

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.

Margaret Mary Theresa Beater

_____ day of _____ 2006

A dissertation submitted to the Faculty of Science, University of the Witwatersrand, in fulfilment of the requirements for the degree of Master of Science.

June, 2006

ABSTRACT

The broad aim of this study was to measure the ecosystem repair of the Sabie River (which traverses through both the grassland and savanna biomes) riparian environment in Mpumalanga, South Africa, in response to the clearing of alien plants by the Working for Water (WfW) alien plant clearing programme. This was done in order to assess the effectiveness of the WfW clearing on the Sabie River riparian plant community composition and associated environmental factors. Although “effectiveness” can be assessed in various ways, in this study it included determining whether there was a reduction in the invasion intensity (defined as the percentage aerial cover of woody alien plants) after clearing. This broad aim was achieved by studying the impacts of the WfW alien plant clearing programme, as well as the invasion of alien plants, on the plant species composition, diversity and vegetation structure of riparian ecosystems on the Sabie River. Hence, in 2005 40 modified Whittaker nested plots were sampled. The impacts on the Sabie River riparian environment were also assessed by measuring various environmental variables that are likely to change as a result of clearing, such as the ground cover (percentages of exposed soil, rock, litter, herbaceous vegetation and grass), as well as various soil chemical and physical properties. Twenty plots were surveyed along the Sabie River in the Hazeyview region (savanna biome), ten in the Sabie region (grassland biome) and ten in the Graskop region (grassland biome). The response of the Sabie River riparian community to invasive alien plant clearing by WfW (and the alien plant invasion itself) was also assessed over time, by comparing the 2005 study with one done in 1996, which used the same plots.

In 2005, a cumulative total of 282 species were found, 222 (79%) of which were indigenous and 60 (21%) alien. The grassland sites had a higher cumulative total of 222 species compared with the 171 species in the savanna sites. A total of 112 (39%) species were common between the biomes, 86 (30%) of which were indigenous and 26 (9%) alien. At the 1000 m² scale, the indigenous species richness (32.4 ± 1.4 (S.E.)) was significantly higher than the alien species richness (12.0 ± 0.5) ($P < 0.001$). Of the 60 alien species, 17 (28%) were shrubs and 15 (25%) trees. The grassland sites were more species rich at the 1000 m² scale (48.8 ± 1.8) and diverse at the 100 m² scale (Simpson’s index of alpha diversity of 0.90 ± 0.01) than the savanna sites (species richness of 40.0 ± 2.1 and alpha diversity of 0.85 ± 0.02 ; $P = 0.003$ for species richness and $P = 0.04$ for alpha diversity). The Sabie sites were more species rich at the 1000 m² scale (52.6 ± 2.8) than the Graskop sites (45.0 ± 1.4) ($P = 0.12$). The higher species richness in the Sabie region contributed to the higher total species richness in the grasslands relative to the savanna sites. At the 1000 m² scale, the overall beta diversity (Sorenson’s coefficient of community) between the biomes was 0.57, and the species complementarity (the Marczewski-Steinhaus distance) between the biomes was 0.60, indicating that the biomes were not that similar in terms of species composition. Even though the grassland was more rich and diverse in terms of species than the savanna, the overall relative abundances of plant species in each biome was very similar (species evenness (Simpson’s measure of evenness), at the 100 m² scale, of 0.52 ± 0.03 in the grassland and 0.51 ± 0.03 in the savanna; $P = 0.74$). The savanna tended to have a higher degree of invasion intensity (aerial cover of woody alien plants of $34.4 \pm 4.6\%$ compared to $29.4 \pm 4.5\%$ in the grassland; $P =$

0.44), possibly due to its position lower in the catchment, and hence a sink for upstream alien plant propagules.

It was hypothesized that higher plant species richness and/or diversity should enhance community resistance to alien plant invasions, in both the grassland and savanna biomes. In the Sabie (grassland) region, there was a negative correlation between the indigenous and alien species richness, thus indicating that the Sabie region plant community may have been more resistant to the invasion of alien plants than the other two regions. Therefore, the hypothesis was not rejected for the Sabie region. On the other hand, in the Graskop (grassland) and Hazeyview (savanna) regions, there were positive correlations between the indigenous and alien species richness, thus indicating that these plant communities may not have been as resistant to the invasion of alien plants. Therefore, the hypothesis was rejected for both the Graskop and Hazeyview regions. When considering the biome scale, the hypothesis was not rejected as the increase in total species richness with increasing invasion intensity in the grassland (which was more diverse than the savanna) indicated that it may have been more resistant to the invasion of alien plants than the savanna, which had a total species richness that decreased with increasing invasion intensity.

In 2005, exposed soil, litter and grass covers tended to be slightly higher in the savanna ($14.4 \pm 1.6\%$; $43.5 \pm 3.0\%$; $21.8 \pm 1.7\%$ respectively) than in the grassland ($12.1 \pm 2.5\%$; $43.2 \pm 4.2\%$; $20.1 \pm 2.3\%$ respectively) ($P = 0.43$, 0.96 and 0.56 respectively). Rock and herbaceous covers were higher in the grassland ($4.3 \pm 1.6\%$ and $20.3 \pm 1.7\%$ respectively) than in the savanna ($0.8 \pm 0.2\%$ and $19.5 \pm 2.2\%$ respectively), but only rock cover was significantly different ($P = 0.04$) ($P = 0.76$ for herbaceous cover). These patterns in ground cover may have been a response to the slightly higher invasion intensity in the savanna. The hypothesis that the lower the degree of alien plant invasion, the higher the understorey vegetation cover, which may result in reduced cover of exposed soil and litter, in both the grassland and savanna biomes, was not rejected as the grassland tended to have a lower degree of alien invasion (although not significant), a higher cover of herbaceous vegetation, and corresponding lower covers of exposed soil and litter. The biomes (in 2005) did not differ significantly in soil pH (grassland pH: 4.6 ± 0.1 ; savanna pH: 4.8 ± 0.1 ; $P = 0.34$). However, the grassland soils were generally more fertile than the savanna soils, i.e. higher organic matter ($4.5 \pm 0.2\%$ versus $3.3 \pm 0.4\%$; $P = 0.01$) and total nitrogen ($0.3 \pm 0.02\%$ versus $0.2 \pm 0.02\%$; $P = 0.03$). The concentrations (mg/l) of most of the nutrients were also higher in the grassland. The lower fertility of the savanna soils may have been related to the higher litter cover of the savanna immobilizing a larger amount of available nutrients than the grassland; another possibility may have been slower rates of soil organic matter decomposition in the slightly cooler (higher altitude) grassland regions. The soils of the grassland sites tended to be more compacted ($0.8 \pm 0.1 \text{ kg/cm}^2$) (but not significantly) than those of the savanna sites ($0.7 \pm 0.1 \text{ kg/cm}^2$) ($P = 0.43$), and the savanna plots were on significantly steeper ground ($12.8 \pm 1.7^\circ$) than the grassland plots ($4.8 \pm 1.1^\circ$) ($P < 0.001$), which may have also contributed to lower fertility through greater leaching and erosion losses. From the detrended correspondence analysis (DCA) of the species by plot data, there were no distinct plant communities separating out between the biomes and regions. This is probably because the Sabie River riparian environment essentially supports a riparian forest/woodland, rather than reflecting the species typically found in the adjoining (more upland) grasslands and savannas. Hence, the

species composition of the riparian environment was fairly uniform throughout the study area. The canonical correspondence analysis (CCA), which also incorporates the environmental variables, showed that altitude, exposed soil cover, soil pH, organic carbon content and slope steepness were the variables that most closely (and significantly) correlated with the species composition, and two of these variables relate directly to soil fertility, and the other three are indirectly related to soil fertility.

Of the original “treatments” of the 1996/1997 study, namely (A) biome (grassland versus savanna), (B) invasion intensity (high (> 50%) versus low (< 50%)), and (C) clearing (cleared versus uncleared), the legacy of the latter two did not persist over time, as there was little or no clear overall relationship between the 1996 and 2005 data when analysed by ANCOVA. The cumulative total species richness sampled in the 40 plots increased from 163 species in 1996, to 282 in 2005 (42% increase). Mean species richness (at the 1000 m² scale) was 24.1 ± 1.0 in 1996 and 44.4 ± 1.5 in 2005 ($P < 0.001$). Trees increased from 28 species in 1996 to 46 in 2005 (39% increase), shrubs from 44 to 82 (46%), herbaceous plants from 71 to 121 (41%), and grasses from 20 to 33 (39%). However, even though the species richness of each growth form increased over time, the proportion of each growth form remained approximately the same, i.e. in 1996, 17% of the species were trees, 27% shrubs, 44% herbaceous and 12% grasses; whereas in 2005, 16% were trees, 29% shrubs, 43% herbaceous and 12% grasses. The greatest increase over time was for category 1, 2 and 3 weed species, namely 25 in 1996 to 50 in 2005, a 50% increase. Although mean alpha diversity was higher in 2005 (0.9 ± 0.01 compared to only 0.3 ± 0.03 in 1996 (at the 100 m² scale); $P < 0.001$), overall beta diversity over time (a change from 1996 to 2005) was relatively low, indicating a small change in overall species composition, despite the increase in species richness.

The invasion intensity (percentage aerial cover of woody alien plants) was similar between the years, i.e. $30.0 \pm 4.6\%$ in 1996 and $31.9 \pm 3.2\%$ in 2005 ($P = 0.73$). When comparing the invasion intensity between the three original treatments over time, the invasion intensity of the 1996 grassland and savanna plots remained unchanged. The invasion intensity of the 1996 high invaded plots also remained unchanged over time, however the low invaded plots had a significantly higher invasion intensity in 2005 ($P = 0.004$). The invasion intensity of the 1996 uncleared plots remained unchanged over time, whereas the cleared plots had a significantly higher invasion intensity in 2005 ($P = 0.03$). These results clearly show that the legacy of the original invasion intensity and clearing treatments measured in the 1996/1997 study did not persist over time, whereas the inherent differences between the biomes did. The hypothesis that higher plant species richness and/or diversity should enhance community resistance to alien plant invasions was rejected, as both the 1996 and 2005 plant communities were not that resistant to the invasion of alien plants, even though there was a significantly higher species richness and diversity in 2005 than in 1996. It is concluded that because of both the similar growth form composition and invasion intensity over time, the WfW clearing efforts are not succeeding in the primary aim of controlling aliens, particularly woody alien species. However, there was a considerable decrease in the aerial cover of large alien plants, namely (a) alien plants > 5 m decreased from $15.8 \pm 4.1\%$ in 1996 to $5.8 \pm 1.2\%$ in 2005 ($P = 0.02$), and (b) those between 2 – 5 m tended to decrease from $13.3 \pm 2.8\%$ in 1996 to $11.1 \pm 2.4\%$ in 2005 ($P = 0.55$). However, these decreases were balanced by a considerable increase in the aerial cover of alien plants < 2 m in height, which

increased from $3.9 \pm 1.0\%$ in 1996 to $15.0 \pm 2.1\%$ in 2005 ($P < 0.001$). This therefore showed that the WfW clearing programme is succeeding, to some extent, in removing most of the larger alien plants but not in controlling the regenerating plants, which recover through post-clearing resprouting and/or newly established seedlings.

