Vegetation responses to invasive alien plant clearing along the Sabie River in and adjacent to the Kruger National Park.

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DECLARATION

I declare that this dissertation is my own, unaided work. It is being submitted for the Degree of Master of Science in the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination in any other university.

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Taryn Lee Morris

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ABSTRACT

Alien plant invasions are a global problem and have widespread ecological and economic impacts. River ecosystems are highly prone to invasion by alien plants due to their dynamic hydrology and the ability of water to efficiently transport alien plant propagules. This, together with continuous access to water and nutrient resources, facilitates invasions. The recognized impact of woody alien species in reducing scarce water resources in South Africa inspired the inception of the Working for Water (WfW) programme. This programme aims to increase future water yields through the large scale clearing of invasive alien plants (IAPs), while simultaneously addressing poverty alleviation. Since its inception, the programme has been operating under the assumption that ecosystems would "self repair" after the removal of IAPs, but little monitoring has occurred to determine if this is in fact the case.

In the Kruger National Park (KNP) invasive alien species have been declared one of the greatest threats to ecosystem biodiversity. Riparian zones are the most invaded systems due to the continuous influx of alien propagules from the poorly managed upper reaches of the major river catchments, combined with the capacity of river systems to facilitate invasions. WfW have executed the majority of the active clearing operations on an ongoing basis in the KNP for several years. However, little monitoring has occurred to determine the efficacy of control operations or the response of both native and alien vegetation to the removal of IAPs. Thus, the major aims of this project were to assess the efficacy of the WfW programme in clearing invasive alien plants in the KNP, and to assess the extent of natural ecosystem recovery after clearing operations.

Vegetation from twelve sites along the Sabie River within and adjacent to the KNP (Mpumalanga, South Africa) was sampled before and after an annual clearing operation by WfW. Results were compared with additional data derived from several historical studies in the area to assess the longer-term efficacy of WfW.

The occurrence of dense stands of IAPs comprising up to 97% of the vegetation density along the Sabie River within the KNP were likely a result of the significantly elevated rainfall in the respective growth season. These dense stands of IAPs were associated with a decline in several diversity measures of native vegetation with a basal stem diameter > 1 cm ($P < 0.05$). However similar negative associations were not observed with understorey vegetation ($P > 0.05$). The annual clearing operations by WfW were highly effective and reduced invasive alien plant densities from 3508 ± 1113 plants per ha to 343 ± 156 plants per ha ($P = 0.002$), translating to an average reduction

of ± 80%. After clearing, indigenous vegetation density increased (*P* = 0.02), despite the reduced rainfall received in that year's growing season. Herbaceous and graminoid growth forms showed the greatest increase in previously densely invaded transects.

In general, alien species richness has increased slightly in the KNP over the last ten years. However, the invasion intensities have remained exceptionally low, even in the face of several large disturbance events that are usually associated with a sharp increase in alien plant invasions. This is more than likely attributable to the continuous annual clearing operations by WfW in the KNP. Continuous clearing acts to effectively limit the establishment and spread of many IAP species despite the ever present threat of invasion from upstream. Furthermore, the continuous clearing of IAP stands in the KNP ensures that stands are relatively short-lived, preventing long lasting negative impacts on the ecosystem. Removal of IAP species reduces their disproportionate competitive influence and facilitates the natural re-establishment of native vegetation.

This study presented important information with regards to the vital need for assessment and monitoring of WfW operations. It also provided KNP management with valuable results pertaining to research and management objectives.

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CHAPTER 1
Introduction

1.1. Invasive alien plants in riparian zones

Riparian zones represent an ecotone between aquatic and terrestrial ecosystems of a river, where important ecological, hydrological and geomorphological processes occur and are among the most diverse, dynamic and complex habitats of all landscapes (Gregory *et al*. 1991, Naiman *et al*. 1993). The nature of a riparian corridor can change continually along its length reflecting both biotic and abiotic conditions of the adjacent upland areas. However, although riparian areas are greatly affected by the nature of upland regions, they in turn can also strongly affect how the entire watershed functions (Tickner *et al*. 2001), and despite their minor extent in most landscapes, riparian ecosystems are disproportionately important for the delivery of a number of key services (Naiman and Décamps 1997).

Riparian vegetation fulfils a number of important ecological functions, such as the regulation of movement of water, nutrients and sediments between terrestrial and aquatic systems (Décamps 1993, Naiman and Décamps 1997) as well as providing both food and habitat for faunal communities (Gregory *et al*. 1991, Naiman and Décamps 1997). Riparian vegetation also exerts strong controls on the microclimate of an area (Naiman *et al*. 1998), regulating air, soil and water temperatures as well as relative humidity (Brosofske *et al*. 1997). Therefore the general condition of riparian zones can have significant environmental consequences and plays an important role in maintaining healthy ecosystem functioning.

One of the largest threats to riparian ecosystems is invasion by alien plants and few, if any, South African river systems remain uninvaded (van Wilgen *et al*. 2001). Several factors render riparian ecosystems highly prone to plant invasions. The dynamic hydrology and frequent disturbances associated with aquatic systems (e.g. floods) provides ideal habitats and conditions for many IAP species by exposing or creating sediment banks that have little or reduced indigenous competitive influence (Tickner *et al*. 2001). This, combined with the efficient ability of water to transport seeds, rhizomes and other vegetative fragments through the riparian corridor, can often facilitate or trigger riparian plant invasions (Thebaud and Debussche 1991, Johansson *et al*. 1996, Macdonald and Frame 1998, Tickner *et al*. 2001). Rivers also provide continual replenishment of nutrients that can be suspended in the water column as well as deposited in stream sediments (Tickner *et al*. 2001).

Degradation to river catchments associated with various human-mediated disturbances further exacerbates the natural susceptibility of riparian systems to invasion by alien plants. These include disturbances associated with cultivation (e.g. vegetation clearance for agriculture, cultivation of crops, logging) (Hancock *et al*. 1996, Kentula 1997, Patten 1998, Apan *et al*. 2002); impacts from livestock (Hancock *et al*. 1996, Mathooko and Kariuki 2000, Robertson and Rowling 2000, Meeson *et al*. 2002); pollution from the surrounding catchment (Ferrar *et al*. 1988, Washitani 2001, Weiersbye *et al*. 2006), and alterations to hydrogeomorpholgical processes as a result of damming, flow regulation and/or water extraction (Dudgeon 1992, Stromberg *et al*. 1996, Patten 1998, Jansson *et al*. 2000, Nilsson and Berggren 2000, Meeson *et al*. 2002, Nilsson and Svedmark 2002, Shafroth *et al*. 2002, An *et al*. 2003, Rood *et al*. 2003).

Impacts of alien plant invasions are extensive and varied and their ability to alter composition, structure and functioning of ecosystems can affect the delivery of key ecosystem services (Gordon 1998, van Wilgen *et al*. 2001, Richardson and van Wilgen 2004, van Wilgen 2004). For example, IAPs often form dense monospecific stands that replace indigenous vegetation and lead to the loss or even extinction of both animal and plant species that can be vital for ecosystem functioning (e.g. dispersers, pollinators, soil engineers) (Breytenbach 1986, Samways *et al*. 1996, Steenkamp and Chown 1996, Higgins *et al*. 1999, French and Major 2001, Leslie and Spotila 2001, Dean *et al*. 2002, Herrera and Dudley 2003, Samways 2004, Nelson and Wydoski 2008). Furthermore, IAPs can lead to alterations in nutrient cycles (Musil and Midgley 1990, Witkowski 1991a, Musil 1993, Ehrenfeld 2003, Kourtev *et al*. 2003) and disturbance regimes such as fire (D’Antonio and Vitousek 1992, Mack and D’Antonio 1998, Brooks *et al*. 2004).

IAPs also have several impacts relating directly to riparian ecosystems and many studies have demonstrated how IAPs impact the hydrogeomorphological processes of riparian zones by altering erosion and sedimentation rates, lowering the water table, and altering patterns of surface flow (Hoffman and Moran 1988, Henderson 1991, Richardson *et al*. 1997, Gordon 1998, Tickner *et al*. 2001, Crooks 2002). But perhaps the most significant impact of IAPs in South Africa is their effect on the availability of water (Enright 2000, Le Maitre *et al*. 2000, Dye and Jarmain 2004, Görgens and van Wilgen 2004). South Africa is known for its highly variable rainfall and inadequate water resources, which are under continual pressure from the expanding population’s demands for agriculture, industry and towns (Binns *et al*. 2001, Everson 2001). The spread of invasive alien tree species across the country is thought to further exacerbate the country's water shortage problem due to their increased water usage (Le Maitre *et al*. 2002, Görgens and van Wilgen 2004). Le Maitre *et al*. (2000) estimated that the incremental water use (water use over and above what indigenous plants would normally use) by IAPs in South Africa and Lesotho was approximately 6.7% of the mean annual rainfall (MAR), almost twice as much as that used by commercial plantation forestry. Several studies have shown that clearing areas invaded by alien trees results in an increase in stream flow of the impacted system (Dye and Poulter 1995, Prinsloo and Scott 1999, Dye and Jarmain 2004). This, together with concerns over future water availability in South Africa, inspired the inception of one of the world's largest initiatives to clear riparian corridors of IAP species - the Working for Water (WfW) programme (van Wilgen *et al*. 1998).

The national WfW programme was launched by the Department of Water Affairs and Forestry (DWAF), in October 1995, with the primary goal of increasing scarce water supplies through the coordination and execution of IAP management. This translated to large-scale manual removal operations of IAPs that doubled to simultaneously address poverty alleviation and social upliftment and development in economically marginalised communities through job creation and skills (Macdonald 2004, Marais *et al*. 2004). With an initial budget of R25 million, the WfW programme established itself by demonstrating significant employment potential and conservation benefits (Marais *et al*. 2004). By 2006 the programme had spent R3.2 billion on clearing 1.6 million ha of invaded land across the country (excluding follow-up control operations of 3 million ha), while providing employment to more than 30 000 people (Marais and Wannenburgh 2008).

A decade after its inception, it is necessary for the WfW programme to secure future funding for the continuation of this highly acclaimed, cross-disciplinary project. To do this, its full socio-economic worth needs to be demonstrated and while much of the success of the programme has stemmed from its socio-political emphasis on poverty alleviation and capacity building, very little attention has been given to its ecological economic value (Turpie 2004). The ecological economic value of the programme is dependent on the success of the alien plant control programmes, leading to the recovery of ecosystems that will ultimately yield an increased water supply. However, despite more than 10 years of implementation, little research on the efficacy of clearing operations has been conducted. This task has been particularly difficult due to the fact that no formal protocols were in place for recording programme activities and details until 2001. Hence only crude estimates of the areas cleared (with little or no density and species information) and aggregate costs of clearing are available for the first six years of the programme (Marais *et al*. 2004). Additionally since its inception, the programme has been operating under the assumption that ecosystems would recover automatically after the removal of IAPs (Esler *et al*. 2008), however very little monitoring has occurred to determine whether this is in fact the case or whether, in some instances, post-clearance restoration actions might be neccessary to accelerate ecosystem recovery (Holmes *et al*. 2005).

1.2. Invasive alien plants in the Kruger National Park

The Kruger National Park (KNP) forms an isolated unit in the landscape, fundamentally affected by various social, economic, environmental and political factors beyond its borders that ultimately influence its management and functioning (Pollard *et al*. 2003). This is particularly true for several of the major rivers running across the breadth of the park. These rivers originate in catchments beyond the parks western boundary and before entering the KNP flow through various land-use areas often associated with a diverse and abundant suite of IAP species, including areas of agriculture, silviculture and dense urban and rural habitation. This provides a continuous source of alien propagules into the system that are efficiently transported via rivers down the catchments into the KNP, providing park management with an ongoing challenge of managing riparian alien plant invasions (Foxcroft and Richardson 2003, Foxcroft *et al*. 2007).

The KNP management aims to "maintain biodiversity in all its natural facets and fluxes and to provide human benefits in keeping with the mission of the South African National Parks …" (Anon. 1997a). The presence and associated impacts of IAPs in the KNP clearly violates this aim, and invasive alien species have in fact been singled out as the greatest threat to biodiversity within the KNP (Anon. 1997b). The park contains 373 species of non-indigenous plants, of which 121 are invaders. The most invaded systems are the riparian zones, hosting 40 invader taxa alone, making these areas a major priority for alien plant management (Foxcroft *et al*. 2003, Foxcroft and Richardson 2003).

1.3. Management of invasive alien species in the Kruger National Park

Management of IAPs in the KNP is a multi-faceted operation and includes monitoring, research and the execution of active IAP clearing. Monitoring programmes for IAPs in the KNP aim to assess and monitor the extent of invasions in the park according to criteria defined in the KNP management plan (Foxcroft and Richardson 2003). The KNP's management plan is arranged in a series of hierarchical objectives (Biggs and Rogers 2003, Foxcroft 2004). To put objectives into practice, KNP management has developed and employed a system 'Strategic Adaptive Management' (SAM), which is simply a variation of 'Adaptive Management' (Biggs & Rogers 2003) that focuses on strategic thinking and continual assessment. 'Thresholds of Potential Concern' (TPCs) form part of SAM, and represent measurable goals for fine-scale or low-level objectives. Biggs & Rogers (2003) define TPCs as hypotheses of spatial and temporal limits of natural ecosystem flux that are described by upper and lower limits of acceptable change of selected environmental indicators, which when reached results in management action or in re-calibration of the threshold to a more realistic and meaningful level.

Falling under the 'ecosystem objective', the main aim of the 'alien impact objective' is "to anticipate, prevent entry and where feasible and/or necessary control invasive alien species in an effort to minimize the impact on, and maintain the integrity of indigenous biodiversity" (Foxcroft and Freitag-Ronaldson 2004). To put these objectives into practice three distinct invasive alien plant TPCs have been developed that relate to invasion processes (Foxcroft and Downey 2008).

Alien TPC 1: deals with new invasions of a species in the KNP and includes both imminent external threats and first ever records in the KNP.

Alien TPC 2: deals with an increase in distribution of a species in the KNP, taking clearing into account. This includes first ever records from a new grid cell (the size of which are currently being explored) or expansion of invasive species through contiguous grid cells which represent more than a 5% increase over the number of grid cells recorded as invaded in the reference (base) year.

Alien TPC 3: deals with an increase in density of a species in the KNP. TPCs are, however not yet operational due to the lack of data and efficient cost-effective monitoring options to date. They are nonetheless described hypothetically and may in future have the potential to be used as surrogates for biodiversity impacts. They potentially involve any increase by two density classes (classes being defined as scattered, low, medium or high) or more in any grid cell or an increase from medium density in any grid cell.

Research into invasive alien species also plays a major role in IAP management and often feeds back to influence management objectives and further refine invasive alien TPCs. The KNP coordinated research programme focuses on providing insights into the impacts of IAPs on the biodiversity and heterogeneity of the KNP and providing guidelines for developing and maintaining cost-effective, sustainable control programmes. Three broad research themes have been identified and linked directly to the KNP's alien objective hierarchy: 1) impacts of alien invasions, 2) ecology of alien invasions, and 3) efficacy of control techniques (Foxcroft and Freitag-Ronaldson 2004).

While monitoring and research are essential components of alien plant management, active clearing of IAPs is the ultimate objective. Various stakeholders are involved in alien plant clearing in the KNP but for the most part, implementation is executed mainly by the WfW programme. The programme was first launched in the park in 1997, and has since become an integral component of IAP management, with over R60 million having been spent to date in the KNP on clearing mostly riparian areas (Foxcroft and Freitag-Ronaldson 2007). The WfW partnership in the KNP is somewhat unique as clearing has occurred on an annual basis since approximately 2000 and will continue to form a major component of active clearing operations in the park, for some years to come. This means that selected areas in the KNP are under continuous control by WfW in contrast to the limited operations executed under normal WfW protocol.

1.4. Rationale for the study

Research on invasive alien plants in the Kruger National Park

The 'efficacy of control techniques' is a broad research theme of the KNP alien research objective and aims to enhance the long-term implementation of control programmes, through developing an understanding of the associated negative impacts of control and further developing techniques for improved control and rehabilitation and incorporates several specific sub-objectives including:

a. To evaluate and quantify the potential impacts of control on non-target (indigenous) species
b. To evaluate and quantify the efficacy of control measures

c. To evaluate and quantify the impacts / effects of control on specific areas under control and after control
d. To develop rehabilitation strategies and monitor these to determine the long-term efficacy thereof
e. To carry out cost/benefit analyses of control
f. To evaluate the establishment and success of new biological control agents following their release
g. To determine the long-term impacts of biological control and quantify its contribution to integrated management
h. To develop detection, diagnostic and vaccination strategies that are safe and effective

Clearing of IAPs in the KNP has occurred on an annual basis for approximately seven years in specific riparian corridors. However, for the most part little monitoring has occurred to assess the efficacy of control measures or the effect of clearing on both alien and indigenous vegetation. Thus the need for information on these KNP research objectives contributed to the inception of this study which then focussed on the first four research objectives.

Active management of invasive alien plants by Working for Water.

The need for monitoring after clearing by the WfW programme has recently been identified as a major priority. In response, WfW commissioned the "Ecosystem Repair" project which comprised several studies, including this one, on various academic levels, spanning the fynbos, grassland and savanna biomes in South Africa. The major objective for the greater project was to derive clear and achievable goals for riparian ecosystem recovery following alien plant control and to develop management tools that could be utilised to effectively promote desired restoration targets. The Ecosystem Repair project was the principal motivation for the inception of this study and results aimed to contribute to answering the following key questions of the overall project.

1. What has been achieved in terms of ecosystem repair following removal of stands of alien plants?
2. Have abiotic or biotic thresholds been passed that prevent natural ecosystem repair?
3. What is achievable in terms of ecosystem repair in each of the different situations studied and how could operations be improved?
4. What are realistic ecosystem repair goals for the different situations?

1.5. Aims and objectives

The broad aims of this study were twofold – firstly to investigate impacts, ecology and efficacy of IAP clearing techniques in order to contribute to the understanding and improvement of KNP alien species management protocols. Results could also potentially contribute to the evaluation and further refinement of alien plant TPCs. Secondly, this study aimed to assess the efficacy of the WfW programme in clearing alien plant invasions and to determine the extent of natural ecosystem recovery after clearing of IAPs in the KNP.

These aims translated into several major objectives for this study:

1) To determine if short-lived alien plant invasions have a significant impact on native vegetation structure and diversity.
2) To investigate the role of native vegetation in influencing the distribution of IAP species on a river bank.
3) To assess the short-term efficacy of IAP clearing operations of WfW after an annual clearing event.
4) To assess the long-term efficacy of IAP clearing operations of WfW over ten years using data from other studies.
5) To investigate the response of riparian vegetation to IAP removal in order to assess the extent of natural ecosystem recovery.

1.6. Dissertation structure

A general introduction into the ecology, impacts and management of invasive alien species in South Africa and particularly in the KNP, as well as the rationale for the inception of the study and the intended aims and objectives were provided in this first chapter. Chapter 2 investigates the impacts of short-lived alien plant invasions on the structure and diversity of larger herbaceous and woody riparian vegetation. The efficacy of clearing operations by WfW over one clearing season as well as the response of indigenous vegetation after clearing was also assessed. Additionally, the role of disturbance in facilitating alien plant invasions along rivers is evaluated, with particular reference to flooding as a disturbance. Chapter 3 investigates the impacts of alien aerial cover on ground cover variables and assesses the response of these variables to the removal of the alien plant invasions. The role of both overstorey aerial and understorey ground cover are considered in conjunction with several other environmental variables to investigate the influence of these variables on the establishment distribution of IAPs. Chapter 4 incorporates results from several other studies spanning the same river catchment. The long-term efficacy of WfW clearing in the KNP is assessed and then related to areas further upstream with a differing management history. A brief concluding discussion, recommendations and future research suggestions for both KNP management and WfW are presented in Chapter 5.

Chapters 2, 3 and 4 present the results of this study and have each been presented in a free-standing format for submission or publication in a scientific journal. Chapter 2 has been published in the South African Journal of Botany in a special issue focusing on results from the Ecosystem Repair project. The publication has been included as an appendix. Consequently, there is a fair degree of repetition in the introduction and methods sections and to a lesser degree the discussions of the three chapters, although an attempt has been made to keep this to a minimum. For convenience, the literature cited in Chapters 1-5 is presented in one reference section at the end of the thesis.

CHAPTER 2

Initial response of riparian plant community structure to clearing of invasive alien plants in Kruger National Park, South Africa[1]

2.1. ABSTRACT

Recovery of indigenous species subsequent to the clearing of invasive alien plants (IAPs) is crucial for ecosystem recovery to occur. However, cleared sites are often just left in the hope that revegetation will occur naturally. In riparian areas of Kruger National Park (KNP), the Working for Water (WfW) Programme has cleared IAPs on a regular basis, but little post-clearance monitoring has taken place. Thus investigating short-term effects of IAPs and IAP clearing on plant community diversity and vegetation recovery after clearing provided an ideal opportunity to assess feasible targets of natural ecosystem recovery in similar areas. Vegetation was sampled from twelve transects along the Sabie River in and adjacent to the KNP, before (March/April 2006) and after (March 2007) the annual clearing of IAPs by WfW. Rarefied species richness, alpha diversity and evenness of distribution of species all declined with increasing density of IAPs ($P < 0.05$). There was a mean reduction of IAP density by 80±6% ($P = 0.002$) through clearing by WfW. After clearing of IAPs, indigenous vegetation densities increased ($P = 0.02$), with herbaceous growth forms showing the largest increase in transects that were previously heavily invaded. Thus, in this system, which is relatively undisturbed by human activities, initial recovery of indigenous vegetation can occur without further restorative interventions. This process is more than likely aided by the continuous clearing of IAPs by WfW as this acts to deplete alien seed banks and maintain IAPs at acceptable and manageable levels.

2.2. INTRODUCTION

The introduction and establishment of invasive alien species is a global problem having severe and wide-spread consequences. Invasive alien plants (IAPs) not only negatively impact the structure and functioning of ecosystems (Vitousek 1990, Witkowski 1991a; b, Richardson *et al*. 1997, Gordon 1998, Witkowski and Wilson 2001), but have also been acknowledged as one of the greatest threats to global biological diversity (Coblentz 1990, Rubec and Ledd 1996), with numerous studies reporting negative effects of IAPs on the diversity of communities (Richardson *et al*. 1989, 1997, Vitousek 1990, Pyšek and Pyšek 1995, Dunbar and Facelli 1999). Although diversity has various ecological definitions, in this study it refers to "the variety and abundance of species in a defined unit of study" and incorporates measures of both species richness and evenness of distribution of species (Magurran 2004).

[1] This chapter has been published in the South African Journal of Botany: Morris, T.L., Witkowski, E.T.F. and Coetzee, J.A. 2008. Initial response of riparian plant community structure to clearing of invasive alien plants in the Kruger National Park, South Africa. *South African Journal of Botany* 74: 485-494.

Considering the detrimental impacts that alien invasions can have, it is not surprising that management of IAPs and restoration of ecosystems impacted by IAPs has become a priority to conservation managers worldwide (Byers *et al.* 2002). South Africa faces a great challenge in managing IAPs, an issue that has received much attention (Richardson and van Wilgen 2004). In 1995, the Department of Water Affairs and Forestry launched the Working for Water (WfW) programme, with the primary goal of securing scarce water resources, by coordinating and conducting active clearing of alien plant invasions across the country, while simultaneously addressing poverty alleviation through job creation (van Wilgen *et al.* 1998). Clearing of IAPs is however, a continual and complex challenge (Manchester and Bullock 2000), and cleared areas often experience further invasion or other secondary problems (Holmes *et al.* 2000, Holmes 2001, Beater *et al*. 2008). Regrowth by indigenous vegetation is essential to minimise the possibility of further problems and to allow ecosystem recovery to ultimately occur. While in some areas this may take place without further management intervention, in others, active maintenance and restoration can sometimes be necessary (D'Antonio and Meyerson 2002, Galatowitsch and Richardson 2004). Post-clearance monitoring is crucial to assess levels of post-clearance ecosystem recovery and to determine if further management is needed. However, this monitoring is rarely performed and in general, sites cleared by WfW are often just left in the hope that indigenous revegetation will occur without further management intervention (Galatowitsch and Richardson 2004).

In the Kruger National Park (KNP), South Africa, invasive alien species have been declared one of the greatest threats to biodiversity, with riparian zones being the most severely invaded systems (Foxcroft and Richardson 2003, Foxcroft *et al*. 2007). Riparian ecosystems are acknowledged to be highly prone to IAP invasions due to the dynamic nature of rivers as well as the efficient ability of rivers to transport and disperse alien propagules (Thebaud and Debussche 1991, Pyšek and Prach 1993, Johansson *et al*. 1996, Tickner *et al*. 2001). Once present in a catchment, many of these IAP species can exploit opportunities provided by both natural and anthropogenic disturbances (Richardson *et al*. 2007). These disturbances include those linked to hydrology (flooding, sedimentation), fire, herbivory and even disturbances associated with IAP clearing (Tang and Montgomery 1995, Naiman and Décamps 1997, Parker-Allie *et al.* 2004, Richardson *et al*. 2007, Witkowski and Garner 2008).

To aid in the management of alien plant invasions, the WfW programme was first launched in the KNP in 1997, and has since become a major component of IAP management, executing annual clearing operations in selected areas. Despite this setting providing an excellent opportunity to assess impacts of IAPs and their clearing on plant community diversity and initial vegetation succession in riparian areas subsequent to clearing, very little monitoring has taken place. Investigating the impacts of and recovery from IAP invasions in such an area with relatively low anthropogenic disturbance, which should be less invaded, should provide indications of benchmark targets for similar vegetation in other areas of land-use. It should also provide a realistic test to assess to what extent natural revegetation actually occurs, subsequent to clearing of IAPs. If revegetation were not to occur in this relatively well managed ecosystem with low anthropogenic disturbance, it definitely can not be expected to occur in highly transformed or degraded areas. Thus, the aims of this study were (a) to assess vegetation diversity along the riparian zone of the Sabie River in and adjacent to the KNP, in relation to the abundance of IAPs and (b) to determine patterns of vegetation regrowth after clearing of IAPs in densely invaded sites.

2.3. MATERIAL AND METHODS

2.3.1. Study Area

This study was conducted along the Sabie River, within and adjacent to, the KNP. The Sabie River is a perennial river (Heritage *et al.* 1999) originating in the escarpment of the Drakensberg Mountains to the west of KNP. It flows eastwards through areas of commercial forestry, agriculture and dense rural habitation before entering the KNP and on to Mozambique (Figure 2.1). The complex pattern of land-use and ownership upstream of the KNP provides a continual source of alien plant propagules into the riparian system, creating a continual challenge for the management of IAPs (Foxcroft and Richardson 2003, Foxcroft *et al*. 2007, Beater *et al*. 2008).

The area is located in the savanna biome and is characterized by a semi-arid to subtropical climate, with hot rainy summers and mild dry winters (Venter *et al.* 2003). There is an increasing rainfall gradient from east to west (Venter *et al.* 2003), with an average annual rainfall of 450-600 mm (van Niekerk and Heritage 1993). Rainfall during the study period recorded at the Skukuza weather station was 70% greater than the 76 year long-term annual average rainfall in 2005/06 and in 2006/07, 35% below the average (Figure 2.2).

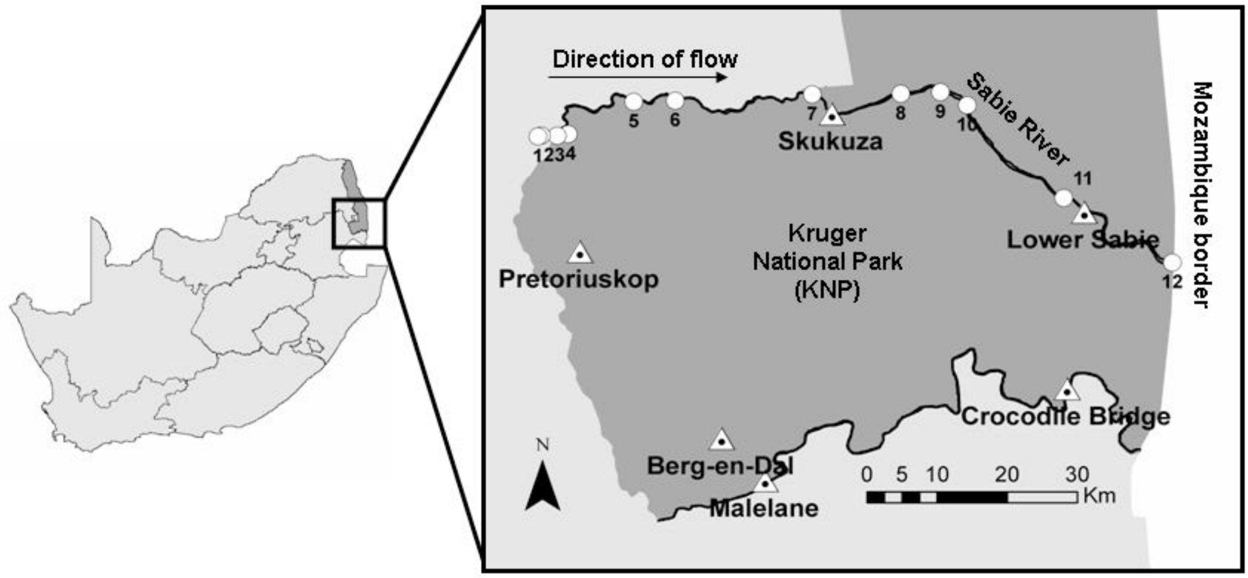


Figure 2.1. Map of the southern section of the Kruger National Park. Transects span the Sabie River and were divided into three zones according to location and propagule pressure. Zone 1: transects 1-3, outside the KNP; Zone 2: transects 4-8, in close proximity to the boundary (transect 8 is situated after Skukuza rest camp which is a propagule source) and Zone 3: transects 9-12, within the confines of the park extending to the Mozambique border.

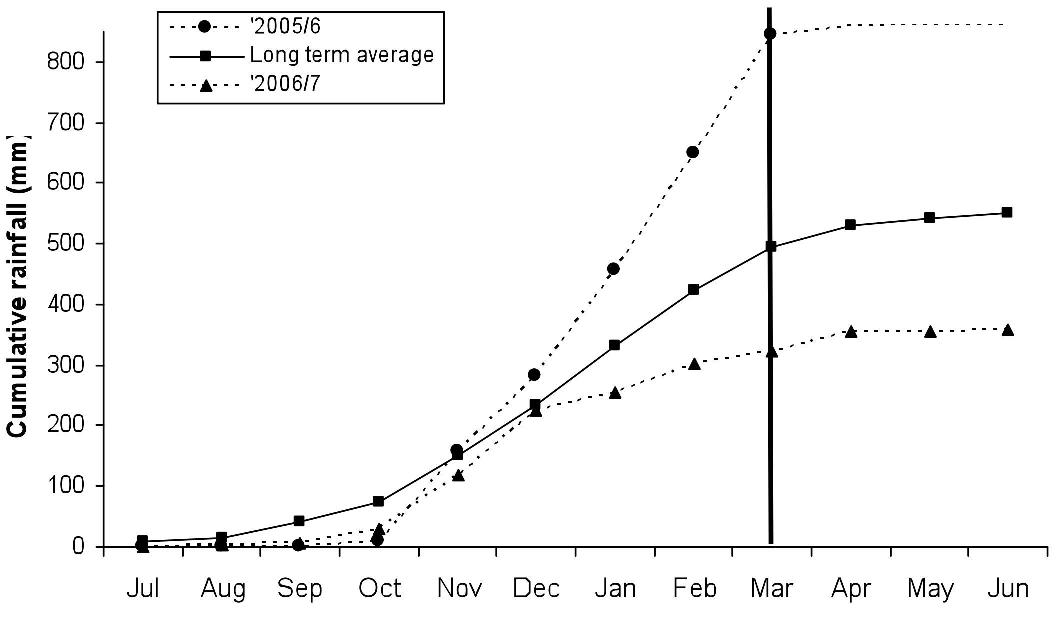


Figure 2.2. Cumulative rainfall (mm) at Skukuza weather station from the beginning of the "annual climatic year" (July). The dotted lines represent the 2005/6 and 2006/7 rainfall seasons, while the solid line represents the long-term average over 76 years. Vegetation sampling occurred in March, indicated by the bold solid bar.

The sites within the park were chosen based on the locations of historical sites for which data were available for comparison. Three sites chosen outside of the park were limited to areas that had not undergone extensive transformation. Each site fell with in a unique "Nbalid". An Nbalid (National Botanical Aliens Database Identifications) is the unique ID, given by WfW to an area of land that is under management. The size of the Nbalid should technically be related to its density of invasive alien plants, as all Nbalids should theoretically be cleared in a standard unit of time. However, these classifications have not been revised in the history of the WfW project, and thus seldomly still represent the density of the alien infestation. They are however, still practical due to the predefined delinieations of land as well as the availability (in some cases) of historical clearing data. Due to institutional fluctuations and subsequent alterations to data organization methods, this information in reality can be very difficult to obtain. Thus the information from each Nbalid for each study site is listed in the table below as best could be deciphered.

Table 2.1. Co-ordinates of each site as well as the corresponding Working for Water Nbalid in which it falls, the size of the Nbalid and the number of times treatment has occurred in that Nbalid.

Site	X co-ordinate	Y co-ordinate	Nbalid	Size (Ha)	Follow up no.
1	31.21668	-25.02002	X31K100171	49.59	8
2	31.22106	-25.01883	x31K100231	20.72	4
3	31.24160	-25.01894	x31K100232	17.37	4
4	31.25560	-25.01676	X31k100174	89.42	5
5	31.33964	-24.97391	X31K100341	243.83	7
6	31.39299	-24.97251	X31M100260	156.03	8
7	31.56878	-24.96425	X31M100244	113.41	5
8	31.68244	-24.96336	X31M100157	194.96	7
9	31.73330	-24.96125	X31M100242	372.94	4
10	31.76772	-24.97856	X31M100243	364.17	4
11	31.89148	-25.10137	X31M100195	163.21	4
12	32.03075	-25.18706	X31m100180	262.43	6

Sampling took place over two periods: in March/April 2006 and in March 2007. Information on the exact clearing dates at each site was unavailable but clearing occurred between May 2006 and Nov 2006, mostly in the autumn and spring months.

Table 2.2. Methods of control for invasive alien plants found within the transects modified from Murray and Powell (2004). 1 = pull out by hand; 2 = remove plants with slasher; 3 use foliar spray; 4 = if plants small – use foliar spray, if too large remove with slasher and use foliar spray 2-3 months later on regrowth; 5 = cut at ground level and apply herbicide; 6 = make downward cuts into trunk and apply herbicide

Species	All sizes	Seedlings	Young plants	Adult plants	Thick stem adults	Regrowth
Argemone spp.	1 or 2					
Cardiospermum halicacabum		3	2 or 3			3
Datura erecta	1	3	2 or 3	5		
Lantana camara		1 or 3	2 or 3	5		3
Leucaena leucocephala		1 or 3	2 or 3	5	6	3
Melia azedarach		1 or 3	2 or 3	5	6	3
Mimosa pigra		1 or 3	2 or 3	5	6	3
Ricinus comunis	1	1	2 or 3	5		3
Senna didymobotrya	1	1	2 or 3	5		3
Senna spp.	1	3	2 or 3	5		3
Sesbania bispinosa	1	3	2 or 3	5		3
Sesbania puniceae	1		2 or 3	5	6	3
Solanum seaforthianum		3	2 or 3			3
Tithonia diversifolia	1	3	2 or 3	5	6	3
Tithonia rotundifolia	1	3	2 or 3	5		3
Xanthium strumarium	1 or 2					

The high rainfall experienced in 2005/2006 (Figure 2.2) enhanced the response of IAP growth and IAP densities were much greater than those reported on the same river in 2004 (Foxcroft *et al*. 2008b). However, IAP patterns are also influenced by the continuous clearing efforts of WfW, who have undertaken annual clearing operations for at least the last four years on the Sabie River. This annual clearance by WfW afforded the opportunity to assess the short-term response of IAPs over just one season of growth, with the large disturbance of a high rainfall bout having occurred since the previous years clearing operations. It also provided the opportunity to assess the response of the indigenous vegetation directly after clearing operations by WfW. Thus for interpretation purposes the terms before (pre-clearance) and after (post-clearance) relate only to the 2006 clearing season which targeted the high IAP densities resulting from the high rainfall season, and not to the long-term clearing operations by WfW.

2.3.2. Vegetation sampling

Sampling took place over two periods: in March/April 2006 and in March 2007. Twelve transects were sampled along the Sabie River from Hazyview (upstream and adjacent to KNP) through the park and terminating at the Mozambique border on the eastern boundary of the park (Figure 2.1). These transects were split into three zones according to their location and hence corresponding propagule pressures: Zone 1 − transects 1-3: situated along the Sabie River outside the KNP; Zone 2 − transects 4-8: situated within the park but in close proximity to the boundary. Transect 8 was included in this zone as it is located near the large Skukuza tourist camp and staff village, which poses a very high threat for IAP invasions, mainly due to the pathway of spread of exotic species from camp and staff gardens (Foxcroft and Richardson 2003, Foxcroft *et al*. 2008a); Zone 3 − transects 9-12: located along the Sabie River within the confines of the KNP extending to the Mozambique border.

Vegetation with a basal stem diameter (BSD) > 1 cm was sampled in a 10 m wide belt transect placed perpendicularly to the river. This belt transect extended from the top of the macro-channel bank to the beginning of the macro-channel floor. However, due to the heterogeneous nature of the riparian zone along the 108 km stretch of the Sabie River, these transects varied in length from 20-90 m. In each transect individual plants were identified and counted, the BSD and height class were recorded and the growth forms were later classified as herb, shrub or tree according to Germishuizen and Meyer (2003).

