CHAPTER 1:

GENERAL INTRODUCTION AND LITERATURE REVIEW

1.1 Rationale of the study

Alien plant invasions are a global problem and, after direct habitat destruction, is the second most important threat to biodiversity (Randall, 1996). Southern Africa is severely affected by alien invasions, and has one of the biggest problems with invasions of any area in the world. Large areas have been transformed as a result of these invasions, and many negative impacts on the economy, in sectors such as health, agriculture, water supply and tourism, have resulted (Macdonald, 1989). The threat posed by alien invasions to biodiversity is significant as biodiversity is a fundamental property of ecological communities. It influences productivity, soil nutrient availability, and invasion resistance, as well as system stability and reliability (Purvis and Hector, 2000; Knops *et al.*, 2001). When biodiversity is reduced, greater rates of loss of limiting soil nutrients through leaching results, which ultimately decreases soil fertility, thus lowering plant productivity (Tilman, 2000). Clearing infestations of invading alien plants will have many benefits. These include increasing the available surface and underground water, preventing the loss of biodiversity, reducing fire hazard, stabilizing catchment areas and preventing erosion (Le Maitre *et al.*, 2002).

Riparian ecosystems constitute the interface between aquatic and terrestrial ecosystems (Gregory *et al.*, 1991), and are particularly prone to alien plant invasions due to the efficient dispersal mechanism, water, which spreads the seeds of aquatic and riparian weeds downstream (Pysek and Prach, 1993; DeFerrari an Naiman, 1994). The frequency of disturbance in this ecosystem is also a contributing factor increasing the invasibility (Rejmanek, 1989; Hobbs and Huenneke, 1992). Disturbances increase the invasibility of an ecosystem due to the creation of new microhabitats and niches for invading species (Carlton 1996, 2000), the direct removal or decrease in populations of indigenous competitor species thereby making them less capable of controlling or resisting a growing population of invading species (Davis *et al.*, 2000), and the introduction of alien species' propagules into areas that were inaccessible to the propagules on their own (Lonsdale, 1999).

The Sabie River catchment in the Mpumalanga province of South Africa, is important from both economic and eco-tourism perspectives. However, the Sabie River riparian ecosystem has been severely affected by invasive alien plants. As a result, the Working for Water (WfW) alien plant clearing programme, a programme initiated in 1995 by the Department of Water Affairs and Forestry (DWAF) in response to the massive threat posed by invasive alien woody plants to ecosystems, has been clearing alien plants along this river over the past 10 years, i.e. from 1995 to 2005. Thus, the main aim of this 2005 study was to measure the ecosystem repair of the Sabie River (which traverses through both the grassland and savanna biomes) riparian environment in response to the clearing of alien plants by WfW. 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, such as determining whether there is an increase in indigenous species richness and/or a decrease in alien species richness, in this study it also includes determining whether there is a reduction

in the invasion intensity (defined as the percentage aerial cover of woody alien plants) after clearing.

This study forms part of a national project in which targets for ecosystem repair in riparian ecosystems in the fynbos, grassland and savanna biomes will be developed (Holmes *et al.*, 2003). This study will develop targets for the grassland and savanna biomes as the Sabie River traverses through both biomes. Ecosystem recovery studies assess the degree of repair that has occurred as a result of alien clearing, based on suitable benchmarks, and an analysis of the information then clarifies whether biotic or abiotic thresholds in the environment have been passed (Whisenant, 1999). It can then be determined whether biotic or abiotic components need to be manipulated in order to facilitate the recovery of the indigenous plant community, which then facilitates the development of achievable targets for ecosystem repair. For example, if an abiotic threshold has been passed, it will be necessary to repair the relevant components of the physical environment before manipulating the vegetation components. If the inputs of physical energy are the dominating forces in structuring an ecosystem, e.g. water and wind movement in riparian zones (Planty-Tabbachi *et al*., 1996), then manipulating these abiotic components is then particularly important in ecosystem repair (Ehrenfeld, 2000).

Data were collected and compared with a similar study conducted in 1996/1997 (Garner, 2005) in order to measure the ecosystem repair of the Sabie River riparian community, and hence the WfW effectiveness. In 1996/1997, 40 permanent Modified Whittaker nested plots were first surveyed along the Sabie River and several variables were measured, such as the plant species composition, diversity and vegetation structure, as well as environmental variables (Garner, 2005). In this 2005 study, these same factors were measured and compared to the 1996 study. The specific aims and objectives are listed on page 33 of this chapter. The results of this 2005 study can then be used to develop suitable targets for ecosystem repair in both biomes. As stated previously, “effectiveness” in this study includes a reduction in the invasion intensity after clearing. In this study, the percentage aerial cover of woody alien plants was used as a measure of the invasion intensity as the aerial cover gives a true reflection of the effects of the woody alien plants on the plant community (as opposed to, for example, using basal density of alien plants as a measure of invasion intensity which does not take into account the effects of the full canopy cover). This measure of invasion intensity was also used in order to be consistent with the 1996 study (Garner, 2005), which used the same measure. The invasion intensity was then used as a measure of the degree of alien plant invasion in this 2005 study.

The national ecosystem repair project (Holmes *et al.*, 2003) has developed key questions relating to the ecosystem repair in the three biomes, and this study will aim to answer these questions in relation to the grassland and savanna biomes. Any relevant gaps in our knowledge or understanding will be identified and prioritised. These questions are:

1) What level of ecosystem repair has been achieved in each of the different situations studied?
2) Are the thresholds derived from ecological theory applicable in practice?
    a) In what situations have biotic thresholds been passed?
    b) In what situations have abiotic thresholds been passed?
3) What is achievable in each of the different situations studied?

4) What could be improved?
5) Have any important ecosystem drivers or keystone species (to facilitate recovery) been identified?
6) What are the realistic goals for the different situations, particularly in relation to vegetation type, river order and level of ecosystem degradation?

1.2 The Working for Water (WfW) alien plant clearing programme

The Working for Water (WfW) alien plant clearing programme focuses on controlling woody alien plants that invade riverine areas (Macdonald, 2004). Because South Africa has such an enormous problem with alien invasive plants, and because it is a semi-arid country with a highly variable rainfall and hydrology, the primary aim of the programme is to increase water supplies by controlling the alien plants. One of the main goals of the programme is to enhance social development. An increasingly important benefit of this programme is maintenance of biodiversity over the long-term, which can be achieved via the restoration of indigenous ecosystems. The WfW programme is one of the world's biggest programmes dealing with invasive alien species, and is one of the most effective poverty eradication programmes in South Africa (Van Wilgen, 2004). The success of the programme is a result of its ability to gain local and international funding and continuing political support (Richardson and Van Wilgen, 2004).

Historically, the removal of invasive alien woody plants in riparian zones by WfW involved felling all alien trees and shrubs, and then treating the stumps of the coppicing species with herbicide (Holmes *et al.*, 2005). The felled material was then either removed from the river corridor or burnt in slash stacks (Holmes *et al.*, 2005). The current method is to use frilling or ring barking to kill the larger trees (> 200 mm basal diameter) as felling and timber removal is too expensive (Holmes *et al.*, 2005). Reinvading aliens are regularly removed by follow-up treatments, which are perceived to be a temporary practice (i.e. 2 – 4 treatments) intended to deplete remnant propagule reserves (Galatowitsch and Richardson, 2004). Satisfactory, sustainable and affordable management of invasive alien plants will be impossible without the integration of biological control as a supplement to other management practices (Zimmermann *et al.*, 2004). As a result much of the progress achieved in recent years in biocontrol has been facilitated by the WfW programme (Olckers, 2004). An example of a WfW clearing contract (for the Barbeton area) is given in Appendix 20, and an example of a WFW worker's contract is given in Appendix 21. There is a contractual agreement between WfW and the landowners, and details of this contract are given in Appendix 23.

1.2.1 History of the WfW programme

In 1995/1996, the WfW programme obtained an initial grant of R25 million from the government's funds for reconstruction and development (Macdonald, 2004). The programme then succeeded in obtaining considerable further funding, largely from the government's poverty relief budget, once it had proven its significant employment potential (Magadlela and Mdzeke, 2004). In 2003/2004, WfW's budget increased to R415 million, with a total of R2.4 billion being spent between 1995 and March 2004 (B. Van Wilgen, *pers. comm.*). As part of the WfW programme's integrated strategic approach to the management of alien plants, the programme

invests about R15 million per annum in research (Macdonald, 2004). The programme has cleared over 1.2 million hectares of infestations, which was estimated to have resulted in the release of 48 – 56 million m^3 of additional water annually (Gorgens and Van Wilgen, 2004). Costs associated with follow-up treatments have grown annually as a result of two or more follow-up treatments being required after the initial clearing, which varies with the species concerned, as well as the density of the invasive alien plant infestations (Marais *et al.*, 2004).

1.2.2 Clearing history of the WfW programme in the study areas along the Sabie River

Since the WfW programme began in 1995, invasive alien plants have been cleared from riparian areas in Mpumalanga and the rest of the country. A large proportion of the Sabie River flows through forest plantations, which have reduced the flow of the river quite dramatically over the years (Le Maitre *et al.*, 2002). Tall invasive alien trees may reduce the mean annual run-off in higher rainfall areas by up to 300 mm/year (Gorgens and Van Wilgen, 2004). Because of this flow reduction and because the Sabie River catchment is important from the ecotourism perspective, WfW has done extensive clearing along this river since 1995, and continue to do so. The history of clearing by WfW in the study areas has not been well documented, and thus a lot of the precise details of what was done and when is lacking. In terms of WfW records post-2000, in the Sabie (grassland) region, clearings took place in some of the plots on the 31st January 2003, with follow-ups on the 26th March 2004 and the 30th November 2004. In some of the plots in the Graskop (grassland) region, clearings took place on the 18th September 2003 with follow-ups on the 18th March 2004. Clearings also took place on the 27th August 2004 in other plots in the Graskop region, with no records of follow-ups. In the Hazeyview (savanna) region, there were records of follow-up clearings on the 8th February 2002 and the 17 January 2003. More recent clearings took place during November 2004 to January 2005, in some of the savanna plots (H. De Lange, *pers. comm.*). A more detailed review of the WfW clearings is given in Appendix 22.

1.2.3 The WfW programme as a social development programme

One of the main focuses of the WfW programme is on job creation and a lot of labour is therefore used. Tens of thousands (>20 000 annually) of previously unemployed people, mainly women, have been trained and employed by this massive catchment rehabilitation programme (Macdonald, 2004). During its first year of operations (from October 1995 to March 1996), the programme employed 6163 people (Anon, 1996). When poverty relief funding was secured in 1997, the employment rate increased substantially and high levels of direct employment have been maintained – some 24 000 people were employed in 2000 (Milton *et al.*, 2003).

The WfW's social development programme has several main components. It has a childcare programme, whereby children are looked after in creches, allowing women time to earn an income; it has an HIV/AIDS programme, to increase HIV/AIDS awareness; and it has an ex-offender reintegration programme; as well as several others (Van Wilgen *et al.*, 2001). The poorest members of the communities closest to the alien infested areas are employed, and women, especially single mothers, are encouraged to join teams of about twenty members with supervisors to

oversee their productivity (Van Wilgen *et al.*, 2001). There are many social benefits from these clearing activities that do not only include employment, but also the improvement of poor people's livelihoods through incomes, resulting in better nutrition for children, better clothing and an ability to pay for education. Opportunities to earn a living outside the programme are created through small business training and skills development for contractors (Van Wilgen *et al.*, 2001).

1.3 Biodiversity

Biodiversity is usually equated with the number of species (species richness) or species density when species are quantified in terms of area (Whittaker, 1972). According to UNEP (1992), biodiversity is the variability among living organisms from all ecosystems and the ecological complexities of which they are a part. This includes diversity within species, between species and of ecosystems (UNEP, 1992). The ease of measurement of biodiversity has led to the development of a number of indices of species diversity including Simpson's index of diversity, Simpson's measure of evenness, Sorenson's coefficient of community, and Marczewski-Steinhaus (MS) distance (as a measure of complementarity). A more detailed review of the various diversity indices is given in Chapter 3.

1.4 Multivariate statistical analyses

If the continuity of change in community composition is stressed, then ordination methods are the best to use. There are two types of ordination methods: indirect gradient analysis (unconstrained) and direct gradient analysis (constrained). The most prominent types of indirect gradient (unconstrained) analysis are the principal component analysis (PCA), correspondence analysis (CA), and detrended correspondence analysis (DCA) (Leps and Smilauer, 2003). The most prominent types of direct gradient analysis (constrained) are the redundancy analysis (RDA) and canonical correspondence analysis (CCA) (Leps and Smilauer, 2003). Ordination methods can also be distinguished according to whether they are linear or unimodal. Linear methods include PCA and RDA, and unimodal methods include CA, DCA and CCA (Leps and Smilauer, 2003). Refer to Chapter 3 for more detailed notes on multivariate statistical analyses.

1.5 Riparian ecosystems

The interface between terrestrial and aquatic ecosystems constitutes the riparian zone (Gregory *et al.*, 1991). These ecosystems are amongst the most structurally complex and biologically diverse ecosystems on earth (Naiman and Decamps, 1997). Riparian zones provide a critical linkage between streams and the catchments they drain, and experience periodic flooding, erosion, siltation and a variety of human-mediated biotic and abiotic stresses (Bennett and Mooney, 2003). The catchment geology combined with the hydrogeomorphic processes of rivers gives rise to a highly heterogeneous landscape consisting of a mosaic of different morphological units which change spatially (vertically, laterally and longitudinally) and temporally (from months and years to decades and centuries) (Van Coller *et al.*, 1997). This heterogeneity in geomorphological structure is an important factor controlling vegetation development (Kalliola and Puhakka, 1988) and is consequently reflected in the distribution of different vegetation types in these riparian systems

(Gregory *et al.*, 1991; Van Coller *et al.*, 1997). This geomorphological complexity leads to a correspondingly high level of diversity in vegetation structure and composition (Van Coller *et al.*, 2000).

The riparian community is an important component of the landscape and is considered a key habitat for biodiversity (Naiman *et al.*, 1993; Toner and Keddy, 1997). Along with connecting terrestrial and aquatic ecosystems, riparian vegetation functions as a corridor for the dispersal of seeds and vegetative propagules of riparian plants (Heartsill-Scalley and Aide, 2003). Riparian vegetation also provides food, controls evapotranspiration and water temperature, filters sediments and nutrients (Peterjohn and Correl, 1984), stabilisers stream banks and supports faunal communities (Barling and Moore, 1994). Riparian vegetation is usually markedly different from the surrounding vegetation as it is generally high in species numbers (Nilsson *et al.*, 1988; Nilsson, 1992), and consists of specialized disturbance-adapted species (Naiman and Decamps, 1997). Riparian plant species have adaptations to fluvial disturbances such as resprouting ability or seed storage, which confer resilience and facilitate regeneration after fire (Dwire and Kauffman, 2003). The riparian community encompasses structurally distinguishable vegetation types, from trees through to shrubs and herbaceous vegetation (Nilsson 1992). Species richness of riparian vegetation is constrained to a large degree by dispersal (Merritt and Wohl, 2002). Riparian vegetation is shaped by disturbance regimes of the surrounding landscape and aquatic systems, e.g. wind, fire, flooding, debris flows and sedimentation processes (Tnag and Montgomery, 1995). However, because soil seed banks are poorly developed in riparian soils (Kalliola *et al.*, 1991) and because wind dispersal may occur over relatively limited distances, water dispersal plays an important role in structuring plant communities along rivers through long-distance and directed dispersal (Merritt and Wohl, 2002). Gradients of available moisture and oxygen are the primary determinants of the distribution of riparian vegetation types, and thus plant communities can be stratified by height above the river channel (Boucher, 2002).

1.5.1 The Sabie River riparian ecosystem

The Sabie River is part of the Sabie-Sand River system which covers approximately 6320 km^2 and forms part of the larger Inkomati system, which extends into Swaziland and Mozambique (Van Coller *et al.*, 1997). The Sabie River is the main stream of the catchment, with the Sand and Marite Rivers being major tributaries and the Mac Mac River being a tertiary draingage system (Van Coller *et al.*, 1997). The Sabie River has its source at 2130 m a.s.l. in the Drakensburg escarpment and drops into the lowveld where it joins the Sand River inside the Kruger National Park (KNP) (Van Niekerk and Heritage, 1993). Most of the Sabie River system is in the lowveld, with sandy, sandy loam and clayey soils overlying iron, jaspilite and granite, which support the sour lowveld bushveld (www.csir.co.za/rhp). Rapids are common in the upper parts of the river, and in the lower parts, the river is wide and has gentle gradients where mature riparian forests are found up to a hundred metres from the river. There is extensive forestry in this region of the Sabie-Sand River catchment, and alien vegetation invasion is a serious threat to the ecosystem health. Roads and plantations close to streams impair the riparian health due to erosion, sedimentation and resulting smothering of habitats (www.csir.co.za/rhp). Along the Sabie River, sawdust from sawmills also impacts on the riparian zone and

washes into the river during rain events. Chemicals leaching out of the sawdust can acidify the soil and water, and the dust itself also smothers the vegetation and in-stream habitats (www.csir.co.za/rhp).

1.5.2 Riparian ecosystems and invasive alien plants

Many invasive species are not able to survive in the surrounding drier areas of the riparian zone; thus the ready access to water in these riparian habitats has enabled a number of species to invade (Le Maitre *et al.*, 2000). Many invasions in riparian areas have resulted from the introduction of invading species in the upper catchments, which subsequently spread rapidly downstream (Le Maitre *et al.*, 2000). Any control program should therefore focus on the upper parts of a catchment first so that control areas are not re-invaded from upstream. Degradation of riparian habitats due to inappropriate land-use practices has also facilitated invasions (Rowntree, 1991).

Alien species replace the rich biodiversity of the riverine forest with a monotonous stand of a few alien species; thus the same diversity of indigenous animals and birds cannot be supported. This loss of species can have a major impact on the ecosystem's resilience or ability to recover after major natural disasters such as floods, drought and disease. Aliens can also alter properties of whole ecosystems, including plant productivity (Midgley *et al*., 1992), nutrient cycling (Witkowski, 1991) and hydrology (Vitousek, 1990). A higher biomass of alien plants as a result of the invasions is related to increased transpiration (e.g. Le Maitre *et al.*, 2002). This is because water use of woody alien plants is a lot higher than the indigenous vegetation in the same setting. Some catchments in the Mpumalanga escarpment have shown 100% reductions in water flow due to dense stands of invasive vegetation greatly reducing the surface water runoff because of increased evapotranspiration (Van Lill *et al*., 1989). Many studies have illustrated increased stream flow in areas cleared of alien plant species and the advantageous effects of their removal in reducing water "wastage" (Dye and Poulter, 1995a). Even though the removal of aliens results in increased stream flow, the removal of transpiring indigenous forests can also have the same effect. Thus, evidence is needed to illustrate that the water "saved" as a result of alien woody plants being cleared is greater than the water "saved" if indigenous forests were removed in the same setting.

1.5.3 Invasive alien plants along Mpumalanga rivers

For a detailed review of alien plants in the Mpumalanga area, the revised list of alien plants for the KNP (Foxcroft *et al.*, 2003) was assessed. A total of 370 alien plant species were listed and 191 of these were found in riparian areas. From the list, two species (0.5%) were transformer weeds (i.e. *Lantana camara* and *Opuntia stricta*), 125 (33.8%) were invasive and 223 (60.2%) were either casual aliens or naturalized species. The long-term average increase in recorded alien plant species, since the first record of alien plants in 1937, was 5.6 alien species per year (Foxcroft *et al.*, 2003). Macdonald and Gertenbach (1988) state that increases in recorded alien plant species was probably due to increased collecting and awareness between 1937 and 1983. Furthermore, the increase in the recorded alien plant species may also be a result of increased tourism (Macdonald and Gertenbach, 1988), which unintentionally brought in seeds from other infested parts of the country, as well as from other countries. Infestations and new species may also have arisen due to the considerable

increase in the size of towns such as Nelspruit and others along the escarpment over the past 50 years (Foxcroft *et al.*, 2003).

1.6 Disturbance regimes

Very few environments are unaffected by disturbances. Important landscape-scale disturbances include fire, drought, floods, infrequent frosts or periods of higher than normal temperatures, severe storms, localized soil disturbance by animals, tree falls and insect outbreaks (Hobbs, 2002). Human disturbance is also an important component of many ecosystems, which includes changed grazing or fire regimes, fragmentation, nutrient enrichment and road construction (Hobbs and Humphries, 1995). Disturbances can increase the invasibility of communities. All aspects of an ecosystem's successional status, including soil development, accumulated nutrient and biomass capital, and nutrient cycling, are likely to be affected by disturbances (Davy, 2002). The components of the disturbance regime will determine the scale and pattern of variation in the vegetation observed, and each disturbance type may produce different vegetation responses (Hobbs, 2002). Individual disturbance types can also produce different responses depending on factors such as environmental variations within the disturbed areas, weather characteristics following the disturbance, and interactions with other disturbances (Hobbs, 2002).

In herbaceous systems, disturbances impose on various processes that affect the colonisation by woody species, including above- and below-ground competition (Hill *et al.*, 1995), inhibition of germination by plant litter (Facelli and Pickett, 1991), herbivory (De Stevens, 1991), and facilitation from established plants (De Stevens, 1991). While disturbances may increase community invasibility, plant life-history traits such as seed size, growth rate and shade tolerance determine the ability of different species to exploit newly created gaps (Bazzaz, 1996). Understanding vegetation response to landscape-scale disturbance is vital to understanding ecosystem structure and function (Lawrence and Ripple, 2000). Riparian corridors may be especially prone to invasion because of their high degree of hydrological disturbance (Tabacchi, 1995), and will often support disturbance-adapted species assemblages (Sher *et al.*, 2002). When historical flooding patterns are changed in intensity or frequency, the likelihood of invasions in riparian zones is increased (Sher *et al.*, 2002).

1.6.1 Floods in riparian ecosystems

Central in structuring the physical environment and in determining the community composition of riverine ecosystems is the variation in streamflow (Hupp and Osterkamp, 1985), i.e. the frequency (Bren, 1992), depth (Carter and Grace, 1990) and duration (Howell and Benson, 2000) of floods. Flow regime influences species abundance by determining the spatial and temporal occurrence of suitable habitat patches (Poff and Allen, 1995). Although extreme flow variation can eliminate species (Bain *et al.*, 1988), floods are necessary for the persistence of some species of plants (Friedman *et al.*, 1996). Therefore, flooding is an important natural phenomenon on most rivers (Gregory *et al.*, 1991).

Catastrophic infrequent flood events have a greater effect on vegetation composition than do regular floods, as they tend to remove more vegetation (James,

2000). Areas on rivers that receive the greatest flooding disturbance tend to have the greatest proportion of alien species (Hood and Naiman, 2000). These episodic disturbance events can spread propagules, reduce indigenous plant species richness and competition or change site conditions to better suit the invader (Leroy, 2003). Floods disturb river-banks and re-route water courses, providing recruitment sites for invading plants with water-borne propagules (Rowntree, 1991). The recovery of a riparian ecosystem after a large disturbance event is governed by the community composition before the event and the dispersal to, and establishment within the disturbed area, of propagules from surrounding areas (Leroy, 2003).

1.6.2 Fires in terrestrial ecosystems

The role of fire in either enhancing or minimizing biological invasions in indigenous communities will depend on the physiological properties of both the indigenous community and the invading organisms, and the fire regime. Fire effects must be evaluated in terms of frequency, intensity, seasonality and stage of vegetation development. Frequent burning favours aggressive competitive introduced species, as many invaders can resprout from rootstocks or bulbs, and thereby survive a wide range of fire regimes (Hughes and Vitousek, 1993). Fire allows wind-blown seeds of grasses and thistles to germinate and establish. Invasive trees and shrubs increase fuel loads thereby increasing fire intensities and frequencies (Van Wilgen and Richardson, 1985; Versfeld and Van Wilgen, 1986). The failure of most of the shrub species to reestablish following fire could be due to a loss of seed viability because of fire and/or an inability to disperse to the sites following fire (Hughes and Vitousek, 1993). The rapid reestablishment and long-term persistence of alien grasses can inhibit shrub colonisation and growth (Hughes and Vitousek, 1993).

Fire can act as a germination cue for many species with soil-stored seeds that may not otherwise be present in the community (Hughes and Vitousek, 1993). Persistence of seeds in the soil provides dispersal in time, which is considered an adaptation to an environment where disturbances are unpredictable (Ferrandis *et al.*, 1999). This minimises germination prior to a fire and maximizes germination following fire, thus increasing their chance of survival. For many species with fire-triggered germination, heat shock has no effect on germination; rather germination is induced by chemicals from combustion products (Ferrandis *et al.*, 1999). It was originally assumed that heat alone from fires cracked seed coats and allowed germination to take place, but a number of fire products have been found to be influential as well (Schlesinger, 1997). These fire products include heat, components of wood smoke, inorganic nutrients, destruction of allelopathic compounds that inhibit germination, oxidation of the seed coat, and unidentified compounds associated with blackened (charred) wood (Schlesinger, 1997). Another fire-associated factor promoting germination includes the seasonal timing of burning. Fire-independent cues, such as incubation temperature and light have also been demonstrated to influence germination in some species of fire-prone habitats (Schlesinger, 1997). Some forms of nitrogen may be important triggers in charred wood or smoke-induced germination, such as nitrate, which increases briefly after fire and induces germination of many weedy species (Schlesinger, 1997).

However, in riparian communities (particularly in summer rainfall areas of South Africa), fire may be excluded (Holmes *et al.*, 2005). This is because the

structural characteristics of the riparian community render them less flammable than the surrounding vegetation (Holmes *et al.*, 2005).

1.6.3 Factors leading to changes in disturbance regimes

Land transformation often leads to changes in disturbance regimes. For example, it is more difficult for fires to spread through areas where the transformed patches are not fire-prone (Le Maitre *et al.*, 2004). Global climate change is another factor and is highly likely to lead to more frequent and intense extreme events, such as droughts and floods, which will create severe disturbances in the affected areas (Schulze *et al.*, 2001). Invaders are also likely to have substantial effects on ecosystems by rapidly changing disturbance regimes.

1.7 Invasive alien plants

'Alien' or 'exotic' species are those that have been introduced from a different area. 'Naturalized' species are those that have become established to the point where they appear to be indigenous species, and many are not seen as being overly abundant or damaging enough to cause them to be placed on lists of noxious weeds or to become targets for control (Myers and Bazely, 2003). 'Established' plant species are introduced species that are on their way to becoming naturalized, and are a permanent feature of a plant community. An 'invasive species' is a species introduced from a different area, most often from a different continent, which first becomes established (colonizes), increases in density and expands rapidly across a new habitat (invades) (Myers and Bazely, 2003).

The Conservation of Agricultural Resources Act (Act 43 of RSA 1983), as amendment in 2001, has listed the Declared Weeds and Invaders of South Africa. The 198 alien species listed as declared weeds and invaders have been divided into three categories:
Declared weeds (category 1 plants): these are prohibited and must be controlled.
Declared invaders (category 2 plants): these are commercially used plants that may be grown in demarcated areas providing that there is a permit and that steps are taken to prevent their spread.
Declared invaders (category 3 plants): these are ornamentally used plants that may no longer be planted; existing plants may remain, as long as all reasonable steps are taken to prevent them spreading, except within the flood line of watercourses and wetlands (Henderson, 2001).

1.7.1 Invasive alien plants in Southern Africa

The influx of alien plant species into South Africa began in the 1600's, when the Cape of Good Hope was a major refurbishing stop for European ships, and over many years, hundreds of species of plants were brought in and cultivated for various purposes (Zimmermann *et al.*, 2004). Some 75% of South Africa's alien weeds were deliberately introduced into the country for commercial gain including forestry, agroforestry, horticulture, agriculture, dune stabilisation and fruit production (Olckers *et al.*, 1998). The uncontrolled spread of invasive alien species is one of the key threats to the indigenous biodiversity. This is because southern Africa is an area of high biological diversity – it is home to some 21 137 species of vascular plants, about

80% of them endemic (Cowling and Hilton-Taylor, 1994). About 750 tree species and around 8000 shrubby, succulent and herbaceous species have been introduced into South Africa (Van Wilgen *et al.*, 2001) and of these, 161 species are regarded as seriously invasive (Van Wilgen and Van Wyk, 1999). The rapid spread of alien vegetation in many areas of southern Africa has been attributed to various factors, including high reproductive potentials and growth rates in the plants concerned (Richardson and Van Wilgen, 2004).

1.7.2 The invasion process

According to Groves (1985), there are three main stages in the invasion process: introduction, colonisation, and naturalisation. Introduction involves a plant (or its propagule) being transported by humans across a major barrier. Naturalisation starts when abiotic and biotic barriers to survival, as well as various barriers to regular reproduction, are overcome. Invasion further requires that introduced plants produce reproductive offspring in areas distant from sites of introduction. The fates of these organisms vary vastly. Many perish en route, and if they succeed in reaching a new site, they are likely to be destroyed quickly by a multitude of physical or biotic agents; however some occasionally survive to reproduce (Mack, 1995). Even then, their descendants may only survive for a few generations before going extinct locally, but some small fraction of these immigrant species persist and become naturalized (Mack *et al.*, 2000). Among the naturalized species that persist after this extremely severe reductive process, a few will go on to become invaders (Mack *et al.*, 2000).

The progression from immigrant to invader often involves a delay or lag phase, followed by a phase of rapid exponential increase that continues until the species reaches the bounds of its new range and its population growth rate slackens (Mack, 1989). Most extinctions of immigrant populations occur during the lag phase (Mack *et al.*, 2000), but some populations overcome these long odds and grow to a threshold size such that extinction from chance events, demographic or environmental, becomes unlikely (Crawley, 1989). Early detection and treatment of invasions in this lag phase before explosive spread occurs will prevent many future problems (Hobbs and Humphries, 1995).

According to Mack *et al.* (2000), any lag phase in the population growth and range expansion of a potential invasion most likely results from several forces and factors operating singly or in combination:

1) *Limits on the detection of a population's growth* – a lag could be perceived through the inability to detect still small and isolated but nonetheless growing populations in a new range (Crooks and Soule, 1996).
2) *The number and arrangement of infestations of immigrants* – an invasion will usually proceed fastest from many small, widely separated infestations compared with a single larger one, and this lag phase could be the result of an initial limitation in widely separated infestations (Moody and Mack, 1988).
3) *Natural selection among rare or newly created genotypes adapted to the new range* – strong selection in a new range can destroy all but the few pre-adapted genotypes. Alternatively, the lag phase could reflect the time for emergence of new genotypes through outcrossing among immigrants.
4) *The vagaries of environmental forces* – a small immigrant population could persist or perish largely as a consequence of a lottery-like array of forces

across time and generations, i.e. whether the first years in the new range are benign or severe; whether environmental forces combine to destroy breeding-age individuals as well as their offspring. Immigrant populations may also be so small that demographic stochasticity, simply the odds that a few reproductive individuals will produce offspring as influenced by endogenous forces, can also be important (Simberloff, 1988).

1.7.3 Factors influencing invasions

There are various factors that influence the invasion of alien species, such as the characteristics of the invading species, as well as the characteristics, dynamics and history of the site being invaded (Hobbs and Humphries, 1995). Once propagules arrive at a site, factors such as the level of disturbance, resource availability, and species interactions may determine the success of an invasion (Meiners *et al.*, 2002). Simberloff and Von Holle (1999) suggest that accumulations of alien species facilitate one another's survival and accelerate the rate of successful invasion. Many international drivers also influence the invasion of alien species, and these include the expansion of international trade and travel links, as well as the increasing volume of travel and trade, thus allowing 'impossible migration' to be possible and common. Globalisation of forestry and agro-forestry, increasing human population, habitat fragmentation and disturbance, changes in resources (pollution and fertilization), and the testing of new species, are other factors influencing invasions.

1.7.4 Factors influencing the invasiveness of species

Invasiveness is defined from the point of view of the species as the capacity to successfully invade communities from which it was previously absent, whereas invasibility is defined from the point of view of the community as the intrinsic susceptibility to invasion from external species (Prieur-Richard and Lavorel, 2000). Very few invasive alien plants are invasive in their countries of origin, as their ability to grow vigorously and produce large amounts of seeds is controlled by a host of co-evolved invertebrates and pathogens (Van Wilgen *et al.*, 2004). When introduced species are transported to a new continent, they can therefore multiply rapidly in the absence of the co-evolved invertebrates and diseases, thus allowing them to spread rapidly and out-compete indigenous species. However, it is often difficult to predict which species will become invasive.