Exposed soil, rock and litter covers were higher in 2005 ($13.3 \pm 1.5\%$; $2.5 \pm 0.8\%$; $43.3 \pm 2.5\%$ respectively) than in 1996 ($2.1 \pm 0.5\%$; $0.9 \pm 0.3\%$; $16.4 \pm 2.7\%$ respectively) ($P < 0.001$ for soil and litter covers, and 0.07 for rock cover). Herbaceous and grass covers were significantly higher in 1996 ($47.8 \pm 2.8\%$ and $32.8 \pm 2.6\%$ respectively) than in 2005 ($20.0 \pm 1.4\%$ and $20.9 \pm 1.4\%$ respectively) ($P < 0.001$ for herbaceous and grass covers). These differences in the ground covers between the years may have partially been a response to the major February 2000 flood event, which cleared a large proportion of the vegetation, resulting in much greater rates of erosion and deposition of soils. The WfW clearing operations also removed a significant proportion of the vegetation, and disturbed much that remained, thus modifying the environment. The increase in litter cover may have also been due to the slightly higher invasion intensity in 2005 than in 1996. Soil pH remained unchanged over time (both years had a pH of 4.7 ± 0.1 ; $P = 0.99$), indicating that pH was unaffected by the invasion and subsequent clearing of alien plants, as well as the 2000 flood event which moved a tremendous amount of sediment. The hypothesis that the lower the degree of alien plant invasion, the higher the understorey vegetation cover, in both 1996 and 2005, was not rejected as the plots in 1996 had a lower degree of alien invasion (although not significant), a higher cover of herbaceous vegetation, and corresponding lower covers of exposed soil and litter.

Along the Sabie River, the alien tree and shrub species with the greatest densities were *Rubus cuneifolius* (American bramble) (1828 plants/ha), *Lantana camara* (Lantana) (1760), *Solanum mauritianum* (Bugweed) (838), *Indigofera macrophylla* (640), *Eucalyptus grandis* (Saligna gum) (560), *Caesalpinia decapetala* (Mauritius thorn) (403), *Agrimonia odorata* (Agrimonia) (220), *Lilium formosanum* (St. Joseph's lily) (218), and *Populus x canescens* (Grey popular) (125). Focusing the clearing efforts on these species will help to reduce the frequency of re-invasions, reduce costs, and increase ease of clearing.

The primary aim of the WfW programme is to increase water supplies by controlling woody alien plants. Therefore, it is concluded that the WfW clearing along the Sabie River has been partially successful, as there has been a significant decrease in the invasion intensity of large (> 5 m) alien trees (which tend to have the highest transpiration rates) over time from 1996 to 2005. In 1996, these large alien trees were represented mainly by *Eucalyptus* spp. However, the WfW programme was not effective in terms of ecosystem repair, as the invasion intensity increased slightly from 1996 to 2005, largely as a result of the significant increase in the aerial cover of smaller alien shrubs (< 2 m). If left unchecked, these will probably in time result in even higher levels of invasion intensity when the individual plants increase in size and cover. Furthermore, the growth form composition remained relatively unchanged over time, and more than half of the alien species found in 2005 were tree and shrub species. Therefore, little or no ecosystem repair has occurred along the Sabie River. In order to improve the effectiveness of the WfW programme, various detailed recommendations are included, which largely revolve around improvements in follow-up treatments.

ACKNOWLEDGEMENTS

I would like to thank the following individuals and organizations for their assistance and support throughout this study:

- Prof. Ed Witkowski, my supervisor, for his help in organising the project, for his assistance in the field, for his positive comments and criticisms given during the write-up, and for his endless enthusiasm throughout this project, which made this project a pleasure to complete.
- My research committee (Prof. Dave Mycock, Prof. Marcus Byrne and Dr. Pat Holmes) for their positive comments and criticisms.
- The Working for Water (WfW) team in Mpumalanga, especially Mr. Hannes De Lange, for assistance in finding the field sites, for providing information about WfW, and for enthusiastic support for this project.
- Penwell Mashego from Komatiland Forests for the use of some of the field equipment.
- My field assistants, Mr. Mahit Anam and Miss Maagreth Masekoane, for their invaluable assistance in the field.
- The staff at Umsonti Lodge for allowing us to stay there, and for being so hospitable.
- The National Research Foundation (NRF), the University of the Witwatersrand, and WfW for their financial assistance during this study.
- The Staff at the Moss Herbarium, especially Donald McCallum, Renee Reddy, as well as Prof. Kevin Balkwill, for their assistance in the identifications of the plant specimens.
- My fellow student Mr. Delali Dovie for his help with the multivariate analyses component of the project.
- My fellow student and friend, Miss Dalit Marom for all her help and advice, and endless support, giving throughout the project.
- Finally to my family and friends, and especially Mahit, for their support throughout the project.

TABLE OF CONTENTS

DECLARATION.....	ii
ABSTRACT.....	iii
ACKNOWLEDGEMENTS.....	vii
TABLE OF CONTENTS.....	viii
LIST OF FIGURES.....	xiii
LIST OF TABLES.....	xxviii
LIST OF APPENDICES.....	xxxiii

CHAPTER 1: GENERAL INTRODUCTION AND LITERATURE REVIEW.....

<u>1.1 Rationale of the study.....</u>	1
<u>1.2 The Working for Water (WfW) alien plant clearing programme.....</u>	3
1.2.1 History of the WfW programme.....	3
1.2.2 Clearing history of the WfW programme in the study areas along the Sabie River.....	4
1.2.3 The WfW programme as a social development programme.....	4
<u>1.3 Biodiversity.....</u>	5
<u>1.4 Multivariate statistical analyses.....</u>	5
<u>1.5 Riparian ecosystems.....</u>	5
1.5.1 The Sabie River riparian ecosystem.....	6
1.5.2 Riparian ecosystems and invasive alien plants.....	7
1.5.3 Invasive alien plants along Mpumalanga rivers.....	7
<u>1.6 Disturbance regimes.....</u>	8
1.6.1 Floods in riparian ecosystems.....	8
1.6.2 Fires in terrestrial ecosystems.....	9
1.6.3 Factors leading to changes in disturbance regimes.....	10
<u>1.7 Invasive alien plants.....</u>	10
1.7.1 Invasive alien plants in Southern Africa.....	10
1.7.2 The invasion process.....	11
1.7.3 Factors influencing invasions.....	12
1.7.4 Factors influencing the invasiveness of species.....	12
1.7.5 Factors influencing the invasibility of plant communities.....	13
<u>1.8 Impacts of invasive alien plants.....</u>	15
1.8.1 Impacts of invasive alien grasses.....	17
1.8.2 Impacts of invasive alien woody plants.....	18
1.8.3 Economic impacts of invasive alien plants.....	19
1.8.4 Examples of the most important invasive alien plants.....	20
<u>1.9 Clearing of invasive alien plants.....</u>	21
1.9.1 Control methods.....	22
<u>1.10 Ecosystem restoration.....</u>	24
1.10.1 The process of ecosystem restoration.....	25
1.10.2 Examples of methods used in restoration projects.....	27
1.10.3 Problems involved in ecosystem restoration.....	28
<u>1.11 Soil seed banks.....</u>	31
<u>1.12 Seed dispersal.....</u>	32
<u>1.13 Soil characteristics.....</u>	33
<u>1.14 Aims, objectives and hypotheses.....</u>	33

1.14.1 Aims.....	33
1.14.2 Objectives.....	34
1.14.3 Hypotheses.....	35
<u>1.15 Dissertation structure.....</u>	35
 <u>CHAPTER 2: STUDY SITE LOCATION, DESCRIPTION AND EXPERIMENTAL DESIGN.....</u>	 37
<u>2.1 Geographical location.....</u>	37
<u>2.2 Climate.....</u>	39
2.2.1 Temperature.....	40
2.2.2 Rainfall.....	43
2.2.3 Humidity.....	43
<u>2.3 Geology.....</u>	44
<u>2.4 Vegetation.....</u>	45
2.4.1 The savanna biome.....	45
2.4.2 The grassland biome.....	46
2.4.3 Vegetation types of the study areas.....	46
<u>2.5 Fauna.....</u>	48
<u>2.6 Invasive alien plants.....</u>	48
<u>2.7 Importance of the Sabie River catchment.....</u>	49
<u>2.8 Experimental design.....</u>	49
 <u>CHAPTER 3: PLANT SPECIES COMPOSITION, DIVERSITY AND VEGETATION STRUCTURE IN RESPONSE TO ALIEN PLANT CLEARING ON THE SABIE RIVER, SOUTH AFRICA, IN 2005.....</u>	 53
<u>3.1 Abstract.....</u>	53
<u>3.2 Introduction.....</u>	54
3.2.1 Biodiversity.....	55
3.2.2 The modified Whittaker nested plot technique.....	56
3.2.3 Aim, objectives and hypothesis.....	57
<u>3.3 Materials and methods.....</u>	57
3.3.1 Field sampling.....	57
3.3.2 Identification of the vegetation.....	59
3.3.3 Data analyses.....	59
<u>3.4 Results.....</u>	63
3.4.1 Plant species richness.....	63
3.4.2 Plant species diversity.....	78
3.4.3 Overstorey aerial cover.....	93
3.4.4 Linear regression analyses of the percentage aerial cover of woody alien plants (invasion intensity), and plant species richness and diversity measures.....	94
3.4.5 Linear regression analyses of the indigenous and alien plant species richness.....	111
3.4.6 Detrended correspondence analysis (DCA) of the indigenous and alien plant species composition between the grassland and savanna plots, in 2005.....	115
<u>3.5 Discussion.....</u>	119
3.5.1 Total plant species richness and diversity.....	119

3.5.2 Invasion intensity, i.e. percentage aerial cover of woody alien plants.....	120
3.5.3 Relationship between total plant species richness and diversity, and invasion intensity.....	122
3.5.4 Relationship between indigenous and alien plant species richness.....	122
3.5.5 Species richness and diversity of tree, shrub, herbaceous, grass and sedge growth forms.....	124
3.5.6 Species richness and diversity of tree, shrub, herbaceous, grass and sedge growth forms in the grassland and savanna biomes.....	126
3.5.7 Relationship between species richness and diversity of tree, shrub, herbaceous, grass and sedge growth forms, and invasion intensity.....	126
3.5.8 The effect of quadrat size on plant species richness measures.....	127
3.5.9 Edge effects on plant species richness measures.....	127
<u>3.6 Conclusions</u>	128
 <u>CHAPTER 4: CHANGES IN PLANT SPECIES COMPOSITION, DIVERSITY AND VEGETATION STRUCTURE IN RESPONSE TO ALIEN PLANT CLEARING FROM 1996 TO 2005, ALONG THE SABIE RIVER, SOUTH AFRICA</u>	
<u>4.1 Abstract</u>	131
<u>4.2 Introduction</u>	132
4.2.1 Impacts of alien plant invasions and subsequent clearing.....	132
4.2.2 The Working for Water (WfW) alien plant clearing programme.....	133
4.2.3 Objectives and hypothesis.....	133
<u>4.3 Materials and methods</u>	134
4.3.1 Experimental design.....	134
4.3.2 Field sampling.....	135
4.3.3 Data analyses.....	135
<u>4.4 Results</u>	137
4.4.1 Plant species richness.....	137
4.4.2 Plant species diversity.....	148
4.4.3 Overstorey aerial cover.....	152
4.4.4 Linear regression analyses of the percentage aerial cover of woody alien plants (invasion intensity), and plant species richness and diversity measures.....	156
4.4.5 Linear regression analyses of the percentage aerial cover of woody alien plants (invasion intensity) in 1996 and 2005.....	159
<u>4.5 Discussion</u>	163
4.5.1 Total plant species richness and diversity.....	163
4.5.2 Species richness of tree, shrub, herbaceous, grass and sedge growth forms.....	167
4.5.3 Invasion intensity, i.e. percentage aerial cover of woody alien plants.....	168
4.5.4 Relationship between total plant species richness and diversity, and invasion intensity.....	170
<u>4.6 Conclusions</u>	171

