover being significantly more in the indigenous treatments (94 ± 2 %) compared to the grass treatments (34 ± 7 %) ($p < 0.001$) ($H = 13.78$). The difference was not significant between the control and the indigenous treatments, and between the grass and control treatments.

5.4.1.2 A. longifolia cover

A. longifolia cover (23 ± 3 %) was significantly higher in the NF dry bank control compared to the grass treatments (0 ± 0 %) ($p < 0.0001$), as well as significantly higher in the indigenous treatment (24 ± 5 %) ($p < 0.00001$) ($H = 33.68$) (Figure 5.2b). Although *A. longifolia* cover was higher in the control treatments compared to the indigenous and grass treatments in the other two zones, differences were not significant.

5.4.1.3 D. eriantha cover

D. eriantha cover was significantly higher in all the grass treatments across all zones ($p < 0.00001$, $H = 57.01$, in NF dry bank, $p < 0.001$ in SF dry bank and WB control plots, and $p < 0.01$ in SF dry bank, $H = 32.61$, and WB, $H = 20.36$, indigenous treatments), as compared to the indigenous and control treatments, which hardly had any *D. eriantha* cover (Figure 5.2c) *D. eriantha* cover was highest in the NF dry bank (96 ± 2 %), followed by 61 ± 11 % in the SF dry bank and 47 ± 8 % in the WB zone.

5.4.1.4 Bare ground cover

The highest cover of bare ground was found in the control treatments across all three zones, and lowest cover in the grass treatments except for the WB zone (Figure 5.2d). Differences were most pronounced in the NF dry bank, being significantly higher in the NF dry bank control (68 ± 4 %) compared to the grass treatments (3 ± 2 %) ($p < 0.0001$) and the indigenous treatment (42 ± 6 %) ($p < 0.01$) ($H = 37.59$). In the SF dry bank there was a significant difference in bare ground cover in the control plots (29 ± 6 %), which was significantly more than in the grass plots (6 ± 5 %) ($p < 0.05$) ($H = 8.14$). The WB zone exhibited the greatest bare ground cover in the control plots (25 ± 4 %), significantly more than the indigenous treatments (3 ± 1 %) ($p < 0.01$) ($H = 8.72$).

5.4.1.5 Correlation analysis

Analysis of treatment effects on vegetation cover, using a Spearman rank correlation analysis, revealed significant relationship correlations between some variables (Table 5.2). The strongest effect was observed in the grass treatment where *D. eriantha* cover was negatively correlated with both *A. longifolia* cover ($r = -0.65$, $p < 0.005$) and indigenous cover ($r = -0.86$, $p < 0.00001$). There were also significant negative correlations between indigenous cover and *A. longifolia* in both the indigenous treatment ($r = -0.68$, $p < 0.0005$) and the control ($r = -0.51$, $p < 0.0005$).

Table 5.2. Correlation between treatments (Spearman Rank correlation analysis) across all zones (only significant relationships are shown)

Treatment	Variables	r	Significance
Grass	*D.eriantha* cover and indigenous cover	-0.86	$p < 0.00001$
	D. eriantha cover and *A. longifolia* cover	-0.65	$p < 0.005$
	Combined indigenous and *D. eriantha* and *A. longifolia* cover	-0.86	$p < 0.00001$
Indigenous	Indigenous cover and *A. longifolia*	-0.68	$p < 0.0005$
Control	Indigenous cover and *A. longifolia*	-0.51	$p < 0.0005$
	Combined indigenous and *D. eriantha* and *A. longifolia* cover	-0.52	$p < 0.0005$

Within zones some of the relationships are more pronounced, e.g. the strongest relationship was found in the SF dry bank between combined *D. eriantha* and indigenous cover, and *A. longifolia* ($r = -0.98$, $p < 0.05$) (Table 5.3).

5.4.1.6 Survival of planted indigenous species

A total of 25 % of the individuals planted survived, and there were no significant differences in percentage survival between zones. There was great variation in percentage survival between the species that were planted in December 2005, ranging from a 7 % survival of *Chironia baccifera* to a 50 % survival rate of *Helichrysum petiolare* (Table 5.4).

Table 5.3. Correlation between treatments (Spearman Rank correlation analysis) within zones (only significant relationships are shown, p < 0.05)

Treatment	Variables	r	Significance
WET BANK			
Grass	Combined indigenous and *D. eriantha* and *A. longifolia* cover	-0.84	$p < 0.0001$
Control	Indigenous and *D. eriantha* cover	-0.97	$p < 0.001$
	Indigenous cover and *A. longifolia* cover	-0.77	$p < 0.05$
SF DRY BANK			
Grass	Indigenous cover and *D.eriantha* cover	-0.82	$p < 0.0005$
	Combined indigenous and *D. eriantha* and *A. longifolia* cover	-0.98	$p < 0.0001$
Control	Indigenous cover and *A. longifolia* cover	-0.75	$p < 0.05$
NF DRY BANK			
Grass	*D. eriantha* cover and *A. longifolia* cover	-0.89	$p < 0.00005$
	D. eriantha cover and indigenous cover	-0.61	$p < 0.0005$
	Combined indigenous and *D. eriantha* and *A. longifolia* cover	-0.91	$p < 0.0005$

The percentage survival of species planted in April 2006 was much higher, with a total survival of 93 %, and a very similar survival rate between species (although survival of *Hypoxis argentea* was slightly lower at 87 %).

Table 5.4. Percentage survival of species planted in indigenous treatment (see also Appendix A)

Species planted in December 2005	**% survival**	**Species planted in April 2006**	**% survival**
Chironia baccifera	7	*Hypoxis argentea*	87
Burchellia bubalina	11	*Helichrysum cymosum*	96
Leonotis leonurus	14	*Chironia baccifera*	96
Halleria lucida	16		
Chrysanthemoides monilifera	18		
Pappea capensis	25		
Searsia dentata	32		
Ochna serrata	34		
Helichrysum petiolare	50		
Total % survival	**25**		**93**

5.4.2 Medium-term effects (2009)

A 100 % vegetation cover had re-established by 2009, but some pronounced differences persisted between the restoration treatments. Again, treatment effects were zone-dependent, with the most marked differences in the NF dry bank, no significant differences in the SF dry bank, and a few significant differences between some variables in the WB. The overall trend was a significant reduction in indigenous cover and species richness with increasing grass cover, especially in the NF dry bank.

5.4.2.1 Introduced grass cover

The highest introduced grass cover (*D. eriantha* and *E. curvula*) was found in the NF dry bank, with 89 ± 5 % cover in the GH and 88 ± 2 % in the GM restoration plots, followed by 62 ± 10 % in the CM and 59 ± 5 % in the CH plots (Figure 5.3). The lowest introduced grass cover was found in the indigenous treatments, with 34 ± 11 % in the IM treatment and 31 ± 7 % in the IH treatment. Differences were significant between the GH treatment and both indigenous treatments ($p < 0.01$), the GH and CH treatments ($p < 0.05$), and the GM and IH treatments ($p < 0.01$).

There was a significant difference ($p < 0.05$) in introduced grass cover between the control plots and the grass treatments in the WB zone, with 28 ± 15 % in the GM plots, 47 ± 8 % in the GH plots, and 4 ± 3 % in the CM plots and 9 ± 5 % in the CH plots. There was also a lower cover in the indigenous plots (9 ± 5 % in the IM and 7 ± 6 % in the IH treatments (but no significant difference).

Overall, the contribution of *E. curvula* to the introduced grasses was highest in the NF dry bank, with a mean cover of 20 ± 2 %, with the highest cover in the control treatments (25 ± 7 % in CM and 30 ± 4 % in CH). *E. curvula* cover was much lower in the WB zone, with a mean cover of 4 ± 1 %, and the highest cover in the CH treatment (6 ± 4 %). Mean *E. curvula* cover was 1 ± 0.6 % in the SF dry bank, with the highest cover (2 ± 1 %) in the CH treatment.

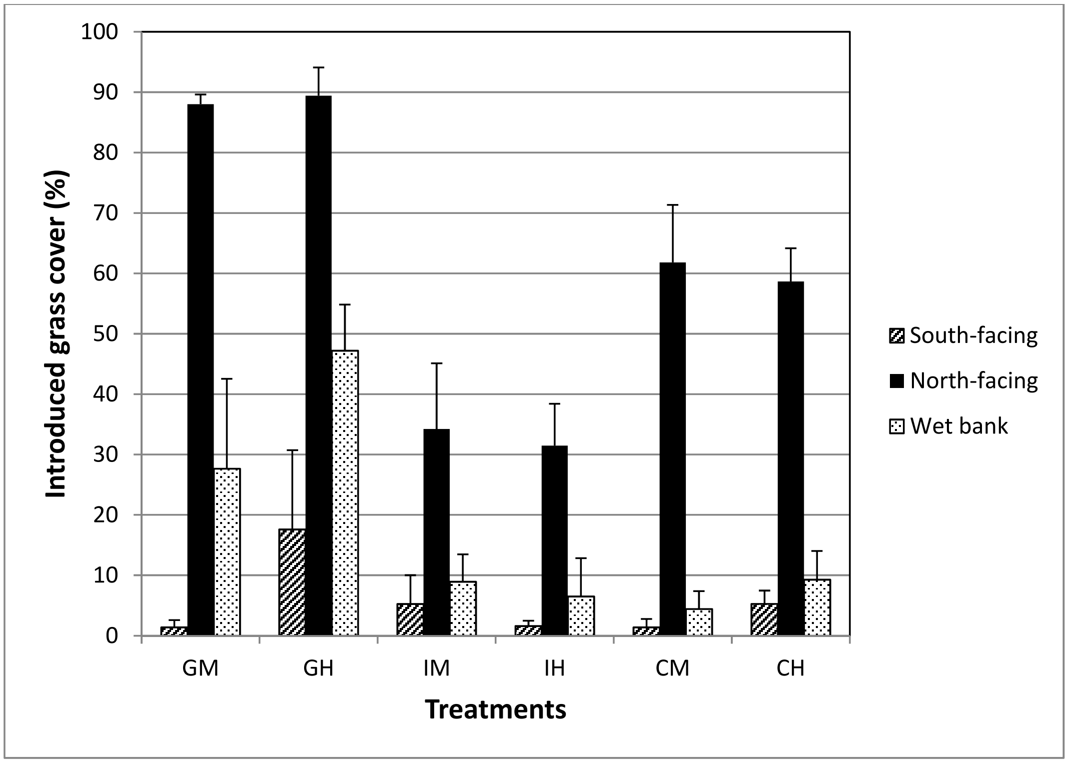


Figure 5.3. Cover of *D. eriantha* and *E. curvula* in response to treatments and across zones in 2009

5.4.2.2 Indigenous species cover

In the NF dry bank there was considerable variation in indigenous species cover (excluding *D. eriantha* and *E. curvula*) (Figure 5.4). This was highest in the indigenous treatments, with 80 ± 16 % indigenous species cover in the IM and 75 ± 7 % in the IH treatments, followed by 50 ± 42 % in the CM treatments and 43 ± 29 % in the CH plots. Lowest indigenous species cover was in the GM treatments (8 ± 2 %) and the GH plots (21 ± 7 %). The differences between the indigenous and control plots were significant (IM & GM, $p < 0.01$; IM & GH, $p < 0.01$; IH & GM, $p < 0.001$; IH & GH, $p < 0.0005$).

There was also a significant difference ($p < 0.05$) in indigenous cover between the CM plots (184 ± 22 %) and the GH treatments (95 ± 17 %) in the WB zone. Indigenous cover in all treatments in the WB zone and SF dry bank was high, with the lowest values (95 % and 125 % respectively) in the GH plots. However, a significant proportion of the indigenous cover in the SF and WB zones consisted of *Pteridium aquilinum.*

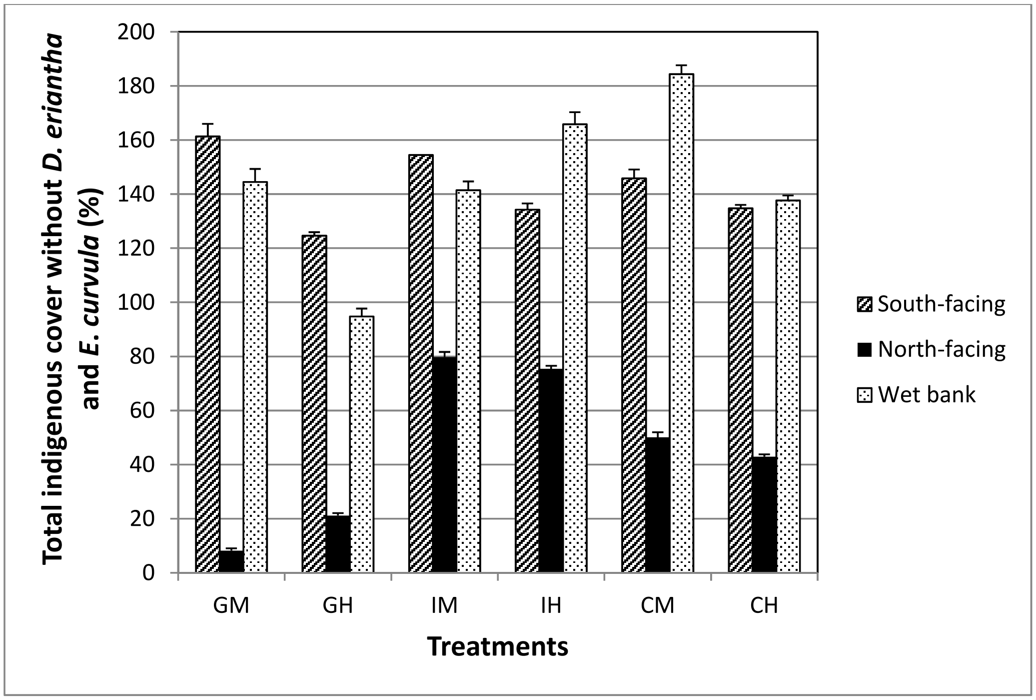


Figure 5.4. Indigenous species cover in response to treatments and across zones in 2009

Overall, *P. aquilinum* was the most dominant regenerating indigenous species, with a mean cover of 33 ± 2 %, followed by *Ehrharta erecta* (20 ± 2 % mean cover) and *Eragrostis curvula*

(11 ± 1 % mean cover). The cover *of P. aquilinum* was significantly dependent on lateral zone, with the highest cover of 66 ± 3 % in the SF dry bank, followed by 40 ± 4 % in the WB zone and lowest in the NF dry bank (13 ± 2 %). The cover of *P. aquilinum* was significantly different between the NF dry bank and WB zone ($p < 0.00001$), between the NF dry bank and SF dry bank ($p < 0.000001$) and the SF dry bank and WB zone ($p < 0.01$). However, there were no significant differences in *P. aquilinum* cover in response to restoration treatment. In the SF dry bank where *P. aquilinum* cover was highest, analysis revealed a weak negative correlation ($r = -0.3870$, $p < 0.05$) between indigenous species cover and *P. aquilinum.*
Other than *P. aquilinum*, *E. erecta* also dominated the SF and WB zones and made up a significant proportion of the indigenous cover in these zones, with a mean cover of 36 ± 4 % *E. erecta* in the WB zone and 36 ± 4 % in the SF dry bank, compared to *E. erecta* cover of 4 ± 1 % in the NF dry bank ($p < 0.000001$). Cover of the remaining indigenous grasses in the SF dry bank was very low: 5 ± 2 %, with a higher cover of 16 ± 2 % in the WB zone and 7 ± 1 % in the NF dry bank. Indigenous grasses were negatively correlated with introduced grasses ($r = - 0.5813$, $p < 0.05$).