2.3.3. Data analysis

The following diversity indices were derived for combined alien and indigenous vegetation using Primer™ v5 (Clarke and Gorley 2001) and utilised to assess possible area effects between transects of differing lengths and hence areas:

a) Observed species richness (S).
b) Rarefied species richness (n=100): the expected number of species for a given number of randomly sampled individuals (McCabe and Gotelli, 2000).
c) Simpson's diversity index (D) and reciprocal (1/D).
d) Simpson's evenness index ($E_{1/D}$)

Densities of alien and indigenous vegetation were assessed before and after the annual clearing by WfW and tested for significant differences over time using Wilcoxon matched pairs tests in Statistica 6.1 (StatSoft 2004). Mann-Whitney *U*-tests were used to assess differences in before clearance alien densities between the three zones along the River. Diversity indices were assessed across the three zones before and after the annual clearing by WfW and were also plotted against alien densities to investigate potential relationships between alien intensity and vegetation diversity.

Indigenous species densities categorised into growth form were considered before and after the annual clearing of IAPs. The densities of species that increased in abundance over time were square-root transformed and the percentage contribution of the species responsible for 70% of the variation within a site before and after clearing of IAPs was calculated. A 70% cut off was used to highlight the species that contributed most to the observed changes. Indigenous herbaceous plant densities that increased over time were tested for a significant difference between heavily- versus lighty-invaded transects using Mann-Whitney *U*-tests.

Transect 3 was omitted from all before versus after analyses as this transect had subsequently been transformed into farmlands by the second data collecting period and hence no “after” data could be collected for this site.

2.4. RESULTS

2.4.1. Effects of variation in transect length (area)

Species richness is expected to increase as area increases. However, as transect areas increased, this expected relationship was not observed, either before (2006) or after clearance (2007) of IAPs. There was no relationship between transect area and species richness ($P > 0.05$) (Figure 2.3a) and, unexpectedly, both species diversity (Figure 2.3b) and evenness (Figure 2.3c) decreased slightly as transect area increased ($P > 0.05$). These results suggest that macro-channel banks along the lower Sabie River are comparable regardless of transect length. This may be of importance when considering future sampling methods as plots of a fixed size may misrepresent the full extent of riparian macro-channel banks, which can vary dramatically down the length of the river, and hence underestimate diversity. Thus regardless of the differing lengths, and hence areas across the sites, data were still considered comparable due to the negligible area effects.

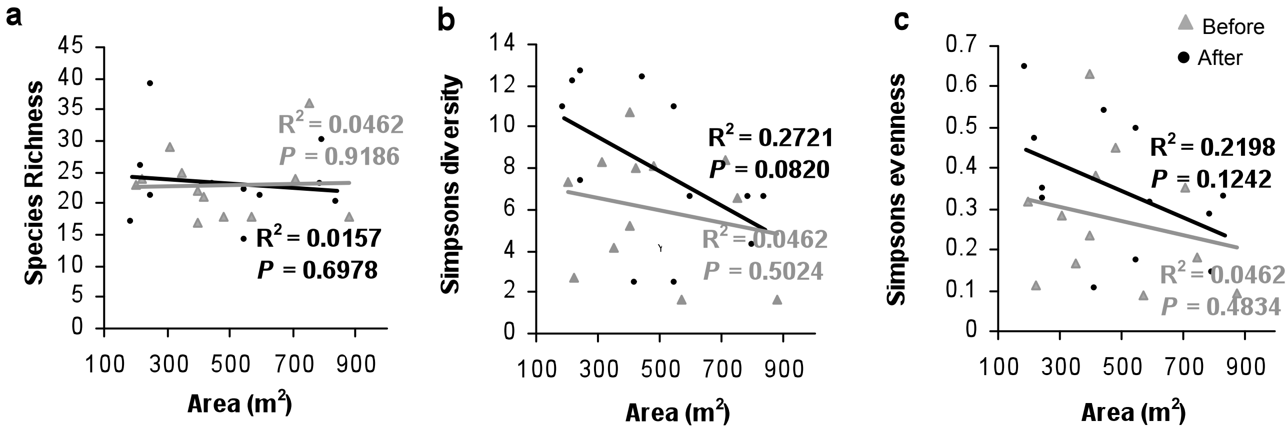


Figure 2.3. Species richness (a), Simpson's diversity (b), and Simpson's evenness (c) as a function of transect area (m^2) before (Mar 2006) and after (Mar 2007) clearance of invasive alien plants. Fitted trend lines are linear.

2.4.2. Densities of invasive alien plants before and after annual clearing

The density of IAPs before clearing by WfW outside the KNP (Zone 1: transects 1-3) was slightly lower than transects within the park in Zone 2 (transects 4-8) although differences were not significant ($Z_{3,5} = -1.34$, $P = 0.18$). Density was lowest in transects further downstream towards the Mozambique border (Zone 3: transects 9-12) ($Z_{4,5} = 2.45$, $P = 0.014$) as would be expected with an increasing distance away from the major propagule sources upstream of the western boundary. Densities of IAPs (per ha) after clearing (343±156), were significantly reduced ($Z_{12} = 3.06$, $P = 0.002$) relative to before clearance levels (3508±1113), with a mean IAP reduction of 80±6% (Figure 2.4).

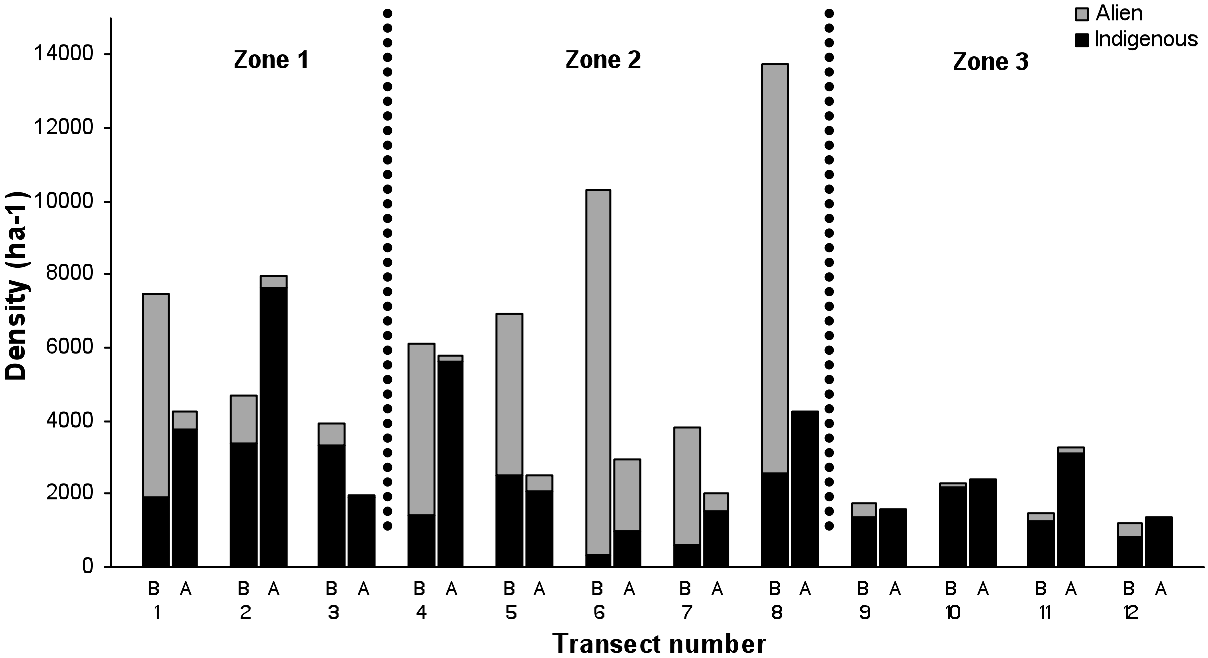


Figure 2.4. Densities (per ha) of indigenous and alien vegetation (basal stem diameter >1 cm) before (B) and after (A) the annual clearing of invasive alien plant species by the Working for Water programme.

Prior to clearing, species that contributed most to the alien plant density of heavily invaded transects were *Acanthospermum hispidium* (DC.), *Lantana camara* (L.), *Senna obtusifolia* ((L.) Irw & Barn.), *Senna occidentalis* ((L.) Link), *Tagetes minuta* (L.) and *Xanthium strumarium* (L.). These six species contributed between 62-93% of all vegetation density at the previously heavily invaded transects (transects 1, 4-8) (Table 2.1).

Table 2.3. Densities of alien species (with a density > 5 plants/ha at any one site) as well as the relative contribution of these species to the total density of all vegetation of transects that were relatively densely invaded (alien density > 50%) prior to the clearing of invasive alien plants.

				Transect number					
Species	Growth form	Longevity	Legal status*	1	4	5	6	7	8
Acanthospermum hispidum	Herb	Annual	-		9	3			
Lantana camara	Shrub	Perennial	DW1		5			1	
Senna obtusifolia	Shrub	Annual	-	31	2	19	9		
Senna occidentalis	Shrub	Perennial	-	1	26		1		56
Tagetes minuta	Herb	Annual	-	36	32	23	5	5	1
Xanthium strumarium	Herb	Annual	DW1	3		18	78	77	24
Total percentage density of abundant alien species				72	74	62	93	83	81
Total percentage density of all invasive alien species				75	77	64	97	84	82
Percentage of total alien density				96	96	98	96	99	99

***Legal status refers to regulation 15 of the Conservation of Agricultural Resources Act, 1983 (Act No. 43 of 1983). DW1 = Declared weed 1 as described in Henderson (2001).**

2.4.3. Effects of invasive alien plant density on plant community diversity

When investigating the effects of IAPs on community diversity, no relationship between alien density and species richness was found (*P* > 0.05) (Figure 2.5a). However when species richness was rarefied to *n* = 100 for comparison across transects, it decreased as alien density increased (*P* < 0.05) (Figure 2.5b). Additionally, alpha diversity and evenness decreased as alien density increased (pre-clearance data: *P* < 0.05) (Figure 2.5c, d). Similar trends occurred irrespective of whether densities were calculated on an absolute or relative basis.

When considering changes in diversity measures before and after clearing, in each zone and overall, no changes in species richness were evident (Figure 2.6a). Alpha diversity and evenness remained unchanged in zone 3, which was mostly unaffected by IAP invasions. However in zone 1 and 2, there was a trend for both alpha diversity and evenness to increase despite the reduced rainfall received in that year (Figure 2.6b, c). This suggests that the drastic reduction of IAPs in these zones may have lead to this initial increase in these diversity measures.

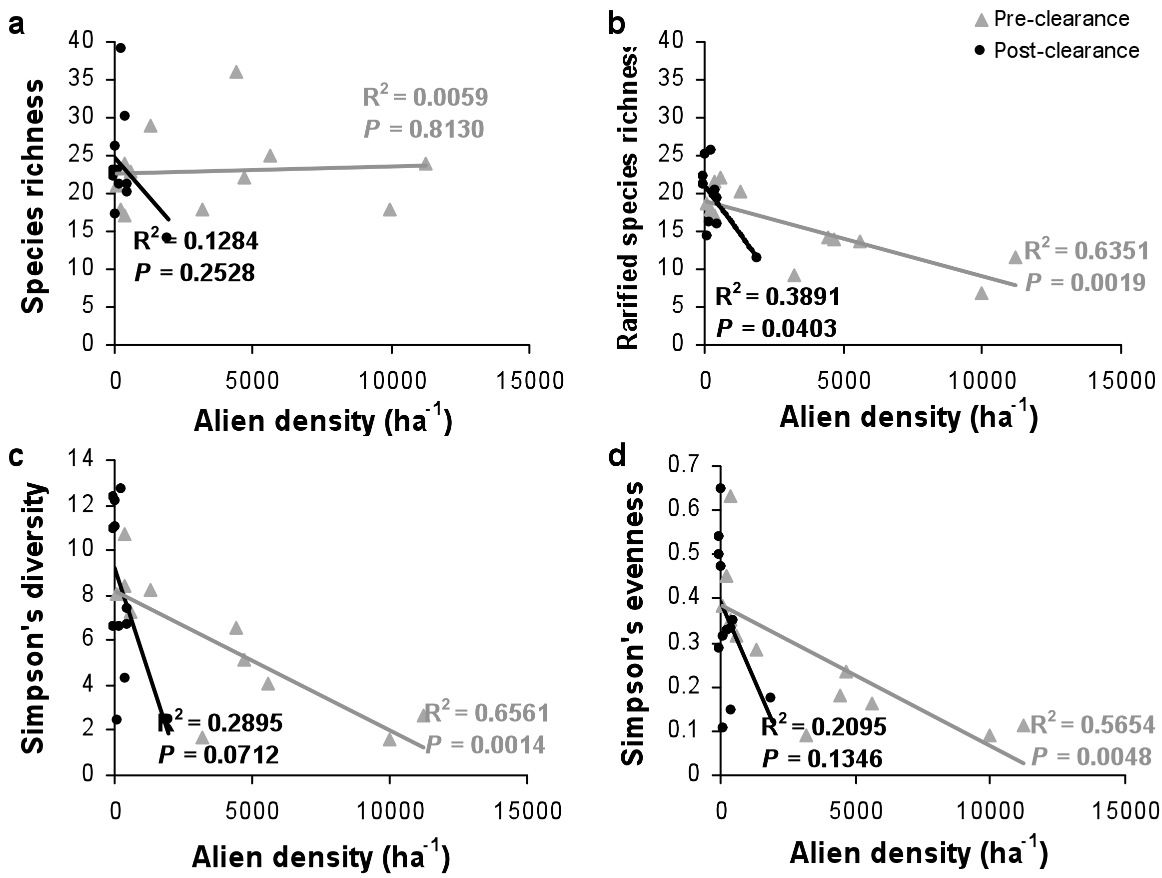


Figure 2.5. Species richness (unadjusted and rarefied) (a, b), Simpson's diversity (c) and Simpson's evenness (d) as a function of alien density (per ha) before (Mar 2006) and after (Mar 2007) the seasonal clearance of invasive alien plants by Working for Water.

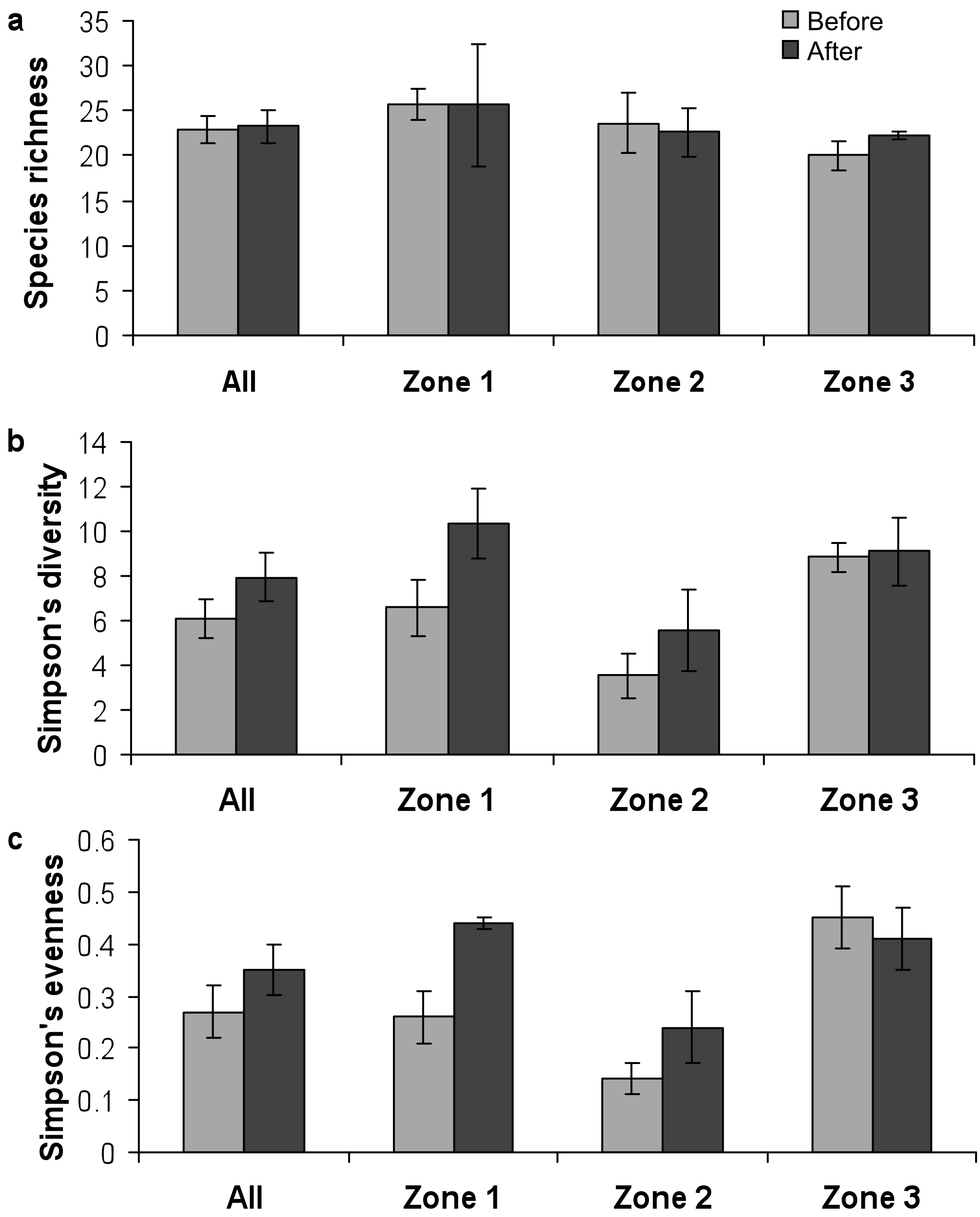


Figure 2.6. Average (± SE) species richness, Simpson's diversity and Simpson's evenness for all transects and each zone, before and after clearing.

2.4.4. Response of indigenous vegetation to annual clearing of invasive alien plants

Overall, densities of indigenous species increased after the clearing of IAPs (Figure 2.7) ($Z_{11} = 2.66$, $P = 0.007$) with both tree and shrub growth forms increasing significantly after clearing ($Z_{11} = 2.93$, $P = 0.003$; $Z_{11} = 2.66$, $P = 0.007$, respectively). Interestingly, species that increased in previously densely invaded transects (alien density >50%), were mostly herbaceous ($Z_5 = -1.92$, $P = 0.055$), whereas species that increased in the less invaded transects were tree species ($Z_5 = 2.31$, $P = 0.021$) (Figure 2.8), as would be expected in relatively undisturbed areas experiencing normal recruitment.

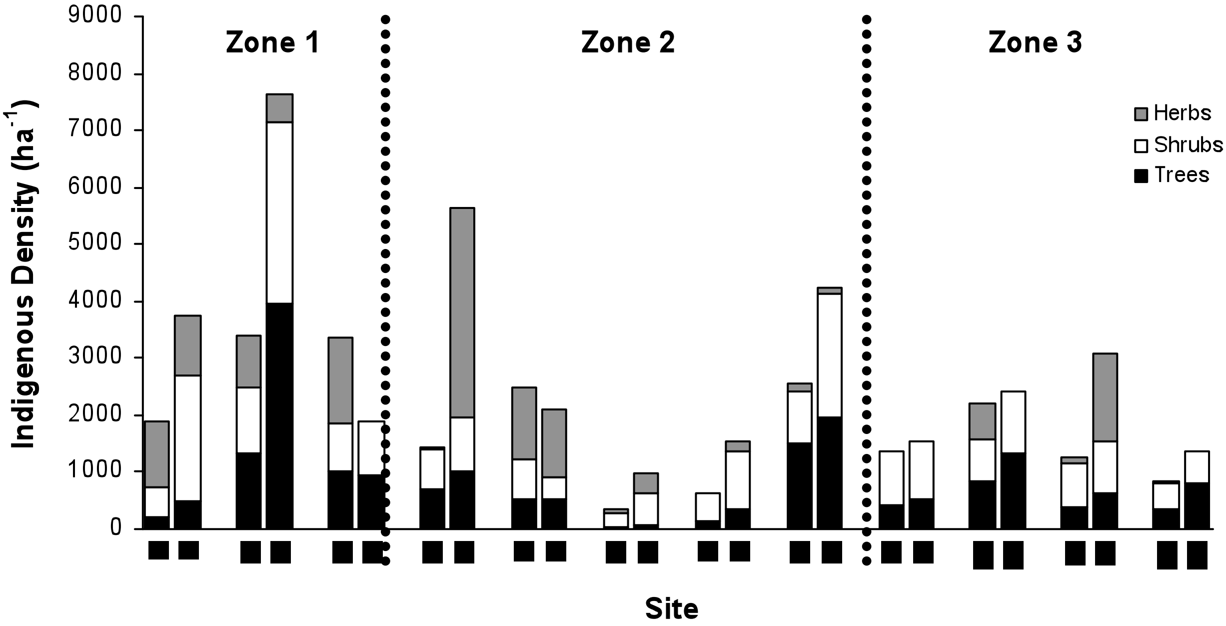


Figure 2.7. Density (per ha) of indigenous vegetation before and after the seasonal clearing by Working for Water. Densities are divided into three growth forms: trees, shrubs and herbs (data could not be collected at transect 3 after clearing of invasive alien plants as this site had been transformed into farm lands and thus post-clearance densities at site 3 were derived from an intermediate data set and were excluded from interpretation).

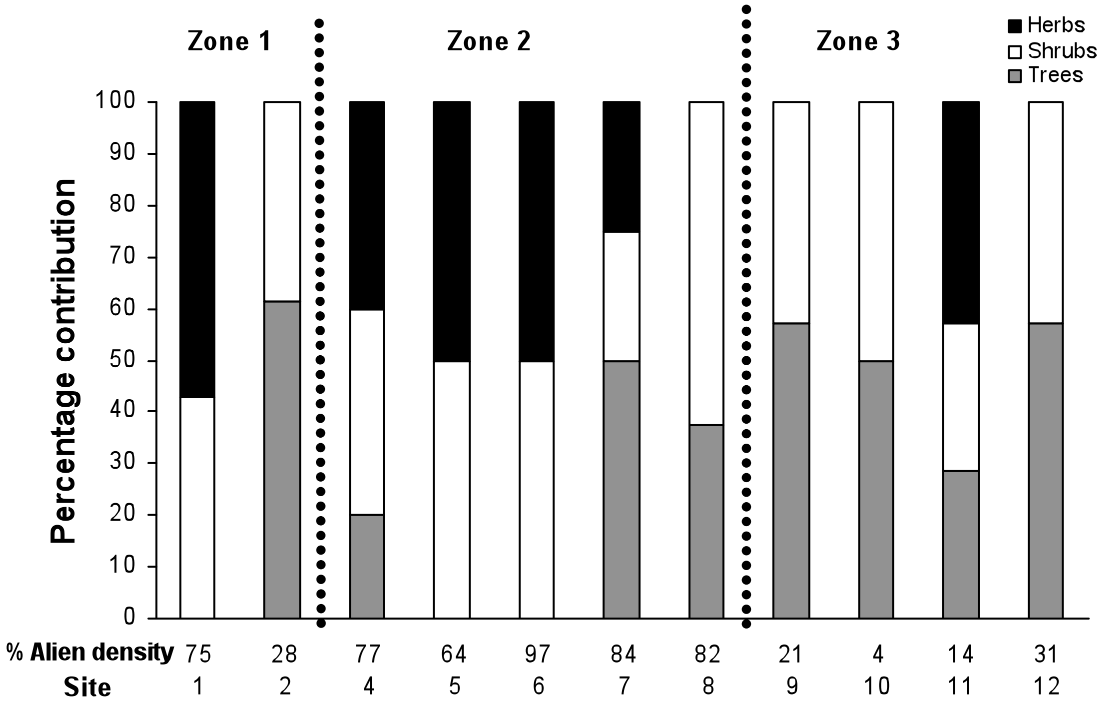


Figure 2.8. Percentage contribution of the growth forms of species that increased after clearing, contributing to 70% of the observed change post-clearance of invasive alien plants.

The herbaceous species that contributed the most to the increase in indigenous non-graminoid plant abundance were *Sida cordifolia* (L.), *Triumfetta rhomboidea* (Jacq.) and *Waltheria indica* (L.); while *Phyllanthus reticulatus* var. *reticulates* (Poir.), *Acacia schweinfurthii* var. *schweinfurthii* (Brenan & Exell) and *Leonotis intermedia* (Lindl.) contributed to the greatest increase in shrub abundance, and *Acacia robusta* subsp. *clavigera* (Burch) contributed to the increase in tree species abundance after clearing (Table 2.2). This supports the use of *A. robusta*, which regenerates relatively easily from seed (E.T.F. Witkowski, unpublished) for restoration planting in riparian areas within this ecoregion (Holmes *et al*. 2008).

Table 2.4. Total percentage contribution of the three indigenous species that contributed most at each site to the increase in indigenous plant density in previously densely invaded sites (alien density >50%).

			Transect number						
Species	**Growth Form**	**Longevity**	**1**	**4**	**5**	**6**	**7**	**8**	**Total**
Sida cordifolia	Herb	Annual		49	48	31	19		146
Phyllanthus reticulatus	Shrub	Perennial	17	9				10	36
Acacia schweinfurthii	Shrub	Perennial			9		14		23
Leonotis intermedia	Shrub	Perennial				21			21
Pluchea dioscoridis	Shrub	Perennial				17			17
Pavetta catophylla	Shrub	Perennial						15	15
Triumfetta rhomboidea	Herb	Annual	14						14
Crotolaria capensis	Shrub	Perennial	14						14
Acacia robusta	Tree	Perennial					9		9
Waltheria indica	Herb	Annual			9				9
Pyrostria hystrix	Shrub	Perennial						9	9
Flueggea virosa ssp. *virosa*	Shrub	Perennial		6					6

2.5. DISCUSSION

2.5.1. Changes in alien densities and community diversities

Prior to clearing by WfW (2006), transects had IAP densities of up to 97%. These high IAP densities appeared to have a negative impact on plant community diversity (Figure 2.5), which is congruous with results of other studies (e.g. Holmes *et al.* 2000, Pyšek and Pyšek 1995). After the reduction in IAP density there was a notable corresponding increase in the alpha diversity and evenness of vegetation in the previously densely invaded sites (Figure 2.6). The major contribution to the high IAP densities was from annual or short-lived perennial species such as *Xanthium strumarium* (L.), *Senna obtusifolia* (L.), *Senna occidentalis* (L.) and *Tagetes minuta* (L.). The short longevity of these species may result in these plants dying off naturally at the end of the annual growing season, making clearing seem redundant. However, the clearing of these species reduces both reseeding and shading out of regenerating indigenous herbaceous species, and thus acts against subsequent reinvasion of herbaceous IAP species. Perhaps clearing the densely invaded areas before these IAPs have the opportunity to set seed, would minimise the perpetuation of these herbaceous IAPs and reduce the overall management effort necessary to control these species in the long-term.

2.5.2. Response of indigenous vegetation to annual clearing of invasive alien plants

Herbaceous growth forms increased in response to clearing of IAPs in transects that were previously densely invaded. This is congruent with the notion that recovery from plant invasion is observed quickest in changes to herbaceous diversity and abundance, followed by shrubs and trees (Connell and Slatyer 1977, Mentis and Ellery 1994). The short time span of this study as well as the compounded effects of annual clearing renders it difficult to fully explore successional changes in the indigenous vegetation. However, the important point with regards to the recovery of the system after clearing, is that recolonisation of vegetation is largely by indigenous species rather than the undesirable situation of reinvasion by the same or other exotic species, as was the case further up in the catchment (Beater *et al*. 2008, Witkowski & Garner 2008). Ground cover of indigenous vegetation also increased after the clearing of IAPs mostly due to an increase in grass cover.

The high levels of observed overall indigenous regrowth indicate that the system shows a relatively high level of resilience to disturbance by IAPs. Resilience is defined as the ability of an ecosystem to return to its former state following a disturbance or stress (Wali 1999). Most riparian species are inherently resilient due to the frequent exposure to disturbance events (e.g. flooding) (Richardson *et al*. 2007). These species typically have dispersal and establishment strategies, such as the ability to colonise bare sediments and aggressive clonal growth that allow for rapid recovery after a disturbance event (Naiman and Décamps 1997).

An important factor that facilitates this resilience in the system is the continuous management and clearing of IAPs by WfW, as the repetitive clearing depletes alien seed banks and maintains IAPs at acceptable levels that are relatively easy to manage. Acceptable levels of IAPs are based upon the KNP management objectives which incorporate the use of "Thresholds of Potential Concerns" (TPCs) concerning the distribution, density and rate of spread of IAPs (Foxcroft and Richardson 2003). Thus the WfW operations ensure that stands of IAPs are present for short periods. This probably improves the chances of natural post-clearing recovery occurring, as the longer an invader has been present, the more dense and widespread its seed bank will become (Witkowski and Wilson 2001), and the greater its contribution to the attrition of native seed banks and its impact on indigenous plant propagule input (Holmes and Cowling 1997a, 1997b).

2.5.3. Spatial variation in alien densities

Densities of IAPs were significantly higher in the first two zones prior to their clearing. This is probably attributable to the greater propagule pressure in these areas. The Sabie River flows through areas of varying land-use including areas of commercial forestry and dense rural habitation even after entering the KNP, as the river acts as a boundary for some distance (Figure 2.1, transects 4-7; Foxcroft *et al*. 2007, Beater *et al*. 2008). This continuous interface with human disturbance allows multiple opportunities for the introduction of alien propagules into the riparian corridor, resulting in recurring germination and establishment of alien plants (Richardson *et al*. 2007, Witkowski and Garner 2008). Interestingly transect 8 situated downstream of Skukuza rest camp had the highest alien density even though it is not on the park boundary. This supports the notion that the gardens of rest camps and staff villages act as major pathways for alien invasions (Foxcroft and Richardson 2003, Foxcroft *et al*. 2008a). Further downstream within the KNP, there are very few, if any, sources of alien propagules besides those originating from alien plants in adjacent reaches, and correspondingly, densities of IAPs are considerably lower.

Transects outside the KNP tended to have lower densities of IAPs than those of 'zone 2' within the park, which is rather surprising as one would expect this area to be subjected to greater human impacts and hence to be more disturbed. The only transect in keeping with this, was transect 1, which was frequently used by both humans and livestock (T. Morris, pers. obs.), and correspondingly supported a relatively high density of IAPs. The other two transects were relatively unutilised, probably due to their inaccessibility and steeper gradients and in contrast supported high densities of indigenous vegetation, and had high alpha diversity and species richness. Thus, the only variable in common between the heavily invaded sites both within and adjacent to the park was the presence of faunal disturbance. Riparian zones within the KNP are heavily utilised by a range of large herbivore species, creating an additional disturbance and perhaps also providing additional vectors for propagule dispersal along the riparian zone by spreading propagules while foraging or by spreading those that attach to their fur (Hood and Naiman 2000).

2.5.4. Role of disturbance in dynamics between indigenous and exotic plant growth

Natural and anthropogenic disturbances such as herbivory, fire, hydrological processes and even disturbances created by IAP mitigation, play a large role in determining patterns of riparian vegetation (Witkowski and O'Connor 1996, Richardson *et al*. 2007). In the KNP where there is an increased use of the riparian zone by mega-herbivores, herbivory may play an important but unexplored disturbance role. Fire on the other hand is generally considered relatively uncommon in the riparian zones of higher order streams in the KNP (Pettit and Naiman 2007a), such as the Sabie River. This is largely due to the high levels of moisture and lower fuel loads in comparison to uplands (Dwire and Kauffman 2003). Additionally, tourist roads are situated along almost the entire length of the southern bank of the Sabie River, where study transects were situated. These roads may be acting as additional "fire-breaks", unintentionally preventing the spread of fires from upland areas into the riparian zone. Thus fire in all likelihood does not play a major role in determining vegetation patterns in the sampled areas. The role of fire however can become more important when it occurs as a result of, or in conjunction with, other disturbances such as floods.

Flooding and water levels play a large role in characterising riparian vegetation (van Coller *et al*. 2000). Opportunities for recruitment and colonisation occur mostly after floods when new patches are exposed either due to the removal of vegetation or through sediment deposition (Richardson *et al*. 2007). In February 2000, severe flooding occurred in the KNP region. The Sabie River flood peaked between 3000 m^3/s and 7000 m^3/s at different points along the river (Heritage *et al*. 2001). When compared to the typical wet season base flow discharges of 15-20 m^3/s, it is clear that this flood was of enormous magnitude. The estimated return interval of the flood was 90-200 years, depending on the position in the catchment (Smithers *et al*. 2001) and was considered a large infrequent disturbance (LID). This LID reduced the extent of tree, shrub, reed and herbaceous patches, and increased the extent of sand, rock and water patches in the Sabie River within the KNP (Parsons *et al*. 2006), thus opening many new areas for colonisation. In this case, it was expected that increased colonisation of exotic species would occur due to the disproportionate propagule input into the system. Large amounts of IAP propagules would have washed down from the highly disturbed and transformed areas of the upper Sabie River catchment (Beater *et al*. 2008), whereas indigenous propagule pressure would be mostly reliant on residual indigenous vegetation, which was relatively sparse after the 2000 flood (Parsons *et al*. 2005). Leroy (2003) confirmed this and showed an increase in alien woody and herbaceous species along the Sabie River directly after the 2000 flood relative to preflood (1997) on the same transects.

Before the 2000 flood, herbaceous IAP species were not a strong focus of IAP management, as they were considered more difficult to control manually and were expected to be reduced naturally over time as competition with native species increased. However, due to the highly dynamic nature and the frequent disturbances experienced along the riparian zone, typical succession seldom occurs, giving IAPs a continual competitive advantage in this largely non-equilibrium system. In this light, the effective clearing of both herbaceous and woody species executed by WfW may play an important role in aiding both the physical and temporal recovery of indigenous vegetation after the LID, by reducing the competitive effects of IAPs.

LIDs can have long-lasting impacts (Foster *et al*. 1998) and can alter important disturbance regimes such as fire. For instance large woody piles deposited after a flood of this magnitude increase fuel loads and therefore the susceptibility of the riparian zone to fire (Dwire and Kauffman 2003). Pettit and Naiman (2007b) illustrated that fires enhanced by these large woody piles had a significant initial effect on Sabie River vegetation and showed how fire could alter pathways of succession after floods by causing the destruction of surviving and regenerating vegetation (Pettit and Naiman 2007b). Thus the dynamics of IAP growth and indigenous vegetation regrowth may still be greatly compounded by the February 2000 floods.

Lastly, clearing operations can also be a source of disturbance whether in the form of physical disturbance, disturbances to ecosystem processes (e.g. erosion) or negative effects on non-target species (Galatowitsch and Richardson 2004, D'Antonio and Meyerson 2002, Parker-Allie *et al*. 2004). However due to the largely dense mono-specific stands of invasion along the Sabie River, as well as the highly specific and largely manual rather than chemical practices utilised by the WfW teams, negative impacts of clearing on native vegetation appeared to be fairly minimal (T. Morris, pers. obs.) compared to upstream in the same catchment (Beater *et al*. 2008).

In 2004, less than 6% of the total plant abundance comprised alien species, which may have indicated the effectiveness of the ongoing clearing programme (Foxcroft *et al.* 2008b), especially in light of the increased levels recorded directly after the large flood disturbance in 2000. However, after just one season of above average rainfall in 2006, alien densities increased up to 97% in isolated areas. Thus, it is important for management to realise that responses of exotic and indigenous vegetation can be complex and highly heterogeneous in both space and time and hence management regimes should correspondingly be fairly flexible. This is of utmost importance when dealing with invasions associated with large disturbances, such as a flood or an escalated rainfall season, so that IAP infestations can be dealt with effectively, timeously and can be maintained at acceptable and manageable levels.

In areas that are relatively undisturbed by human activity, such as reserves or conservation areas, revegetation and recovery of indigenous vegetation after the clearing of IAPs should occur without further management steps being necessary. However the continuous mitigation of reinvasion by IAPs plays a vital role in this and boosts the resilience of the system, making rapid recovery viable. In the short-term, monitoring the response of both alien and indigenous vegetation to clearing of IAPs has provided several worthy insights. However long-term monitoring is crucial to build upon our understanding of the role of seed banks, environmental influences and disturbances, in perpetuating IAP invasions and hence allowing us to advance and optimise management operations accordingly.

CHAPTER 3

Relationships of under- and over-storey vegetation cover to changes in alien plant invasions along the Sabie River, South Africa

3.1 ABSTRACT

Overstorey canopy cover is an important determinant of understorey vegetation growth. Changes in aerial cover associated with alien plant invasions can alter the structure and composition of understorey attributes. These changes can have further consequences by altering important environmental processes such as fire regimes, nutrient cycles, trophic webs, and soil dynamics. Conversely both overstorey and understorey covers can influence the distribution of invasive alien plant (IAP) growth. Repeat follow-up clearings of IAPs by the Working for Water (WfW) programme in the Kruger National Park (KNP) provided ideal circumstances a) to assess the effects of short lived alien stands on understorey ground cover, b) to determine the understorey response to the removal of dense alien stands and c) to investigate the role of aerial and ground vegetation cover in influencing the distribution of IAP growth. Aerial and ground cover were measured in twelve transects spanning the Sabie River in the KNP. Additionally, several environmental variables were measured in each transect. Results showed a significant decrease in alien aerial and ground cover after the annual WfW clearing ($P < 0.05$). Furthermore, IAP invasions seemed to have very little impact on ground cover variables or indigenous ground vegetation diversities. This reinforces the importance of continuous IAP clearing practices so that alien stands remain short lived and the negative consequences often associated with long lived alien invasions are prevented. Canonical correspondence analyses revealed that aerial cover and native species richness played a large role in the distribution patterns of IAP growth, with very few IAP species associated with high levels of native aerial cover. This is of particular importance when considering the occurrence of frequent disturbances in riparian zones that often result in a marked reduction in native canopy cover. Clearing of IAPs after such disturbance events would be important to mitigate the establishment of IAPs that grow opportunistically in newly opened areas.