<u>CHAPTER 5: RELATING PLANT SPECIES COMPOSITION, DIVERSITY AND VEGETATION STRUCTURE TO ENVIRONMENTAL FEATURES ON THE SABIE RIVER, SOUTH AFRICA, FROM 1996 TO 2005.....</u>	175
<u>5.1 Abstract.....</u>	175
<u>5.2 Introduction.....</u>	176
5.2.1 Effects of alien plant invasions on the environment.....	176
5.2.2 Effects of alien plant clearing on the environment.....	177
5.2.3 Effects of flooding on the riparian vegetation.....	178
5.2.4 Aim, objectives and hypothesis.....	178
<u>5.3 Materials and methods.....</u>	179
5.3.1 Experimental design.....	179
5.3.2 Field sampling.....	179
5.3.3 Data analyses.....	180
<u>5.4 Results.....</u>	182
5.4.1 Slope steepness.....	182
5.4.2 Ground cover.....	183
5.4.3 Soil.....	187
5.4.4 Linear regression analyses of the percentage aerial cover of woody alien plants (invasion intensity), and litter cover and soil organic matter.....	195
5.4.5 Principal component analysis (PCA) of the environmental variables between the grassland and savanna plots, in 2005.....	201
5.4.6 Correspondence analysis (CA) and canonical correspondence analysis (CCA) of the environmental variables and indigenous and alien plant species composition between the grassland and savanna plots, in 2005.....	203
<u>5.5 Discussion.....</u>	211
5.5.1 The effects of alien plant invasion and subsequent clearing on the ground cover in the grassland and savanna biomes in 2005.....	211
5.5.2 The effects of alien plant invasion and subsequent clearing on the soil environment in the grassland and savanna biomes in 2005.....	213
5.5.3 The influence of the biomes and environmental variables on the indigenous and alien plant species composition in 2005.....	215
5.5.4 The effects of alien plant invasion and subsequent clearing on the environment over time, i.e. from 1996 to 2005.....	215
<u>5.6 Conclusions.....</u>	217
5.6.1 Grassland and savanna biomes (in 2005).....	218
5.6.2 Change over time (from 1996 to 2005).....	220
<u>CHAPTER 6: SUMMARY OF RESULTS, GENERAL CONCLUSIONS AND RECOMMENDATIONS.....</u>	222
<u>6.1 Summary of the rationale of the study.....</u>	222
<u>6.2 Summary of the aims, objectives and hypotheses.....</u>	222
6.2.1 Aims.....	223
6.2.2 Objectives.....	223
6.2.3 Hypotheses.....	224
<u>6.3 Summary of the most important results.....</u>	224

6.3.1 Impacts of alien plant species invasion and subsequent clearing on the Sabie River riparian plant species composition, diversity and vegetation structure of the grassland and savanna biomes in 2005 (Chapter 3).....	224
6.3.2 Impacts of alien plant species invasion and subsequent clearing on the Sabie River riparian plant species composition, diversity and vegetation structure over time, i.e. from 1996 to 2005 (Chapter 4).....	226
6.3.3 Impacts of alien plant species invasion and subsequent clearing on the Sabie River riparian environment of the grassland and savanna biomes in 2005, as well as over time, i.e. from 1996 to 2005 (Chapter 5).....	229
<u>6.4 Key questions relating to the ecosystem repair of the grassland and savanna biomes</u>	232
<u>6.5 Recommendations to WfW</u>	237
<u>6.6 Future areas of research</u>	238
<u>6.7 Final concluding points</u>	239
 <u>CHAPTER 7: REFERENCES</u>	 243
 <u>CHAPTER 8: APPENDICES</u>	 267

LIST OF FIGURES

Figure 2.1.	(A) Map of the Mpumalanga province in South Africa, with the study areas highlighted. Study areas were located near the Sabie (grassland), Graskop (grassland) and Hazeyview (savanna) regions. (B) Map of the study areas in the Mpumalanga province (Samancor Chrome, 2006).....	38
Figure 2.2.	Photographs of representative plots in the (A) grassland and (B) savanna biomes. The savanna tended to have a higher invasion intensity than the grassland, which can be seen by the high invasion of <i>Solanum mauritianum</i> (Bugweed) (one of the dominant alien species).....	39
Figure 2.3.	Mean monthly (A) maximum and (B) minimum temperatures (°C) from the nearest South African weather bureau climate station in Graskop, for the last 12 years, i.e. from 1994 until 2005. Note: the long-term mean is from 1994-2005. The arrows are pointing to the months of the 2005 study period (i.e. February to April).....	41
Figure 2.4.	Total monthly rainfall (mm) from the nearest South African weather bureau climate station in Graskop, for the last 12 years, i.e. from 1994 until 2005. Note: the long-term mean is from 1994-2005. The arrows are pointing to the months of the 2005 study period (i.e. February to April). Note the very high rainfall in February 2000, which was when flooding occurred.....	43
Figure 2.5.	Mean monthly humidity (%) from the nearest South African weather bureau climate station in Graskop, for the last 12 years, i.e. from 1994 until 2005 (data was not available for the years 1999, 2000, 2001 and 2002). Note: the long-term mean is from 1994-2005. The arrows are pointing to the months of the 2005 study period (i.e. February to April).....	44
Figure 2.6.	Geological map of the study areas. The study areas near the Sabie (grassland) and Graskop (grassland) regions are composed of Malmani Group Dolomite and Timeball Hill Formation Shale, and the study area near the Hazeyview (savanna) region is composed of Nelspruit Suite Granite (Samancor Chrome, 2006).....	45
Figure 2.7.	Acocks' veld types of South Africa. The study areas and the relevant veld types in the Mpumalanga province are highlighted	47
Figure 2.8.	Flow diagram summarising the experimental design of the sampling during 1996/1997 (Garner, 2005) and 2005 (this study), and the comparisons made between the two data sets.....	50
Figure 2.9.	The modified Whittaker nested plot design (from Stohlgren <i>et al.</i> , 1995).....	51
Figure 2.10.	Placement of the modified Whittaker nested plots centrally within the 30 m cleared zone relative to the river (from Garner (2005)).....	52
Figure 3.1.	Plant species richness (mean ± S.E.) as a function of quadrat size (log scale), at the 1 m ² (10 quadrats per plot for 20 plots in each biome), 10 m ² (2 quadrats per plot for 20 plots in each biome), 100 m ² (1 quadrat per plot for 20 plots in each biome),	

	and 1000 m ² (the experimental unit) (20 plots in each biome) scales within the grassland and savanna biomes, along the Sabie River. Data points with different superscript letters within the same quadrat size are significantly different using t-tests (for independent-samples) ($P < 0.05$). $N = 20$ for all quadrat scales; $d.f. = 38$	63
Figure 3.2.	Plant species richness (mean $\pm$ S.E.) as a function of quadrat size (log scale), at the 1 m ² (10 quadrats per plot for 10 plots in Sabie and Graskop, and 10 quadrats per plot for 20 plots in Hazeyview), 10 m ² (2 quadrats per plot for 10 plots in Sabie and Graskop, and 2 quadrats per plot for 20 plots in Hazeyview), 100 m ² (1 quadrat per plot for 10 plots in Sabie and Graskop, and 1 quadrat per plot for 20 plots in Hazeyview), and 1000 m ² (the experimental unit) (10 plots in Sabie and Graskop, and 20 plots in Hazeyview) quadrat scales within Sabie, Graskop and Hazeyview, along the Sabie River. Data points with different superscript letters within the same quadrat size are significantly different using Tukey's honest significant difference (HSD) tests ($P < 0.05$). $N = 10$ for all quadrat scales in Sabie and Graskop, and 20 for all quadrat scales in Hazeyview; $d.f. = 2,37$	64
Figure 3.3.	The total density (plants/ha) of alien (a) trees, (b) shrubs and (c) herbaceous plants at the 0.01 ha scale (i.e. 100 m ²), along the Sabie River (species names and invasive status are given in Appendix 3).....	66
Figure 3.4.	The density (plants/ha) of alien (1) trees, (2) shrubs and (3) herbaceous plants at the 0.01 ha scale (i.e. 100 m ²), in the (a) grassland biome and (b) savanna biome (species names and invasive status are given in Appendix 3).....	68
Figure 3.5.	The density (plants/ha) of alien (1) trees, (2) shrubs and (3) herbaceous plants at the 0.01 ha scale (i.e. 100 m ²), in the (a) Sabie, (b) Graskop and (c) Hazeyview regions (species names and invasive status are given in Appendix 3).....	70
Figure 3.6.	Species richness (mean $\pm$ S.E.) for (a) tree, (b) shrub, (c) herbaceous, and (d) grass and sedge growth forms in the grassland and savanna biomes, at the (A) 1 m ² , (B) 10 m ² , (C) 100 m ² and (D) 1000 m ² quadrat scales. Columns with different superscript letters within the same growth form are significantly different using t-tests (for independent-samples) ($P < 0.05$). $N = 20$ for all growth forms and quadrat scales; $d.f. = 38$	71
Figure 3.7.	Species richness (mean $\pm$ S.E.) for (a) tree, (b) shrub, (c) herbaceous, and (d) grass and sedge species in the Sabie (grassland), Graskop (grassland) and Hazeyview (savanna) regions, at the (A) 1 m ² , (B) 10 m ² , (C) 100 m ² and (D) 1000 m ² quadrat scales. Columns with different superscript letters within the same growth form are significantly different using Tukey's honest significant difference (HSD) tests ($P < 0.05$). $N = 10$ for all growth forms and quadrat scales in Sabie and Graskop, and 20 for all growth forms and quadrat scales in	

	Hazeyview; <i>d.f.</i> = 2,37.....	72
Figure 3.8.	Total, indigenous and alien species richness for (a) tree, (b) shrub, (c) herbaceous, and (d) grass and sedge growth forms (mean $\pm$ S.E.), for all 40 plots at the 1000 m ² quadrat scale. Comparing the indigenous with the alien species, the stacked columns with different superscript letters within the same growth form are significantly different using t-tests (for dependent-samples) ($P < 0.05$). <i>N</i> = 40 for all growth forms; <i>d.f.</i> = 39.....	73
Figure 3.9.	Total, indigenous and alien plant species richness (mean $\pm$ S.E.) for plots in the grassland and savanna biomes at the 1000 m ² quadrat scale. Stacked columns with different superscript letters within the same growth form, within the same category (i.e. total or indigenous or alien) and are significantly different using t-tests analyses (for independent-samples) ($P < 0.05$). <i>N</i> = 20 for all growth forms; <i>d.f.</i> = 38.....	74
Figure 3.10.	Total, indigenous and alien plant species richness (mean $\pm$ S.E.) for plots in the Sabie (grassland), Graskop (grassland) and Hazeyview (savanna) regions at the 1000 m ² quadrat scale. Stacked columns with different superscript letters within the same growth form, within the same category (i.e. total or indigenous or alien) and are significantly different using Tukey's honest significant difference (HSD) tests ($P < 0.05$). <i>N</i> = 10 for plots in Sabie and Graskop, and 20 for plots in Hazeyview; <i>d.f.</i> = 2,27 for Sabie and Graskop, and 2,57 for Hazeyview.....	74
Figure 3.11.	Total plant species richness (mean $\pm$ S.E.) of quadrats (1 m ² and 10 m ²) occurring on the roadside and riverside of (A) each of the 40 modified Whittaker nested plots, (B) the modified Whittaker nested plots occurring in the grassland and savanna biomes, and (C) the modified Whittaker nested plots occurring in the Sabie, Graskop and Hazeyview regions. Columns with different superscript letters within the same quadrat size are significantly different using t-tests (for dependent-samples) ($P < 0.05$). <i>N</i> = 40 for total plots, <i>N</i> = 20 for savanna, grassland and Hazeyview plots, and <i>N</i> = 10 for Sabie and Graskop plots; <i>d.f.</i> = 39 for total plots, <i>d.f.</i> = 19 for savanna, grassland and Hazeyview plots, and <i>d.f.</i> = 9 for Sabie and Graskop plots.....	76
Figure 3.12.	Alien plant species richness (mean $\pm$ S.E.) of quadrats (1 m ² and 10 m ²) occurring on the roadside and riverside of (A) each of the 40 modified Whittaker nested plots, (B) the modified Whittaker nested plots occurring in the grassland and savanna biomes, and (C) the modified Whittaker nested plots occurring in the Sabie, Graskop and Hazeyview regions. Columns with different superscript letters within the same quadrat size are significantly different using t-tests (for dependent-samples) ($P < 0.05$). <i>N</i> = 40 for total plots, <i>N</i> = 20 for savanna, grassland and Hazeyview plots, and <i>N</i> = 10 for Sabie and Graskop plots; <i>d.f.</i> = 39 for total plots, <i>d.f.</i> = 19 for savanna, grassland and Hazeyview plots, and <i>d.f.</i> = 9 for Sabie and Graskop plots.....	78