According to Rejmanek (1989), there are several factors that could be used to predict which species will become invasive. Plants having at least some of these characteristics may more easily reach new sites and/or more rapidly compete with and eventually become dominant over plants that have evolved at that site (Rejmanek, 1989). These factors, which act either alone or together to increase the chance of a plant becoming invasive, are:

1) *Taxonomic position* – certain groups of plants have become more invasive in most regions than other taxonomic groupings;
2) *Homoclines* – if an organism is transported to a climate similar to that of its country of origin it may be better able to colonise and spread rapidly;
3) *Ecological status* – if a plant is a 'coloniser' in its country of origin, it seems more likely to become invasive in its new country;

4) *Dispersal characteristics* – invaders often have fruits that are morphologically adapted to disperse efficiently. Such plants are more likely to be moved around accidentally by wind or birds or grazing animals on or in their products, thus arriving at a new site;
5) *Seed dormancy* – many invasives show some level of seed dormancy, the effect of which usually is to spread the time for germination and establishment. The chances for effective colonisation are therefore increased; and
6) *Mode of reproduction* – once a propagule has arrived at a new site it is advantageous to be able to reproduce rapidly and enter the colonisation stage of invasion. Plants having the ability to produce large numbers of seeds or those having both sexual and asexual (vegetative) mode of reproduction are advantaged.

Weed populations have a high capacity to adapt to various environmental factors and control measures, due to the genetic diversity within these populations (Jordan and Jannink, 1997). This promotes diversity in biological and ecological properties, such as germination behaviour, growth form, seed size and dormancy (Warwick, 1990), and also the development of specific adaptations such as resistance to herbicide and biocontrol agents (Gould, 1991). Many introduced plant species rely on mutualisms in their new habitats to become invasive, and mutualisms involving animal-mediated pollination and seed dispersal, and symbioses between plant roots and microbiota often facilitate invasions (Richardson *et al.*, 2000). Flowing water and wind are often very important vectors of dispersal for propagules of initial invaders (Richardson *et al.*, 2000).

The invasiveness of woody species in disturbed landscapes is associated with small seed mass, short juvenile period (< 10 yrs), and short intervals between large seed crops (1 – 4 years) (Rejmanek and Richardson, 1996). Long fruiting periods seem to be also associated with invasiveness (Reichard, 1994). Vertebrate dispersal is responsible for the success of many woody invaders in disturbed as well as 'undisturbed' habitats (Rejmanek and Richardson, 1996). Plant species depending on non-specific mutualisms (root symbionts, pollinators, and seed dispersers) are more likely to overcome many abiotic and biotic barriers in new environments (Baker, 1974).

1.7.5 Factors influencing the invasibility of plant communities

An ecosystem's susceptibility to invasion may be influenced by many factors, such as disturbance, resource availability, habitat fragmentation and accessibility, evolutionary history, propagule pressure, predation, mutualism and competition (Kolb *et al.*, 2002), and the composition and diversity of resident species (Dukes, 2001). These factors interact with each other and with the characteristics of individual species, making it difficult to identify the causes of invasibility in individual cases (Kolb *et al.*, 2002).

Diversity and invasibility

It is commonly hypothesized that diverse communities use resources more completely than simple communities (thus leaving little space for individuals of new

species) and are thus more resistant to invasion by alien species (Levine and D'Antonio, 1999; Tilman, 1999). Therefore, species-rich communities may be less invasible, as resource niches are more fully occupied (Moulton and Pimm, 1986). If this is the case, diverse communities might buffer ecosystem processes against invader-driven perturbations for two reasons: reduced success of invading species, and reduced likelihood that an invading species will introduce some new property or process to the system (Chapin *et al.*, 1998).

However, some studies have described both positive (Robinson *et al.*, 1995; Palmer and Maurer, 1997) and negative (McGrady-Steed *et al.*, 1997; Tilman, 1997; Stachowicz *et al.*, 1999) relationships between diversity and invasibility, and in some cases have found no relationship (Lavorel *et al.*, 1999). For example, Palmer and Maurer (1997) point out that due to differences among plants in canopy height, rooting depth, rhizosphere microbial communities, etc., diverse communities contain more micro-heterogeneity than monocultures (Aarssen, 1983), and might therefore be more invasible. Therefore, while it is commonly believed that diversity should enhance resistance to invasion, arguments can be made that diversity may promote invasion (Levine and D'Antonio, 1999).

Species composition

Species composition may be an important component of habitat invasibility for potential invaders (Symstad, 2000). If changes in species composition result in changes in plant functional types, the effects may be even more pronounced (Grime, 2001; Lawton, 2001). Changes in the composition of (co-)dominant species in a community can result in substantial variability in community invasibility for certain invaders (Woitke and Dietz, 2002). Species composition can be changed by clearing existing vegetation, and thus altering the availability of nutrients and water (Luken, 1990).

Resource availability

The susceptibility of a community to invasion will be influenced by the supply of resources and their uptake, and this fluctuating resource availability is the key to understanding invasibility (Davis *et al.*, 2000). The basis for this suggestion is that a plant community with unused resources such as water, nutrients, space, or light, is more susceptible to invasion. Any factor that makes resources more available, e.g. a wet spell, the input of nutrients or the removal of a species, will promote invasion by new species.

According to Myers and Bazely (2003), the proposed relationship between resource abundance and invasion generates several predictions. Firstly, environments most likely to be invaded are those with periodic enrichment or an abrupt increase in the supply of resources such as by fire or flooding. Secondly, environments in which a decline in the uptake of resources has occurred will be susceptible to invasion. Thirdly, because conditions can change, no consistent relationship between the species diversity of a plant community and its susceptibility to invasion is expected. Finally, there will be no general relationship between the average productivity of a plant community and its susceptibility to invasion. What matters is the variation in productivity.

Edge effects

Corridors may facilitate the spread of invasive species, particularly if they are associated with long edges of disturbed habitat. Roads and streams act as corridors or agents for dispersal, provide suitable habitat, and retain reserves of propagules for future invasion following disturbance for some species of alien plants (Parendes and Jones, 2000). Roads are particularly good corridors as they alter conditions, stress indigenous species, and allow easier access of humans and other vectors of plant dispersal. They have higher light conditions and bare soil, which favours alien plant establishment (Pauchard and Alaback, 2004). Fortunately, most alien species growing along roadsides are incapable of colonizing less disturbed natural environments, as they are generalist species with short life cycles and high reproductive rates. Roadsides, however, still may serve as starting points from which some species spread from the edges to the interiors of pristine or naturally disturbed environments. These edge effects may either be beneficial or detrimental to the conservation of biodiversity. On the one hand, edges imply increased structural diversity and heterogeneity, often enhancing species diversity. Furthermore, edge effects constrict habitat size of interior species due to a change in the microclimatic conditions near the border and through the invasion of weedy species, competitors, parasites and predators.

1.8 Impacts of invasive alien plants

Historically, the concerns about the impacts of invading alien plants were mainly about the impacts on human society, but there is growing recognition of the impacts on biodiversity and natural systems in general (IUCN, 1997). The adverse consequences of biotic invasions vary enormously. At one extreme, the mere presence of alien species could be detrimental (Mack *et al.*, 2000), and at the other extreme, ecosystem processes are affected such as water purification, soil generation, waste decomposition and nutrient cycling, which are critical to human survival (Le Maitre *et al.*, 2004). The biggest ecological threat posed by invasive species is the disruption of entire ecosystems (Mack *et al.*, 2000).

According to Vitousek (1990), there are three principal effects of alien plants on ecosystems: the alteration of the flow, availability or quality of nutrient resources within biogeochemical cycles; of trophic resources within food webs; and of physical resources such as living space, sediment, light, or water. The impacts of invasive alien plants on natural ecosystems have been well documented in South Africa and abroad, and these include: (a) a reduction in biodiversity, (b) changes to soil and hydrological cycles, (c) changes to fire regimes, and (d) evolutionary changes.

(a) Reduction in biodiversity

One of the major threats of alien invasions is the loss of biodiversity, with invasions resulting in the replacement of diverse ecosystems with alien (sometimes monoculture) stands. This loss of ecological diversity can lead to reduced stability and resilience within ecosystems (Reinhardt and Rossouw, 2000). Once in a community, aliens may suppress indigenous species or prevent tree regeneration (Meiners *et al.*, 2002). Vegetation sampling studies indicate that alien plant species are often associated with a decrease in the number of species in natural communities

(Richardson *et al.*, 1989; Woods 1993; Wyckoff and Webb, 1996; McCarthy, 1997; Hutchinson and Vankat, 1997; Christian and Wilson, 1999), which suggests that invading alien species do not just fill vacant niches in natural communities (Tilman, 1997; D'Antonio, 1998) or replace indigenous species, but that they displace species disproportionately from the community, lowering diversity (Meiners *et al.*, 2002).

In cases where alien species have caused biodiversity loss, their effects are typically manifested through direct species interactions in the form of predation, competition, or hybridisation (Roemer *et al.*, 2002). Competition is increasingly recognized as a major means through which alien species impact and displace indigenous species (Settle and Wilson, 1990; Petren and Case, 1996; Kupferberg, 1997; Juliano, 1998; Byers, 2000). Well-adapted indigenous species would usually be expected to have a marked competitive advantage over newly arriving species that are adapted to different habitats and resource availabilities (Vermeij and Dudley, 2000). However, this is usually not the case. Competition for light is one of the primary mechanisms for change following alien invasions, resulting in shading of indigenous plants by invasive trees, shrubs, ferns and vines (Standish *et al.*, 2001). Invasion by alien plants also results in the decline of soil-stored seed banks of indigenous plants, leading to the local extinction of indigenous species (Richardson and Van Wilgen, 2004).

In general, however, it is not known whether alien species are stronger competitors than indigenous species (Meiners *et al.*, 2002). It is difficult, if not impossible, to differentiate the effects of the alien species on the plant community from the effects of the disturbance that lead to the initial plant invasion (Woods, 1997). It is not the invasion of an alien plant that reduces species richness but the dominance of a patch by alien species that may result in reduced species richness (Meiners *et al.*, 2002). It has also been found that the species richness of natives and aliens were positively associated, thereby showing no effects of alien invasion on indigenous species richness (Meiners *et al.*, 2002). However, when alien plants made up a large proportion of the total cover of a plot, they observed reductions in the community richness (Meiners *et al.*, 2002). Therefore, restoration efforts should be focused on controlling species that have the potential to dominate local plant communities.

(b) Changes to soil and hydrological cycles

It has been implicated that invasive alien plants have resulted in changes to soil nitrogen and associated biota, altered nutrient and hydrological cycles (Merrian and Feil, 2002), as well as plant productivity (Bertness, 1984; Vitousek, 1990). Increased soil erosion (Merrian and Feil, 2002), and decreased soil and above ground water supplies (Van Wilgen and Richardson, 1985), are further possible changes caused by alien invasions.

(c) Changes to fire regimes

Because of the high density of invasive alien plants, an increase in the fuel load and fire frequency results; often, key indigenous species are not adapted to this new fire regime (Mack *et al.*, 2000). This increased intensity of fires makes them more difficult to control (Chandler *et al.*, 1983). The increased severity of the fires

also results in greater damage to soils through heating and combustion of the organic matter which, in turn, can result in water repellency and severe soil erosion (Euston-Brown, 2000). The risk of severe flooding is also increased by the increased surface runoff and higher peak flood water volumes (Scott *et al.*, 1991; Van Wilgen *et al.*, 2001). The risks of damage to property and the loss of human lives or severe injuries are also greatly increased (Le Maitre *et al.*, 2002). Seeds in the soil, as well as sprouting plant species, can be killed by these severe fires (Holmes *et al.*, 2000).

(d) Evolutionary changes

Alien species invasions may be effective drivers of evolutionary change (Chornesky and Randall, 2003). Successful invaders may cause genetic changes in populations of indigenous species by hybridisation or by qualitatively or quantitatively altering selection pressures through ecological interactions or through changes in important habitat qualities or ecosystem processes (Chornesky and Randall, 2003). In heavily invaded landscapes, indigenous species are often restricted to small, refugial populations in marginal habitats. These populations may be particularly susceptible to extinction, because inbreeding depression and stochastic events can exacerbate the effect of the original invasion (Seabloom *et al.*, 2003). This spatial isolation raises issues for management and restoration of indigenous communities.

1.8.1 Impacts of invasive alien grasses

Over the past three decades in South Africa, alien grasses have become increasingly widespread and problems associated with these invasions are likely to increase as a result of global change (Milton, 2004). Alien grasses are an important component of the naturalized alien flora. However, they are often overlooked in reviews of the effects of invasive alien plants, and are seldom considered to have the potential to reduce the biodiversity and productivity of natural ecosystems, despite the growing global evidence that alien grasses can transform ecosystems (Richardson *et al.*, 2002; Richardson and Van Wilgen, 2004). They are often overlooked because of the major problems associated with alien woody plant invasions (Richardson and Van Wilgen, 2004).

The worldwide invasion of alien grasses has occurred due to seed introductions, tree and shrub clearing for pasture and grazing intensification, and crop production (Milton, 2004), and fragmentation of natural vegetation by roads (Hobbs, 2001). Alien grasses are a costly problem for agriculture, biodiversity conservation, fire and water management and rehabilitation following disturbance or clearing of woody weeds. D'Antonio and Vitousek (1992) propose that grass invasions are becoming important at local and global scales because grass flammability prevents recovery of woody vegetation, maintaining grass dominance, changing the microclimate and causing nutrient losses. Alien grasses are efficiently dispersed by wind, vehicles and animals, produce many small seeds and generally maintain persistent seed banks with few specialized seed predators. These factors extend their chances of persistence and eventual naturalization (Milton, 2004).

1.8.2 Impacts of invasive alien woody plants

While invasive plant species of all life forms are capable of having major impacts upon natural ecosystems, invasive trees are among the most damaging species, owing to their ability to become structurally dominant in terrestrial situations (Panetta and Sparkes, 2001). Invasive alien tree species may rapidly spread into riparian zones, eventually forming dense thickets that are expensive to eradicate (Dye and Poulter, 1995a). Riparian alien woody plants greatly reduce surface water runoff, and evapotranspiration by these plant communities is markedly greater than by indigenous plant communities in the same setting (Dye *et al.*, 2001; Everson *et al.*, 2001). Commercial plantation forestry has been one of South Africa's major sources of alien infestation (Richardson, 1998) – a large proportion (38%) of the area invaded by woody alien plants is occupied by species used in commercial forestry (Van Wilgen *et al.*, 2001). Because natural forests in southern Africa cover less than 0.25% of the landscape (Low and Rebelo, 1996; Midgley *et al.*, 1997), there is no natural source of fast growing timber trees, which has thus led to the establishment of these plantations of alien species (Le Maitre, 1998).

Impacts of commercial plantation forestry

Plantations of alien trees cover 1.52 million ha in South Africa (FOA, 1998). Many of the plantation species have become major invaders, thus spreading the negative impacts far beyond the afforested areas (Le Maitre *et al.*, 2002). These plantation species have become major invaders due to various factors. Firstly, the tree species themselves are often highly invasive (Richardson, 1998). Secondly, forestry operations often facilitate invasions through poor weed control in the plantations, and by transporting alien seeds on forestry machinery (Donald, 1971). Thirdly, the growing demand for forestry products is leading to an increase in the area under plantations and, therefore, in propagule sources (Jobs, 2002). Furthermore, agricultural and forestry enterprises are finding and testing new plant species and varieties with commercial value or potential (Le Maitre *et al.*, 2004). The exchange and trade in plant materials often involves species known to be invasive elsewhere in the world but this is ignored because of the perceived benefits of these plants (Mack, 2001).

Afforestation has substantial impacts on the biodiversity and functioning of natural ecosystems (Armstrong and Van Hensbergen, 1996; Allen *et al.*, 1997). Forest management, especially intensive forest management, is a major contributor to the loss of species from forest communities and the creation of biological deserts or monocultures. Each silvicultural intervention (i.e. harvesting, site preparing, planting, and tending) may affect species richness, abundance, and evenness differently, with the net result being the combined affect of all interventions (Bell and Newmaster, 2002). Plantation forestry has resulted in an increase in soil nitrate in many areas, possibly due to greater mineralization under forests than, for example, grasslands (Mills and Fey, 2003). Planting trees such as *Pinus* and *Eucalyptus* spp. invariably alters many soil properties – soils typically become more acidic, the effect usually being ascribed to the uptake of basic cations into the forest biomass (Mills and Fey, 2003).

One of the most severe impacts of afforestation is the significant reduction in surface streamflow (Bosch and Von Gadow, 1990). At the national scale, surface runoff was estimated to have been reduced by about 1.4 billion m^3 (3.2%) per year (Le Maitre *et al.*, 1997; Scott *et al.*, 1998a). These reductions are significant because South Africa has a mean annual rainfall of only 490 mm and less than 10% of this becomes surface runoff (Alexander, 1985). After clearing of dense and extensive stands of alien trees, it may take several years before streamflow recovery approaches pre-planting levels, indicating that soil water resources can be depleted and need replenishment (Dye and Bosch, 1999). The forestry industry says that it recognises the problems of invaders and says that it subscribes to a code of conduct that, amongst other things, requires that riparian zones and non-afforested areas within the forest estates are kept clear of invading alien plant species (FIEC, 1995). They also recognise that the impacts of plantation trees on streamflow are far greater in the riparian zone than outside it (Scott and Lesch, 1995; Scott *et al.*, 1999), and follow a policy of non-afforestation of such zones (FIEC, 1995). However, how well these policies are actually implemented is a matter that needs to be looked at.

Despite all the negative impacts of plantation forestry, it is an important part of the South African economy, as it contributes US$ 300 million (2%) to GDP (1996/1997 values) and employs over 100 000 people (Van Wilgen *et al.*, 2001; Le Maitre *et al.*, 2002). Downstream industries, based on forestry, produce timber products worth a further US$ 1.6 billion (1996/1997 values) much of which is exported, earning valuable foreign exchange (FOA, 1998; Van Wilgen *et al.*, 2001).

1.8.3 Economic impacts of invasive alien plants

The threats that alien invasions pose to biodiversity and to ecosystem-level processes translate directly into economic consequences such as losses in crop production, fisheries, forestry, and grazing capacity (Mack *et al.*, 2000). Other economic impacts include the direct cost of combating invasions, including all forms of quarantine, control, and eradication (U.S. Congress, 1993).

Invasive alien plants cost South Africans tens of billions of rand annually in lost agricultural productivity and resources spent on weed control (Van Wilgen *et al.*, 2001). A study was conducted to estimate the predicted impacts of invasive alien trees at a national level, and found that about 10.1 million ha (6.8%) of South Africa has been invaded to some degree (Versfeld *et al.*, 1998). The incremental water use of these invaders was an estimated 3300 million m^3/yr or 6.7% of the mean annual runoff (Le Maitre *et al.*, 2000), and would cost an estimated US$ 1.2 billion to clear using chemical and mechanical methods, or roughly US$ 60 million per year for the estimated 20 years that it will take to deal with the problem (Versfeld *et al.*, 1998; Le Maitre *et al.*, 2000). Substantial amounts would then be required to keep the areas clear. In many situations the costs of control will greatly exceed the value of the land, making clearing operations difficult to justify (Olckers *et al.*, 1998). However, clearing invasive alien plants is a good investment simply to prevent water losses (Hosking and Du Preez, 1999), as water is a limiting resource in South Africa and water losses restrict the potential for economic growth (Van Wilgen *et al.*, 2001). Furthermore, failure to clear stands of invading trees will result in exponential increases in the costs of clearing as catchment areas become further invaded (Le Maitre *et al.*, 2002).

1.8.4 Examples of the most important invasive alien plants

Trees in the genus *Eucalyptus* number approximately 400 species, almost all of them endemic to Australia (Williams and Woinarski, 1997). In South Africa, eucalypts have many benefits. They are used for timber, poles, firewood, ornamentals, and are valuable sources of nectar and pollen necessary for the production of honey (Poynton, 1979). However, some eucalypts are considered invasive with potentially negative effects on natural habitats (Forsyth *et al.*, 2004). Eucalypt plantations use large amounts of water. For example, the afforestation of catchments in Mpumalanga with eucalypts resulted in the total drying-up of streams 6-12 years after planting (Van Lill *et al.*, 1989). While many species of eucalypts have been here for over a 100 years, only a few have become truly invasive, such as red river gum (*Eucalyptus camaldulensis*), flooded gum (*Eucalyptus grandis*) and spider gum (*Eucalyptus lehmanii*) (Forsyth *et al.*, 2004). Forsyth *et al.* (2004) recommend that clearing projects should focus on removing eucalypts from riparian areas (where water use is likely to be excessive) and nature reserves (where all eucalypts have undesirable effects on biodiversity), but that clearing projects outside of these areas should focus only on the invasive species.

Several Australian *Acacia* species have also become highly invasive weeds in South Africa where they form dense thickets which impair agriculture, create fire hazards, smother natural vegetation and associated fauna, and drastically reduce flow rates of rivers and streams (Henderson, *et al.*, 1987). Besides being problematic, some of these *Acacia* species are also of considerable commercial value as a source of high-grade pulp-wood and tannin (*A. mearnsii*), furniture timber (*A. melanoxylon*), agroforestry (*A. saligna)* and firewood (*A. cyclops*) (Hoffmann *et al.*, 2002). *A. cyclops* and *A. longifolia* are important species used in dune stabilisation.

Black wattle (*A. mearnsii*) was imported to South Africa in the mid-nineteenth century (De Wit *et al.*, 2001). It has been widely planted and now forms the basis of a small but significant commercial plantation industry. In addition, many black wattle woodlots provide rural communities with firewood. The species is also highly invasive, and it commonly invades many forms of indigenous vegetation, developing into dense, evergreen thickets, particularly along riparian zones (Dye and Jarmain, 2004). It produces copious amounts of hard-coated seeds which are relatively long-lived (Garner, 2005), and are spread rapidly down water courses and through the movement of soil (De Wit *et al.*, 2001). The wattle has spread over an area of almost 2.5 million ha in South Africa, where it has significant negative impacts on water resources, biodiversity, and the stability and integrity of riparian ecosystems (Versfeld *et al.*, 1998). Serious infestations occur in the higher rainfall regions of the country (Le Maitre *et al.*, 2000). An assessment of the economic impact of Black wattle gives a net cost of R9.8 billion (De Wit *et al.*, 2001). The costs associated with the invasion by black wattle are partly offset by the substantial social and economic benefits derived from the wattle industry (Le Maitre *et al.*, 2004). Only one biocontrol agent (a seed-feeding weevil) has been released against this species, but only in areas where the wattle is not grown commercially (De Wit *et al.*, 2001). De Wit *et al.* (2001) conducted an analysis of the costs and benefits associated with *A. mearnsii* in South Africa at a national level, and found that the most attractive option was to combine physical and biological control with the continuation of the commercial growing activities.

Other species used for commercial gain include *Pinus* species (used in forestry), *Prosopis species* and *Melia azedarach* (used in horticulture) and *Opuntia ficus-indica* (used in fruit production) (Olckers *et al.*, 1998). Important invasive species that invade the grassland and savanna biomes include *Rubus* species and *Opuntia stricta* (Richardson and Van Wilgen, 2004). *Opuntia stricta* currently infests about 40 000 ha of the KNP and is the greatest threat to biodiversity in veld habitats (Reinhardt and Rossouw, 2000). It was found that most of the water used in an invaded area, is by *Acacia mearnsii* and *A. cyclops*, followed by pines, eucalypts, *Prosopis* species and *Melia azadarach* (Le Maitre *et al.*, 2000). Another important invasive of grasslands and savannas, is *Chromolaena odorata*, which suppresses the regeneration of primary forest trees, and also provides feeding niches that can sustain other pests (Mack, *et al.*, 2000). This species also has secondary compounds that are of medicinal interest (Ambika, 2002).

A good example of a plant that has been spread around the world is *Lantana camara*, which is on various lists of the top invasive woody weeds (Cronk and Fuller, 1995; Rejmanek and Richardson, 1996; Binggeli *et al.*, 1998). Its ability to invade and dominate new environments was not recognized until after it had become widely spread (Myers and Bazely, 2003). This species also has medical properties – it contains iridoid glycosides that may have potential for use as anti-cancer drugs (Ghisalberti, 2000). In addition to its medicinal properties, *L. camara* and relatives are widely valued as popular garden plants with many different brightly coloured cultivars (Myers and Bazely, 2003). Furthermore, many agricultural benefits of *Lantana* have been reported, among them improved soil fertility and slowed soil erosion (Ghisalberti, 2000). Despite these beneficial properties, *L. camara* can have negative effects on the biodiversity of an area.

1.9 Clearing of invasive alien plants

Removing dense stands, as opposed to individuals, of invasive alien plants has the greatest effect. Also, removing the invasive alien plants from riparian areas has a greater effect than clearing them from upland areas (Macdonald, 2004). There is evidence that, without sufficient planning, successful eradications can have unwanted and unexpected impacts on indigenous species and ecosystems (Zavaleta *et al.*, 2001). For example, removal of one alien species can lead to the establishment or increase of one or more other invasive species (Zavaleta *et al.*, 2001). Also, removal of invasive plant species can reduce habitat or resources available for indigenous fauna if the removal is not accompanied by further restoration measures (Zavaleta *et al.*, 2001). Therefore, eradication must be followed by additional site restoration. With the removal of alien species, the availability of resources required by plants such as light, water and nutrients reaches a peak soon afterwards (Canham and Marks 1985). There is increased soil moisture, soil temperature and improved substrate quality, which stimulates nitrogen mineralization and increases nitrogen pool sizes, and consequently increases short-term nitrogen availability (Agrawal and Tiwari, 1987; Matson *et al.*, 1987). The first plants to establish after a disturbance should thus encounter a greater availability of resources, improving the probability of survival and establishment in the community. The initial colonizer's competitive advantage and consequent dominance could inhibit establishment by other species as succession proceeds and resources become more limited (Hughes and Vitousek, 1993).

The regeneration of trees by coppicing (resprouting) is an important process that needs to be considered when dealing with the removal of woody species. Relatively little is known concerning the persistence and regeneration of African savanna trees (Wilson and Witkowski, 1998, 2003; Witkowski and Garner, 2000). Often, when the above ground parts of a tree are removed or killed, resprouting occurs soon afterwards. Examples of this are trees of the distinctive miombo (savanna) woodlands of south-central and eastern Africa (Luoga *et al.*, 2004). These trees resprout from roots and stumps once the above ground parts have been removed or killed by harvesting or fire damage (Grundy, 1995; Frost, 1996). These shoots grow faster than newly established seedlings, because they already have a well-established root system with stored reserves (Chidumayo, 1993; Grundy, 1995). Species with seeds already in the disturbed environment have an advantage over species that are some distance away as they do not have the delay of dispersal. Therefore it is important to consider the soil seed bank composition in order to determine the regeneration and species structure of the community after a disturbance.

In early phases of recovery from plant invasion, the changes in diversity of herbaceous plants is the quickest, followed by the increased abundance of indigenous woody plants (Sousa, 1984). Therefore, an increase in floral diversity is expected after clearing of alien species from the community (Sousa, 1984). The reason for this increased diversity is that clearing and exclusion of invasive species, functions as a disturbance and in essence resets the successional sequence of the vegetation (Mentis and Ellery, 1994). A period of many years will be required to regain the same successional stage that was present prior to the disturbance. Therefore, there is a need for long-term observations in the assessment of vegetation restoration in areas that have been disturbed by clearing of invasive species.

1.9.1 Control methods

Once a species has reached the point where it is recognized as a problem, eradication is not likely to be achievable even with massive economic investment. An option, therefore, is to attempt to control the species to some acceptable level through various control methods (Myers and Bazely, 2003). Three main approaches are widely used to control invasive plants: chemical, mechanical, and biological control (biocontrol).

Chemical control methods

Chemical control probably remains the chief tool in combating alien plants in agriculture. However, chemical controls have too often created health hazards for humans and non-target species. However, newer herbicides are less toxic, have shorter residence times, and are more specific (Hobbs and Humphries, 1995). Although herbicides can be applied more readily to larger areas than physical control, many broad-scale problems may not be treatable with herbicides (Hobbs and Humphries, 1995).

Mechanical control methods

Mechanical methods include hand-pulling, cutting and burning. The timing of pulling and cutting is very important. If plants are pulled out while they are

flowering, their transport and removal may spread seeds far and wide. Consistent and continued pulling can work to remove invasive species from small areas and even achieve very local eradication. But as long as there is a source of seeds or cuttings for reinvasion, the control effort must continue. Manual removal has been advocated as the most environmentally friendly method of weed removal, but this type of control is labour intensive and can be applied only to relatively small areas where labour volunteer groups or other bodies are available (Hobbs and Humphries, 1995). Mechanical methods of control are sometimes effective and usually do not stimulate public criticism. Sometimes they can even be used to generate public interest in and support for control of invasive species (Mack *et al.*, 2000).

Biological control methods

Problems with both chemical and mechanical controls have focused attention on biological control. Biocontrol involves the deliberate introduction of host-specific natural enemies (invertebrates or diseases) of the invasive alien plant from its original native range to reduce its adverse effects, and arriving at a situation where the plant is returned to the status of a non-invasive naturalized alien (an alien plant that is able to survive, and even reproduce, but does not invade aggressively in its new habitat) (Fowler *et al.*, 2000; Van Wilgen *et al.*, 2004). The ecological foundation to this form of biological control is that the vigour of plants can be reduced by being attacked by their natural enemies (Fowler *et al.*, 2000). Usually, weeds are partially controlled by introduced biocontrol agents and other control methods are required to maintain the weed at tolerable levels. Biocontrol should therefore be viewed as a means of increasing the efficacy of other control methods and should thus assume a key role in all integrated weed management programmes (Olckers *et al.*, 1998).

(a) Advantages

Biological control is a particularly attractive option as a management tool for weeds as it is cost-effective and safe compared to herbicidal and mechanical operations, it can be successfully integrated with other management practices, and it is self-sustaining (Zimmermann *et al.*, 2004), but there are also drawbacks. However, the advantages outweigh the disadvantages, provided projects are carefully selected and follow rigorous procedures to minimize risk (Fowler *et al.*, 2000).

(b) Disadvantages

Biocontrol has recently been critically scrutinized on the grounds that non-target species, some of them the focus of conservation efforts, have been attacked and even driven to extinction by non-indigenous biocontrol agents (Howarth, 1991; Simberloff and Stiling, 1996). Controversy about the extent of such problems focuses primarily on two issues: whether there is sufficient monitoring to detect such non-target impacts, and the likelihood that an introduced biocontrol agent will evolve to attack new hosts (Mack *et al.*, 2000). The fact that biocontrol agents can disperse and evolve, as can any other species introduced to a new range, implies that their preliminary testing should be extensive and conducted under extremely secure settings (Mack *et al.*, 2000).

(c) History of biological control in South Africa

Biocontrol has been practiced in South Africa since 1910 to control invasive alien plants. To date (2004), 103 biocontrol agents (including invertebrates and pathogens) have been released against 47 weed species (Olckers and Hill, 1999), making South Africa the third most active country in biological control after the U.S.A. and Australia (Van Wilgen *et al.*, 2004). An example of one of the first biocontrol experiments was in 1913, when introduced insects were used to control alien cacti (*Opuntia* species) that were invading semi-arid rangelands (Macdonald, 2004).

Integrated control methods

Experience has shown that satisfactory control of weeds is usually only achieved when several complementary methods, including biocontrol, improved land management practices, herbicides and mechanical methods, are carefully integrated (Richardson *et al.*, 1997). Typically, mechanical and chemical control methods are used to clear invaded areas which are then managed with thorough rehabilitation programmes that rely heavily on biological control to alleviate the problems in the long-term (Olckers *et al.*, 1998). Integrated control of invasive alien plants in Southern African dates back to about 1940 when *Opuntia ficus-indica* was controlled with a combination of biocontrol and mechanical methods (Pettey, 1943).

1.10 Ecosystem restoration

Because of the scale of habitat loss, fragmentation, and degeneration, ecosystem restoration is an increasingly valuable conservation strategy (Webb, 1996; Fahrig, 1997). It is an integral component of land management, and restoration activities should ideally be placed within a broader context of sustainable land use and conservation (Hobbs and Harris, 2001). Restored ecosystems are more likely to be self-maintaining if restoration is carried out at the landscape level (Cairns, 2002). When it is carried out at this level, then restored sites need to be compared to reference sites to measure success (McCoy and Mushinsky, 2002). According to Bradshaw (2002), restoration is the approximate return of an ecosystem to its original condition prior to disturbance. The goal of restoration is to emulate a natural functioning, self-regulating system that is integrated with the ecological landscape in which it occurs (National Research Council, 1992). This definition has been broadened by the Society for Ecological Restoration (1996), which states that 'ecological restoration is the process of assisting the recovery and management of ecological integrity'.