There was a significant negative correlation ($r = - 0.6027$, $p < 0.05$) between cover of *D. eriantha* and the remaining indigenous cover (other than *P. aquilinum* and *E. curvula*) across all zones and treatments. A stronger negative correlation ($r = -0.6784$, $p < 0.05$) was found when introduced grasses included both *D. eriantha* and *E. curvula*. This relationship is strongest in the NF dry bank ($r = -0.6751$ for both *D. eriantha* and *E. curvula*), weaker in the WB zone ($r = -0.4568$, $p < 0.05$) and not significant in the SF dry bank. Within the indigenous guild, indigenous grasses exhibited a significant negative correlation with introduced grasses across all three lateral zones ($r = -0.5813$, $p < 0.05$), with the strongest response within a lateral zone in the WB zone ($r = -0.5245$, $p < 0.05$) and the weakest correlation in the NF dry bank ($r = -2867$, $p < 0.05$).

Restionaceae cover throughout the restoration area was low, with the highest cover in the NF CM treatment (4 ± 1 %), followed by 3 ± 1 % in the NF IH treatment. There was less than 0.1 % in Restionaceae cover in all grass treatments. On the NF bank, there was a significant difference Restionaceae cover between the GH and IH treatments ($p < 0.05$) and the GH and CM treatment ($p < 0.05$).

Sedge (Cyperaceae) cover was also lower in the grass treatments (5 ± 2 %) as opposed to the indigenous and control treatments (9 ± 2 % and 8 ± 2 % respectively). However, IM had significantly more sedge cover (14 ± 4 %) than GM (3 ± 2 %), GH (6 ± 2 %) and CH (7 ± 4 %) ($p < 0.05$). Both IH and CH (herbicide) treatments had lower sedge cover than their respective paired IM and CM (manual) treatments, indicating that the herbicide adversely affects sedge cover. The difference in sedge cover was most pronounced in the NF dry bank, with 0.5 ± 0.5 % cover in the GM treatment, and 0.2 ± 0.1 % in the GH treatments, as opposed to 7 ± 3 % in IM and 5 ± 1 % in IH.

Average shrub cover across all zones and treatments was 5 %, compared to a pre-fire shrub cover of 3.5 % in 2004, and 8.3 % in 2005. The grass treatments exhibited a significantly reduced shrub cover and richness as compared to the indigenous treatments, especially the GH treatment. Differences in shrub cover and richness between treatments was most pronounced in NF dry bank. Here the highest shrub cover (10 ± 3 %) was found in the IH treatment, followed by 9 ± 2 % in the IM treatment. Lowest shrub cover was found in the GH treatment (2 ± 1 %) and GM treatment (3 ± 1 %). There was a significant difference between the indigenous treatments and the grass treatment (GH & IM, $p < 0.05$; GH & IH, $p < 0.01$).

Thin-leaved shrubs showed a greater response to treatments, with significantly less cover in both grass treatments as well as the CH treatment ($p < 0.05$), all of which had less than 1 % thin-leaved shrub cover, as opposed to thin-leaf shrub cover in the indigenous treatments (7 ± 2 % in IM and 3 ± 1 % in IH plots). All herbicide treatments had the lowest thin-leaved shrub cover compared to the respective paired manual treatments. There was a significant reduction in shrub cover between GH and IH ($p < 0.05$) in the WB zone.

5.4.2.3 Indigenous species richness

Indigenous species richness followed a similar trend in response to the restoration treatments, with treatment effects most pronounced in the NF dry bank and the highest species richness in the indigenous treatments, followed by the control treatments and lowest in the grass restoration treatments (Figure 5.5).

The WB zone exhibited the highest species richness across all treatments (except the IH treatment), with the highest richness in the IM treatment (27 ± 3 species). In the NF dry bank indigenous species richness was lower in both control and grass treatment plots compared to the indigenous; from 19 ± 2 in IM and 18 ± 1 in IH, to 7 ± 1 in both GM and GH and 11 ± 2 in CM and 10 ± 1 in CH. Reduction in species richness was significant between the indigenous and grass restoration plots (GM & IM, $p < 0.05$; GM & IH, $p < 0.01$; GH & IM, $p < 0.001$; GH & IH, $p < 0.00001$) and the IH treatment and CH treatment ($p < 0.01$). On the SF bank there was a significant reduction in shrub richness between GH and IH ($p < 0.05$).

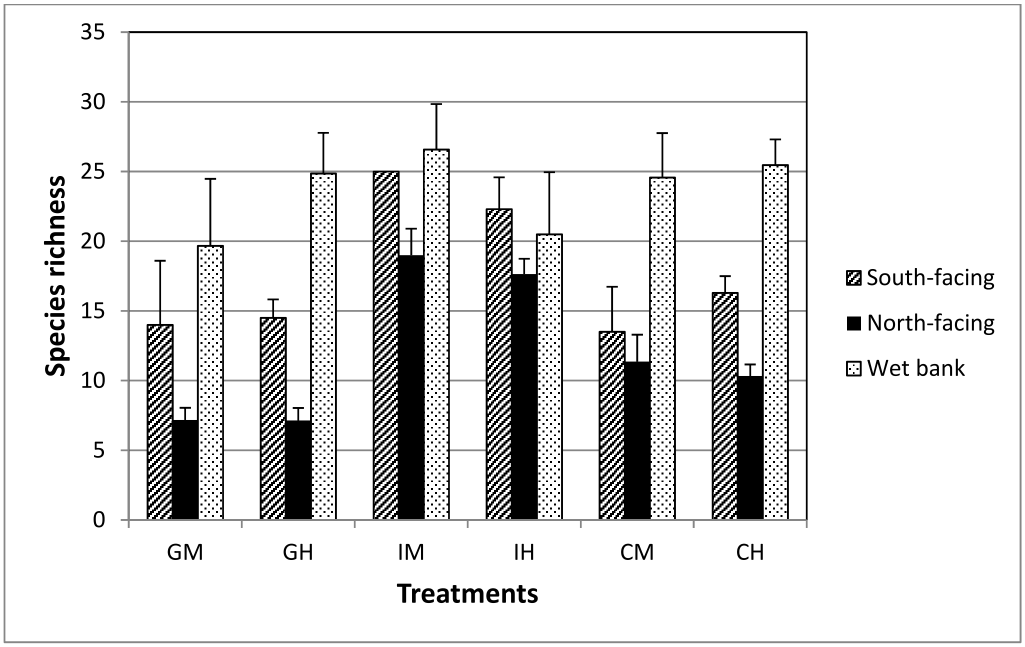


Figure 5.5. Species richness per zone and treatment in 2009

5.4.2.4 Alien species

Total exotic cover was lowest in the grass plots and highest in the control plots, with a significant difference between the GH (3 ± 1 %) treatment and CM (15 ± 4 %) ($p < 0.05$) and CH plots (22 ± 5 %) ($p < 0.001$).

5.4.2.5 Multi-dimensional scaling

Multi-dimensional scaling of species data indicates an overriding effect of lateral zonation over treatment effect, with a clear separation between the NF and SF dry banks but less pronounced in the WB zone (Figure 5.6).

There was little clear treatment effect across all zones, due to the strong lateral zone effect. The only treatment that showed a clear grouping was the GH treatment, with an average similarity of 55 %, followed by the IH treatment (45 %). The main indicator species were *D. eriantha* and *P. aquilinum*, and between some treatments *E. curvula*. Interestingly enough, all indicator species were aggressive or alien species such as *D. eriantha*, *E. curvula*, *P. aquilinum*, *A. longifolia* and *C. canadensis. P. aquilinum* cover was much lower in the GH treatment (average abundance 21 %), as opposed to an average abundance of 38 % in the GM treatment. *E. curvula* had greatest contribution in the GH treatment (avg. abundance 11 %), and *D. eriantha* was much higher in the grass treatments (avg. abundance 56 % in GH and 43 % in GM) as opposed to 13 % in IM and 13 % in IH.

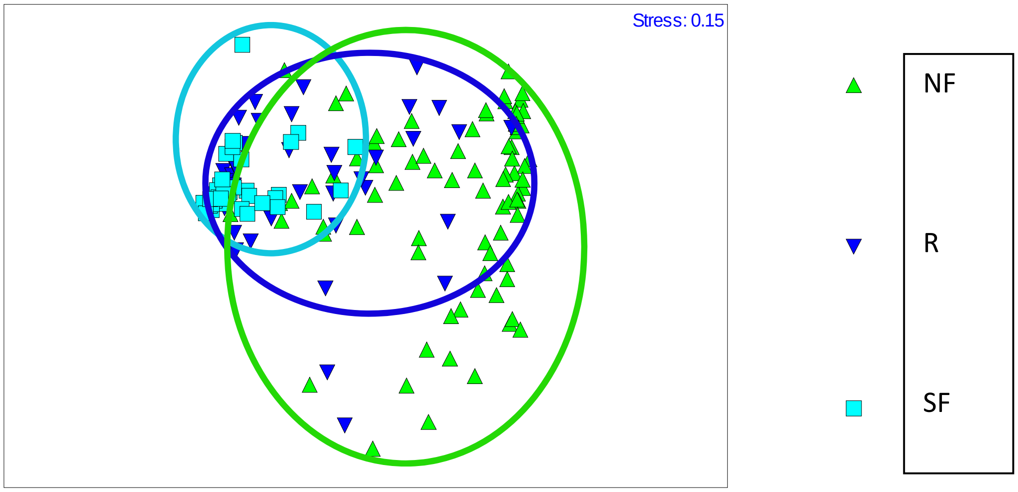


Figure 5.6. Multi-dimensional scaling according to lateral zone and aspect

Analysis of the treatments per zone revealed the lowest variance in the grass treatments in the NF dry bank: 89 % similarity in the GM and 72 % in the GH treatments. There was much higher variance in the indigenous and control treatments, with similarity values all lower than 45 %. *D. eriantha* is also the main indicator species for similarity for all treatments in the NF dry bank, except in the CH treatment, where *E. curvula* was the main indicator species. The main indicator species in the SF dry bank and WB zone were *D. eriantha*, *E.*

erecta and *P. aquilinum*. The reference and chronosequence data also indicate much lower riparian indigenous grass cover: 16 % in the reference sites, and ranges of 6 – 32 % in the cleared sites (although some grass restoration had taken place in the site that had 32 % grass cover). Pre-fire indigenous grass cover on the restoration site was 1 % in 2004, and had increased to 15 % in 2005.

MDS analysis reveals the highest similarity between the indigenous treatments and the reference sites, and highest dissimilarity between the grass treatments and the reference sites (Table 5.5 and Figure 5.7). This is more pronounced when growth form guilds are compared. Figure 5.7 also indicates the relationship of the reference sites and restoration treatments to the various cleared chronosequences, and Table 5.6 lists the abundance of the most indicator species and groups.

Table 5.5. Percentage dissimilarity between restoration treatments and reference sites, analysed according to species and growth form guilds

	GM	GH	IM	IH	CM	CH
Reference (species)	91	91	83	82	88	90
Reference (guilds)	85	86	62	61	71	79

Some clear differences between the reference sites, cleared chronosequences and restoration treatments emerge from the analyses (Table 5.6). Key guilds such as Cyperaceae and Restionaceae are missing or occur in low abundance in the restoration treatments. These guilds are also missing or occur in low abundance in the cleared chronosequences, except in the FKW site, which is a wetland and where Cyperaceae cover is very high (81 %). *P. aquilinum* abundance in the reference site is much lower (3 %) than any of the other sites, other than the GM treatment (0 %) and the FKW wetland (0 %).

Key riparian indicator species such as *Cliffortia graminea*, *Erica caffra* and *Anthospermum ciliare* are also missing from both restoration treatments and chronosequences.

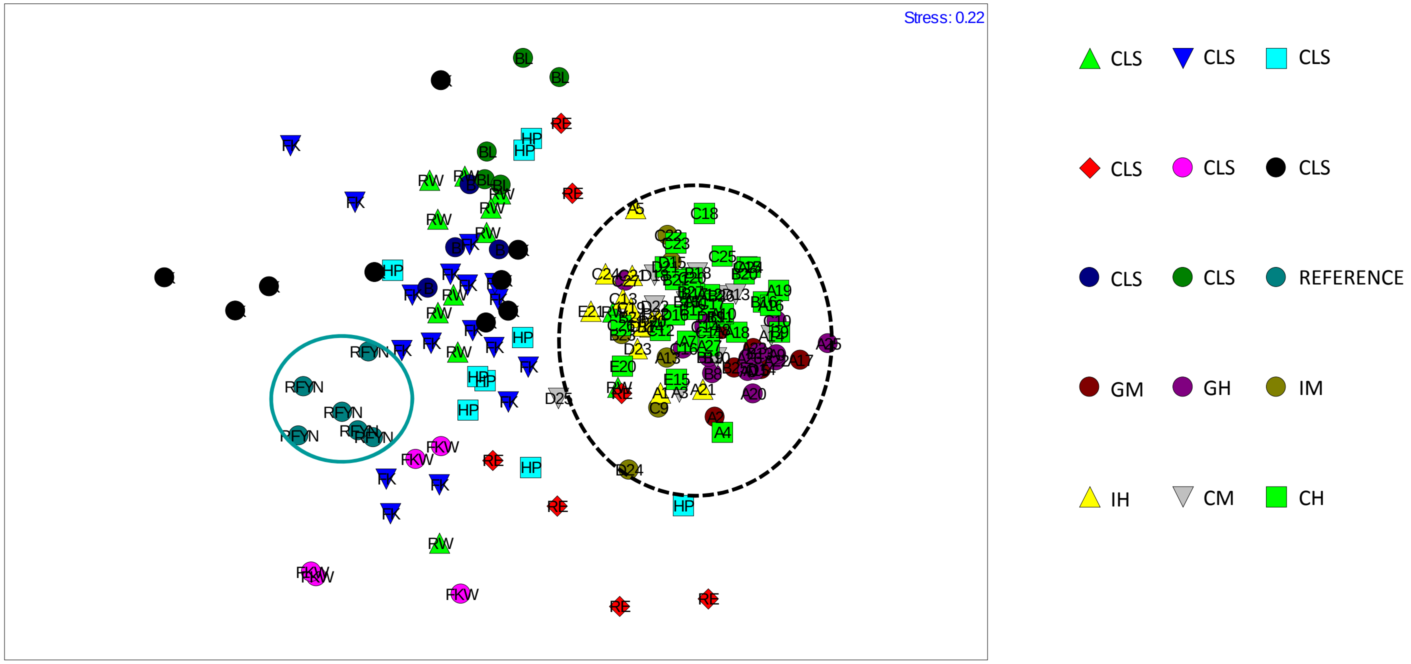


Figure 5.7. Multi-dimensional scaling plot of treatments in the NF dry bank, reference sites and chronosequences (4rth root transformed) (The dashed circle represents the restoration treatments, and the blue circle the reference community (REFERENCE). The remainder represents the cleared chronosequences (CLS)

Table 5.6. Analysis of dissimilarity between treatments in the NF dry bank, reference sites and chronosequences. Values in table represent the average abundance (in % cover) of species/guild.