Figure 3.13.	Simpson's index of diversity (alpha diversity) (mean $\pm$ S.E.) for total plant species in the grassland and savanna biomes, at the 1 m ² , 10 m ² and 100 m ² quadrat scales. Columns with different superscript letters within the same quadrat size are significantly different using t-tests (for independent-samples) ($P < 0.05$). N = 20 for all quadrat scales; $d.f. = 38$	79
Figure 3.14.	Simpson's index of diversity (alpha diversity) (mean $\pm$ S.E.) for total plant species in the Sabie (grassland), Graskop (grassland) and Hazeyview (savanna) regions, at the 1 m ² , 10 m ² and 100 m ² quadrat scales. Columns with different superscript letters within the same quadrat size are significantly different using Tukey's honest significant difference (HSD) tests ($P < 0.05$). N = 10 for all quadrat scales in Sabie and Graskop, and 20 for all quadrat scales in Hazeyview; $d.f. = 2,37$	79
Figure 3.15.	Simpson's index of diversity (alpha diversity) (mean $\pm$ S.E.) for (a) tree, (b) shrub, (c) herbaceous, and (d) grass and sedge species in the grassland and savanna biomes, at the (A) 1 m ² , (B) 10 m ² and (C) 100 m ² quadrat scales. Columns with different superscript letters within the same growth form are significantly different using t-tests (for independent-samples) ($P < 0.05$). N = 20 for all growth forms and all quadrat scales; $d.f. = 38$	81
Figure 3.16.	Simpson's index of diversity (alpha diversity) (mean $\pm$ S.E.) for (a) tree, (b) shrub, (c) herbaceous, and (d) grass and sedge species in the Sabie (grassland), Graskop (grassland) and Hazeyview (savanna) regions, at the (A) 1 m ² , (B) 10 m ² and (C) 100 m ² quadrat scales. Columns with different superscript letters within the same growth forms are significantly different using Tukey's honest significant difference (HSD) tests ($P < 0.05$). N = 10 for all growth forms and quadrat scales in Sabie and Graskop, and 20 for all growth forms and quadrat scales in Hazeyview; $d.f. = 2,37$	82
Figure 3.17.	Species evenness (mean $\pm$ S.E.) for total plant species in the grassland and savanna biomes, at the 1 m ² , 10 m ² and 100 m ² scales. Columns with different superscript within the same quadrat scale are significantly different using t-tests (for independent-samples) ($P < 0.05$). N = 20 for all quadrat scales, $d.f. = 38$	83
Figure 3.18.	Species evenness (mean $\pm$ S.E.) for total plant species in the Sabie (grassland), Graskop (grassland) and Hazeyview (savanna) regions, at the 1 m ² , 10 m ² and 100 m ² scales. Columns with different superscript letters within the same quadrat size are significantly different using Tukey's honest significant difference (HSD) tests ($P < 0.05$). N = 10 for all quadrat scales in Sabie and Graskop, and 20 for all quadrat scales in Hazeyview; $d.f. = 2,37$	84
Figure 3.19.	Species evenness (mean $\pm$ S.E.) for (a) tree, (b) shrub, (c) herbaceous, and (d) grass and sedge species in the grassland and savanna biomes, at the (A) 1 m ² , (B) 10 m ² and (C) 100 m ² quadrat scales. Columns with different superscript letters	

	within the same growth form are significantly different using t-tests (for independent-samples) ($P < 0.05$). $N = 20$ for all growth forms and all quadrat scales; $d.f. = 38$	85
Figure 3.20.	Species evenness (mean $\pm$ S.E.) for (a) tree, (b) shrub, (c) herbaceous, and (d) grass and sedge species in the Sabie (grassland), Graskop (grassland) and Hazeyview (savanna) regions, at the (A) 1 m ² , (B) 10 m ² and (C) 100 m ² quadrat scales. Columns with different superscript letters within the same growth forms are significantly different using Tukey's honest significant difference (HSD) tests ($P < 0.05$). $N = 10$ for all growth forms and quadrat scales in Sabie and Graskop, and 20 for all growth forms and quadrat scales in Hazeyview; $d.f. = 2,37$	87
Figure 3.21.	Percentage aerial cover of alien vegetation (mean $\pm$ S.E.) from the 1000 m ² plots in the grassland and savanna biomes. Columns with different superscript letters within the same height class are significantly different using t-tests (for independent-samples) ($P < 0.05$). $N = 20$ for all height classes; $d.f. = 38$	93
Figure 3.22.	Percentage aerial cover of alien vegetation (mean $\pm$ S.E.) from the 1000 m ² plots in the Sabie (grassland), Graskop (grassland) and Hazeyview (savanna) regions. Columns with different superscript letters within the same height class are significantly different using Tukey's honest significant difference (HSD) tests ($P < 0.05$). $N = 10$ for all quadrat scales in Sabie and Graskop, and 20 for all quadrat scales in Hazeyview; $d.f. = 2,37$	94
Figure 3.23.	The linear relationship between total plant species richness (at the 1000 m ² scale) and 1) total invasion intensity (% aerial cover of large alien trees, small alien trees and alien shrubs); 2) invasion intensity – aerial cover (%) of large alien trees; 3) invasion intensity – aerial cover (%) of small alien trees; and 4) invasion intensity – aerial cover (%) of alien shrubs, for plots in the (A) grassland biome and (B) savanna biome. The linear regression relationship for 1) (A) is $r^2 = 0.003$, $y = 0.02x + 48.15$ and (B) is $r^2 = 0.09$, $y = -0.14x + 44.74$; for 2) (A) is $r^2 = 0.24$, $y = 0.58x + 46.05$ and (B) is $r^2 = 0.01$; $y = -0.14x + 40.95$; for 3) (A) is $r^2 = 0.004$; $y = 0.05x + 48.50$ and (B) is $r^2 = 0.17$, $y = 0.22x + 43.63$; and for 4) (A) is $r^2 = 0.03$, $y = -0.07x + 50.20$ and (B) is $r^2 = 0.14$, $y = 0.61x + 33.15$. The slopes of these regression lines between the two biomes were not significantly different ($P > 0.05$).....	96
Figure 3.24.	The linear relationship between total plant species richness (at the 1000 m ² scale) and 1) total invasion intensity (% aerial cover of large alien trees, small alien trees and alien shrubs); 2) invasion intensity – aerial cover (%) of large alien trees; 3) invasion intensity – aerial cover (%) of small alien trees; and 4) invasion intensity – aerial cover (%) of alien shrubs, for plots in the (A) Sabie, (B) Graskop and (C) Hazeyview regions. The linear regression relationship for 1) (A) is $r^2 = 0.01$, $y = -0.03x$	

+ 53.48, (B) is $r^2 = 0.45$, $y = 0.14x + 40.46$, and (C) is $r^2 = 0.09$, $y = -0.14x + 44.74$; for 2) (A) is $r^2 = 0.28$, $y = 0.59x + 49.49$, (B) is $r^2 = 0.29$, $y = 0.42x + 43.21$, and (C) is $r^2 = 0.01$, $y = -0.14x + 40.95$; for 3) (A) is $r^2 = 0.07$, $y = 0.57x + 50.88$, (B) is $r^2 = 0.21$, $y = 0.17x + 43.55$, and (C) is $r^2 = 0.17$, $y = -0.22x + 43.63$; and for 4) (A) is $r^2 = 0.13$, $y = -0.17x + 55.51$, (B) is $r^2 = 0.15$, $y = 0.11x + 42.81$, and (C) is $r^2 = 0.14$, $y = 0.61x + 33.15$. The slopes of these regression lines were not significantly different between the three regions ($P > 0.05$), except the slopes between Sabie and Hazeyview (3A and 3C) ($P < 0.05$)..... 98

Figure 3.25. The linear relationship between tree species richness (at the 1000 m² scale) and 1) total invasion intensity (% aerial cover of large alien trees, small alien trees and alien shrubs); 2) invasion intensity – aerial cover (%) of large alien trees; 3) invasion intensity – aerial cover (%) of small alien trees; and 4) invasion intensity – aerial cover (%) of alien shrubs, for plots in the (A) grassland biome and (B) savanna biome. The linear regression relationship for 1) (A) is $r^2 = 0.06$, $y = 0.03x + 4.61$ and (B) is $r^2 = 0.004$, $y = 0.01x + 5.62$; for 2) (A) is $r^2 = 0.21$, $y = 0.14x + 4.69$ and (B) is $r^2 = 0.02$, $y = 0.05x + 5.53$; for 3) (A) is $r^2 = 0.01$, $y = 0.02x + 5.22$ and (B) is $r^2 = 0.02$, $y = -0.02x + 6.22$; and for 4) (A) is $r^2 = 0.004$, $y = 0.01x + 5.22$ and (B) is $r^2 = 0.14$, $y = 0.18x + 3.87$. The slopes of these regression lines between the two biomes were not significantly different ($P > 0.05$)..... 100

Figure 3.26. The linear relationship between tree species richness (at the 1000 m² scale) and 1) total invasion intensity (% aerial cover of large alien trees, small alien trees and alien shrubs); 2) invasion intensity – aerial cover (%) of large alien trees; 3) invasion intensity – aerial cover (%) of small alien trees; and 4) invasion intensity – aerial cover (%) of alien shrubs, for plots in the (A) Sabie, (B) Graskop and (C) Hazeyview regions. The linear regression relationship for 1) (A) is $r^2 = 0.001$, $y = -0.003x + 5.57$, (B) is $r^2 = 0.29$, $y = 0.05x + 3.49$, and (C) is $r^2 = 0.004$, $y = 0.01x + 5.62$; for 2) (A) is $r^2 = 0.11x$, $y = 0.09x + 5.05$, (B) is $r^2 = 0.43$, $y = 0.24x + 4.17$, and (C) is $r^2 = 0.02$, $y = 0.05x + 5.53$, for 3) (A) is $r^2 = 0.36$, $y = 0.30x + 4.61$, (B) is $r^2 = 3 \times 10^{-6}$, $y = -0.001x + 5.21$, and (C) is $r^2 = 0.02$, $y = -0.02x + 6.22$; and for 4) (A) is $r^2 = 0.09$, $y = -0.03x + 6.06$, (B) is $r^2 = 0.27$, $y = 0.07x + 3.82$, and (C) is $r^2 = 0.14$, $y = 0.18x + 3.87$. The slopes of these regression lines were not significantly different between the three regions ($P > 0.05$), except the slopes between Sabie and Hazeyview (3A and 3C) ($P < 0.05$)..... 102

Figure 3.27. The linear relationship between total plant species Simpson's index of diversity (alpha diversity) (at the 100 m² scale) and 1) total invasion intensity (% aerial cover of large alien trees, small alien trees and alien shrubs); 2) invasion intensity – aerial cover (%) of large alien trees; 3) invasion intensity – aerial cover (%) of small alien trees; and 4) invasion intensity – aerial cover (%) of alien shrubs, for plots in the (A) grassland biome

and (B) savanna biome. The linear regression relationship for 1) (A) is $r^2 = 0.02$, $y = 0.0003x + 0.89$ and (B) is $r^2 = 0.02$, $y = 0.001x + 0.83$; for 2) (A) is $r^2 = 0.002$, $y = 0.0003x + 0.90$ and (B) is $r^2 = 0.05$, $y = -0.002x + 0.87$; for 3) (A) is $r^2 = 0.09$, $y = 0.002x + 0.91$ and (B) is $r^2 = 0.01$, $y = 0.001x + 0.85$; and for 4) (A) is $r^2 = 0.09$, $y = 0.001x + 0.88$ and (B) is $r^2 = 0.22$, $y = 0.01x + 0.78$. The slopes of these regression lines between the two biomes were not significantly different ($P > 0.05$)..... 104