The return of a degraded system to its original state prior to human-induced damage may not be possible. Recent experimental work indicates that some degraded systems are resistant to traditional restoration efforts due to constraints such as changes in landscape connectivity and organization, loss of indigenous species pools, shifts in species dominance, trophic interactions and/or invasion by aliens, and associated effects on biogeochemical processes (Suding, *et al.*, 2004). For restoration to be considered a 'success', a suitable end point must be reached whereby the particular species or community is restored within a self-sustaining, semi-natural habitat (under a given management regime) (Wheeler, 1995; Macdonald *et al.*, 2002).

For successful river restoration, rivers must be viewed in the context of dynamic ecosystems (Downs *et al.*, 2002). River restoration projects based solely on recreating desired river morphology are unlikely to succeed. Cairns (1991a) defines full river restoration as 'the complete structural and functional return to a pre-disturbance state'.

Van Diggelen *et al*. (2001) suggested that there are three levels of ecosystem restoration:
1). *Reclamation* – defined as attempting to increase biodiversity in highly disturbed sites, benefiting the landscape as a whole but not the protection of red list species. "Revegetation" may be included as a subset of reclamation as it aims to reinstate a cover of vegetation that may or may not be a derivative of the prior vegetation.
2). *Rehabilitation* – defined as the reintroduction of certain ecosystem functions such as improving water infiltration, that benefits ecosystem functioning at the landscape scale, but not necessarily biodiversity;
3). *Restoration* – consists of a reconstruction of a prior ecosystem and includes the re-establishment of former functions and characteristic species, communities and structure, and generally is impossible at the landscape scale because of land use conflicts and other reasons.

The term "ecosystem repair" refers to actions that overcome limitations in both the abiotic and biotic components of the ecosystem. In order to fully understand and assess the process of revegetation after alien invasive species removal, and the impacts of invasion intensity on revegetation, the role of key species must be analysed as well as vegetation structure and regeneration potential (seed propagules and seed banks).

1.10.1 The process of ecosystem restoration

According to Hobbs (2002), there are a number of steps in the development of a programme of landscape-scale restoration. Firstly, assessment needs to be done to establish whether there is a problem that requires attention. Secondly, the causes of the problem need to be determined. Thirdly, realistic goals for restoration need to be set up, and lastly, cost-effective planning and management tools for achieving the agreed goals, needs to be developed, i.e. monitoring must be done.

Goal setting

To achieve a successful monitoring programme, goals must first be clearly defined from the beginning. The restoration goals should focus on the desired characteristics for the system in the future, rather than in relation to what these were in the past (Hobbs and Harris, 2001). To succeed, restoration activities need not only to be based on sound ecological principles and information, but also to be economically possible and practically achievable (Hobbs and Harris, 2001).

Properly functioning ecosystems have natural recovery processes that maintain sustainable flows of soil, nutrients, water and organic materials (Whisenant, 2002). During degradation, positive feedback mechanisms reinforce and accelerate damaging processes, leading to irreversible vegetation change once a site's capacity for self-repair has been exceeded (Rietkerk and Van de Koppel, 1997). Designing restoration

strategies that overcome threshold barriers to natural recovery processes is one of the more important challenges for ecological restoration (Whisenant, 2002). The concept of restoration thresholds suggests that options are determined by the current state of the system in relation to biotic and abiotic thresholds (Hobbs and Harris, 2001). In other words, the type of restoration response needed will depend on which thresholds (biotic or abiotic) have been crossed.

If a system has degraded mainly due to biotic changes (such as grazing-induced changes in vegetation composition), restoration efforts need to focus on biotic manipulations which remove the degrading factor (e.g., the grazing animal) and adjust the biotic composition (e.g., replant desired species) (Hobbs and Harris, 2001). If, on the other hand, the system has degraded due to changes in abiotic features (such as through soil erosion or contamination), restoration efforts need to focus first on removing the degrading factor and repairing the physical and/or chemical environment (Hobbs and Harris, 2001). Considering the functioning of a system will provide a useful framework for the initial assessment of the state of the system and the subsequent selection of repair measures (Tongway and Ludwig, 1996; Ludwig *et al.*, 1997).

Monitoring

Restoration is often viewed as a product rather than an ongoing process. However, if restoration is viewed as an ongoing process resulting in self-maintaining dynamic systems, then monitoring of invasive aliens and the impacts of their removal is essential to success (Holl and Cairns, 2002). Thus, once the goals have been set, specific monitoring protocols must be outlined and criteria for success must be determined. This should be done during the planning phase of the project, and not after implementation (Kondolf and Micheli, 1995). It is also essential at an early stage in project planning to develop a feedback loop of how monitoring will inform subsequent management decisions (Shabman, 1995). Early on in a restoration project, monitoring should be conducted more frequently to determine whether restoration efforts are proceeding along the predicted trajectory (Holl and Cairns, 2002).

Monitoring the effects of invasive species and the efforts to remove them is extremely difficult. Ideally, removal and monitoring efforts lead to insights on way of reducing the problem, but they are unlikely to lead to total eradication. As a consequence, monitoring both the ecological effects of invasive aliens and the efficacy of control measures will almost certainly be an ongoing expense, justified by the enormous ecological and economic impacts caused by aliens (Holl and Cairns, 2002). The effects of removal efforts must be monitored, not only on the target species, but also on the indigenous ecosystem.

Temporal and spatial scales

Temporal and spatial scales need to be considered in restoration projects. It is important to realize that there is usually a great variation between the rate at which humans damage ecosystems and the rate at which a damaged system can be restored, even with active intervention (Lake, 2001). Thus, even though it might only take a few months for an ecosystem to be damaged, it will take much longer for it to be restored.

Many ecosystems may naturally fluctuate through cycles related to disturbance regimes or climatic patterns (Kondolf, 1995). Therefore, data must be collected over a sufficient time period in order to incorporate the natural cycles of variation, such as fire intervals, periodic flooding or cyclical population fluctuations (Sutter, 1996). Ecosystem monitoring must also be conducted at large spatial scales that may include surrounding, non-restored areas, as human actions often affect ecosystems over large areas (Holl and Cairns, 2002). The scale selected for monitoring must be appropriate for the population/community or process being monitored. Technologies that allow work at larger spatial scales are improving. Increasingly, geographic information systems (GIS) are being used to overlay land-use coverage with soil types, elevation, parcel ownership and other parameters to prioritise restoration efforts (Holl and Cairns, 2002). The rates at which natural processes operate, are usually positively correlated with the spatial scale (Wiens, 1989). Therefore, this spatial-temporal scale correlation may govern the rate of restoration (Lake, 2001).

Ideally, all restoration projects should be monitored at large spatial scales, for long time periods, and at high levels of detail (National Research Council, 1992). In reality, the opposite is usually true. A trade-off usually occurs between: 1) frequently sampling a number of parameters at a few points; 2) infrequently sampling many parameters at relatively few locations; and 3) infrequently sampling a few parameters at many locations (Michener and Houhoulis, 1997). How best to allocate monitoring efforts over space and time will depend on the goals of the project and the ecosystem being monitored.

1.10.2 Examples of methods used in restoration projects

The use of fire

Fire is a form of management that essentially reverses or arrests succession of plant communities. Fire is potentially selective, because species differ in their sensitivity to fire and because the duration and temperature of fires can be controlled (Davy, 2002). Fire is an integral part of the ecology of certain ecosystems, and plants in them have evolved considerable resistance to its damaging effects (Davy, 2002). Burning in such communities can be used to the disadvantage of less-tolerant aliens and invaders.

The use of soil seed banks

The starting point for the restoration of plant communities must be the restoration of physical and soil environments appropriate to them. Spatially, the highest amount of regeneration often corresponds to a zone with the highest amount of seed deposition (Titus, 1991; Houle, 1995). Indigenous populations might be re-established from relict propagules in topsoil and litter retained from the original site, or by importing equivalent materials from nearby similar sites; furthermore, the genetic structure of such populations might be expected to closely resemble the pre-disturbance populations (Davy, 2002). Where the use of seed banks is feasible, it is likely to be a highly cost-effective method of re-establishing natural vegetation (Van der Valk and Pederson, 1989).

Soil nitrogen and the addition of carbon

The outcome of competition between indigenous vegetation and weeds may often depend on nitrogen (N) availability, with high levels of N increasing weed invasion and/or decreasing the success of indigenous species (Smith *et al.*, 1999). High N availability may be problematic in the restoration of indigenous plant communities, where prolific weed growth can delay or even prevent the reestablishment of indigenous species (NRC, 1992; Packard and Mutel, 1997). Therefore, carbon (C) addition has been suggested as a method for immobilizing plant-available N and increasing the success of indigenous species (Morgan, 1994). Additions of organic C induce soil microorganisms to immobilize available N (Blumenthal *et al.*, 2003). Decreased N, in turn, reduces the growth of nitrophilic weeds, thereby releasing indigenous species from competitive suppression (Blumenthal *et al.*, 2003).

Re-establishing pollination relationships

The return of a rich invertebrate fauna to restored areas is important, as these invertebrates are associated with the full range of ecosystem functions and processes (Majer *et al.*, 2002). Pollination is an important ecosystem function as it maintains plant species through sexual reproduction (Majer *et al.*, 2002). Thus, pollination relationships in restored communities should be re-established in order to produce self-sustaining plant populations. The role of insects in this function is therefore critical to consider in restoration (Majer *et al.*, 2002).

1.10.3 Problems involved in ecosystem restoration

Selection of a suitable reference site

One of the most problematic questions in designing monitoring plans is identifying a suitable reference site or criteria (White and Walker, 1997). Reference sites must be selected to compare with restored areas. It is impossible to find an identical system, as other sites may be surrounded by different land uses; vary inherently along abiotic gradients, such as soil types or slope aspect; and may have been subjected to different disturbance regimes (Holl and Cairns, 2002). Usually, either historic reference data are used, baseline data are taken before a site is damaged, or restored sites are compared with other nearby sites that are judged to be more ‘intact’ (often, a combination of these comparisons is used) (Holl and Cairns, 2002). Each of these approaches presents a number of problems. In many cases, historic data before the influence of humans are not available. For thousands of years, humans have influenced many ecosystems worldwide to some degree. Therefore, the selection of a reference historical state is subjective (Holl and Cairns, 2002). Often, extensive damage has occurred before baseline data can be collected to provide a reference (Holl and Cairns, 2002).

Another problem with selecting a reference site is deciding with which successional stage to compare a restored site (Holl and Cairns, 2002). This selection is problematic for rivers, as rivers reflect the geology and management practices of the entire watershed, which are impossible to replicate. Therefore, a good approach is to select a range of reference sites to assess the natural variation and define boundary

conditions for parameters to be monitored. A final problem in selecting a reference site is that species and biotic communities are naturally patchily distributed spatially, as well as temporally (Holl and Cairns, 2002). Therefore, reference systems must be sampled across a sufficient spatial scale to incorporate natural variability within systems.

Restoration of the entire ecosystem

Even though it has been clearly defined what restoration of an ecosystem involves, restoration projects often only recreate the vegetation. However, restoration of a system requires more than just recreating the vegetation assemblage (Horwitz *et al.*, 1999). Restoration may be thought to have failed unless the services of nutrient retention and cycling, purification of air and water, detoxification and decomposition of wastes, pollination, dispersal of seeds, and other ecosystem services are recovered (Majer *et al.*, 2002).

Spatial scale

Most of the information and methodologies on ecological restoration centre on individual sites, and ultimately restoration activities have to be conducted in particular sites (Hobbs, 2002). However, site-based restoration is often insufficient on its own to deal with large-scale restoration problems (Hobbs, 2002). Landscape- or regional-scale processes are often either responsible for ecosystem degradation at particular sites, or alternatively have to be restored to achieve restoration goals. Hence, restoration is often needed both within particular sites and at a broader landscape scale (Hobbs, 2002). However, although it is technically possible to "recreate" some former communities on a local scale and at high costs, true restoration is generally impossible at the landscape scale because of land use conflicts and long distance effects of other activities (Van Diggelen *et al.*, 2001).

Setting of restoration goals

Ecosystems are naturally dynamic entities, and hence the setting of restoration goals in terms of static compositional or structural attributes is problematic (Hobbs and Harris, 2001). In practice, a discrepancy exists between the high ideals of restoration goals and reality, where one often encounters limiting factors (Pfadenhauer, 2001). These limiting factors can include the conflict between different restoration goals, the unpredictability of restoration goals owing to long-term effects and stochastic events, the insufficient social acceptance of landscape change during restoration processes, and the use of restoration processes themselves (Pfadenhauer, 2001).

Monitoring and time

A critical aspect of monitoring is the time scale, including length of monitoring and frequency (Holl and Cairns, 2002). Time-frames for both monitoring and restoration are typically short (example, five to ten years). They are commonly limited by budget constraints, as well as the need to demonstrate compliance with regulatory standards, rather than being based on ecological principles (Holl and Cairns, 2002). As a result, many restoration projects are aimed at achieving short-

term goals, which may inhibit long-term ecosystem restoration. Ideally, monitoring should be continued until the ecosystem is self-regulating for some particular time period (Cairns, 1991b).

Outdated ecological concepts

There is a need for a much firmer ecological foundation for developing and implementing restoration projects (Clewell and Rieger, 1997). In addition, it is becoming increasingly apparent that the assumptions underlying many restoration projects have their roots in outdated concepts of how ecological systems function (Hobbs and Harris, 2001).

Invasive alien plant species

The control of alien plant species is usually the key to ecological restoration. However, invasive species are the most difficult to control due to various factors such as reinvasion. Reinvasion may occur either through *in situ* recruitment (e.g., regeneration from a persistent seed bank) or through immigration (Panetta and Sparkes, 2001). The management of seed banks is therefore a critical aspect of revegetation following the removal of invasive plants (Panetta and Groves, 1990). However, effective planning for restoration requires an understanding of the potential for reinvasion by both means (Panetta and Sparkes, 2001). Because the control of invasive species is so difficult, the removal of such species must be highly selective (Davy, 2002). Neither the establishment of crucial plant species nor the removal of deleterious ones can immediately restore target plant communities – some degree of development is likely to be necessary (Davy, 2002).

Use of soil seed banks

Reconstructing the soils is difficult because a soil comprises both organic and inorganic components that have weathered *in situ* for a very long time. As such, soils that have been reconstructed always contain early-successional characteristics (Allen *et al.*, 2002). In most situations, the plants that colonise early-successional sites and are capable of surviving on these soils are not those that are considered desirable for restoration success (Allen *et al.*, 2002). The most fundamental questions raised by the seed-bank approach concern the extent to which the composition of the seed bank reflects that of the established vegetation prior to disturbance, or even that of an earlier successional stage that could be an appropriate target for restoration (Davy, 2002). There are often large disparities between the vegetation composition and the seed bank in the underlying soil, even in the absence of any disturbance, which may be partly because seed banks accumulate species that have been prominent over a series of successional stages at the site and partly because of differential survival of species in the seed bank (Davy, 2002).

Ecological resistance of degraded systems to restoration efforts

The new species (indigenous or alien) that comprise the degraded community often have distinctive traits that can change ecosystem characteristics such as rates of resource turnover, nutrient distribution and disturbance regimes (D'Antonio and Meyerson, 2002). Once species have changed ecosystem processes, positive

feedbacks can increase the resistance of the system in its degraded state and make it resistant to restoration efforts (Scheffer, 2001). Declines of source populations of indigenous species as a consequence of habitat destruction and fragmentation limit the effectiveness of regional pools as a source of propagules for recolonisation (Suding *et al.*, 2004). This, combined with the absence of indigenous species in the degraded site and the loss of an indigenous seedbank, limits the regenerative ability of many indigenous species in restoration projects (Pywell, 2002; Smith, 2002).

1.11 Soil seed banks

Soil seed banks have been defined as all viable seed present under and on the surface of the soil. Soil seed banks are important to plant population dynamics and community structure (Teo-Sherrell *et al.*, 1996), and are essential to ecosystem development following disturbance (Keddy *et al.*, 1989). Soil seed banks can serve as pools of genetic material, enabling a range of responses to ordinary environmental variability, and can buffer populations against temporarily extreme adverse conditions (Teo-Sherrell *et al.*, 1996).

Most plant communities have populations of viable seed buried in the soil (Thompson, 2000), a proportion of which is usually capable of germinating as soon as they are exposed to suitable conditions (Davy, 2002). Therefore, the species that dominate the seed bank have an advantage when disturbance creates opportunities for recruitment. The remaining seeds may exhibit a variety of types of dormancy (Davy, 2002). Seed dormancy in the soil could be considered a form of long-distance dispersal in that it separates parents and offspring in time (Dean *et al*., 1986). Seed banks of different species differ in their persistence, depending on seed longevity in the soil and their tendency to germinate (Thompson and Grime, 1979). Persistent seed banks may often be available for use in restoration and the more persistent they are the more likely they are to be usable (Davy, 2002).

The majority of alien plant species have soil-stored seeds, and these seeds tend to occur in abundance and persist in the soil seed bank as viable entities for long periods (Auld, 1995). Many of the most problematic invader species have persistent seed banks, hindering restoration efforts (Holmes, *et al.*, 2005), for example *Acacia mearnsii* (Pieterse and Boucher, 1997) and *Solanum mauritianum* (Garner, 2005). The soil seed banks play an important role in the regeneration of alien species, and thus there is a real need to determine the success of invasive alien species clearing operations in reducing seed banks. One way of controlling large soil seed banks is by felling the plants and burning them to destroy or to stimulate seeds to germinate, so that the resulting seedlings may be controlled (Pieterse and Boucher, 1997).

In some cases, disturbances are required for seeds to germinate. The absence of disturbances causes seed banks to become stagnant, with seeds becoming older and a decrease in viability occurring, thus reducing the regeneration potential (Auld, 1995). There are a number of processes that directly and indirectly affect the persistence of seeds in the soil. For example, fire may destroy seeds that are not buried deep enough in the soil, but it also functions as a germination cue for some species (Morgan and Neuenschwander, 1988). However, McGee and Feller (1993) showed that the number of germinants generally decreases with increased sample depth and that burial depth significantly affects seed germination in many species,

especially those with small seeds. Hence, the establishment of seedlings from the seed bank will be a function of the depth to which the soil is disturbed and the kind of disturbance imposed (McGee and Feller, 1993).

A major problem with most studies of seed banks is that estimates of seed numbers in the soil are very imprecise (Bigwood and Inouye, 1988). One reason for this is that the spatial pattern of seeds in the soil is usually unknown prior to sampling, and consequently the sampling strategy is far from optional (Witkowski and Garner, 2000). The spatial pattern of seeds in the soil is a response to the spatial pattern of parent trees, the agents of seed dispersal, and the dynamics of seeds in the soil (Witkowski and Garner, 2000). The spatial distribution of seeds has major implications for seedling recruitment as seed predation and density-dependent competition among seedlings results in increased mortality if seeds are clumped (Lamont *et al.*, 1993; Lamont and Witkowski, 1995). The typical distribution of seed banks tends to be highly over-dispersed (Lamont and Witkowski, 1995).

1.12 Seed dispersal

In an ecosystem, the most important interaction between plants and animals is seed dispersal (Gomez *et al.*, 2003), which ultimately determines the character of the vegetation. The study of the dispersal of seeds can contribute greatly to understanding the regeneration ecology of species within an ecosystem (Leck, 1989). An animal-mediated dispersal process provides an efficient way of spreading seeds from one suitable habitat patch to another, especially in the context of increasingly fragmented landscapes (Schiffman, 1997). When introduced species produce fleshy fruits, generalist frugivores can greatly enhance the invasion process (Richardson *et al.*, 2000). Alien plants that produce such fruits benefit from newly established mutualisms involving a wide range of animals (Panetta and Sparkes, 2001). Because birds and mammals can be highly mobile, the potential exists for some seeds to be transported for greater distances than is generally possible via physical dispersal vectors (Panetta and Sparkes, 2001). For invasive plants that are animal-dispersed, the pattern of reinvasion is likely to be determined by the relative locations of seed sources and seed 'sinks' (i.e. the foci for seed deposition) (Panetta and Sparkes, 2001).

An understanding of the mechanisms underlying seed dispersal is a prerequisite to the formulation of effective strategies for addressing alien invasions, as the management of invasive species is critically dependent upon their rates and patterns of spread (Panetta and Sparkes, 2001). The importance of patterns of seed dispersion is determined by the extent to which the abundance and distribution of recruits depends upon the pattern of seed availability (seed limitation), as opposed to the pattern of establishment success (establishment limitation) (Nathan and Muller-Landau, 2000). This suggests two broad approaches for the prevention or slowing of alien invasions: (a) seed immigration to uninfested sites could be regulated, either by eliminating sources of seeds or by direct intervention with the dispersal process (Brown and Carter, 1998); or (b) levels of alien recruitment could be reduced by creating conditions under which germination or seedling establishment were prevented (Panetta and Sparkes, 2001).

Successful alien plant species in the different southern African biomes are characterised by different modes of dispersal. Dispersal by animals is of importance in the forest, karoo, desert and savanna biomes (Kruger *et al*., 1986). In grasslands and the fynbos, wind is an important dispersal agent, though sometimes dispersal by animals (mainly birds) occurs (Richardson, 1985). The majority of seeds that are dispersed by wind fall close to the parent plant. However, the few that are carried in turbulent air are crucial in the colonisation of new habitats/regions (Harper, 1977). In riparian ecosystems, seeds are dispersed by water as soil seed banks are poorly developed in riparian soils (Kalliola *et al.*, 1991) and wind dispersal occurs over relatively limited distances. Water dispersal therefore plays an important role in structuring plant communities along rivers through long-distance and directed dispersal (Merritt and Wohl, 2002). Water may facilitate dispersal to a greater degree than might normally be expected (Kruger *et al*., 1986). Even seeds that are typically not adapted to dispersal by water are dispersed by water movement.

1.13 Soil characteristics

Soil characteristics dictate the type, structure and health of vegetation that grows in it, and vary in space and over time as does vegetation type and structure (Thwaites, 2000). Invasive species alter soil processes and may create changes that have the potential to radiate through the ecosystem. Highly disturbed sites are often highly acidic and may be low in macronutrients, such as nitrogen (N), phosphorus (P) and potassium (K), as well as micronutrients (Holl and Cairns, 2002). The removal of vegetation has an affect on nitrogen mineralization processes and thus affects the concentration of nutrients in the soil. Other changes resulting from alien plant species include a change in soil biota (i.e. bacteria and fungi) (Belnap and Phillips, 2001). In a study by Kourtev *et al.* (2003), it was clearly shown that alien plant species rapidly altered soil microbial communities. Changes in microbial structure and function were accompanied by changes in ecosystem-level soil characteristics (N concentrations and pH) and processes (nitrogen mineralisation) (Kourtev *et al.*, 2003).

The length of the nutrient gradient, the correlation with other nutrients present and the influence of pH on nutrient availability may all influence the shape of the response of species richness to a nutrient (Pausas and Austin, 2001). Many studies have found relationships between changes in species richness and a gradient of nutrient availability.

1.14 Aims, objectives and hypotheses

1.14.1 Aims

As stated previously, 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 response to the clearing of alien plants by WfW. 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. More specifically, to:

1) Assess how the WfW alien plant clearing (and any subsequent further alien plant invasions post-clearing) affected the plant species composition, diversity

and vegetation structure along riparian corridors on the Sabie River in both the grassland and savanna biomes, in 2005 (Chapter 3).
2) Assess how the WfW alien plant clearing (and any subsequent further alien plant invasions post-clearing) affected the plant species composition, diversity and vegetation structure of the Sabie River over time, i.e. from 1996 to 2005 (Chapter 4).
3) Investigate the relationship between the Sabie River riparian environment (i.e. ground cover, and soil chemical and physical properties) and the invasion of alien plant species and their removal (Chapter 5).

These were accomplished using two fundamental approaches:
a) By resurveying existing permanent plots that were established and first sampled in 1996/1997 (Garner, 2005) to assess riparian vegetation recovery.
b) By observing the effects of alien plant species invasion and clearing on plant species diversity and composition, vegetation structure and habitat characteristics.

1.14.2 Objectives

The objectives of Chapter 3 were to:
1) Determine the alien and indigenous plant species composition of the Sabie River riparian vegetation in both the grassland and savanna biomes in 2005, and compare them.
2) Determine the alien and indigenous plant species diversity (alpha and beta), species evenness and species complementarity of the Sabie River riparian vegetation in both the grassland and savanna biomes in 2005, and compare them.
3) Determine the vegetation structure of the Sabie River riparian vegetation in both the grassland and savanna biomes in 2005, and compare them.
4) Use the information from objectives 1-3 to assess the effectiveness of the WfW clearing. Note: "effectiveness" can be assessed in various ways, such as determining whether there is an increase in indigenous species richness and/or a decrease in alien species richness. In this study it also includes determining whether there is a reduction in the invasion intensity (defined as the percentage aerial cover of woody alien plants) after clearing.

The objectives of Chapter 4 were to:
1) Compare the alien and indigenous plant species composition of the Sabie River riparian vegetation between 1996 and 2005.
2) Compare the alien and indigenous plant species diversity (alpha and beta) of the Sabie River riparian vegetation between 1996 and 2005.
3) Compare the vegetation structure of the Sabie River riparian vegetation between 1996 and 2005.
4) Use the information from objectives 1-3 to assess the effectiveness of the WfW clearing over time, i.e. from 1996 to 2005.

The objectives of Chapter 5 were to:
1) Measure and compare the cover of exposed soil, rock, litter, herbaceous vegetation (except graminoids) and grass between the grassland and savanna biomes in 2005.

2) Compare the cover of exposed soil, rock, litter, herbaceous vegetation and grass between 1996 and 2005.
3) Measure and compare various soil chemical and physical properties of the grassland and savanna biomes in 2005.
4) Compare various soil chemical and physical properties between 1996 and 2005.
5) Use the information from objectives 1-4 to assess the effectiveness of the WfW clearing over time, i.e. from 1996 to 2005.

1.14.3 Hypotheses

It is important to note that the invasion intensity (i.e. percentage aerial cover of woody alien plants) was used as a measure of the degree of alien plant invasions.

1) Higher plant species richness and/or diversity should enhance community resistance to alien plant invasions, in both the grassland and savanna biomes (Chapter 3), and in both 1996 and 2005 (Chapter 4).
2) 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, and in both 1996 and 2005 (Chapter 5).

1.15 Dissertation structure

Chapter 1 gives a general introduction to the project, along with the aims, objectives and hypotheses, and a literature review. Chapter 2 gives a description of the study sites, which includes the geographical location, climate, geology, vegetation, fauna, invasive alien plants, and ecological and economic importance of the Sabie River catchment. Chapter 2 also gives a description of the overall experimental design. Chapter 3 assesses the impact of the WfW alien plant clearing on the plant species composition, diversity and vegetation structure of riparian ecosystems on the Sabie River in 2005. This is done by determining and comparing the plant species richness, alpha and beta diversities, species evenness and species complementarity between the grassland and savanna biomes in 2005, as well as conducting a multivariate statistical analysis (detrended correspondence analysis (DCA)) of the indigenous and alien plant species composition between the grassland and savanna plots (in 2005). Chapter 4 assesses the response of the plant species composition, diversity and vegetation structure along the Sabie River to the WfW clearing over time, by comparing the data from the 2005 study to the data of the 1996/1997 study (Garner, 2005). Chapter 5 assesses the effects of alien plant clearing by WfW on the Sabie riverine environment by measuring various environmental variables, such as the ground cover (percentages of exposed soil, rock, litter, herbaceous vegetation and grass), as well as various soil chemical and physical properties, that are likely to change as a result of the clearing from 1996 to 2005. Multivariate statistical analyses were also conducted, namely (1) a principal component analysis of the environmental variables between the grassland and savanna plots (in 2005), (2) a correspondence analysis (CA) of the species by plot data, and (3) a canonical correspondence analysis (CCA) of the environmental variables and the indigenous and alien plant species composition between the grassland and savanna plots (in 2005). The response of the environmental variables to the clearing in the

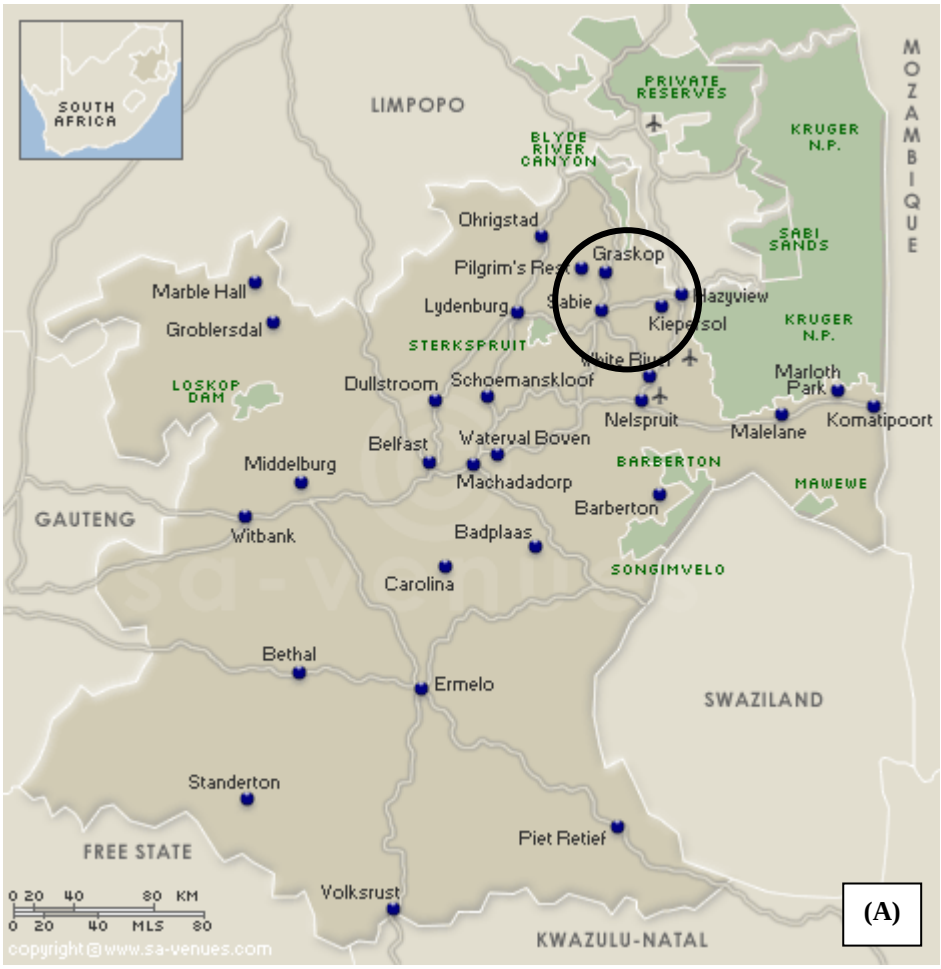
grassland and savanna biomes (in 2005), as well as over time (from 1996 to 2005), is determined. Chapter 6 gives a summary of the results and draws the conclusions of the study, as well as makes various recommendations to WfW. Finally, future possible areas of research are suggested. Chapter 7 lists the references used and chapter 8 contains the appendices.

CHAPTER 2:

STUDY SITE LOCATION, DESCRIPTION AND EXPERIMENTAL DESIGN

2.1 Geographical location

This study took place in the Sabie River catchment, situated in the lowveld region of the Mpumalanga province, South Africa (Figure 2.1(A)). Study plots were located near the Sabie (grassland biome), Graskop (grassland biome) and Hazeyview (savanna biome) regions, with grassland plots situated at higher altitudes than savanna plots (Figures 2.1(B) and 2.2; study plot locations, altitudes and co-ordinates are given in Appendix 1). The Sabie River has its source on the Drakensberg escarpment at an altitude of 2200 m, and it runs through Sabie to Graskop and then to Hazeyview, and enters the Kruger National Park (KNP) 104 km downstream (450 m a.s.l.) (Van Niekerk and Heritage, 1993). It then flows a further 110 km before exiting the KNP (110 m a.s.l.) and confluencing with the Inkomati River in Mozambique (Van Coller *et al*., 1997). The catchment has an area of approximately 7096 km^2 (Van Coller *et al*., 1997). The South Eastern boundary of the Sabie River catchment is formed by the Sabie Road at the Bergvliet plantation (near Hazeyview). Long Tom Pass at the top of the catchment forms the South Western boundary, and the North Eastern boundary is formed by the top corner of the Bergvliet plantation, immediately below the Mac Mac River. From here the northern boundary runs west in a straight line to the Drakensberg Escarpment.