3.2. INTRODUCTION

Invasive alien plants (IAPs) are becoming an increasingly large problem in South Africa. In the Kruger National Park (KNP), invasive alien species have been declared one of the greatest threat to biodiversity (Foxcroft and Richardson 2003, Foxcroft *et al*. 2007), with riparian zones being the most severely invaded systems. This is largely due to the major river systems originating upstream of the KNP, and flowing through areas of various land-uses often associated with large numbers of IAPs. These include commercial agriculture, forestry and dense human habitation, and provide a continual source of alien propagules into the rivers. The dynamic nature of riparian corridors as well as the efficient ability of water in transporting these alien propagules, facilitates the establishment and spread of IAP invasions (Thebaud and Debussche 1991, Johansson *et al*. 1996, Macdonald and Frame 1998, Tickner *et al*. 2001), creating an ongoing challenge for management of riparian invasions in the KNP (Foxcroft and Richardson 2003, Foxcroft *et al*. 2007, Beater *et al*. 2008).

Invasive alien plants often form dense monospecific stands, replacing indigenous vegetation and impacting upon ecosystem structure and function in various ways (Breytenbach 1986, Witkowski 1991b, Samways *et al*. 1996, Steenkamp and Chown 1996, Gordon 1998, Higgins *et al*. 1999, Enright 2000, Le Maitre *et al*. 2000, French and Major 2001, Leslie and Spotila 2001, Alvarez and Cushman 2002, Dean *et al*. 2002, Herrera and Dudley 2003, Richardson and van Wilgen 2004, Samways 2004). A study in a catchment upstream of the KNP showed that increased alien canopy cover due to IAPs suppressed indigenous herbaceous and grass cover, resulting in an increase in bare soil and litter (Beater *et al*. 2008).

Canopy cover is an important determinant of understorey growth as it regulates the amount of light able to reach the ground (Werner *et al*. 1990, Cowling and Gxaba 1990). Alien plants, especially trees, usually grow faster and taller than indigenous species and often form dense closed canopies that shade out indigenous ground cover (Witkowski 1991b, Standish *et al*. 2001). This results in a modification of the understorey environment by altering the levels of litter, bare soil, and exposed rock present, often resulting in further negative feedbacks (Witkowski 1991a, Richardson *et al*. 1997, Witkowski and Wilson 2001, Standish *et al*. 2001, Iponga *et al*. 2008). For example, changes in the quality, chemical composition, rate of production, or rate of decomposition of litter, can have varying effects on biotic and abiotic factors and ecosystem processes. An increase in litter, often associated with exotic species, especially exotic grass species, can greatly affect fire regimes by increasing the susceptibility, probability, extent and severity of fires in the riparian zone, causing alterations to the structure and composition of riparian species (D'Antonio and Vitousek 1992, Busch 1995, Ellis *et al*. 1998). Changes in litter can also affect nutrient cycling by altering soil pH and levels of C, N and P, among others. This can ultimately affect net primary productivity and plant growth rates and often favours fast growing alien species (Pastor *et al*. 1984, Doescher *et al*. 1987, Witkowski and Mitchell 1987, Witkowski 1991a, Hooper and Vitousek 1998, Hector *et al*. 1999, Holmes and Richardson 1999, Yelenik *et al*. 2004). Changes in litter and plant cover can also affect animal distribution and abundance, by influencing habitat selection and impacting critical resources for survival and reproduction. For example, changes in litter properties are likely to indirectly affect the performance of aquatic decomposers such as fungi and detritivorous invertebrates by modifying both quality and quantity of the detritus pool, potentially causing further impacts on trophic cascades and food webs (Cummins *et al*. 1989, Dangles *et al*. 2002). Lastly, ground cover, whether in the form of live plant matter or litter, is one of the primary factors controlling soil erosion (Davenport *et al*.1998). Plant cover not only binds the soil, but in conjunction with the litter layer, increases infiltration rates and thus slows surface runoff, reducing soil erosion (Wood *et al*. 1987, Davenport *et al*. 1998). Therefore decreases in the amount of ground cover associated with alien invasions often leads to increased soil erosion (Pieper 1990, Davenport *et al*. 1998, Holmes *et al*. 2000). Thus, alterations of ground states through alien invasions can have varying and extensive consequences by altering both the physical and chemical understorey environment (Facelli and Picket 1991, Fogarty and Facelli 1999, Ervin and Wetzel 2002, Wearn and Morgan 2004).

In light of these and other known negative impacts of IAPs, effective management of invasive species has become a priority worldwide (Byers *et al*. 2002). In 1995, the South African government launched the Working for Water (WfW) initiative with the aim of securing scarce water resources through large-scale manual IAP clearing programmes across the country, while simultaneously addressing unemployment and poverty alleviation. The WfW programme was first launched in the KNP in 1997 and has since become a major component of alien plant management, executing annual clearing operations in selected areas, mostly along major riparian corridors. However, I have shown in chapter 2 that IAP invasions are highly dynamic in space and time and are strongly influenced by disturbance events and suggest that perhaps management should be more dynamic and reactive. This would mean that a greater understanding of factors influencing the distribution of IAPs would be necessary.

Many studies have investigated factors that either facilitate or impede IAP invasions (e.g. Kennedy *et al*. 2002, Stohlgren *et al*. 2003). Foxcroft *et al*. (2008b) showed that certain patches in the river landscape within the KNP are more prone to IAPs than others, and furthermore, that individual alien species are more clearly associated with certain patch types. Their study assessed various patch types within the macro-channel floor. The macro-channel bank, which is less influenced by hydrological and geomorphological disturbance, was assessed as its own patch type. The macro-channel bank forms an interface between aquatic and terrestrial ecosystems (Richardson *et al*. 2007) and hence other more terrestrial factors, influencing the germination and establishment of IAPs, must come into play.

This study aimed a) to determine if alteration of aerial canopy cover due to dense stands of IAPs affected ground cover attributes and ground cover vegetation diversity; b) to determine the understorey response to the removal of dense alien invasions; and c) to assess the role of environmental variables, including understorey and overstorey cover, in influencing the distribution of IAPs on macro-channel banks.

3.3. MATERIAL AND METHODS

3.3.1. Study site

The study took place along the Sabie River, within and adjacent to the KNP. The Sabie River is a 210 km perennial river originating in the Mpumalanga Highlands, flowing eastwards through the KNP for 108 km before entering Mozambique where it confluences with the Incomati River (Figure 3.1).

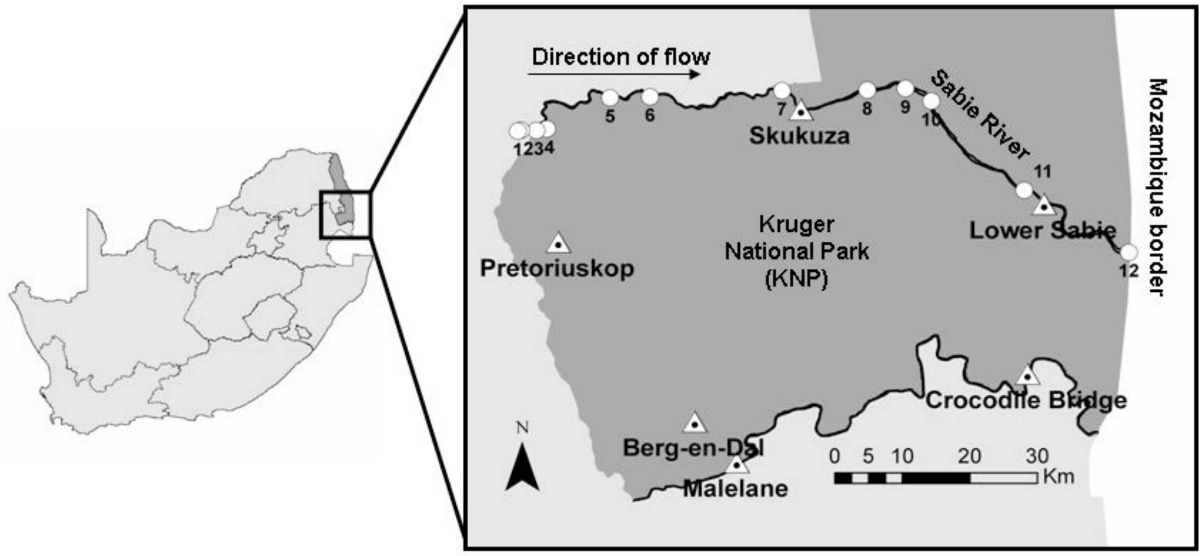


Figure 3.1. Map of the Southern section of the Kruger National Park. Transects span the Sabie River and were divided into three zones according to situation and propagule pressure. Zone 1: transects 1-3, outside the KNP; Zone 2: transects 4-8, in close proximity to the boundary (transect 8 is situated after Skukuza rest camp which is a high propagule source) and Zone 3: transects 9-12, within the confines of the park extending to the Mozambique border.

The KNP is located in the savanna biome, experiencing mild dry winters and hot rainy summers (Venter *et al*. 2003), with an annual average rainfall of 450-600mm (van Niekerk and Heritage 1993). However, the rainfall received during the study period, recorded at the Skukuza weather station in 2005/2006, was 70% greater than the 76 year long-term annual average and the next season in 2006/2007, 35% below this average (Figure 3.2).

This high rainfall received in 2005/06 resulted in an enhanced IAP growth along the Sabie River, yielding alien densities much greater than those reported on the same River in 2004 (Foxcroft *et al*. 2008b, chapter 2). Vegetation was not only greatly influenced by the abnormally high rainfall in the beginning of the study period, but annual clearing efforts of riparian IAPs by the WfW programme also play a large role in shaping vegetation patterns. Annual clearances of IAPs have been executed along the Sabie River in the KNP for between 4-7 years.

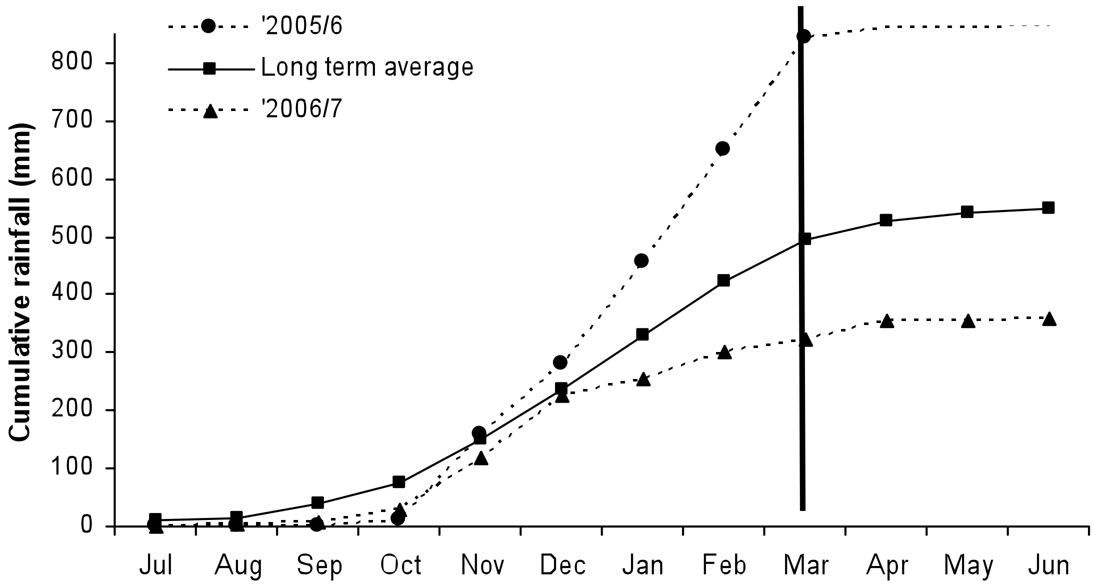


Figure 3.2. Cumulative rainfall (mm) at Skukuza weather station from the beginning of the "annual climatic year" (July). The dotted lines represent the 2005/6 and 2006/7 rainfall seasons, while the solid line represents the long-term average over 76 years. Vegetation sampling occurred in March, indicated by the bold solid bar.

Ground cover species are dynamic and often short lived. Thus, investigating the change in ground cover over time from a state of high invasion intensity after the elevated rainfall to that of a low intensity after the annual clearing by WfW, allowed for the opportunity to assess if short lived IAP invasions have any marked effect on ground cover. If an effect was present it would also be possible to determine the initial response of ground cover to the removal of these IAPs.

Woody vegetation (trees and shrubs) forms the dominant native plant canopy of the macro-channel banks along the Sabie River. This includes species such as *Spirostachys africana*, *Diospyros mespiliformis*, *Dichrostachys cinerea*, *Euclea natalensis* and *Grewia bicolor*, among others (van Coller *et al.* 1997). Understorey vegetation is composed of short lived annual, as well as longer lived perennial species, many of which are clonal and have rhizomes and stolons that effectively cover the ground surface. Many fast growing weedy species, both indigenous and alien, are often present in the understorey layer.

3.3.2. Vegetation sampling

Sampling was carried out in two periods: March/April 2006 and March 2007. Twelve belt transects were sampled along the Sabie River inside and adjacent to the KNP. For ease of interpretation of results these transects were split into three zones according to their location and hence corresponding propagule pressures. Zone 1: transects 1-3 – situated on the Sabie River outside the KNP; Zone 2: transects 4-8 – situated within the park but in close proximity to a boundary or main camp as is the case with transect 8 (transect 8 is in close proximity to the large Skukuza tourist camp and staff village, which poses a high threat for IAP invasions due to the pathway of spread of exotic species from staff and camp gardens (Foxcroft and Richardson 2003, Foxcroft *et al.* 2008a)); Zone 3: transects 9-12 – situated along the Sabie River within the confines of the park, extending towards the Mozambique border.

Aerial cover of indigenous and alien overstorey was measured using the line intercept method. Alien overstorey cover was used as a surrogate for alien invasion intensity. Three lines were positioned perpendicular to the river at the boundaries and centre line of each determined transect. The lengths of these lines varied between 20-90m due to the heterogenous nature of the channel width and hence riparian zone. Overstorey aerial cover was measured in four different height classes: 0-1 m (herbaceous or small woody vegetation), 1-2 m (shrubs and saplings), 2-5 m (small trees) and >5 m (large trees). Along each line, the length which fell under each individual plant canopy in the four height classes was recorded. The relative overstorey aerial cover of each species in each of the different height classes was determined before and after the annual clearing by WfW and the invasive status of each species was classified according to Regulation 15 of the Conservation of Agricultural Resources Act, 1983 (Act No. 43 of 1983) as described in Henderson (2001).

Ground cover was visually estimated in 1x1 m quadrats placed every 5 m along the outside lengths of the belt transect, which also varied in length. Percentages of native and alien vegetation, litter cover, rock and exposed soil were estimated. However, rock cover was omitted from all analyses as it was almost nonexistent. Each plant species was identified and categorized according to growth form as either tree, shrub, herbaceous or graminoid species.

Each of the twelve transects were also subsampled in 10x10 m plots in which alien species were identified and the number of stems of alien plants with a basal stem diameter greater than 1 cm were counted.

Environmental variables were determined for each 10x10 m plot as described in Table 3.1. Distance along the river from its entry point into the KNP; closest distance to boundary of the KNP and closest distance to a major alien propagule source, were all highly correlated ($r > 0.98$) and were thus represented by one variable 'Boundary distance'. 'Boundary distance' was considered a covariable as distance along the river from entry into the KNP has already been shown to have a marked effect on the invasion intensity of IAPs (chapter 2). Distance to the major river channel was recorded per 10x10 m plot, with plots adjacent to the river being labelled as 0 and increasing with each plot away from the river channel.

Table 3.1. Environmental variables used in canonical correspondence analyses.

Environmental variable	Code used in ordination
Total native aerial cover	Total N. aerial cover
>5 m native aerial cover	>5m N. aerial cover
2-5 m native aerial cover	2-5m N. aerial cover
1-2 m native aerial cover	1-2m N. aerial cover
0-1 m native aerial cover	0-1m N. aerial cover
Native ground vegetation cover	N. ground veg.
Alien ground vegetation cover	A. ground veg.
Soil cover	Soil
Litter cover	Litter
Total native species richness	N. species richness
Distance from major channel	Channel
*Distance along the river from its entry point into the KNP	
*Closest distance to boundary of the KNP	Boundary distance
*Closest distance to a major alien propagule source	

***Variables highly correlated ($r > 0.98$) and therefore combined and used as a covariable.**

3.3.3. Data analysis

Area effect

Transects situated along the Sabie River extended from the top to the bottom of the macro-channel bank (i.e. before the start of the macro-channel floor). Due to the dynamic nature of the river, these transect lengths varied greatly across the 12 transects. The average transect length was 50±20 m, with lengths ranging from 30-90 m. As ground cover was sampled every 5m along the transect boundaries, longer transects would obviously have had a greater number of samples. Observed species richness (S), Simpson's diversity index (D) and its reciprocal (1/D), and Simpson's evenness index ($E_{1/D}$) of ground cover vegetation were derived using Primer^{TM} v5 (Clarke and Gorley 2001) and plotted against area sampled per transect to determine if any area effects occurred between transects of differing length and thus differing areas sampled.

Aerial cover

Changes in absolute native and alien overstorey aerial cover per height class were compared before and after clearing by WfW and were tested for significant change over time using Wilcoxon matched pairs tests in Statistica 6.1. Relative native and alien percentages of total vegetation aerial cover were assessed per site for the total, 0-1 m and 1-2m height classes. The 2-5 m and >5m height classes were omitted from the results as almost no alien cover existed in these height classes.

Ground cover

Total ground covers were compared before and after clearing of IAPs by WfW and tested for significant differences over time using Wilcoxon matched pairs tests. Cover variables were also assessed per zone. Native ground vegetation cover was further assessed in terms of growth forms per zone before and after clearing. Percentages of each ground cover variable were plotted against total aerial cover as well as alien aerial cover to assess if any relationships were present.

Native ground cover diversity indices were determined per zone and plotted against alien invasion intensity (alien aerial cover) to determine whether any relationships were prevalent. The relationship between alien aerial cover and herbaceous and grass diversities was also plotted to determine if distinct relationships occurred in the different growth forms (R^2 values from linear regression analyses are presented). Species abundances were square root transformed and Bray-Curtis similarities of total, native and alien ground vegetation were derived per site to assess species similarities per site before and after clearing of IAPs by WfW.

Environmental predictors of alien plant distribution

Ordinations were performed in CANOCO™ (ter Braak and Smilauer 2003) to evaluate the relationships and importance of environmental variables in influencing IAP distribution on the macro-channel bank of the Sabie River. The number of woody invasive alien plants (BSD > 1 cm) and the percentage aerial cover of herbaceous alien vegetation were derived for each 10m plot. Thus two species data sets and a set of environmental data were derived for each 10m plot. Each data set was considered unimodal, which was confirmed by the maximum gradient length exceeding 4 standard deviations in respective detrended correspondence analyses. Thus, canonical correspondence analyses were performed on the square root transformed data of both the woody and herbaceous species to determine relationships between species and environmental variables. The statistical significance of patterns was determined using a Monte Carlo permutation test.

3.4. RESULTS

3.4.1. Area effect

Ground cover plant species richness tended to show a positive relationship with area sampled ($P < 0.05$) (Figure 3.3a). No relationship was evident, however, between area sampled and vegetation species diversity and evenness (Figure 3.3b, c). The positive correlation between species richness and area does not follow trends seen in larger herbaceous and woody vegetation (basal stem diameter > 1 cm) in the same transects (chapter 2), which may perhaps be due to the comparatively small areas sampled for ground cover. However, to avoid possible area effects, results were not compared between transects and zones but rather only within the same transects and zones over time.

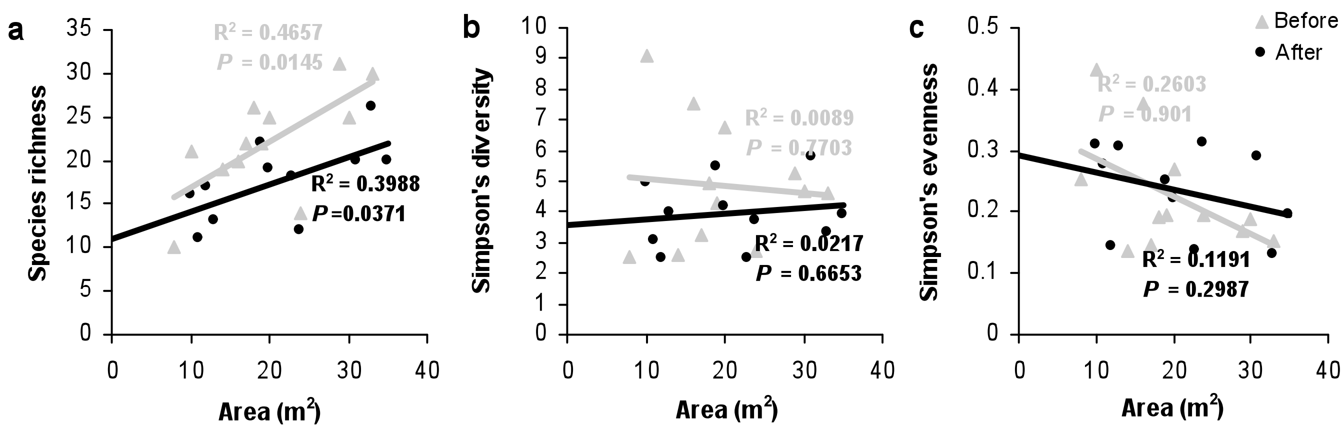


Figure 3.3. Species richness (a), Simpson's diversity (b), and Simpson's evenness (c) of all ground vegetation as a function of ground area sampled before (Mar 2006) and after (Mar 2007) clearing of invasive alien plants.

3.4.2. Aerial cover

Alien aerial cover was predominantly composed of woody plants in the 0-1 m and 1-2 m height classes and was significantly reduced in those classes and in total ($P < 0.05$) after the clearing of IAPs by WfW (Figure 3.4a). Indigenous aerial cover was evenly represented across all height classes and very little difference in the average indigenous aerial cover was evident over time ($P > 0.05$) (Figure 3.4b).

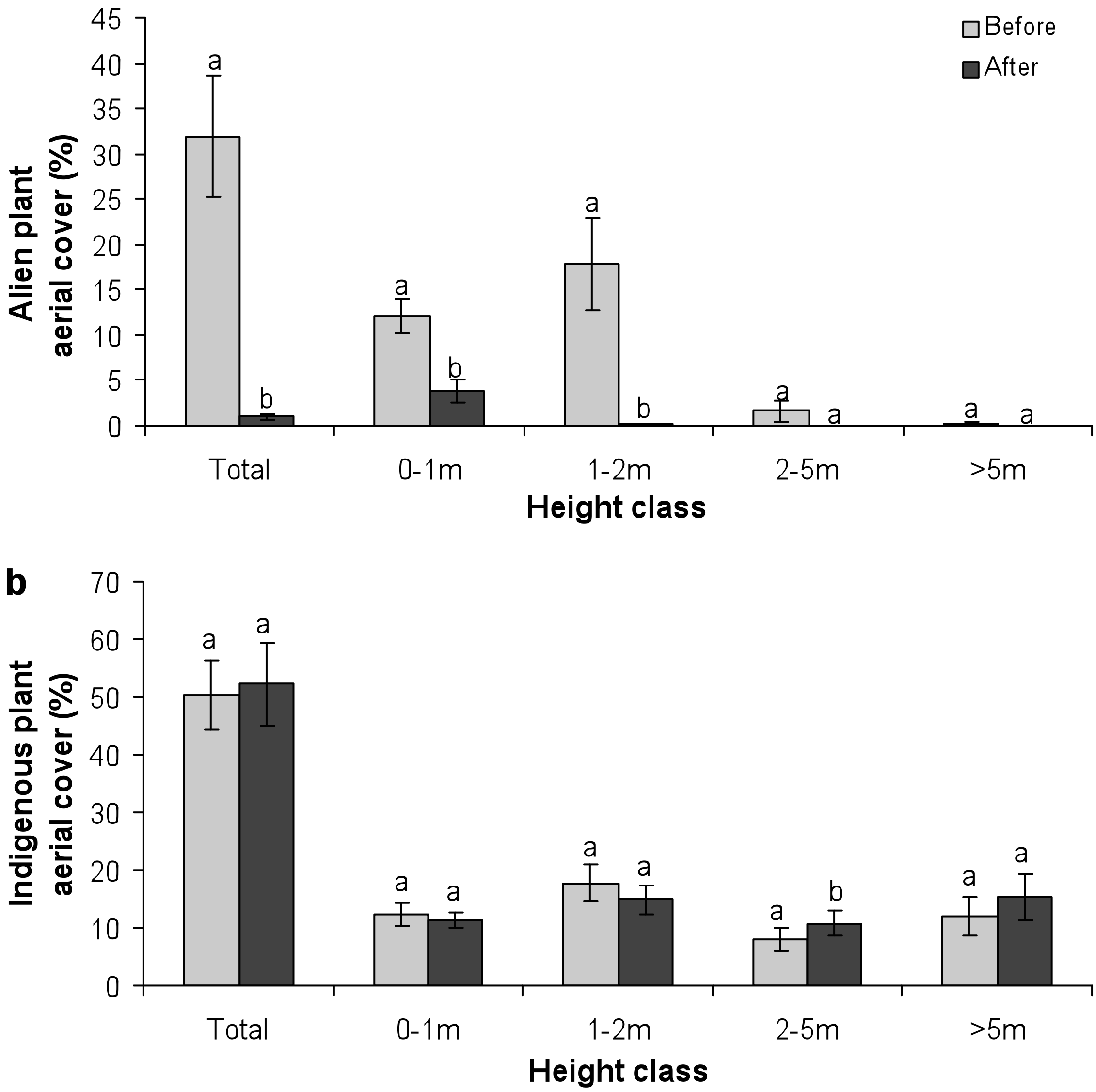


Figure 3.4. Percentage (a) alien and (b) indigenous plant aerial cover (mean ± SE) across all transects per height class, before and after the annual clearance by Working for Water. Columns with different superscript letters within the same class are significantly different from each other (Wilcoxon's matched pairs tests, d.f. = 11, $P < 0.05$).

Relative alien aerial cover was reduced in total (Figure 3.5a, b) from an average of 37±7% to 8±3%. In the 0-1 m height class the average relative alien aerial cover of 48±5% was reduced to 23±6% (Figure 3.5c, d) and in the 1-2m height class the average relative alien aerial cover of 44±10% was reduced to 2±1% (Figure 3.5e, f). After clearing, a low level of alien aerial cover was still present in the 0-1m height class (Figure 3.5c, d).

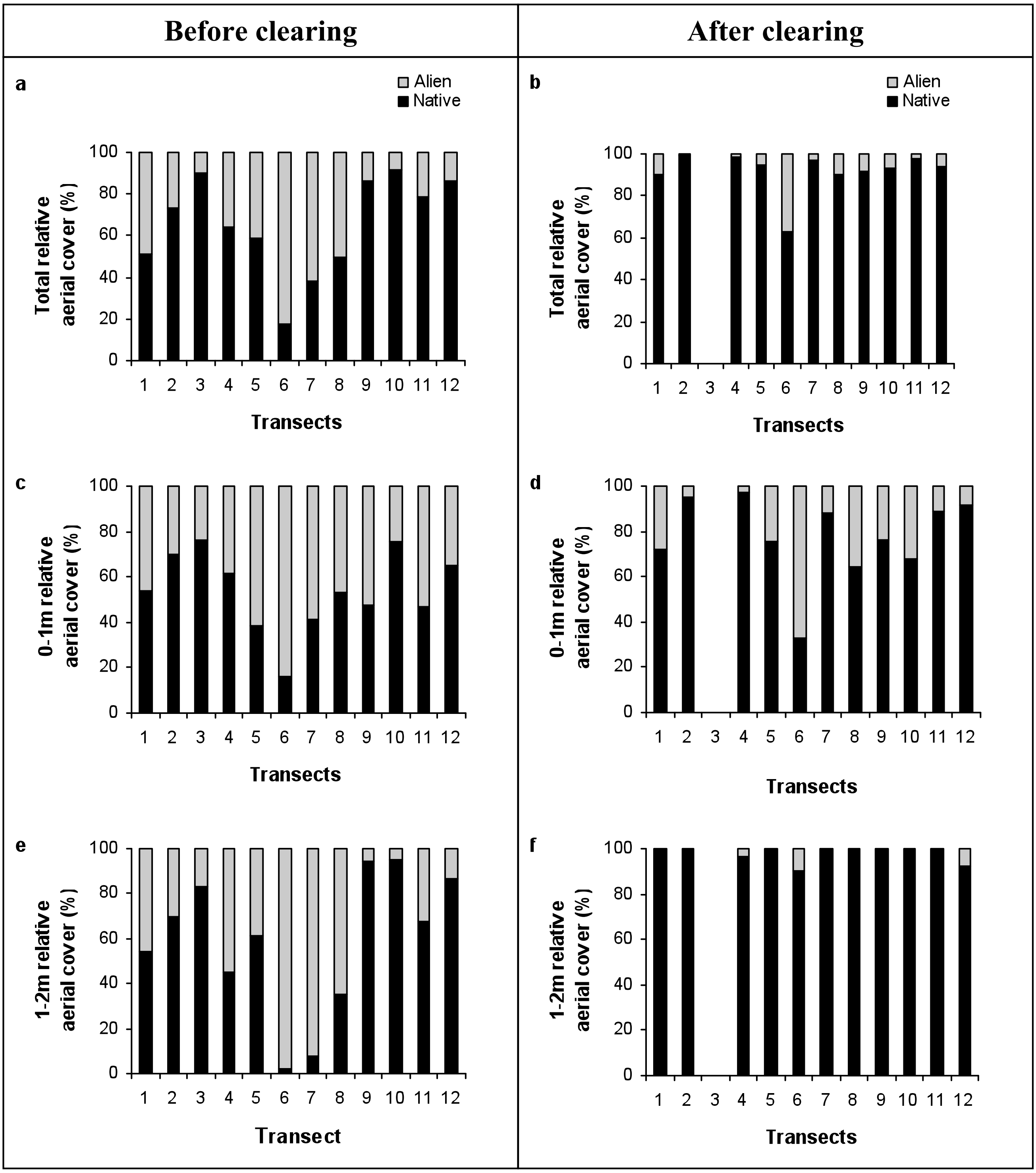


Figure 3.5. Relative alien and native aerial cover of total vegetation (a, b) as well as vegetation in the 0-1 m (c, d) and 1-2 m (e, f) height classes per transect, before and after clearing of invasive alien plants by Working for Water. Transect 3 was cleared for agriculture prior to "after" clearing sampling and is thus missing in "after" data sets.

3.4.3. Ground cover

In total, alien ground cover comprised a small proportion of the total ground cover (10±1%) and was significantly lower after the annual clearing by WfW (2±0.5%) (Z_{11} = 2.93; $P = 0.003$) (Figure 3.6). There was little change in the percentage of native vegetation (Z_{11}= 1.24, $P = 0.213$) and bare soil cover (Z_{11} = 1.33; $P = 0.182$) and a small increase in litter cover over time (Z_{11} = 2.76; $P = 0.006$) (Figure 3.6). However, when the data were broken down into the three zones that were differentially invaded, different patterns were observed. Alien vegetation cover decreased in all zones after clearing. In zone 1, representing transects outside the KNP, there was an increase in native ground cover, with a corresponding decrease in the amount of exposed soil. In Zone 2 there was no change in the proportions of native vegetation, litter and soil cover over time. Zone 3 showed a marked decrease in native vegetation cover and a corresponding increase in litter cover and exposed soil (Figure 3.7). The observed changes in native ground cover in each zone were predominantly due to fluctuations in native grass cover (Figure 3.8).

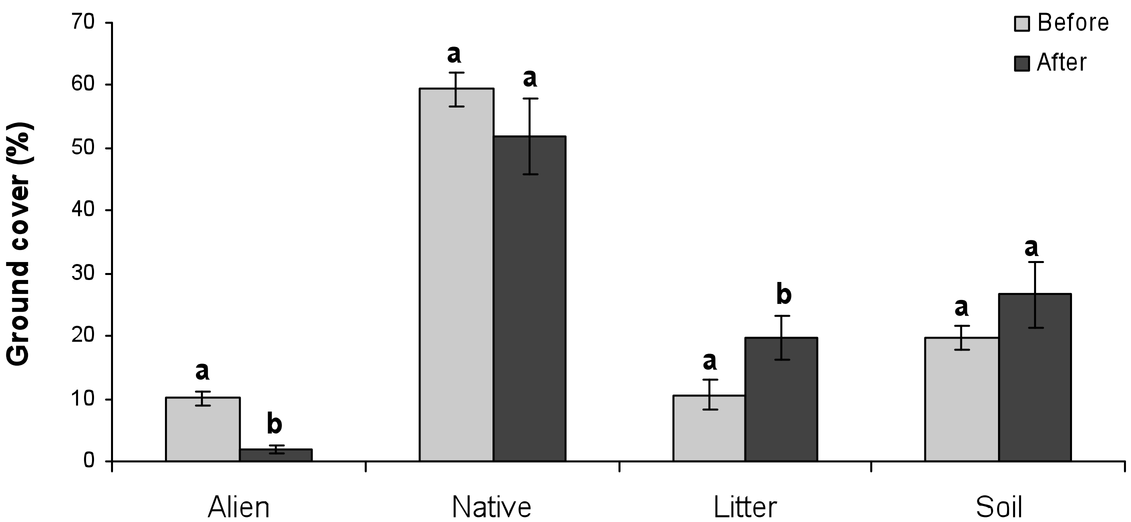


Figure 3.6. Percent ground cover (mean ± SE) of alien vegetation, native vegetation, litter and bare soil, before and after clearing by Working for Water. Columns with different superscript letters within the same class are significantly different from each other (Wilcoxon's matched pairs tests, d.f. = 11, $P < 0.05$).

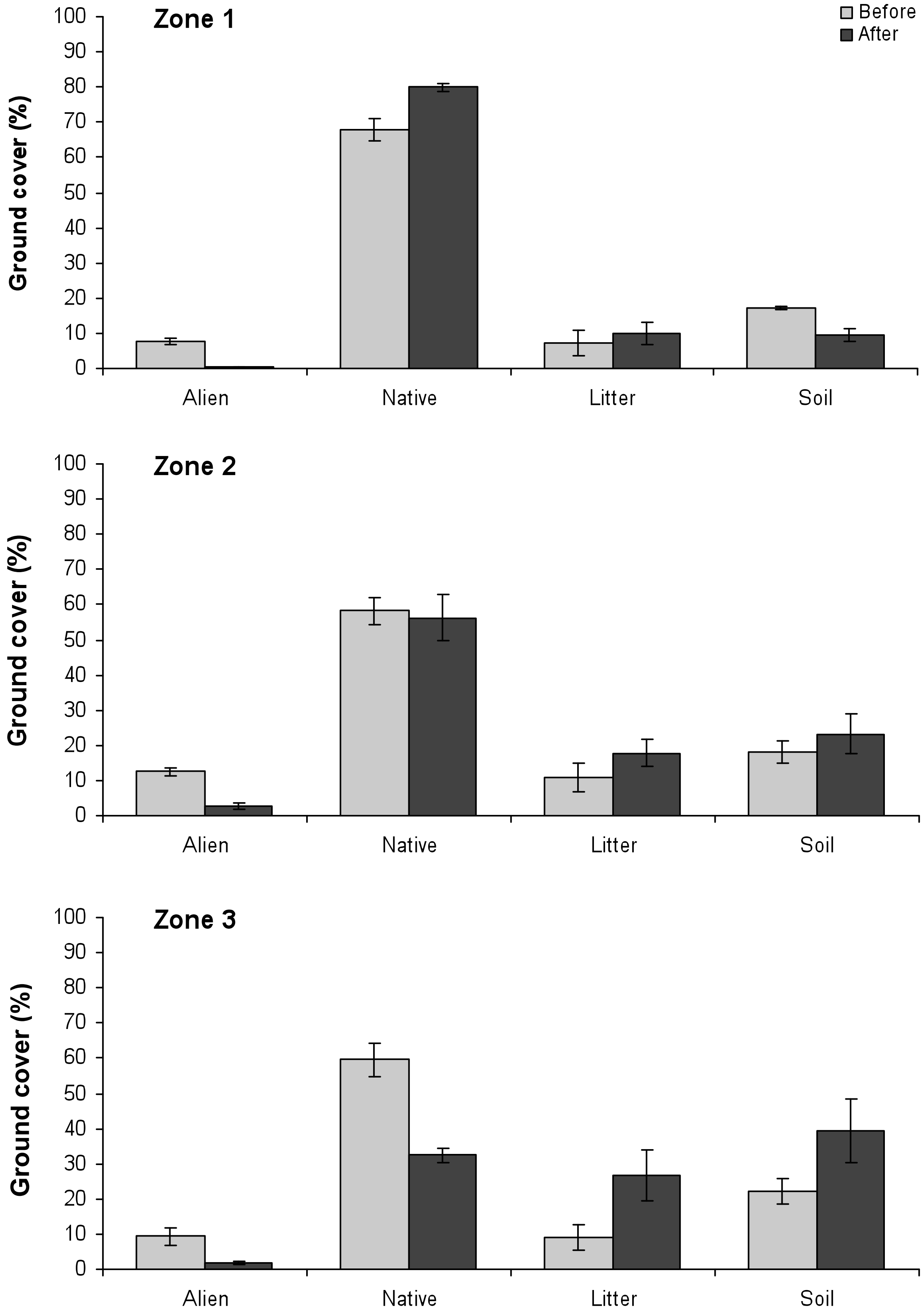


Figure 3.7. Percentage ground cover of alien vegetation, native vegetation, litter and bare soil per zone (mean ± SE), before and after clearing by Working for Water.