Figure 3.28. The linear relationship between total plant species Simpson's index of diversity (alpha diversity) (at the 100 m² scale) and 1) total invasion intensity (% aerial cover of large alien trees, small alien trees and alien shrubs); 2) invasion intensity – aerial cover (%) of large alien trees; 3) invasion intensity – aerial cover (%) of small alien trees; and 4) invasion intensity – aerial cover (%) of alien shrubs, for plots in the (A) Sabie, (B) Graskop and (C) Hazeyview regions. The linear regression relationship for 1) (A) is $r^2 = 0.06$, $y = 0.001x + 0.87$, (B) is $r^2 = 0.002$, $y = -8 \times 10^{-6}x + 0.91$ and (C) is $r^2 = 0.02$, $y = 0.001x + 0.83$; for 2) (A) is $r^2 = 0.02$, $y = 0.001x + 0.89$, (B) is $r^2 = 0.03$, $y = -0.001x + 0.91$ and (C) is $r^2 = 0.05$, $y = -0.002x + 0.87$; for 3) (A) is $r^2 = 0.002$, $y = 0.001x + 0.89$, (B) is $r^2 = 0.49$, $y = -0.002x + 0.92$ and (C) is $r^2 = 0.01$, $y = 0.001x + 0.85$; and for 4) (A) is $r^2 = 0.03$, $y = 0.001x + 0.88$, (B) is $r^2 = 0.29$, $y = 0.001x + 0.88$ and (C) is $r^2 = 0.22$, $y = 0.01x + 0.78$. The slopes of these regression lines between the three regions were not significantly different ($P > 0.05$)..... 106

Figure 3.29. The linear relationship between tree species Simpson's index of diversity (alpha diversity) (at the 100 m² scale) and 1) total invasion intensity (% aerial cover of large alien trees, small alien trees and alien shrubs); 2) invasion intensity – aerial cover (%) of large alien trees; 3) invasion intensity – aerial cover (%) of small alien trees; and 4) invasion intensity – aerial cover (%) of alien shrubs, for plots in the (A) grassland biome and (B) savanna biome. The linear regression relationship for 1) (A) is $r^2 = 0.17$, $y = 0.01x + 0.20$ and (B) is $r^2 = 0.05$, $y = -0.004x + 0.63$; for 2) (A) is $r^2 = 0.14$, $y = 0.01x + 0.29$ and (B) is $r^2 = 0.08$, $y = -0.01x + 0.59$; for 3) (A) is $r^2 = 0.01$, $y = 0.003x + 0.35$ and (B) is $r^2 = 0.03$, $y = -0.003x + 0.56$; and for 4) (A) is $r^2 = 0.09$, $y = 0.005x + 0.28$ and (B) is $r^2 = 0.02$, $y = 0.01x + 0.44$. The slopes of these regression lines between the two biomes were not significantly different ($P > 0.05$)..... 108

Figure 3.30. The linear relationship between tree species Simpson's index of diversity (alpha diversity) (at the 100 m² scale) and 1) total invasion intensity (% aerial cover of large alien trees, small alien trees and alien shrubs); 2) invasion intensity – aerial cover (%) of large alien trees; 3) invasion intensity – aerial cover (%) of small alien trees; and 4) invasion intensity – aerial cover (%) of alien shrubs, for plots in the (A) Sabie, (B) Graskop and (C) Hazeyview regions. The linear regression relationship for 1) (A) is $r^2 = 0.13$, $y = 0.01x + 0.21$, (B) is $r^2 = 0.19$, $y = 0.01x +$

	0.20 and (C) is $r^2 = 0.05$, $y = -0.004x + 0.63$; for (2) (A) is $r^2 = 0.10$, $y = 0.01x + 0.28$, (B) is $r^2 = 0.23$, $y = 0.02x + 0.29$ and (C) is $r^2 = 0.08$, $y = -0.01x + 0.59$; for (3) (A) is $r^2 = 6 \times 10^{-6}$, $y = 0.001x + 0.34$, (B) is $r^2 = 0.01$, $y = 0.002x + 0.38$ and (C) is $r^2 = 0.03$, $y = -0.003x + 0.56$; and for (4) (A) is $r^2 = 0.05$, $y = 0.003x + 0.28$, (B) is $r^2 = 0.14$, $y = 0.01x + 0.26$ and (C) is $r^2 = 0.02$, $y = 0.01x + 0.44$. The slopes of these regression lines between the three regions were not significantly different ($P > 0.05$).....	110
Figure 3.31.	The linear relationship between the total indigenous and alien plant species richness ($r^2 = 0.04$). The linear relationship is $y = 0.06x + 9.83$	111
Figure 3.32.	The linear relationship between the indigenous and alien plant species richness for plots in the (A) grassland biome ($r^2 = 5 \times 10^{-6}$, $y = 0.02x + 36.3$) and (B) savanna biome ($r^2 = 0.12$, $y = 1.08x + 15.7$). The slopes of these regression lines were not significantly different ($P > 0.05$).....	112
Figure 3.33.	The linear relationship between the indigenous and alien plant species richness for plots in the (A) Sabie ($r^2 = 0.06$, $y = -0.59x + 47.06$), (B) Graskop ($r^2 = 0.20$, $y = 0.88x + 24$) and (C) Hazeyview ($r^2 = 0.12$, $y = 1.08x + 15.71$) regions. The slopes of these regression lines were not significantly different ($P > 0.05$), except between Graskop and Hazeyview ($P < 0.05$).....	113
Figure 3.34.	The linear relationship between the (A) indigenous and alien tree species richness ($r^2 = 0.10$, $y = 0.39x + 3.02$), (B) indigenous and alien shrub species richness ($r^2 = 0.11$, $y = -0.71x + 12.10$), (C) indigenous and alien herbaceous species richness ($r^2 = 0.12$, $y = 0.95x + 8.28$) and (D) indigenous and alien grass species richness ($r^2 = 0.04$, $y = 1.30x + 5.53$), for all 40 plots. The slopes of these regression lines were not significantly different ($P > 0.05$).....	114
Figure 3.35.	Detrended correspondence analysis (DCA) of plant species (with a weight of 10 – 100%) in the 40 plots at the 100 m ² scale, in 2005. Plots were categorised into grassland and savanna, and species into indigenous and alien. Species are labeled by the first four letters of the generic name and the first four letters of the specific name (refer to Appendix 2 for species names).....	116
Figure 3.36.	Detrended correspondence analysis (DCA) of plant species in the 40 plots at the 100 m ² scale, in 2005. Only the indigenous species are shown (with a weight of 10 – 100%). Plots were categorised into grassland and savanna. Species are labeled by the first four letters of the generic name and the first four letters of the specific name (refer to Appendix 2 for species names)....	117

Figure 3.37.	Detrended correspondence analysis (DCA) of plant species in the 40 plots at the 100 m ² scale, in 2005. Only the alien species are shown (all of them). Plots were categorized into grassland and savanna. Species are labeled by the first four letters of the generic name and the first four letters of the specific name (refer to Appendix 2 for species names). The black arrows are pointing to the alien species that are declared weeds and invaders (category 1 and 2).....	118
Figure 3.38.	Summary diagram of the most important results from chapter 3.	128
Figure 4.1.	Flow diagram of the experimental layout of the plots, showing the three different experimental treatments, i.e. high altitude (grassland) versus low altitude (savanna) plots (biome), high invaded versus low invaded plots (invasion intensity) and cleared versus uncleared plots (clearing). These categorizations were made in 1996/1997 and are used again in 2005, despite all the changes over time.....	135
Figure 4.2.	Total, indigenous and alien plant species of each of the 40 1000 m ² plots, in 1996 and 2005, along the Sabie River.....	137
Figure 4.3.	Total plant species richness (mean ± S.E.) for all 40 plots in 1996 and 2005, at the 1 m ² , 10 m ² , 100 m ² and 1000 m ² quadrat scales. Columns with different superscript letters within the same quadrat size are significantly different using t-tests (for independent-samples) ($P < 0.05$). $N = 40$ for quadrat scales; $d.f. = 78$	139
Figure 4.4.	Total plant species richness (mean ± S.E.) for plots in the grassland and savanna biomes in 1996 and 2005, at the 1 m ² , 10 m ² , 100 m ² and 1000 m ² quadrat scales. Columns with different superscript letters within the same quadrat size and biome are significantly different using t-tests (for independent-samples) ($P < 0.05$). $N = 20$ for all quadrat scales and biomes; $d.f. = 38$	140
Figure 4.5.	Species richness (mean ± S.E.) for (a) tree, (b) shrub, (c) herbaceous, and (d) grass and sedge growth forms in all 40 plots in 1996 and 2005, at the (A) 1 m ² , (B) 10 m ² , (C) 100 m ² and (D) 1000 m ² quadrat scales. Columns with different superscript letters within the same growth form are significantly different using t-tests (for independent-samples) ($P < 0.05$). $N = 40$ for all growth forms and quadrat scales; $d.f. = 78$	142
Figure 4.6.	Simpson's index of diversity (alpha diversity) (mean ± S.E.) for total plant species for all 40 plots in 1996 and 2005, at the 100 m ² quadrat scale. Columns with different superscript letters are significantly different using t-tests (for independent-samples) ($P < 0.05$). $N = 40$ for each year; $d.f. = 78$	148
Figure 4.7.	Simpson's index of diversity (alpha diversity) (mean ± S.E.) for total plant species for plots in the grassland and savanna biomes in 1996 and 2005, at the 100 m ² quadrat scale. Columns with different superscript letters within the same biome are significantly different using t-tests (for independent-samples) ($P < 0.05$). $N = 20$ for each biome; $d.f. = 38$	149
Figure 4.8.	Percentage aerial cover of alien vegetation (mean ± S.E.) for all	

	40 plots in 1996 and 2005. Columns with different superscript letters within the same height class are significantly different using t-tests (for independent-samples) ($P < 0.05$). $N = 40$ for all height classes; $d.f. = 78$	152
Figure 4.9.	Percentage aerial cover of alien vegetation (mean $\pm$ S.E.) for plots in the grassland and savanna biomes in 1996 and 2005. Columns with different superscript letters within the same height class and biome are significantly different using t-tests (for independent-samples) ($P < 0.05$). $N = 20$ for each height class and biome; $d.f. = 38$	152
Figure 4.10.	Total percentage aerial cover of alien vegetation (mean $\pm$ S.E.) for plots of the three different experimental treatments in 1996 and 2005, i.e. grassland and savanna (= biome), high and low invasion (= invasion intensity), and cleared and uncleared (= clearing). Columns with different superscript letters within the same treatment are significantly different using t-tests (for independent-samples) ($P < 0.05$). $N = 20$ for each treatment; $d.f. = 38$	156
Figure 4.11.	The linear relationship between total plant species richness (at the 1000 m ² scale) and invasion intensity (% aerial cover of woody alien plants) for each of the 40 plots in (A) 2005 ($r^2 = 0.03$) and (B) 1996 ($r^2 = 0.26$). The linear regression relationship for (A) is $y = -0.09 + 47.15x$, and for (B) is $y = -0.11x + 27.33$. The slopes of these regression lines were significantly different ($P < 0.05$).....	157
Figure 4.12.	The linear relationship between tree species richness (at the 1000 m ² scale) and invasion intensity (% aerial cover of woody alien plants) for each of the 40 plots in (A) 2005 ($r^2 = 0.02$) and (B) 1996 ($r^2 = 0.01$). The linear regression relationship for (A) is $y = 0.02x + 5.05$ and for (B) is $y = -0.01x + 3.66$. The slopes of these regression lines were significantly different ($P < 0.05$)..	158
Figure 4.13.	The linear relationship between Simpson's index of diversity (plant alpha diversity) (at the 100 m ² scale) and invasion intensity (% aerial cover of woody alien plants) for each of the 40 plots in (A) 2005 ($r^2 = 0.01$) and (B) 1996 ($r^2 = 0.14$). The linear regression relationship for (A) is $y = 0.0003x + 0.87$ and for (B) is $y = 0.002x + 0.24$. The slopes of these regression lines were significantly different ($P < 0.05$).....	159
Figure 4.14.	The linear relationship between the invasion intensity (% aerial cover of woody alien plants) in 1996 and the invasion intensity in 2005 (for each of the 40 plots) ($r^2 = 0.03$). The linear regression relationship is $y = 0.12x + 28.18$	160
Figure 4.15.	The linear relationship between the invasion intensity (% aerial cover of woody alien plants) in 1996 and the invasion intensity in 2005, for plots in the (A) grassland biome ($r^2 = 0.04$) and (B) savanna biome ($r^2 = 0.02$). The linear regression relationship for (A) is $y = 0.13x + 25.80$ and for (B) is $y = 0.09x + 31.31$. The slopes of these regression lines were not significantly different ($P > 0.05$).....	161
Figure 4.16.	The linear relationship between the invasion intensity (% aerial	