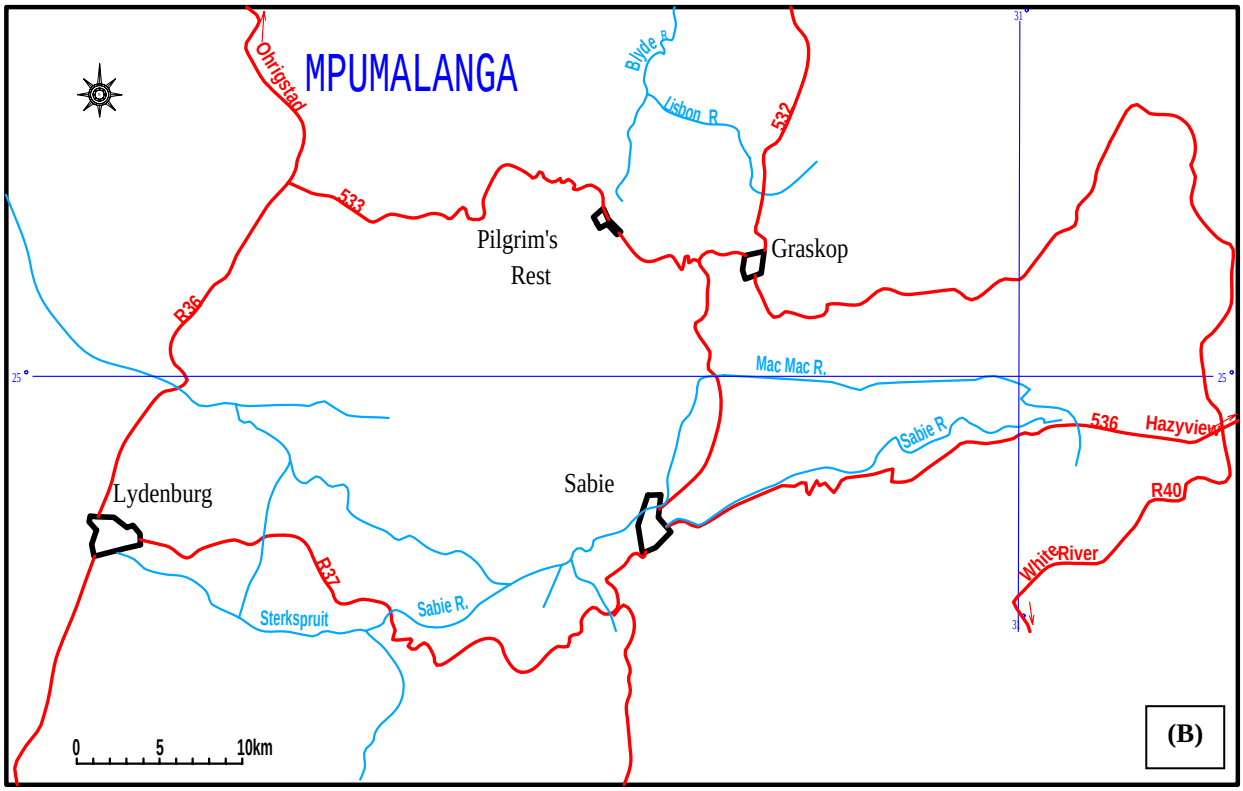


Figure 2.1. (A) Map of the Mpumalanga province in South Africa, with the study areas highlighted. Study areas were located near the Sabie (grassland), Graskop (grassland) and Hazeyview (savanna) regions. (B) Map of the study areas in the Mpumalanga province (Samancor Chrome, 2006).

(A)

(B)

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 *Solanum mauritianum* (Bugweed) (one of the dominant alien species).

2.2 Climate

The Sabie River is situated in a semi-arid to sub-tropical climate which experiences hot, rainy summers and warm, dry winters. The flow of the river is perennial and flooding is closely associated with the highly seasonal rainfall. Climate is a major driving force influencing magnitudes and recurrence frequencies of fluvial processes (Patton and Schumm, 1981). Floods are the primary source of disturbance in river ecosystems and are considered the driving force behind riparian vegetation persistence and survival (Junk *et al*., 1989). Many of the taxa occurring in riparian communities appear well adapted to flooding (Busch and Smith, 1995).

During the past 60 years (from the 1940's to the early 2000's), there have been four flood events in the Sabie River that exceeded mean flow by more than two standard deviations (Heritage *et al.*, 2000). There were also seven droughts during this period (Rogers and O'Keeffe, 2003). A severe drought in 1991/1992 reduced the flow in the Sabie River on the Mozambique border to previously unrecorded low discharges, measured in the KNP, of only 0.33 m^3s^{-1} (Weeks *et al*., 1996). The prolonged low flows and decreased frequencies of high flows resulted in a significant accumulation of sediment and development of sedimentary features, which were then colonized by vegetation (Heritage and Van Niekerk, 1995). A high magnitude flood with a peak discharge of 2200 m^3s^{-1} (Birkhead *et al*., 2005) and an estimated return interval of 1 in 50 years then followed in 1996 (Rountree *et al*., 2000). This flood was expected to have removed vegetation from the macro-channel by flood scour and so halt or reverse the trend of increasing vegetation establishment which had been observed since the 1940's (Carter and Rogers, 1995).

However, very heavy rainfall in February 2000 resulted in a much more severe flood over Mpumalanga and Limpopo provinces, as well as Zimbabwe and Mozambique. These 2000 floods were caused by a tropical depression sustained between the 4th and 14th of February 2000, but subsequent to this, cyclone Eline hit Mozambique which also brought rain to the northern parts of South Africa (Heritage *et al*., 2001). The rainfall of the Sabie region was 428% above the long-term average for February in 2000 (Heritage *et al*., 2001). The subsequent flood was termed a Large Infrequent Disturbance (LID) event due to the infrequent nature of this type of event (Heritage *et al*., 2001). Alexander (2000), using the South Africa Weather Bureau's monthly distinct rainfall database, showed that the February 2000 rainfall slightly exceeded the 100-year return period event. The 2000 flood resulted in a major change in the vegetation distribution along the Sabie River in the KNP. Using line transects across the river, Leroy (2003) showed that the flood reduced the number of woody species occurrences and woody plant density per transect. Leroy (2003) also found an increase in the herbaceous and grass species richness (Leroy, 2003). The number of alien species along the river increased quite considerably, which was expected as the flood brought in large quantities of propagules from the surrounding catchment (Leroy, 2003). Along the Sabie River in the upper catchments outside of the KNP, Garner (2005) found that the soil seed banks in the community were limited in their species richness and were dominated by propagules of four species – two aliens (*Eucalyptus grandis* and *Solanum mauritianum*), one indigenous shrub (*Clutia monticola*) and one indigenous herb (*Ipomoea* sp.). Therefore, these species would have been expected to have arrived from the upper catchment.

2.2.1 Temperature

There were no weather stations in or near Sabie or Hazeyview, therefore all the weather data, i.e. mean maximum and minimum temperatures, total rainfall and mean humidity, was obtained from the South African weather bureau climate station in Graskop. Weather data was obtained for the years from 1994 until 2005. Note: the study period in 2005 was from February to April.

In 2005, there were no temperatures below 0ºC, and therefore no frost. The relative change in the mean maximum temperatures from the long-term means (i.e. from 1994-2005) was an increase of 10.1% in February 2005, 3.1% in March 2005 and 1.5% in April 2005 (Figure 2.3; Table 2.1). The relative change in the mean minimum temperatures from the long-term means was a 2.0% increase in February 2005, a 2.9% decrease in March 2005 and a 5.1% increase in April 2005 (Figure 2.3; Table 2.1).

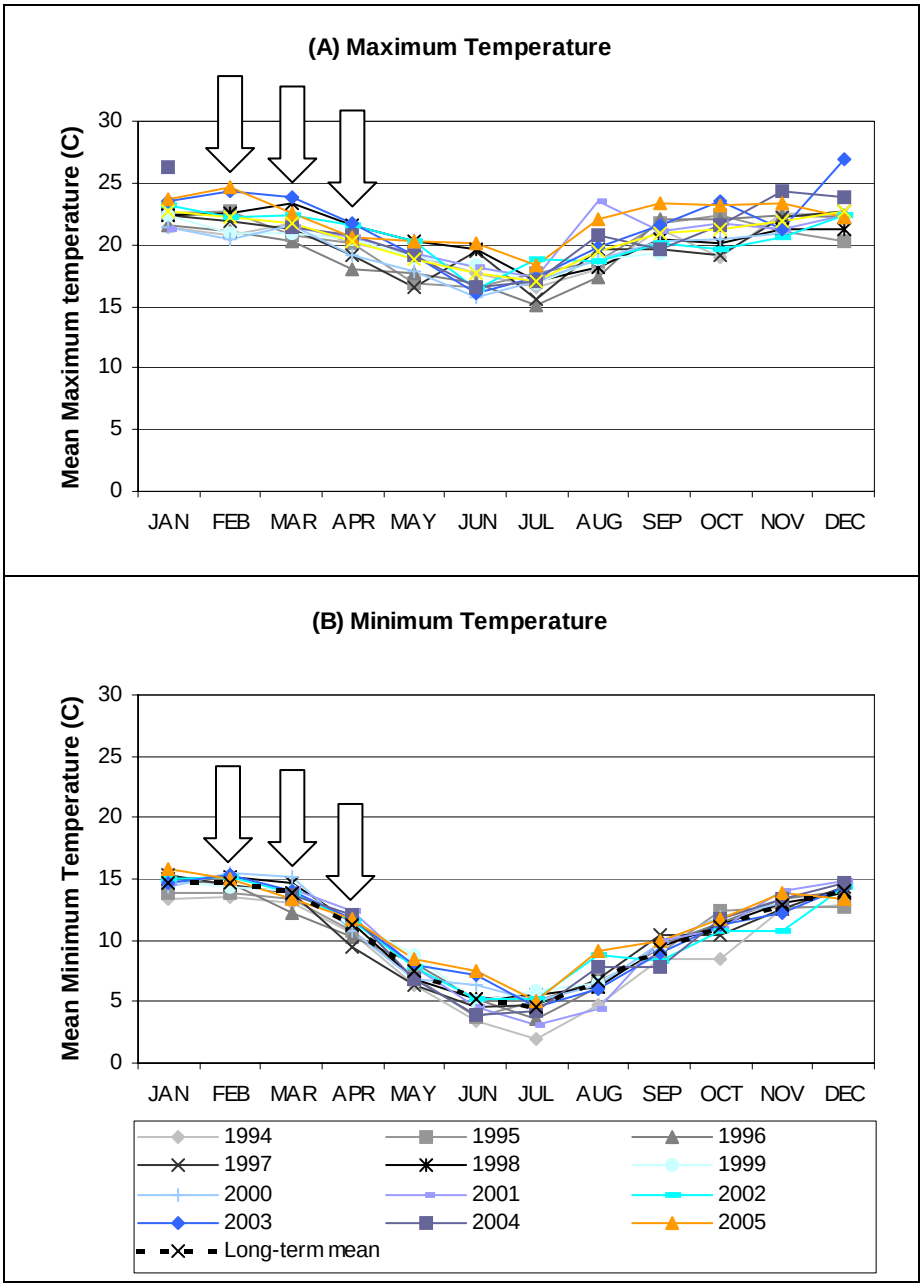


Figure 2.3. Mean monthly (A) maximum and (B) minimum temperatures (ºC) from the nearest South African weather bureau climate station in Graskop, for the last 12 years, i.e. from 1994 until 2005. Note: the long-term mean is from 1994-2005. The arrows are pointing to the months of the 2005 study period (i.e. February to April).

Table 2.1. Mean maximum and minimum temperatures (ºC), 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.

Month	Year	Mean maximum temperature (ºC)	Mean minimum temperature (ºC)	Total rainfall (mm)	Mean humidity (%)
February	1994	20.7	13.5	102.4	94
	1995	22.7	13.9	15.8	89
	1996	21.1	14.6	606.4	96
	1997	21.9	14.5	5.8	96
	1998	22.6	15.1	201.6	96
	1999	21.0	14.3	401.6	
	2000	20.5	15.5	999.8	
	2001				
	2002	22.2	15.1	16.4	
	2003	24.3	15.3	18.0	83.9
	2004	23.7	15.1	406.6	94.9
	2005	24.7	15.0	0.4	90.6
	Long-term mean (1994-2005)	22.2	14.7	252.3	92.6
March	1994	21.7	13.0	130.2	91
	1995	20.8	13.4	134.4	91
	1996	20.2	12.2	110.2	95
	1997	21.2	13.9	0.0	97
	1998	23.3	14.6	3.8	94
	1999	21.0	14.1	230.2	97
	2000	21.6	15.1	415.0	
	2001	21.4	14.2	113.6	
	2002	22.4	13.9	86.4	
	2003	23.8	14.0	26.4	85.2
	2004	21.4	13.7	148.4	95.4
	2005	22.5	13.4	33.8	94.9
	Long-term mean (1994-2005)	21.8	13.8	119.4	92.9
April	1994	20.1	10.6	30.0	88
	1995	20.1	10.7	105.8	88
	1996	18.1	10.2	86.8	94
	1997	19.2	9.5	0.0	90
	1998	21.6	11.4	84.4	93
	1999	20.4	11.6	130.4	
	2000	19.2	10.8	133.6	
	2001	20.6	12.4	178.6	
	2002	21.5	11.6	42.9	
	2003	21.8	11.7	9.4	87.2
	2004	20.8	12.0	60.8	92.6
	2005	20.6	11.8	25.0	92.4
	Long-term mean (1994-2005)	20.3	11.2	74.0	90.7

2.2.2 Rainfall

The relative change in the total rainfall from the long-term means (i.e. from 1994-2005) was a decrease of 99.8% in February 2005, 71.7% in March 2005 and 66.2% in April 2005 (Figure 2.4; Table 2.1).

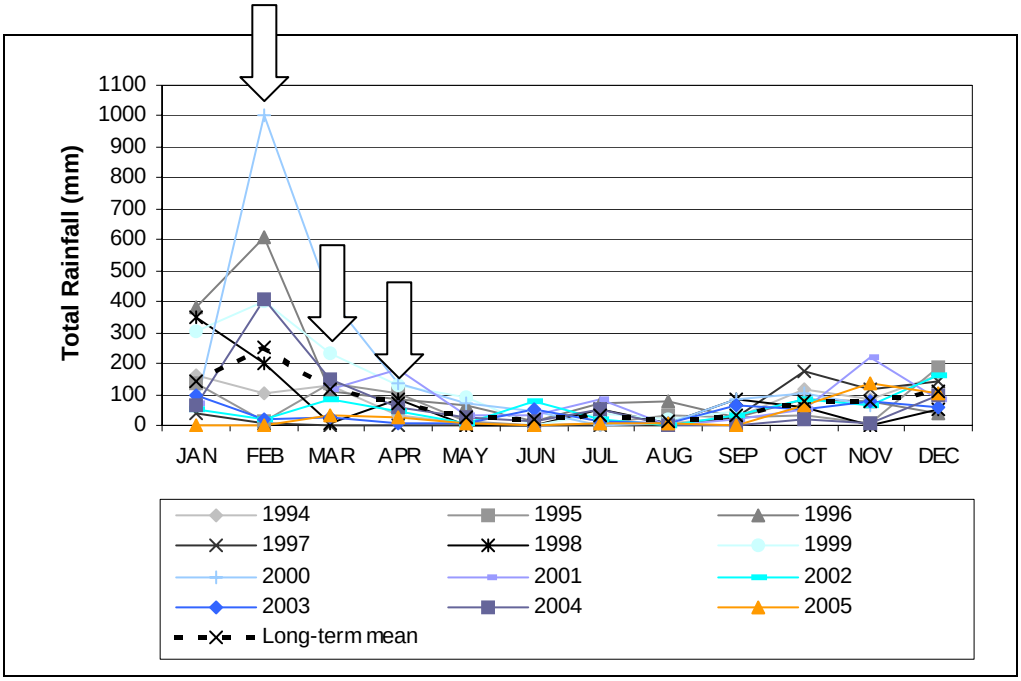


Figure 2.4. Total monthly rainfall (mm) from the nearest South African weather bureau climate station in Graskop, for the last 12 years, i.e. from 1994 until 2005. Note: the long-term mean is from 1994-2005. The arrows are pointing to the months of the 2005 study period (i.e. February to April). Note the very high rainfall in February 2000, which was when flooding occurred.

2.2.3 Humidity

The relative change in the mean humidity from the long-term means (i.e. from 1994-2005) was a 2.2% decrease in February 2005, a 2.1% increase in March 2005 and a 1.8% increase in April 2005 (Figure 2.5; Table 2.1).

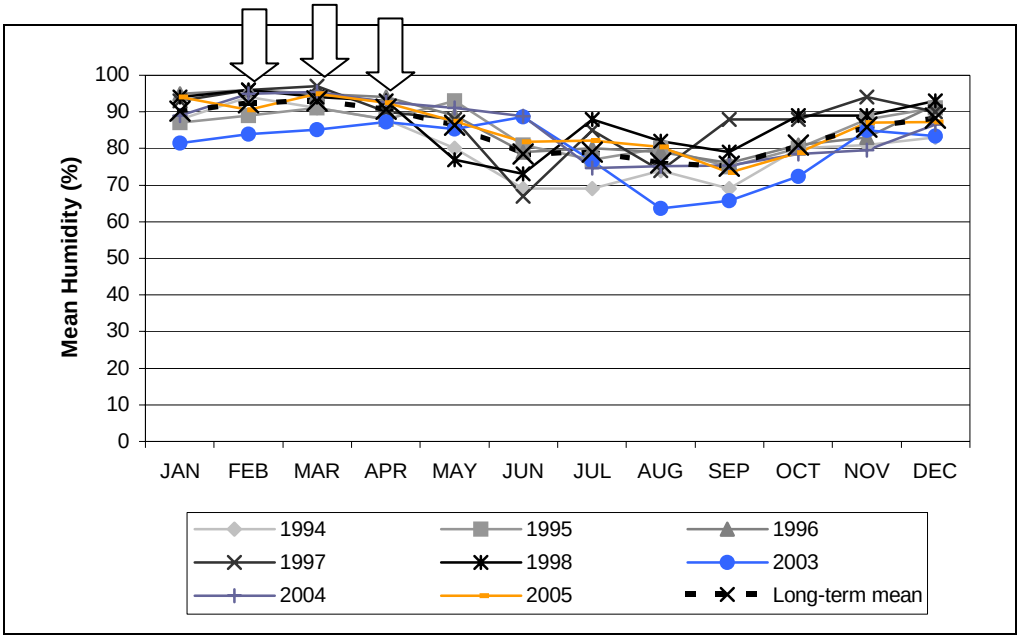


Figure 2.5. Mean monthly humidity (%) from the nearest South African weather bureau climate station in Graskop, for the last 12 years, i.e. from 1994 until 2005 (data was not available for the years 1999, 2000, 2001 and 2002). Note: the long-term mean is from 1994-2005. The arrows are pointing to the months of the 2005 study period (i.e. February to April).

2.3 Geology

The Sabie River is a bedrock-influenced system (Heritage *et al.*, 1999) and is geomorphologically complex (Van Niekerk *et al.*, 1995). Uplift in the recent geological past and subsequent incision into the bedrock during the last 10 000 years has generated a river with steep valley sides and a 'flood-plain' restricted by the width of the incised channel (Partridge and Maude, 1987). Soils in the area are derived from the Transvaal system complex/super-group that consists of the black reef series, dolomite series and the Archaean basement complex (Visser, 1989). The grassland plots (in the Sabie and Graskop regions) overlay Timeball Hill Formation Shale and Malmani Group Dolomite (Figure 2.6). The savanna plots (in the Hazeyview region) overlay Nelspruit Suite Granite (Figure 2.6).

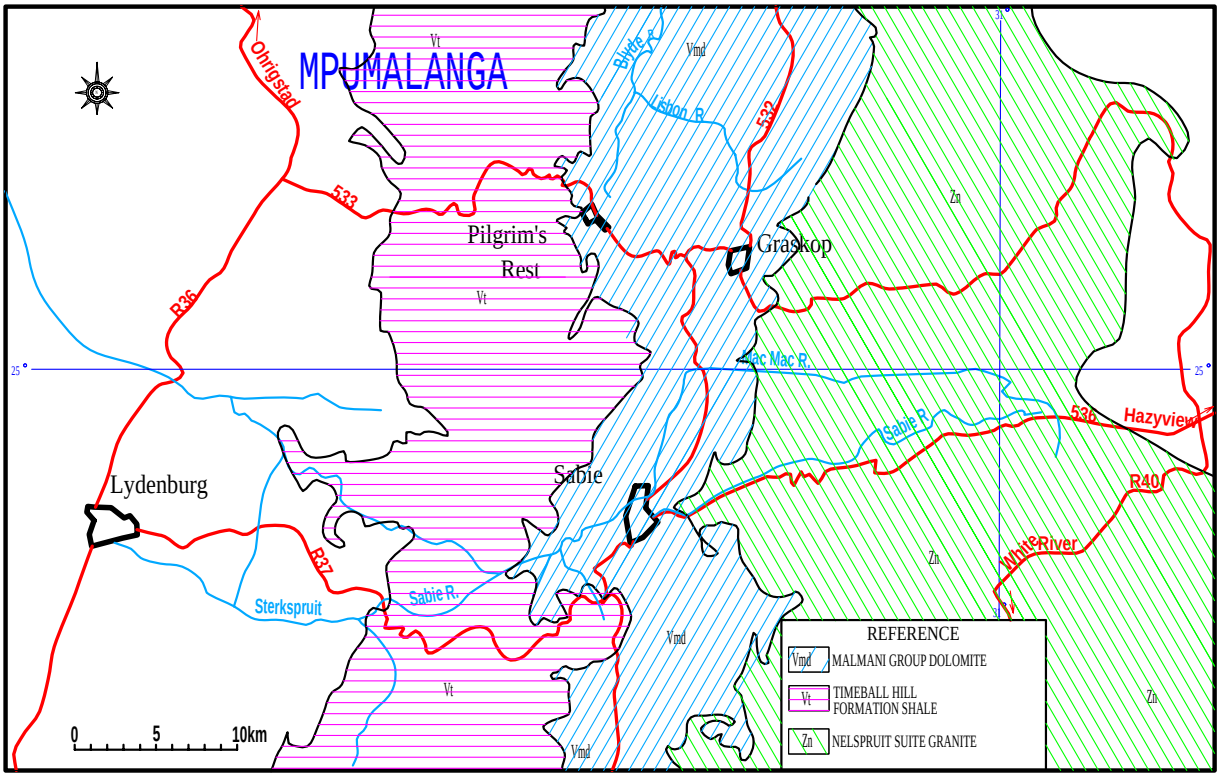


Figure 2.6. Geological map of the study areas. The study areas near the Sabie (grassland) and Graskop (grassland) regions are composed of Malmani Group Dolomite and Timeball Hill Formation Shale, and study area near the Hazeyview (savanna) region is composed of Nelspruit Suite Granite (Samancor Chrome, 2006).

2.4 Vegetation

The Sabie River catchment is part of the Wolkberg centre of biodiversity (Cowling and Hilton-Taylor, 1994), with about 163 red data book plant species (Matthews *et al.*, 1993; Nel *et al.*, 1999). The natural vegetation in the upper reaches of the Sabie River is winter-dormant, temperate grassland with extensive areas of Afromontane forest in the valleys and the sheltered slopes of the escarpment (Nel *et al.*, 1999). The vegetation of the lower areas comprises closed to open woodlands, savannas and grasslands with forests along the main rivers (Le Maitre *et al.*, 2002). Both the savanna and grassland biomes meet in the vicinity of the study areas of this project.

2.4.1 The savanna biome

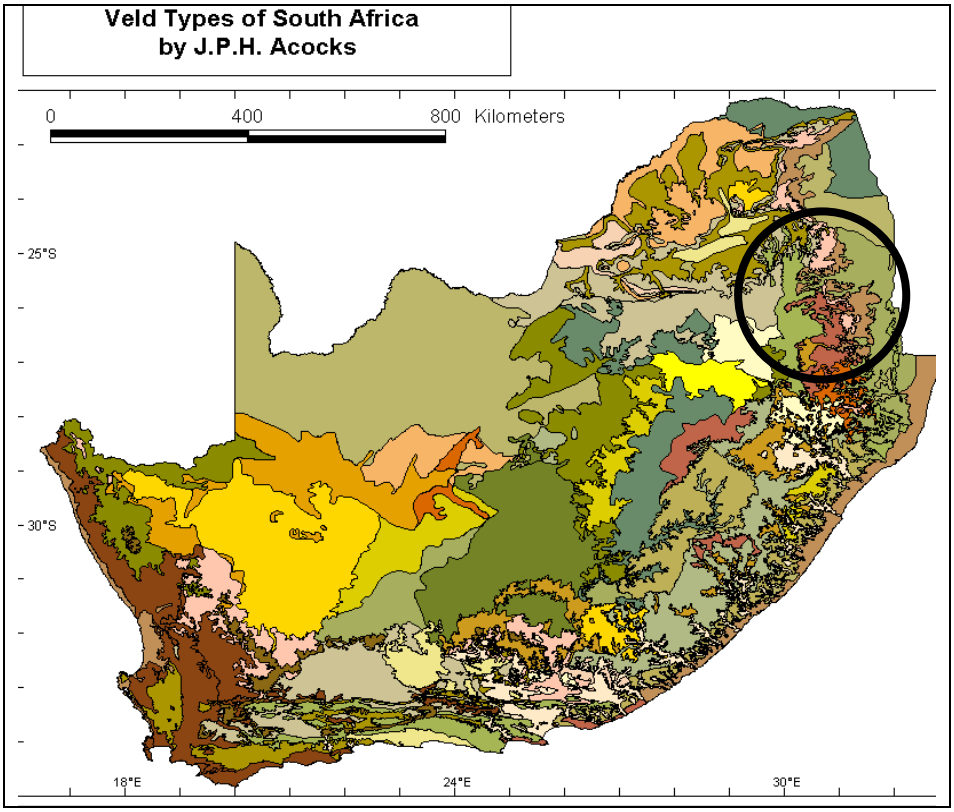
The word ‘savanna’ describes vegetation with a herbaceous, usually graminoid, layer with an upper layer of woody plants, which can vary from widely spaced to 75% canopy cover (Edwards, 1983). The savanna biome is the largest biome in South Africa, comprising approximately 46.2% of southern Africa (one third of South Africa) (Rutherford and Westfall, 1994). Savannas extend between altitudes of 2000 m down to a few hundred metres above sea level (Rutherford and Westfall 1994). The co-dominant life forms at the biome scale are hemicryptophytes and

phanerophytes. Rutherford and Westfall (1994) defines hemicryptophytes as perennial plants, generally herbaceous, with the renewal buds at or, more often, close to ground level, but seldom exceeding 0.1 m in height; and phanerophytes as perennial plants, usually woody, with the mean height of the renewal buds greater than 0.7 m above ground level, and because plant height is usually greater than the mean height of renewal buds, the mean plant height is seldom less than 1.0 m. Plant species diversity may be classed as average relative to that of the other biomes. Invasive alien plants are generally only locally important in savannas, for example various species along water courses (Rutherford and Westfall, 1994).

2.4.2 The grassland biome

This biome has an area of 343 000 km^2 (16.5% of South Africa) and is found mainly on the high central plateau of South Africa, inland areas of the seaboard of Natal and mountain areas of the south eastern Cape Province (Rutherford and Westfall, 1994). Topographically, grasslands are found on flat to rolling coastal plateaus, but also occur in mountainous areas and typically range in altitude from 300 m to 2850 m above mean sea level (Rutherford and Westfall, 1994). The vegetation is physiognomically monolithic and is characterized by a strong dominance of hemicryptophytes of the Poaceae (Rutherford and Westfall, 1994). Probably the most noteworthy species with wide distribution is *Themeda triandra*. Alien plant species have not invaded much of the area of this biome outside streambank habitats (Henderson and Musil, 1984). The main woody plant invaders are wattles (*Acacia* species).

2.4.3. Vegetation types of the study areas



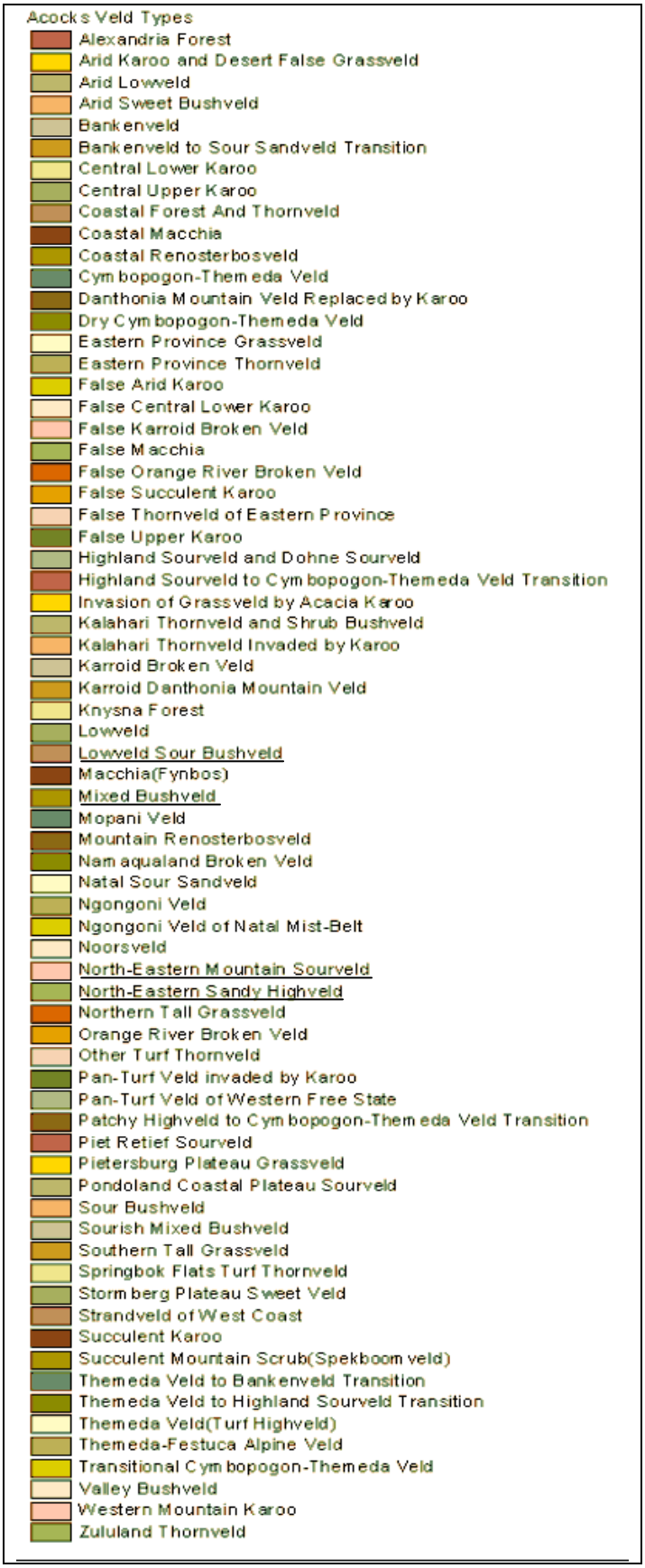


Figure 2.7. Acocks' veld types of South Africa. The study areas and the relevant veld types in the Mpumalanga province are highlighted.

Vegetation mapping and research in South Africa was based on the research and work conducted by Acocks (1988), and these maps were established as the standard by which all national vegetation changes were measured. These maps were then updated in 1996 (Low and Rebelo, 1996) (Figure 2.7). The grassland biome in Mpumalanga consists of several veld types. These include moist clay highveld grassland, moist cool highveld grassland, moist sandy highveld grassland, rocky highveld grassland, wet cold highveld grassland, and north-eastern mountain grassland (Low and Rebelo, 1996), with moist sandy highveld grassland and north-eastern mountain grassland occurring in the study areas (Figure 2.7). The veld types of the savanna biome in Mpumalanga includes clay thorn bushveld, lebombo arid mountain bushveld, mixed bushveld, mixed lowveld bushveld, mopane bushveld, mopane shrubveld, natal lowveld bushveld, sour lowveld bushveld, and sweet lowveld bushveld (Low and Rebelo, 1996), with mixed lowveld bushveld and sour lowveld bushveld occurring in the study areas (Figure 2.7).