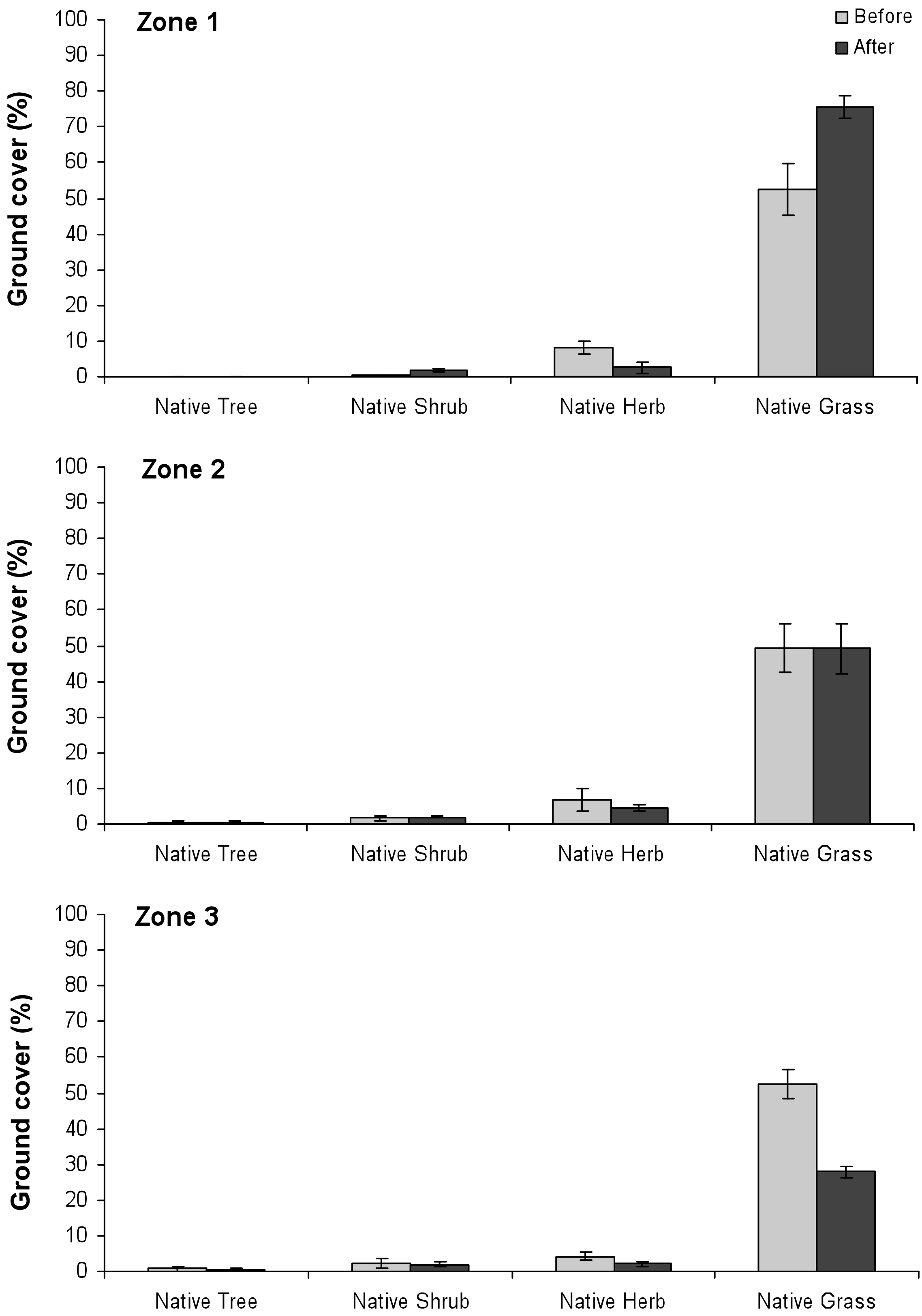


Figure 3.8. Percentage native vegetation cover divided into tree, shrub, herb and grass growth forms per zone (mean ± SE), before and after clearing by Working for Water.

3.4.4. Effect of aerial cover on ground cover

There were no effects of total (alien and indigenous) aerial cover on any of the measured ground covers ($P > 0.05$) (Figure 3.9a-d). Additionally, when assessing the effects of alien aerial cover, there were also no effects on the ground cover measures ($P > 0.05$), except for alien ground cover, which increased as alien aerial cover increased ($P < 0.05$) (Figure 3.9e-h). The positive relationship between alien aerial and ground cover was not due to seedlings of the same species but rather due to different alien species with different growth forms (i.e. woody or shrubby aerial vs. herbaceous ground species. This would be expected as the sites that are more invaded, and thus have a higher alien aerial cover, more than likely face a higher level of alien propagule input from outside the KNP and would have correspondingly high herbaceous alien propagules. Furthermore, seedlings from overstorey aliens would be present in the herbaceous understorey layer.

3.4.5. Ground cover vegetation diversity

Species richness declined in zone 1 and 3 but remained unchanged in zone 2 (Figure 3.10a). In total there was a significant decrease in ground species richness after clearing by WfW ($Z_{11} = 2.45$, $P = 0.014$). Although not significant, there were consistent trends for alpha diversity to decrease in all three zones and in total ($Z_{11} = 1.51$, $P = 0.131$) (Figure 3.10b). Simpson's evenness increased slightly only in zone 3 but in total remained unchanged ($Z_{11} = 0.27$, $P = 0.79$) (Figure 3.10 c).

There was no relationship between alien aerial cover and ground cover vegetation diversity measures, either before or after the clearing by WfW (Figure 3.10 d-f). There were also no significant relationships between alien aerial cover and grass and herbaceous diversity measures (Table 3.2).

Bray-Curtis similarities showed that individual sites had a marked shift in species compositions between the two sampling seasons as similarity values were low for native (55.1 ± 3.3), alien (23.4 ± 4.5) and total ground species (49.8 ± 2.5) (Table 3.3).

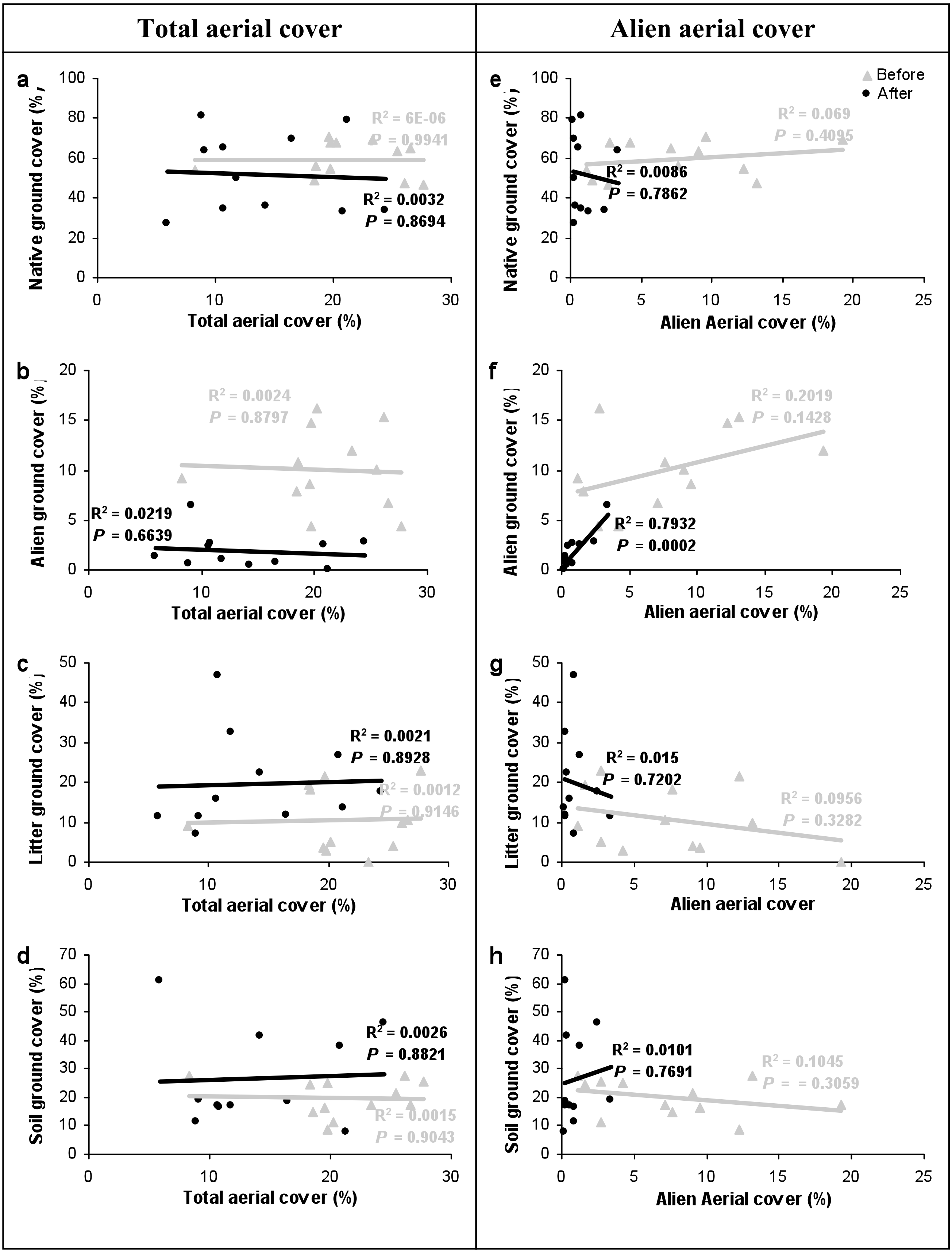


Figure 3.9. Relationship between total (a-d) and alien (e-h) aerial cover with native vegetation ground cover, alien vegetation ground cover, litter cover and bare soil before (Mar 2006) and after (Mar 2007) clearing of invasive alien plants by Working for Water.

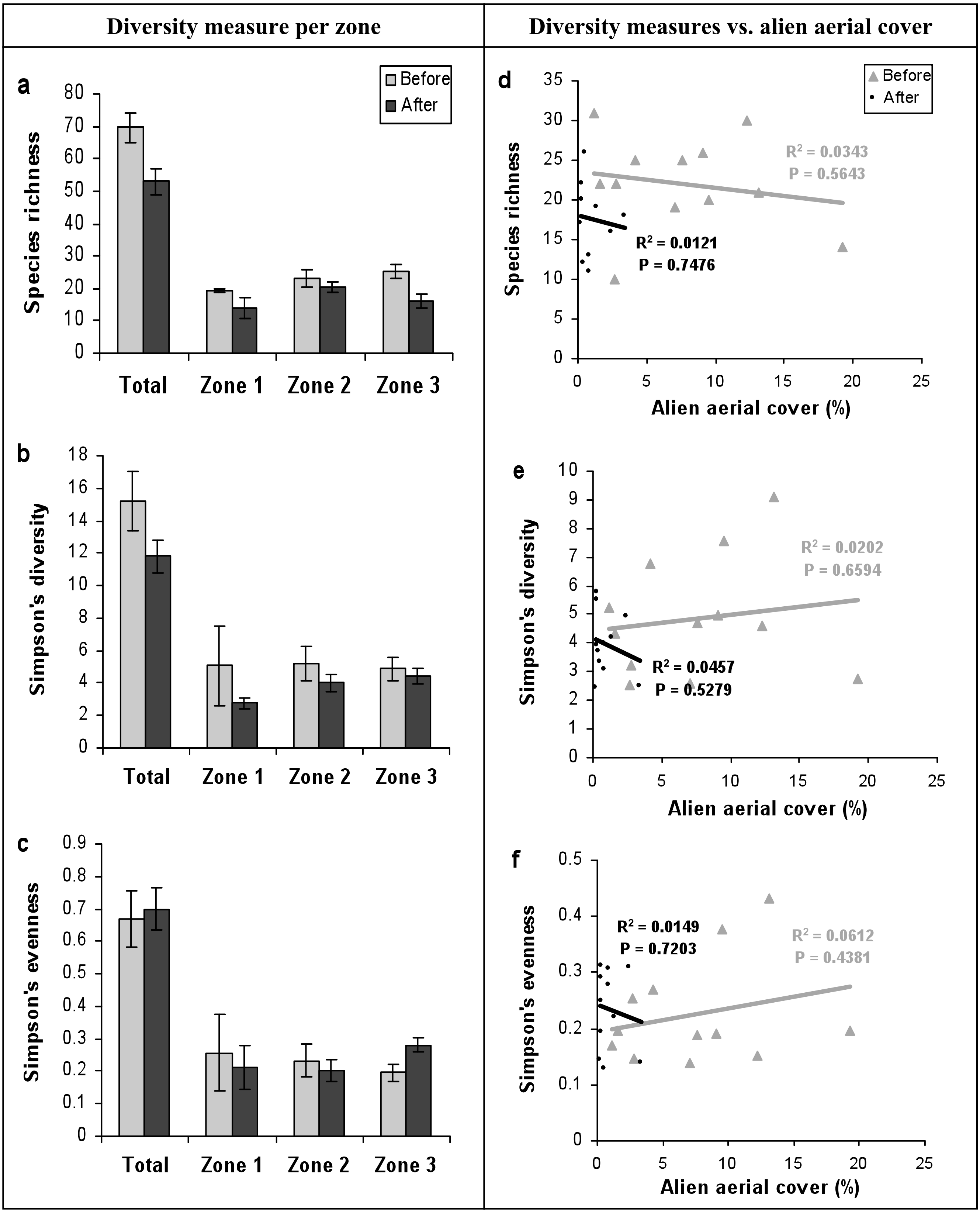


Figure 3.10. Species richness, Simpson's diversity and Simpson's evenness per zone and in total for all ground cover vegetation, before and after clearing by Working for Water (a-c); and as a function of alien aerial cover before and after clearing by Working for Water (d-f).

Table 3.2. R^2 values of the linear regressions of grass and herbaceous species richness, diversity and evenness before and after clearing in relation to alien vegetation aerial cover. None of the R^2 values were significant (n = 11, *P* > 0.05).

	Grass species		Herb species	
	R^2		R^2	
	Before	**After**	**Before**	**After**
Species richness	0.1215	0.3826	0.0469	0.3217
Simpson's alpha	0.0017	0.3083	0.0564	0.2195
Simpson's evenness	0.2563	0.0495	0.1370	0.0005

Table 3.3. Bray-Curtis similarity values of total, native and alien ground cover species compositions at each site before and after clearing by Working for Water.

	Bray-Curtis similarity		
Site	**All species**	**Native species**	**Alien species**
1	54.2	58.9	22.4
2	41.3	45.8	0
4	51.7	59.1	10.8
5	58.2	65.3	28.3
6	57.6	63.5	44.4
7	54.8	63.7	23.2
8	41.8	44.7	33.6
9	33.0	32.1	36.1
10	46.5	48.7	37.8
11	57.7	65.3	0
12	51.4	59.0	20.7
Average	49.8 ± 2.5	55.1 ± 3.3	23.4 ± 4.5

3.4.6. Environmental predictors of alien plant distribution

Woody species

Canonical correspondence analysis of the woody alien vegetation and environmental factors revealed that total aerial cover and native species richness at the 10x10m plot scale were important factors influencing invasion patterns (Figure 3.11). The first three CCA axes accounted for 76.2% of the total variance explained by the species correspondence analysis. The first environmental axis was correlated with 'Total native aerial cover' (r = 0.88) and 'Native species richness' (r = 0.63) and accounted for 42% of the variance. The second environmental axis was positively related to 'overstorey native aerial cover' composed of plants >5 m in height (r = 0.69) and negatively related with native ground cover (r = -0.32) and accounted for 21.6% of the variance. The third environmental axis described 12.6% of the variance and was negatively correlated with understorey cover (plants in 0-1 m height class) (r = -0.49) and soil cover (r = -0.30). Lastly the fourth axis was negatively correlated with midstorey aerial cover (plants in the 2-5m height class) (r = -0.61) and native species richness (r = -0.37) and accounted for 7.3% of the variance. However the Monte Carlo significance test revealed that all canonical axes were not significant (P = 0.55).

The analyses showed that most woody alien species were not associated with areas of high total aerial cover, especially tall overstorey aerial cover composed of plants >5 m in height or in those areas with a high native plant species richness. However certain species such as *Lantana camara* (4), *Senna occidentalis* (8) and *Solanum seaforthianum* seem to be able to tolerate more shaded areas caused by relatively high over- and mid-storey aerial cover. Most alien species were found closer to the active channel although *Xanthium strumarium* (13), an alien species that was found in extremely high densities in several transects in 2005, seemed to have no preference and was widely spread across the bank.

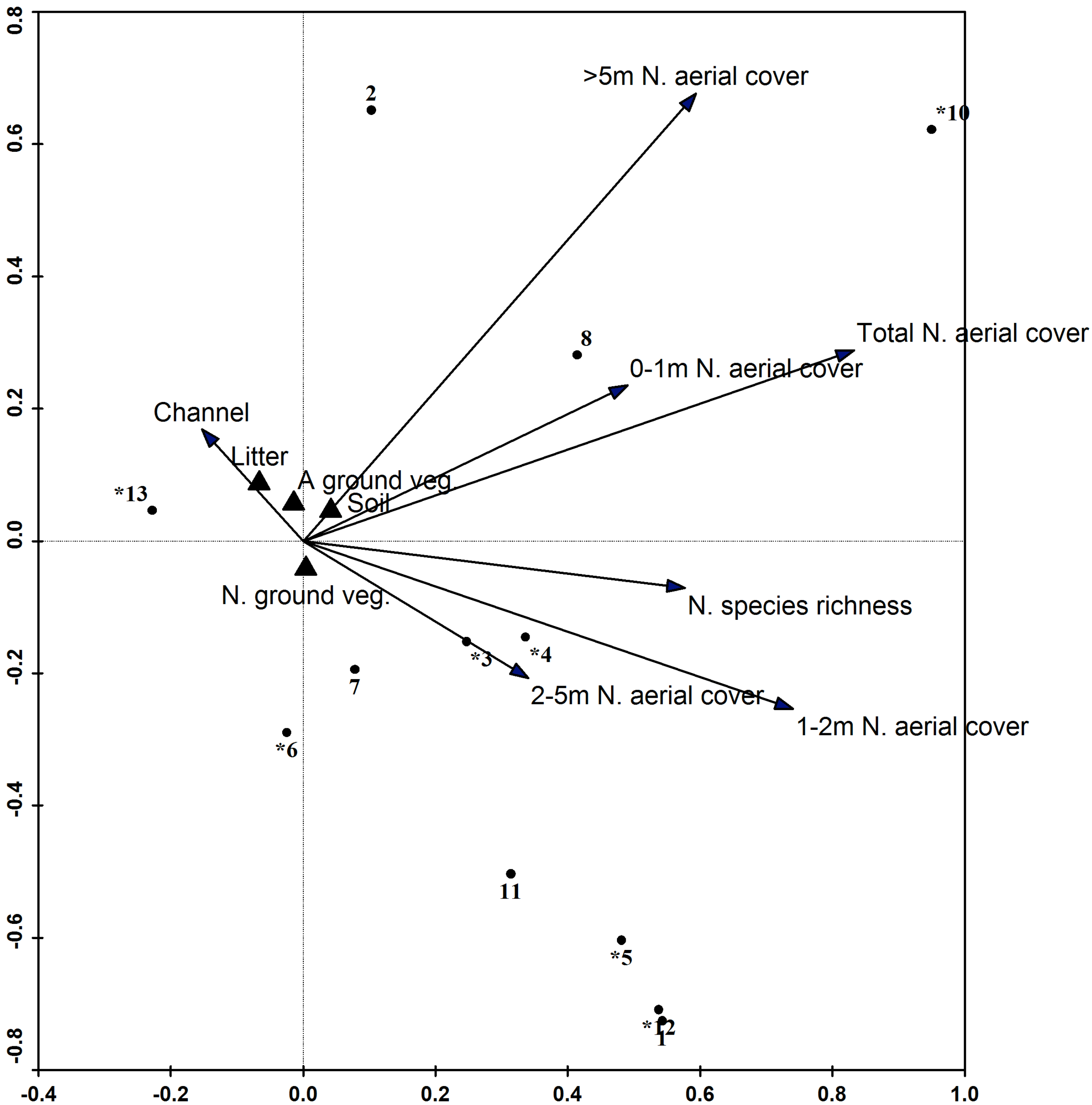


Figure 3.11. Canonical correspondence analysis (CCA) biplot for woody alien plant species (n=13) along the Sabie River. Environmental variables are indicated by biplot arrows and triangles (nominal variables). Asterisks (*) mark species that are declared weeds according to regulation 15 of the Conservation of Agricultural Resources Act, 1983 (Act No. 43 of 1983) as described in Henderson (2001). N is an abbreviation for native. Species are numbered as: (1) *Amaranthus spinosus*, (2) *Corchorus trilocularis*, (3) *Datura stramonium*, (4) *Lantana camara*, (5) *Melia azedarach*, (6) *Mimosa pigra*, (7) *Senna obtusifolia*, (8) *Senna occidentalis*, (9) *Sesbania puniceae*, (10) *Solanum seaforthianum* var. *disjunctum*, (11) *Stachytarpetta mutabilis*, (12) *Tithonia diversifolia*, (13) *Xanthium strumarium*.

Herbaceous species

The CCA for herbaceous species and the environmental variables revealed that total native aerial cover, especially midstorey cover (2-5 m), native species richness, litter cover and distance from channel are all important factors influencing the distribution of herbaceous alien species (Figure 3.12). The first three CCA axes explained 65.1% of the total variance shown by the species correspondence analysis. The first environmental axis was related to intermediate native aerial cover comprising plants in the 2-5 m height class (r = 0.79) as well as litter cover (r = 0.62) and accounts for 25.2% of variance. The second axes accounted for 20.9% of the variance and is positively correlated with soil cover (r = 0.56) and negatively correlated with ground cover vegetation whether alien (r = -0.52) or native (r = -0.36). The third axis correlated with total aerial cover (r = 0.75), specifically overstorey aerial cover (plants >5 m in height class) (r = 0.84) and contributed 19% of the variance. The fourth axis contributing 9.9% of the variance was negatively correlated with intermediate aerial cover (plants in 1-2 m height class) (r = -0.59) and positively correlated with native species richness (r = 0.41). The Monte Carlo significance test revealed that all canonical axes were not significant (P = 0.11).

In contrast to the woody vegetation results, the herbaceous vegetation was not influenced as much by overstorey aerial cover (>5m) but rather more influenced by midstorey cover (2-5 m) with only species such as *Achyranthes aspera* (15) and *Cardiospermum halicacabum* (19) tolerating high levels of shading.

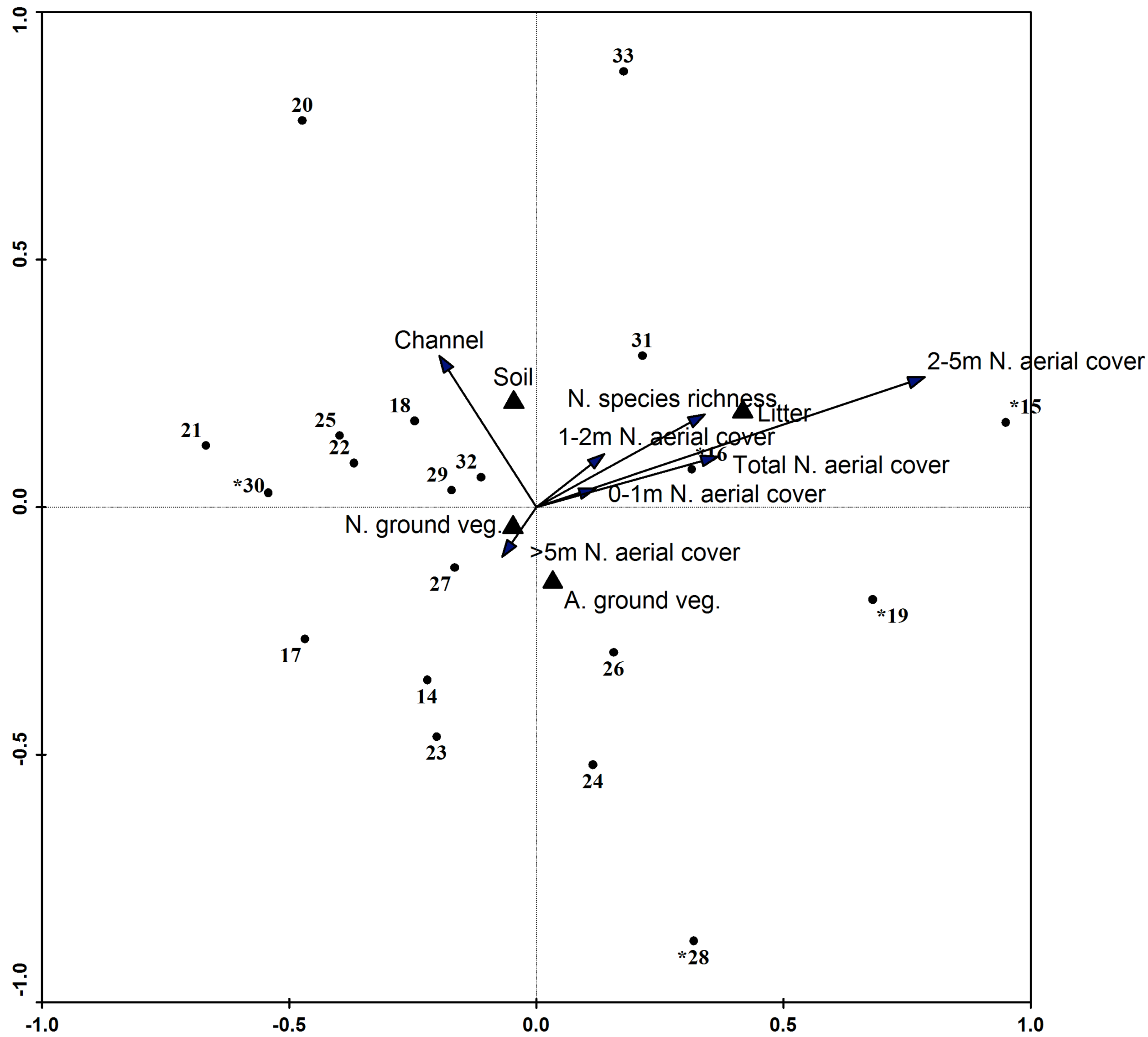


Figure 3.12. Canonical correspondence analysis (CCA) biplot for herbaceous alien plant species (n = 21) along the Sabie River. Environmental variables are indicated by biplot arrows and triangles (nominal variables). Asterisks (*) mark species that are declared weeds according to regulation 15 of the Conservation of Agricultural Resources Act, 1983 (Act No. 43 of 1983) as described in Henderson (2001). N is an abbreviation for native. Species are numbered as follows: (14) *Acanthospermum hispidum*, (15) *Achyranthes aspera* var. *aspera*, (16) *Ageratum conyzoides*, (17) *Amaranthus virosa*, (18) *Bidens pilosa*, (19) *Cardiospermum halicacabum*, (20) *Conyza albida*, (21) *Corchorus tridens*, (22) *Euphorbia hirta*, (23) *Euphorbia heterophylla*, (24) *Euphorbia prostrata*, (25) *Gomphrena celosiodes*, (26) *Malvastrum coromandelianum*, (27) *Momordica charantia*, (28) *Parthenium hysterophorus*, (29) *Richardia brasiliensis*, (30) *Sphagneticola trilobata*, (31) *Tagetes minuta*, (32) *Triumfetta pentandra*, (33) *Tridax procumbens*.

3.5. DISCUSSION

3.5.1. Effect of invasive alien plant invasions on understorey ground cover

Indigenous species aerial cover did not change over time. There was however a significant decrease in alien plant aerial cover after clearing, specifically in the 0-1 and 1-2m height classes where alien cover had been predominant. Therefore if any changes occurred in ground cover as a result of changes in aerial cover it would be due to the significant reduction in alien aerial cover as indigenous aerial cover remained unchanged. A low level of alien cover was still present in the 0-1m height class after the annual clearing by WfW, due to the combination of expected reseeding of IAPs as well as a minimal occurrence of substandard clearing practices by WfW (pers. obs.) resulting in resprouting of IAPs (see also Witkowski and Garner 2008). Some level of IAP presence is to be expected, however, as complete removal of IAPs is unrealistic, and the aim and expectation of IAP clearing is to rather maintain IAPs at acceptably low and manageable levels as defined by KNP management (Foxcroft and Richardson 2003).

High levels of alien aerial cover had no effect on the levels of understorey ground cover variables or on the richness and diversity of native ground vegetation. However, when this was considered on a finer scale per zone, different patterns arose. Before clearing of IAPs by WfW, zone 1 had high densities of IAPs with associated high levels of aerial cover. After clearing this was significantly reduced, and native ground cover in the form of indigenous grass species took advantage of increased resources due to the reduction in canopy cover, and increased, covering patches of bare soil. This is important as it not only combats soil erosion, common after the clearing of IAPs (Holmes *et al.* 2000), but it also shows that native species were regenerating in the gaps created by clearing, rather than the more common scenario of alien species re-invading (Beater *et al.* 2008). Patterns of native herbaceous regeneration are congruous with patterns seen in the woody vegetation in the same study (chapter 2). However, similar patterns were not seen in zone 2, which differed from zone 1 by being inside the KNP where perhaps increased disturbance due to large herbivore usage in the riparian zone may have played a role. In zone 3, native ground cover decreased significantly with a corresponding increase in litter and bare soil. This zone was relatively uninvaded and thus changes in ground cover are not the result of a reduction in alien canopy cover, but may rather have been affected by the differential rainfall experienced in the two sampling seasons. In the first sampling season (2005), rainfall was 70% above the 76 year long-term annual average, which would have caused escalated plant growth especially in herbaceous species. The following season's rainfall (2006) was approximately two thirds less than the previous seasons and 35% below the long-term average, and would thus have had a strong negative influence on plant growth. However, if this was the expected pattern from season to season due to the decreased rainfall, similar changes should have existed in the other two zones. In zone 1, where dense stands of IAPs were removed, the opposite occurred and so the increase in native grass cover after the removal of IAPs in zone 1 is a response to the removal of IAPs.

There was very little change in ground cover diversities in response to IAP removal. Alpha diversity and evenness of distribution of species did not change over time, but species composition differed substantially, which once again may be due to the large differences in rainfall received influencing the species compositions.

Understorey ground cover has been documented to be affected by changes to overstorey aerial cover, often associated with IAP invasions (Sheppard *et al*. 2000, Wearn and Morgan 2004, Beater *et al*. 2008). In this study though, similar patterns were not evident and overstorey aerial cover had very little effect on understorey cover or richness. The major difference separating other studies from this one is that most studies focused on scenarios where IAP invasions have been present for an extended period of time, long enough to have a definitive effect on understorey vegetation (e.g. Wearn and Morgan 2004). In this study, however, the dense alien stands were newly developed having arisen largely over one season of growth, since the last clearing by WfW, in response to the exceptionally high rainfall. This allowed for an excellent opportunity to assess how quickly, if at all, new invasions could affect the understorey environment. Results indicated that short-lived alien invasions did not have a marked affect on understorey composition or structure and thus no likely effect on function. This demonstrates the importance of maintaining invasions at short-lived, low levels using continuous or repeat follow-ups to ensure that impacts to the surrounding environment are negligible.

3.5.2. Environmental predictors of alien plant distribution

Aerial cover seemed to have a large influence on the spatial distribution of alien species. The ordinations show that alien species tended to prefer open areas with a number of different species having strong associations with the main channel. However, most species associated with the channel are undeclared annual herbaceous weeds which can be expected closer to the channel where a greater level of disturbance exists due to frequent fluctuations in the water level, and these are generally thought not to be a cause for concern. The association of IAPs with open areas is of particular importance on the Sabie River when taking the large February 2000 infrequent flood event into account. The flood was of an extremely large magnitude and depending on the position in the catchment, had a return interval of between 90-200 years (Smithers *et al*. 2001). Woody vegetation and in particular large trees were greatly reduced (van der Velde 2001, Parsons *et al*. 2006), which resulted in an increase in open spaces and bare soil (Parsons *et al*. 2006). The increase in light and space as resources, as well as the large number of alien propagules washed down from further up the catchment, provided an ideal establishment opportunity for invasive alien species after the flood. Studies by Beater *et al*. (2008) and Leroy (2003) indicated a marked increase of invasive alien plants after the 2000 flood in both the upper catchments of the Sabie River as well as in the lower reaches within the KNP respectively. Due to the known strong competitive influence of alien species, it was expected that the high levels of IAPs present after the large flood may have had long-term repercussions for the recovery of the system. However, the continual IAP clearing by WfW since the 2000 flood acted to reduce the competitive advantage of alien plants and promoted recovery of indigenous vegetation in the riparian zone (chapter 2).

IAPs on the macro-channel bank grew predominantly in areas with less overstorey aerial cover. A reduction in canopy cover is often associated with large disturbance events such as floods or fires but can also be the result of seasonal or continuous heavy usage by mega-herbivores. Thus, in instances where canopy cover of indigenous vegetation has been reduced, it is important for timely clearing of IAPs to occur, so that establishment of IAPs while the increased levels of light and space are at a maximum can be countered and native vegetation recovery can be enhanced.

3.6. CONCLUSION

Alien plant cover occurred predominantly in the shorter height classes and was significantly reduced ($P < 0.05$) after the annual clearing of IAPs by WfW. Elevated levels of IAP canopy cover had very little effect on understorey cover variables or diversities. This is most likely due to the repetitive follow-up clearing by WfW that prevents invasions from being present for periods long enough to dramatically alter the understorey environment. Native understorey cover showed a slight increase in previously densely invaded transects in response to the removal of IAPs. However, the variable rainfall over the sampling seasons seemed to mask stronger patterns expected in response to alien canopy cover reduction.

Ground cover variables did not influence the distribution of IAPs to the same extent as overstorey aerial cover did. IAPs tended to grow in areas that were less shaded by overstorey aerial cover. This factor is of significant importance when considering the frequent disturbances that occur in riparian zones often resulting in a reduction of the native overstorey canopy. This study has demonstrated that the dynamic response of IAP management in clearing IAPs in such instances is imperative to mitigate the opportunistic and highly competitive growth of IAPs in newly opened areas and hence enhance the preferred growth of indigenous vegetation after a large disturbance.

CHAPTER 4

Temporal and spatial variation of invasive alien plants in response to clearing by the Working for Water programme – a catchment level assessment of the Sabie River, South Africa.

4.1. ABSTRACT

The Kruger National Park (KNP) incorporates the lower reaches of several major river catchments, including the Sabie River catchment. Commercial land-types, including forestry and agriculture, in the upper catchments watersheds provide a continual supply of alien plant propagules into the riparian corridors. This provides KNP management with an ongoing challenge to combat alien plant invasions. Management of invasive alien plants (IAPs) in the KNP is continuous and is conducted largely by the national Working for Water (WfW) programme which aims to increase water yields through the large-scale clearing of IAPs, while simultaneously addressing rural economic upliftment. WfW have also cleared alien plant invasions upstream of the KNP in previous years. However, the once-off clearing protocol combined with limited follow-up control efforts failed to reduce IAPs and the cleared areas have returned to pre-clearance invasion levels. This study utilised various historical data sets from the region and aimed to 1) investigate if riparian alien plant species found in the KNP are similar to those found upstream in order to assess the extent of invasion threat from the upper catchment, and 2) assess the role of continuous clearing by WfW in controlling alien plant invasions in the KNP over time. Data were collected from 12 sites on the Sabie River and were compared to IAP data collected in the upper and mid Sabie River catchment in 1996/7 and 2001, as well as to several data sets collected within the KNP over the last 10 years. For the catchment scale assessment, alien species richness and alien invasion intensity were compared between the upper, mid and lower catchments of the Sabie River over time. Results were tested for significance using Chi-square tests and Wilcoxon's matched paired tests. Similarities in species suites between the catchments over time were compared using a Bray Curtis similarity matrix.
To assess temporal changes within the lower reach of the KNP, species composition and abundances were compared in five transects over time. Results show that IAP species have increased in the KNP over time, with alien plants outside the borders presenting a large threat through the continuous input of propagules into the system. Although species richness has increased over time, the densities of IAPs have remained very low and relatively stable over the past 10 years despite frequent flooding disturbance. A key factor that sustains IAPs at such low intensities in the KNP is the annual clearing by WfW which acts to control and monitor existing alien species as well as to suppress any new infestations that may enter the park through its riparian corridors. This comparison has therefore not only highlighted the benefit of ongoing clearing practices but has also emphasised the need for integrated catchment management plans in order to optimally reduce alien plant invasions to sustainable levels.