	cover of woody alien plants) in 1996 and the invasion intensity in 2005, for plots with a (A) high invasion ($r^2 = 2 \times 10^{-5}$) and (B) low invasion ($r^2 = 0.20$). The linear regression relationship for (A) is $y = -0.01x + 35.55$ and for (B) is $y = 0.89x + 16.98$. The slopes of these regression lines were not significantly different ($P > 0.05$).....	162
Figure 4.17.	The linear relationship between the invasion intensity (% aerial cover of woody alien plants) in 1996 and the invasion intensity in 2005, for plots that are (A) cleared ($r^2 = 0.02$) and (B) uncleared ($r^2 = 0.03$). The linear regression relationship for (A) is $y = 0.14x + 26.63$ and for (B) is $y = 0.12x + 28.69$. The slopes of these regression lines were not significantly different ($P > 0.05$).....	163
Figure 4.18.	Summary diagram of the most important results from chapter 4.	172
Figure 5.1.	Degree of slope steepness (mean $\pm$ S.E.) of plots in the grassland and savanna biomes in 2005. Columns with different superscript letters are significantly different using t-tests (for independent-samples) ($P < 0.05$). $N = 20$ for each biomes; $d.f. = 38$	182
Figure 5.2.	Degree of slope steepness (mean $\pm$ S.E.) of plots in the Sabie (grassland), Graskop (grassland) and Hazeyview (savanna) regions in 2005. Columns with different superscript letters are significantly different using Tukey's honest significant difference (HSD) tests ($P < 0.05$). $N = 10$ for Sabie and Graskop, and 20 for Hazeyview; $d.f. = 2,37$	183
Figure 5.3.	Percentage ground cover estimates (mean $\pm$ S.E.) of (a) exposed soil, (b) rock, (c) litter, (d) herbaceous vegetation and (e) grass from plots in the grassland and savanna biomes in 2005. Columns with different superscript letters within the same ground cover variable are significantly different using t-tests (for independent-samples) ($P < 0.05$). $N = 20$ for all ground cover variables; $d.f. = 38$	183
Figure 5.4.	Percentage ground cover estimates (mean $\pm$ S.E.) of (a) exposed soil, (b) rock, (c) litter, (d) herbaceous vegetation and (e) grass from plots in the Sabie (grassland), Graskop (grassland) and Hazeyview (savanna) regions in 2005. Columns with different superscript letters within the same ground cover variable are significantly different using Tukey's honest significant difference (HSD) tests ($P < 0.05$). $N = 10$ for all ground cover variables in Sabie and Graskop, and 20 for all ground cover variables in Hazeyview; $d.f. = 2,37$	184
Figure 5.5.	Percentage ground cover estimates (mean $\pm$ S.E.) of (a) exposed soil, (b) rock, (c) litter, (d) herbaceous vegetation and (e) grass from all 40 plots along the Sabie River, in 1996 and 2005. Columns with different superscript letters within the same ground cover variable are significantly different using t-tests (for independent-samples) ($P < 0.05$). $N = 40$ for each ground cover variable; $d.f. = 78$	185
Figure 5.6.	Percentage of soil organic matter (mean $\pm$ S.E.) for plots in the grassland and savanna biomes in 2005. Columns with different	

	superscript letters are significantly different using t-tests (for independent-samples) ($P < 0.05$). $N = 20$ for each biome; $d.f. = 38$	188
Figure 5.7.	Percentage of total nitrogen (mean $\pm$ S.E.) for plots in the grassland and savanna biomes in 2005. Columns with different superscript letters are significantly different using t-tests (for independent-samples) ($P < 0.05$). $N = 20$ for each biome; $d.f. = 38$	188
Figure 5.8.	pH (mean $\pm$ S.E.) for plots in the grassland and savanna biomes in 2005. Columns with different superscript letters are significantly different using t-tests (for independent-samples) ($P < 0.05$). $N = 20$ for each biome; $d.f. = 38$	189
Figure 5.9.	Concentration of soil elements (mg/L) (mean $\pm$ S.E.) for plots in the grassland and savanna biomes in 2005. Soil elements include phosphate (indicated as P), exchangeable potassium (K), exchangeable calcium (Ca), exchangeable magnesium (Mg), total zinc (Zn), total manganese (Mn) and total copper (Cu). Columns with different superscript letters within the same soil element are significantly different using t-tests (for independent-samples) ($P < 0.05$). $N = 20$ for each soil element; $d.f. = 38$	189
Figure 5.10.	Soil compaction (mean $\pm$ S.E.) of plots in the grassland and savanna biomes in 2005. Columns with different superscript letters are significantly different using t-tests (for independent-samples) ($P < 0.05$). $N = 20$ for each biome; $d.f. = 38$	190
Figure 5.11.	Percentage of soil organic matter (mean $\pm$ S.E.) for plots in the Sabie (grassland), Graskop (grassland) and Hazeyview (savanna) regions in 2005. Columns with different superscript letters are significantly different using Tukey's honest significant difference (HSD) tests ($P < 0.05$). $N = 10$ for Sabie and Graskop, and 20 for Hazeyview; $d.f. = 2,37$	191
Figure 5.12.	Percentage of total nitrogen (mean $\pm$ S.E.) for plots in the Sabie (grassland), Graskop (grassland) and Hazeyview (savanna) regions in 2005. Columns with different superscript letters are significantly different using Tukey's honest significant difference (HSD) tests ($P < 0.05$). $N = 10$ for Sabie and Graskop, and 20 for Hazeyview; $d.f. = 2,37$	191
Figure 5.13.	pH (mean $\pm$ S.E.) for plots in the Sabie (grassland), Graskop (grassland) and Hazeyview (savanna) regions in 2005. Columns with different superscript letters are significantly different using Tukey's honest significant difference (HSD) tests ($P < 0.05$). $N = 10$ for Sabie and Graskop, and 20 for Hazeyview; $d.f. = 2,37$	192
Figure 5.14.	Concentration of soil elements (mg/L) (mean $\pm$ S.E.) for plots in the Sabie (grassland), Graskop (grassland) and Hazeyview (savanna) regions in 2005. Soil elements include phosphate (indicated as P), exchangeable potassium (K), exchangeable calcium (Ca), exchangeable magnesium (Mg), total zinc (Zn), total manganese (Mn) and total copper (Cu) in 2005. Columns with different superscript letters within the same soil element	

	are significantly different using Tukey's honest significant difference (HSD) tests ($P < 0.05$). $N = 10$ for Sabie and Graskop, and 20 for Hazeyview; $d.f. = 2,37$	192
Figure 5.15.	Soil compaction (mean $\pm$ S.E.) for plots in the Sabie (grassland), Graskop (grassland) and Hazeyview (savanna) regions in 2005. Columns with different superscript letters are significantly different using Tukey's honest significant difference (HSD) tests ($P < 0.05$). $N = 10$ for Sabie and Graskop, and 20 for Hazeyview; $d.f. = 2,37$	193
Figure 5.16.	pH (mean $\pm$ S.E.) for all 40 plots in 1996 and 2005, along the Sabie River. Columns with different superscript letters are significantly different using t-tests (for independent-samples) ($P < 0.05$). $N = 40$ for each year; $d.f. = 78$	194
Figure 5.17.	The linear relationship between percentage litter cover and invasion intensity (% aerial cover of woody alien plants) for plots in the (A) grassland biome ($r^2 = 0.004$) and (B) savanna biome ($r^2 = 0.38$) in 2005. The linear regression relationship for (A) is $y = -0.06x + 44.93$ and for (B) is $y = 0.40x + 29.64$. The slopes of these regression lines were not significantly different ($P > 0.05$).....	196
Figure 5.18.	The linear relationship between percentage of soil organic matter and invasion intensity (% aerial cover of woody alien plants) for plots in the (A) grassland biome ($r^2 = 0.13$) and (B) savanna biome ($r^2 = 0.09$) in 2005. The linear regression relationship for (A) is $y = 0.02x + 4.04$ and for (B) is $y = 0.02x + 2.50$. The slopes of these regression lines were not significantly different ($P > 0.05$).....	197
Figure 5.19.	The linear relationship between percentage litter cover and invasion intensity (% aerial cover of woody alien plants) for plots in the (A) Sabie ($r^2 = 0.60$), (B) Graskop ($r^2 = 0.34$) and (C) Hazeyview ($r^2 = 0.38$) regions in 2005. The linear regression relationship for (A) is $y = -0.79x + 63.04$, for (B) is $y = 0.52x + 26.31$ and for (C) is $y = 0.40x + 29.64$. The slopes of these regression lines were not significantly different ($P > 0.05$).....	198
Figure 5.20.	The linear relationship between percentage of soil organic matter and invasion intensity (% aerial cover of woody alien plants) for plots in the (A) Sabie ($r^2 = 0.001$), (B) Graskop ($r^2 = 0.47$) and (C) Hazeyview ($r^2 = 0.07$) regions in 2005. The linear regression relationship for (A) is $y = 0.002x + 4.21$, for (B) is $y = 0.02x + 3.93$ and for (C) is $y = 0.02x + 2.66$. The slopes of these regression lines were not significantly different ($P > 0.05$).....	199
Figure 5.21.	The linear relationship between percentage litter cover and invasion intensity (% aerial cover of woody alien plants) for each of the 40 plots in (A) 2005 ($r^2 = 0.05$) and (B) 1996 ($r^2 = 0.41$). The linear regression relationship for (A) is $y = 0.17x + 37.78$ and for (B) is $y = 0.37x + 5.22$. The slopes of these regression lines were significantly different ($P < 0.05$).....	200
Figure 5.22.	The linear relationship between percentage of soil organic	

	matter in each of the 40 plots in 1996 and 2005 ($r^2 = 0.13$). The linear regression relationship is $y = 0.92x + 2.85$	201
Figure 5.23.	Principal component analysis (PCA) of the environmental variables of the 40 plots, in 2005. Plots were categorised into grassland and savanna. Environmental variables include phosphate (PO_4^{3-}), exchangeable potassium (K), calcium (Ca), and magnesium (Mg), total zinc (Zn), manganese (Mn), and copper (Cu), organic C, total N, acidity, cations, acid saturation (AcidSat), soil pH, altitude, slope steepness (Slope), compaction (Compactn), and the percentage cover of exposed soil, rock, litter, herbaceous vegetation (Herbs) and grass, and the invasion intensity (InvInt) (i.e. percentage aerial cover of woody alien plants).....	202
Figure 5.24.	Correspondence analysis (CA) of the plant species of the 40 plots, in 2005. Plots were categorised into grassland and savanna, and species into indigenous and alien. Only those species with a weight range of 10-100% were included, i.e. the less abundant species were not included. For clarity, the species labels were not included.....	204
Figure 5.25.	Canonical correspondence analysis (CCA) of the plant species and environmental variables, within the 40 plots (in 2005). Environmental variables are not shown in this ordination diagram, only the species (all of them), which were categorised into alien and indigenous. For clarity, species labels were not included.....	207
Figure 5.26.	Canonical correspondence analysis (CCA) of the plant species and environmental variables, within the 40 plots (in 2005). Only environmental variables and plots (which were categorised into grassland and savanna) are shown in this ordination diagram. Only those environmental variables that significantly explained the species composition patterns were included in the CCA. These environmental variables include the slope steepness (Slope), altitude, organic C, exposed soil cover (Soil) and soil pH.....	208
Figure 5.27.	Canonical correspondence analysis (CCA) of the plant species and environmental variables, within the 40 plots (in 2005). Only those environmental variables that significantly explained the species composition patterns were included in the CCA, namely slope steepness (Slope), altitude, organic C, exposed soil cover (Soil) and soil pH. Plots were categorised into grassland and savanna, and species into indigenous and alien. All of the species were included, but for clarity, the species labels were not included.....	209
Figure 5.28.	Canonical correspondence analysis (CCA) of the plant species and environmental variables, within the 40 plots (in 2005). Only alien species (all of them) are included in the ordination diagram. Only those environmental variables that significantly explained the species composition patterns were included in the CCA, namely slope steepness (Slope), altitude, organic C, exposed soil cover (Soil) and soil pH. Plots were categorised	

	into grassland and savanna. The black arrows are pointing to the alien species that are declared weeds and invaders (category 1 and 2). Species are labeled by the first four letters of the generic name and the first four letters of the specific name (refer to Appendix 2 for species names).....	210
Figure 5.29.	Summary diagram of the most important results from chapter 5.	218
Figure 6.1.	The total density (plants/ha) of indigenous and alien tree and shrub species at the 0.01 ha scale (i.e. 100 m ²), along the Sabie River in the grassland biome (species names and invasive status are given in Appendix 3).....	235
Figure 6.2.	The total density (plants/ha) of indigenous and alien tree and shrub species at the 0.01 ha scale (i.e. 100 m ²), along the Sabie River in the savanna biome (species names and invasive status are given in Appendix 3).....	236