2.5 Fauna

As stated previously, the Sabie River catchment is part of the Wolkberg centre of biodiversity (Cowling and Hilton-Taylor, 1994), with red data bird species (Allen *et al.*, 1997), reptiles, amphibians and mammals. This river system also supports a rich aquatic fauna, including endemic fishes (Russel and Rodgers, 1989; O'Keeffe *et al.*, 1996; Weeks *et al.*, 1996). Fruit eating bird species exist in abundance within this region, and are directly involved in the distribution of propagules. Examples include pigeons (*Columbidae* species), Barbetts (*Pogoniulus* species), common Bulbul (*Pycnonotus barbatus*) and Francolins (*Francolinus* species). There are also a number of indigenous herbivores that exist in the region, such as the red duiker (*Cephalophus natalensis*), common duiker (*Sylvicapra grimmia*), bush buck (*Tragelaphus scriptus*), hippopotamus (*Hippopotamus amphibius*) (lower altitude areas only), vervet monkey (*Cercopithecus aethiops*) and baboon (*Papio ursinus*) (Garner, 2005).

2.6 Invasive alien plants

On a national scale, in 2002, the total flow reduction due to invasive aliens (estimated at 69 million m^3 per year) was about half that due to plantations, but it is predicted that it could exceed that of plantations in the next 25 – 30 years (Le Maitre *et al.*, 2002). On a unit area basis the invaders were estimated to reduce the flow, in 2002, by about 2192 m^3 per year compared with plantations at 1344 m^3 per year (Le Maitre *et al.*, 2002). Eucalypts accounted for 24% of the total flow reduction, followed by pines (18%), *Solanum* (14%), *Lantana* (13%) and *Acacia* species (10%) (Le Maitre *et al.*, 2002). It was estimated that a programme to bring invasions under control through clearing would cost R650 million per year (from 2002) for the next 20 years (Le Maitre *et al.*, 2002).

More than half of the Sabie River catchment has been transformed by forestry plantations, and about 23% of the catchment has already been invaded by alien species (Le Maitre *et al.*, 2002). In both the grassland and savanna areas, the major woody plant invaders are wattles (*Acacia* spp.), and some commercially utilized species such as *Eucalyptus* spp. and *Pinus* spp. (Rutherford and Westfall, 1994). Other invaders include *Solanum mauritianum*, *Lantana camara* and *Rubus* species. In

the middle and lower reaches of the Sabie River, *Caesalpinia decapetala* is a major invader (Le Maitre *et al.*, 2002). In 1987, it was estimated that plantations in the upper reaches of the Sabie River reduced the natural flow by about 45%, and irrigation used about 14% of the natural flow, while human use and water for livestock accounted for about 1% (Nel *et al.*, 1999).

2.7 Importance of the Sabie River catchment

The Sabie River is important from both the agricultural and eco-tourism perspectives. The study area is highly utilised by the silvicultural industry, and the predominant crops are bluegums (*Eucalyptus grandis*) and pines (*Pinus patula*). Other plantations occur, but on a smaller scale. The silvicultural industry is an important part of the South African economy. Plantation forestry provides the raw materials for downstream activities such as pulpmilling, paper manufacturing, sawmilling and some furniture manufacturing (SAFIMA, 2005). Plantations also provide the inputs required for mining timber, pole manufacturing, fibreboard manufacture, charcoal and wood chip production (SAFIMA, 2005). Plantation forestry companies have, over the past two decades, contracted out the bulk of their low-skilled labour requirements, and it is estimated these independent plantation forestry contractors have a workforce of up to 35 000 and that they have a combined annual turnover of R600 million (SAFIMA, 2005). In 2005, the timber-producing industry (excluding any downstream activities) was a net generator of foreign exchange (i.e. money not previously available in the South African economy) to the value of almost R2 billion (SAFIMA, 2005). The Sabie River is also important as it is the major water source in the town of Sabie, as well as in towns and villages east of Sabie, where it eventually flows through numerous private game reserves and into the KNP and Mozambique.

2.8 Experimental design

In 1996/1997, 40 permanent modified Whittaker nested plots were first surveyed along the Sabie River and several variables were measured, such as the plant species composition, diversity and vegetation structure, as well as environmental variables (Garner, 2005). Three different experimental treatments, i.e. (A) high altitude (grassland) versus low altitude (savanna) plots (=biome), (B) high invaded versus low invaded plots (=invasion intensity), and (C) cleared versus uncleared plots (=clearing), were assessed (Table 2.2). These data were collected over a single time period, i.e. 1996/1997, across the three treatments, and were compared using various statistical analyses. Within each biome, i.e. the high altitude, grassland biome and the low altitude, savanna biome, plots of different degrees of invasion intensity were chosen subjectively in 1996/1997 (Garner, 2005). The following categories were used: (a) a low to moderate invasion (0-50% of alien vegetation aerial cover); and (b) a high invasion (50-100% of alien vegetation aerial cover). Therefore, each biome contained plots of ‘high invasion’ and ‘low invasion’. For each ‘invasion intensity’ treatment, ten modified Whittaker nested plots were completed (Figure 2.9; Table 2.2). Therefore, each ‘biome’ treatment contained 20 plots, giving a total of 40 modified Whittaker nested plots (Table 2.2). For each ‘invasion intensity’ treatment, plots were chosen that had been cleared of alien plants, as well uncleared plots. Therefore, each ‘invasion intensity’ treatment consisted of ‘cleared’ and ‘uncleared’

plots. For each 'clearing' treatment, five modified Whittaker nested plots were completed (Table 2.2).

This study, with field work done in 2005, was then conducted using the 40 modified Whittaker nested plots positioned as close as possible to the original 1996/1997 plots, as the floods of 2000 had removed all the concrete-embedded corner markers that were used to "permanently" mark the plots (Garner, 2005). The floods of 2000 also resulted in considerable changes to river morphology, with considerable erosion of the banks, and so plots could not always be in exactly the same place as before. The same three treatments were used, i.e. (A) biome, (B) invasion intensity and (C) clearing. However, because WfW had been clearing alien plants over the last 8 years, i.e. from 1996/1997 to 2005, there were no longer any uncleared plots, as all of the plots had been cleared to some degree, and therefore the 'clearing' treatment was really only an historical initial clearing prior to 1996/1997 (Garner, 2005). Furthermore, alien plants had invaded the 40 plots to a similar degree over the last eight years, and therefore most of the plots had a much more similar degree of invasion in 2005 compared with much more variation in 1996/1997. Therefore, the 'invasion intensity' category also differed, and thus the degree of invasion intensity in 2005 was only re-assessed once the sites were visited. The 2005 data were compared across the same three treatments, and, in addition, the changes over the last eight years (i.e. 1996/1997 versus 2005) were analysed. Figure 2.8 summarises the experimental design of the 1996/1997 and 2005 studies.

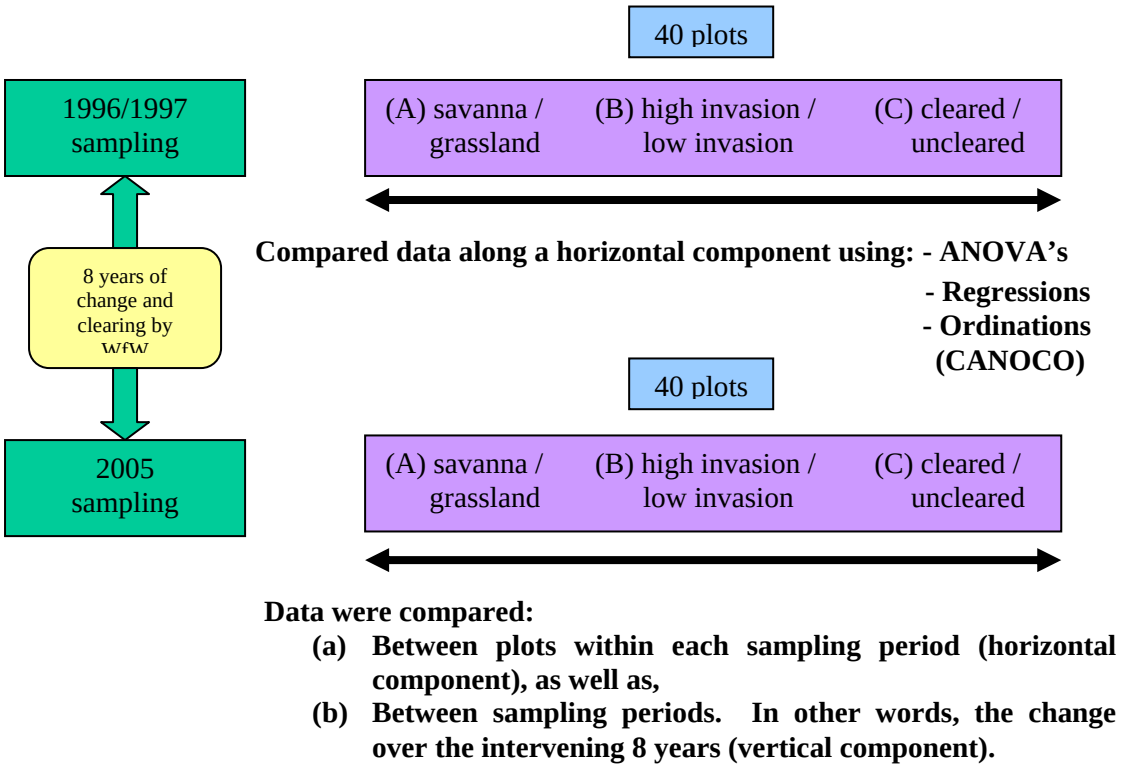


Figure 2.8. Flow diagram summarising the experimental design of the sampling during 1996/1997 (Garner, 2005) and 2005 (this study), and the comparisons made between the two data sets.

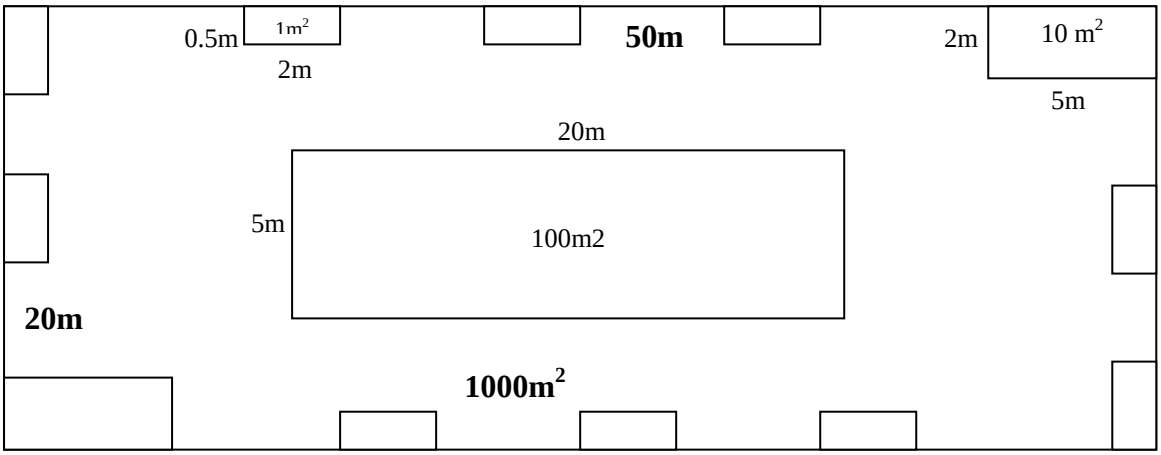


Figure 2.9. The modified Whittaker nested plot design (from Stohlgren *et al*., 1995).

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.

(A) High altitude (grassland) (20 plots)				(A) Low altitude (savanna) (20 plots)			
(B) High invasion, i.e. 50-100% aerial cover of alien vegetation (10 plots)		(B) Low invasion, i.e. 0-50% aerial cover of alien vegetation (10 plots)		(B) High invasion, i.e. 50-100% aerial cover of alien vegetation (10 plots)		(B) Low invasion, i.e. 0-50% aerial cover of alien vegetation (10 plots)	
(C) Cleared (5 plots)	(C) Uncleared (5 plots)	(C) Cleared (5 plots)	(C) Uncleared (5 plots)	(C) Cleared (5 plots)	(C) Uncleared (5 plots)	(C) Cleared (5 plots)	(C) Uncleared (5 plots)
21.1±11.8	72.2±7.5	3.3±1.1	11.0±3.8	29.1±8.0	69.1±11.2	11.0±3.7	23.0±6.6

Similar to Garner (2005), each modified Whittaker nested plot was positioned centrally within the 30 m cleared riverine zone/corridor on either side of the river and orientated with the long axis lying parallel to the river bank (there is a 30 m exclusion zone defined by WfW which means that no plantations can be closer than 30 m to the river) (Figure 2.10). Each modified Whittaker nested plot was located using a Global Positioning System (GPS) (Garmin GPS V). Even though the 2005 plots were positioned as close as possible to the original 1996/1997 plots, certain criteria for the placements (that Garner (2005) also used) of the plots had to be used. These were that (a) areas with steep slopes (>20^{o}) were avoided for practical reasons, and (b) that plots were relatively uniform in terms of substrate, i.e. areas of > 35% exposed rock cover were excluded. Therefore, this was consistent with the 1996/1997 study. It is important to note that the 2000 flood event caused major changes to the river morphology, and hence the plots of 2005 differed in terms of their morphology to those of 1996/1997.

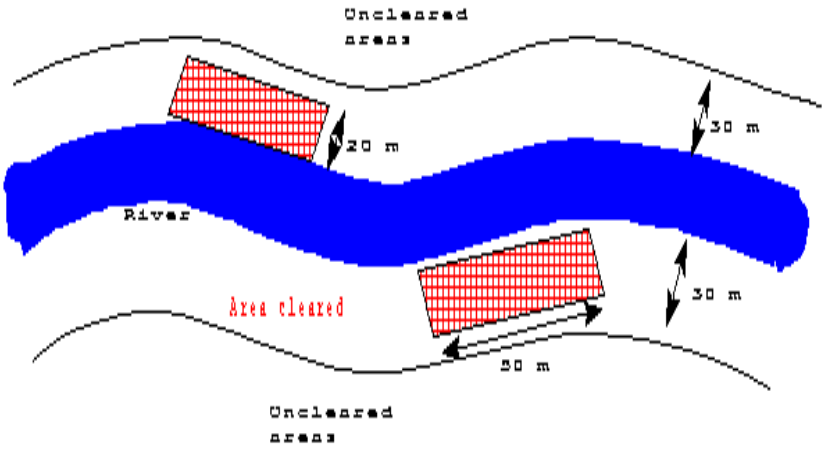


Figure 2.10. Placement of the modified Whittaker nested plots centrally within the 30 m cleared zone relative to the river (from Garner (2005)).

Within each 20 x 50 m modified Whittaker nested plot, one 5 x 20 m, two 2 x 5 m and ten 0.5 x 2 m quadrats were positioned in fixed locations as described by Stohlgren *et al.* (1995) (Figure 2.9). The 0.5 x 2 m (1 m^2) quadrats were positioned using a tape measure and marked out using a rigid steel quadrat, which was removed once the sampling was completed. The 2 x 5 m (10 m^2), 5 x 20 m (100 m^2) and 20 x 50 (1000 m^2) quadrats were all positioned using a tape measure and marked out using red barrier tape (as the boundary) between fence droppers hammered into the ground as non-permanent markers.

The field work and data collection for the 1996/1997 study, took place from October 1996 to the end of February 1997, and for the 2005 study, took place from the 14th February 2005 to the 6th April 2005. Laboratory analyses of the 2005 field samples and specimens took two and a half months, and were completed in June 2005. Details of the sampling will be discussed under the materials and methods section of the relevant chapters.

CHAPTER 3:

PLANT SPECIES COMPOSITION, DIVERSITY AND VEGETATION STRUCTURE IN RESPONSE TO ALIEN PLANT CLEARING ON THE SABIE RIVER, SOUTH AFRICA, IN 2005

3.1 Abstract

The impacts of the Working for Water (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, which traverses through both the grassland and savanna biomes, was investigated in 2005 using 40 modified Whittaker nested plots. 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).

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 m^2 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. Of the 282 species, 121 (43%) were herbaceous, 82 (29%) were shrubs, 46 (16%) were trees and 33 (12%) were grasses. The grassland sites were more species rich at the 1000 m^2 scale (48.8 ± 1.8) and diverse at the 100 m^2 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 m^2 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 m^2 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 m^2 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 ± 4.6% compared to 29.4 ± 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.

More than half of the alien species were trees and shrubs, showing that the WfW clearing programme was not achieving its primary aim of removing woody alien plants. More focus should therefore be placed on the few dominant alien species that were not being effectively removed due to their resprouting potentials. In the 1996/1997 study, it was found that resprouting was a significant issue for *Eucalyptus grandis* and *Solanum mauritianum* (two of the dominant aliens along the Sabie River). Currently, follow-up clearings are taking place about a year after the initial clearings, with further follow-up clearings taking place about eight months later. It is recommended that the frequency of the follow-up clearings should increase to about four, spread over three years. This will help to reduce the number of resprouting alien plants.

3.2 Introduction

There are many negative impacts of alien plant invasions, such as decreasing biodiversity (particularly of indigenous species), reduced water flow, as well as various negative impacts on the economy (Le Maitre *et al.*, 2004). Clearing the alien plant infestations will have many benefits, not only to the environment, but to society as well. Thus, the removal of these alien plants is of the utmost importance. However, it is very difficult to achieve complete eradication of any alien plant species. Thus, focus should be on the control of these alien plants, i.e. reducing the invasion intensity of the alien plants. Without sufficient planning, control may not be successful, thus it must be followed by restoration planting with indigenous species on cleared sites. Along with all the benefits of removing alien plants, comes a change in the species richness, structure and diversity of the plant community (Le Maitre *et al.*, 2004).

The control, i.e. reduction, of alien plants from an area usually results in an increase in the richness and diversity of the plant community (Mentis and Ellery, 1994). The reason for this increase is that the WfW clearing functions as a disturbance and resets the successional sequence of the vegetation (Mentis and Ellery, 1994). The removal of these aliens results in an increase in the availability of essential plant resources such as light, nutrients and water. The first plants to establish after a disturbance will therefore encounter a greater availability of resources, thus improving their probability of survival and establishment in the community.

After clearing, changes in the richness and diversity of herbaceous plants is the quickest, followed by an increased abundance of indigenous woody plants (Sousa, 1984). However, these herbaceous plants are often of a weedy nature or are alien

species (Venter *et al.*, 1989). Often, when the above ground parts of invasive woody plants are removed or killed, resprouting occurs soon afterwards (Garner, 2005). Thus, the regeneration of trees by resprouting is an important process that needs to be considered when dealing with the removal of woody species.

3.2.1 Biodiversity

Biodiversity has traditionally been equated with the number of species (species richness) or species density when species are quantified in terms of area (Whittaker, 1972). These values, species diversity and richness, constitute a measure of diversity. Biodiversity is simply the number and abundance of plant and animal species in an area (O'Connell and Noss, 1992). However, it not only involves species, but also their genetic composition, the ecosystems in which they live, and the ecological and evolutionary processes that sustain them (O'Connell and Noss, 1992).

Whittaker (1972) described three terms for measuring biodiversity over spatial scales: alpha (α), beta (β) and gamma (γ) diversity. Alpha diversity refers to the diversity within a particular area or ecosystem and is usually expressed by the number of species (i.e. species richness) in that ecosystem. Beta diversity is a comparison of diversity between ecosystems or along gradients and is usually measured as the amount of species change between the ecosystems (or species turnover). Gamma diversity is a measure of the overall diversity within a large region, i.e. geographic-scale species diversity. In this study, alpha and beta diversity were focused upon. Measurement of beta diversity is important in at least three ways: (i) it indicates the degree to which habitats have been partitioned by species; (ii) values of beta diversity can be used to compare the habitat diversity of different study systems; (iii) beta diversity and alpha diversity together measure the overall diversity or biotic heterogeneity of an area (Wilson and Shmida, 1984).

Species diversity measures take into account two factors: species richness and evenness. Species richness is a measure of the number of species per sample, but on its own takes no account of the number of individuals of each species present (Magurran, 2004). It gives as much weight to those species which have very few individuals as those which have many individuals. Evenness is a measure of the relative abundance of the different species making up the richness of an area (Magurran, 2004). As the species richness and evenness increase, so the diversity increases. Diversity indices provide important information about the rarity and commonness of species in a community (Magurran, 2004). The ability to quantify diversity in this way is an important tool to understand community structure. The ease of measurement of biodiversity has led to the development of a number of indices of species diversity, such as (a) Simpson's index of diversity, (b) Simpson's measure of evenness, (c) Sorenson's coefficient of community, and (d) the Marczewski-Steinhaus (MS) distance (species complementarity).

Simpson's index of diversity is used as a measure of alpha diversity. Simpson's index of diversity uses species abundance data and gives more weight to the more abundant species in a sample, while being less sensitive to species richness, than other indices (Magurran, 2004). This index represents the probability that individuals randomly selected from a sample will belong to different species. The value of this index ranges between 0 and 1, and the greater the value, the greater the

sample diversity. According to Magurran (2004) this index is one of the most meaningful and robust diversity measures available. Although Simpson's index of diversity emphasizes the dominance, as opposed to the richness, component of diversity, it is not strictly speaking a pure evenness measure. Therefore, Simpson's measure of evenness is used and also ranges from 0 to 1 and is not sensitive to species richness, compared to other indices (Magurran, 2004). A low evenness means a high dominance in the presence of a few species. When all species are equally abundant in a sample, the evenness index is at a maximum of 1, and decreases towards zero as the relative abundances of the species diverge away from evenness. Sorenson's coefficient of community is a measure of the beta diversity of a community. It uses abundance data (quantitative index) as well as presence/absence data (qualitative index). In this study, the qualitative index was used, and as such focused on the species richness element of diversity. Sorenson's measure is regarded as one of the most effective presence/absence similarity measures (Magurran, 2004). A larger value means that the areas are more similar in their diversity. The Marczewski-Steinhaus (MS) distance is a measure of species complementarity. The term complementarity describes the difference between areas in terms of the species they support, and can therefore be used in interpreting the uniqueness of a given area or habitat (Magurran, 2004). The more complementary two areas are, the lower their beta diversity. The MS distance is the complement of the Jaccard similarity index.

There are various ways in which biodiversity can be measured in the field, but the most common method for plant diversity is by the modified Whittaker nested plot technique.

3.2.2 The modified Whittaker nested plot technique

The use of sampling areas employing plots that increase in size from a small quadrat, then enlarging the area to ten times the size, then to one hundred and one thousand times the size, etc. has been performed numerously in the past (Stohlgren *et al*., 1995). These increases in quadrat size normally follow a $\log_{10}$ distribution pattern with the smallest plot being 1 m^2 (log 1 = 0) and increasing at one unit intervals (i.e. log 10 = 1; log 100 = 2; log 1000 = 3). These are then plotted to give a species area curve and hence the species richness of the study areas. This method forms the basis of the Whittaker nested plot design. The Whittaker nested plot also consists of quadrats of unequal shapes from a 1 x 1 m square to a 2 x 5 m rectangle to a 10 x 10 m square, and then back to a 20 x 50 m rectangular plot (Stohlgren *et al*., 1995).

A number of modifications are possible to the nested plot technique, and have been applied in the past (Westfall *et al.*, 1983). Apart from the standard nested plot used in many studies (with plot sizes of 1, 5, 10, 100, and 1000 m^2), other sizes of plots have been used, and the shapes of the plots and quadrats inside the large plot have been modified (Stohlgren *et al*., 1995). The reason for these modifications is that the original technique had a number of flaws (Stohlgren *et al*., 1995). Besides these, the advantages of the method meant that it provided (1) a standardized approach to quantifying species richness in different plant communities, and (2) it supplied indices into the effects of quadrat size when determining species-area relationships (Stohlgren *et al*., 1995).

Firstly, if the habitat is not strictly homogenous, species richness is influenced by plot shape. Circular or square plots (with reduced perimeter to surface areas ratio) will have fewer species, in general, than a long thin rectangle covering a more heterogeneous area. Secondly, plot size and shape interactions may influence species richness. The sampling plot design was modified in order to overcome these flaws and designed to minimise the size and perimeter effects of the plots and subplots with all subplots being of the same shape (Stohlgren *et al*., 1995). There was also a problem of sample overlap within the original sampling design, which was avoided by Stohlgren *et al*. (1995) who had quadrats within the sample plot in fixed positions (Chapter 2, Figure 2.9).

3.2.3 Aim, objectives and hypothesis

In the 10 year period from 1995 to 2005, WfW has been clearing invasive alien plants along the Sabie River, which included the study areas. The upper catchment of the Sabie River traverses through the grassland biome, whereas the lower catchment occurs in the savanna biome. The aim of this chapter was therefore to assess how the WfW alien plant clearing (and any subsequent further alien plant invasions post-clearing) affected the plant species composition, diversity and vegetation structure along riparian corridors on the Sabie River in both the grassland and savanna biomes, in 2005.

The objectives of this chapter were to:

1) Determine the alien and indigenous plant species composition of the Sabie River riparian vegetation in both the grassland and savanna biomes in 2005, and compare them.
2) Determine the alien and indigenous plant species diversity (alpha and beta), species evenness and species complementarity of the Sabie River riparian vegetation in both the grassland and savanna biomes in 2005, and compare them.
3) Determine the vegetation structure of the Sabie River riparian vegetation in both the grassland and savanna biomes in 2005, and compare them.
4) Use the information from objectives 1-3 to assess the effectiveness of the WfW clearing. Note: “effectiveness” can be assessed in various ways, such as determining whether there is an increase in indigenous species richness and/or a decrease in alien species richness. In this study it also includes determining whether there is a reduction in the invasion intensity (defined as the percentage aerial cover of woody alien plants) after clearing.

It is hypothesized that higher plant species richness and/or diversity should enhance community resistance to alien plant invasions, in both the grassland and savanna biomes. It is important to note that the invasion intensity was used as a measure of the degree of alien plant invasions.

3.3 Materials and methods

3.3.1 Field sampling

The field work and data collection for this 2005 study, took place from the 14th February to the 6th April 2005. Field sampling took place along the Sabie River near

the Sabie and Graskop regions (both regions in the grassland biome) and about 30 km outside of Sabie towards the Hazeyview region (in the savanna biome). In each biome, 20 modified Whittaker plots were completed (ten in the Sabie region, ten in the Graskop region and 20 in the Hazeyview region). Plot numbers 1 – 10 occurred in the Sabie region, 11- 20 in the Graskop region and 21 – 40 in the Hazeyview region (refer to Chapter 2).

Descriptive variables

For each plot, the co-ordinates, altitude (m.a.s.l.), landscape context, slope steepness (^{o}), aspect and position relative to the river, i.e. north, south, etc., were determined. The co-ordinates and altitude were determined from GPS readings (Garmin GPS V). The slope steepness, aspect and position relative to the river were all determined using a compass with a built-in clinometer (Brunton Prismatic Compass). The landscape context was determined by observing what the surrounding land-use was – in all 40 plots it was *Eucalyptus* plantations.

Plant species composition, diversity and vegetation structure

Within the 1 m^2, 10 m^2 and 100 m^2 quadrats (refer to Chapter 2, Figure 2.9), all species were identified and number of individuals rooted in the quadrat counted. The percentage aerial cover of each species in the quadrats was estimated visually. Plant voucher specimens for each species were collected and pressed for later identification. The growth form for each species was also identified as either (1) trees, (2) shrubs, (3) grasses and sedges, and (4) other herbaceous plants. Trees were defined as multi- or single stemmed perennial woody plants with a distinct upper crown, that remained erect unassisted and were ≥ 2 m in height (Van Wyk and Van Wyk, 1997). Shrubs were defined as multi- or single stemmed perennial woody plants that arose from or near the ground and remained erect unassisted with a maximum height of < 2 m (Van Wyk and Van Wyk, 1997) (they differed from trees in that they were smaller and did not have a trunk). Herbaceous plants were defined as plants whose stems were not woody. Even though some species were both trees and shrubs, the seedlings of the trees were classified as "shrubs" if they were < 2 m in height, and as "trees" if they were ≥ 2 m in height. When counting the rhizomatous grasses, the "individuals" were counted by counting the individual clumps of grass. In the final species list, each species was classified into a unique class based on its adult growth form.

Within the "matrix" of the 1000 m^2 plot (refer to Chapter 2, Figure 2.9), any other species that had not been identified in the smaller quadrats, were noted. The overstorey aerial cover of the woody alien plants was determined by the line intercept method. At 10 m intervals along the 50 m length of the plot, markers were placed. At each marker, 20 m was measured out across the plot using a tape measure (perpendicular to the river). This 20 m line was walked with a ranging rod and the following were noted: the plant identity, the plant height class, distance of aerial cover, i.e. the length of the tape measure that was under the tree canopy, and distance under no vegetation, i.e. vegetation < 1 m in height. The plant height classes were: (a) large trees (> 5 m in height), (b) small trees (between 2 – 5 m), and (c) saplings and shrubs (between 1 and 2 m).

3.3.2 Identification of the vegetation

Using the species list in Garner (2005) for 1996/1997, as well as the revised alien plant list for the riparian areas of the Kruger National Park (Foxcroft *et al.*, 2003), a species 'photo-catalogue' was created. All of the species from both lists were either scanned from herbarium specimens taken from the University of the Witwatersrand's Moss Herbarium, or from field guides if they were not found in the herbarium. These scanned photographs were then put together to form an identification kit to assist in the identification of the plant specimens. New specimens were keyed out and identified using the Wits Herbarium and various reference works in the library. These field guides and reference works included Sheat, 1982; Macoboy, 1983; Onderstall, 1984; Pienaar, 1984; Palgrave, 1988; Van Wyk and Malan, 1988; Van Oudtshoorn, 1992, 1999; Pooley, 1993, 1998; Bromilow, 1995; Onderstall, 1996; Fabian and Germishuizen, 1997; Jacana and Twisisa, 1997; Grant and Thomas, 1998; and Schmidt *et al.*, 2002. Any specimens that could still not be identified were sent to the South African National Biodiversity Institute (SANBI) herbarium (PRE) in Pretoria for identification. All these latter specimens were identified to genus level and, in most cases, to species level. The species were also classed as either alien or indigenous, and their present status was specified (for example, a weed or invader, etc.) using the field guides and books listed above.

3.3.3 Data analyses

Plant species richness

Total plant species richness was determined at each quadrat scale, i.e. 1 m^2, 10 m^2, 100 m^2 and 1000 m^2. There are ten 1 m^2 quadrats in order to get a good estimate of the 1 m^2 richness as it is very variable within the 1000 m^2 plot, and two 10 m^2 quadrats as it is also variable but less than the 1 m^2 quadrat. Species richness was also determined in total and for each growth form, i.e. (1) trees, (2) shrubs, (3) herbs, and (4) grasses and sedges, for aliens versus indigenous species, for each biome (grassland and savanna), and for each region (Sabie, Graskop and Hazeyview). Each species was assigned to a single growth form category – the seedlings of trees were classified as "shrubs" if they were < 2 m in height and as "trees" if they were ≥ 2 m in height. However, as stated previously, each species was classified into a unique class based on its adult growth form in the final species list. The indigenous and alien species richness was determined at the 1000 m^2 quadrat scale for each biome and region. The total species richness was also then determined at the roadside (opposite side away from the river) and riverside 1 m^2 and 10 m^2 quadrat scales separately.

(a) Statistical analyses

Total plant species richness, as well as (a) tree, (b) shrub, (c) herbaceous, and (d) grass and sedge species richness, were statistically compared between the grassland and savanna biomes (at the 1 m^2, 10 m^2, 100 m^2, and 1000 m^2 quadrat scales) using t-tests (for independent-samples). They were also compared between the Sabie, Graskop and Hazeyview regions (at each quadrat scale) using one-way analysis of variances (ANOVA's) and Tukey's honest significant difference (HSD) test. The programme STATISTICA (1999 edition) was used for the statistical analyses. Data were checked for normality, and were transformed if not.