4.2. INTRODUCTION

Protected areas form isolated units in the landscape but are fundamentally affected by various social, economic, environmental and political factors beyond their borders that ultimately influence their management and functioning (Pollard *et al*. 2003). The Kruger National Park (KNP) is no exception and due to its elongated shape (length:width ratio ≈ 5:1) has a large interface with the surrounding landscape. Several of the major rivers in the KNP originate in catchments beyond the western boundaries of the park and flow through areas varying in land-use, including agriculture, silviculture and dense urban and rural habitation before entering into and flowing across the KNP. These land-uses host a diverse and abundant suite of invasive alien plant (IAP) species and provide a continuous source of alien propagules into the river systems. The efficient ability of rivers in spreading and transporting these alien propagules along their corridors presents KNP management with the ongoing challenge of managing IAP invasions in the KNP (Foxcroft and Richardson 2003, Foxcroft *et al*. 2007).

IAPs have been declared one of the greatest ecosystem threats in the KNP, with riparian corridors being the most invaded systems (Foxcroft and Richardson 2003, Foxcroft *et al*. 2007). This is not only due to the ability of rivers to transport alien propagules from the invaded upper catchments, but also due to the dynamic hydrology of rivers and frequent disturbance by floods in the riparian zone, providing favourable growth conditions for IAPs (Tickner *et al*. 2001). In February 2000, an extreme flood occurred on the Sabie River with peak flows between 3000 m^3/s and 7000 m^3/s (Heritage *et al*. 2001) and an estimated return interval of 90-200 years, depending on the position in the catchment (Smithers *et al*. 2001). The flood caused considerable transformation to both biotic and abiotic components of the riparian corridor. Large amounts of vegetation were stripped from the river corridor that resulted in a corresponding increase in bare patches of sand and rock (Parsons *et al*. 2006). This, combined with the numerous alien propagules that were washed down from higher in the catchment (Foxcroft *et al*. 2007), triggered substantial recruitment of IAPs in the KNP (Leroy 2003, Parsons *et al*. 2005; 2006).

The escalated levels and continuous threat of IAPs in the KNP in recent years has lead to the establishment of large-scale, integrated management operations aiming to control IAPs to an acceptable extent as defined by the KNP management (Foxcroft and Richardson 2003). These acceptable limits are defined in the KNP strategic adaptive management plan using a set of "Thresholds of Potential Concern" (TPCs). TPCs are defined as "hypotheses of spatial and temporal limits of natural ecosystem flux that are described by upper and lower limits of acceptable change of selected environmental indicators", which when reached result in management action or in readjustment of the threshold to a more realistic and meaningful level (Biggs and Rogers 2003). The invasive alien species TPCs are divided into three major themes. The first TPC targets new invasions or incursions within the KNP; the second targets increases in the distribution of an alien species already within the KNP; and the third targets increases in the density of an alien species in the KNP. This last TPC however, is hypothetical and is not yet operational due to a lack of data and efficient cost-effective monitoring options to detect such thresholds (Foxcroft and Downey 2008).

Active management of IAPs in the KNP is largely executed by the Working for Water (WfW) programme who clear selected areas (mostly major riparian areas) on an annual basis. WfW is a government funded, national programme that aims to secure scarce water resources through the large-scale clearing of IAPs while simultaneously addressing poverty alleviation through job creation (van Wilgen *et al*. 1998, Macdonald 2004). WfW have also executed clearing operations further up in the Sabie River catchment. However, clearing protocols there differed from the annual clearing practices within and adjacent to the KNP and instead were executed in the customary WfW fashion of a single large-scale clearing event followed by a limited number of (usually a maximum of three) follow-up clearances in subsequent years. Since clearing, alien plant invasions in the upper catchment have re-established to levels similar to those present prior to control efforts (Beater *et al*. 2008, Witkowski and Garner 2008).

This and many other examples around the country have not only highlighted the importance for an assessment of the manner in which national operations are executed, but have also emphasized the importance for a move towards co-ordinated clearing efforts. This is significant for the KNP where management of IAPs is increasingly seen as redundant due to the continuous influx of alien propagules from the poorly managed upper reaches. Thus, the aim of this paper was to analyse data from this and several previous studies in order to 1) assess the extent to which alien species from the upper reaches of the Sabie River have spread into the lower reaches within and adjacent to the KNP, and 2) assess the efficacy of continuous clearing operations, by WfW, within the KNP over the last decade and compare these results to failures further upstream.

4.3. MATERIALS AND METHODS

4.3.1. Study area

The Sabie River catchment is situated in the Mpumalanga province and has a catchment of 7096 km^2. The area is characterised by semi-arid to subtropical climate, with hot rainy summers and warm dry winters (Venter *et al*. 2003). The Sabie River, a perennial river, originates in the escarpment of the Drakensburg Mountains at an altitude of 2200 m, where the rainfall is between 500-1000 mm p.a. It flows eastwards for 104km through the Sabie, Graskop and Hazyview regions before entering the KNP at an altitude of 450 m where the rainfall averages between 450-600 mm p.a. It then flows a further 108 km through the KNP before exiting into Mozambique at an altitude of 110 m (van Niekerk and Heritage 1993) (Figure 4.1).

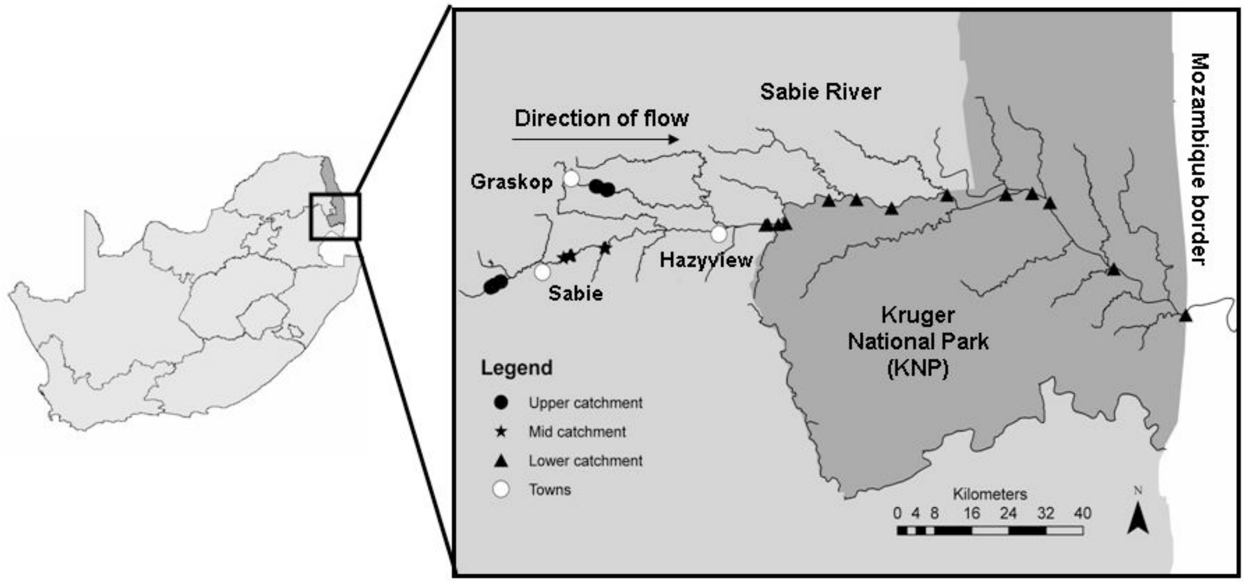


Figure 4.1. Map of sites sampled along the Sabie River contributing to the upper, mid and lower catchment data.

The Sabie catchment area, within South Africa, has a complex pattern of land ownership with almost half (48%) of it occurring within the KNP. Outside of the KNP, 50% of the catchment area comprises natural vegetation, 20% cultivated lands, 20% *Pinus* and *Eucalyptus* plantations, 7% degraded lands and 3% other uses such as urban and rural habitation (Foxcroft *et al*. 2007). These areas contain an abundant and diverse array of IAP species, which pose a significant threat to the conserved riparian areas of the KNP lower down in the catchment (Foxcroft *et al*. 2007, Beater *et al*. 2008, Witkowski and Garner 2008).

Studies analysed in this paper include data from the upper, mid and lower Sabie River catchment (Table 4.1). Vegetation in the elevated "upper catchment" is winter-dormant grassland interspersed with afromontane forest in valleys and sheltered slopes (Nel *et al*. 1999). More than three quarters of these natural grasslands have been converted into plantations dominated by pine and eucalypt forestry (Le Maitre *et al*. 2002), which are heavily invaded with several other IAP species, including Australian wattles (*Acacia* spp.), *Solanum mauritianum*, *Lantana camara* and *Rubus* spp. (Garner 2006). The "middle catchment" is characterised by mixed savanna and grassland vegetation dominated mainly by commercial agriculture and densely populated rural communities practicing subsistence farming. The major IAP species in this area include *Lantana camara* and *Caesalpinia decapetala*. The "lower catchment" is characterised mainly by conserved open woodlands, savannas and mixed grasslands with riparian forest along the major rivers (Le Maitre *et al*. 2002). The major woody alien plants controlled by WfW within and adjacent to the KNP include *Chromolaena odorata*, *Lantana camara*, *Melia azedarach*, *Nicotiana glauca*, *Ricinus communis* and *Senna didymobotrya*, while the herbaceous alien plants include *Argemone* spp., *Datura* spp., *Senna* spp. and *Xanthium strumarium* (Foxcroft *et al*. 2008b, chapter 2).Vegetation in these lower reaches tends to be shaped by the strongly bedrock influenced system (Heritage *et al*. 1999), leading to characteristic relatively steep macro channel banks either side of a wide macro channel floor, each of which have distinct vegetation associations as described by van Coller *et al*. (1997).

Table 4.1. Descriptions of all studies used in the comparative analysis including: the study area, the catchment region, altitude, the year and season of the study, the number of sites sampled (N), the type of data collected and the use in this comparison. Aim 1 refers to comparisons between alien species richness and invasion intensities along the Sabie River between upper, mid and lower reaches. Aim 2 refers to comparisons of alien species richness and invasion intensities along the Sabie River within the KNP.

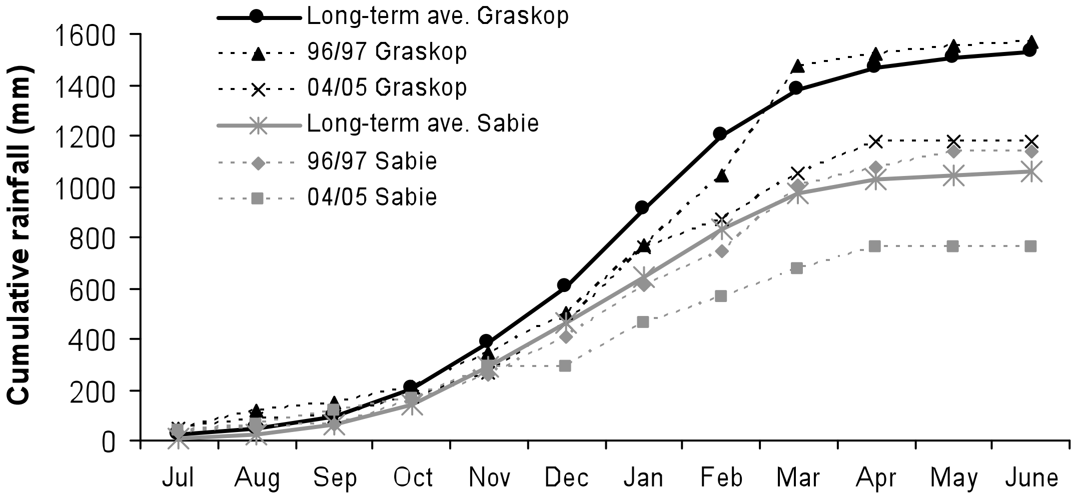
Study	Study region	Catchment region	Altitude (m)	Year	Season	N	Data collected	Data for aim:	
Garner 2006	Sabie Graskop Hazyview	Upper Mid	±1000-1150 ±750-900	1996/7	Oct96-Feb97 (Spring/ summer)	40	Herb Woody	1	
Beater 2006	Sabie Graskop Hazyview	Upper Mid	±1000-1150 ±750-900	2005	Feb- Apr (Autumn)	40	Herb Woody	1	
Leroy 2003	KNP	Lower	±110-450	1997	Jun-Jul (Winter)	7	Herb Woody	1	2
Parsons *et al*. 2006	KNP	Lower	±110-450	2000	Oct (Spring)	11	Woody		2
Leroy 2003	KNP	Lower	±110-450	2001	Jun-Jul (Winter)	7	Herb Woody	1	2
Foxcroft *et al*. 2008b	KNP	Lower	±110-450	2005	Jul- Oct (Winter)	12	Herb Woody	1	2
Morris 2008, this study	KNP	Lower	±110-450	2006 2007	Apr-May (Autumn)	12	Herb Woody	1	2

4.3.2. Rainfall for study periods.

Cumulative rainfall for the annual climatic season (July-June) showed that rainfall in the 96/97 study period was similar to the 48 year long-term average in the Graskop region and the 31 year long-term average in the Sabie Region, whereas the rainfall in the 04/05 study period was lower than the long-term average (Figure 4.2a).

Rainfall in the KNP, measured at the Skukuza weather station (Figure 4.2b), was greatly escalated in the 05/06 annual climatic year when sampling took place (dashed line) in comparison to the 76 year long-term average (solid bold line). Rainfall in the 99/00 annual climatic year indicates the escalated rainfall that occurred in the region and resulted in the large floods in February 2000.

a



b

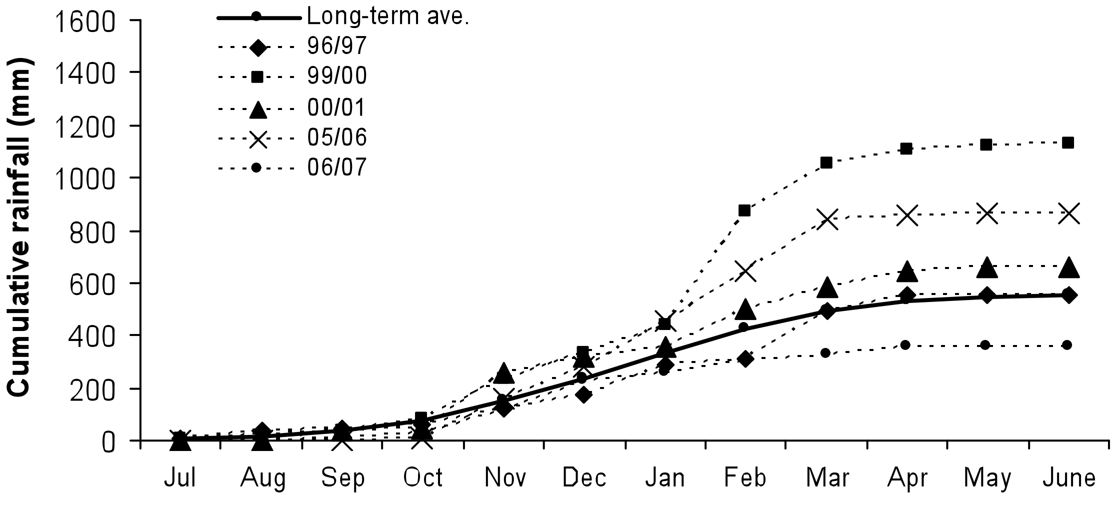


Figure 4.2. Cumulative rainfall (mm) per "annual climatic year" (July-June), for the mid and upper catchment recorded at the Graskop and Sabie weather stations (a) and the lower catchment recorded at the Skukuza weather station (b). Dotted lines represent rainfall that occurred in study years while the bold solid lines indicate the long-term average cumulative rainfalls. The 99/00 line in graph b indicates the high rainfall that resulted in the large February 2000 floods.

4.3.3. Vegetation sampling

Sampling of recent IAP levels inside and adjacent to the KNP was carried out in three periods: March/April 2006, Nov/Dec and March 2007. The March sampling was considered end of summer sampling as it occurred after seasonal rains and hence the summer growth period, whereas the November sampling occurred before the seasonal rains when vegetation still resembled the "dormant" winter state (Figure 4.2a). Vegetation was sampled on the macro-channel bank in twelve belt transects spanning the Sabie River inside (n=9) and adjacent (n=3) to the KNP (Figure 4.1). Due to the heterogeneous nature of the riparian zone in the lower reaches of the Sabie River, transects varied in length from 20-90 m.

Vegetation with basal stem diameters (BSDs) >1 cm was recorded in a 10 m wide belt transect, and vegetation with BSDs > 3 cm was recorded in a neighbouring 10m wide belt transect. In the >1 cm transect all alien plants (> 1 cm) were identified and counted and the density (per ha) of each IAP species was determined. Herbaceous species were recorded in 1x1 m quadrats placed every 5 m along the two outside lengths of the transect. Additionally, extensive sampling took place within a further two 20 m wide transects located 15 m in either direction of the main transect, in which the presence of all alien species was recorded (Figure 4.3).

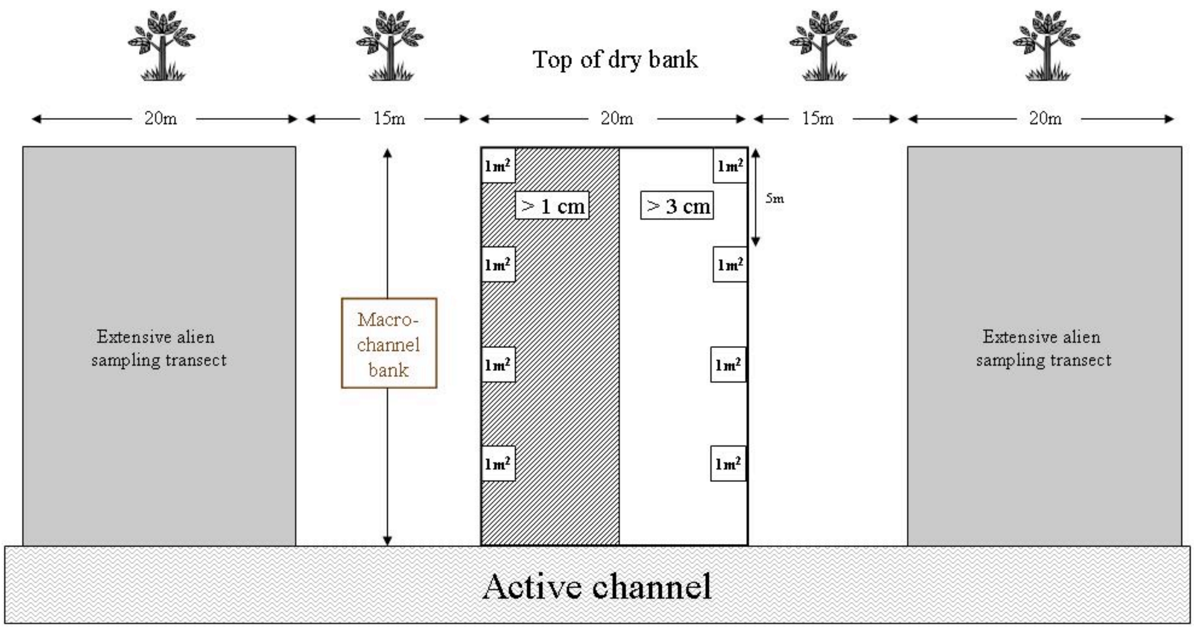


Figure 4.3. Sampling layout of the series of belt transects sampled down the macro-channel bank at each of the twelve sites on the Sabie River. All woody species were recorded in the >1 cm and >3 cm transects. Alien species densities were determined in the >1 cm transect. Herbaceous species were recorded in the 1 m^2 quadrats along the lengths of the transect. Additional alien species were recorded in the two extensive sampling transects.

Overstorey alien plant aerial cover, used as a surrogate for alien invasion intensity, was measured using the line intercept method along three lines, positioned perpendicular to the river at the boundaries and centre line of the 20 m wide belt transect. Overstorey aerial cover was measured in each of four different height classes: 0-1 m (small woody plants and herbaceous vegetation), 1-2 m (shrubs and saplings), 2-5m (small trees) and >5 m (large trees). Along each line, the length which fell under each individual plant canopy in the four height classes was recorded. The species of each plant was recorded and the average percent overstorey aerial cover of each species, in each of the different height classes, was determined. The national invasive status of each alien species was recorded, according to Regulation 15 of the Conservation of Agricultural Resources Act, 1983 (Act No. 43 of 1983) as described in Henderson (2001).

Transect 3 was omitted from the 2007 data as this transect had subsequently been transformed into farmlands and hence no data could be re-collected for this site.

4.3.4. Data analysis

In order to "assess the extent to which alien species from the upper reaches of the Sabie River have spread into the lower reaches within and adjacent to the KNP" (aim 1), the following were assessed:

1. The number of IAP species expressed as a percentage of all vegetation was compared between the upper and mid catchments in 1996/7 (Garner 2006) and 2005 (Beater 2006); and in the lower catchment in 1997, 2001(Leroy 2003); 2005 (Foxcroft *et al*. 2008b); and 2006 and 2007 (this study). The percentage was used to take annual or climatic variations in that year into account. Contingency table χ^2 tests with Yates correction were performed on proportions of alien plants to assess differences in species richness between reaches.
2. The invasion intensity (using alien aerial cover as a surrogate) was compared between the upper, mid and lower catchments in 1996/7 (Garner 2006), 2005 (Beater 2006), as well as 2006 and 2007 (this study). Contingency table χ^2 tests with Yates correction were also performed on data to assess differences in alien invasion intensities between 2006/7 data and the previous years. Differences between the more comparable 2006 and 2007 data, were compared using Wilcoxon's matched pairs tests.

3. The co-occurrence of alien species between the upper, mid and lower catchments was compared using species lists from 1996/7 (Garner 2006), 1997, 2001(Leroy 2003), 2005 (Beater 2006, Foxcroft *et al*. 2008b), 2006 and 2007 (this study). Bray-Curtis similarities for total alien species (undeclared and declared) and declared alien species were calculated between data from the combined mid and upper catchments from 1996/7 (Garner 2006) and 2005 (Beater 2006); and the lower catchment from 1997, 2001 (Leroy 2003) and 2005-2007 (Foxcroft *et al*. 2008b, and this study).

When considering aim (2) to: "assess the efficacy of continuous clearing operations within the KNP over the last decade and to compare these results to results from studies further upstream" the following was assessed:

1. The species composition and alien abundance of data from 5 transects along the Sabie River within the KNP were compared between 1997, 2001 (Leroy 2003), 2006 and 2007 (this study).
2. The species composition and where possible, abundance of alien vegetation along the macro-channel bank of the Sabie River within the KNP was compared between 1997 (Leroy 2003), 2000 (Parsons *et al*. 2006), 2001 (Leroy 2003), 2005 (Foxcroft *et al*. 2008b), 2006 and 2007 (this study) (Table 4.1).

4.4. RESULTS

4.4.1. Catchment scale assessment of invasive alien plants

Alien species richness

Woody alien plant species percentages in the mid/upper catchment in 1996/7 were similar to percentages in the lower catchment ($\chi^2_1 = 1.05$, $P > 0.05$). However, by 2005, levels of woody alien plant species were higher in the mid/upper catchment than in the lower catchment ($\chi^2_1 = 4.93$, $P < 0.05$). In contrast, herbaceous alien plant species tended to be greater in the lower catchment in 2006/2007 than further upstream, although this was not significant in either 1996/7 ($\chi^2_1 = 0.99$, $P > 0.05$) or 2005 ($\chi^2_1 = 1.43$, $P > 0.05$). In total, IAP species richness in the lower catchment was similar to the IAP species richness higher in the catchment ($\chi^2_1 = 0.15$, $P > 0.05$) (Figure 4.4).

The number of declared woody alien species in the lower reach was fairly uniform over time and did not differ significantly from the number of declared woody alien species in the mid/upper catchments in either year (1996/7: $\chi^2_1 = 1.35$, $P > 0.05$; 2005: $\chi^2_1 = 1.74$, $P > 0.05$). Declared alien herbaceous species levels did not differ noticeably across the catchment ($\chi^2_1 = 0.01$, $P > 0.05$) and were relatively low in all years. In total, the number of declared alien species is less than 10% for all studies, with current levels of declared IAPs in the lower reach being similar to the levels in the upper reaches ($\chi^2_1 = 0.09$, $P > 0.05$) (Figure 4.4).

Alien species invasion intensity

Alien invasion intensity was greatest in the taller height classes in the upper and mid reaches in 1996/7. The overall alien intensity had not changed significantly in the upper and mid reaches by 2005 but it had switched to being greater in the shorter height classes as reported by Beater *et al*. (2008) (Figure 4.5). In the lower reach, the levels of alien invasion intensity were very low in the taller height classes with the predominant portion stemming from invasive alien plants <2 m in height. Additionally in 2006, after the escalated rainfall, total levels were comparable to those found upstream, and were significantly higher in the <2 m class. By 2007, the levels in the <2 m height class had been significantly reduced ($Z_{11} = 2.85$, $P = 0.004$) with no alien plants present at a height greater than 2 m, and the overall 2007 alien invasion levels in the KNP were significantly reduced in comparison to the previous year ($Z_{11} = 2.93$, $P = 0.003$). The 2007 invasion intensities in the KNP were significantly lower than intensities further up in the catchment ($\chi^2_1 = 12.63$, $P < 0.001$).

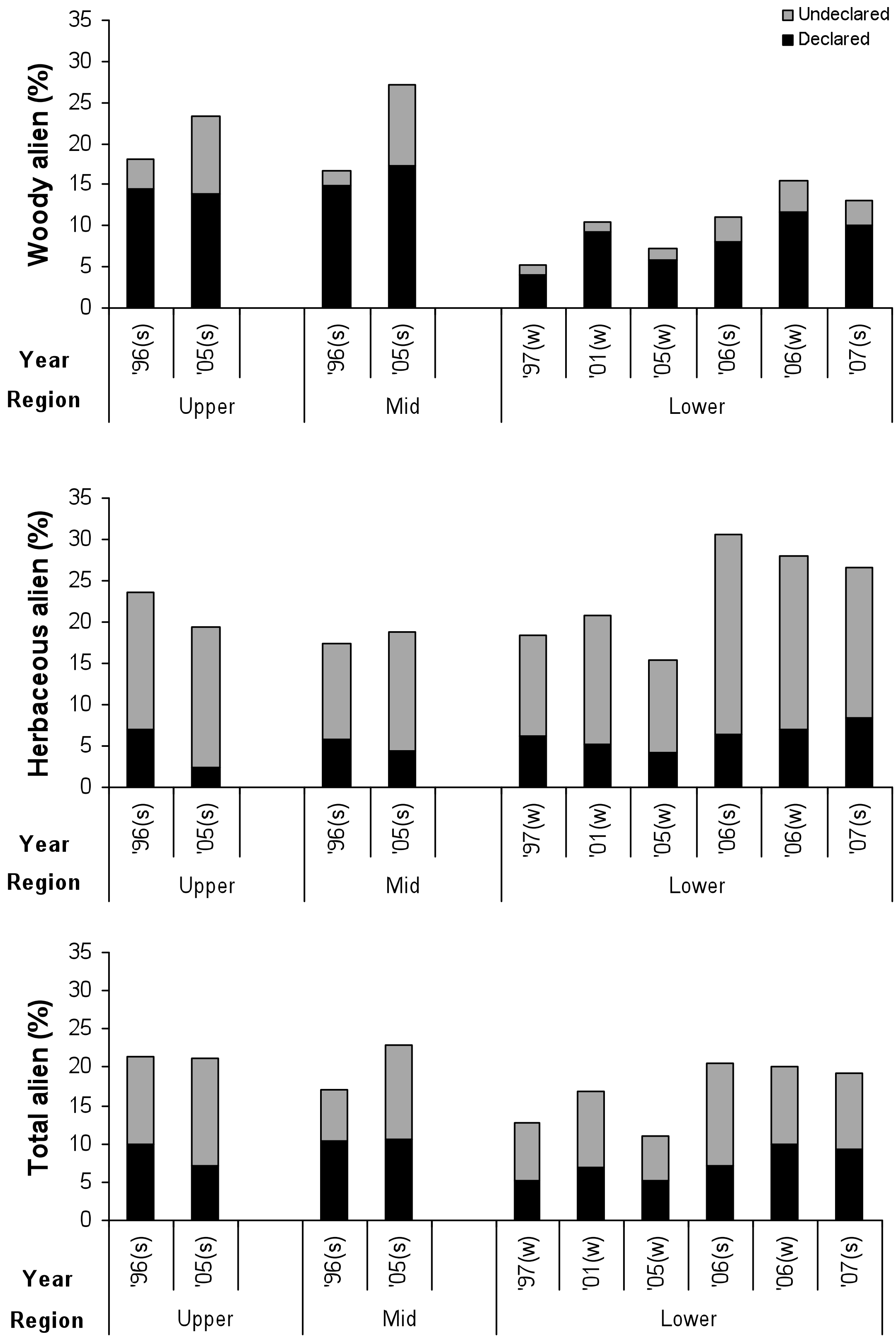


Figure 4.4. Percentages of the number of declared and undeclared alien species along the Sabie River in the upper, mid and lower reaches over time. Declared species refer to those alien species with a declared legal status according to regulation 15 of the Conservation of Agricultural Resources Act, 1983 (Act No. 43 of 1983) as described in Henderson (2001). w = winter, s = summer.

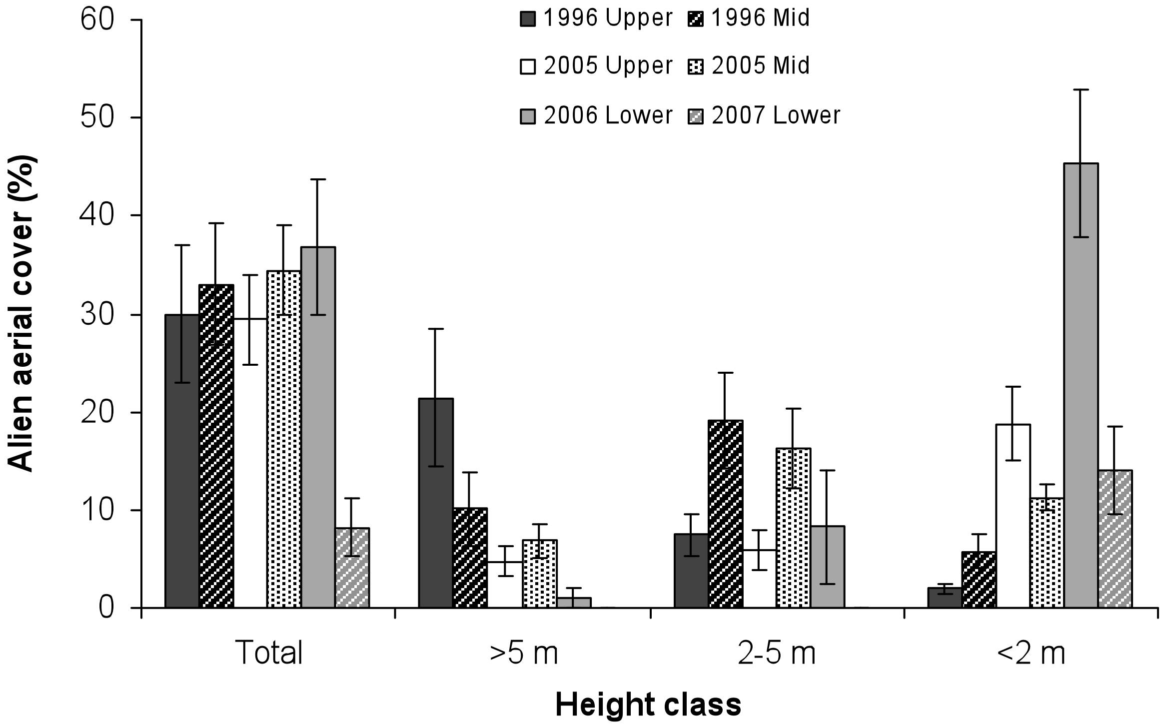


Figure 4.5. Alien species aerial cover (as a surrogate for alien invasion intensity) across the catchment over time, for all the height classes (total), and for the >5 m, 2-5 m and <2 m height classes

Alien species similarity

The suite of alien species of the upper and mid reaches that were in common with the lower reach only differed by one species and were thus assessed as a combination (Table 4.2). In total, only 20% of the alien species found in the lower reach were also found in the upper reaches. Of the species in common, approximately 30% were woody and 70% were herbaceous. Almost half the species were declared alien species according to the CARA legislation of 1983 (Henderson 2001) (Table 4.2). Many of the species in common were widespread opportunistic alien species which are often found on roadsides and other disturbed areas (such as *Lantana camara*, *Bidens pilosa*, *Tagetes minuta*, *Achyranthes aspera* and *Verbena bonariensis*) (Table 4.3). Other species however, were not as widespread and may have been present in the lower reach due to dispersal from higher up in the catchment. For example, *Solanum mauritianum* found in the upper and mid reaches in 1996/7 and 2005 was only found once in the lower reaches of the KNP in 2001 (Table 4.3 and 4.4). This species was most likely brought into the lower reaches by the large February 2000 flood. Similarly, only one specimen of each of the woody species *Rubus cuneifolius*, *Senna septemtrionalis* and *Caesalpinia decapetala* was found in the lower reach of the Sabie River (Table 4.3 and 4.4). Thus, the presence of several species in the lower reach was only due to a minimal number of individuals. An overall comparison of suites of alien species and suites of declared alien species (Table 4.5) between the upper, mid and lower reaches revealed that species suites within a reach did not differ markedly over time, but that the upper and mid reaches showed very little similarity (<25%) to the lower reach at any time.

Table 4.2. Percentage of alien species in common between the lower reach and the upper/mid combined reaches (these were combined as they only differed by one species).

	Upper/Mid
Alien species in common with lower reach	20% (16/81)
- Woody alien species	31% (5/16)
- Herbaceous alien species	69% (11/16)
- Declared alien species	38% (6/16)

Table 4.3. Co-occurrence of alien species in common to both the lower and mid/upper reaches of the Sabie River over time.

Species	Status	Growth form	Upper '96/7	Mid '96/7	Upper '05	Mid '05	Lower '97	Lower '01	Lower '05	Lower '06/07
Achyranthes aspera	Weed (1)	Herb	X	X		X	X	X		X
Ageratum conyzoides	Weed (1)	Herb			X	X	X	X		X
Bidens pilosa	-	Herb	X	X	X	X		X	X	X
Caesalpinia decapetala	Weed (1)	Woody	X	X	X	X			X	X
Centella asiatica	-	Herb			X	X	X	X		
Conyza bonariensis	-	Herb			X	X				X
Lantana camara	Weed (1)	Woody	X	X	X	X	X	X	X	X
Oxalis corniculata	-	Herb	X		X	X	X	X		
Pseudognaphalium luteo-album	-	Herb	X		X		X			
Richardia brasiliensis	-	Herb			X	X		X		X
Rubus cuneifolius	Weed (1)	Woody	X	X	X	X				X
Senna septemtrionalis	-	Woody		X		X			X	
Solanum mauritianum	Weed (1)	Woody	X	X	X	X		X		
Solanum nigrum	-	Herb	X		X	X				X
Tagetes minuta	-	Herb			X	X	X	X	X	X
Verbena bonariensis	-	Herb	X	X	X	X		X		X

Table 4.4. Number of individuals of transient woody species common to the upper/mid and lower reaches of the Sabie River. These species appeared in the lower reaches in minimal numbers and did not seem to persist for any appreciable period of time.

Species	Number of individuals
Caesalpinia decapetala '05	1
Caesalpinia decapetala '06	1
Rubus cuneifolius	1
Senna septemtrionalis	7
Solanum mauritianum	1

Table 4.5. Bray-Curtis similarity indices for total (declared and undeclared) and declared alien plant species across the upper, mid and lower reaches from 1996/7-2007.

	Upper ’96/7	Mid ’96/7	Lower ’97	Lower ’01	Upper ’05	Mid’05
	All alien species					
Mid ’96/7	71					
Lower ’96/7	15	10				
Lower ’01	19	20	63			
Upper ’05	43	35	20	25		
Mid ’05	39	44	21	29	64	
Lower ’05 -’07	15	17	32	37	19	24
	Declared alien species					
Mid ’96/7	85					
Lower ’96/7	17	21				
Lower ’01	22	26	70			
Upper ’05	62	56	18	23		
Mid ’05	53	62	26	30	62	
Lower ’05 - 07	20	22	41	53	20	24

4.4.2. Temporal assessment of invasive alien plants in the Kruger National Park

Direct comparison over time

Five of the transects along the Sabie River were sampled in 1997, 2001, 2006, and 2007, providing informative data for long-term monitoring. The first of the five transects sampled was located 24km along the Sabie River from the point where it enters the KNP. Sites located higher up the river could not be matched between 1997/2001 and 2005/6 and could thus not be compared. The five transects compared unfortunately had the lowest IAP densities of all the sites along the river in all years (chapter 2), most likely due to the lower propagule pressure further down the river. Although comparisons of the sites situated closer to the border of the KNP may have been more informative, dynamics over time of the sites compared will nonetheless still be useful.

The total number of woody species found in the transects in all years was very low. An increase in numbers occurred in 2006, associated with the increased rainfall. These were reduced to lower levels after the annual clearing of alien plants by WfW later in 2006 (Figure 4.6a). Besides the outlying value in transect 12 in 2001, woody alien species contributed relatively little to the total suite of alien species, with the total percentage of woody alien species in all years being less than 10%. Overall, the proportions of woody species have remained low and fairly constant over the past 10 years (Figure 4.6b).

The number of herbaceous alien species generally increased in 2001 after the occurrence of the large 2000 flood. Numbers increased again in 2006, in response to the elevated rainfall. However, by the following year, numbers of herbaceous alien species had been reduced to levels similar to those found in 2001. This occurred after the winter season had passed and many herbaceous plants had died off, as well as after the annual clearing by WfW had occurred (Figure 4.7a). Similar patterns were seen in the relative values of herbaceous alien species and in total, across the 5 transects, the relative number of alien herbaceous species remained fairly stable between 20-30% over time (Figure 4.7b).