LIST OF TABLES

Table 2.1.	Mean maximum and minimum temperatures (°C), total rainfall (mm) and mean humidity (%) from the nearest South African weather bureau climate station in Graskop, for the months of the study period, i.e. February, March and April, for the last 12 years, i.e. 1994 until 2005, and over the long-term (i.e. the mean from 1994-2005). Note: grey highlight = data unavailable.....	41
Table 2.2.	The degree of invasion intensity (%) (shown in the last row of the table) of each of the experimental categories, i.e. (A) high (grassland) and low altitude (savanna) plots (biome), (B) high and low invaded plots (invasion intensity) and (C) cleared and uncleared plots (clearing), from the 1996/1997 study.....	51
Table 3.1.	Total, indigenous, alien, shrub, tree, grass, and other herbaceous species (cumulative number and percentage) in all 40 modified Whittaker nested plots in 2005, as well as the number and percentage of species common to the grassland and savanna biomes, and the Sabie (grassland), Graskop (grassland) and Hazeyview (savanna) regions.....	64
Table 3.2.	Sorenson's coefficient of community (mean $\pm$ S.E.) for all pair-wise comparisons of the total plant species of all pooled plots for the grassland and savanna biomes (i.e. 20 plots pooled for each biome). This index was calculated at the 1 m ² , 10 m ² , 100 m ² and 1000 m ² quadrat scales.....	87
Table 3.3.	Sorenson's coefficient of community (mean $\pm$ S.E.) for all pair-wise comparisons of the total plant species of all pooled plots for the Sabie (grassland), Graskop (grassland) and Hazeyview (savanna) regions (i.e. 10 plots pooled for both Sabie and Graskop, and 20 plots pooled for Hazeyview). This index was calculated at the 1 m ² , 10 m ² , 100 m ² and 1000 m ² quadrat scales.....	87
Table 3.4.	Sorenson's coefficient of community (mean $\pm$ S.E.) for all pair-wise comparisons of the (a) tree, (b) shrub, (c) herbaceous, and (d) grass and sedge species of all pooled plots for the grassland and savanna biomes (i.e. 20 plots pooled for each biome). This index was calculated at the 1 m ² , 10 m ² , 100 m ² and 1000 m ² quadrat scales.....	88
Table 3.5.	Sorenson's coefficient of community (mean $\pm$ S.E.) for all pair-wise comparisons of the (a) tree, (b) shrub, (c) herbaceous, and (d) grass and sedge species of all pooled plots for the Sabie (grassland), Graskop (grassland) and Hazeyview (savanna) regions (i.e. 10 plots pooled for both Sabie and Graskop, and 20 plots pooled for Hazeyview). This index was calculated at the 1 m ² , 10 m ² , 100 m ² and 1000 m ² quadrat scales.....	89
Table 3.6.	Species complementarity (mean $\pm$ S.E.) for all pair-wise comparisons of the total plant species of all pooled plots for the grassland and savanna biomes (i.e. 20 plots pooled for each biome). This index was calculated at the 1 m ² , 10 m ² , 100 m ² and 1000 m ² quadrat scales.....	90
Table 3.7.	Species complementarity (mean $\pm$ S.E.) for all pair-wise	

	comparisons of the total plant species of all pooled plots for the Sabie (grassland), Graskop (grassland) and Hazeyview (savanna) regions (i.e. 10 plots pooled for both Sabie and Graskop, and 20 plots pooled for Hazeyview). This index was calculated at the 1 m ² , 10 m ² , 100 m ² and 1000 m ² quadrat scales.....	90
Table 3.8.	Species complementarity (mean ± S.E.) for all pair-wise comparisons of the (a) tree, (b) shrub, (c) herbaceous, and (d) grass and sedge species of all pooled plots for the grassland and savanna biomes (i.e. 20 plots pooled for each biome). This index was calculated at the 1 m ² , 10 m ² , 100 m ² and 1000 m ² quadrat scales.....	91
Table 3.9.	Species complementarity (mean ± S.E.) for all pair-wise comparisons of the (a) tree, (b) shrub, (c) herbaceous, and (d) grass and sedge species of all pooled plots for the Sabie (grassland), Graskop (grassland) and Hazeyview (savanna) regions (i.e. 10 plots pooled for both Sabie and Graskop, and 20 plots pooled for Hazeyview). This index was calculated at the 1 m ² , 10 m ² , 100 m ² and 1000 m ² quadrat scales.....	92
Table 3.10.	Summary of the detrended correspondence analysis (DCA).....	115
Table 4.1.	Total, indigenous, alien, herbaceous, shrub, tree, grass and weed species (counts and percentages) of each of the 40 plots in 1996 and 2005; the percentage increases in these species over time (i.e. from 1996 to 2005); as well as the number of these species common between 1996 and 2005.....	137
Table 4.2.	Total, indigenous, alien, herbaceous, shrub, tree, grass and weed species (counts and percentages) of the grassland and savanna biomes in 1996 and 2005, as well as the percentage increases in these species in the grassland and savanna biomes over time (i.e. from 1996 to 2005).....	138
Table 4.3.	Total plant species richness (mean ± S.E.) for 1996 and 2005. Values with different subscript letters within the same experimental category of the three different experimental treatments and same quadrat size in 1996 and 2005 are significantly different using t-tests (for independent-samples) ($P < 0.05$). Values with different superscript letters within rows are significantly different using Tukey's honest significant difference (HSD) tests ($P < 0.05$) (probability values are given in Appendix 17).....	140
Table 4.4.	Total plant species richness probability values for: ((a) and (b)) three-way ANOVA's between the three different experimental treatments, i.e. (A) biome (BIOME), (B) invasion intensity (INVIN) and (C) clearing (CLEAR), for plots in 1996; and for plots in 2005 ($d.f. = 1,32$); and (c) a three-way ANCOVA between the three different experimental treatments, with the 1996 data as the covariate ($d.f. = 1,31$). Bold text indicates $P < 0.05$	141
Table 4.5.	Tree species richness (mean ± S.E.) for 1996 and 2005. Values with different subscript letters within the same experimental category of the three different experimental treatments and same quadrat size in 1996 and 2005 are significantly different using t-	

	tests (for independent-samples) ($P < 0.05$). Values with different superscript letters within rows are significantly different using Tukey's honest significant difference (HSD) tests ($P < 0.05$) (probability values are given in Appendix 17).....	143
Table 4.6.	Tree species richness probability values for three-way ANOVA's between the three different experimental treatments, i.e. (A) biome (BIOME), (B) invasion intensity (INVIN) and (C) clearing (CLEAR), for plots in 1996, and for plots in 2005. <i>d.f.</i> = 1,32 for all main effects and interaction terms. Bold text indicates $P < 0.05$	143
Table 4.7.	Shrub species richness (mean $\pm$ S.E.) for 1996 and 2005. Values with different subscript letters within the same experimental category of the three different experimental treatments and same quadrat size in 1996 and 2005 are significantly different using t-tests (for independent-samples) ($P < 0.05$). Values with different superscript letters within rows are significantly different using Tukey's honest significant difference (HSD) tests ($P < 0.05$) (probability values are given in Appendix 17).....	144
Table 4.8.	Shrub species richness probability values for three-way ANOVA's between the three different experimental treatments, i.e. (A) biome (BIOME), (B) invasion intensity (INVIN) and (C) clearing (CLEAR), for plots in 1996, and for plots in 2005. <i>d.f.</i> = 1,32 for all main effects and interaction terms. Bold text indicates $P < 0.05$	145
Table 4.9.	Herbaceous species richness (mean $\pm$ S.E.) for 1996 and 2005. Values with different subscript letters within the same experimental category of the three different experimental treatments and same quadrat size in 1996 and 2005 are significantly different using t-tests (for independent-samples) ($P < 0.05$). Values with different superscript letters within rows are significantly different using Tukey's honest significant difference (HSD) tests ($P < 0.05$) (probability values are given in Appendix 17).....	145
Table 4.10.	Herbaceous species richness probability values for three-way ANOVA's between the three different experimental treatments, i.e. (A) biome (BIOME), (B) invasion intensity (INVIN) and (C) clearing (CLEAR), for plots in 1996, and for plots in 2005. <i>d.f.</i> = 1,32 for all main effects and interaction terms. Bold text indicates $P < 0.05$	146
Table 4.11.	Grass and sedge species richness (mean $\pm$ S.E.) for 1996 and 2005. Values with different subscript letters within the same experimental category of the three different experimental treatments and same quadrat size in 1996 and 2005 are significantly different using t-tests (for independent-samples) ($P < 0.05$). Values with different superscript letters within rows are significantly different using Tukey's honest significant difference (HSD) tests ($P < 0.05$) (probability values are given in Appendix 17).....	147
Table 4.12.	Grass and sedge species richness probability values for three-way ANOVA's between the three different experimental	

	treatments, i.e. (A) biome (BIOME), (B) invasion intensity (INVIN) and (C) clearing (CLEAR), for plots in 1996, and for plots in 2005. <i>d.f.</i> = 1,32 for all main effects and interaction terms. Bold text indicates $P < 0.05$	147
Table 4.13.	Total plant species Simpson's index of diversity (alpha diversity) (mean $\pm$ S.E.) for 1996 and 2005, at the 100 m ² scale. Values with different subscript letters within the same experimental category of the three different experimental treatments and same quadrat size in 1996 and 2005 are significantly different using t-tests (for independent-samples) ($P < 0.05$). Values with different superscript letters within rows are significantly different using Tukey's honest significant difference (HSD) tests ($P < 0.05$) (probability values are given in Appendix 17).....	149
Table 4.14.	Total plant species Simpson's index of diversity (alpha diversity) (at the 100 m ² scale) probability values for: ((a) and (b)) three-way ANOVA's between the three different experimental treatments, i.e. (A) biome (BIOME), (B) invasion intensity (INVIN) and (C) clearing (CLEAR), for plots in 1996, and for plots in 2005 (<i>d.f.</i> = 1,32); and (c) a three-way ANCOVA between the three different experimental treatments, with the 1996 data as the covariate (<i>d.f.</i> = 1,31). Bold text indicates $P < 0.05$	150
Table 4.15.	Matrix of Sorenson's coefficient of community (beta diversity) for total plant species in plots in each of the eight experimental categories of the three different experimental treatments in 1996 and 2005, at the 100 m ² quadrat scale. Bold = beta diversity between plots in 1996 and 2005; dark grey = beta diversity between plots in 1996; and light grey = beta diversity between plots in 2005.....	151
Table 4.16.	Percentage aerial cover of alien vegetation (mean $\pm$ S.E.) for 1996 and 2005. Values with different subscript letters within the same experimental category of the three different experimental treatments and same aerial cover category in 1996 and 2005 are significantly different using t-tests (for independent-samples) ($P < 0.05$). Values with different superscript letters within rows are significantly different using Tukey's honest significant difference (HSD) tests ($P < 0.05$) (probability values are given in Appendix 17).....	153
Table 4.17.	Percentage aerial cover of alien vegetation probability values for: ((a) and (b)) three-way ANOVA's between the three different experimental treatments, i.e. (A) biome (BIOME), (B) invasion intensity (INVIN) and (C) clearing (CLEAR), for plots in 1996, and for plots in 2005 (<i>d.f.</i> = 1,32); and (c) a three-way ANCOVA between the three different experimental treatments, with the 1996 data as the covariate (<i>d.f.</i> = 1,31). Bold text indicates $P < 0.05$	154
Table 5.1.	Percentage ground cover estimates (mean $\pm$ S.E.) of exposed soil, rock, litter, herbaceous vegetation and grass for 1996 and 2005. Values with different subscript letters within the same	