The indigenous and alien species richness for (a) tree, (b) shrub, (c) herbaceous, and (d) grass and sedge growth forms at the 1000 m^2 scale (in all 40 plots), was compared using t-tests (for dependent-samples). The indigenous species richness, as well as the alien species richness, for each growth form for plots (1000 m^2 scale) in the grassland and savanna biomes, was also compared using t-tests (for independent-samples). The indigenous species richness, as well as the alien species richness, for each growth form, for plots (1000 m^2) in the Sabie, Graskop and Hazeyview regions, was then compared using one-way ANOVA'S and Tukey's HSD tests. The total species richness of the roadside 1 m^2 (five replicates per 1000 m^2 plot) and 10 m^2 quadrats (one replicate per 1000 m^2 plot), were compared with the total species richness at the riverside 1 m^2 (five replicates per 1000 m^2 plot) and 10 m^2 (one replicate per 1000 m^2 plot) quadrats, using t-tests (for dependent-samples).

Plant species diversity

There is an array of diversity indices that expresses species diversity as a single statistic. Using the programme *EstimateS* (Version 7.5) (Colwell, 2005), various diversity measures were computed directly. In this study, (a) Simpson's index of diversity (as a measure of alpha diversity), (b) Simpson's measure of evenness (as a measure of species evenness), (c) Sorenson's coefficient of community (as a measure of beta diversity), and (d) the Marczewski-Steinhaus (MS) distance (as a measure of species complementarity), were used.

(a) Simpson's index of diversity (1-D)

Simpson's index of diversity was the index used to measure the alpha diversity of species independently for each plot. Species abundance data (as opposed to presence/absence data) were used, together with the following equation:

$$1 - D = 1 - \Sigma \{[n_i - (n_i - 1)] / [N (N - 1)]\}$$

where n_i = the number of individuals in the i^{th} species,

N = the total number of individuals.

Simpson's index of diversity was calculated for total plant species, as well as (a) tree, (b) shrub, (c) herbaceous, and (d) grass and sedge species in each of the 40 plots. These values were then meaned to give an overall measure in each biome (i.e. grassland and savanna) and in each region (i.e. Sabie, Graskop and Hazeyview). Simpson's index of diversity was calculated at the 1 m^2, 10 m^2 and 100 m^2 scales. Because this index uses species abundance data, it could not be calculated for the 1000 m^2 quadrat scale, as only species presence/absence was collected at this scale. The index at the 1 m^2, 10 m^2 and 100 m^2 scales was then compared statistically between the grassland and savanna biomes using t-tests (for independent-samples). It was also compared at the 1 m^2, 10 m^2 and 100 m^2 scales between the Sabie, Graskop and Hazeyview regions using one-way ANOVA's and Tukey's HSD tests.

(b) Simpson's measure of evenness (E 1/D)

Simpson's measure of evenness was the measure of species evenness selected, and the following equation was used:

$$E\ 1/D = (1/D) / S$$

where D = Simpson's index,

S = the number of species in the sample.

Simpson's measure of evenness was calculated for total species, as well as for (a) tree, (b) shrub, (c) herbaceous, and (d) grass and sedge species in each of the 40 plots. These values were then meaned to give an overall evenness measure in each biome and in each region. This index was calculated at the 1 m^2, 10 m^2 and 100 m^2 quadrat scales. The index at each of these quadrat scales was then compared statistically between the grassland and savanna biomes using t-tests (for independent-samples). The values for the Sabie, Graskop and Hazeyview regions were compared statistically (at each of the above-mentioned quadrat scales) using one-way ANOVA's and Tukey's HSD multiple range tests.

(c) Sorenson's coefficient of community (CC)

Sorenson's coefficient of community was used as a measure of beta diversity and uses species presence/absence data. The following equation was used:

$$CC = 2S_s / (S_j + S_k)$$

where S_s = the number of species shared by both samples,
S_j = the number of species present in sample 1,
S_k = the number of species present in sample 2.

Sorenson's coefficient of community was calculated at the 1 m^2, 10 m^2, 100 m^2 and 1000 m^2 quadrat scales. This index was calculated for all pair-wise comparisons of all pooled plots for the grassland and savanna biomes (i.e. 20 plots pooled for each biome), and the Sabie, Graskop and Hazeyview regions (i.e. 10 plots pooled for both Sabie and Graskop, and 20 plots pooled for Hazeyview).

(d) The Marczewski-Steinhaus (MS) distance

The MS distance was used as a measure of species complementarity. It uses species presence/absence data and the following equation:

$$C_{MS} = 1 - [a / (a - b + c)]$$

where a = the total number of species present in both quadrats or samples,
b = the number of species present only in quadrat 1,
c = the number of species present only in quadrat 2.

The MS distance was calculated at the 1 m^2, 10 m^2, 100 m^2 and 1000 m^2 quadrat scales. This index was calculated for all pair-wise comparisons of all pooled plots for the grassland and savanna biomes (i.e. 20 plots pooled for each biome), and the Sabie, Graskop and Hazeyview regions (i.e. 10 plots pooled for both Sabie and Graskop, and 20 plots pooled for Hazeyview).

Overstorey aerial cover

The percentage aerial cover of woody alien plants was calculated for each height class, i.e. (a) large trees (> 5 m in height), (b) small trees (between 2 – 5 m), and (c) saplings and shrubs (between 1 and 2 m), and in total. The aerial cover for each plot was then meaned for plots occurring in the grassland and savanna biomes, and in the Sabie, Graskop and Hazeyview regions. The percentage aerial cover for plots in the grassland and savanna, were then statistically compared using t-tests (for

independent-samples). This was done for each of the height classes, and in total. The percentage aerial cover (for each height class and in total) for plots in the Sabie, Graskop and Hazeyview regions, were statistically compared using one-way ANOVA's and Tukey's HSD tests.

The total percentage aerial cover of woody alien plants, i.e. large trees (> 5m), small trees (between 2 – 5 m), and saplings and shrubs (< 2 m), was used as a measure of the invasion intensity. Linear regression analyses were then performed whereby the relationships between the invasion intensity (independent variable) and various species richness and species diversity measures (dependent variables) were determined. The percentage aerial cover of large alien trees, small alien trees and alien shrubs, was then regressed separately against various species richness and diversity measures.

Multivariate statistical analysis

Variation in biotic communities can be summarized using a wide range of statistical methods. If the continuity of change in community composition is stressed, then ordination methods are the best to use. The goal of ordination is to find axes of the greatest variability in the community composition (the ordination axes) for a set of samples and to visualize (using an ordination diagram) the similarity structure for the samples and species (Leps and Smilauer, 2003). There are two types of ordination methods: indirect gradient analysis (unconstrained) and direct gradient analysis (constrained).

(a) Indirect gradient analysis (unconstrained)

The indirect gradient analysis is used when there is a single response variable and no predictors available. The most prominent types of this analysis are the principal component analysis (PCA), correspondence analysis (CA), and detrended correspondence analysis (DCA) (Leps and Smilauer, 2003). In this unconstrained ordination, any variable that best explains the species composition (which is taken as the ordination axis) is searched for. The unconstrained ordination axes correspond to the directions of the greatest variability within the data set.

(b) Direct gradient analysis (constrained)

If there are predictors for a set of response variables, the relations between multiple response variables (typically species) and one or several predictors, can be summarized using direct gradient analysis. The most prominent types of this analysis are the redundancy analysis (RDA) and canonical correspondence analysis (CCA) (Leps and Smilauer, 2003). The aim of constrained ordination is to find the variability in species composition that can be explained by the measured environmental variables. The ordination axes are weighted sums of environmental variables, and correspond to the directions of the greatest data set variability that can be explained by the environmental variables (Leps and Smilauer, 2003).

(c) Linear and unimodal methods

Ordination methods can also be distinguished according to whether they are linear or unimodal. Linear methods are based on a model of linear species response to the underlying environmental gradient, and include PCA and RDA, whereas unimodal methods are weighted-averaging ordination methods corresponding to a model of unimodal species response, and include CA, DCA and CCA (Leps and Smilauer, 2003).

Multivariate analyses were undertaken on the species data using the multivariate package CANOCO (Leps and Smilauer, 2003). CANOCO is a FORTRAN programme for *cano*nical *c*ommunity *o*rdination by [partial] [detrended] [canonical] correspondence analysis, principal components analysis and redundancy analysis (Leps and Smilauer, 2003). An analysis was done to determine if there were any relationships between the species and the plots. The indirect gradient method, detrended correspondence analysis (DCA), was used because only a single response variable, i.e. the species, was used with no predictors. Species abundance data from the 100 m^2 quadrat from each of the 40 plots were used in this analysis.

3.4 Results

3.4.1 Plant species richness

Total plant species richness

(a) As a function of quadrat size

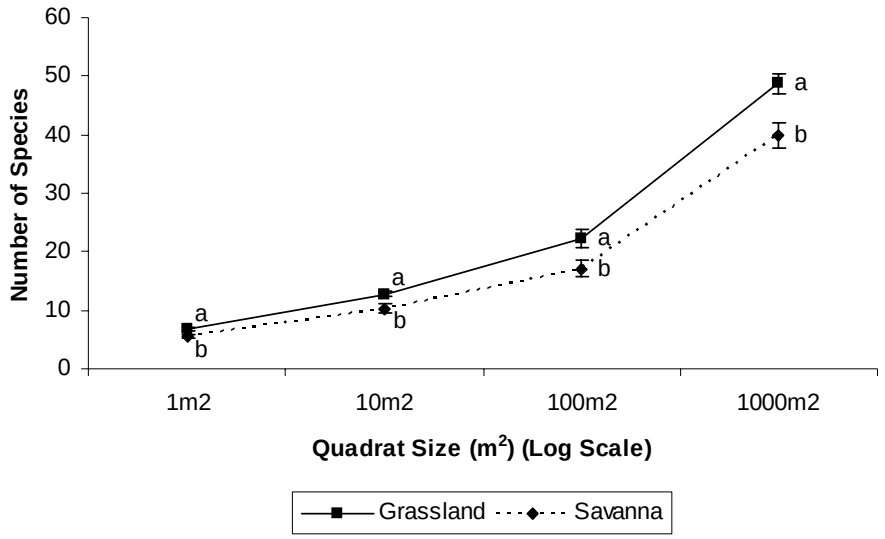


Figure 3.1. Plant species richness (mean ± S.E.) as a function of quadrat size (log scale), at the 1 m^2 (10 quadrats per plot for 20 plots in each biome), 10 m^2 (2 quadrats per plot for 20 plots in each biome), 100 m^2 (1 quadrat per plot for 20 plots in each biome), and 1000 m^2 (the experimental 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.

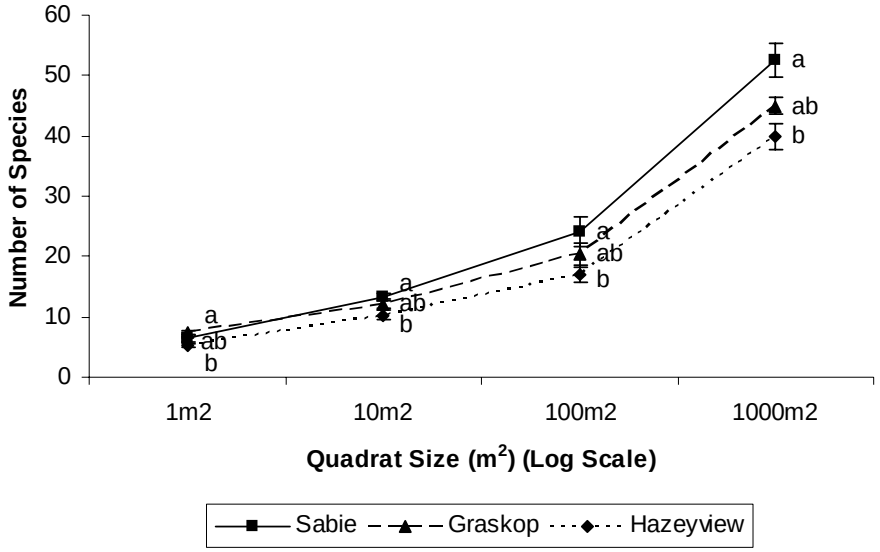


Figure 3.2. Plant species richness (mean ± S.E.) as a function of quadrat size (log scale), at the 1 m^2 (10 quadrats per plot for 10 plots in Sabie and Graskop, and 10 quadrats per plot for 20 plots in Hazeyview), 10 m^2 (2 quadrats per plot for 10 plots in Sabie and Graskop, and 2 quadrats per plot 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.

As the quadrat size increased, the species richness increased (Figures 3.1 and 3.2). Therefore, the size of the quadrat used affected the measure of species richness. At each quadrat scale, the species richness was significantly greater in the grassland biome than in the savanna biome (Appendix 5 for probability values). At all quadrat scales (except the 1 m^2 scale), the species richness was greatest in the Sabie region, followed by the Graskop region, and then the Hazeyview region, which had a species richness that was significantly lower than that of the Sabie region (Appendix 6 for probability values). At the 1 m^2 scale, the species richness was greatest in the Graskop region and lowest in the Hazeyview region. These values were significantly different.

(b) Total plant species composition

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.

Species	Total number (and percentage) of species present in all 40 plots	Number (and percentage) of species common to the:			
		Grassland and savanna biomes	Sabie (grassland) and Graskop (grassland) regions	Sabie (grassland) and Hazeyview (savanna) regions	Graskop (grassland) and Hazeyview (savanna) regions
TOTAL	**282**	112 (39%)	81 (28%)	97 (34%)	81 (28%)
Indigenous	222 (79%)	86 (30%)	63 (22%)	71 (25%)	64 (22%)
Alien	60 (21%)	26 (9%)	18 (6%)	26 (9%)	17 (6%)
Herbaceous	121 (43%)	46 (16%)	42 (15%)	44 (16%)	35 (12%)
Shrub	82 (29%)	32 (11%)	17 (6%)	24 (8%)	21 (7%)
Tree	46 (16%)	18 (6.4%)	9 (3%)	14 (5%)	13 (5%)
Grass	33 (12%)	16 (5.6%)	13 (4%)	15 (5%)	12 (4%)

A total of 282 species were found in the study area along the Sabie River (Table 3.1; Appendix 3). Of these species, 60 (21%) were alien and 222 (79%) were indigenous (Table 3.1; Appendix 3). The herbaceous species composition was the greatest (121 species (43%)), followed by the shrubs (82 species (29%)) and then the trees (46 species (16%)) (Table 3.1; Appendix 3). The grass species composition was the lowest with a total of 33 species (12%) (Table 3.1; Appendix 3). 27 (45%) of the 60 alien species were herbs, 17 (28%) were shrubs, 15 (25%) were trees, and 1 (2%) was a grass (Appendix 3). Therefore, more than half of the alien species were trees and shrubs. A total of 222 species were present in the grassland biome (178 in Sabie and 124 in Graskop), and 171 in the savanna biome (Appendix 3).

A total of 112 (39% of the total species of 282) were common to both biomes, with 86 indigenous species (30%) and 26 alien species (9%) common (Table 3.1). 46 Herbaceous species (16%), 32 shrub species (11%), 18 tree species (6.4%) and 16 grass species (5.6%) were common to both biomes (Table 3.1). A total of 81 species (28%) were common to the Sabie and Graskop regions, with 63 indigenous species (22%) and 18 alien species (6%) common (Table 3.1). 42 Herbaceous species (15%), 17 shrub species (6%), 9 tree species (3%) and 13 grass species (4%) were common to these two regions (Table 3.1). A total of 97 species (34%) were common to the Sabie and Hazeyview regions, with 71 indigenous species (25%) and 26 alien species (9%) common (Table 3.1). 44 Herbaceous species (16%), 24 shrub species (8%), 14 tree species (5%) and 15 grass species (5%) were common to Sabie and Hazeyview (Table 3.1). A total of 81 species (28%) were common to the Graskop and Hazeyview regions, with 64 indigenous species (22%) and 17 alien species (6%) common (Table 3.1). 35 Herbaceous species (12%), 21 shrub species (7%), 13 tree species (5%) and 12 grass species (4%) were common to these two regions (Table 3.1).

(c) Total alien plant species density, i.e. of all 40 plots combined

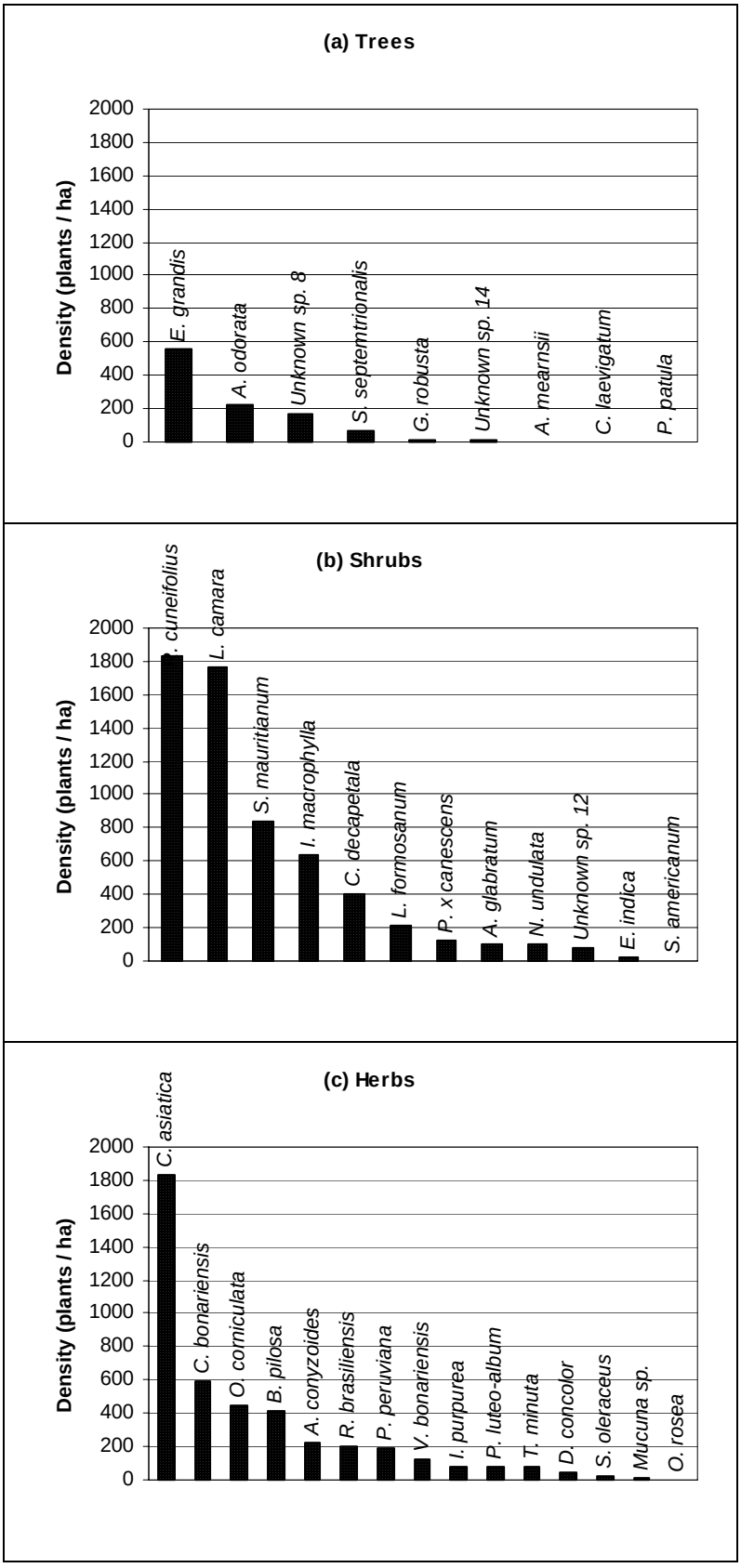
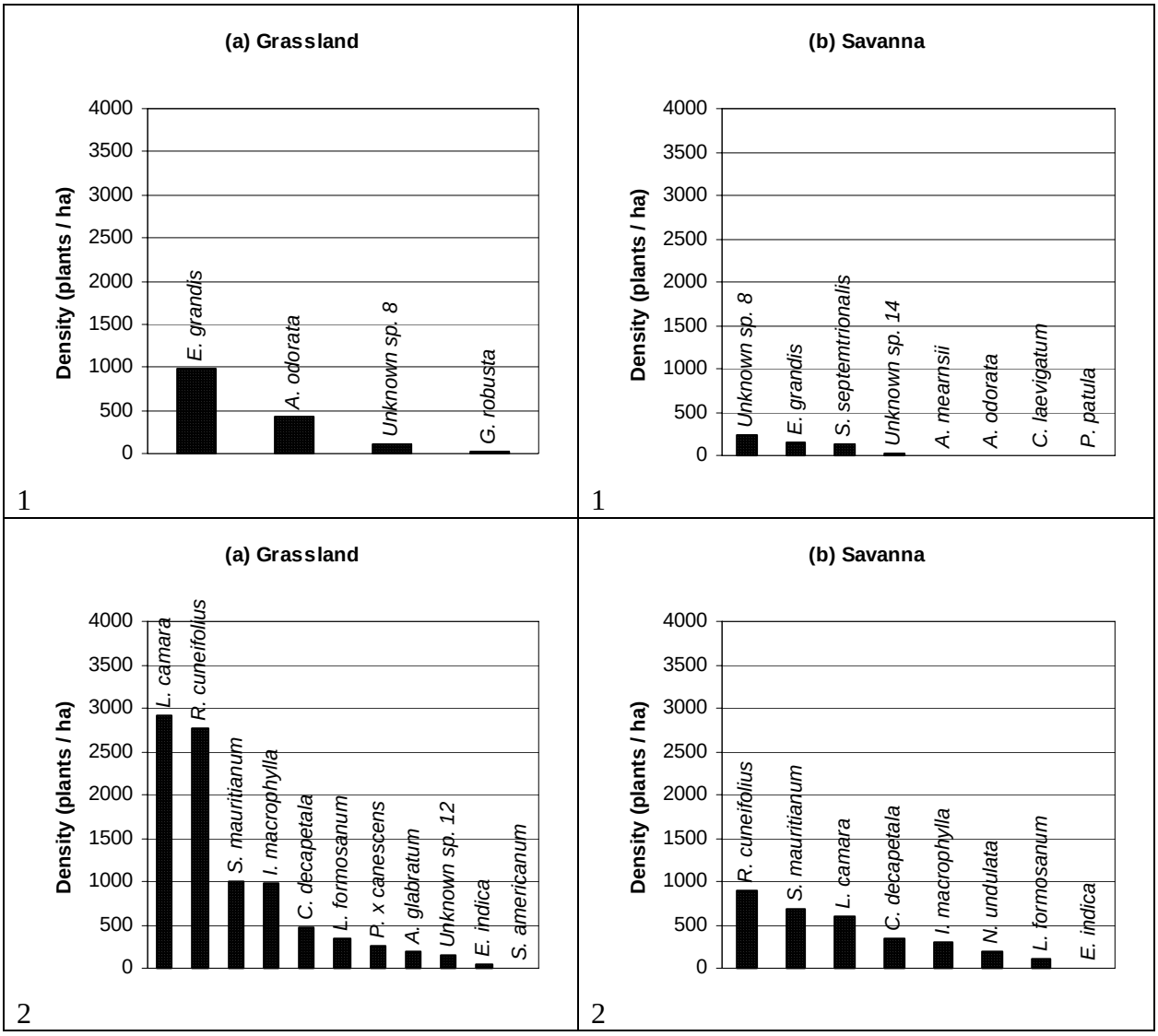


Figure 3.3. The total density (plants/ha) of alien (a) trees, (b) shrubs and (c) herbaceous plants at the 0.01 ha scale (i.e. 100 m^2), along the Sabie River (species names and invasive status are given in Appendix 3).

Within the total 40 plots along the Sabie River, the densest alien tree species was *Eucalyptus grandis*, the densest alien shrub species were *Rubus cuneifolius*, *Lantana camara* and *Solanum mauritianum*, and the densest alien herbaceous species was *Centella asiatica* (Figure 3.3).

(d) Biome comparison of alien plant species density: grassland and savanna biomes



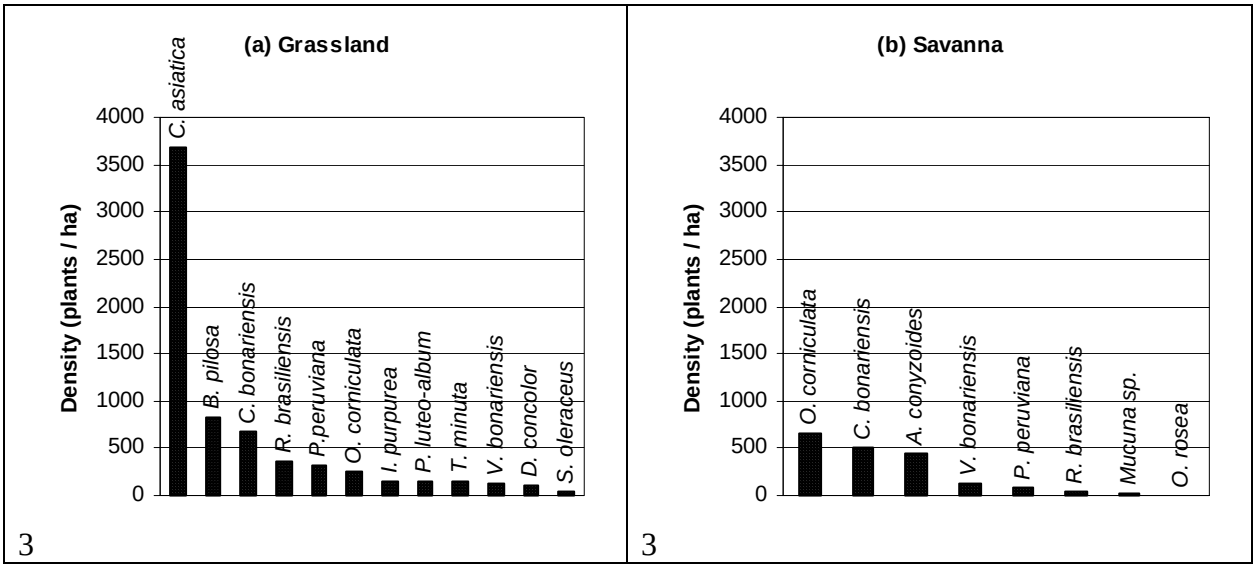
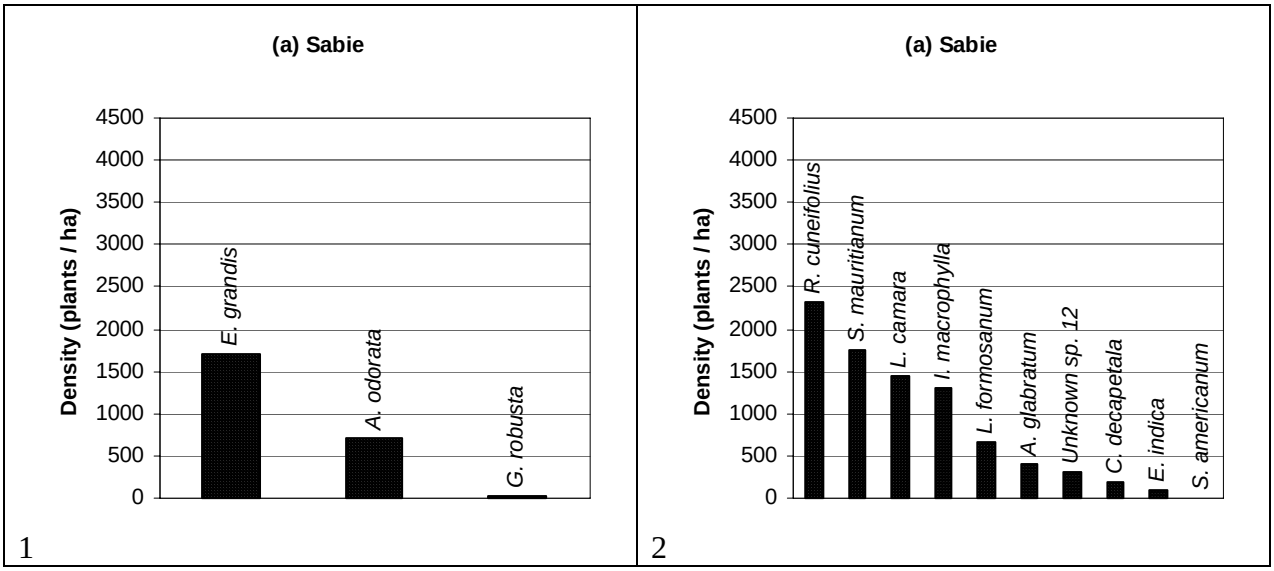
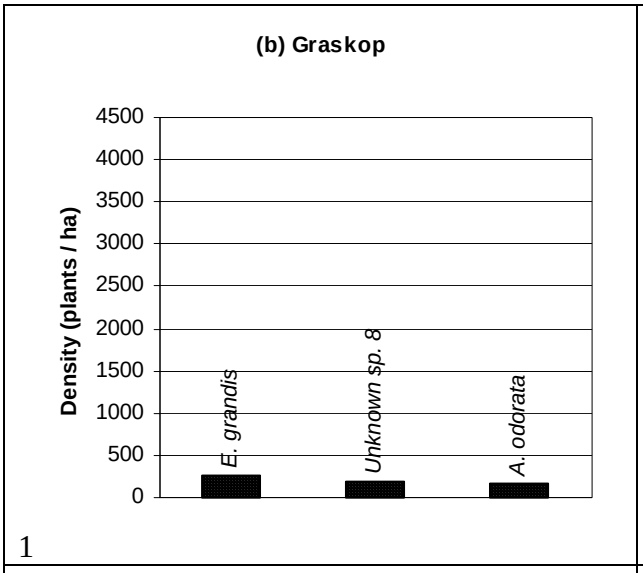


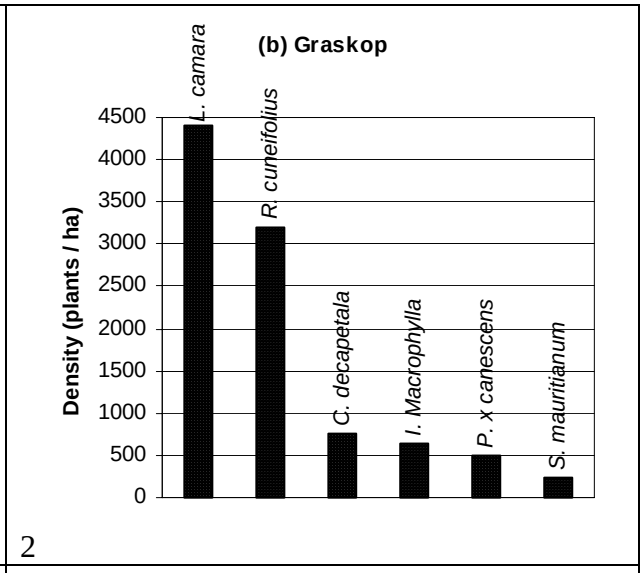
Figure 3.4. The density (plants/ha) of alien (1) trees, (2) shrubs and (3) herbaceous plants at the 0.01 ha scale (i.e. 100 m^2), in the (a) grassland biome and (b) savanna biome (species names and invasive status are given in Appendix 3).

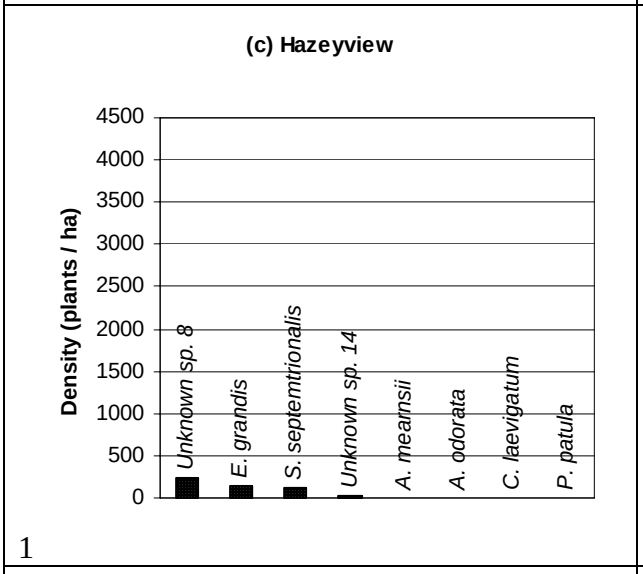
In the grassland, the densest alien tree species were *Eucalyptus grandis* and *Agrimonia odorata*, the densest alien shrub species were *Lantana camara* and *Rubus cuneifolius*, and the densest alien herbaceous species was *Centella asiatica* (Figure 3.4). In the savanna, the densest alien tree species were an unknown species and *Eucalyptus grandis*, the densest alien shrub species were *Rubus cuneifolius* and *Solanum mauritianum*, and the densest alien herbaceous species was *Oxalis corniculata* (Figure 3.4).