When considering the changes in specific alien woody species across the 5 transects over time, *Lantana camara* only appeared in these transects further downstream after the 2000 flood. Since then, *L. camara* has persisted in the sites but in very low numbers, and in total, has remained fairly stable over time. This is more than likely due to the continuous control efforts by WfW as *L. camara* is one of their prioritized and highly targeted species (Foxcroft *et al*. 2008b). *Senna obtusifolia* and *S. occidentalis* were only present in 2006/2007 and although numbers were relatively low in the 5 transects, both species were found upstream in far greater numbers (roughly 50 times greater for *S. obtusifolia*, and 25 times greater for *S. occidentalis*) (chapter 2). Another species that was also only present in 2006/2007 was *Xanthium strumarium*, which was only prominent in transect 7, although once again this species was found in the thousands (± 250-8000 plants per ha) further upstream (chapter 2) (Table 4.6).

Herbaceous species were variable over time with many wide-spread species occurring in all transects in most years (e.g. *Ageratum conyzoides*, *Bidens pilosa* and *Malvastrum coromandelianum*). By 2007, very few alien herbaceous species were still present in the five transects (Table 4.7).

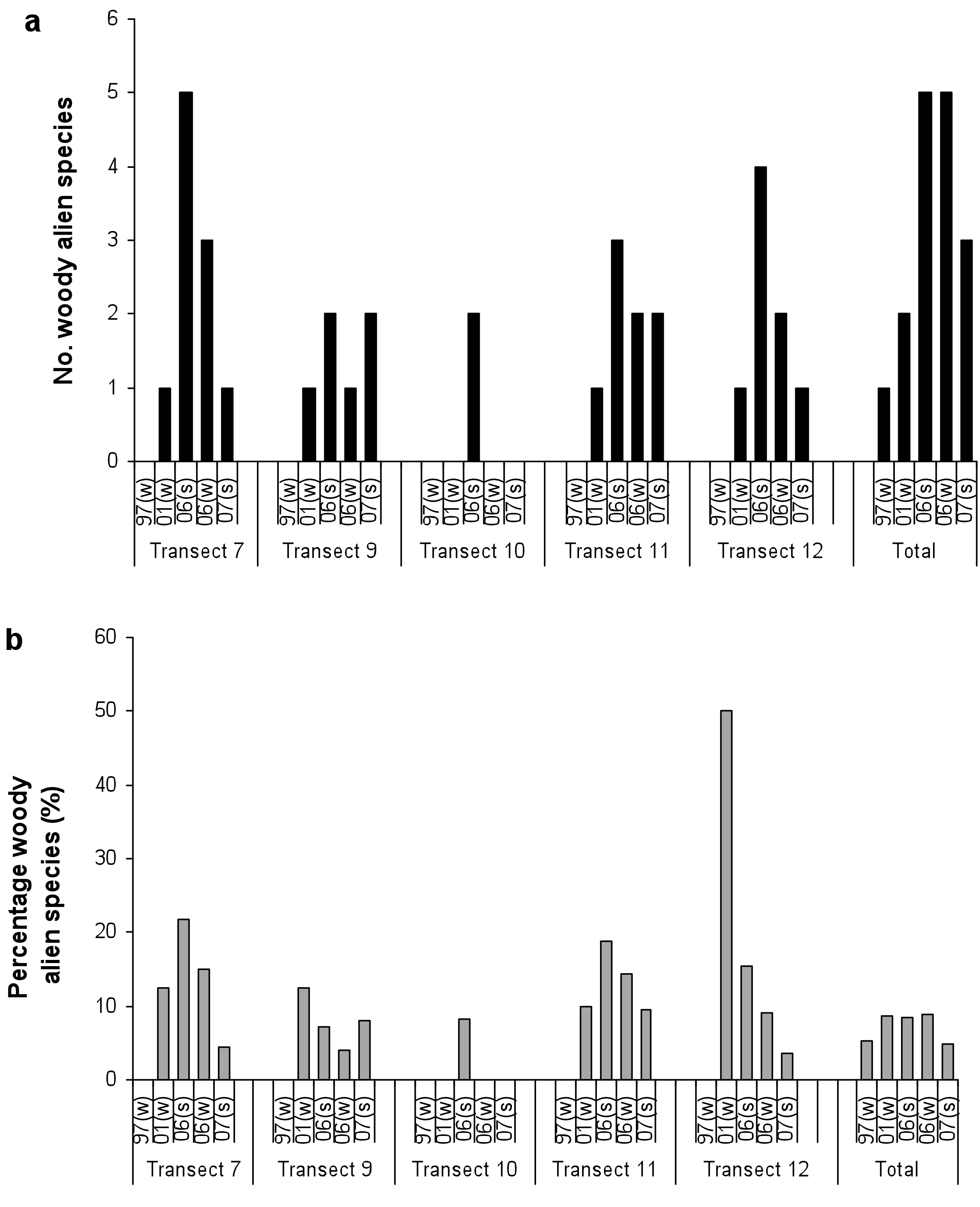


Figure 4.6. Absolute number of woody alien species (a) and percentage of woody alien species in relation to the total number of woody species (b) in 5 transects along the Sabie River in the Kruger National Park (lower reach) in 1997, 2001, 2006 and 2007. w = winter, s = summer.

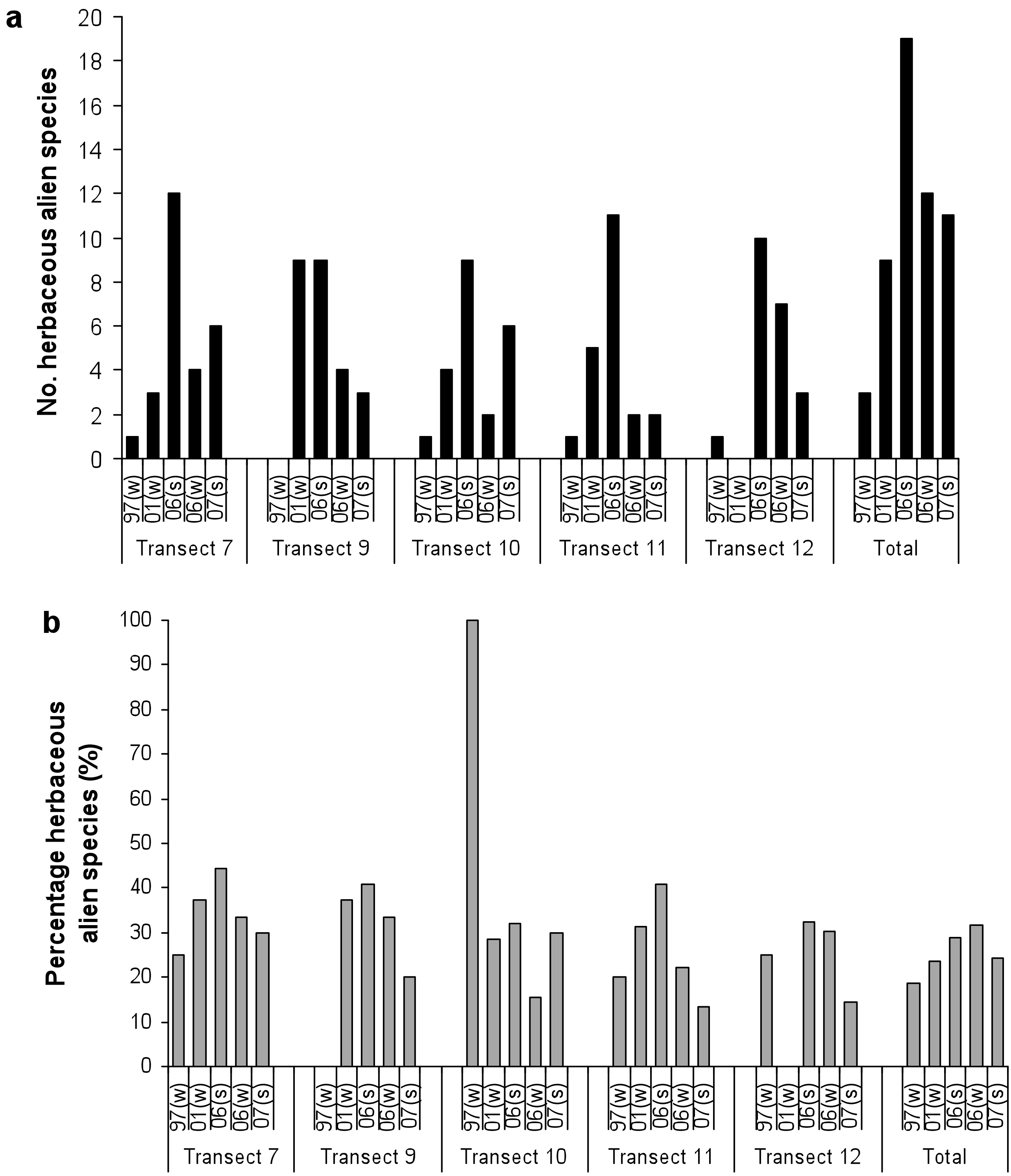


Figure 4.7. Number of herbaceous alien species (a) and percentage of alien herbaceous species relative to the total number of herbaceous species (b) in 5 transects along the Sabie River in the Kruger National Park (lower reach) in 1997, 2001, 2006 and 2007. w = winter, s = summer.

Table 4.6. Comparison of counts of woody alien species found in five transects along the Sabie River in the Kruger National Park (lower reach) in 1997, 2001, 2006 and 2007. Frequencies have been left as counts as discrepancies exist in areas sampled.

Transect	Transect 7				Transect 9				Transect 10				Transect 11				Transect 12			
Year	‘97	‘01	‘06	‘07	‘97	‘01	‘06	‘07	‘97	‘01	‘06	‘07	‘97	‘01	‘06	‘07	‘97	‘01	‘06	‘07
Area (m^2)	450	450	880	840	600	600	400	550	450	450	420	450	400	400	480	600	250	250	710	790
Lantana camara		1	2	3		1		1						2		1		1		
Senna obtusifolia											2								3	
Senna occidentalis			1												2	10			1	
Xanthium strumarium			261	37			2				2									

Table 4.7. Occurrence of herbaceous alien species found in five transects along the Sabie River in the Kruger National Park (lower reach) in 1997, 2001, 2006 and 2007. Presence indicated by an X.

Transect	Transect 7				Transect 9				Transect 10				Transect 11				Transect 12			
Year	‘97	‘01	‘06	‘07	‘97	‘01	‘06	‘07	‘97	‘01	‘06	‘07	‘97	‘01	‘06	‘07	97	01	06	07
Acanthospermum hispidum						X								X						
Achyranthes aspera					X					X		X	X	X						
Ageratum conyzoides	X	X			X	X		X	X	X			X	X				X		
Alternanthera pungens											X				X			X		
Bidens pilosa		X	X			X				X	X							X	X	
Cardiospermum halicacabum	X				X											X				
Chaemaescyne hirta					X															
Conyza albida																		X		
Conyza bonariensis																			X	
Corchorus tridens														X						
Euphorbia hirta		X																X		
Euphorbia prostrata														X						
Gomphrena celosiodes														X				X		
Malvastrum coromandelianum		X	X		X	X	X		X	X	X			X				X		
Parthenium hysterophorus						X	X													
Richardia brasiliensis		X	X						X		X									
Solanum seaforthianum var. *disjunctum*												X								
Tagetes minuta		X	X		X								X							
Tridax procumbens			X							X								X	X	
Triumfetta pentandra var. *pentandra*		X				X														
Verbena brasiliensis	X				X				X				X							
Vincia major					X															

Overall comparison of the Sabie River invasive alien species over time

Absolute and relative numbers of woody alien plants increased along the banks of the Sabie River over time, although the current levels remained relatively low at less than 15% (Figure 4.8a). A large proportion of the woody species are declared alien species according to CARA legislation (Henderson 2001) (Figure 4.8b). Herbaceous alien species were more seasonally variable with a greater number of alien species occurring in the summer sampling seasons (2006 and 2007) (Figure 4.8c). Proportionally, there were very few declared alien herbaceous species, and besides the winter 2005 sampling where aliens contributed very little to the total herbaceous vegetation, alien herbaceous species have remained relatively stable over the last 10 years at approximately 20-30% (Figure 4.8d). The total number of alien species along the Sabie River within the KNP increased from 1997 to 2001 probably as a result of the large February 2000 floods. Since then, the number of alien species, and particularly the number of declared alien species, has increased further (Figure 4.8e). Total alien species have increased over the years from about 10% to approximately 20% (Figure 4.8f).

It is clear that the number of alien species has increased slightly over time but what may be more informative is the change in densities of IAPs along the Sabie River banks over time. Many of the species representing the elevated species richness are actually only present in extremely low densities (e.g. *Caesalpinia decapetala*, *Chromolaena odorata*, *Melia azedarach*, *Mimosa pigra*, *Ricinus communis*, *Senna didymobotrya*, *Tithonia diversifolia*) (Table 4.8). *Lantana camara* increased after the February 2000 flood but has since been maintained at fairly low levels. Species such as *Senna obtusifolia*, *Senna occidentalis* and *Xanthium strumarium*, which have only been present in more recent years increased dramatically in 2006, most likely due to the abundant rainfall in that year. Their numbers were significantly reduced by 2007 due to the annual WfW clearing efforts. However, a substantial number of plants understandably still remained, either due to re-establishment, resprouting or the rare case of lack of removal by the WfW teams.

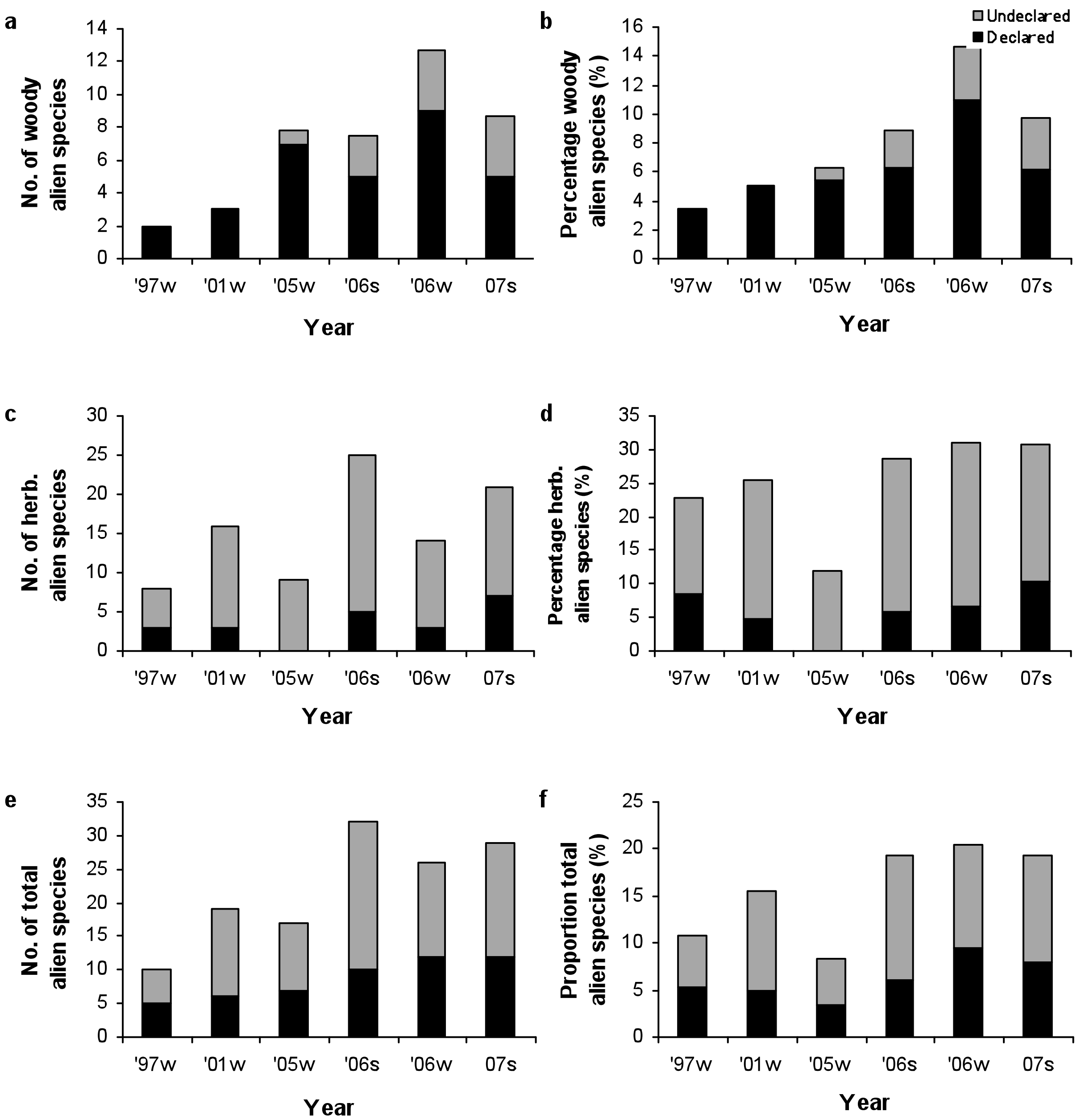


Figure 4.8. Number (a-c) and percentages (b-d) of woody, herbaceous and total undeclared and declared alien species along the macro-channel banks of the Sabie River in the Kruger National Park (lower reach) in 1997, 2001, 2005, 2006, 2006, 2007. w= winter, s = summer.

Table 4.8. Densities (per ha) of woody alien species on macro-channel banks of the Sabie River in the Kruger National Park (lower reach) in 1997, 2001 (n = 14), 2005 (n = 12), 2006 and 2007 (n = 9). w = winter, s = summer. * indicates alien species declared as weeds according to Regulation 15 of the Conservation of Agricultural Resources Act, 1983 (Act No. 43 of 1983) as described in Henderson (2001).

Species	'97(w)	'01(w)	'05(w)	'06(s)	'07(s)
*Caesalpinia decapetala**			0.1		
*Chromolaena odorata**			0.4		
*Datura strumarium**				10	
*Lantana camara**	13	45	25	31	12
*Melia azederach**			0.7		
*Mimosa pigra**					2
*Ricinus communis**			0.5		
*Senna didymobotrya**			1.0		
Senna obtusifolia				325	59
Senna occidentalis			39	501	21
Senna septemtrionalis *			0.9		
*Sesbania punicea**			9		
*Solanum mauritianum**		2			
Solanum seaforthianum var. *disjunctum* *				2	4
Stachytarpetta mutabilis				4	4
Tagetes minuta			56	565	2
*Tithonia diversifolia**					2
*Xanthium strumarium**			172	843	272

4.5. DISCUSSION

4.5.1. Catchment level assessment of invasive alien plants

Alien species richness in the lower reach (including KNP) was similar to that found in reaches further upstream. However, the intensity at which alien species were found was dramatically lower, often with only a few individuals representing a particular species. Additionally, the suite of alien species found in the lower reach was markedly different from the suites of alien species in the mid and upper catchments, having only 20% of their alien species in common. The dissimilar suites of alien species also differed in dominant growth forms. Species in the mid and upper catchments comprised predominantly woody alien species whereas in the lower reach in the KNP, herbaceous alien species were more prominent. Most of the woody alien species found in the reaches were declared aliens which are known to cause widespread environmental impacts in the Sabie catchment and many other areas. The difference of alien species suites can however be somewhat expected due to differences in both habitat and climate between the cooler, wetter upper reaches and the warmer, dryer lower reaches of the cathcment. However several species, for example wattles (*Acacia* spp.) and Bugweed (*Solanum* *mauritianum*) are known to be generalist invader species capable of colonising many and varied habitats including savannas, and it is thus surprising that these and other more tolerable species have not spread down the catchment.

The predominantly woody alien species found in the upper reaches are proposed to have an increased water usage, resulting in negative impacts to surface runoff yields (Le Maitre, *et al*. 2000, Le Maitre *et al*. 2002, Dye and Jarmain 2004). In the lower reaches, in the KNP, the greater predominance of herbaceous species often elicits a lower management concern. While this may be tolerable for certain species, other herbaceous alien species can have detrimental environmental impacts often only associated with their larger counterparts. Many examples exist in the literature illustrating the widespread and detrimental impacts that herbaceous alien species can elicit both in South Africa and abroad (Macdonald and Frame 1988, D'Antonio and Vitousek 1992, Williams and West 2000, Navie *et* al. 2004, Sharma *et* al. 2005). For example Erskine Ogden and Rejmánek (2005) provide several examples showing how fennel, an exotic herb to Santa Cruz Island in the USA, reduced native species populations and negatively impacted indigenous species richness and diversity. *Tradescantia fluminensis* Vell., a perennial herb originating from South America prevents forest regeneration of native species through shading in many invaded forest remnants in New Zealand and Australia (Standish *et al*. 2001). Similarly, results from this study revealed that dense mono-specific stands of the herbaceous alien species *Xanthium strumarium*, were associated with decreased levels of indigenous species richness and diversity along the Sabie River within the KNP (chapter 2). Thus although alien species within the KNP are dominated more by herbaceous species, it is no less cause for concern, and perhaps management should focus on negating impacts to ecosystem functioning rather than on species specific management, although this can often be limited by time and economic constraints.

Riparian corridors are non-equilibrium ecosystems with dynamic fluvial and hydrological processes and are subject to frequent disturbance events. Flooding in a river can often cause widespread mortality or removal of established riparian vegetation and create new habitats for plant colonisation that are usually reduced to early successional stages through the fluvial erosion-deposition process (Kalliola and Puhakka 1988, Gregory *et al*. 1991, Pollock *et al*. 1998, Parsons *et al*. 2005; 2006, Richardson *et al*. 2007). Many alien species are early seral species that thrive in these low competition, frequently disturbed environments (Huston 2004, Richardson *et al*. 2007). This phenomenon combined with the efficient ability of river corridors to transport alien propagules throughout the landscape, increases the susceptibility of riparian corridors to invasion by exotic species after a large flood (Thebaud and Debussche 1991, Pyšek and Prach 1993, Planty-Tabacchi *et al*. 1996). The extreme flood event in February 2000 caused considerable transformation to the biotic and abiotic components of the riparian corridor (Parsons *et al*. 2006) and an associated increase in IAPs was recorded (Leroy 2003, Parsons *et al*. 2006). However, in years after the flood, alien plants represented only a small portion of KNP Sabie River vegetation (Foxcroft *et al*. 2008b) and it has become evident that many of the species present after the flood were transient species that did not increase or persist over time. As proposed by Foxcroft *et al*. (2008b), the failure of many alien species to establish on the Sabie River after the 2000 flood is likely due to a combination of two factors: the competition from the abundant and rich native vegetation and the continuous clearing operations executed by WfW.

Riparian vegetation is inherently resilient due to the frequent and intense disturbance that occurs in the system - with resilience being defined as the ability to return to a former state, following a disturbance or stress (Wali 1999). Parsons *et al*. (2005) revealed that 75% of woody plant abundance after the large 2000 flood on the Sabie River, within the KNP, was composed of plants that had established after the flood, and only 25% was residual vegetation that had survived the flood. Results from chapter 2 showed that native herbaceous species along the Sabie River increased in density after the disturbance of the removal of dense stands of IAPs. Both these examples illustrate a certain level of resilience of riparian vegetation in the KNP. However, a factor which seems to be important in enhancing this observed resilience is the continuous removal of IAPs by WfW. Invasive alien species have the ability to compromise resilience due to their efficient ability to exert disproportionate competitive influences on other species (Esler *et al*. 2008). Thus, through WfW's continuous clearing efforts, the competitive influence from IAPs is reduced, allowing for a greater opportunity for the establishment and growth of the preferred native species. This has feed-back effects since enhancing the resilience and increasing the competitive influence of the system acts to further minimize the growth and establishment of IAPs. In the KNP, where native species are rich and abundant, and where WfW have been executing IAP removal operations for a prolonged period, it is difficult to determine the hierarchy of each factor in mitigating establishment of IAPs. While further manipulations and studies may provide more insight into this, what is evident is that the combination of the two appears successful in limiting the establishment and spread of alien plant invasions in the KNP.

The lack of species similarity between the upper and mid reaches and the lower reach of the Sabie River catchment is unexpected. However, several factors may have contributed to the lack of similarity or spread of IAPs down the Sabie River catchment. Firstly, studies used for data from the mid and upper catchments were more than 40km upstream of the first sites sampled adjacent to the KNP. Thus there is a large section of river that was not included in this study that could perhaps show a greater level of similarity to species found within the KNP. Furthermore, species found on the Sabie River in the KNP may be from an alternative source other than the riparian corridor. For example, staff and tourist gardens have been shown to be a significant potential source of alien propagules into the system (Foxcroft and Richardson 2003, Foxcroft *et al*. 2008a). Additionally, the road network in the KNP can also be an important pathway for the spread of invasive alien species, as the continuous flux of vehicles traversing in and out the park along tourist roads (many of which are situated along major river systems), could provide a continuous source of alien propagules into the system. While these sources may well add to the spread, riparian corridors are still thought to be the major pathway of spread of IAP species into the KNP.

4.5.2. Temporal assessment of invasive alien plants in the Kruger National Park

The number of alien plant species has increased along the banks of the Sabie River within the KNP over the last 10 years. However, the invasion intensities of most species have remained very low with several records often being the only representation of a species. Certain species are more widespread and often fluctuate in association with environmental fluctuations or disturbances such as the February 2000 flood or the elevated rainfall in 2006, but escalations are usually counteracted by the annual clearing efforts of WfW who reduce IAPs to acceptable and maintainable levels.

Thus, the role of WfW in diminishing the occurrence of alien invasions within the KNP seems paramount. Upstream, where clearing occurred only once with a limited series of follow-ups, invasion intensities returned to pre-clearance levels with a changed structure of invasive alien plants. This has not only made initial clearing efforts redundant but has also created a state that will potentially require greater time at greater economic costs to clear in the future (Beater *et al*. 2008).

The management process developed for managing invasive species in the KNP is still evolving and has undergone substantial changes since its inception in 1997 (Foxcroft and Downey 2008). In particular, TPCs are continually reassessed and adjusted as more information is gathered. While TPC 1 and 2 concerning the distribution of alien species adjacent to and within the KNP are established and operational, TPC 3 regarding alien plant densities is still hypothetical. Results from this study emphasise the need to further develop this TPC as it has been seen that the presence of a species may only be due to a limited number of individuals that do not spread or persist. While monitoring the spread and distribution of alien species as outlined in TPCs 1 and 2 is important, it is equally important to monitor the intensity of invasions once the infestations have been recognised. This is of significant importance when taking the invasion process into consideration as naturalised species can often exist at low levels for extended periods of time, termed a "lag phase", before a rapid exponential increase and spread of the invasion occurs (Mack 1989).

This study has not only reiterated the advantages of repetitive IAP clearing but has also highlighted the need for integrated regional management plans. Although relatively few invasive alien species from upstream have established within the KNP, it does not necessarily mean that the threat has not been present, but rather, that continual clearing efforts have controlled and also potentially mitigated the establishment of many IAP species. If clearing was orchestrated in a coordinated and successional manner along the catchment, pressures on the lower reaches would be substantially lower and resources used in this area for clearing could ultimately be reduced or spread to other areas of need.

However, in a time where protected areas are subject to increasingly greater threats from habitat transformation and climate change, among others (Sala *et al*. 2000), preserving current protected areas is critical. Thus with the lack of integrated control of IAPs further up in the catchment and the ever expanding pressures from IAPs entering the KNP, the need for regular maintenance of the area is essential. Management need not occur on a strictly annual basis but may be more optimal following a dynamic, flexible and reactive schedule that responds to increased threats of IAPs usually associated with a level of disturbance in the area.

CHAPTER 5

Discussion and recommendations

5.1. GENERAL DISCUSSION

By the end of 2006, the highly acclaimed Working for Water (WfW) programme had spent R3.2 billion on clearing 1.6 million ha of invaded land across South Africa (excluding follow-ups of 3.1 million ha), while providing employment to approximately 30 000 people (Marais and Wannenburgh 2008). To secure further funding and ensure the long-term continuation of the programme, its full socio-economic worth needs to be demonstrated. While much of the success of the programme has stemmed from its socio-political emphasis on poverty alleviation and capacity building, very little attention has been given to its environmental and associated economic significance (Turpie 2004). Le Maitre *et al*. (2000) estimated that the incremental water use by invasive alien plants (IAPs) in South Africa was almost twice that used by commercial forestry. This has significant future environmental and economic implications for a country that is already water stressed. WfW was established to remove large tracts of IAPs along riparian corridors with the aim of increasing future water yields. However, despite more than a decade of implementation, little research has been executed to determine whether IAPs in targeted areas have been maintained. Since its inception, the programme has been operating under the assumption that ecosystems "self repair" after the removal of IAPs (Esler *et al*. 2008) and until recently very little monitoring has taken place to determine whether this is in fact the case or whether in some instances further management is necessary (Holmes *et al*. 2005).

A recent project commissioned by WfW, the Ecosystem Repair project, incorporated several studies (including this one) from across the country and aimed a) to assess what level of ecosystem repair is achieved in different situations after IAP clearing; b) to determine achievable targets for repair after clearing of IAPs and c) to use this information to develop management tools that could be incorporated into clearing operations to enhance ecosystem repair after clearing. Results and recommendations from the studies have been pooled and will be published in an upcoming special issue in the "South African Journal of Botany".

One of the studies already mentioned in previous chapters was that by Beater *et al*. (2008), which showed that despite targeted control operations in the upper reaches of the Sabie River catchment, ten years later, invasive alien plants had returned to levels similar to those present prior to clearing by WfW. This has not only made clearing in the area redundant but has also resulted in an altered state of the invasion which is likely to require greater time at greater economic costs to clear in the future. In contrast, results from this study show that in the KNP, over the last ten years, densities and numbers of invasive alien species have remained surprisingly low, despite the frequency of disturbance in the system, as well as the ever increasing threat from substandard management practices further upstream. Much of the success in controlling invasive alien plants over the last decade in the KNP has been attributed to the continuous clearing operations executed by WfW. The three main themes emerging from this study that are essential to enhance successful control of IAPs are 1) post-clearance monitoring; 2) ecosystem repair; and 3) follow-up clearing.

5.1.1. Post clearance monitoring

Monitoring of the system after IAP removal operations is essential (e.g. Woolsey *et al*. 2007). However, this is rarely, if ever executed and has been identified as an important subject that is severely lacking (especially with reference to WfW, Holmes *et al*. 2003). Monitoring is imperative in assessing the efficacy of clearing practices. For example, Witkowski and Garner (2008) found that substandard clearing practices in the upper Sabie River catchment resulted in resprouting of targeted *Solanum mauritianum* plants, making much of the clearing operations redundant. A simple solution of ensuring plants were cut below the correct height resulted in 100% mortality of the plants. A further example is a study by Blanchard and Holmes (2008) who used monitoring to assess whether fell and remove, fell and burn or fell only clearing methods resulted in the best ecosystem repair after invasive alien tree removal in the Western Cape. Monitoring after clearing operations showed that fell and remove methods were most suitable for promoting ecosystem recovery and minimising reinvasion by alien species in a fynbos region.

Monitoring is also imperative when aiming to assess whether the expected outcomes of clearing or controlling IAPs has been acheived. The immediate goal after clearing of IAPs is to prevent reinvasion or secondary invasion by other alien species so that the ultimate outcome of restoring the system to a desired state can be achieved. To limit reinvasion we assume that natural revegetation must occur (Holmes *et al*. 2008). Monitoring is essential after the removal of IAPs to assess whether natural indigenous revegetation of indigenous plants has occurred or whether further management steps in the form of additional follow-up operations or active restoration efforts are necessary.

Monitoring in this study revealed that through regular clearing, effective reduction in IAP numbers and densities had occurred. Indigenous vegetation re-established after the removal of IAPs and re-invasion by the same or other alien species was minimal.

5.1.2. Ecosystem repair

It has been recognized that regrowth of indigenous vegetation after clearing of IAPs is fundamental not only to exert a competitive force on alien species that acts to further suppress re-invasion (Pyšek and Pyšek 1995, Bakker and Wilson 2004, Taylor and McDaniel 2004), but is also necessary to fulfil basic ecological functioning (Holmes *et al*. 2008). Depending on the type, size and periodicity of the invasions, the survival strategy of contributing invasive species and the efficacy of control measures, sites can sometimes recover naturally. Bay and Sher (2008) provide several examples where native species regenerated naturally after the removal of invasive *Tamarix* trees along several rivers in the USA. However, Shafroth and Briggs (2008) provide examples from the USA showing the alien tree *Tamarix* often reinvades after removal operations on rivers with regulated flows, in contrast to rivers with natural flow regimes where natural revegetation usually occurs after clearing. Results from this study, as well as several others in South Africa (e.g. Holmes *et al*. 2008), have shown that removal of IAPs alone, in most cases, improves ecosystem integrity and facilitates the re-establishment of native riparian vegetation structure and functioning. However, in other instances, for example where stands of IAPs have been present for extended periods or when hydrological regimes of the river have been altered the need for active intervention in order for native vegetation to recover is required (Holmes *et al*. 2008).

This example highlights that river ecosystems are part of the broader landscape and the scale and potential for riparian restoration depends on the condition, land-use and management of adjacent systems throughout the catchment area (Richardson *et al*. 2007). Restoration requires the consideration of ecological factors such as the extent of degradation and availability of indigenous propagules, as well as non ecological, human mediated factors (Holmes *et al*. 2008). For example, several studies have shown that successful restoration often hinges on re-establishing the hydrological regime of the river (Stromberg 2001, Rood *et al*. 2003). Restoration targets should thus be realistic and feasible and based on desired future characteristics rather than restricted to some historical target that is more than likely unattainable (Hobbs and Harris 2001, Hughes *et al*. 2005, Holmes *et al*. 2005, Richardson *et al*. 2007).

Techniques used in ecosystem restoration are many and wide-ranging and include re-establishing soil seed banks (van der Valk and Pederson 1989, Prins *et al*. 2004); the use of fire, not only to reset plant community succession (Davy 2002) but also to stimulate seedbank activation as is necessary for many species in the fynbos (Le Maitre and Midgley 1992, Holmes and Newton 2004) and manipulation of growth conditions (e.g. impeding growth of IAPs by reducing the amount of N in the soil (Blumenthal *et al*. 2003)).

However, revegetation of indigenous species in the system alone is not always sufficient and an integrated management plan, including follow-up clearing is often necessary. Pretorius *et al*. (2008) in the Western Cape, revealed that sites cleared of dense *Acacia mearnsii* stands that were actively revegetated by sowing seeds into the system showed promising recovery of indigenous species richness and abundance. However, seven years later, after receiving only one follow-up clearing operation in the year subsequent to active restoration, *A*. *mearnsii* had reinvaded the area and again dominated the vegetation.

5.1.3. Follow-up clearing

Follow-up clearing is essential to gain long-term control of IAPs. Results from this study show that repetitive clearing of IAPs is successful in limiting the extent of invasions. However, the situation in the KNP, with the continuous presence of WfW is an uncommon scenario. Continuous follow-up clearing on such a large and extended scale is not practical elsewhere and would be very costly on a wider scale. Thus under normal circumstances across the country where IAP control occurs, best efforts should be made to utilise integrated management plans that incorporate monitoring, ecosystem repair and feasible follow-up clearing operations. The use of biocontrol should also be considered where possible as this is often seen as a sustainable and cost effective option when aiming for long-term control of certain invasive alien species (Olckers *et al*. 1998, Olckers and Hill 1999).

5.2. RECOMMENDATIONS

Working for Water

While WfW have made great achievements in the effort to control alien plant invasions in South Africa, the funding of the programme is insufficient to effectively curb further invasion. This fact, together with the reality that as fast as alien clearing occurs, old invasions expand, and new invasions sprout, makes the task of clearing IAPs an ongoing challenge (Turpie 2004). In order to make headway in the monumental task of controlling IAPs, there is a need to optimise operations and prevent reinvasion in areas that have already been cleared. To do this the following is suggested:

- Execute a greater number of follow-up clearing operations – several studies have shown the need for greater follow-up clearing (Beater *et al*. 2008, Pretorius *et al*. 2008).
- Optimise clearing operations – many recent examples have shown that alien clearing alone in most cases facilitated restoration of riparian vegetation. Further investigation needs to be undertaken to test which clearing methods or combination of clearing methods results in the best ecosystem recovery (e.g. Blanchard and Holmes 2008).
- Strategic catchment control – WfW's strategic planning prioritises invasion fronts and outliers thus preventing further invasion and degradation (Anon. 2004). However, sustainable long-term control in the upper catchments is important to prevent the spread of invasions in the first place, and operations should hence be executed systematically down the catchment.
- Increased monitoring – monitoring is essential, not only to learn from successful control efforts but just as importantly, to learn from failures so that clearing operations can ultimately be executed in the most optimal fashion.
- Need for research – combined with monitoring, future research is needed to investigate the long-term effectiveness of different control and repair strategies and to assess the benefits of each in terms of associated costs.

Kruger National Park

The position of the KNP in the lower reaches of several major river catchments provides an ongoing management challenge with regards to IAPs. The KNP is one of the largest conservation areas in the world and is dedicated to "preserving biodiversity in its natural facets and fluxes". Impacts and threats of IAPs clearly contravene conservation efforts and thus will always be a major concern for management. The WfW partnership in the KNP has been instrumental in combating alien plant invasions, and to date has spent well over R20 million in the KNP alone (Foxcroft and Richardson 2003). WfW have provided an indispensable service on a large scale that KNP management would not be able to replicate with their limited budget. Thus the ongoing partnership of SANParks with WfW is extremely valuable in the endeavour to preserve KNP biodiversity.