Species / guild	**Uninvaded**	**Restoration treatments**						**Cleared chronosequences**						
	Reference	**GH**	**GM**	**IH**	**IM**	**CH**	**CM**	**CLS**	**CLS**	**CLS**	**CLS**	**CLS**	**CLS**	**CLS**
D. eriantha	0	74	80	22	21	28	37	0	0	0	0	0	0	0
Cyperaceae	36	0	1	5	7	3	7	10	18	9	81	14	6	0
Thamnocortus spp.	23	0	0	0	0	0	0	0	0	0	0	0	0	0
E. curvula	0	15	8	9	13	30	25	0	0	0	0	0	0	0
A. ciliare	15	0	0	0	0	0	0	0	7	0	9	0	0	0
C. graminia	22	0	0	0	0	0	0	0	0	0	0	0	0	0
E. caffra	13	0	0	0	0	0	0	0	0	0	0	0	0	0
Indigenous grasses	16	5	3	16	12	15	11	32	21	20	26	6	11	6
B. bubalina	8	0	1	0	1	1	1	1	2	0	0	0	1	3
P aquilinum	3	11	0	17	11	15	13	27	7	7	0	40	5	9
H. petiolare	3	1	0	12	0	1	1	0	0	3	0	28	3	16
R. melanophloeos	5	0	0	0	0	0	0	0	0	0	0	0	5	0
M. muricata	4	0	0	0	0	0	0	0	0	0	0	0	0	0
Plectranthus spp.	7	0	0	0	0	0	0	0	0	0	0	4	20	0
A. herbaceum	2	0	0	0	0	0	1	1	0	0	8	0	0	0
R. adiantiformis	0	0	0	0	0	0	0	3	6	0	0	5	6	0
P. dilatatum	0	0	0	0	0	0	0	9	0	10	0	0	0	0
H. lucida	0	0	0	2	0	0	6	0	0	0	0	7	2	4
H. cymosum	0	0	0	0	0	0	0	0	0	7	0	0	0	5
S. dentata	2	0	0	0	0	0	0	0	0	0	0	7	0	0
S. corymbosa	0	0	0	1	3	0	0	0	0	0	0	0	0	0
A. aethiopicum	0	0	0	2	3	0	0	0	0	0	0	0	0	0
P. glabra	0	0	0	0	3	0	0	0	0	0	0	0	0	0

5.5 DISCUSSION

5.5.1 Use of grasses in restoration of grassy fynbos

The re-establishment of a vegetation cover through the planting of grasses was extremely successful, although establishment was dependent on zone and then decreased over time, and also compromised diversity (see Sections 5.5.2 and 5.5.3). Unassisted grass establishment, as evidenced by *D. eriantha* and *E. curvula* cover in the control treatments, was also relatively high, but to a lesser degree in the indigenous treatments. Grass cover in the restoration plots was much higher than normally occurs in grassy fynbos - an average grass cover of 36 %, with C3 grasses consisting of 14.4 % and C4 grasses 21.6 % of total vegetation cover (Cowling 1983). The reference and chronosequence data from this study also indicate much lower riparian indigenous grass cover. Species exchange between restoration treatments has been found in other trials (Baasch *et al.* 2012), with increasing similarity over time between treatments. The disturbed nature of the area will also facilitate the increase of grasses in the control and indigenous treatments. In particular, the increase in nitrogen levels through the invasion process (Marchante *et al.* 2009; Drake 2011; Tye and Drake 2011) favours grasses over species which have evolved with low soil nutrient levels, enabling them to outcompete indigenous species, especially slower-growing indigenous shrubs (Milton 2004; Musil *et al.* 2005).

Although burning may reduce total soil nitrogen immediately after the fire, NH_4 – and NO_3 – nitrogen often increases (Korb *et al.* 2004; Drake 2011; Tye and Drake 2011) and van der Waal (2009) reported an increase in acidity, N, P, K, Mn, Zn and Ca on invaded and cleared slopes. This creates further favourable conditions for nitrophilous, non-fynbos species (Holmes and Cowling 1997b), which have the potential to permanently transform the community into a weedy grass community (Vitousek and Walker 1989; Yelenik *et al.* 2004) and can be resistant to natural restoration (Milton 2004, Reinecke *et al.* 2008) and subject to secondary invasions (Blanchard and Holmes, 2008). Didham *et al.* (2005) have also suggested that ecosystems that are naturally subject to extreme abiotic regimes, which would include riparian ecosystems, have greater tendency to display alternative stable states that may be resilient to restoration interventions. Two of the dominant grass species in the restoration trials, *D. eriantha* and *E. curvula*, are vigorous C4 species, and have become invasive in other parts of the world (Nakayama *et al.* 2007) where they displace indigenous species. *Paspalum dilatatum*, an invasive species from South America, was also found on the site, which is of concern. *E. erecta*, the other dominant grass found in the restoration trials, is indigenous to Southern Africa but a declared weed species in other parts of the world (McIntryre and Ladiges 1985; Jacobs and Hastings 1993; USDA 2012).

There is increasing concern about grass invasions worldwide (D'Antonio and Vitousek 1992; Keeley 2004), including in South Africa (Milton 2004). Invasive grasses reduce biodiversity and there is growing evidence that grasses can transform ecosystem processes and reduce the productivity of natural systems. The increased and more continuous grass cover increases flammability and fire connectivity, thus promoting more frequent and extensive fires (Pyke *et al.* 2010) which prevents the establishment of woody species (Milton 2004; Sankaran *et al.* 2008). This creates feedback loops which promote a high grass cover, at the expense of other fynbos growth forms, resulting in continued grass dominance (D'Antonio and Meyerson 2002; Bond 2008). Grass invasions will be further favoured by increases in atmospheric nitrogen levels, warmer climates and greater variability in rainfall quantity and seasonality.

Any change in vegetation will result in some change in ecosystem function(s), seldom predictably and not always in tandem (Tickner *et al.* 2001; Le Maitre *et al.* 2011). The greatest functional changes will occur if the abundance of the dominant species changes, as they are most influential (Richardson *et al.* 2007). The greater the difference in morphology, growth rate and other traits between previously dominant vegetation and new dominant species, the greater the change in function (Richardson *et al.* 2007). This will be irrespective of whether the new dominant species is an indigenous or invader species. Based on the above, the deliberate introduction or spontaneous invasion of grass after clearing can therefore have unforeseen consequences for riparian function. Given the competitiveness of grasses and their ability to change fire behaviour and transform ecosystems, it is not certain whether the other guilds (forbs, shrubs, restios) will be able to re-establish over time. Baasch *et al.* (2012) found that grass re-introduction through hay transfer and sowing resulted in long-term effects on species composition, with a permanently higher abundance of grassland species. However, the effectiveness of the grass treatments in suppressing regrowth and achieving biotic resistance in these trials is undisputable, and grass could be a very valuable management tool if used correctly. This is discussed further in Sections 5.5.3 and 6.5.

5.5.2 Re-establishment of indigenous vegetation

The findings show that different restoration treatments result in very different rates and trajectories of recovery of indigenous vegetation. Active intervention in the form of seed and established plant additions resulted in a significantly higher indigenous cover after seven months as compared to the grass or passive restoration (control) treatments. Indigenous cover was lower, and appeared to be suppressed by grass in the grass treatment, as opposed to controls. Indigenous cover and composition was also strongly influenced by lateral zonation, and was lowest across all treatments in the NF dry bank, although undesirable species such as *P. aquilinum* comprised a large portion of the initial post-fire indigenous cover in the moister SF and WB zones. The dynamics and impacts of *P. aquilinum* on the restoration of the site are discussed in Section 5.5.2.5. In the NF dry bank there was no indigenous cover in the grass treatments after seven months, whereas the grass cover of the grass treatments was highest in this zone, and bare ground was highest in the control and indigenous treatments.

Methods of species addition, for example seeds versus seedlings and methods of seeding (e.g. seeds drilled, broadcast or through additions of seed- rich mulch), can have a great impact on the resultant plant community (Klimkowska *et al.* 2010, Middleton *et al.* 2010; Nyamai *et al.* 2011; DeFalco *et al.* 2012). These may differ between different sites (Larson *et al.* 2011). There is not much information available on the relative success of seeding versus transplanting seedlings, but some studies indicate that transplanted seedlings have a higher survival rate than seedlings germinating from seed in the field (Page and Bork 2005; Buisson *et al.* 2006). This is because transplanted seedlings are nurtured during a critical life stage. The immediate post-fire environment is harsh, even more so in riparian areas (Naiman and Décamps 1997), and restoration by seeds alone can be limited through unsuccessful recruitment (Clark and Wilson 2003). Once seedlings have survived into the second growing season, they have a high chance of survival. Recovery through seeding can also take much longer, as has been reported by Pretorius *et al.* (2008). Middleton *et al.* (2010) found that using seedlings in combination with seed is more successful than seed alone, and that adding established plants resulted in a community closer to the reference condition in terms of diversity and richness. Investing effort in growing plants and transplanting these increases the target species establishment. It is recommended that early successional pioneer species should be introduced through seeding, especially if the seed can swamp the exotic seed bank (Simmons 2005), and that growing effort is invested in perennial species. Establishing grown plants may be especially useful for obligate mycorrhizal species where they are transplanted into degraded mycorrhizal-poor areas (Richter and Stutz 2002).

This post-fire cover was higher than the post-clearing, pre-fire indigenous vegetation cover, which was 15 % in 2004, a few months after clearing was completed, and 57 % 15 months after clearing and shortly before the controlled burn. The low pre-fire vegetation cover can be explained in part by the high brush cover after the felling of *A. longifolia*: 61 % in the NF dry bank and WB zone, and 60 % in the SF dry bank. Many indigenous fynbos seeds also need a fire (smoke and heat) stimulus to germinate (Keeley *et al.* 1985; Le Maitre and Midgley 1992; Brown 1993). The increase in indigenous vegetation after clearing before the fire, over the space of 15 months, is interesting, as it is generally believed that little inter-fire recruitment takes place in fynbos and that all species establish immediately after fire (Kruger 1983; Le Maitre and Midgley 1992; Holmes and Richardson 1999). This may be more relevant to the shrub component, as Le Maitre and Midgley (1992) have found that most dominant woody shrubs establish in open environments after fires. However, the overall pre-fire shrub cover was 3.5 % in 2004, which increased to 8.3 % in 2005, but reduced to 5 % three years after the fire, as measured in 2009. It is likely that the high fire severity was responsible for reducing shrub cover.

5.5.2.1 Impact of season and climatic variability on restoration

Climatic variability between years is also an important factor for regeneration and restoration (Moreno *et al.* 2011), both active and passive. The large deviations from average rainfall, shortly before the fire and especially during the first months and year of the restoration trials, may result in very different trajectories and different final end-states of the treatments compared to a year with different rainfall patterns, as the effect of moisture stress is especially important during the recruitment phase (Richardson and Cowling 1992; Moreno *et al.* 2011). Competition between the plants increases with increasing moisture stress, and C4 grasses, through their greater water use efficiency, have a greater competitive advantage over C3 grasses and plants (Cowling 1983). C4 grasses have their main growing season during summer, when they exert the greatest competitive effect. This competition during the critical germination and early seedling establishment phase of the non-grass component can result in high seedling mortality and reduced cover of other species (D'Antonio and Vitousek 1992). The effect of soil moisture stress and grass competition on the restoration outcomes is discussed in Section 5.5.3.2.

Although survival of the planted individuals did not differ across zones, there was a marked difference between percentage survival of species planted in summer and those planted in autumn, as well as between the species planted in summer. Overall, 25 % of the species planted in summer survived, as opposed to a much higher survival rate of 93 % of the species planted in autumn. This is a clear indication of the importance of timing of restoration actions and how stochastic events, such as rainfall, can vastly change the outcome of a restoration project. High mortality of *Acacia* seedlings was also observed in January 2006 (see Plate 12) and it is hypothesised that the seasonal timing of fire can be used to manipulate the successful recruitment of indigenous species to suppress *Acacia* seedlings. Other authors (Bakker *et al.* 2003; Middleton *et al.* 2010) have also reported that the success of restoration interventions is contingent on the year and site, and multiple introductions may be required if any one year fails. Moreno *et al.* (2011) reported a high variation of recruitment (varying by factors of three to ten) between years subject to rainfall, with species-specific (e.g. *Erica*) sensitivity to dry conditions after fire.

Different species showed a wide variation in survival, with the highest survival exhibited by *H. petiolare* (50 %), which is considered a suitable indigenous restoration species, since it is fast-growing, produces large quantities of seeds that are easy to collect, propagates easily and provides a good groundcover. Shrubs such as *Burchellia*, *Halleria* and *Searsia* are also desirable species; once established, these will resprout and provide stability after fire, but their establishment success was much lower. They also attract frugivorous birds, which may bring in more seed.

5.5.2.2 Recruitment from soil seed bank

Germination from seeds was much slower, and unassisted recovery (control plots) was very slow, especially in the NF dry bank (indigenous cover < 10 % in July 2006). This is surprising, as the post-fire soil seed bank density was highest in the NF dry bank (> 1 661 seeds/m^2), mostly through the contributions of Asteraceous annual and short-lived perennial species such as *Senecio rigidus* and *Conyza pinnata* (Chapter 2 and Appendix A). The NF dry bank was more exposed to solar radiation and with the dry December month, it is likely that soil moisture was initially the limiting factor in the successful germination and establishment of indigenous seedlings in this zone.