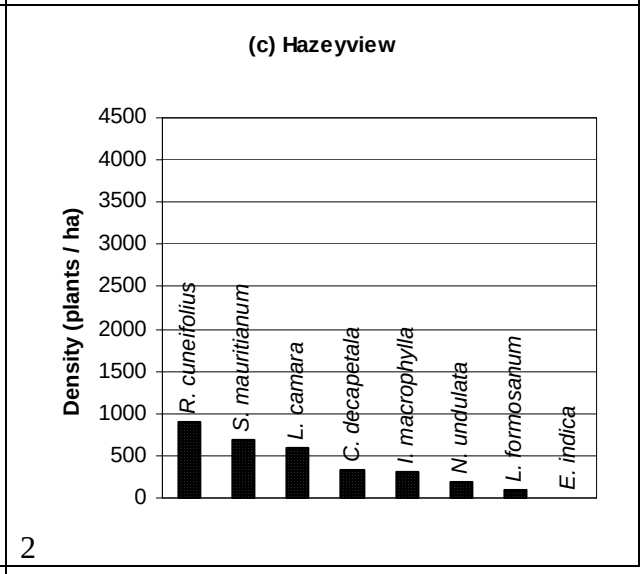
(e) Regional comparison of alien plant species density: Sabie (grassland), Graskop (grassland) and Hazeyview (savanna)

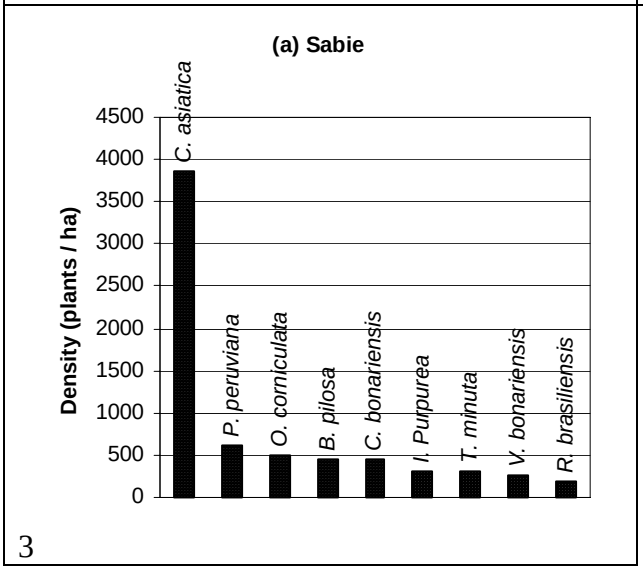



(b) Graskop
Density (plants / ha)
4500
4000
3500
3000
2500
2000
1500
1000
500
0
E. grandis
Unknown sp. 8
A. odorata
1


(b) Graskop
Density (plants / ha)
4500
4000
3500
3000
2500
2000
1500
1000
500
0
L. camara
R. cuneifolius
C. decapetala
I. Macrophylla
P. x canescens
S. mauritianum
2


(c) Hazeyview
Density (plants / ha)
4500
4000
3500
3000
2500
2000
1500
1000
500
0
Unknown sp. 8
E. grandis
S. septemtrionalis
Unknown sp. 14
A. mearnsii
A. odorata
C. laevigatum
P. patula
1


(c) Hazeyview
Density (plants / ha)
4500
4000
3500
3000
2500
2000
1500
1000
500
0
R. cuneifolius
S. mauritianum
L. camara
C. decapetala
I. macrophylla
N. undulata
L. formosanum
E. indica
2


(a) Sabie
Density (plants / ha)
4500
4000
3500
3000
2500
2000
1500
1000
500
0
C. asiatica
P. peruviana
O. corniculata
B. pilosa
C. bonariensis
I. Purpurea
T. minuta
V. bonariensis
R. brasiliensis
3

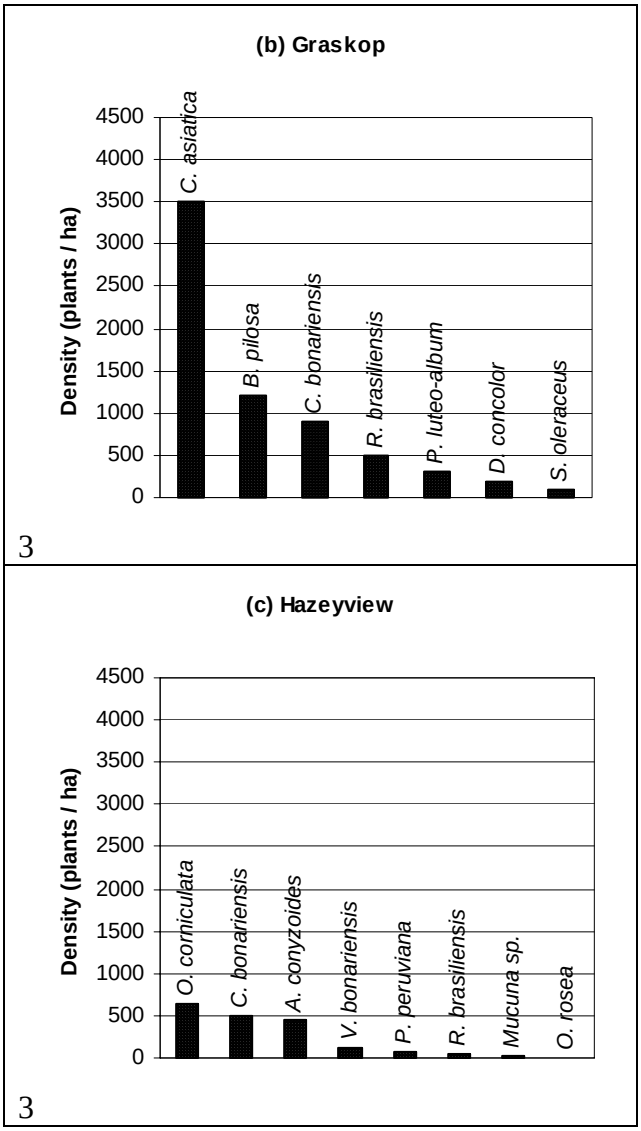


Figure 3.5. The density (plants/ha) of alien (1) trees, (2) shrubs and (3) herbaceous plants at the 0.01 ha scale (i.e. 100 m^2), in the (a) Sabie, (b) Graskop and (c) Hazeyview regions (species names and invasive status are given in Appendix 3).

In the Sabie region, the alien tree species with the highest density was *Eucalpytus grandis*, the densest alien shrubs were *Rubus cuneifolius*, *Solanum mauritianum* and *Lantana camara*, and the densest alien herb was *Centella asiatica* (Figure 3.5). In the Graskop region, *Eucalpytus grandis* was the densest alien tree species, *Lantana camara* and *Rubus cuneifolius* were the densest alien shrub species, and *Centella asiatica* was the densest alien herbaceous species (Figure 3.5). In the Hazeyview region, the densest alien tree species were an unknown species and *Eucalyptus grandis*, the densest alien shrub species were *Rubus cuneifolius* and *Solanum mauritianum*, and the densest alien herbaceous species was *Oxalis corniculata* (Figure 3.5).

Species richness (tree, shrub, herbaceous, and grass and sedge growth forms)

(a) Biome comparison: grassland and savanna biomes

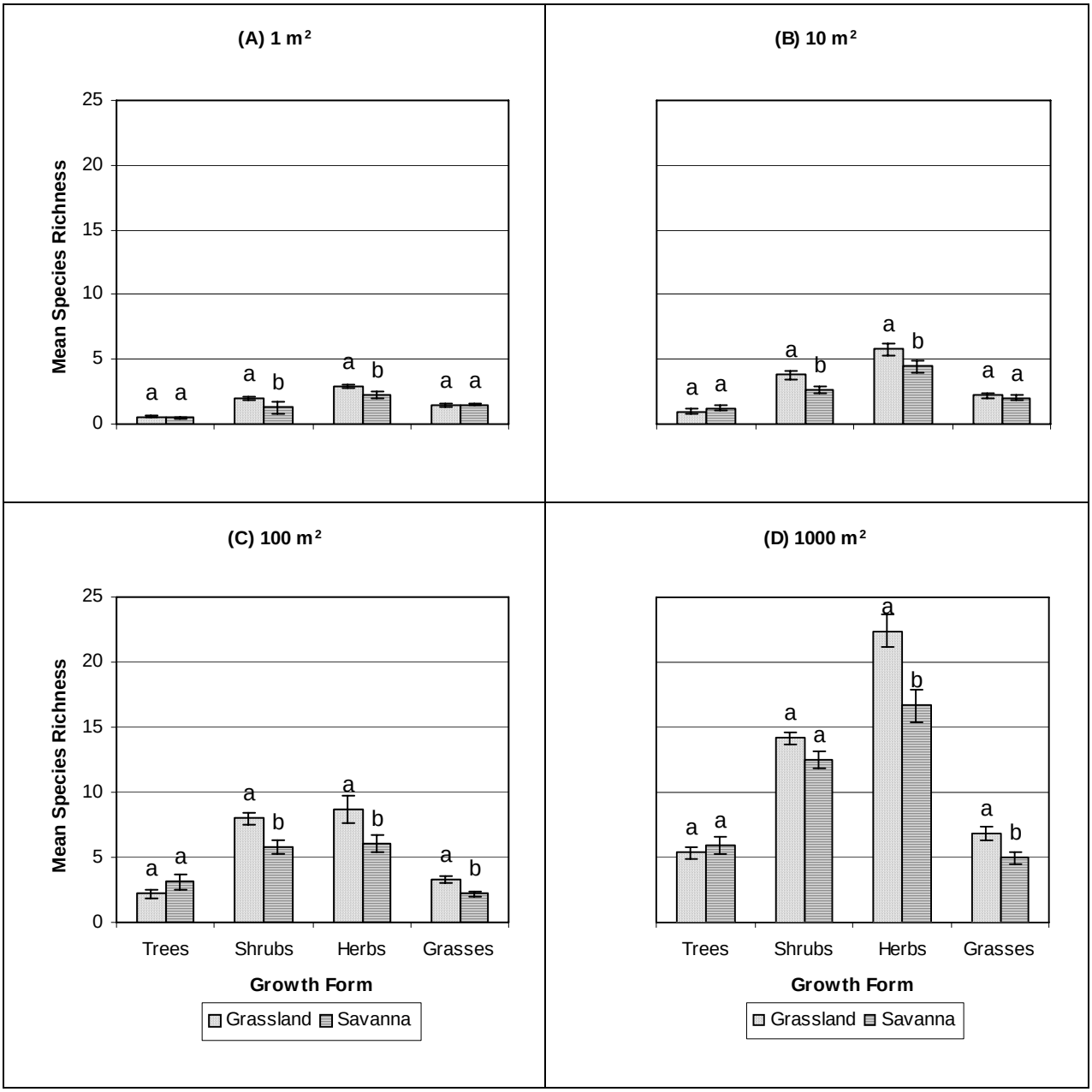


Figure 3.6. Species richness (mean ± S.E.) for (a) tree, (b) shrub, (c) herbaceous, and (d) grass and sedge growth forms in the grassland and savanna biomes, at the (A) 1 m^2, (B) 10 m^2, (C) 100 m^2 and (D) 1000 m^2 quadrat scales. Columns with different superscript letters within the same growth form are significantly different using t-tests (for independent-samples) ($P < 0.05$). N = 20 for all growth forms and quadrat scales; *d.f.* = 38.

At all quadrat scales (in both biomes), the herbaceous species richness was the greatest, followed by the shrub, grass and tree species richness (Figure 3.6). The exception to this pattern was found at the 100 m^2 and 1000 m^2 scales, where there were more tree than grass species measured in the savanna biome. This point is expected due to the larger sizes of trees and shrubs relative to herbaceous plants and hence the requirement for larger plot sizes in order to sample them adequately. The grassland biome contained more shrub (significant at all scales expect 1000 m^2), herbaceous (significant at all scales) and grass species (significant at the 100 m^2 and

1000 m^2 scales) (Appendix 7 for probability values) than the savanna biome. The exception to this pattern occurred at the 1 m^2 scale, where there was approximately the same grass species richness in both biomes. On the other hand, the savanna biome tended to contain more (but not significantly more (Appendix 7 for probability values)) tree species than the grassland biome, except at the 1 m^2 scale, where there was approximately the same tree species richness in both biomes.

(b) Regional comparison: Sabie (grassland), Graskop (grassland) and Hazeyview (savanna)

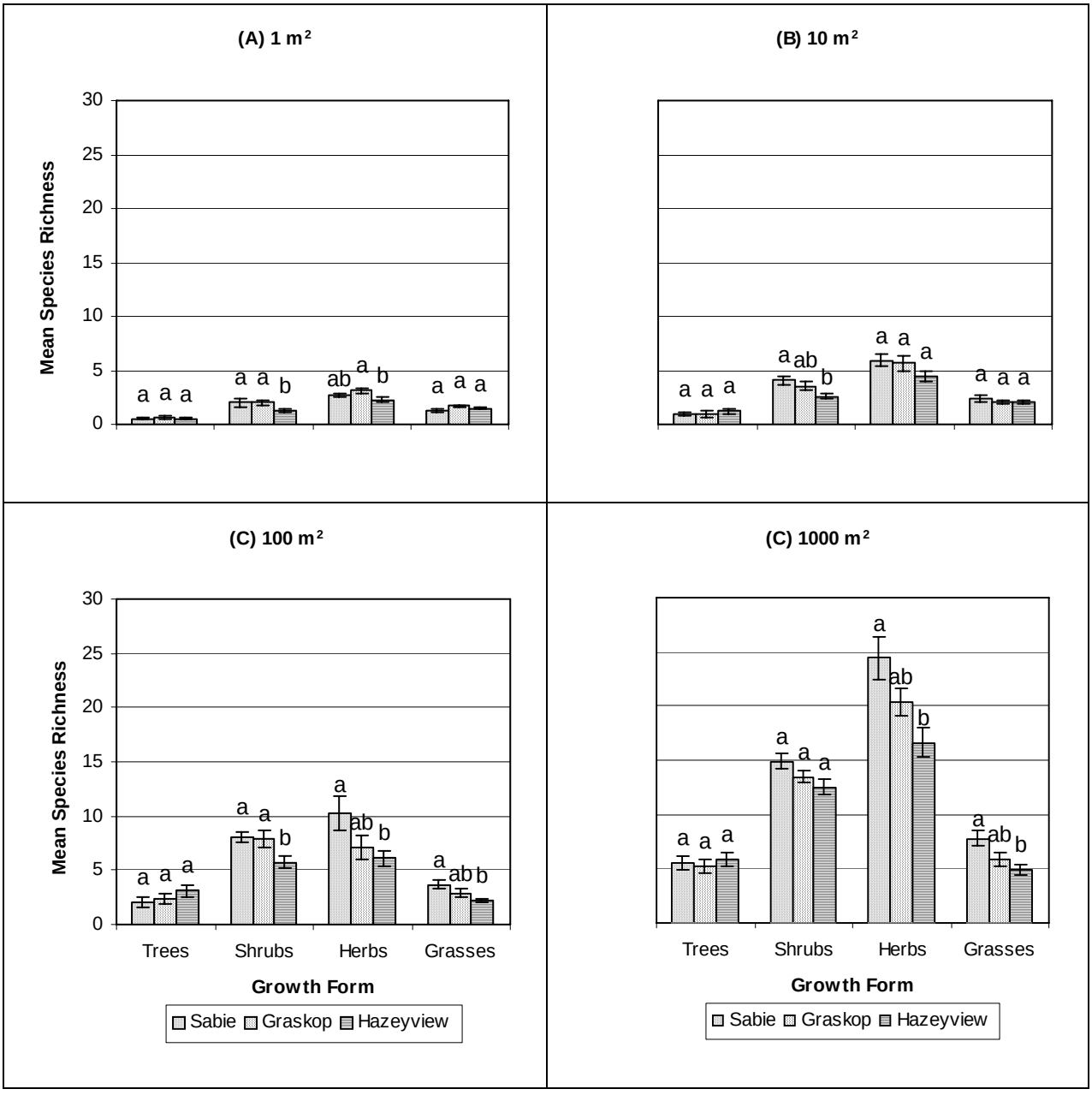


Figure 3.7. Species richness (mean ± S.E.) for (a) tree, (b) shrub, (c) herbaceous, and (d) grass and sedge species in the Sabie (grassland), Graskop (grassland) and Hazeyview (savanna) regions, at the (A) 1 m^2, (B) 10 m^2, (C) 100 m^2 and (D) 1000 m^2 quadrat scales. Columns with different superscript 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; *d.f.* = 2,37.

The Sabie region had the highest number of shrub, herbaceous and grass species, and the Hazeyview region had the lowest (expect at the 1 m^2 scale where there is no distinct pattern) (Figure 3.7). There were significantly more shrub (at all scales expect the 1000 m^2 scale), more herbaceous (at the 100 m^2 and 1000 m^2) and more grass species (at the 100 m^2 and 1000 m^2 scales), in the Sabie than Hazeyview regions (probability values are given in Appendix 8). The Graskop region had significantly more shrub (at the 1 m^2 and 100 m^2 scales) and herbaceous species (at the 1 m^2 scale) than those in the Hazeyview region (probability values are given in Appendix 8). There was no real pattern in tree species richness, with no significant difference in tree species richness at all quadrat scales and between any of the regions (probability values are given in Appendix 8).

Total, indigenous and alien plant species richness

(a) For all 40 plots

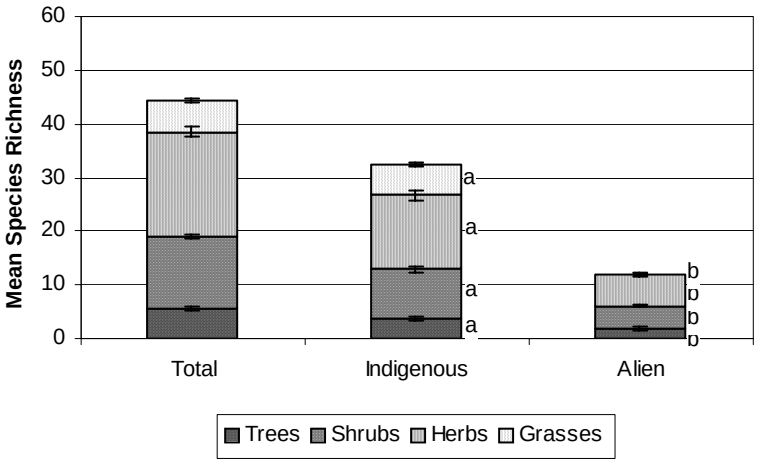


Figure 3.8. Total, indigenous and alien species richness for (a) tree, (b) shrub, (c) herbaceous, and (d) grass and sedge growth forms (mean ± S.E.), for all 40 plots at the 1000 m^2 quadrat scale. Comparing the indigenous with the alien species, the stacked columns with different superscript letters within the same growth form are significantly different using t-tests (for dependent-samples) ($P < 0.05$). N = 40 for all growth forms; *d.f.* = 39.

The indigenous species richness of each growth form was significantly higher than the alien species richness of each growth form ($P < 0.001$) (Figure 3.8).

(b) Biome comparison: grassland and savanna biomes

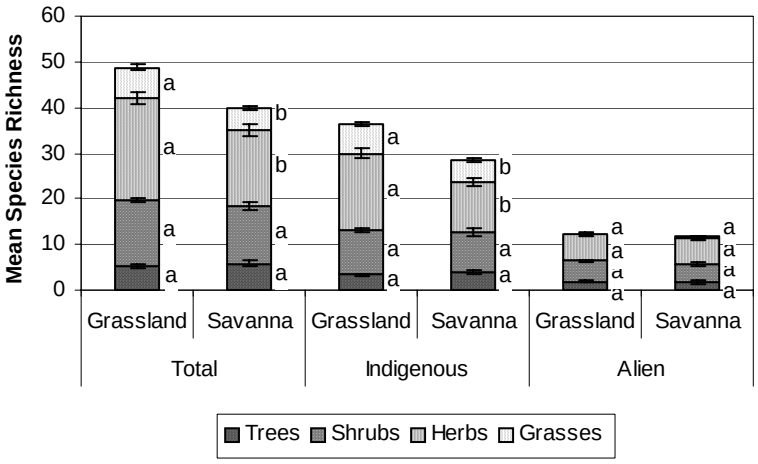


Figure 3.9. Total, indigenous and alien plant species richness (mean ± S.E.) for plots in the grassland and savanna biomes at the 1000 m^2 quadrat scale. Stacked columns with different superscript letters within the same growth form, within the same category (i.e. total or indigenous or alien) and are significantly different using t-tests analyses (for independent-samples) ($P < 0.05$). N = 20 for all growth forms; *d.f.* = 38.

In total, the grassland had a greater shrub, herbaceous (significantly greater) and grass (significantly greater) species richness, whereas the savanna had a greater tree species richness (Figure 3.9; Appendix 9 for probability values). The grassland also had a greater indigenous shrub, herbaceous (significantly greater) and grass (significantly greater) species richness, whereas the savanna had a greater indigenous tree species richness (Figure 3.9; Appendix 9 for probability values). The grassland had a greater (but not significantly greater) alien tree, shrub and grass species richness, whereas the savanna had a greater (but not significantly) alien herbaceous species richness (Figure 3.9; Appendix 9 for probability values).

(c) Regional comparison: Sabie (grassland), Graskop (grassland) and Hazeyview (savanna)

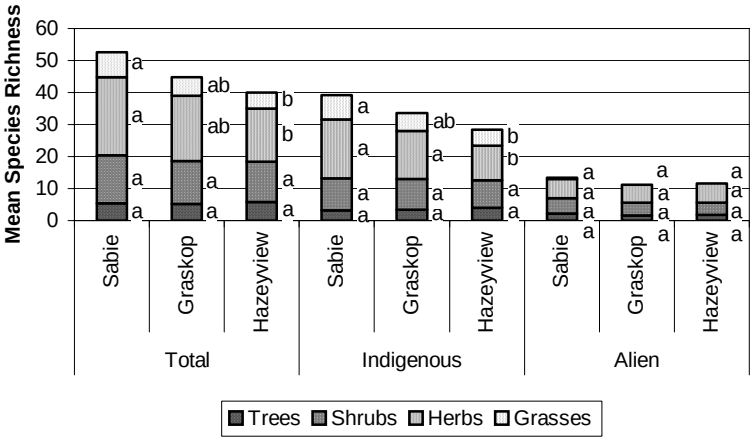
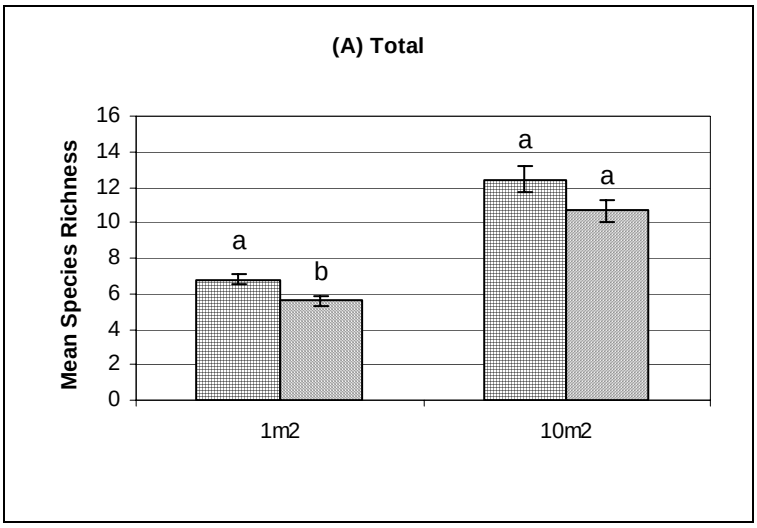


Figure 3.10. Total, indigenous and alien plant species richness (mean ± S.E.) for plots in the Sabie (grassland), Graskop (grassland) and Hazeyview (savanna) regions at the 1000 m^2 quadrat scale. Stacked columns with different superscript letters

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 ($P < 0.05$). N = 10 for plots in Sabie and Graskop, and 20 for plots in Hazeyview; *d.f.* = 2,27 for Sabie and Graskop, and 2,57 for Hazeyview.

In total, the Sabie region had a greater shrub (but not significantly greater), herbaceous (significantly greater than Hazeyview) and grass (significantly greater than Hazeyview) species richness than the Graskop and Hazeyview regions (Figure 3.10; Appendix 10 for probability values), whereas the Hazeyview region had a greater (but not significantly greater) tree species richness than the Sabie or Graskop regions (Figure 3.10; Appendix 10 for probability values). The Sabie region had a greater indigenous shrub (but not significantly greater), herbaceous (significantly greater than Hazeyview) and grass (significantly greater than Hazeyview) species richness than the Graskop and Hazeyview regions, whereas the Hazeyview region had a greater (but not significantly greater) indigenous tree species richness than the Sabie or Graskop regions (Figure 3.10; Appendix 10 for probability values). The Sabie region had a greater alien tree, shrub, herbaceous and grass species richness than the Graskop and Hazeyview regions; however, this was not significant (Figure 3.10; Appendix 10 for probability values).

Total plant species richness at the roadside and riverside quadrats



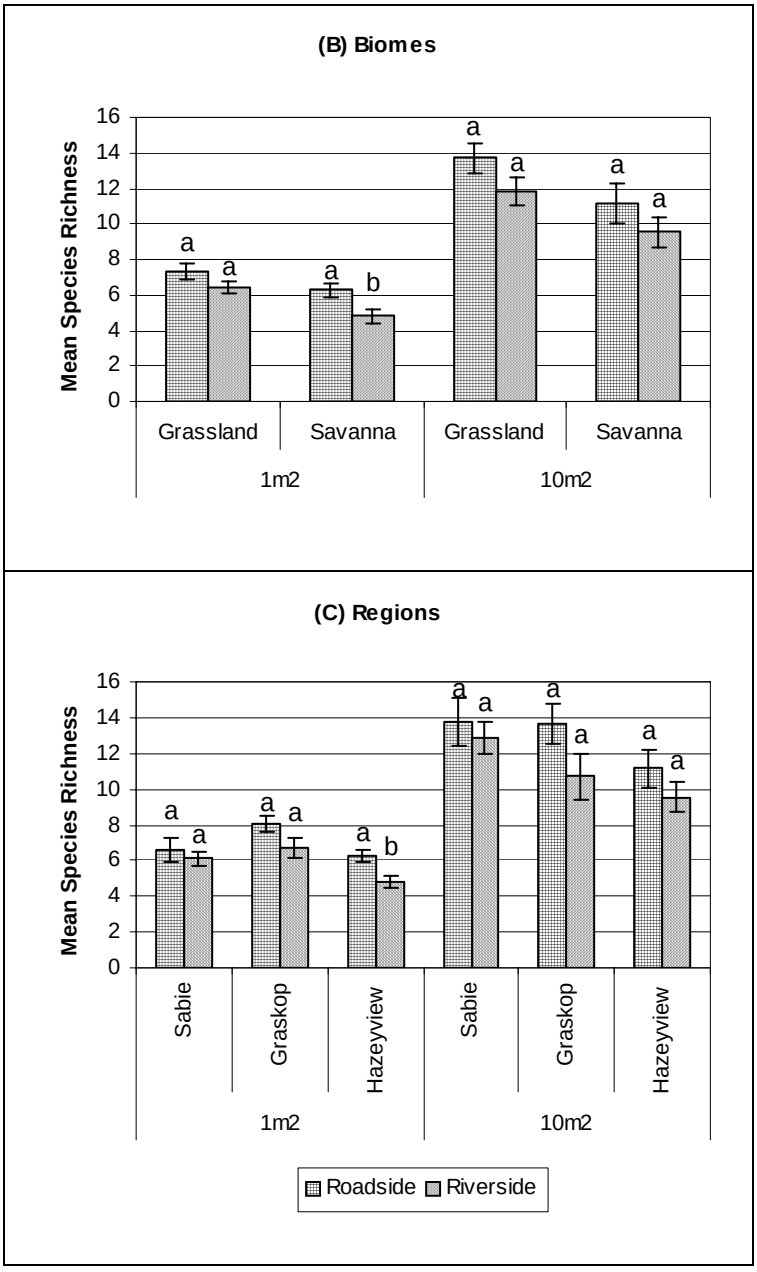
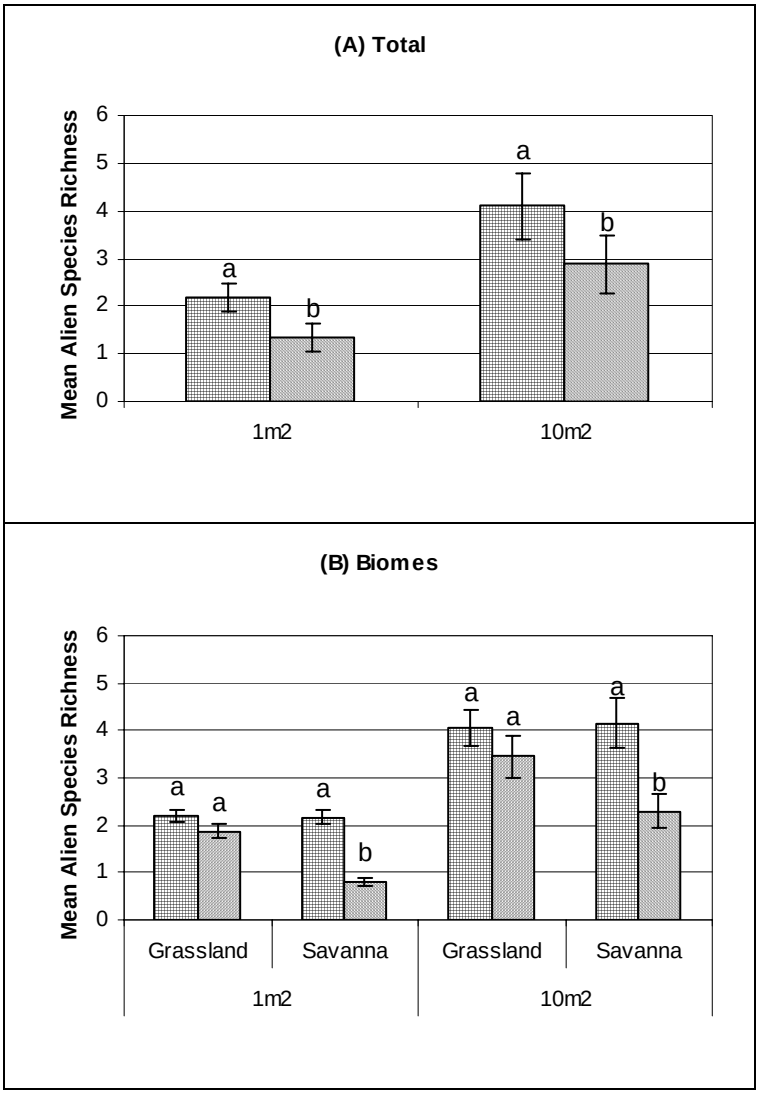


Figure 3.11. Total plant species richness (mean ± S.E.) of quadrats (1 m^2 and 10 m^2) occurring on the roadside and riverside of (A) each of the 40 modified Whittaker nested plots, (B) the modified Whittaker nested plots occurring in the grassland and savanna biomes, and (C) the modified Whittaker nested 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) ($P < 0.05$). N = 40 for total plots, N = 20 for savanna, grassland and Hazeyview plots, and N = 10 for Sabie and Graskop plots; *d.f.* = 39 for total plots, *d.f.* = 19 for savanna, grassland and Hazeyview plots, and *d.f.* = 9 for Sabie and Graskop plots.

The species richness of the roadside quadrats was greater than that of the riverside quadrats, at both the 1 m^2 and 10 m^2 quadrat scales (Figure 3.11 (A)(B)(C)). However, only the 1 m^2 roadside quadrats in total (Figure 3.11 (A)), and those in the savanna biome (and therefore the Hazeyview region) (Figure 3.11 (B)(C)), had a

significantly greater total species richness than the 1 m^2 riverside quadrats (Appendix 11 for probability values).