This study has provided valuable information with regards to the research objectives outlined by KNP alien management. It has also highlighted the importance of further refining alien TPCs. TPCs 1 and 2 concerning alien species distribution are currently operational whereas TPC 3 concerning the density of alien plant invasions is still hypothetical, due to the lack of efficient cost-effective monitoring protocols. As seen from this study, several alien species may be transient in the KNP and while TPC 1 and 2 may raise the alarm to their presence, the extent of invasion by a particular species and its possible associated impacts, go unchecked. Thus, the need for development of TPC 3 concerning the density of an invasive alien species is of utmost importance. While resources are understandably limited for the monitoring needs that would be associated with this TPC, efforts to investigate alternative methods or strategies need to be made. Perhaps integrating monitoring by trained designated persons associated with the annual clearing operations of WfW could provide the necessary information as well as vital data needed for long-term monitoring operations.

Several recommendations are made for KNP management:

- Efforts should be made to continue the successful partnership of KNP management with WfW.
- The permanent presence of WfW in the KNP provides ideal research and monitoring opportunities and efforts should be made to further integrate KNP alien species management and research teams with WfW operations.
- Levels of IAPs further downstream in the KNP are considerably lower, however most of the time these areas are still subject to annual clearing operations.

Defining a hierarchy of target areas that are attended to accordingly would stretch resources into other areas of need. For example, areas in the lower reaches of the Sabie River within the KNP perhaps need not be cleared every year but may only need attention every second or third year to prevent any small level of invasion that may be present from expanding or spreading further downstream into Mozambique.

- Disturbance has a large influence on IAP dynamics within savanna riparian zones. Once again, making clearing operations dynamic and responsive, enforcing clearing when we know there to be a potentially large threat (e.g. after floods or extreme rainfall events), may be more optimal than having a standard, routine clearing schedule.
- As IAPs exist at greater intensities closer to the western border of the park, clearing these areas at certain times of the year would be better than random scheduling. For example, clearing dense stands of IAPs before they have the opportunity to set seed (which once cleared are usually just left in the system), will prevent further spread and re-invasion in the following season.

5.3. FUTURE AREAS OF RESEARCH

From this study in connection with the Ecosystem repair project, several further areas of research need have been identified.

1) Research into the cost benefit ratios of continuous follow-ups vs. follow-ups integrated with restoration is important for long-term management considerations by WfW.
2) Monitoring of alien species on the Sabie River within the 40 km zone above the western border that was not included in any of the studies compared in this project may provide more information concerning the nature of spread of IAPs down the catchment as well as also potential information on the rate of spread.
3) Research into the relative processes of reinvasion by alien plants (e.g. recruitment from seedbank, new propagule arrival, recruitment from seeds dispersed by surviving adult plants, resprouting of cleared plants etc.) may help to management of invasive plants in riparian areas.
4) Monitoring, perhaps integrated with other studies or programmes in the area, is essential. Many studies along the Sabie River have provided excellent baseline data to which future comparisons can be made.

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APPENDICES

Appendix 1. Coordinates of study sites within and adjacent to the Kruger National Park.

Transect no.	In/Out KNP	Coordinates (Dec. deg.)	
		S	E
1	Out	25.02002	31.21668
2	Out	25.01883	31.22106
3	Out	25.01894	31.24160
4	In	25.01676	31.25560
5	In	24.97391	31.33964
6	In	24.97251	31.39299
7	In	24.96425	31.56878
8	In	24.96336	31.68244
9	In	24.96125	31.73330
10	In	24.97856	31.76772
11	In	25.10137	31.89148
12	In	25.18706	32.03075

Appendix 2. List of plant species found along the Sabie river in this study including: naming authorities; taxonomic family; native or alien status and in which transects the species were found. The invasive status of alien plants is noted in brackets according to Regulation 15 of the Conservation of Agricultural Resources Act, 1983 (Act No. 43 of 1983) as described in Henderson (2001). DW1= Declared weed category 1; DI2 = Declared invader category 2; DI3 = Declared invader category 2; P3 = Proposed category 3.

Species	Authorities	Family	Alien/ Indigenous	Growth form	Transect											
					1	2	3	4	5	6	7	8	9	10	11	12
Acanthospermum hispidium	DC.	Asteraceae	Alien	Herb	X			X	X	X	X	X	X	X	X	
Achyranthes aspera var. *aspera*	L.	Amaranthaceae	Alien (DW1)	Herb			X	X			X	X	X	X	X	
Ageratum conyzoides	L.	Asteraceae	Alien (DW1)	Herb	X	X	X	X	X	X	X	X	X	X	X	X
Alternanthera pungens	H.B.K.	Amaranthaceae	Alien	Herb										X	X	X
Amaranthus spinosus	L	Amaranthaceae	Alien	Herb	X	X	X									
Amaranthus virosa	L.	Amaranthaceae	Alien	Herb				X		X						
Argemone ochroleuca	L.	Papavaraceae	Alien (DW1)	Herb												X
Bidens pilosa	L.	Asteraceae	Alien	Herb	X	X	X	X	X	X	X	X	X	X	X	X
Caesalpinia decapetala	(Roth) Alston	Caesalpiniaceae	Alien (DW1)	Shrub					X							
Cardiospermum grandiflora	L.	Sapindaceae	Alien (DW1)	Shrub	X											
Cardiospermum halicacabum	L.	Sapindaceae	Alien (P3)	Shrub	X			X		X	X	X	X		X	X
Cocculus hirsutus	L.	Menispermaceae	Alien	Herb											X	
Conyza albida	Spreng,	Asteraceae	Alien	Herb												X
Conyza bonariensis	(L.) Cronq.	Asteraceae	Alien	Herb												X
Corchorus tridens	L.	Tiliaceae	Alien	Herb				X	X						X	
Corchorus trilocularis L.	L.	Tiliaceae	Alien	Herb						X						
Datura stramonium	L.	Solanaceae	Alien (DW1)	Shrub	X			X	X	X	X	X				
Duranta erecta	L.	Verbenaceae	Alien (P3)	Shrub			X									
Euphorbia heterophylla	L.	Euphorbiaceae	Alien	Herb				X		X						
Euphorbia hirta	L.	Euphorbiaceae	Alien	Herb							X	X				X
Euphorbia prostrata	Aiton	Euphorbiaceae	Alien	Herb											X	
Glinus lotoides	L.	Molluginaceae	Alien	Herb												X
Gomphrena celosioides	Mart.	Amaranthaceae	Alien	Herb									X		X	X
Hyptis pectinata	Poit.	Lamiaceae	Alien	Herb								X				
Lantana camara	L.	Verbenaceae	Alien (DW1)	Shrub	X	X	X	X	X	X	X	X	X		X	X

Species	Authorities	Family	Alien/ Indigenous	Growth form	Transect											
					1	2	3	4	5	6	7	8	9	10	11	12
Leucaena leucocephala	(Lam.) de Wit	Fabaceae	Alien (DI2)	Tree		X										
Malvastrum coromandelianum	(L.) Garcke	Malvaceae	Alien	Herb		X		X	X	X	X	X	X	X	X	X
Melia azedarach	L.	Burseraceae	Alien (DI3)	Tree	X	X										
Mimosa pigra	L.	Fabaceae	Alien (DI3)	Shrub	X				X							
Momordia charantia	L.	Cucurbitaceae	Alien	Herb				X	X	X	X				X	
Nicotiana glauca	Graham	Solanaceae	Alien (DW1)	Shrub							X					
Parthenium hysterophorus	L.	Asteraceae	Alien (DW1)	Herb	X								X			
Richardia brasiliensis	Gomez	Rubiaceae	Alien	Herb	X	X	X	X	X	X	X		X	X		
Ricinus comunis	L.	Euphorbiaceae	Alien (DI2)	Shrub	X											
Rubus cuneifolius	Pursh.	Rosaceae	Alien (DW1)	Shrub		X										
Senna didymobotrya	(Fresen.) Irw. & Barn.	Fabaceae	Alien (DI3)	Shrub	X					X						
Senna obtusifolia	(L.) Irw. & Barn.	Fabaceae	Alien	Shrub	X		X	X	X	X	X	X		X	X	X
Senna occidentalis	(L.) Link	Fabaceae	Alien	Shrub	X	X	X	X		X	X	X	X	X	X	X
Sesbania bispinosa var. *bispinosa*	(Jacq.) W.Wight	Fabaceae	Alien	Herb	X	X										
Sesbania puniceae	(Cav.) Benth.	Fabaceae	Alien (DW1)	Tree		X		X	X	X		X				
Solanum nigrum	L.	Solanaceae	Alien	Herb			X									
Solanum seafotheanum var. *disjunctum*	Andrews	Solanaceae	Alien (DW1)	Herb				X				X		X		
Sphagneticola trilobata	(L.) Pruski	Asteraceae	Alien	Herb				X		X						
Stachytarpetta mutabilis	(Jacq.) Vahl.	Verbenaceae	Alien	Shrub		X		X								
Tagetes minuta	L.	Asteraceae	Alien	Herb	X	X	X	X	X	X	X	X	X	X	X	X
Tithonia diversifolia	(Hemsl.) A.Gray	Asteraceae	Alien (DW1)	Herb	X		X		X							
Tithonia rotundifolia	S.F. Blake	Asteraceae	Alien (DW1)	Herb					X							
Tridax procumbens	L.	Asteraceae	Alien	Herb		X			X		X			X		X
Triumfetta pentandra var. *pentandra*	A.Rich	Tiliaceae	Alien	Herb	X		X	X	X	X	X	X	X	X	X	X
Verbena bonariensis	L.	Verbenaceae	Alien	Herb		X		X	X				X			
Xanthium strumarium	L.	Asteraceae	Alien (DW1)	Herb	X	X			X	X	X	X	X	X		

Species	Authorities	Family	Alien/ Indigenous	Growth form	Transect											
					1	2	3	4	5	6	7	8	9	10	11	12
Abutilon angulatum	(Guill. & Perr.) Mast.	Malvaceae	Indigenous	Herb	X											
Abutilon austro-africanum	Hochr.	Malvaceae	Indigenous	Herb									X	X		
Abutilon ramosum	(Cav.) Guill. & Perr.	Malvaceae	Indigenous	Herb				X	X	X	X	X	X	X	X	
Acacia ataxacantha	DC.	Mimosaceae	Indigenous	Shrub	X											
Acacia grandicornuta	Gerstner	Mimosaceae	Indigenous	Tree					X			X	X	X		
Acacia nigrescens	Oliv	Mimosaceae	Indigenous	Tree					X				X			X
Acacia robusta subsp. *clavigera*	Burch	Mimosaceae	Indigenous	Tree					X	X	X	X	X	X		X
Acacia schweinfurthii var. *schweinfurthii*	Brenan & Exell	Mimosaceae	Indigenous	Shrub					X	X	X		X			
Acacia sieberiana var. *woodii*	(Burt Davy) Keay & Bren.	Mimosaceae	Indigenous	Tree		X										
Acacia xanthophloea	Benth	Mimosaceae	Indigenous	Tree			X									
Acalypha glabrata	Thunb.	Euphorbiaceae	Indigenous	Tree							X		X	X		
Acalypha indica var. *indica*	L.	Euphorbiaceae	Indigenous	Herb								X		X	X	X
Acalypha villicaulis	Hochst.	Euphorbiaceae	Indigenous	Herb		X		X								X
Agathisanthemum bojeri	Klotzsch	Rubiaceae	Indigenous	Herb				X								
Albizia forbesii	Benth.	Mimosaceae	Indigenous	Tree									X	X		
Albizia harveyi	Fourn.	Mimosaceae	Indigenous	Tree	X	X								X		
Albizia versicolor	Welw. Ex Oliv.	Mimosaceae	Indigenous	Tree	X											
Antidesma venosum	E.Mey. ex Tul.	Euphorbiaceae	Indigenous	Tree		X										
Asparagus setaceus	(Kunth) Jessop	Asparagaceae	Indigenous	Shrub							X					
Balanites pedicillaris subsp. *pedicillaris*	Mildr. Schlect.	Balanitaceae	Indigenous	Shrub										X		X
Barleria elegans	S.Moore ex C.B.Clarke	Acanthaceae	Indigenous	Herb				X	X	X		X	X			
Bauhinia galpinii	N.E.Br.	Caesalpiniaceae	Indigenous	Shrub	X	X										
Berchemia discolor	(Klotzsch) Hemsl.	Rhamnaceae	Indigenous	Tree				X			X	X	X	X		
Bothriochloa insculpta	(Hochst.) A.Camus	Poaceae	Indigenous	Graminoid		X			X				X			

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					1	2	3	4	5	6	7	8	9	10	11	12
Brachiaria brizantha	(A.Rich.) Stapf	Poaceae	Indigenous	Graminoid		X										
Bridelia cathartica	Bertol. f.	Euphorbiaceae	Indigenous	Tree	X	X							X	X	X	X
Bridelia micrantha	(Hochst.) Baill.	Euphorbiaceae	Indigenous	Tree		X										
Capparis fascicularis var. *fascicularis*	DC.	Capparaceae	Indigenous	Shrub								X				
Capparis tomentosa	Lam.	Capparaceae	Indigenous	Shrub					X	X	X	X	X	X		
Cassia abbreviata subsp. *beareana*	Oliv./ (Holmes) Brenan	Caesalpiniaceae	Indigenous	Tree								X				
Cenchrus ciliaris	L.	Poaceae	Indigenous	Graminoid	X				X				X			X
Chamaecrista absus	(L.) Irwin & Barneby	Fabaceae	Indigenous	Herb	X						X			X		X
Chamaecrista mimosoides	(L.) Greene	Fabaceae	Indigenous	Herb	X	X			X							
Chenopodium involuta	L.	Chenopodiaceae	Indigenous	Herb												X
Chloris gayana	Kunth.	Poaceae	Indigenous	Graminoid		X										
Chloris virgata	Sw.	Poaceae	Indigenous	Graminoid									X	X		X
Cissus cornifolia	(Baker) Planch.	Vitaceae	Indigenous	Shrub												X
Clerodendrum ternatum	Schinz	Lamiaceae	Indigenous	Shrub					X							
Combretmu imberbe	Wawra	Combretaceae	Indigenous	Tree							X	X			X	
Combretum apiculatum subsp. *apiculatum*	Sond.	Combretaceae	Indigenous	Tree												X
Combretum erythrophyllum	(Burch.) Sond.	Combretaceae	Indigenous	Tree	X	X			X		X	X				
Combretum heroroense	Schinz	Combretaceae	Indigenous													X
Combretum microphyllum	Klotzsch	Combretaceae	Indigenous	Shrub								X		X	X	
Combretum molle	R.Br. Ex G.Don.	Combretaceae	Indigenous	Tree					X			X		X		
Combretum mossambicense	(Klotzsch)	Combretaceae	Indigenous	Tree									X			
Combretum zeyheri	Sond.	Combretaceae	Indigenous	Tree												X
Commelina benghalensis	L.	Commelinaceae	Indigenous	Herb		X						X				
Commicarpus plumbagineus	Standl.	Nyctaginaceae	Indigenous	Herb								X				
Crabbea velutina	S.Moore	Acanthaceae	Indigenous	Herb							X					X

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					1	2	3	4	5	6	7	8	9	10	11	12
Crinum delagoense	Baker	Amaryllidaceae	Indigenous	Herb			X									
Crotalaria capensis	Jacq.	Fabaceae	Indigenous	Shrub	X											
Crotalaria lanceolata subsp. *lanceolata*	E.Mey.	Fabaceae	Indigenous	Herb	X	X	X									
Crotalaria pallida var. *pallida*	Aiton.	Fabaceae	Indigenous	Herb				X								
Crotalaria sphaerocarpa subsp. *sphaerocarpus*	Perr. Ex DC.	Fabaceae	Indigenous	Herb	X			X	X			X			X	
Cynadon dactylon	(L.) Pers.	Poaceae	Indigenous	Graminoid	X	X	X	X	X	X	X	X	X	X	X	X
Cyperus esculentus	L.	Cyperaceae	Indigenous	Graminoid												X
Cyperus sexangularis	Nees	Cyperaceae	Indigenous	Graminoid						X					X	X
Dactyloctenium giganteum	B.S.Fisher & Scweick	Poaceae	Indigenous	Graminoid					X							X
Dalbergia armata	E.Mey.	Fabaceae	Indigenous	Shrub					X							
Dalbergia melanoxylon	Guill. & Perr.	Fabaceae	Indigenous	Tree		X	X	X								X
Deinbollia oblongifolia	(E.Mey. Ex Arn.) Radlk.	Sapindaceae	Indigenous	Shrub												X
Desmodium tortuosum	(Sw.) DC.	Fabaceae	Indigenous	Herb	X	X	X		X	X						
Dichrostachys cinerea	(L.) Wight & Arn.	Mimosoideae	Indigenous	Shrub	X	X	X	X	X	X	X	X	X	X	X	
Dicliptera clinopodia	Nees	Acanthaceae	Indigenous	Herb								X	X			
Digitaria eriantha	Steud.	Poaceae	Indigenous	Graminoid	X			X	X		X		X			X
Diospyros mespiliformis	Hochst. Ex A.DC.	Ebenaceae	Indigenous	Tree	X	X	X	X	X	X	X	X	X	X	X	X
Diospyros whyteana	(Hiern)	Ebenaceae	Indigenous	Shrub							X					
Dombeya rotundifolia	(Horchst.) Planchon	Sterculiaceae	Indigenous	Tree		X										
Dovyalis caffra	(Hook.f. & Harv.) Hook.f.	Flacourtiaceae	Indigenous	Shrub		X										
Ehretia amoena	Klotzsch	Boraginaceae	Indigenous	Shrub	X	X	X	X			X	X			X	X
Ehretia rigida	(Thunb.) Druce	Boraginaceae	Indigenous	Shrub	X	X						X	X			X

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					1	2	3	4	5	6	7	8	9	10	11	12
Elaeodendron transvaalense	(Burtt Davy) R.H.Archer	Celastraceae	Indigenous	Tree					X							
Eleusine coracana	Gaertn.	Poaceae	Indigenous	Graminoid										X	X	
Eragrostis ciliaris	Kunth.	Poaceae	Indigenous	Graminoid				X								
Eragrostis pseudosclerantha	Chiov.	Poaceae	Indigenous	Graminoid												X
Eragrostis rigidior	Pilg	Poaceae	Indigenous	Graminoid				X								
Eragrostis superba	Peyr.	Poaceae	Indigenous	Graminoid				X			X				X	X
Eragrostis tricophora	Coss. & Durieu	Poaceae	Indigenous	Graminoid		X		X		X	X	X	X	X		X
Eriochloa meyeriana	(Nees) Pilg.	Poaceae	Indigenous	Graminoid	X									X		X
Eriosema psoraleoides	(Lam.) G. Don	Fabaceae	Indigenous	Shrub	X	X										
Euclea daphnoides	Hiern.	Ebenaceae	Indigenous	Tree												X
Euclea divinorum	Hiern	Ebenaceae	Indigenous	Tree				X	X		X	X	X			
Euclea natalensis subsp. *natalensis*	A.DC/ F.White	Ebenaceae	Indigenous	Tree	X	X	X	X	X	X	X	X	X	X	X	X
Euclea shimperi	(A.DC.) Dandy	Ebenaceae	Indigenous	Tree						X				X		
Ficus capreifolia	Delile	Moraceae	Indigenous	Shrub					X		X				X	
Ficus sycomorus subsp. *sycomorus*	L.	Moraceae	Indigenous	Tree		X	X	X								
Flacourtia caffra	Merr.	Flacourtiaceae	Indigenous	Tree		X										
Flueggea virosa subsp. virosa	(Pax & K.Hoffm.	Euphorbiaceae	Indigenous	Shrub	X	X		X	X		X	X	X	X	X	X
Galpinia traansvaalica	N.E.Br.	Lythraceae	Indigenous	Tree												X
Gardenia volkensii subsp. *volkensii*	K.Schum	Rubiaceae	Indigenous	Tree					X		X		X	X		
Grewia bicolor	Juss.	Malvaceae	Indigenous	Shrub					X			X	X	X	X	
Grewia flavescens var. *flavescens*	Juss.	Malvaceae	Indigenous	Shrub		X			X	X	X	X	X	X	X	X
Grewia hexamita	Burret	Tiliaceae	Indigenous	Shrub								X				
Grewia monticola	Sond.	Malvaceae	Indigenous	Shrub		X		X	X			X			X	
Grewia villosa	Willd.	Malvaceae	Indigenous	Shrub							X	X	X	X	X	X
Gymnosporia glaucophylla	M.Jordaan	Celastraceae	Indigenous	Tree								X	X			

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					1	2	3	4	5	6	7	8	9	10	11	12
Gymnosporia senegelensis	(Lam.) Loes.	Celastraceae	Indigenous	Tree	X	X	X	X	X	X	X	X	X	X	X	X
Hermania boraginiflora	Hook.	Sterculiaceae	Indigenous	Herb											X	
Hermania c.f. glanduligera	k. ex Schinz	Sterculiaceae	Indigenous	Herb		X										X
Heteropogon contortus	(L.) Roem. & Schult.	Poaceae	Indigenous	Graminoid		X		X								X
Heteropyxis natalensis	Harv.	Heterpyxidaceae	Indigenous	Tree		X			X							
Hibiscus calyphyllus	Cav.	Malvaceae	Indigenous	Herb						X			X			
Hibiscus engleri	K.Schum	Malvaceae	Indigenous	Herb	X	X			X							X
Hibiscus micranthus var. *micranthus*	L.f.	Malvaceae	Indigenous	Shrub											X	
Hibiscus surratensis	L.	Malvaceae	Indigenous	Herb	X											
Hyperthelia dissoluta	(Nees ex Steud.) Clayton	Poaceae	Indigenous	Graminoid	X	X	X	X					X			
Hypoestes forskaali	(Vahl) R.Br.	Acanthaceae	Indigenous	Herb	X	X					X	X		X	X	
Indigofera arrecta	Hochst. ex A.Rich	Fabaceae	Indigenous	Herb	X	X			X		X				X	
Indigofera astragalina	DC.	Fabaceae	Indigenous	Herb				X		X	X	X		X		
Indigofera tinctoria var*. arcuata*	L. / J.B.Gillet	Fabaceae	Indigenous	Herb											X	
Ipomea dichroa	Choisy	Convolvulaceae	Indigenous	Herb			X									
Jacquemontia tamnifolia	(L.) Griseb.	Convolvulaceae	Indigenous	Herb						X						
Jasminum fluminense subsp. *fluminense*	Vell.	Oleaceae	Indigenous	Shrub				X								
Justicia flava	(Vahl.) Vahl	Acanthaceae	Indigenous	Herb		X				X				X		X
Justicia protracta subsp*. protracta*	(Nees) T.Anderson	Acanthaceae	Indigenous	Herb		X	X	X	X		X	X	X	X	X	
Kigelia africana	(Lam.) Benth.	Bignoniaceae	Indigenous	Tree		X		X		X				X	X	
Kohautia virgata	(Willd.) Bremek.	Rubiaceae	Indigenous	Herb												X
Kraussia floribunda	Harv.	Rubiaceae	Indigenous	Tree	X			X	X	X		X				X
Lannea schweinfurthii	(Engl.) Engl.	Anacardiaceae	Indigenous	Tree					X							

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					1	2	3	4	5	6	7	8	9	10	11	12
Lantana rugosa	Thunb.	Verbenaceae	Indigenous	Shrub								X				
Leonotis intermedia	Lindl.	Lamiaceae	Indigenous	Shrub					X	X	X				X	
Leucas glabrata	R. Br.	Lamiaceae	Indigenous	Herb	X	X	X		X	X						
Lippia javanica	(Burm.f.) Spreng	Verbenaceae	Indigenous	Shrub	X	X	X	X	X		X	X	X	X	X	X
Lippia wilmsii	H.Pearson	Verbenaceae	Indigenous	Shrub					X							
Litogyne gariepina	(DC.) Anderb.	Asteracea	Indigenous	Herb												X
Maclura africana	(Bereau) Corner	Moraceae	Indigenous	Shrub												X
Melhania forbesii	Planch. Ex Mast.	Sterculiaceae	Indigenous	Herb					X			X		X		X
Monechma debile	(Forssk.) Nees	Acanthaceae	Indigenous	Herb	X	X	X	X								
Monechma divarticum	Nees	Acanthaceae	Indigenous	Shrub											X	
Mystroxylon aethiopicum	Thunb. Loes.	Celastraceae	Indigenous	Shrub				X	X							
Nuxia oppositifolia	(Hochst.) Benth.	Buddlejaceae	Indigenous	Tree					X		X					
Ochna natalensis	(Meisn.) Walp.	Ochnaceae	Indigenous	Tree										X		
Ocimum americanum var. *americanum*	L.	Lamiaceae	Indigenous	Herb				X	X						X	X
Ocimum gratissimum	Forssk.	Lamiaceae	Indigenous	Herb				X								X
Onconoba spinosa	Forssk.	Flacourtiaceae	Indigenous	Shrub		X										
Oxyganum sinuatum	Dammer	Polygonaceae	Indigenous	Herb						X						
Panicum coloratum	L.	Poaceae	Indigenous	Graminoid								X				
Panicum deustum	Thunb.	Poaceae	Indigenous	Graminoid					X		X	X	X	X		X
Panicum maximum	Jacq.		Indigenous	Graminoid	X	X	X	X	X	X	X	X	X	X	X	X
Pavetta catophylla	K.Schum	Rubiaceae	Indigenous	Shrub								X	X	X		
Pavetta lanceolata	Eckl.	Rubiaceae	Indigenous	Tree								X				
Peltophorum africanum	Sond.	Caesalpiniaceae	Indigenous	Tree		X						X				
Perotis patens	Gand.	Poaceae	Indigenous	Graminoid				X								
Philinoptera violaceae	Rolfe	Papiloinoideae	Indigenous	Tree		X	X	X	X	X		X	X	X	X	X

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Phragmites mauritinus	Kunth.	Poaceae	Indigenous	Graminoid	X					X					X	
Phyllanthus asperulatus	Hutch.	Euphorbiaceae	Indigenous	Herb		X		X			X				X	X
Phyllanthus reticulatus var. *reticulatus*	Poir.	Euphorbiaceae	Indigenous	Shrub	X	X	X	X	X	X	X	X	X	X	X	X
Piliostigma thonningii	(Schumach.) Milne-Redh.	Caesalpiniaceae	Indigenous	Tree		X										
Plectroniella armata	(K.Schum) Robyns	Rubiaceae	Indigenous	Shrub										X		
Pluchea dioscoridis	(L.) DC.	Asteracea	Indigenous	Shrub		X	X		X	X		X				X
Pogonarthria squarrosa	Pilg.	Poaceae	Indigenous	Graminoid				X								
Pouzolzia mixta	Solms	Urticaceae	Indigenous	Shrub		X										
Pristomera longpetiolata	(Oliv.) N.Hallé	Celestraceae	Indigenous	Shrub		X			X		X		X	X		
Ptaeroxylon obliquum	(thunb.) Radlk.	Ptaeroxylaceae	Indigenous	Tree												X
Pterocarpus rotundifolius subsp. *rotundifolius*	(Sond.) Druce	Fabaceae	Indigenous	Tree		X										
Pupalia lappacea var. *lappaceae*	(L.) A.Juss	Amaranthaceae	Indigenous	Herb							X		X	X		X
Pyrenacantha grandiflora	Baill.	Icacinaceae	Indigenous	Shrub		X			X	X						
Pyrostria hystrix	(Bremek.) Bridson.	Rubiaceae	Indigenous	Shrub								X		X		
Rhinacanthus xerophilus	A.Meeuse	Acanthaceae	Indigenous	Herb								X				
Rhoicissus tridentata subsp. *cuneifolia*	(L.f.) Wild & R.B.Drumm.	Vitaceae	Indigenous	Herb		X										
Rhus guenzii	Sond.	Anacardiaceae	Indigenous	Tree					X			X	X	X		
Rhus pentherii	Zahlbr.	Anacardiaceae	Indigenous	Tree	X	X		X	X							
Rhus pyroides var. *pyroides*	Burch.	Anacardiaceae	Indigenous	Tree			X	X								
Rhynchosia minima var. *minima*	(L.) DC.	Fabaceae	Indigenous	Herb		X	X		X				X			
Ruellia cordata	Thunb.	Acanthaceae	Indigenous	Herb										X		
Ruellia patula	Jacq.	Acanthaceae	Indigenous	Herb									X	X		X
Schotia brachypetala	Sond.	Caesalpiniaceae	Indigenous	Tree	X	X		X			X					

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Sclerocarya birrea subsp. *caffra*	(A.Rich) Hochst.	Anacardiaceae	Indigenous	Tree	X	X	X	X								X
Senna petersiana	(Bolle) Lock	Fabaceae	Indigenous	Shrub				X	X					X		
Setaria incrassata	(Steud.) Dur. & Shinz	Poaceae	Indigenous	Graminoid					X							
Sida acuta subsp. *acuta*	(Burm.) F.	Malvaceae	Indigenous	Shrub	X	X			X	X			X		X	
Sida alba	L.	Malvaceae	Indigenous	Herb					X		X	X	X	X	X	X
Sida cordifolia	L.	Malvaceae	Indigenous	Herb	X			X	X	X	X	X	X	X	X	
Smilax anceps	Willd.	Smilacaceae	Indigenous	Shrub		X										
Solanum panduriform	E.Mey.	Solanaceae	Indigenous	Herb	X		X							X	X	X
Sorghum bicolour	L.	Poaceae	Indigenous	Graminoid	X	X		X								
Spermacoce senensis	(Klotzsch) Hiern.	Rubiaceae	Indigenous	Herb				X						X		
Sphaeranthus peduncularis subsp. *peduncularis*	DC.	Asteraceae	Indigenous	Herb												X
Spirostachys africana	Sond.	Euphorbiaceae	Indigenous	Tree							X	X	X			
Sporobolus fimbriatus	(Trin.) Nees	Poaceae	Indigenous	Graminoid	X	X			X	X	X		X		X	X
Strychnos madagascariensis	Poir.	Strychnaceae	Indigenous	Tree					X							
Strychnos spinosa	Lam.	Strychnaceae	Indigenous	Tree		X										
Tacazzea apiculata	Oliv.	Apocynaceae	Indigenous	Shrub			X		X							
Talinum caffrum	Eckl. & Zeyh.	Portulacaceae	Indigenous	Herb					X							
Tephrosia purpurea	Pers.	Fabaceae	Indigenous	Herb				X								
Terminalia prunioides	C.Lawson	Combretaceae	Indigenous	Tree									X			
Terminalia sericea	Burch. Ex DC.	Combretaceae	Indigenous	Tree		X		X	X							
Themeda triandra	Forssk.	Poaceae	Indigenous	Graminoid	X	X			X							X
Tragia cf rupestris	Sond.	Euphorbiaceae	Indigenous	Herb								X				
Tragus berteronianus	Schult.	Poaceae	Indigenous	Graminoid										X		
Trema orientalis	(L.) Blume	Celtidaceae	Indigenous	Tree	X	X	X		X					X		
Trichilia emetica subsp. *emetica*	Vahl.	Meliaceae	Indigenous	Tree			X						X			
Triumfetta annua	L.	Tiliaceae	Indigenous	Herb	X	X			X							

Species	Authorities	Family	Alien/ Indigenous	Growth form	Transect											
					1	2	3	4	5	6	7	8	9	10	11	12
Triumfetta rhomboidea	Jacq.	Tiliaceae	Indigenous	Herb	X											
Urochloa mosambicensis	(Hack.) Dandy	Poaceae	Indigenous	Graminoid	X	X	X	X	X	X	X	X	X	X	X	X
Vangueria infausta subsp. *infausta*	Burch.	Rubiaceae	Indigenous	Tree			X					X		X		
Vernonia colorata subsp. *colorata*	(Willd.) Drake	Asteraceae	Indigenous	Tree	X		X									
Vitex harveyana	H.Pearson	Verbenaceae	Indigenous	Shrub												X
Waltheria indica	L.	Sterculiaceae	Indigenous	Herb				X	X	X	X			X		
Withonia somnifera	(L.) Dunal	Solanaceae	Indigenous	Shrub												X
Ximenia caffra	Sond.	Olacaceae	Indigenous	Shrub					X							X
Ziziphus mucronata	Willd.	Rhamnaceae	Indigenous	Tree		X	X	X								X

Appendix 3. Chapter 2 published in the South African Journal of Botany.

To follow on the next page

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Initial response of riparian plant community structure to clearing of invasive alien plants in Kruger National Park, South Africa

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Abstract

Recovery of indigenous species subsequent to the clearing of invasive alien plants (IAPs) is crucial for ecosystem recovery to occur. However, cleared sites are often just left in the hope that revegetation will occur naturally. In riparian areas of Kruger National Park (KNP), the Working for Water (WfW) Programme has cleared IAPs on a regular basis, but little post-clearance monitoring has taken place. Thus investigating short-term effects of IAPs and IAP clearing on plant community diversity and vegetation recovery provided an ideal opportunity to assess feasible targets of natural ecosystem recovery in similar areas. Vegetation was sampled from twelve transects along the Sabie River in and adjacent to the KNP, before (March/April 2006) and after (March 2007) the annual clearing of IAPs by WfW. Rarefied species richness, alpha diversity and evenness of distribution of species all declined with increasing density of IAPs ($P<0.05$). There was a mean reduction in IAP density of 80% (S.E ± 6%) ($P=0.002$) through the clearing by WfW. After clearing of IAPs, indigenous vegetation densities increased, with herbaceous growth forms showing the largest increase in transects that were previously heavily invaded. Thus, in this system, which is relatively undisturbed by human activities, initial recovery of indigenous vegetation can occur without further restorative interventions. This process is more than likely aided by the continuous clearing of IAPs by WfW as this acts to deplete alien seed banks and maintain IAPs at acceptable and manageable levels.

Keywords: Biological invasions; Ecosystem repair; Exotic plants; Diversity; Resilience; Restoration; Working for Water

1. Introduction

The introduction and establishment of invasive alien species is a global problem having severe and wide-spread consequences. Invasive alien plants (IAPs) not only negatively impact the structure and functioning of ecosystems (Vitousek, 1990; Witkowski, 1991a,b; Richardson et al., 1997; Gordon, 1998; Witkowski and Wilson, 2001), but have also been acknowledged as one of the greatest threats to global biological diversity (Coblentz, 1990; Rubec and Ledd, 1996), with numerous studies reporting negative effects of IAPs on the diversity of communities (Richardson et al., 1989, 1997; Vitousek, 1990; Pyšek and Pyšek, 1995; Dunbar and Facelli, 1999). Although diversity has various ecological definitions, in this study it refers to "the variety and abundance of species in a defined unit of study" and incorporates measures of both species richness and evenness of distribution of species (Magurran, 2004).

When considering the detrimental impacts that IAPs can have, it is not surprising that management of IAPs and restoration of ecosystems impacted by IAPs have become priorities to conservation managers worldwide (Byers et al., 2002). South Africa faces a great challenge in managing IAPs, an issue that has received much attention (Richardson and Van Wilgen, 2004). In 1995, the Department of Water Affairs and Forestry launched the "Working for Water" programme (WfW), with the primary goal of securing scarce water resources, by coordinating and conducting active clearing of IAPs across the country, while simultaneously addressing poverty alleviation through job creation (Van Wilgen et al., 1998). Clearing of IAPs is, however, a continual and complex challenge (Manchester and Bullock, 2000), and cleared areas often experience further invasion or

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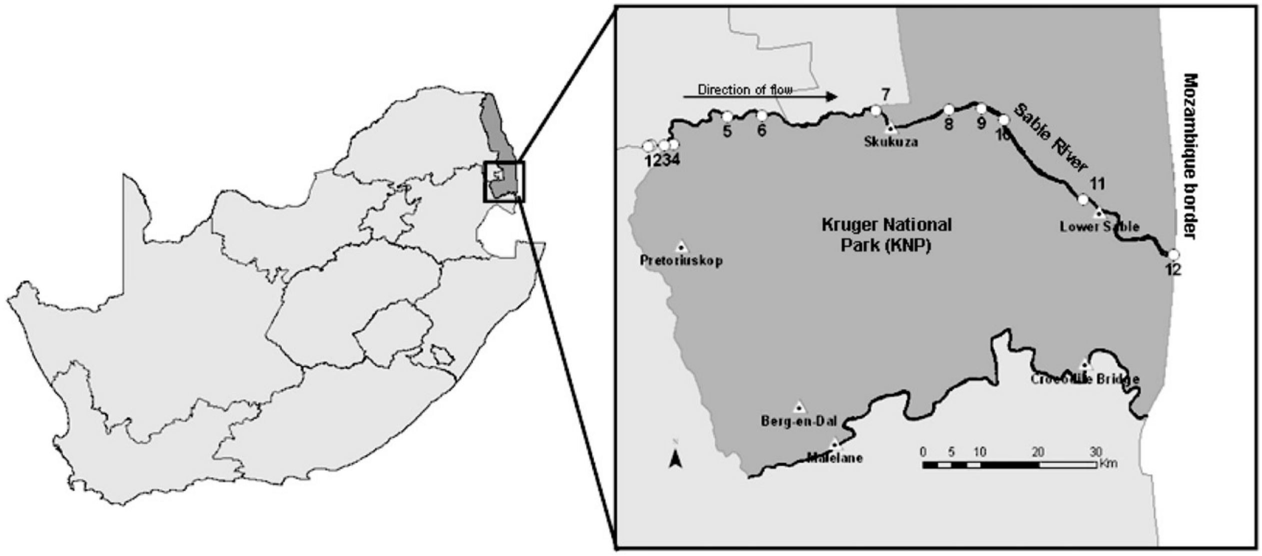

Fig. 1. Map of the Southern section of the Kruger National Park. Transects span the Sabie River and were divided into three zones according to location and propagule pressure. Zone 1: transects 1–3, outside the KNP; Zone 2: transects 4–8, in close proximity to the boundary (transect 8 is situated after Skukuza rest camp which is a propagule source) and Zone 3: transects 9–12, within the confines of the park extending to the Mozambique border.

other secondary problems (Holmes et al., 2000; Holmes, 2001; Beater et al., 2008-this issue). Regrowth by indigenous vegetation is essential to minimise the possibility of further problems and to allow ecosystem recovery to ultimately occur. While in some areas this may take place without further management intervention, in others, active maintenance and restoration can sometimes be necessary (D'Antonio and Meyerson, 2002; Galatowitsch and Richardson, 2004). Post-clearance monitoring is crucial to assess levels of post-clearance ecosystem recovery and to determine if further management is needed. However this monitoring is rarely performed and in general, sites cleared by WfW are often just left in the hope that indigenous revegetation will occur without further management intervention (Galatowitsch and Richardson, 2004).