	experimental category of the three different experimental treatments and same ground cover category in 1996 and 2005 are significantly different using t-tests (for independent-samples) ($P < 0.05$). Values with different superscript letters within rows are significantly different using Tukey's honest significant difference (HSD) tests ($P < 0.05$) (probability values are given in Appendix 17).....	185
Table 5.2.	Probability values of percentage ground cover estimates for: ((a) and (b)) three-way ANOVA's between the three different experimental treatments, i.e. (A) biome (BIOME), (B) invasion intensity (INVIN) and (C) clearing (CLEAR), for plots in 1996, and for plots in 2005 ($d.f. = 1,32$); and (c) a three-way analysis of covariance between the three different experimental treatments, with the 1996 data as the covariate ($d.f. = 1,31$). Bold text indicates $P < 0.05$	186
Table 5.3.	Probability values of percentage ground cover estimates for two-way ANOVA's between the biomes (BIOME) and times (YEAR) ($d.f. = 1,76$). Bold text indicates $P < 0.05$	187
Table 5.4.	Soil pH (mean $\pm$ S.E.) for 1996 and 2005. Values with different subscript letters within columns are significantly different using t-tests (for independent-samples) ($P < 0.05$). Values with different superscript letters within rows are significantly different using Tukey's honest significant difference (HSD) tests ($P < 0.05$) (probability values are given in Appendix 17).....	194
Table 5.5.	Soil pH probability values for three-way ANOVA's between the three different experimental treatments, i.e. (A) biome (BIOME), (B) invasion intensity (INVIN) and (C) clearing (CLEAR), for plots in 1996, and for plots in 2005. $d.f. = 1,32$ for all main effects and interaction terms. Bold text indicates $P < 0.05$	194
Table 5.6.	Soil pH probability values for two-way ANOVA's between the biomes (BIOME) and times (YEAR) ($d.f. = 1,76$). Bold text indicates $P < 0.05$	195
Table 5.7.	Summary of the principal component analysis (PCA) of the environmental variables, and the grassland and savanna plots.....	201
Table 5.8.	Summary of the correspondence analysis (CA) of the indigenous and alien plant species, and the grassland and savanna plots.....	204
Table 5.9.	Marginal and conditional effects obtained from the summary of the forward selection (using the Monte Carlo permutation tests) during the CCA. Bold text indicates $P < 0.05$	205
Table 5.10.	Summary of the canonical correspondence analysis (CCA) (using the simplified model) of the indigenous and alien plant species, the environmental variables, and the grassland and savanna plots.....	206

LIST OF APPENDICES

Appendix 1.	Study plot locations, altitudes and co-ordinates of the 2005 plots.....	267
Appendix 2.	Codes used for species names in the multivariate statistical analyses.....	268
Appendix 3.	List of plant species with their authorities, taxonomic family, and invasive status for grass and sedge, herbaceous, shrub, and tree species along the Sabie River in 2005. Presence (1) and absence (0) of species in each biome (grassland and savanna) and in each region, i.e. Sabie and Graskop (grassland) and Hazeyview (savanna), is given. Underlined species are those that are common to both 1996 and 2005. Note: “transformers” = plants which can as monospecies dominate or replace any canopy or subcanopy layer of a natural or semi-natural ecosystem, thereby altering its structure, integrity and functioning; “potential transformers” = plants that are already invading natural or semi-natural habitats, and have the potential to dominate a vegetation layer but not yet having a marked effect; “special effect weeds” = plants which can as monospecies significantly degrade the value or purpose for which a natural or semi-natural ecosystem is valued without necessarily dominating it or greatly altering its vegetational structure or functioning; and “minor weeds” = plants that invade and persist in any layer of a natural or semi-natural ecosystem but are not particularly aggressive and cannot or do not as monospecies dominate that layer or seriously alter the vegetation structure or its functioning although the accumulation of several to many species may do so (Henderson, 2001).....	272
Appendix 4.	List of plant species with their authorities, taxonomic family, and invasive status for grass and sedge, herbaceous, shrub, and tree species found along the Sabie River in 1996. Presence (1) and absence (0) of species in each biome (grassland and savanna) is given. Underlined species are those that are common to both 1996 and 2005; therefore the remaining species are those that have been lost since 1996. Note: “transformers” = plants which can as monospecies dominate or replace any canopy or subcanopy layer of a natural or semi-natural ecosystem, thereby altering its structure, integrity and functioning; “potential transformers” = plants that are already invading natural or semi-natural habitats, and have the potential to dominate a vegetation layer but not yet having a marked effect; “special effect weeds” = plants which can as monospecies significantly degrade the value or purpose for which a natural or semi-natural ecosystem is valued without necessarily dominating it or greatly altering its vegetational structure or functioning; and “minor weeds” = plants that invade and persist in any layer of a natural or semi-natural ecosystem but are not particularly aggressive and cannot or do	

	not as monospecies dominate that layer or seriously alter the vegetation structure or its functioning although the accumulation of several to many species may do so (Henderson, 2001).....	282
Appendix 5.	Statistical <i>P</i> -values for t-tests (for independent-samples) for differences in several tested variables between the grassland and savanna biomes. <i>d.f.</i> = 38. Bold text indicates <i>P</i> < 0.05...	289
Appendix 6.	Statistical <i>P</i> -values for one-way ANOVA analyses for differences in several tested variables between the Sabie (grassland), Graskop (grassland) and Hazeyview (savanna) regions. <i>d.f.</i> = 2,37. Bold text indicates <i>P</i> < 0.05.....	289
Appendix 7.	Statistical <i>P</i> -values for t-tests (for independent-samples) for differences in several tested variables of (a) tree, (b) shrub, (c) herbaceous, (d) grass and sedge growth forms, between the grassland and savanna biomes. <i>d.f.</i> = 38. Bold text indicates <i>P</i> < 0.05.....	290
Appendix 8.	Statistical <i>P</i> -values for one-way ANOVA's for differences in several tested variables of (a) tree, (b) shrub, (c) herbaceous, (d) grass and sedge growth forms, between the Sabie (grassland), Graskop (grassland) and Hazeyview (savanna) regions. <i>d.f.</i> = 2,37. Bold text indicates <i>P</i> < 0.05.....	291
Appendix 9.	Statistical <i>P</i> -values for t-tests (for independent-samples) for differences in the total, indigenous and alien species richness of each growth form, between the grassland and savanna biomes (in 2005), at the 1000 m ² quadrat scale. <i>d.f.</i> = 38. Bold text indicates <i>P</i> < 0.05.....	292
Appendix 10.	Statistical <i>P</i> -values for Tukey's honest significant difference (HSD) tests for differences in the total, indigenous and alien species richness of each growth form, between the Sabie (grassland), Graskop (grassland) and Hazeyview (savanna) regions (in 2005), at the 1000 m ² quadrat scale. <i>d.f.</i> = 2,27 for Sabie and Graskop, and 2,57 for Hazeyview. Bold text indicates <i>P</i> < 0.05.....	292
Appendix 11.	Statistical <i>P</i> -values for t-tests (for dependent-samples) for differences in the total and alien species richness of the roadside and riverside quadrats (1 m ² and 10 m ²) of all 40 plots, plots occurring in the savanna and grassland biomes, and plots occurring in the Sabie (grassland), Graskop (grassland) and Hazeyview (savanna) regions. <i>d.f.</i> = 39 for total plots, <i>d.f.</i> = 19 for savanna, grassland and Hazeyview plots, and <i>d.f.</i> = 9 for Sabie and Graskop plots. Bold text indicates <i>P</i> < 0.05.....	293
Appendix 12.	Statistical <i>P</i> -values for t-tests (for independent-samples) for differences in several tested variables between 1996 and 2005. <i>d.f.</i> = 78. Bold text indicates <i>P</i> < 0.05.....	293
Appendix 13.	Statistical <i>P</i> -values for t-tests (for independent-samples) for differences in several tested variables of the grassland biome between 1996 and 2005, and the savanna biome between 1996 and 2005. <i>d.f.</i> = 38. Bold text indicates <i>P</i> < 0.05.....	294
Appendix 14.	Statistical <i>P</i> -values for t-tests (for independent-samples) for	

	differences in the species richness of (a) tree, (b) shrub, (c) herbaceous, and (d) grass and sedge growth forms between 1996 and 2005, for quadrat sizes of 1 m ² , 10 m ² , 100 m ² and 1000 m ² . <i>d.f.</i> = 78. Bold text indicates <i>P</i> < 0.05.....	294
Appendix 15.	Statistical <i>P</i> -values for t-tests (for independent-samples) for differences in several tested variables of each of the eight experimental categories of the three different experimental treatments between 1996 and 2005. <i>d.f.</i> = 8. Bold text indicates <i>P</i> < 0.05. Note H = High altitude (i.e. grassland)/High invasion; L = Low altitude (i.e. savanna)/Low invasion; C = Cleared; and U = Uncleared.....	294
Appendix 16.	Statistical <i>P</i> -values for t-tests (for independent-samples) for differences in the species richness of (a) tree, (b) shrub, (c) herbaceous, and (d) grass and sedge growth forms of each of the eight experimental categories of the three different experimental treatments between 1996 and 2005, for quadrat sizes of 1 m ² , 10 m ² , 100 m ² and 1000 m ² . <i>d.f.</i> = 8. Bold text indicates <i>P</i> < 0.05. Note H = High altitude (i.e. grassland)/High invasion; L = Low altitude (i.e. savanna)/Low invasion; C = Cleared; and U = Uncleared.....	295
Appendix 17.	Statistical <i>P</i> -values for Tukey's honest significant difference (HSD) tests for differences in several tested variables between each of the eight experimental categories of the three different experimental treatments in 1996, and each of the eight experimental categories of the three different experimental treatments in 2005. <i>d.f.</i> = 1,32. Bold text indicates <i>P</i> < 0.05. Note H = High altitude (i.e. grassland)/High invasion; L = Low altitude (i.e. savanna)/Low invasion; C = Cleared; and U = Uncleared.....	296
Appendix 18.	Statistical <i>P</i> -values for t-tests (for independent-samples) for differences in the total percentage aerial cover of alien vegetation of the plots of the three different treatments, i.e. biome, invasion intensity and clearing, between 1996 and 2005. <i>d.f.</i> = 38. Bold text indicates <i>P</i> < 0.05.....	307
Appendix 19.	Methodology used by the Soil Fertility and Analytical Services Section of the KwaZulu-Natal Department of Agriculture and Environmental Affairs at Cedara for soil sample analyses (Manson and Roberts, 2000).....	307
Appendix 20.	Example of a Working for Water (WfW) clearing contract (for the Barbeton area).....	309
Appendix 21.	Example of a Working for Water (WFW) worker's contract....	313
Appendix 22.	Details of the clearing history by Working for Water (WfW) in each of the 40 plots along the Sabie River. Note: N/A = Not Applicable.....	315
Appendix 23.	Details of the contractual engagement of Working for Water (WfW) with the landowners.....	316