A number of authors hypothesise that early successional communities are often seed-limited (Turnbull *et al.* 2000; Seabloom *et al.* 2003; Young *et al.* 2005) and therefore contain unoccupied microsites which are available for the establishment of IAPs. This may be exacerbated if connectivity to intact source sites is low, as seed dispersal in fynbos is limited (Brits 1987; Le Maitre and Midgley 1992). Seed limitation will also affect the rate of re-assembly (Bischoff *et al.* 2009), and a lack of suitable microsites may in turn limit regeneration (Young *et al.* 2005). It is also not known what fraction of seed will successfully recruit, i.e. whether higher density is actually required for the establishment of a successful cover. Results from the soil seed bank study (Chapter 2) indicate that indigenous recovery does not appear to be seed-limited, although there may be localised impacts, e.g. where fire severity was high under large brush stacks. It is likely that post-fire conditions, especially during the recruitment phase, may be more limiting on recovery than seed densities.

The establishment of a post-fire vegetation cover is also influenced by the temporal dynamics of the seeds in the soil, about which much is still poorly understood (Donohue 2005). The implications of the relative timing of germination of different species from the soil seed bank on succession and community development have been discussed in Chapter 4. Moreno and Oechel (1991) also found germination under controlled conditions to be much greater than in field germination.

5.5.2.3 Fire and impacts on re-establishment

The effects of fires are difficult to predict, due to the high number of variables that can affect fire response, such as large numbers of co-existing species, heterogeneous landscapes, fire intensity and season, weather conditions during recruitment phase and ecological complexity (Pyke *et al.* 2010). Each fire (or even part of the same fire) is unique (Bond and van Wilgen 1996; Baker 2009; Mandle *et al.* 2011; Moreno *et al.* 2011) and responses will vary according to pre-fire factors such as the age and composition of standing vegetation at the time, the seed banks, the fire intensity and post-fire conditions (Richardson and Cowling 1992). Successive fires and fire intervals will result in different trajectories and combinations of co-existing species. Each fire will therefore result in unique, event-dependent plant populations (Bond and van Wilgen 1996). Fire can affect the following plant community variables: seedling production, adult plant persistence and the post-fire performance of plants (Knox and Clarke 2006; Moreno *et al.* 2011). These effects are most apparent during the immediate post-fire period but also translate into subsequent vigour (e.g. survival of herbivory and future reproductive output) (Moreno and Oechel 1991). Varying fire intensities may result in differential germination and survival of species (Stromberg *et al.* 2008), varying ratios of seedlings vs. resprouters, as well as changes in competitive interactions. During this study, fire resulted in reduction in the above-ground cover of some guilds, e.g. resprouting shrubs; an impact which was still evident three years after the fire. It also resulted in a reduction of shrub soil seed banks. The relative cover of other species was favoured, e.g. bracken, which had a much larger contribution to indigenous cover after the fire. Survival depends on type and intensity of fire, the height of the plant, insulating capacity of the bark, and resprouting or coppicing ability (Pyke *et al.* 2010).

Fire intensities vary according to the age of the IAP stand, the season, weather, fuel moisture and topography (Moreno and Oechel 1991). Higher fire intensities can result in greater mortality of resprouters, which creates more gaps for the re-establishment of seedlings, although higher seed mortality due to lethal soil temperatures can co-occur. Little above-ground vegetation remained after the hot fire experienced during this study (only in the river channel), although some vegetation managed to resprout after the fire. Lower fire intensities can result in a higher percentage survival of resprouters, which can intensify competitive interactions between seedlings and resprouters on one hand, but facilitation effects between resprouters and seedlings can also be enhanced, e.g. where resprouters provide suitable micro-sites and aid establishment of seedlings (Moreno *et al.* 2011). Post-fire conditions of high solar radiation, more extreme temperature shifts, wind, higher water loss, increased erosion, changing soil properties including water holding-capacity and short-term soil nutrient availability, all influence the re-establishment of vegetation (Mandle *et al.* 2011). The most vulnerable stage in the life history of plants is the germination and establishment phase (Quintana *et al.* 2004), and environmental conditions during this phase can completely alter the trajectory of re-assembly. However, pre-fire moisture stress combined with the subsequent fire may have depleted the reserves of any resprouting species and reduced their survival after the fire. Annual post-fire rainfall was much higher, although the rainfall in the first two summer months immediately after the fire was much lower than average, and this is likely to have had a significant impact on the successful recruitment of seedlings.

Fires, especially high-intensity fires, as occurred where the stacks burnt (Chapter 3), often result in changes of the chemical and physical properties of the soil, which will influence the successful establishment of seedlings during the post-fire period. Post-fire germination conditions are a vital determinant of the success of post-clearing recovery. Factors such as a decreased vegetation cover (DeBano 2000a), increased soil water repellency and erosion (Scott and van Wyk 1992; DeBano 2000a, b, c), a reduction in soil micro-organisms (especially arbuscular mycorrhizas) (Pietikäinen *et al.* 2000) can all exacerbate the impact of fire and compromise the establishment of a viable community.

The removal of plant cover will increase the risk of erosion immediately after the fire (DeBano 2000a). High-severity fires will kill off many resprouters, which provide soil stability. This is exacerbated by the changes in the physical and chemical composition of the soil due to heating (DeBano 2000a, b, c), which will hinder the recovery of the ecosystem. The increase in water repellency that can occur as a result of the heating of soil during fires also affects the post-fire germination and ability of seedlings to establish. The phenomenon of water repellent soil is complex, with severe fires capable of destroying the repellency of the upper layer of water repellent soils (Doerr *et al.* 2004), but enabling the layer underneath to remain or increase in repellency. Heavy rainfalls can cause the upper layer to be lost to overland flow, with loss of the remaining soil seed bank further compromising natural recovery. Van der Waal (2009) reported an increase in soil water repellency and a decrease in soil surface hardness after invasion and clearing (including fires).

An additional effect of severe fires that will influence the post-fire establishment, succession and growth of the indigenous vegetation is the reduction of soil micro-organisms (Pietikäinen *et al.* 2000; Bárcenas-Moreno and Bååth 2009; Collier and Bidartondo 2009). Arbuscular mycorrhizas (AMs) play an important role in plant nutrition, nutrient cycling and the development of soil structure (Korb *et al.* 2004). Other authors (Pietikäinen *et al.* 2000; Korb *et al.* 2004.) have also reported changes in the biomass and activity of soil microbes after heating. Fire may either kill the soil microbes directly or change the soil organic matter, indirectly affecting the soil microbes (Pietikäinen *et al.* 2000). Although little work has been done in fynbos systems on the effect of invasion and high-intensity fires on soil micro-organisms, Allsopp (2010) reported that approximately 62 % of the flora from the Cape Floristic Region form AMs, and that without the presence of these AMs in the soil, these species will not establish. If these AMs are killed by the high-intensity fires during fell-and-burn, it will limit the recovery of a functional community, as has been found in other studies. Collier and Bidartondo (2009) have found that ericoid mycorrhizal communities play a significant role in the recovery of heathlands after invasions, with a lack of fungi limiting establishment. These effects can be long-lasting and Korb *et al.* (2004) found that the burning of slash piles, in addition to nearly eliminating viable seeds in the soil seed bank, also nearly decimated AM propagules, as well as altering soil chemical properties, and that these effects were still evident after two years. Changes in soil biota can also result in changes in competitive interactions between indigenous species and can favour invasive species (Callaway *et al.* 2003a, 2004), although no information is available for fynbos.

The findings of this study indicate that some guilds, e.g. sedges and shrubs, are adversely affected through the application of herbicide during the management of regrowth. Rhoades *et al.* (2002) found that the combined impact of fire and herbicide on the establishment of indigenous vegetation is much more severe than either variable alone, resulting in increased bare ground as well as significantly increasing the available soil nitrogen, with will favour grass species.

5.5.2.4 Longer term recovery

By 2009, there were no significant differences between overall indigenous cover. It can therefore be concluded that treatments had little effect on overall indigenous cover in the SF and WB zones, but significantly increased indigenous cover in the NF dry bank (compared to the controls), whereas the grass restoration treatment significantly inhibited the growth of other indigenous species. Species richness followed a similar pattern in response to the treatments and across zones, with the most significant decrease in species richness exhibited in the NF dry bank in response to the grass treatments.

Comparison with the vegetation of intact sites indicates that some key guilds (e.g. Restionaceae) and species (e.g. *Erica caffra*, *Anthospermum ciliare* and *Cliffortia graminia*) are missing or present in much lower densities. Cover of Restionaceae species, which form an important component of fynbos, was very low throughout the restoration area, with the lowest cover in the grass treatments, especially the GH treatment. Another key guild that occurred in much lower densities and richness in the treatment site compared to the reference sites was the shrub guild, which again appears to be suppressed by the grass treatments, especially the GH treatment. Fire appeared to have an effect in reducing shrub cover throughout the restoration area, similar to the findings of Blanchard and Holmes (2008) and Reinecke *et al.* (2008). Sedges, which form another important guild in riparian areas, were also lower in the grass treatments, as opposed to the indigenous and control treatments), and results also indicate that herbicide adversely affects sedge cover.

As discussed in Chapter 1, succession after disturbances such as invasion and fire may proceed along many permutations and combinations of trajectories, determined by the interaction of a host of factors. Full recovery to pre-disturbance conditions can take decades and may never be achieved (Holmes *et al.* 2008), and many different stable end-states may be possible. Analyses of the chronosequences indicate that there is much variation in community composition between the various sites; this can be attributed to either the inherent variability of riparian vegetation in the fynbos biome or the various successional stages, trajectories or end-states of these communities.

The lack of some keystone species and low numbers of some guilds in the field site after three years is a matter for concern. Some keystone species can be important in biotic resistance, as they can affect both the number of invading species and the total biomass of invasive species, to a greater degree than species richness does (Callaway and Davis 1999; Pokorny *et al.* 2005). These missing keystone species will have to recruit from other areas. Long-term monitoring will reveal whether any abiotic or biotic thresholds have been crossed that will prevent their establishment and full recovery to a functional riparian system which contains the full complement of key species and/or guilds (Rejmánek *et al.* 2005).

5.5.2.5 Pteridium aquilinum

During the first survey in 2006, seven months after the fire, most of the vegetation cover on the SF dry bank was *P. aquilinum* (bracken); to such a degree that it masked any restoration treatment impacts (see Plates 13-16). Bracken prefers mesic soils (Ershova 2010), which explains it’s higher cover in the wetter SF and WB zones, and can make it a potential problem in moist and riparian areas. Bracken cover increased after clearing to 10 % cover just before the fire and the high post-fire bracken cover indicates that it was stimulated by the fire. This response persisted, and during the survey in 2009, it was still the dominant species, making up 46 % of overall indigenous species cover in the SF dry bank, 25 % in the WB zone and 12 % in the NF dry bank. In such high cover, bracken appears to suppress the regrowth of alien species as well as other indigenous species, as indicated by the negative correlation with indigenous species, especially in the SF dry bank.

Although it is a cosmopolitan species and also indigenous to South Africa, the spread and encroachment of bracken in many part of the world is problematic (Pakeman *et al.* 2002; Ghorbani *et al.* 2007; Cox *et al.* 2008) due to its contribution to species decline and habitat degradation (Pakeman and Marrs 1992). Bracken suppresses and displaces other indigenous species, impoverishes the indigenous soil seed bank and lowers the diversity of plant communities (Pakeman and Marrs 1992; da Silva and Matos 2006; Ghorbani *et al.* 2007). It has been classified as a landscape transformer, due to its ability to change ecosystem structure and function (Novak 2007; Ehrenfeld 2010). This takes place through a number of interacting processes, one of which is fire. Recent research in South African montane grasslands (Adie *et al.* 2011) found that above-ground fire temperatures and intensity were much higher in bracken stands than in the grassland habitat, which resulted in a high mortality of woody seedlings and reduced woody species density. Predominance of bracken can also result in more frequent fires, suppressing the establishment of woody species (Cox *et al.* 2008), damaging older woody plants by killing coppicing resprouts (Adie *et al.* 2011) and maintaining the dominance and increasing the spread of bracken. These effects also appear to facilitate the establishment of IAPs like *Rubus cuneifolius*.

In addition to the above, bracken has fire-resistant spores, underground rhizomes that are immune to fire, stores carbohydrates, as well as a large number of dormant buds; all traits which enables it to tolerate fires and resprout immediately after fire (da Silva and Matos 2006; Novak 2007) and outcompete other species for resources, especially during recruitment stage (Humphrey and Swaine 1997). It has the ability to re-establish first which enables it to exploit resources earlier and more quickly than other species, and thus suppress the establishment of other species (Leffler *et al.* 2011). Once established, it is very persistent, making restoration of infested sites difficult (Pakeman *et al.* 2000). Since its spread and dominance is aided by fire, suppressing fire and minimising fuel loads are recommended to mitigate the impact of bracken (da Silva and Matos 2006), although control can yield highly variable results (Le Duc *et al.* 2000, 2007; Cox *et al.* 2008), due to localised effects. Although its contribution to fire intensity and frequency has not been measured in grassy fynbos, it is likely to behave in a similar fashion, and may transform the vegetation to such a degree that it presents a biotic barrier to recovery (Pretorius *et al.* 2008). The invasion of *Pteridium* may be an example of “invasion meltdown”, where its spread is facilitated through previous invasions of other species, and effects are compounded (Simberloff and Von Holle 1999; Montgomery *et al.* 2012).

5.5.3 Biotic resistance

The results from this the restoration trials indicate that it is possible to achieve biotic resistance through restoration, and that this can significantly suppress the regeneration of *A. longifolia* (or other invasive Acacias[3]). The degree of biotic resistance achieved during this study was dependent on lateral zonation and aspect, and it is likely that the main variable determining the success of the grass restoration treatment (see Plates 13-15) in suppressing regrowth and achieving biotic resistance is related to competition for moisture during the critical recruitment phase of *A. longifolia*. The suppression of regrowth of IAPs through the planting of *D. eriantha* was most pronounced in the NF dry bank. Indigenous vegetation also appears to suppress the regeneration of alien seedlings (Plates 13-16), although to a lesser degree, and this effect is especially pronounced in the WB zone and SF dry bank where the rate of indigenous vegetation recovery was good.

The initial results clearly indicated the achievement of biotic resistance through reinstating a vegetation cover. It will only be possible to quantify the degree of long-term biotic resistance over time, with continued monitoring, especially after disturbance events such as fire. However, it is likely that the high vegetation cover that has been achieved on the site will remain fairly resistant to re-invasion, through a number of mechanisms. The high grass cover is likely to repel invaders through competition and interaction with fire, as its more flammable nature will result in more frequent and higher-intensity fires, which will prevent the establishment of woody species (Bond 2008). The high bracken cover is likely to fulfil the same role, by suppressing the establishment of woody IAPs. However, the high grass and bracken cover is equally likely to suppress the establishment of a more natural and diverse fynbos community, through the same mechanisms mentioned above. It may be considered to have caused long-term alterations in the natural successional trajectories (D'Antonio and Chambers 2006; Baasch *et al.* 2012) and be resilient to recovery to a more natural structure and composition (Reinecke *et al.* 2008).