In the Kruger National Park (KNP), South Africa, invasive alien species have been declared one of the greatest threats to biodiversity, with riparian zones being the most severely invaded systems (Foxcroft and Richardson, 2003; Foxcroft et al., 2007). Riparian ecosystems are acknowledged to be highly prone to IAP invasions due to the dynamic nature of rivers as well as the efficient ability of rivers to transport and disperse alien propagules (Thebaud and Debussche, 1991; Pyšek and Prach, 1993; Johansson et al., 1996; Tickner et al., 2001). Once present in a catchment, many of these IAP species can exploit opportunities provided by both natural and anthropogenic disturbances that are known to play a large role in determining patterns of riparian vegetation (Richardson et al., 2007). These disturbances include those linked to hydrology (flooding, sedimentation), fire, herbivory and even disturbances associated with IAP clearing (Tang and Montgomery, 1995; Naiman and Décamps, 1997; Parker-Allie et al., 2004; Richardson et al., 2007; Witkowski and Garner, 2008-this issue).

To aid in the management of IAPs, the WfW programme was first launched in the KNP in 1997, and has since become a major component of IAP management, executing annual clearing operations in selected areas. Despite this setting providing an excellent opportunity to assess impacts of IAPs and their clearing on plant community diversity and initial vegetation succession in riparian areas subsequent to clearing, very little monitoring has taken place. Investigating the impacts of and recovery from IAP invasions in such an area with relatively low anthropogenic disturbance, which should be less invaded, should provide indications of benchmark targets for similar vegetation in other areas of land-use. It should also provide a realistic test to assess to what extent natural revegetation actually occurs, subsequent to clearing of IAPs. If revegetation were not to occur in this relatively well-managed ecosystem with low anthropogenic disturbance, it definitely cannot be expected to occur in highly transformed or degraded areas. Thus, the aims of this study were to (a) assess the plant diversity of sites along the riparian zone of

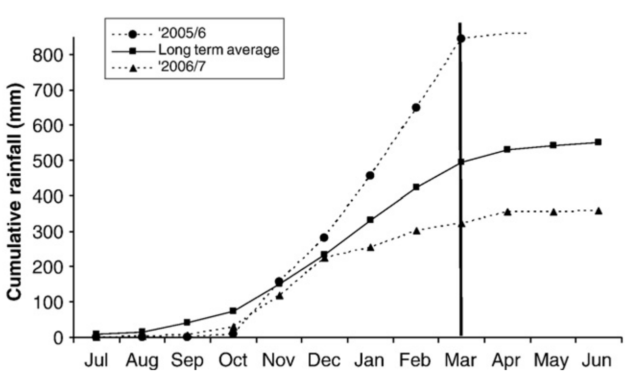

Fig. 2. Cumulative rainfall (mm) at Skukuza weather station from the beginning of the "annual climatic year" (July). The dotted lines represent the 2005/6 and 2006/7 rainfall seasons, while the solid line represents the long term average over 76 years. Vegetation sampling occurred in March, indicated by the bold solid bar.

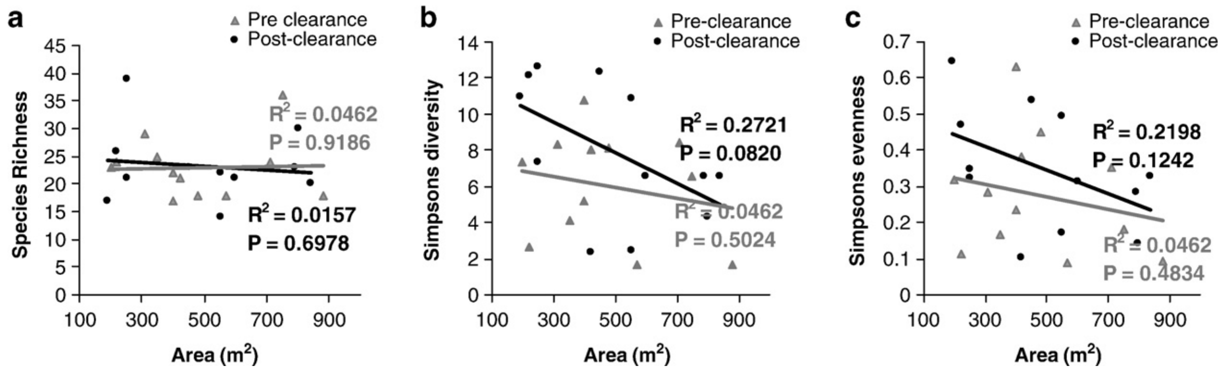

Fig. 3. Species richness (a), Simpson's diversity (b), and Simpson's evenness (c) as a function of transect area (m^2) for pre-(Mar 2006) and post-(Mar 2007) clearance of invasive alien plants. Fitted trend lines are linear.

the Sabie River in and adjacent to the KNP, in relation to the abundance of IAPs and (b) determine patterns of vegetation regrowth after clearing of IAPs in densely invaded sites.

2. Material and methods

2.1. Study area

This study was conducted along the Sabie River, in and adjacent to, the KNP. The Sabie River is a perennial river (Heritage et al., 1999) originating in the escarpment of the Drakensberg Mountains to the west of KNP. It flows eastwards through areas of commercial forestry, agriculture and dense rural habitation before entering the KNP and on to Mozambique (Fig. 1). The complex pattern of land-use and ownership upstream of the KNP provides a continual source of alien plant propagules into the riparian system, creating a continual challenge for the management of IAPs (Foxcroft and Richardson, 2003; Foxcroft et al., 2007; Beater et al., 2008-this issue).

The area is located in the savanna biome and is characterized by a semi-arid to subtropical climate, with hot rainy summers and mild dry winters (Venter et al., 2003). There is an increasing rainfall gradient from east to west (Venter et al., 2003), with an average annual rainfall of 450–600 mm (Van Niekerk and Heritage, 1993). Rainfall during the study period recorded at the Skukuza weather station was 70% greater than the 76 year long-term annual average rainfall in 2005/06, and 35% below in 2006/07 (Fig. 2).

The high rainfall experienced in 2005/2006 (Fig. 2) enhanced the response of IAP growth, and IAP densities were much greater than those reported on the same river in 2004 (Foxcroft et al., 2007). However IAP patterns are also influenced by the continuous clearing efforts of WfW, who have undertaken annual clearing operations for at least the last four years on the Sabie River. This annual clearance by WfW afforded the opportunity to assess the short-term response of IAP over just one season of growth, with the large disturbance of a high rainfall bout having occurred since the previous year's clearing operations. It also

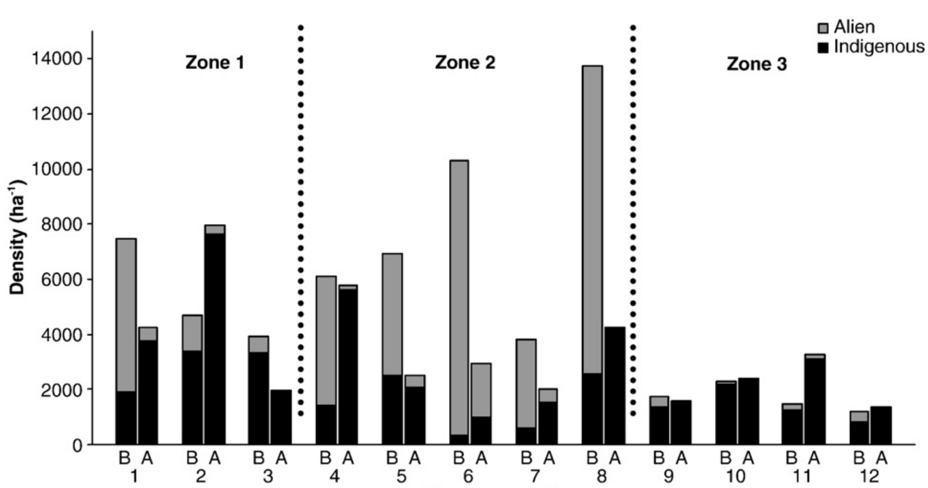

Fig. 4. Densities (per ha) of indigenous and alien vegetation (basal stem diameter > 1 cm) before (B) and after (A) the annual clearing of invasive alien plant species by the Working for Water Programme.

Table 1
Densities of alien species with a density > 5 plants/ha at any one site as well as the relative contribution of these species to the total density of all vegetation of transects with an alien density > 35% prior to the clearing of invasive alien plants

Species	Growth form	Longevity	Legal status	Density (per ha) per site					
				1	4	5	6	7	8
Acanthospermum hispidum	Herb	Annual	–		9	3			
Lantana camara	Shrub	Perennial	DW1		5			1	
Senna obtusifolia	Shrub	Annual	–	31	2	19	9		
Senna occidentalis	Shrub	Perennial	–	1	26		1		56
Tagetes minuta	Herb	Annual	–	36	32	23	5	5	1
Xanthium strumarium	Herb	Annual	DW1	3		18	78	77	24
Total percentage density of abundant alien species				72	74	62	93	83	81
Total percentage density of all invasive alien species				75	77	64	97	84	82
Percentage of total alien density				96	96	98	96	99	99

Legal status refers to regulation 15 of the Conservation of Agricultural Resources Act, 1983 (Act No. 43 of 1983).
DW1 = Declared weed 1 as described in Henderson (2001).

provided the opportunity to assess the response of the indigenous vegetation directly after clearing operations by WfW. Thus for interpretation purposes the terms before (pre-clearance) and after (post-clearance) relate only to the 2006 clearing season which targeted the high IAP densities resulting from the high rainfall season, and not to the long term clearing operations by WfW.

2.2. Vegetation sampling

Sampling took place over two periods: in March/April 2006 and in March 2007. Twelve transects were sampled along the Sabie River from Hazyview (upstream and adjacent to KNP) through the park and terminating at the Mozambique border on the eastern boundary of the park (Fig. 1). These transects were split into three zones according to their locality and hence corresponding propagule pressures: Zone 1 — transects 1–3: situated along the Sabie River outside the KNP; Zone 2 — transects 4–8: situated within the park but in close proximity to the boundary. Transect 8 was included in this zone as it is located near to the large Skukuza tourist camp and staff village, which poses a high threat for IAP invasions, mainly due to the pathway of spread of exotic species from camp and staff

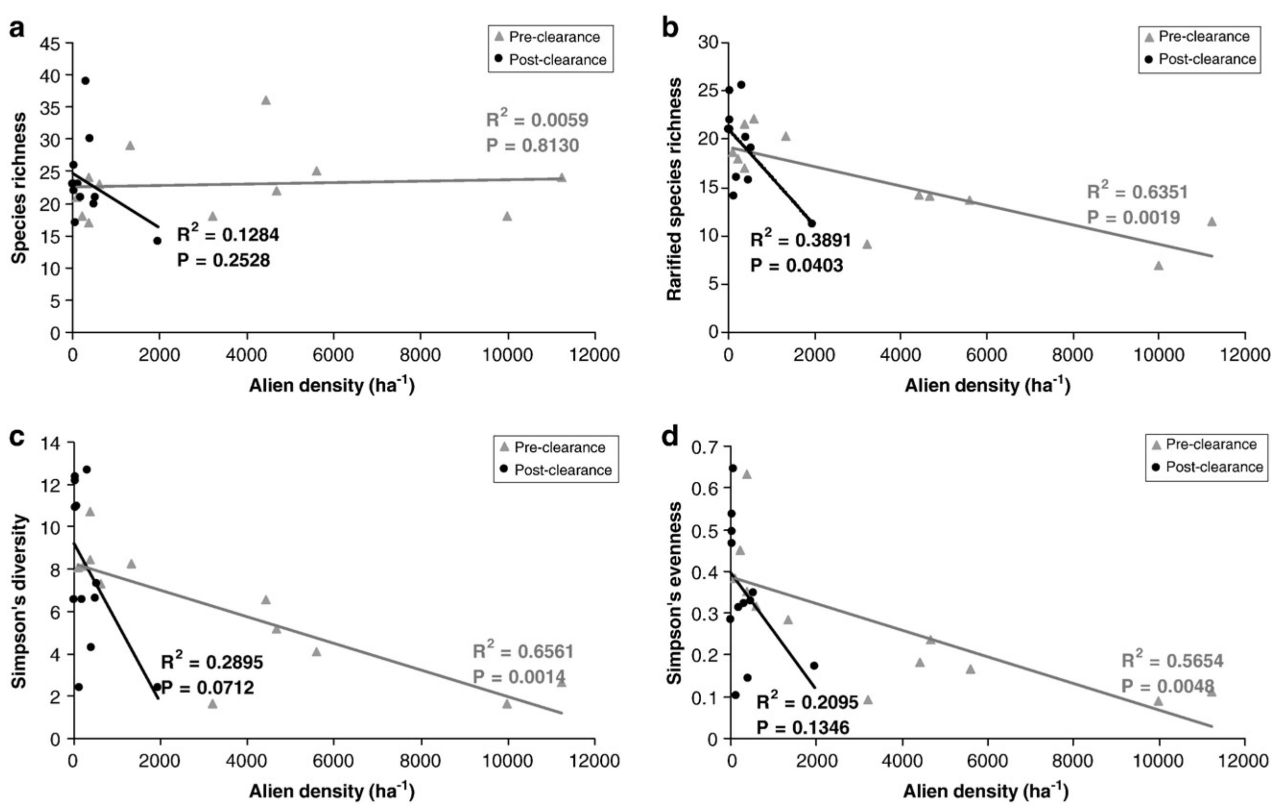

Fig. 5. Species richness (unadjusted and rarefied) (a, b), Simpson's diversity (c) and Simpson's evenness (d) as a function of alien density (per ha) before (Mar 2006) and after (Mar 2007) the seasonal clearance of invasive alien plants by Working for Water.

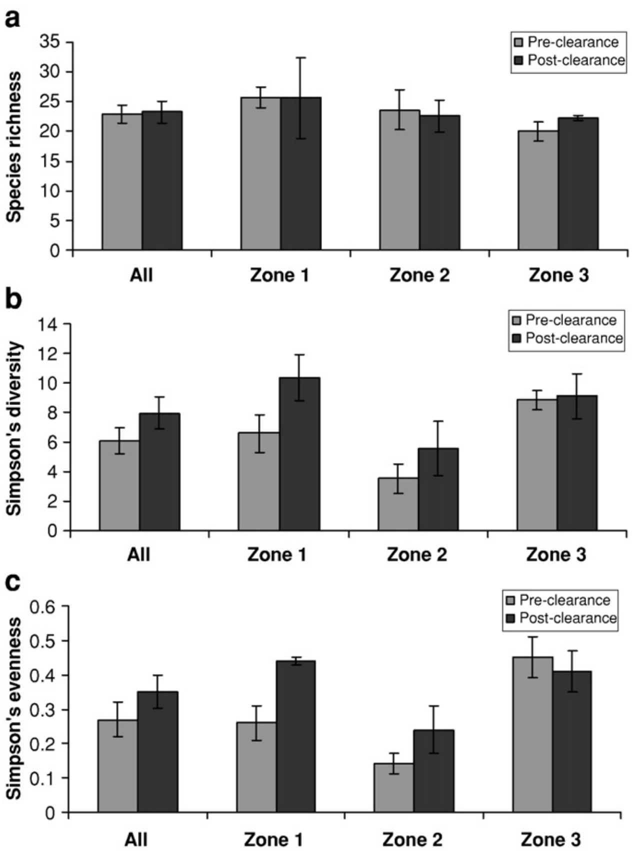

Fig. 6. Pre- and post-clearance species richness, Simpson's diversity and Simpson's evenness for all transects and each zone.

gardens (Foxcroft and Richardson, 2003); Zone 3 — transects 9–12: located along the Sabie River within the confines of the KNP extending to the Mozambique border.

Vegetation with a basal stem diameter (BSD) > 1 cm was sampled in a 10 m wide belt transect placed perpendicular to the river. This belt transect extended from the top of the macro-channel bank to the beginning of the macro-channel floor. However, due to the heterogeneous nature of the riparian zone along the 108 km stretch of the Sabie River, these transects varied in length from 20–90 m. In each transect individual plants were identified and counted, the BSD and height class were recorded and the growth forms were later classified as herb, shrub or tree according to Germishuizen and Meyer (2003).

Transect 3 was omitted from all before versus after analyses as this transect had subsequently been transformed into farm-lands by the second data collecting period and hence no "after" data could be collected for this site.

2.3. Data analysis

The following diversity indices were derived for combined alien and indigenous vegetation using Primer™ v5 (Clarke and Gorley, 2001) and utilised to assess possible area affects between transects of differing lengths and hence areas:

a) Observed species richness (S)
b) Rarefied species richness ($n = 100$): the expected number of species for a given number of randomly sampled individuals (McCabe and Gotelli, 2000).
c) Simpson's diversity index (D) and reciprocal ($1/D$).
d) Simpson's evenness index ($E_{1/D}$).

Densities of alien and indigenous vegetation were assessed before and after the annual clearing by WfW and tested for significant differences over time using Wilcoxon matched pairs tests in Statistica 6.1 (StatSoft, 2004). Mann−Whitney U-tests were used to assess differences in before clearance alien densities between the three zones along the River. Diversity indices were assessed across the three zones before and after the annual clearing by WfW and were also plotted against alien densities to investigate potential effects of alien intensity on vegetation diversity.

Indigenous densities categorised into growth form were considered before and after the annual clearing of IAPs. The densities of species that increased in abundance over time were square-root transformed and the percentage contribution of the

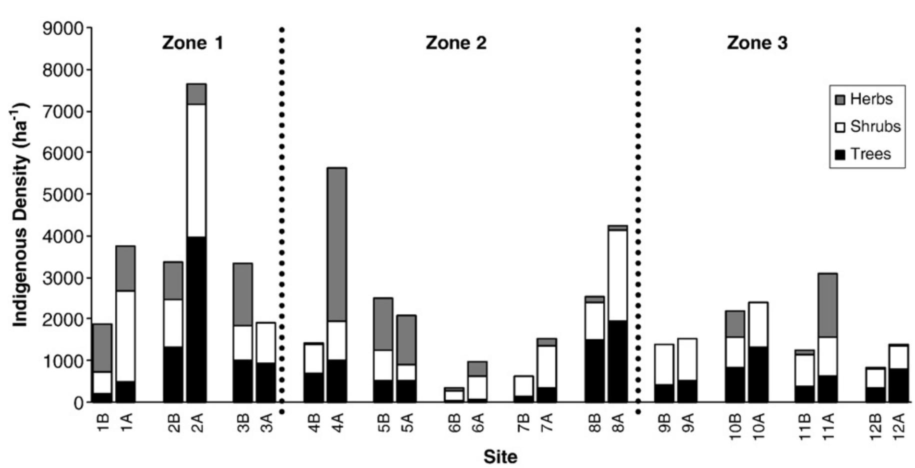

Fig. 7. Density (per ha) of indigenous vegetation before and after the seasonal clearing by Working for Water. Densities are divided into three growth forms: trees, shrubs and herbs. *Data could not be collected at transect 3 after clearing of invasive alien plants as this site had been transformed into farm lands. Thus post-clearance densities are derived from an intermediate data set and were excluded from interpretation.

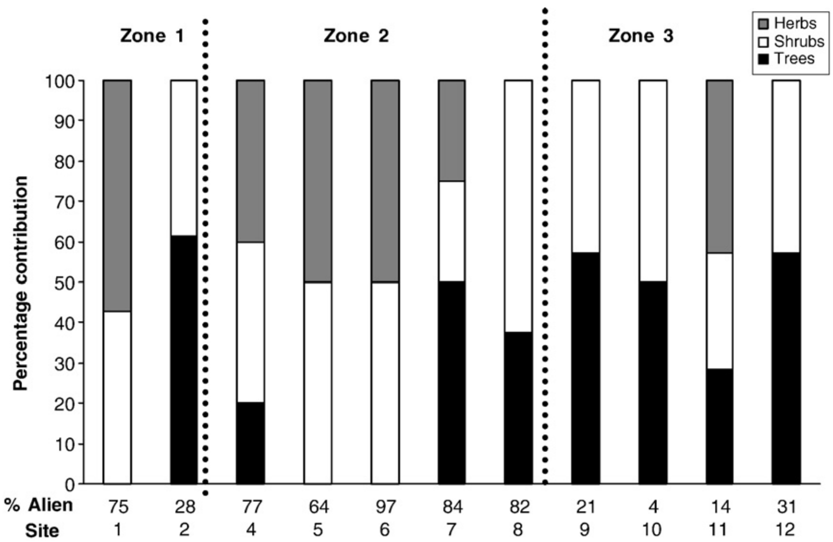

Fig. 8. Percentage contribution of the growth forms of species that increased after clearing, contributing to 70% of the observed change post-clearance of invasive alien plants.

species responsible for 70% of the variation within a site before and after clearing of IAPs was calculated. A 70% cut off was used to highlight the species that contributed most to the observed changes. Indigenous herbaceous plant densities that increased over time were tested for a significant difference between heavily- versus lighty-invaded transects using Mann−Whitney *U*-tests.

3. Results

3.1. Effects of variation in transect length (area)

Species richness is expected to increase as area increases. However, as transect areas increase, this expected relationship is not observed, either before (2006) or after clearance (2007). There is no relationship between transect area and species richness ($P>0.05$) (Fig. 3a) and, unexpectedly, both species diversity (Fig. 3b) and evenness (Fig. 3c) decrease slightly as transect area increases ($P>0.05$). These results suggest that macro-channel banks along the lower Sabie River are comparable regardless of transect length. This may be of importance when considering future sampling methods as plots of a fixed size may misrepresent the full extent of riparian macro-channel banks, which can vary dramatically down the length of the river, and hence underestimate diversity. Thus regardless of the differing lengths, and hence areas across the sites, data were still considered comparable due to the negligible area effects.

3.2. Densities of invasive alien plants before and after annual clearing

The density of IAPs before (B) clearing by WfW outside the KNP (Zone 1: transects 1–3) was slightly lower than for transects within the park in Zone 2 (transects 4–8) although differences were not significant ($P=0.18$). Density was lowest in transects further downstream towards the Mozambique border (Zone 3: transects 9–12) ($P=0.014$) as would be expected with an increasing distance away from the major propagule sources upstream of the western boundary. Densities of IAPs (plants/ha) after clearing (343 ± 156), were significantly reduced ($P=0.002$) relative to before clearance levels (3508 ± 1113), with a mean IAP reduction of 80 ± 6% (Fig. 4).

Prior to clearing, species that contributed most to the alien plant density of heavily-invaded transects were *Acanthospermum hispidium* (DC.), *Lantana camara* (L.), *Senna obtusifolia* (L.), *Senna occidentalis* (L.), *Tagetes minuta* (L.) and *Xanthium strumarium* (L.). These six species contributed between 62–93% of all vegetation density at the previously highly-invaded transects (transects 1, 4–8) (Table 1).

3.3. Effects of invasive alien plant density on community diversity

When investigating the effects of IAPs on community diversity, there was no relationship between alien density and species richness ($P>0.05$) (Fig. 5a). However when species

Table 2
Total percentage contribution to change (600%) of the three highest indigenous species per site that increased in the previously densely invaded sites (>50% density alien invasion)

Species	Growth Form	Longevity	Transect number						Total
			1	4	5	6	7	8	
Sida cordifolia	Herb	Annual		49	48	31	19		146
Phyllanthus reticulatus	Shrub	Perennial	17	9				10	36
Acacia schweinfurthii	Shrub	Perennial			9		14		23
Leonotis intermedia	Shrub	Perennial				21			21
Pluchea dioscoridis	Shrub	Perennial				17			17
Pavetta catophyla	Shrub	Perennial						15	15
Triumfetta rhomboidea	Herb	Annual	14						14
Crotolaria capensis	Shrub	Perennial	14						14
Acacia robusta	Tree	Perennial					9		9
Waltheria indica	Herb	Annual			9				9
Pyrostria hystrix	Shrub	Perennial						9	9
Flueggea virosa ssp. *virosa*	Shrub	Perennial		6					6

richness was rarefied to $n=100$ for comparison across transects, it decreased as alien density increased ($P<0.05$) (Fig. 5b). Additionally, alpha diversity and evenness decreased as alien density increased (pre-clearance data: $P<0.05$) (Fig. 5c,d). These results occurred irrespective of whether densities were calculated on an absolute or relative basis (Morris, 2008).

When considering changes in diversity measures before and after clearing, in each zone and overall, there were no change in species richness (Fig. 6a). Alpha diversity and evenness remained unchanged in zone 3, which was mostly unaffected by IAP invasions. However in zone 1 and 2, there was a trend for both alpha diversity and evenness to increase despite the reduced rainfall received in 2006/07 (Fig. 6b,c). This suggests that the drastic reduction of IAPs in these zones may have lead to this initial increase in these diversity measures.

3.4. Response of indigenous vegetation to the seasonal clearing of invasive alien plants

Overall, densities of indigenous species increased after the clearing of IAPs (Fig. 7) ($P=0.02$) with both tree and shrub growth forms increasing significantly after clearing ($P=0.04$, $P=0.015$, respectively). Interestingly, the species that increased in previously densely-invaded transects (alien density > 50%), were mostly herbaceous ($P=0.067$). Species that increased in the less invaded transects, however, were tree species ($P=0.022$) (Fig. 8), as would be expected in relatively undisturbed areas experiencing normal recruitment.

The herbaceous species that contributed the most to the increase in indigenous plant abundance after clearing were *Sida cordifolia*, *Triumfetta rhomboidea* and *Waltheria indica*; while *Acacia schweinfurthii* var. *schweinfurthii*, *Leonotis intermedia* and *Phyllanthus reticulatus* var. *reticulatus* contributed to the greatest increase in shrub abundance, and *Acacia robusta* contributed to the increase in tree species abundance (Table 2). This supports the use of *A. robusta*, which regenerates relatively easily from seed (Witkowski, E.T.F., unpublished) for restoration planting in riparian areas within this ecoregion (Holmes et al., 2008-this issue).

4. Discussion

4.1. Changes in alien densities and community diversities

Prior to clearing by WfW (2006), transects had IAP densities of up to 97%. These high IAP densities appeared to have a negative impact on community diversity (Fig. 5), which is congruous with results of numerous other studies (e.g. Pyšek and Pyšek, 1995; Holmes et al., 2000). After the reduction in IAP density, there was a notable corresponding increase in the alpha diversity and evenness of vegetation in the previously densely-invaded sites (Fig. 6). The major contribution to the high IAP densities was from annual or short-lived perennial species such as *X. strumarium* (L.), *S. obtusifolia* (L.), *S. occidentalis* (L.) and *T. minuta* (L.). The short longevity of these species may result in these plants dying off naturally at the end of the annual growing season, making clearing seem redundant. However clearing of these species reduces both reseeding and the shading out of regenerating indigenous herbaceous species, and thus acts against the annual reinvasion of herbaceous IAP species. Perhaps clearing the densely-invaded areas before these IAPs have the opportunity to set seed, would minimise the perpetuation of these herbaceous IAPs and reduce the overall management effort necessary to control these species in the long term.

4.2. Response of indigenous vegetation to the seasonal clearing of invasive alien plants

Herbaceous growth forms increased in response to clearing of IAPs in transects that were previously densely-invaded. This is congruent with the notion that recovery from plant invasion is observed quickest in changes to herbaceous diversity and abundance, followed by shrubs and trees (Mentis and Ellery, 1994; Connel and Slayter, 1977). The short time span of this study, as well as the compounded effects of annual clearing, renders it difficult to fully explore successional changes in the indigenous vegetation. However, the important point with regards to the recovery of the system after clearing, is that recolonisation of vegetation is largely by indigenous species rather than the undesirable situation of reinvasion by the same or other exotic species, as was the case further up in the catchment (Beater et al., 2008-this issue; Witkowski and Garner, 2008-this issue).Vegetative ground cover of indigenous vegetation also increased after the clearing of IAPs mostly due to an increase in grass cover (Morris, 2008).

The high levels of observed overall indigenous regrowth indicate that the system shows a relatively high level of resilience to disturbance by IAPs. Resilience is defined as the ability of an ecosystem to return to its former state following a disturbance or stress (Wali, 1999). Most riparian species are inherently resilient due to frequent and intense disturbance (Richardson et al., 2007) and have dispersal and establishment strategies, such as the ability to colonise bare sediments and aggressive clonal growth that allow for rapid recovery after a disturbance event (Naiman and Décamps, 1997).

The continuous management and clearing of IAPs by WfW is an important factor that facilitates this resilience in the system, as the repetitive clearing depletes alien seed banks and maintains IAPs at acceptable levels that are relatively easy to manage. Acceptable levels of IAPs are based upon the KNP management objectives which incorporate the use of “Thresholds of Potential Concerns” (TPCs) concerning the distribution, density and rate of spread of IAPs (Foxcroft and Richardson, 2003). Thus the WfW operations ensure that stands of IAPs are present for short periods. This probably improves the chances of natural post-clearing recovery occurring, as the longer an invader has been present, the more dense and widespread its seed bank will become (Witkowski and Wilson, 2001), and the greater its contribution to the attrition of native seed banks and its impact on indigenous plant propagule input (Holmes and Cowling, 1997a,b).

4.3. Spatial variation in alien densities

Densities of IAPs were significantly higher in the first two zones prior to their clearing. This is probably attributable to the combination of two factors: the aforementioned above average rainfall and the higher propagule pressure. The Sabie River flows through areas of varying land-use including areas of commercial forestry and dense rural habitation even after entering the KNP, as the river acts as a boundary for some distance (Fig. 1, transects 4–7) (Foxcroft et al., 2007; Beater et al., 2008-this issue). This continuous interface with human disturbance allows multiple opportunities for introduction of alien propagules into the riparian corridor, resulting in recurring germination and establishment of alien plants (Richardson et al., 2007; Witkowski and Garner, 2008-this issue). Interestingly, transect 8, situated downstream of Skukuza rest camp, had the highest alien density even though it is not on the park boundary. This supports the notion that the gardens of rest camps and staff villages act as major pathways for alien invasions (Foxcroft and Richardson, 2003). Further downstream within the KNP, there are very few, if any, sources of alien propagules besides those originating from alien plants in adjacent reaches and correspondingly, densities of IAPs are considerably lower.

Transects outside the KNP tended to have lower densities of IAPs than those of zone 2 within the park, which is rather surprising as one would expect this area to be subjected to greater human impacts and hence to be more disturbed. The only transect in keeping with this, appearing to be highly disturbed, was transect 1, which was frequently used by both humans and livestock (T. Morris, pers. obs.), and correspondingly supported a relatively high density of IAPs. The other two transects were relatively unutilised, probably due to their inaccessibility and steeper gradients and in contrast supported high densities of indigenous vegetation, and had high alpha diversity and species richness. Thus, the only variable in common between the heavily-invaded sites both within and adjacent to the park was the presence of faunal disturbance. Riparian zones within the KNP are heavily utilised by a range of large herbivore species who create a further disturbance and perhaps also provide additional vectors for propagule dispersal along the riparian zone by spreading propagules while foraging or by spreading those that attach to their fur (Hood and Naiman, 2000).

4.4. Role of disturbance in the dynamics between indigenous and exotic plant growth

Natural and anthropogenic disturbances, such as herbivory, fire, hydrological processes and even disturbances created by IAP mitigation, play a large role in determining patterns of riparian vegetation (Witkowski and O'Connor, 1996; Richardson et al., 2007). In the KNP where there is an increased use of the riparian zone by mega-herbivores, herbivory may play an important but unexplored disturbance role. On the other hand, fire is generally considered relatively uncommon in the riparian zones of higher order streams in the KNP (Pettit and Naiman, 2007a), such as the Sabie River. This is largely due to the high levels of moisture and lower fuel loads in comparison to uplands (Dwire and Kauffman, 2003). Additionally, tourists roads are situated along almost the entire length of the southern bank of the Sabie River, where study transects were situated. These roads may be acting as additional "fire-breaks", unintentionally preventing fires spreading from upland areas into the riparian zone. Thus fire in all likelihood does not play a major role in determining vegetation patterns in the sampled areas. However, the role of fire can become more important when it occurs as a result of, or in conjunction with, other disturbances such as floods.

Flooding and water levels play a large role in characterising riparian vegetation (Van Coller et al., 2000). Opportunities for recruitment and colonisation occur mostly after floods when new patches are exposed either due to the removal of vegetation or through sediment deposition (Richardson et al., 2007). In February 2000, when severe flooding occurred in the KNP region, the Sabie River flood peaked between 3000 m^3/s and 7000 m^3/s at different points along the river (Heritage et al., 2001). When compared to the typical wet season base flow discharges of 15–20 m^3/s, it is clear that this flood was of enormous magnitude. The estimated return interval of the flood was 90–200 years, depending on the position in the catchment (Smithers et al., 2001) and was considered a large infrequent disturbance (LID). This LID reduced the extent of tree, shrub, reed and herbaceous patches, and increased the extent of sand, rock and water patches on the Sabie River within the KNP (Parsons et al., 2006), thus opening many new areas for colonisation. In this case, it was expected that increased colonisation of exotic species would occur due to the disproportionate propagule input into the system. Large amounts of IAP propagules would have washed down from the highly disturbed and transformed areas of the upper Sabie River catchment (Beater et al., 2008-this issue), whereas indigenous propagule pressure would be mostly reliant on residual indigenous vegetation, which was relatively sparse after the 2000 flood (Parsons et al., 2005). Leroy (2003) confirmed this and showed an increase in alien woody and herbaceous species along the Sabie River directly after the 2000 flood relative to preflood (1997) on the same transects.

Before the 2000 flood, herbaceous IAP species were not a strong focus of IAP management, as they were considered more difficult to control manually and were expected to eventually be reduced naturally over time as competition with native species increased. Competition between alien and native species tends to increase as the native community matures during the course of succession. However due to the highly dynamic nature and the frequent disturbances experienced along the riparian zone, typical succession seldom occurs, giving IAPs a continual competitive advantage in this largely non-equilibrium system. In this light, the effective clearing of both herbaceous and woody species executed by WfW may play an important role in aiding both the physical and temporal recovery of indigenous vegetation after the LID, by reducing the competitive effects of IAP.

LIDs may have long-lasting influences on ecosystems (Foster et al., 1998) and can also alter other important disturbance regimes such as fire. For instance, large woody piles deposited after a flood of this magnitude increase fuel loads and therefore the susceptibility of the riparian zone to fire (Dwire and Kauffman, 2003). Pettit and Naiman (2007b) illustrated that fires enhanced by these large woody piles had a significant initial effect on Sabie River vegetation and showed how fire could alter pathways of succession after floods by causing the destruction of surviving and regenerating vegetation. Thus the dynamics of IAP growth and indigenous vegetation regrowth may still be greatly compounded by the February 2000 floods.

Lastly, clearing operations can also be a source of disturbance whether in the form of physical disturbance, disturbances to ecosystem processes (e.g. erosion) or negative effects on non-target species (D'Antonio and Meyerson, 2002; Galatowitsch and Richardson, 2004; Parker-Allie et al., 2004). However, due to the dense, largely mono-specific stands of invasion along the Sabie River, as well as the highly-specific and largely manual rather than chemical practices utilised by the WfW teams, negative impacts of clearing on native vegetation appeared to be fairly minimal (T. Morris, pers. obs.) compared to upstream in the catchment (Beater et al., 2008-this issue).

In 2004, less than 6% of the total plant abundance was composed of alien species, which may have indicated the effectiveness of the ongoing clearing programme (Foxcroft et al., 2008-this issue), especially in light of the increased levels recorded directly after the large flood disturbance in 2000. However, after just one season of above average rainfall in 2006, alien densities increased up to 97% in isolated areas. Thus it is important for management to realise that the responses of exotic and indigenous vegetation can be complex and highly heterogeneous in both space and time and hence management regimes should correspondingly be fairly flexible. This is of utmost importance when dealing with invasions associated with large disturbances, such as a flood or an escalated rainfall season, so that IAPs infestations can be dealt with effectively and without delay so that IAPs can be maintained at acceptable and manageable levels.

In areas that are relatively undisturbed by human activity, such as reserves or conservation areas, revegetation and recovery of indigenous vegetation after the clearing of IAPs should occur without further management steps being necessary. However, continuous management of IAPs plays a vital role in management, boosting the resilience of the system, and making rapid recovery viable. Over a short term, monitoring the response of both alien and indigenous vegetation to clearing of IAPs has provided several worthy insights. However, long term monitoring is crucial to build upon our understanding of the role of seed banks, environmental influences and disturbances in perpetuating IAP invasions and hence allowing us to advance and optimise management operations accordingly.

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