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[3] Biological control has hugely reduced the invasive threat of *A. longifolia* (Moran and Hoffmann, 2011), although the legacy of the long-lived soil seed still remains a challenge, and suppression of regeneration from the soil seed bank is thus an important management tool. Many other invasive *Acacia* species still present a severe threat to South African ecosystems, for example, *A. mearnsii* is considered South Africa's worst invader species, and is a problem in many other coutries as well (Le Maitre *et al.* 2011). The principles discussed in this section are thus also relevant in the management of these species.

5.5.3.1 Role of propagule pressure

The highest density of *A. longifolia* seeds occurred in the NF dry bank zone, with approximately 4 500 seeds/m^2 before the fire. After the fire, approximately 2 500 seeds/m^2 were recorded, with losses attributed to the high fire intensities. Both pre- and post-fire *A. longifolia* seed densities are much higher than indigenous seed densities, and the post-fire IAP seed density is still enough to maintain high levels of recruitment and present a serious challenge for management after clearing and fire (Richardson and Kluge 2008; Strydom *et al.* 2012). High propagule pressure is one of the main factors that have been implicated in plant community invasions (Richardson and Pyšek 2006; Tanentzap and Bazely 2009). Fires provide a heat germination cue to the alien *Acacia* seeds (Kulkarni *et al.* 2007), resulting in mass germination from the soil seed bank, although mortality in the upper layer would have occurred under larger brush piles. It is likely that the hoeing of the indigenous plots assisted the germination of indigenous seeds as well as *Acacia* seeds, as evidenced from the higher *A. longfolia* density and cover in the indigenous treatments, through disturbance of the soil surface and bringing viable seeds from lower depths to the surface.

Most invasive *Acacia* species accumulate large (Holmes *et al.* 1997 reported more than 45 000 seeds/m^2) and viable soil seed banks. It is therefore very important to account for the propagule pressure in assessments of biotic resistance (Lonsdale 1999; Eschtruth and Battles 2011; Warren *et al.* 2011a). It will be easier to achieve almost 100 % biotic resistance when propagule pressure is low (early in the invasion process at low-residence time rather than later), when propagule pressure is high. Currently, control and restoration in fynbos have inherited a legacy of large numbers of accumulated IAP propagules, and the achievement of biotic resistance can be a phased process: firstly, managing and reducing the IAP propagules, and secondly, reassembling a community that can repel, or mostly repel, entry of new invasions. Ideally, these processes should operate in tandem, where restoration is used as part of the management of IAPs to reduce propagule pressure, as appears to have been achieved during this study. Figure 6.1 illustrates the relationship between IAP propagule pressure, management and biotic resistance.

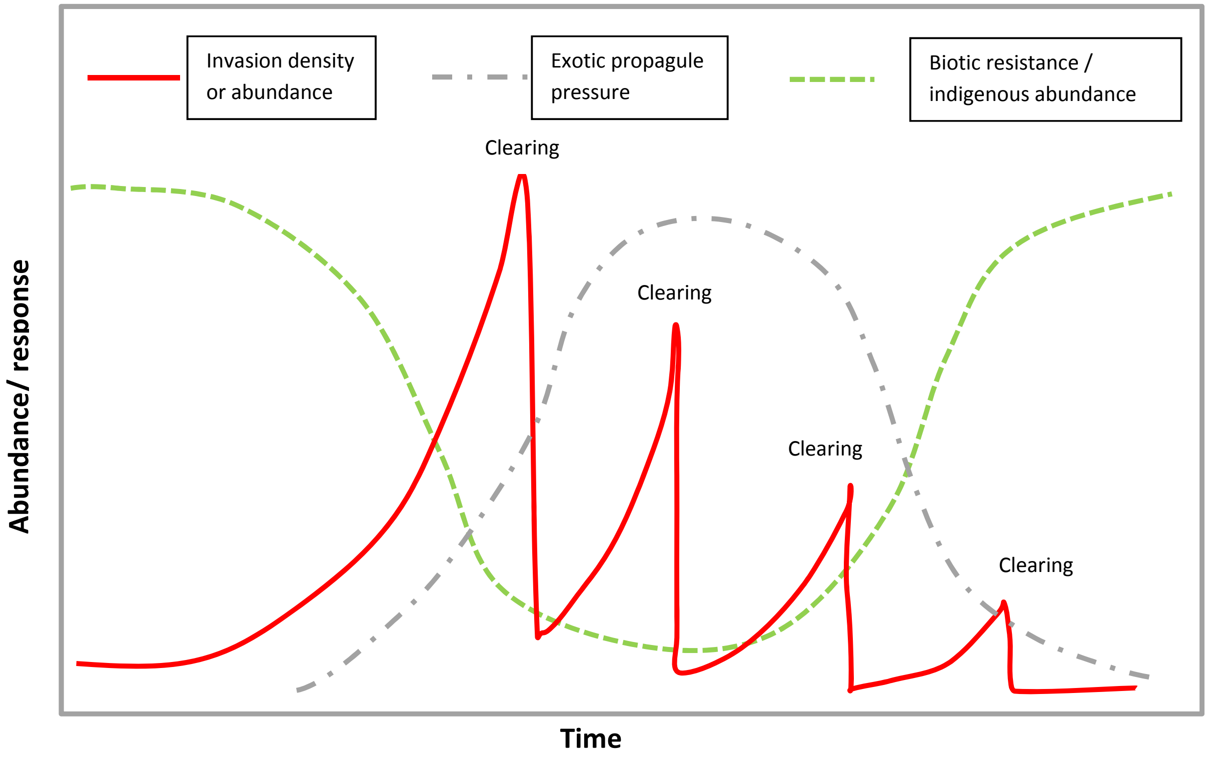

Figure 6.1. The interaction of invasion, indigenous cover, biotic resistance, management and exotic propagule pressure. This diagram indicates a reduction in invasion abundance through clearing. The indigenous abundance cover can be equated with either passive or active restoration

Figure 6.1 illustrates the typical expansion of an IAP in a new range. This shows an initial low abundance of IAPs after introduction, a lag phase with a slow increase in abundance, followed by an exponential increase in abundance. With increasing residence time, both propagule pressure and IAP abundance increase, and indigenous vegetation cover and biotic resistance decrease. This process needs to be reversed for biotic resistance to be re-instated, through decreasing propagule pressure and increasing indigenous vegetation cover.

Managing the legacy of a large viable soil seed bank, where mass germination is triggered through fire, is therefore a crucial first step in the restoration process (Richardson and Kluge 2008). Biological control forms an important component of the integrated IAP management strategy of WfW, and has reduced the seed production of many Australian *Acacia* species in

South Africa. Biological control (the gall wasp *Trichilogaster acaciaelongifolia*) was introduced in South Africa in 1982 and 1983 to reduce seed output, and has proven very successful in reducing seed output as well as vegetative growth. Dennil (1985) has recorded a mean reduction in seed production of *A. longifolia* of 96 % in the South-western Cape, and a reduction of 50 % in vegetative growth. This may explain the lower *Acacia* seed bank densities compared to what has been found for other invasive *Acacia* species (Holmes *et al.* 1987). In many situations, biocontrol is considered the most effective and practical means of reducing seed numbers, and provides a long-term solution (Impson *et al.* 2008, van Wilgen *et al.* 2012). However, due to the longevity of most *Acacia* seeds, a viable IAP seed bank will remain for many future decades, requiring on-going management. Conflicts of interest with the commercial use of wattle also impact on the use of biocontrol to reduce seeds.

Typically, managers have used fire to stimulate mass germination (treating the regrowth with herbicides) as a method for decreasing the soil seed bank, but this often requires repeated fire and herbicide treatments with often severe associated impacts on the soil, soil seed bank and indigenous vegetation. In this study, between 11 % and 40 % of the pre-fire *A. longifolia* soil seed bank remained after the fire and first germination flush, and unless suppressed, repeated follow-ups will be required to kill regrowth. A restoration strategy aimed at achieving biotic resistance in wattle-infested fynbos therefore has to take fire into account, and optimise its use, especially since fires form an integral and inevitable component of fynbos (Roura-Pascual *et al.* 2010). Essentially, the restoration strategy during these trials employed fire to stimulate the mass germination of wattle seedlings, and then used competitive species to outcompete the wattle seedlings and prevent their establishment. Possible mechanisms of achieving biotic resistance after fire are discussed below.

5.5.3.2 Mechanisms of biotic resistance

Since there are no functionally (morphologically) similar species to wattles in fynbos, other options of preventing re-invasion and achieving biotic resistance have to be explored. The planting of grasses was implemented in this study and resulted in significant biotic resistance. Previous studies suggest that grasses can successfully prevent the establishment of tree seedlings (Bond 1989; Milton 2004; Kraaij and Ward 2006; Schutz *et al.* 2010;

Kambatuku *et al.* 2011). Richardson and Cowling (1992) hypothesised that the grass component in fynbos may suppress the establishment of woody IAPs, and Milton (2004) suggested that alien grasses could outcompete wattle seedlings. Bond (1989, 2008) found that the competitive strength of grasses prevents the establishment of woody species, an effect which is magnified by frequent fires (van Wilgen *et al.* 1990). Vlok and Yeaton (1999) also hypothesised that the fast-growing C4 grasses which are more common in eastern fynbos communities may outcompete slower-growing shrubs (proteoids). There has been much research on the interaction and balance between grasses and woody elements globally (D'Antonio and Vitousek 1992), mostly in the context of savannas (Scholes 2003; Kraaij and Ward 2006; Bond 2008; Schutz *et al.* 2010; Kambatuku *et al.* 2011) and, more recently, in the restoration of old fields in America and Europe (Davis *et al.* 2005).

Although grasses are not functionally similar, it appears that their competitive ability and timing of resource use enables them to often successfully suppress the regrowth of woody plants, including IAPs, and provide biotic resistance. Cramer *et al.* (2007) found that competition with grasses significantly reduced the establishment of indigenous *A. karroo*, *A. tortilis*, *A. nilotica* and *A. nigrescens* seedlings, and similar results were found by Riginos (2009) on *A. drepanolobium*. Pot experiments with *A. mellifera* (Kambatuku *et al.* 2011) have yielded the same results, as has recent research by Ward and Esler (2011) on the encroachment of *A. mellifera.* Suppressing effects of herbaceous vegetation and grasses on growth and survival of different *Acacia* species have also been shown by Knoop and Walker (1985).

C4 grasses have high water- and nitrogen-use efficiencies, compared to less efficient C3 grasses, forbs and woody plants (van der Waal *et al.* 2009). C4 grasses also differ from C3 grasses in their growth phenology, e.g. cool vs. warm season growth (Cowling 1983), an effect which is important in manipulating the timing of biotic resistance. Grasses can also outcompete woody elements through the greater allocation of biomass to resource-capturing tissue such as photosynthetically-active leaves, which results in faster growth rates (Poorter and Nagel 2000). This has a greater effect under dry conditions, and Meyer *et al.* (2007), in modelling woody distribution in grassy communities, have found that three out of the four most important parameters to explain density of woody species relate to soil moisture, one of which includes moisture availability to seeds, emphasising the importance of adequate moisture during the recruitment phase. The mild moisture deficits experienced in fynbos during summer may alleviate seedling mortality and may be one of the explanations why fynbos is invasible to woody alien species (Richardson and Cowling 1992). In the longer term, grass-fire interactions will also assist with preventing the establishment of woody IAPs.

Another strategy is to attempt to increase the density of an indigenous, non-graminoid species. This could be achieved either through seed additions or the planting of established (potted) plants, although the latter method is likely to be prohibitively expensive on a large scale. Increasing seed density to achieve biotic resistance to control undesirable plants has been used successfully in agriculture for years (Simmons 2005), especially when selective herbicide is not available, and has also been used successfully in the restoration of degraded systems (Middleton *et al.* 2010). Simmons (2005) achieved a 72 % reduction in the above-ground biomass of an IAP through the sowing of indigenous seeds, at a rate of 100 kg/ha, compared to the 26 kg/ha used during these trials. The importance of early establishment in succession and community development has been discussed in Chapter 4, and the timing of fire can be manipulated in combination with seed additions to increase the density of selected, competitive species.

Using an indigenous species such as *Virgilia* which has similar functional and reproductive life-history traits (Lavorel and Garnier 2002) may produce better results. *Virgilia* is functionally the closest indigenous genus to Australian Acacias. Successful restoration may depend on building communities with traits similar to the invader species (Funk *et al.* 2008), by using the biological attributes of the threatened plant community and artificially increasing the density of competitive species to selectively suppress growth of invasive species and achieve biotic resistance (Blumenthal 2005; Simmons 2005). *Virgilia* exhibits similar fire-responses as invasive *Acacia* species, i.e. fire-dominated recruitment dynamics and seed germination cues, and may be able to fulfil the role of a competitive species with functionally similar traits. This tree is leguminous, able to survive on poor soil, germinates and grows fast (up to 2m/annum) and has fire-resistant seeds which are heat-stimulated, and has been observed to compete with *A. mearnsii* after fire when it germinates in high abundance. McDowell and Moll (1981) have also observed the seedlings of this species to outcompete *Acacia longifolia* under both high- and low-nutrient conditions, with competitive effects being most pronounced underground. As it is a relatively short-lived tree (Coates Palgrave 1992), it could be very effective if it were established in high densities to outcompete *Acacia* species, after which it could be succeeded by a greater diversity of species.

Virgilia trees are forest-pioneer species in the Southern and Western Cape and do not naturally occur in the Eastern Cape. However, the use of extra-limital species or even benign exotics should be considered in the management of invasive alien species (D'Antonio and Meyerson 2002; Ewel and Putz 2004; Reid *et al.* 2009). This can result in the creation of novel ecosystems (Hobbs *et al.* 2006), but the benefits of these systems must be weighed up against the feasibility of attempting to restore pre-invasion ecosystems.

5.5.3.3 Timing of biotic resistance

The timing of restoration interventions to suppress regrowth, i.e. when the mechanisms above are likely to be most successful, can be crucial in determining the difference between success and failure (Funk and Vitousek 2007; Young *et al.* 2011). The results of this study suggest that competitive effects and biotic resistance are most effective at the IAP establishment phase. Other authors have also highlighted that the period of germination and early establishment is the time when a plant is probably most vulnerable (Vilà and Weiner 2004; Fenner and Thompson 2005; Akasaka and Tsuyuzaki 2009). A restoration strategy should therefore aim to increase competition during the establishment phase of *Acacia* species, to achieve biotic resistance. The following key attributes of *Acacia* species that increase their competitive abilities during the establishment phase will have to be factored into this strategy: a large and long-lived soil-stored seed bank, rapid germination triggered after fire, high abundance of IAP seedlings, rapid root development and rapid growth (Witkowski 1991; Morris *et al.* 2011).

One of the mechanisms employed during this study was to establish grass plugs before the *Acacia* seedlings germinated, giving them greater competitive advantage in terms of resource (light and moisture) use. Cramer *et al.* (2007) have found that tree seedlings are suppressed when trying to establish in grasslands, as the seedlings need to grow through the grass root layer to reach deeper soil layers. Establishing a grass layer before *Acacia* seedlings germinate will reduce recruitment success of Acacias. The effect of biotic resistance is also likely to be most effective during the early regeneration phase, as grasses are superior competitors for moisture in upper soil layers (Cramer *et al.* 2007; Kambatuku *et al.* 2011). Equally, if a genus such as *Virgilia* is tested, seeds will have to be introduced before a fire, to enable rapid germination alongside *Acacia* seeds. Baasch *et al.* (2012) and Temperton and Zirr (2004) also emphasised the importance of initial floristic composition, order of species arrival and priority effects of competitive species in vegetation development.

Using a species with a similar timing of resource acquisition can be key to biotic resistance (Funk and Vitousek 2007; Young *et al.* 2009). Timing of resource use was found to be more important than similarities in morphology, life cycle, root architecture and phenology. The main growing season of C4 grasses, such as *D. eriantha*, is in the summer (Cowling 1983), and the increased photosynthetic rates during summer reduce water availability in the soil. This, coupled with a lack of rain and high temperatures, places more stress on woody seedlings and enables the grasses to outcompete the woody seedlings during a critical stage in their establishment (van der Waal *et al.* 2009). This study indicates that the timing of resource utilisation appears to have had a greater impact on biotic resistance than morphological or phenological similarities, a finding that is supported by the results of Young *et al.* (2009).

5.6 CONCLUSIONS

The findings show that different restoration treatments result in very different rates and trajectories of recovery of indigenous vegetation. Active intervention in the form of seed and plant additions resulted in a significantly higher indigenous cover after seven months, compared to restoring with grass or passive restoration. Indigenous cover was lower, and appeared to be suppressed by grass in the grass treatment, as opposed to controls. Indigenous cover and composition was also strongly influenced by lateral zonation, and was lowest across all treatments in the NF dry bank, although undesirable species such as P. aquilinum comprised a large portion of the initial post-fire indigenous cover in the moister SF and WB zones. There was no indigenous cover in the grass treatments of the NF dry bank after seven months, whereas the grass cover of the grass treatments was highest in this zone, and bare ground was highest in the control and indigenous treatments compared to the SF and WB zones. Suppression of the regrowth of *A. longifolia* was achieved to varying degrees as a result of the different restoration interventions, and was very successful in the grass restoration treatment.

Comparison with the vegetation of intact sites indicates that some key guilds and species are missing or present in much lower densities. Cover of Restionaceae species, which form an important component of fynbos, was very low throughout the restoration area, with the lowest cover in the grass treatments, especially the GH treatment. Another key guild that occurred in much lower density and richness was the shrub guild, which declined after fire and was also suppressed by the grass treatments, especially the GH treatment. Key riparian dominants such as *Erica caffra, Anthospermum ciliare* and *Cliffortia graminia* were missing altogether. Sedges, which form another important guild in riparian areas, were also lower in the grass treatments (as opposed to the indigenous and control treatments), and findings also indicate that follow-up using herbicide adversely affects sedge cover.

The results of these trials were site-specific, as was evidenced by the variation within a relatively small site, as well as species-specific, and many variables such as timing of the fire event, moisture availability, soil seed bank, a different combination of species interacting over different temporal scales and sites can result in different trajectories and outcomes (McLachlan and Bazely 2003; Ward and Esler 2011). It is therefore not possible to develop a "one-size-fits-all" strategy (Cox et al. 2008), although the principles and mechanisms applied and described during this study are likely to be effective in other contexts as well.

The results from this study indicate that it is possible to achieve biotic resistance through restoration, and that this can significantly suppress the regeneration of *A. longifolia*. This was achieved through the high-density planting of an indigenous grass species, and has the potential to be a powerful management tool in suppressing regrowth of IAPs. Whether this will compromise biodiversity in the long term remains to be seen. It may also be possible to achieve biotic resistance without compromising ecosystem integrity and diversity, by using a broader mix of indigenous grasses, more C3 grasses, as well as fast-growing indigenous species with a range of competitive characteristics (Simmons 2005), using varying densities and methodologies such as seeding or planting, or a functionally similar genus to wattle. Manipulating soil nitrogen by additions of carbon (Blumenthal et al. 2003; Corbin and D'Antonio 2004; Yelenik et al. 2004) to control grasses in combination with phased planting, as well as manipulating the timing and frequency of fires (Adie et al. 2011) are also techniques that may improve results. Testing phased approaches over longer time-frames is recommended.

6 SYNTHESIS

This study investigated the process of restoring a long-invaded riparian zone in grassy fynbos. It set out to establish the factors that facilitate or constrain spontaneous recovery and influence the trajectories of succession; these factors included the management of IAPs, especially regarding the use of fire. It implemented active restoration interventions with the aim of reinstating indigenous vegetation, with a structure and function representative of natural vegetation, and which is resistant to re-invasion.

The process of degradation, reassembly and recovery consists of a series of complex interactions and responses between many biotic and abiotic variables. There is often insufficient consideration as to the impacts of invasion and the longer-term outcomes of control efforts, which simply aim to remove IAPs (Le Maitre et al. 2011). Wattles have transformed many riparian systems in South Africa, and have displaced indigenous vegetation, altered fire regimes and soil properties, reduced water yield and biodiversity, destabilised river banks and degraded many other ecosystem services. The above interactions often occur in a simultaneous manner, and result in innumerable permutations and combinations of responses. In addition to this, the management of IAPs and restoration of alien-invaded areas have further impacts, and often do not achieve sustainable mitigation of the impacts caused by invasive species, often resulting in unplanned and undesirable outcomes (Le Maitre *et al.* 2011). Manipulating any one of the variables can create unexpected responses, which is compounded by variable site histories even prior to the initiation of invasion or degradation.

Riparian fynbos communities are naturally in a state of flux, due to the dynamic, disturbance-mediated nature of both fynbos and riparian zones. The post-management community thus represents the sum of numerous complex trajectories, which makes accurate predictions of the outcomes of restoration interventions difficult. An understanding of the interaction of the impacts, and the processes that govern trajectories and processes leading to degradation or altered ecosystem functioning as well as reassembly, is required to mitigate these impacts and enable the manipulation of selected variables to steer succession towards a desired state (Cabin *et al.* 2010; le Maitre *et al.* 2011).

IAP management should be viewed as one of the components of restoration (Reid *et al.* 2009), as in most cases the removal of the IAPs does not reverse the residual impacts they have. The structure and function of invaded systems may thus be permanently affected unless other actions are implemented (Reid *et al.* 2009). The recovery of invaded and cleared areas is critical to the long-term success of WfW (Holmes *et al.* 2005), and the establishment of functional vegetation cover after clearing is one of the most important factors in creating a self-sustaining and resilient ecosystem (D'Antonio and Chambers 2006). In the light of the above, there has been a shift towards viewing restoration as an ecologically-based, longer-term solution (Sheley and Krueger-Mangold 2003; Svejcar 2003; Simmons 2005) which can form an integral part of the management and control of IAPs as well as reinstating the ecological functioning of riparian systems (Taylor and McDaniel 2004). Key to this objective is the reassembly of plant communities that are resistant to re-invasion (D'Antonio and Meyerson 2002; Funk *et al.* 2008). Substantial short- to medium-term investments are required for control and restoration, and although active restoration can add additional expenses, it can be effective in reducing the long-term costs of follow-up and maintenance operations, as well as reducing losses of biodiversity and ecosystem services, and the costs to society in the long term (Le Maitre *et al.* 2011).

This chapter provides a synthesis of the main findings of this study, and discusses the implications of these findings to the management and restoration of alien-invaded riparian systems, with the goal of achieving a resilient, self-sustaining and invasion-resistant system.

6.1 AVAILABILITY OF PROPAGULES IN THE SOIL SEED BANK

The study indicated a relatively intact soil seed bank in a long- and densely-invaded riparian zone. The average seed density was 1 582 seeds/m^2 with the family Asteraceae best represented. Species from the soil seed bank represented 30% of the full post-fire above-ground community, and some key fynbos and riparian guilds, e.g. Restionaceae, were absent altogether. However, it is fairly common for many above-ground species not to be represented in the soil seed bank (Valkó *et al.* 2011). However, representatives of all structural growth forms were present. There was a general shift in floristic composition across the lateral zones and moving upslope, and these data can assist the selection of suitable species for reintroductions.

No data exist on the soil seed banks of intact riparian systems in grassy fynbos, and it is therefore unclear whether the seed bank is sufficiently intact to allow succession to proceed spontaneously to pre-invasion conditions without additional interventions. It is possible that species could have set seed during previous clearing intervals or some seed may have dispersed into the site by floods or animals. However, it is inferred that the majority of the seeds of these species are persistent and were able to remain viable for more than 30 years. The presence of a significant seed bank at the 4-8 cm depth supports the persistence hypothesis. These seeds in the deeper layers may not be able to germinate, especially small-seeded species, unless brought closer to the surface through some form of disturbance of post-fire interventions. However, they do represent a reservoir of propagules, should the upper layer be lost to fire damage or erosion after severe fires.

The study also recorded a high pre-fire density of IAP propagules of more than 4 500 seeds/m^2 in some zones. This is much higher than the indigenous seed density, even though biocontrol has been active in the vicinity of the study area for many years. This IAP propagule pressure therefore poses a significant challenge to the management and restoration of this system, and impacts on the ability of the indigenous vegetation to offer biotic resistance.

Since long-distance dispersal of seeds in fynbos is rare (Brits 1987; Le Maitre and Midgley 1992; Morzaria-Luna and Zedler 2007), the reassembly of fynbos systems after invasion (and fire) relies heavily on the soil seed bank, especially if connectivity with intact source areas is low (Bischoff *et al.* 2009). Generally, seed limitation is one of the main constraints in the restoration of disturbed or degraded communities. Although seed availability represents the regeneration potential, other factors, including post-clearing management and conditions, will dictate whether the seeds in the soil seed bank will be able to establish successfully.

6.2 IMPACT OF FIRE ON THE SOIL SEED BANK

This study specifically investigated the impact of fire on soil seed banks, motivated by the importance of soil seed banks in the regeneration of fynbos and the use of fire in the management of IAPs. Burning has formed an integral part of IAP management strategies (CSIR 2000; van Wilgen *et al.* 2011) and this, combined with the fire-prone nature of fynbos, means that fires are inevitable (van Wilgen 2009). It is hypothesised that fire, in combination with the high volumes of alien plant biomass, has the greatest potential to damage alien-invaded riparian ecosystems, and alter or arrest the trajectories of recovery, as compared to other management actions. This is supported by Roura-Pascual *et al.* (2010), who suggest that fire is both a crucial driver of invasion in fynbos. The event-dependent hypothesis (Bond and van Wilgen 1996; Moreno *et al.* 2011) states that the unique character of a fire event, e.g. intensity, season and pre- and post-fire conditions, will result in unique changes in a plant population, and that no two fires will result in the same community. A large part of this study has therefore assessed the role and impacts of fire on the regeneration of vegetation as part of IAP control.

The results of this study indicated that extremely high temperatures (in excess of 900 ^{o}C) were reached at the soil surface under 90 % of the larger stacks of felled *Acacia* biomass, 63 % of the medium stacks and 17 % of the low stacks, although the duration of exposure is not known. There was a significant reduction in soil seed bank density after the fire across the landscape in the upper 4 cm, and a less pronounced reduction in the deeper 4-8 cm layer. However, where large slash stacks were concentrated, seed densities were reduced by as much as 76 %. The response also varied according to the lateral zone. The most pronounced reduction in seed density at both depths took place in the WB zone, from 1 677 seeds/m^2 to 340 seeds/m^2 at 0-4 cm depth.

Some guilds were more affected by fire than others, e.g. woody shrub seeds were almost eliminated from the post-fire soil seed bank, especially species such as *E. caffra* and *H. lucida*. It is possible that some species set seed in the period after clearing and before the fire, or that the germination requirements of this species were perhaps not met during the pre-fire soil seed bank study. If this is the case, the relative impact of fire on the soil seed bank may be underestimated. The indigenous Fabaceae as well as Restionaceae were missing from both the pre- and post-fire soil seed bank, even though the fire should have provided any dormancy-breaking (heat) or germination cues that were missing during the pre-fire soil seed bank study. It can be assumed that these groups are absent from the soil seed bank. Geophyte and graminoid seed densities were very low throughout all zones, and the seed density of *Hypoxis argentea*, a geophyte, was significantly reduced after the fire. The results of this study support the findings of Blanchard and Holmes (2008), who also reported reduced restioid and shrub cover after fell-and-burn treatments, as well as the failed re-establishment of mycorrhizal *Erica* species.

Fire also reduced *Acacia* seed density, but a high viable seed density still remained, exceeding 2 500 seeds/m^2 in some lateral zones. This presents a considerable challenge for management and restoration of indigenous vegetation, as well as achieving biotic resistance. Fire can be used to kill seeds of undesirable species (Pyke *et al.* 2010) and has been advocated in the management of wattles (Richardson and Kluge 2008; van Wilgen *et al.* 2011). However, it is likely that more damage will be inflicted on indigenous soil seed banks than on the fire-resistant *Acacia* soil seed banks. The use of fire to reduce *Acacia* soil seed banks is therefore not advocated.

The response of the soil seed bank to fire intensity is one of the variables that determine the restoration of an alien-invaded plant community. However, impacts on the soil seed bank do not occur in isolation but interact with other abiotic and biotic fire-induced changes, e.g. changes in soil properties, which will influence the trajectory of succession after clearing (and fire) and the composition of the vegetation (Pyšek *et al.* 2004a). It is also impossible to separate the effects of the fire intensity, season of burn and temporal dynamics of the soil seed bank on the subsequent trajectories of succession and resultant vegetation, and the following sections therefore deal with these components.

Overall, this study indicates that the high-intensity fires generated through the burning of felled IAP biomass have a negative impact on the indigenous soil seed bank, which will compromise the regeneration of indigenous vegetation, and recovery of riparian structure and function. Poor management and lack of timeous follow-up may result in the re-establishment of IAPs and a build-up of biomass, which necessitates additional cycles of clearing and the inevitable fire impacts to soil seed banks and other community components. It is crucial that timeous follow-ups of regrowth are implemented to prevent this.

6.3 THE TEMPORAL PATTERNS OF SEEDLING EMERGENCE IN GRASSY FYNBOS

Knowledge of seed germination responses, including timing of emergence, is important for plant conservation, management of diversity and restoration. It can also assist restoration practitioners in understanding the processes and sequences of re-assembly, resulting in more efficient restoration practices (French *et al.* 2011). Soil-stored seeds generally have fairly complex germination requirements and will often only germinate after the appropriate combination and sequence of cues (Le Maitre and Midgley 1992; Brown and Botha 2004; Cowling *et al.* 2005). Although smoke can provide a cue for germination, most fynbos species then need the correct combination of fluctuating temperatures and duration of light and dark (Pierce and Moll 1994) or other combinations of cues, e.g. heat followed by smoke (Musil and de Witt 1990; Musil 1991).

Since fire is central to regeneration of fynbos, an understanding of the reproductive ecology and germination responses after fire is crucial to inform fire management (Pyke *et al.* 2010). Much of the fire management policies in fynbos have been based on the recruitment responses of serotinous overstorey species such as Proteaceae and Bruniaceae in the Western Cape, especially in response to the season of fire. Very little is known about the impact of the season of fire on the regeneration of the soil seed bank in either the typically Mediterranean-climate Western Cape fynbos or the eastern extent of fynbos which experiences more aseasonal and unpredictable rainfall. Also, little is known about the timing of germination of the soil seed bank from this area, and how the timing of emergence affects the trajectories of post-fire succession and plant community development.

This current study shows that emergence is not synchronous after fire and is uncoupled to the availability of moisture, and it appears that physiological dormancy of seeds recorded during this study may control the timing of germination. Results indicate clear germination sequences and patterns of emergence over time for different species, with many species exhibiting delayed emergence relative to the time of the fire. Existing literature suggests that early emergence as opposed to delayed emergence can increase the success of recruitment and vigour which can last throughout the life cycle of the plant (De Luis *et al.* 2005; Verdú and Traveset 2005). Timing of emergence will therefore also alter successional trajectories and the composition of subsequent populations Some species exhibited a wider window of emergence, which may be a risk-spreading mechanism in response to more unpredictable rainfall patterns (Moreno *et al.* 2011), or a reflection of linkages to both the predominantly winter-germinating Cape flora and more tropical spring and summer-germinating flora. This study also suggests that there is no optimal season of fire for facilitating regeneration from the soil seed bank.

It is proposed that the manipulation of the season of fire can be used to selectively optimise the order of arrival and therefore superior recruitment of some species over others in the Eastern Cape fynbos. This will influence trajectories of recovery and direct the succession of the vegetation towards a more desirable state. A species with no seasonal requirements will have competitive advantage under certain fire regimes, while a delayed germination response until a particular season can result in a competitive disadvantage, especially if co-occurring species have faster post-fire response. However, the interaction of facilitation and competition between different species and the effect that this has on establishment and re-assembly is not known, and remains to be tested.

The rapid emergence of invasive species, before the emergence of any of the indigenous species, is obviously one of the strategies that enable these IAPs to establish and gain a competitive advantage. Although rapid growth rates are one of several traits commonly associated with IAPs (Castro-Díez *et al.* 2011; Morris *et al.* 2011), the rapid germination after fire allows *A. longifolia* to take advantage of the increased resources immediately after fire. This, in combination with the relatively high remaining seed bank, presents challenges to the management of this species (Strydom *et al.* 2012). As the period of germination and early establishment is the time when a plant is probably most vulnerable (Vilà and Weiner 2004; Fenner and Thompson 2005; Akasaka and Tsuyuzaki 2009), I hypothesise that this is the stage in the life-history of an IAP during which biotic resistance could have the greatest effect. *A. longifolia* seeds are physically dormant and dormancy is broken by heat, where after germination can take place as soon as moisture becomes available, irrespective of season. Fire should thus be timed to coincide with the seasonal germination of an indigenous species which can germinate at the same time and offer sufficient competition to reduce the successful establishment and/or vigour of *A. longifolia*. Alternatively, enough physically dormant seeds with the same germination response of another competitive indigenous species, e.g. from the Fabaceae family, must be present or be introduced into the system before fire. Although this method may not be able to fully suppress the regrowth of *A. longifolia*, it may reduce the successful establishment of *A. longifolia* seedlings, therefore reducing post-fire densities, follow-up efforts, costs and negative impacts from follow-up treatments (see Section 6.5).

6.4 ACTIVE AND PASSIVE RESTORATION

The findings show that different restoration treatments result in very different rates and trajectories of recovery of indigenous vegetation. Active intervention in the form of seed and plant additions resulted in a significantly higher indigenous cover after seven months, compared to restoring with grass or passive restoration. Indigenous cover is lower, and appears to be suppressed by grass in the grass treatment, as opposed to controls. Indigenous cover and composition is also strongly influenced by lateral zonation, and is lowest across all treatments in the NF dry bank, although undesirable species such as *P. aquilinum* make up a large portion of the initial post-fire indigenous cover, in the moister SF and WB zones. In the NF dry bank there is no indigenous cover in the grass treatments after seven months, whereas the grass cover of the grass treatments is highest in this zone, and bare ground is highest in the control and indigenous treatments, compared to the SF and WB zones.

Although survival of the planted individuals did not differ across zones, there was a marked difference between percentage survival of species planted in summer and those planted in autumn, as well as between the species planted in summer. Overall, 25 % of the species planted in summer survived, as opposed to a much higher survival rate of 93 % of the species planted in autumn. Different species showed a wide variation in survival. Other authors (Bakker *et al.* 2003; Middleton *et al.* 2010) have also reported that the success of restoration interventions is very much contingent on the year and site, and multiple introductions may be required if efforts in any one year fail. Germination from seeds was much slower, and unassisted recovery (control plots) was very slow, especially in the NF dry bank (indigenous cover < 10 % in July 2006). This is surprising, as the post-fire soil seed bank density was highest in the NF dry bank (> 1 661 seeds/m^2), mostly through the contributions of indigenous Asteraceous annual and short-lived perennial species such as *Senecio rigidus* and *Conyza pinnata* (Chapter 2). Post-fire conditions may limit field recovery in this zone.

By 2009, there were no significant differences between overall indigenous cover (excluding introduced grasses) in the control and indigenous restoration plots in the WB zone and SF dry bank, although a significant proportion of this still comprised *P. aquilinum* (see Plate 13 and 14). Combined indigenous vegetation cover of all structural layers exceeded 95 % in the control and indigenous treatments, and even without *P. aquilinum*, the lowest indigenous cover (in the GH treatment) was still more than 65 % in the WB and SF zones. However, the cover of indigenous species was significantly less in the NF dry bank, with the highest cover in the indigenous treatments (80 % in IM and 75% in IH), and significantly less in the grass treatments, with the lowest cover of 8 % in the GM treatment (and no bracken cover). It can therefore be concluded that treatments had little effect on overall indigenous cover in the SF and WB zones, but significantly increased indigenous cover in the NF dry bank (compared to the controls), where the grass restoration treatment significantly inhibited the growth of other indigenous species. Species richness followed a similar pattern in response to the treatments and across zones, with the most significant decrease in species richness exhibited in the NF dry bank, in response to the grass treatments.

Comparison with the vegetation of intact sites indicates that some key guilds and species are missing or present in much lower densities. Cover of Restionaceae species, which form an important component of fynbos, was very low throughout the restoration area, with the lowest cover in the grass treatments, especially the GH treatment. Another key guild that occurred in much lower density and richness was the shrub guild, which declined after fire and was also suppressed by the grass treatments, especially the GH treatment. Key riparian dominants such as *Erica caffra*, *Anthospermum ciliare* and *Cliffortia graminia* were missing altogether. *Erica* and *Anthospermum* seeds both formed a significant percentage of the seed mix used in the indigenous restoration seed mix, which indicates that the lack of establishment of these species is not due to a lack of seed supply (Turnbull *et al.* 2000), but rather inhospitable post-fire conditions (Mandle *et al.* 2011). Sedges, which form another important guild in riparian areas, were also lower in the grass treatments as opposed to the indigenous and control treatments), and findings also indicate that follow-up using herbicide adversely affects sedge cover.

As fire plays such an important role in management and the regeneration of fynbos, the full effects of fire will be discussed in some more detail. Fire regimes are defined by the following three variables: intensity, frequency and season; and these factors determine the development, structure and composition of vegetation communities (Le Maitre and Midgley 1992; Bond and Keeley 2005). It is hypothesised that fire, in combination with the high volumes of alien plant biomass, has the greatest potential to damage alien-invaded riparian ecosystems, and alter or arrest the trajectories of recovery, as compared to other management actions. Knowledge of the interactions of plant responses and survival mechanisms to the fire regime and the drivers that influence the regime is important for restoration ecology (Pyke *et al.* 2010). Fire can affect the following community variables: seedling production, adult plant persistence and the post-fire performance of plants (Knox and Clarke 2006; Moreno *et al.* 2011). These effects are most apparent during the immediate post-fire period but also translate into subsequent vigour (e.g. survival of herbivory and future reproductive output) (Moreno and Oechel 1991).

The development of a plant community after fire is thus the product of an intricate set of factors and processes. In the review of the use of fire as restoration tool, Pyke *et al.* (2010) refer to the first-order effects or responses to fire, which consist of individual plant responses to fire, and which set the stage for trajectories and succession. These are largely influenced by the fire event itself, but also reflect the history of the site, including previous fire events. This has been referred to as the “invisible mosaic” (Parr and Andersen 2006). Second-order effects consist of the complex interaction of ecological processes, which depend on the timing of many biotic and abiotic factors, which direct plant trajectories, succession and community development following fire (Pyke *et al.* 2010).

Fire intensities vary by orders of magnitude, with very different impacts on biotic and abiotic variables according to the age of the IAP stand, the season, weather, fuel moisture and topography (Moreno and Oechel 1991). Higher fire intensities can result in greater mortality of resprouters, which creates more gaps for the re-establishment of seedlings, although higher seed mortality due to lethal soil temperatures can co-occur. Survival depends on type and intensity of fire, the height of the plant, insulating capacity of the bark, and resprouting or coppicing ability (Pyke *et al.* 2010). Lower fire intensities can result in a higher percentage survival of resprouters, which can intensify competitive interactions between seedlings and resprouters on one hand, but facilitation effects between resprouters and seedlings can also be enhanced, e.g. where resprouters provide suitable micro-sites and aid establishment of seedlings (Moreno *et al.* 2011). Varying fire intensities may result in differential germination and survival of species (Stromberg *et al.* 2008), varying ratios of seedlings vs. resprouters, as well as changes in competitive interactions.

In the context of riparian systems invaded by woody alien species such as wattles, the most important consideration would be to reduce fire intensity. Timing of the fire, e.g. which season a prescribed burn takes place, as well as the particular weather conditions (e.g. cool weather and wet soil after a rain event), can be used to reduce fire intensity and the impacts on the soil seed bank. High fire intensities can result in higher above-ground kill rate of some species, thus shaping the post-fire community, while reduced fire intensities will decrease heat penetration into the soil. The extent and duration of temperature levels will differentially affect germination responses and mortality rates of seeds, which in turn affect the trajectories of succession and the resultant plant community.

Post-fire conditions of high solar radiation, more extreme temperature shifts, wind, higher water loss, increased erosion and changing soil properties (including water-holding capacity and short-term soil nutrient availability) all influence the re-establishment of vegetation (Mandle *et al.* 2011). No above-ground vegetation remained after the hot fire experienced during this study, although some vegetation managed to resprout after the fire. Soil moisture is probably the most limiting factor for survival once germination has taken place (Moreno and Oechel 1992) and mortality is typically high during the first few months (Quintana *et al.* 2004). This was observed during this study. Climatic conditions after fire are thus crucial in determining the survival of seedlings. Fire can also affect soil biota, but little is known about the role that soil biota may play in the re-establishment of plants in fynbos. It has been estimated that 62 % of Cape flora require arbuscular mycorrhizas (AMs) to establish (Allsopp 2010), and evidence from other studies (Korb *et al.* 2004; Collier and Bidartondo 2009) has shown that AMs are sensitive to high temperatures caused by the burning of slash piles. Plant re-establishment can thus be significantly retarded after the burning of slash piles, with long-lasting effects.

Autumn fires are considered more likely to result in communities with structural and floristic properties similar to intact sites in Mediterranean environments (Moreno and Oechel 1991; van Wilgen *et al.* 2010), but this is largely based on the response of natural vegetation containing serotinous species. Aseasonal fires have been shown to have devastating effects on the re-establishment of species with canopy-stored seed banks in Mediterranean vegetation (Bond 1984; Vlok and Viviers 1984; Cowling and Lamont 1987; Knox and Clarke 2006), although Heelemann *et al.* (2008) have shown that the season of fire does not affect the re-establishment of serotinous species in the Eastern Cape. More severe, dry-season fires, which result from the fell-and-burn, may kill the above-ground populations, including any canopy-stored seeds. This, in combination with IAP shading and competition, can eliminate the serotinous fynbos species in invaded stands altogether. It is recommended that the impacts of an aseasonal fire on recruitment be weighed up against the benefits of reduced fire intensities resulting from cooler weather burns, especially when serotinous species are not present.

Although more difficult to control, fire frequency is also an important component, and short fire intervals can also have devastating consequences on plant populations, especially when combined with the high fire intensities caused by felled biomass. Invasion by alien plant species often increases fire frequency, as does the use of fire as a management tool in the control of woody IAPs. Timeous follow-ups to prevent the build-up of biomass from invasions will ameliorate this impact. Restoring alien-invaded sites to prevent re-invasions is another way in which repeated fire impacts can be avoided. There is evidence that shorter fire intervals are becoming more common in fynbos, partly due to an increase of anthropogenic sources of ignition (van Wilgen 2008). This can also result in shifts in fire season, with detrimental impacts on indigenous plant communities as well as aggravating the invasive plant problem. Climate change will result in further changes in fire regimes, with potentially devastating consequences for indigenous plant communities.

Although succession towards woody species can be prevented by fast-growing grasses which out-compete seedlings of perennial plants (Bond 1989; van der Waal *et al.* 2009; Hobbs 2001; Heelemann *et al.* 2008), this process, in combination with fire and invasion legacies such as an increase in soil nutrients, can irreversibly change shrublands to grasslands (D'Antonio and Vitousek 1992). These end-states can be very resilient to change, especially if the dominant species have the ecosystem-altering attributes of grasses and bracken. Any change in vegetation will result in some change in ecosystem function(s), seldom predictably and not always in tandem (Tickner *et al.* 2001; Le Maitre *et al.* 2011). The greatest functional changes will occur if the abundance of the dominant species changes, as they are most influential (Richardson *et al.* 2007). The greater the differences in morphology, growth rates and other traits between the previously-dominant species and the new dominant species, the greater the change in function (Richardson *et al.* 2007). This will be irrespective of whether the new dominant species is an indigenous or invader species. The interaction of fire and invasion impacts has serious potential to permanently alter fynbos communities in favour of grassy species. When IAPs alter fuel characteristics, they change ecosystem dynamics (D'Antonio and Vitousek 1992; Brooks *et al.* 2004). Based on the above, the deliberate introduction, or spontaneous invasion of grass, after clearing can therefore have unforeseen consequences to riparian function. Given the competitiveness of grasses and their ability to change fire behaviour and transform ecosystems, it is not certain whether the other guilds (forbs, shrubs, restios) will be able to re-establish over time.

It is therefore hypothesised that species diversity and composition in the grass and control treatments will not increase and return to pre-invasion levels, but are likely to decrease, due to the aggressive nature and ecosystem-transforming traits of the grasses and bracken and the fact that they are favoured by changes in fire cycles and climate. However, our understanding of the long-term recovery of invaded and degraded systems is still poor, due to a lack of long-term data, as it can take decades for the eventual outcomes of competitive interactions to be revealed (Rejmánek *et al.* 2005). Only long-term monitoring of restored sites will reveal whether these systems can recover a representative vegetation structure and function.

6.5 BIOTIC RESISTANCE

The findings of this study indicate that it is possible to achieve biotic resistance through restoration, and that this can significantly suppress the regeneration of *A. longifolia* or other invasive Acacias, although this may be at the cost of biodiversity. However, other methods which may facilitate the development of a more diverse community and draw on similar principles of competition can be explored. The degree of biotic resistance achieved during this study was dependent on lateral zonation and aspect, and it appears that the main variable determining the success of the grass restoration treatment in suppressing regrowth and achieving biotic resistance is related to competition for moisture during the critical recruitment phase of the *A. longifolia*. The suppression of regrowth of IAPs through the planting of *D. eriantha* was most pronounced in the NF dry bank. This zone also had the highest pre- and post-fire *A. longifolia* soil seed bank (3 918 and 2 536 seeds/m^2 respectively). Indigenous vegetation also appears to suppress the regeneration of alien seedlings, although to a lesser degree, and this effect is especially pronounced in the WB zone and SF dry bank where the rate of indigenous vegetation recovery was good: 59 to 66 % within seven months, but it had no effect in the NF dry bank, where indigenous recovery was low (34 % in indigenous treatments and 9 % in the control treatment) in the first seven months.

Although the initial results clearly indicate the achievement of biotic resistance through reinstating a vegetation cover, it will only be possible to quantify the degree of long-term biotic resistance over time, with continued monitoring, especially after disturbance events such as fire. However, it is likely that the high vegetation cover that has been achieved on the site will remain fairly resistant to re-invasion, through a number of mechanisms. The high grass cover is likely to repel invaders through competition and interaction with fire, as its more flammable nature will result in more frequent and higher-intensity fires that will prevent the establishment of woody species. The high bracken cover is likely to fulfil the same role, by suppressing the establishment of woody IAPs. However, the high grass and bracken cover appears to equally suppress the establishment of a more natural and diverse fynbos community, through the same mechanisms mentioned above. Long-term alterations in the natural successional trajectories may thus have taken place (D’Antonio and Chambers 2006; Baasch *et al.* 2012); these could be resilient to succession towards a more natural structure and composition (Reinecke *et al.* 2008).

High propagule pressure is one of the main factors associated with invasions (Lonsdale 1999; Richardson and Pyšek 2006; Warren *et al.* 2011a). It is therefore very important to account for the propagule pressure in the assessment and development of biotic resistance (Lonsdale 1999; Eschtruth and Battles 2011; Warren *et al.* 2011a). It will be easier to achieve almost 100 % biotic resistance when propagule pressure is low (early in the invasion process at low residence time rather than later when propagule pressure is high). Currently, control and restoration in fynbos has inherited a legacy of large numbers of accumulated IAP propagules, and the achievement of biotic resistance may require a phased process: firstly, managing and reducing the IAP propagules, and secondly reassembling a community that can repel, or mostly repel, re-invasion. Ideally, these processes should operate in tandem, where restoration is used as part of the management of IAPs to reduce propagule pressure, as appears to have been achieved during this study.

Understanding the mechanisms of biotic resistance is essential in achieving successful restoration (Hooper and Dukes 2010) and necessarily has to include the traits of the successful invader as well as the factors that make the community invasible. As research suggests that diversity in functional traits is better correlated with resistance to invasion than species diversity per se (Tilman 1997; Funk *et al.* 2008; Hooper and Dukes 2010), restored communities may better be able to resist re-invasion when they contain species functionally similar to known high-risk invaders (Zavaleta and Hulvey 2007). The timing of restoration interventions to suppress regrowth can also be crucial in determining the difference between success and failure (Funk and Vitousek 2007; Young *et al.* 2011). Competition at different life stages differs, e.g. between establishment versus growth phases, and biotic resistance will vary accordingly (Hooper and Dukes 2010). The results of this study suggest that competitive effects and biotic resistance are most effective at the IAP establishment phase. A restoration strategy should therefore aim to increase competition during the establishment phase of *Acacia* species to achieve biotic resistance. This has effectively been achieved by planting grasses soon after a controlled fire, before *Acacia* seedlings germinated.

Another proposed strategy which may better facilitate the development of diverse indigenous communities than the planting of grass, is to increase the density of an indigenous, non-graminoid species. This could be achieved either through seed additions or the planting of established (potted) plants, although the latter method is likely to be prohibitively expensive on large scales. Introducing seeds from a genus such as *Virgilia* - which exhibits similar fire responses as invasive *Acacia* species, i.e. fire-dominated recruitment dynamics, may be able to fulfil the role of a competitive species with functionally similar traits.

6.6 CONCLUSION

The findings of this study indicate the presence of a viable and persistent riparian soil seed bank. It shows that the management practice of fell-and-burn results in high soil temperatures, and that this has a negative impact on the soil seed bank. This will retard spontaneous succession and the re-assembly of an indigenous intact and functional riparian community. It is hypothesised that fire, in combination with invasion legacies including the high volumes of alien plant biomass, has the greatest potential to damage alien-invaded riparian ecosystems, and to alter or arrest the trajectories of recovery, as compared to other management actions. However, it is often impossible to avoid the high-severity fires resulting from the biomass generated by woody IAPs. A solution is not easy and this will remain a dilemma for managers, often dictated by logistical constraints and budget. Methods of restoring and mechanisms for achieving biotic resistance therefore have to factor in an attempt to optimise fire. Managers may be faced with a number of factors to consider in weighing up the benefits of fire with the potential impacts in any particular situation. It is critical that fire is used appropriately to achieve set objectives, with cognisance of the potential impacts. The large number of variables that can affect fire responses and lack of experimental evidence make these decisions more challenging. A fire management decision framework that integrates plant growth forms and survival strategies with fire regime characteristics to optimise desired outcomes, such as the one produced by Pyke *et al.* (2010), and which also incorporates costs and practical constraints, may be useful for IAP management.

Restoration is a costly process and often takes many years to deliver desired outcomes (Wilson *et al.* 2011b). However, where riparian ecosystem services have been lost, active restoration may be worthwhile to restore these functions. Diversity in functional groups and responses increases the resilience of an ecosystem to natural disturbances, and probably also to novel disturbances (White and Stromberg 2011). Deciding where, when and how restoration should take place is difficult and fraught with uncertainty, and many factors will influence these decisions (Lemons and Victor 2008).

The results from this study indicate that it is possible to achieve biotic resistance and significantly suppress the regeneration of *A. longifolia*, which has the potential to be a powerful management tool in suppressing regrowth of IAPs. However, the deliberate introduction or spontaneous invasion of grass after clearing also reduces biodiversity, and can have unforeseen consequences to riparian function. Given the competitiveness of grasses and their ability to change fire behaviour and transform ecosystems, it is not certain whether the other guilds (forbs, shrubs, restios) representative of a more natural riparian structure will re-establish over time. The promising results indicate the need to implement more small-scale trials. The efficacy of different mixes of indigenous grass and forb species which have a range of competitive characteristics (Simmons 2005) should also be tested, as well as varying densities and methodologies such as seeding or planting (Klimkowska *et al.* 2010; DeFalco *et al.* 2012). It may also be possible to achieve biotic resistance without compromising ecosystem integrity and diversity by using a broader mix of indigenous grasses, more C3 grasses, fast-growing forbs or a functionally similar genus.

Appendix A. Species recorded on study site. Lateral zonation is only recorded for species which emerged during the soil seed bank studies.

Guilds: A = alien, F = forb, G = graminoid, Ge = geophyte, S = shrub, T = tree. Zones: WB = Wet bank, NF = North-facing dry bank, SF = South-facing dry bank, LH = Lower hill slope, UH = Upper hill slope

Species	Family	Alien (A) / Indigenous (I)	Guild	Zone (species recorded during SSB)
Rumohra adiantiformis (G.Forst) Ching	Dryopteridaceae	I	F	WB, AN, AS, LH, UH
Cheilanthes viridis (Forssk.) Sw.	Pteridaceae	I	F	WB, AN, AS, LH, UH
Cheilanthes hirta Sw.	Pteridaceae	I	F	AS, LH, UH
Pteridium aqualinum (L.) Kuhn	Dennstaedtiaceae	I		
Ficinia oligantha (Steud.) J.Raynal	Cyperaceae	I	G	WB, AN, AS, LH, UH
Cyperus esculentus L.	Cyperaceae	I	G	WB, AN, AS, LH, UH
Isolepis cernua (Vahl) Roem. & Schult.	Cyperaceae	I	G	WB, AN, LH
Isolepis prolifer R.Br.	Cyperaceae	I	G	WB, AN, LH, UH
Ficinia capillifolia (Schrad.) C.B. Clarke	Cyperaceae	I	G	WB, AN, LH, UH
Scirpus thunbergii (Schrad.) L.B. Clarke	Cyperaceae	I	G	WB, AS
Cynodon dactylon (L.) Pers.	Poaceae	A	G	LH, UH
Digitaria eriantha Steud.	Poaceae	I	G	WB, AN, AS, UH
Eragrostis obtusa Munro ex Ficalho & Hiern	Poaceae	I	G	WB, AN, AS, LH, UH
Panicum maximum Jacq.	Poaceae	I	G	WB, AN, AS, LH, UH
Ehrharta erecta Lam.	Poaceae	I	G	
Eragrostis curvula (Schrad.) Nees	Poaceae	I	G	
Cymbopogon plurinodis (Stapf) Burtt Davy	Poaceae	I	G	
Eragrostis tef (Zuccagni) Trotter	Poaceae	A	G	
Paspalum dilatatum Poir.	Poaceae	A	G	
Merxmuellera cincta (Nees) Conert	Poaceae	I	G	
Hypoxis argentea Harv. ex Baker	Hypoxidaceae	I	Ge	WB, AN, AS, LH, UH
Aristea anceps Eckl. ex Klatt	Iridaceae	I	Ge	WB, AN
Burchellia bubalina (L.f.) Sims	Rubiaceaea	I	S	
Leonotis leonurus (L.) R.Br.	Lamiaceae	I	S	
Ochna serrulata (Hochst.) Walp.	Ochnaceae	I	S	
Pappea capensis Eckl. & Zeyh.	Sapindaceae	I	T	
Searsia dentata (Thunb.) F.A. Barkley	Anacardiaceae	I	S	
Centella asiatica (L.)	Araliaceae	I	F	WB, AN
Chrysanthemoides monilifera (L.) Norl.	Asteraceae	I	S	WB, AN, LH
*Conyza canadensis**	Asteraceae	A	A	WB, AN, AS, LH, UH
Conyza pinnata (L.f.) Kuntze	Asteraceae	I	P	WB, AN, AS, LH, UH
Haplocarpha lyrata Harv.	Asteraceae	I	F	WB, AN, AS
Helichrysum cymosum (L.) D.Don.	Asteraceae	I	F	WB, AN, AS, LH, UH
Helichrysum petiolare Hilliard & B.L. Burtt	Asteraceae	I	F	WB, AN, AS, LH, UH
Helichrysum cephaloideum DC.	Asteraceae	I	F	AN, AS, LH, UH
Helichrysum subglomeratum Less	Asteraceae	I	F	WB, AN, LH, UH
Helichrysum odoratissimum (L) Sweet	Asteraceae	I	F	AN
Helichrysum spp.	Asteraceae	I	F	WB, AN, AS, LH, UH
Helichrysum epapposum Bolus	Asteraceae	I	F	R
*Pseudognaphalium luteo-album**	Asteraceae	A	F	WB, AN, AS, LH, UH
Senecio pterophorus DC.	Asteraceae	I	P	WB, AN, AS, LH, UH
Senecio chrysocoma Meerb.	Asteraceae	I	F	AS, LH, UH
Senecio rigidus L.	Asteraceae	I	P	WB, AN, AS, LH, UH
Lobelia tomentosa L.f.	Campanulaceae	I	F	WB, LH, UH
Drosera aliciae Raym.-Hamet	Droseraceae	I	F	LH, UH
Erica chamissonis Klotzsch ex Benth.	Ericaceae	I	S	WB, AN, AS, LH, UH
Erica caffra L.	Ericaceae	I	S	WB, AN, AS, LH, UH
Acacia longifolia (Andrews) Willd.*	Fabaceae	A	A	WB, AN, AS, LH, UH

Psoralea pinnata L.	Fabaceae	I	S	WB, LH
Virgilia divaricate Adamson	Fabaceae	I	T	
Virgilia oroboides (P.J. Bergius) Salter	Fabaceae	I	T	
Chironia baccifera L.	Gentianaceae	I	F - S	WB, AN, AS, LH, UH
Sebaea micracantha (Cham. & Schltdl.) Schinz	Gentianaceae	I	F	WB, AS, LH, UH
Pelargonium alchemilloides (L) L'Hér.	Geraniaceae	I	F	WB, AN, UH
Pelargonium radens H.E Moore	Geraniaceae	I	F	UH
Polygala hispida Burch.	Polygalaceae	I	F	UH
Anthospermum herbaceum L.f.	Rosaceae	I	F	WB, AS, LH, UH
Anthospermum ciliare L.	Rosaceae	I	S	
Cliffortia graminea L.f.	Rosaceae	I	S	
Halleria lucida L.	Scrophulariaceae	I	S	WB, AN, AS, LH, UH
Selago corymbosa L.	Scrophulariaceae	I	P	WB, AS, LH, UH
Solanum mauritianum Scop.*	Solanaceae	A	A	WB, AN, AS, LH, UH
Solanum nigrum L.*	Solanaceae	A	A	WB, AN, AS, LH, UH
Struthiola macowanii C.H. Wr.	Thymelaceae	I	F	UH

* alien species, ** extralimital

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