Alien plant species richness at the roadside and riverside quadrats



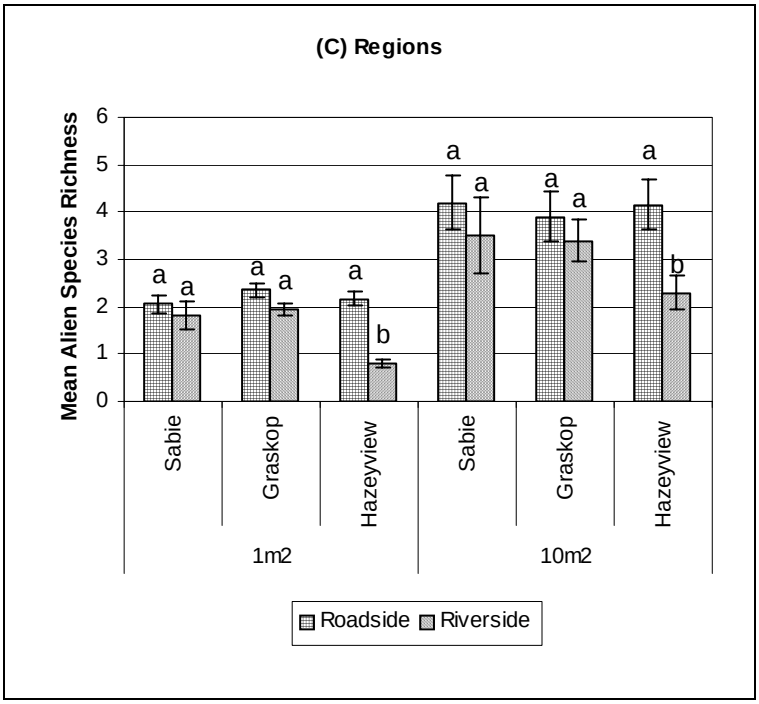


Figure 3.12. Alien plant species richness (mean ± S.E.) of quadrats (1 m^2 and 10 m^2) occurring on the roadside and riverside of (A) each of the 40 modified Whittaker nested plots, (B) the modified Whittaker nested plots occurring in the grassland and savanna biomes, and (C) the modified Whittaker nested 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) ($P < 0.05$). N = 40 for total plots, N = 20 for savanna, grassland and Hazeyview plots, and N = 10 for Sabie and Graskop plots; *d.f.* = 39 for total plots, *d.f.* = 19 for savanna, grassland and Hazeyview plots, and *d.f.* = 9 for Sabie and Graskop plots.

The alien species richness of the roadside quadrats was greater than that of the riverside quadrats, at both the 1 m^2 and 10 m^2 quadrat scales (Figure 3.12 (A)(B)(C)). The 1 m^2 and 10 m^2 roadside quadrats in total (Figure 3.12 (A)), and those in the savanna biome (and therefore the Hazeyview region) (Figure 3.12 (B)(C)), had a significantly greater alien species richness than the 1 m^2 and 10 m^2 riverside quadrats (Appendix 11 for probability values).

3.4.2. Plant species diversity

Simpson's index of diversity (1-D)

(a) Biome comparison of total plant species: grassland and savanna biomes

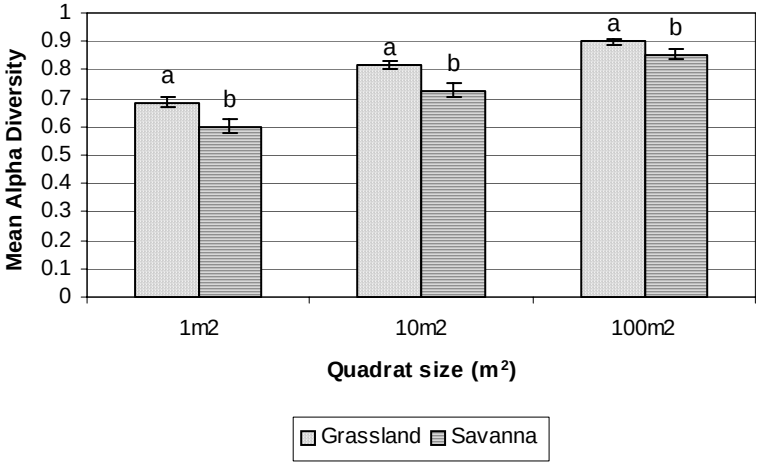


Figure 3.13. Simpson's index of diversity (alpha diversity) (mean ± S.E.) for total plant species in the grassland and savanna biomes, at the 1 m^2, 10 m^2 and 100 m^2 quadrat scales. Columns with different superscript letters within the same quadrat size are significantly different using t-tests (for independent-samples) ($P < 0.05$). N = 20 for all quadrat scales; *d.f.* = 38.

The alpha diversity was significantly greater in the grassland than in the savanna, at the 1 m^2, 10 m^2 and 100 m^2 quadrat scales (Figure 3.13; probability values are given in Appendix 5). Species diversity increased as quadrat size increased (Figure 3.13), as expected.

(b) Regional comparison of total plant species: Sabie (grassland), Graskop (grassland) and Hazeyview (savanna)

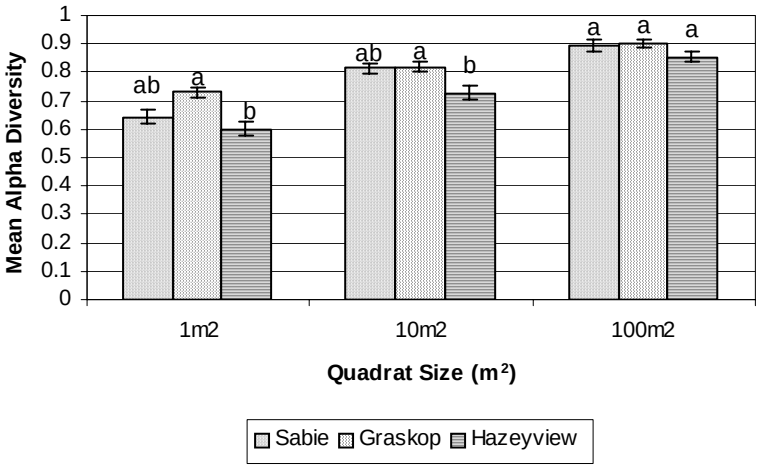
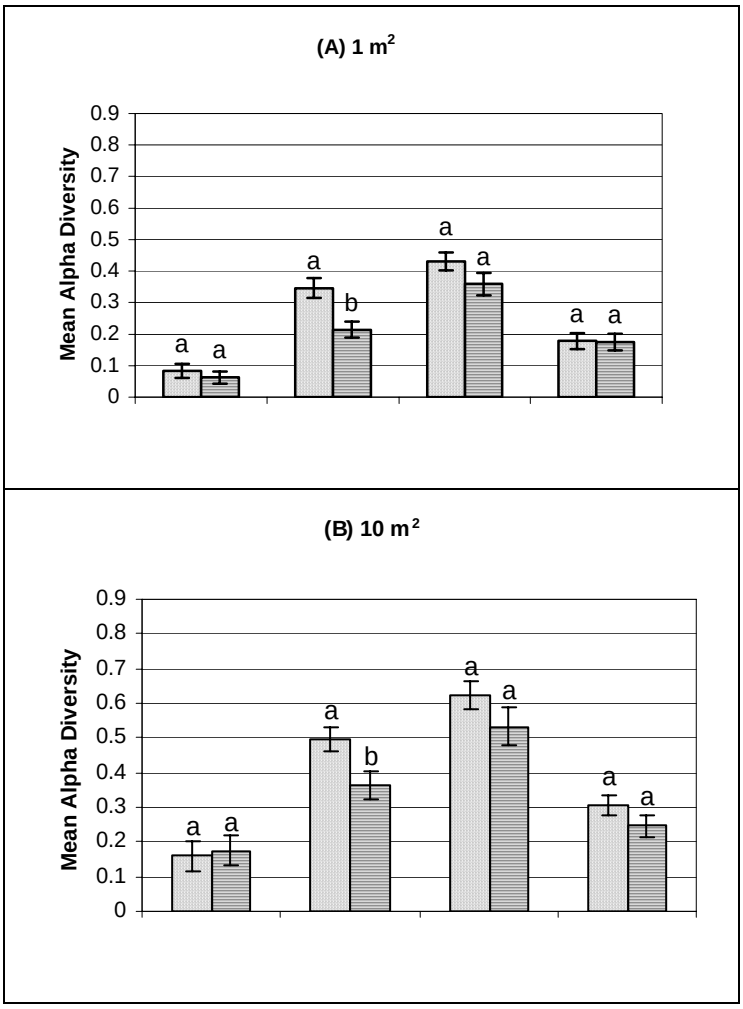


Figure 3.14. Simpson's index of diversity (alpha diversity) (mean ± S.E.) for total plant species in the Sabie (grassland), Graskop (grassland) and Hazeyview (savanna) regions, at the 1 m^2, 10 m^2 and 100 m^2 quadrat scales. Columns with different superscript letters within the same quadrat size are 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.

The alpha diversity was the greatest in the Graskop region, followed by the Sabie and Hazeyview regions (at all three quadrat scales) (Figure 3.14). The alpha diversity in the Graskop region was significantly greater than that in the Hazeyview region at the 1 m^2 and 10 m^2 quadrat scales (probability values are given in Appendix 6).

(c) Biome comparison of tree, shrub, herbaceous, and grass and sedge growth forms: grassland and savanna biomes



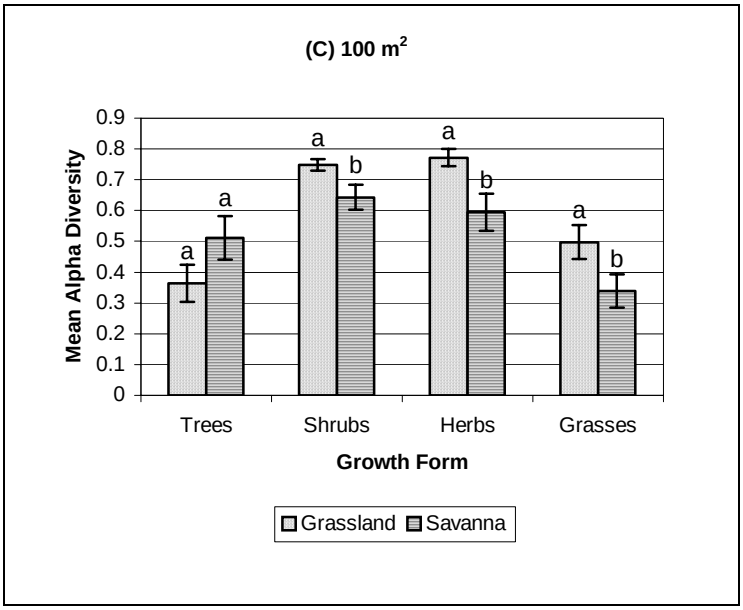


Figure 3.15. Simpson's index of diversity (alpha diversity) (mean ± S.E.) for (a) tree, (b) shrub, (c) herbaceous, and (d) grass and sedge species in the grassland and savanna biomes, at the (A) 1 m^2, (B) 10 m^2 and (C) 100 m^2 quadrat scales. Columns with different superscript letters within the same 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.

At all quadrat scales (1 m^2, 10 m^2 and 100 m^2), the grassland biome had a significantly higher shrub, herbaceous (only significant at 100 m^2) and grass (only significant at 100 m^2) species diversity than the savanna biome (Figure 3.15; Appendix 7 for probability values). On the other hand, the savanna biome had a higher (but not significantly higher) tree species diversity, expect at the 1 m^2 scale. The herbaceous species diversity was the highest, followed by the shrub and then the grass species diversity. The tree species diversity was the lowest, except at the 100 m^2 scale, where both the grass and tree species had approximately the same diversity. Again this is because trees, being larger plants, require larger sample areas to adequately sample their diversity.

(d) Regional comparison of tree, shrub, herbaceous, and grass and sedge growth forms: Sabie (grassland), Graskop (grassland) and Hazeyview (savanna)

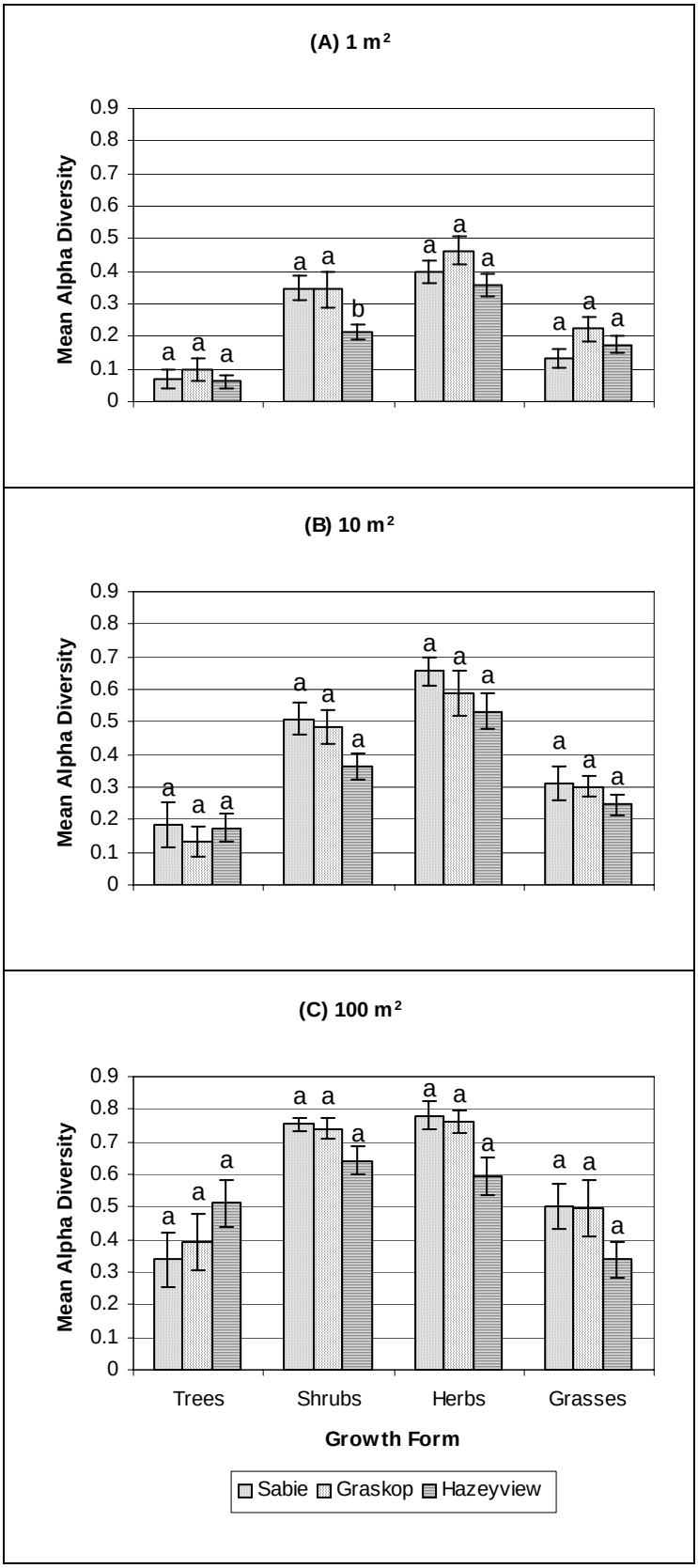


Figure 3.16. Simpson's index of diversity (alpha diversity) (mean ± S.E.) for (a) tree, (b) shrub, (c) herbaceous, and (d) grass and sedge species in the Sabie (grassland), Graskop (grassland) and Hazeyview (savanna) regions, at the (A) 1 m^2, (B) 10 m^2 and (C) 100 m^2 quadrat scales. Columns with different 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.

The Sabie region had the greatest shrub, herbaceous and grass species diversity, followed by the Graskop and Hazeyview regions (this pattern was not seen at the 1 m^2 scale) (Figure 3.16). At the 100 m^2 scale, the Hazeyview region had the highest tree species diversity, followed by Graskop and then Sabie. The diversity of the total species did not differ significantly between the regions (at all scales), except at the 1 m^2 scale where the Hazeyview region had a significantly lower shrub species diversity than Sabie and Graskop (Appendix 8 for probability values).

Simpson's measure of evenness (E 1/D)

(a) Biome comparison of total plant species: grassland and savanna biomes

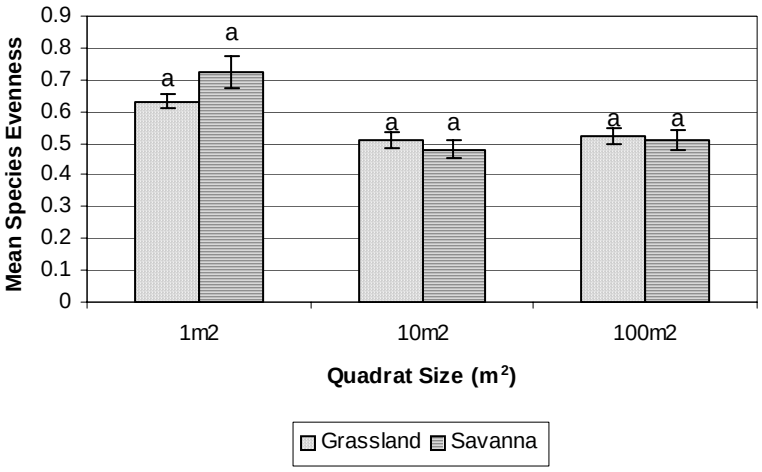


Figure 3.17. Species evenness (mean ± S.E.) for total plant species in the grassland and savanna biomes, at the 1 m^2, 10 m^2 and 100 m^2 scales. Columns with different superscript within the same quadrat scale are significantly different using t-tests (for independent-samples) ($P < 0.05$). N = 20 for all quadrat scales, *d.f.* = 38.

The species evenness in the grassland and savanna biomes was approximately the same (Figure 3.17; Appendix 5 for probability values). At the 1 m^2 scale, the species evenness was the highest.

(b) Regional comparison of total plant species: Sabie (grassland), Graskop (grassland) and Hazeyview (savanna)

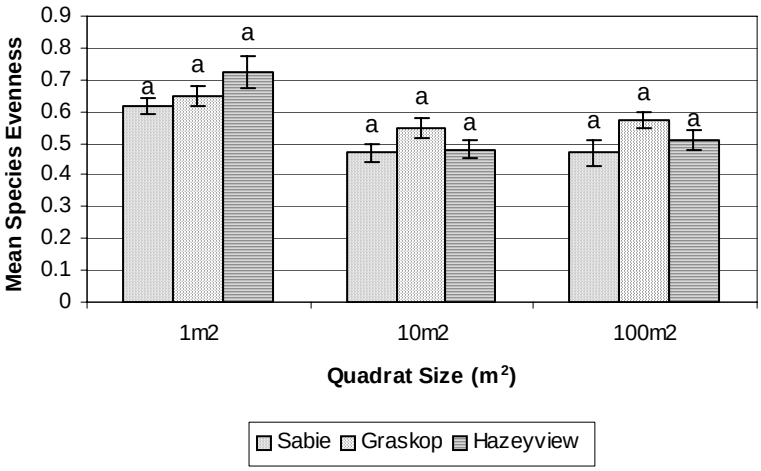
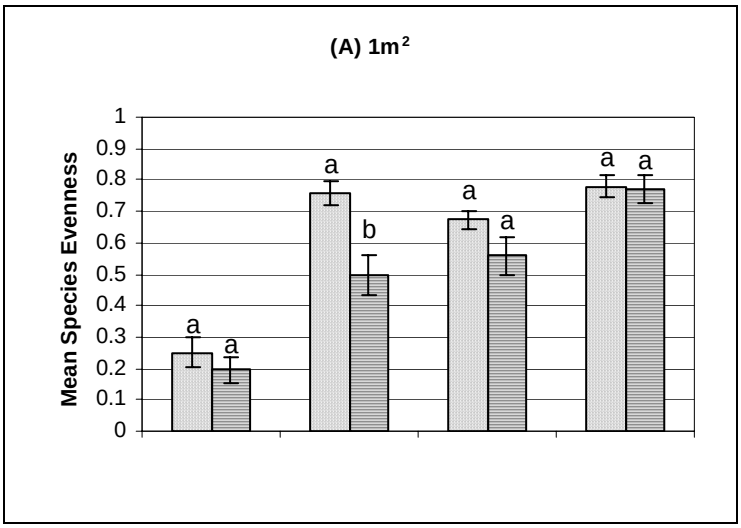


Figure 3.18. Species evenness (mean ± S.E.) for total plant species in the Sabie (grassland), Graskop (grassland) and Hazeyview (savanna) regions, at the 1 m^2, 10 m^2 and 100 m^2 scales. Columns with different superscript letters within the same quadrat size are significantly different using Tukey's 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.

At the 10 m^2 and 100 m^2 scales, the species evenness was highest in the Graskop region and lowest in the Sabie region, and at the 1 m^2 scale, it was highest in the Hazeyview region and lowest in the Sabie region (Figure 3.18). However, the species evenness was not significantly different between the three regions (Figure 3.18; Appendix 6 for probability values). The species evenness was the highest at the 1 m^2 scale.

(c) Biome comparison of tree, shrub, herbaceous, and grass and sedge growth forms: grassland and savanna biomes



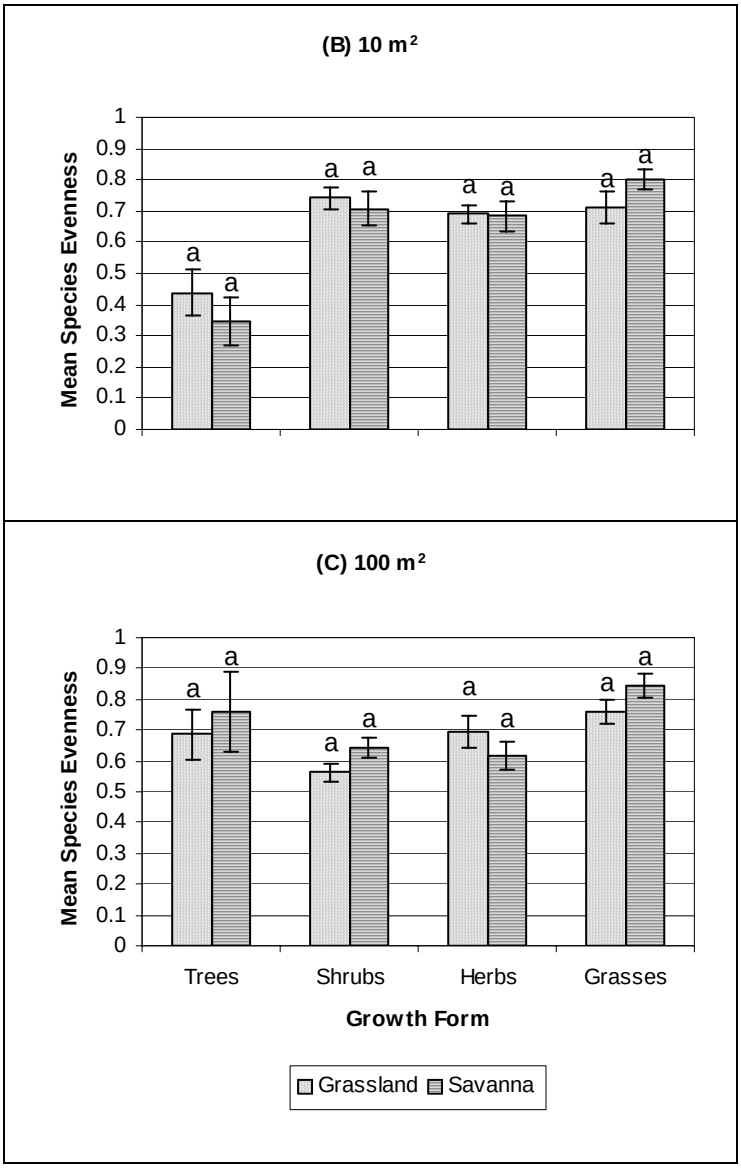


Figure 3.19. Species evenness (mean ± S.E.) for (a) tree, (b) shrub, (c) herbaceous, and (d) grass and sedge species in the grassland and savanna biomes, at the (A) 1 m^2, (B) 10 m^2 and (C) 100 m^2 quadrat scales. Columns with different superscript letters within the same growth form are significantly different using t-tests (for independent-samples) ($P < 0.05$). N = 20 for all growth forms and all quadrat scales; *d.f.* = 38.

At the 1 m^2 and 10 m^2 scales, the species evenness (for all growth forms) was higher in the grassland (except for the grasses at the 10 m^2 scale) (Figure 3.19 (A)(B)). At the 100 m^2 scale, the species evenness was higher in the savanna for all growth forms except herbs (Figure 3.19 (C)). However, the species evenness was not significantly different between the biomes, only for shrub species at the 1 m^2 scale, which had an evenness significantly higher in the grassland (Appendix 7 for probability values). Grasses had the highest species evenness, trees had the lowest, and shrubs and herbs had approximately the same. At the 100 m^2 scale (Figure 3.19 (C)), the tree species evenness was slightly higher than the shrub and herbaceous species evenness. Grasses had the highest evenness (Figure 3.19 (C)).

(d) Regional comparison of tree, shrub, herbaceous, and grass and sedge growth forms: Sabie (grassland), Graskop (grassland) and Hazeyview (savanna)

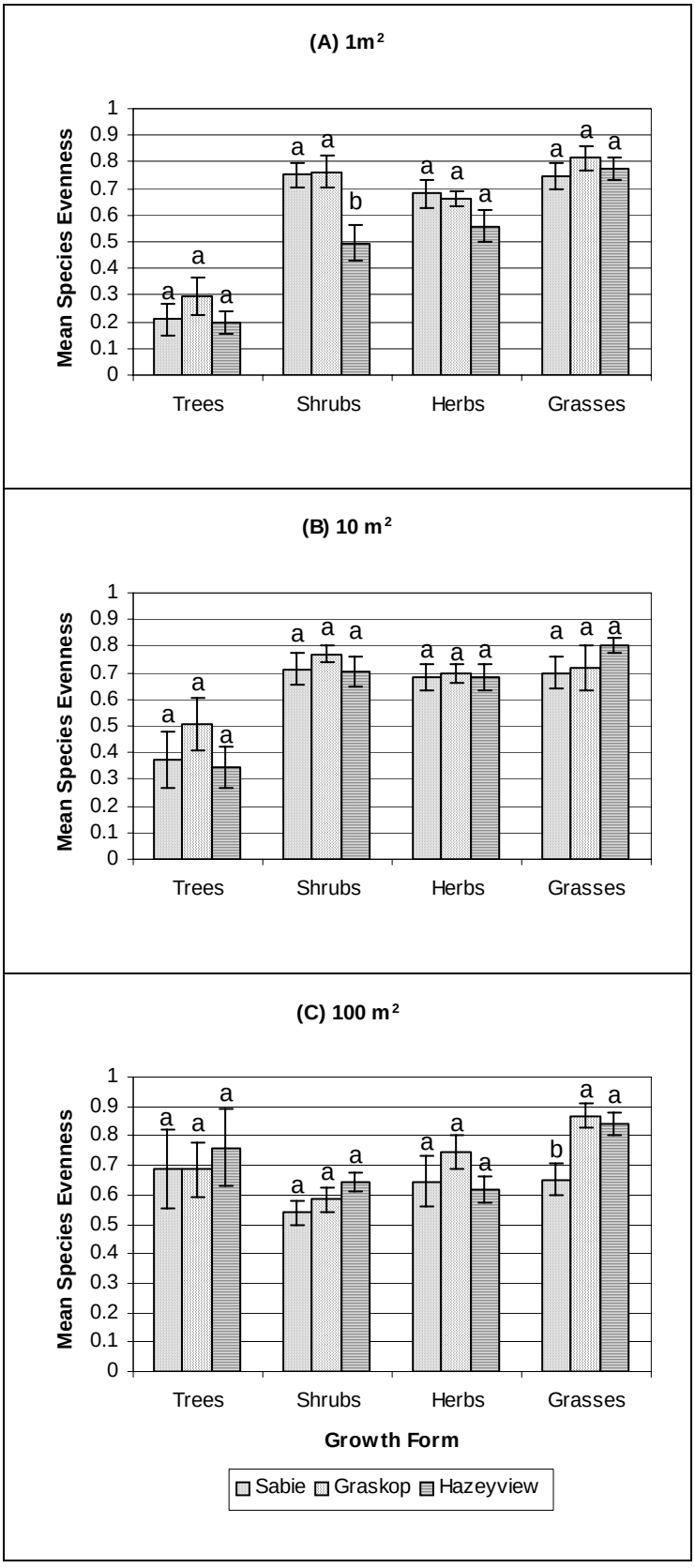


Figure 3.20. Species evenness (mean ± S.E.) for (a) tree, (b) shrub, (c) herbaceous, and (d) grass and sedge species in the Sabie (grassland), Graskop (grassland) and Hazeyview (savanna) regions, at the (A) 1 m^2, (B) 10 m^2 and (C) 100 m^2 quadrat scales. Columns with different superscript letters within 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.

The species evenness was almost always higher in the Graskop region than in the Sabie region for all growth forms (Figure 3.20). The species evenness was not significantly different between the three different regions, except for the shrub species evenness at the 1 m^2 scale, which was significantly lower in the Hazeyview region than in the Sabie and Graskop regions, and for the grass species evenness at the 100 m^2 scale, which was significantly lower in the Sabie region than in the Graskop and Hazeyview regions (Appendix 8 for probability values).

Sorenson's coefficient of community (CC)

(a) Biome comparison of total plant species: grassland and savanna biomes

Table 3.2. Sorenson's coefficient of community (mean ± 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.

Quadrat Size	Sorenson's Coefficient
1 m^2	0.60
10 m^2	0.63
100 m^2	0.53
1000 m^2	0.57

Sorenson's coefficient of community indicates how similar two communities are in terms of the species they support. The grassland and savanna biomes were between approximately 50 – 60 % similar in terms of the species composition (Table 3.2).

(b) Regional comparison of total plant species: Sabie (grassland), Graskop (grassland) and Hazeyview (savanna)

Table 3.3. Sorenson's coefficient of community (mean ± 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.

1 m^2	Graskop	Hazeyview
Sabie	0.58	0.58
Graskop		0.62
10 m^2	Graskop	Hazeyview
Sabie	0.55	0.57
Graskop		0.62
100 m^2	Graskop	Hazeyview
Sabie	0.50	0.50
Graskop		0.50
1000 m^2	Graskop	Hazeyview
Sabie	0.53	0.55
Graskop		0.55

The Sabie, Graskop and Hazeyview regions were between approximately 50 – 60 % similar in terms of the species composition (Table 3.3).

(c) Biome comparison of tree, shrub, herbaceous, and grass and sedge growth forms: grassland and savanna biomes

Table 3.4. Sorenson's coefficient of community (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.

Growth Form	Quadrat Size	Sorenson's Coefficient
Trees	1 m^2	0.63
	10 m^2	0.56
	100 m^2	0.58
	1000 m^2	0.57
Shrubs	1 m^2	0.51
	10 m^2	0.56
	100 m^2	0.60
	1000 m^2	0.55
Herbs	1 m^2	0.60
	10 m^2	0.64
	100 m^2	0.45
	1000 m^2	0.56
Grasses	1 m^2	0.68
	10 m^2	0.79
	100 m^2	0.52
	1000 m^2	0.65

The grassland and savanna biomes were not that similar in terms of the (a) tree, (b) shrub, (c) herbaceous, and (d) grass species, expect the grass species at the 10 m^2 scale where there was a 79% similarity between the biomes (Table 3.4). The tree and grass species similarities between the biomes were slightly higher than the herb and shrub species similarities; therefore there were more changes in the shrub and herbaceous species than the tree and grass species between the biomes (Table 3.4).

(d) Regional comparison of tree, shrub, herbaceous, and grass and sedge growth forms: Sabie (grassland), Graskop (grassland) and Hazeyview (savanna)

Table 3.5. Sorenson's coefficient of community (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.

(a) Trees		
1 m^2	Graskop	Hazeyview
Sabie	0.50	0.41
Graskop		0.52
10 m^2	Graskop	Hazeyview
Sabie	0.55	0.52
Graskop		0.73
100 m^2	Graskop	Hazeyview
Sabie	0.48	0.39
Graskop		0.59
1000 m^2	Graskop	Hazeyview
Sabie	0.45	0.50
Graskop		0.54
(b) Shrubs		
1 m^2	Graskop	Hazeyview
Sabie	0.51	0.47
Graskop		0.50
10 m^2	Graskop	Hazeyview
Sabie	0.48	0.49
Graskop		0.55
100 m^2	Graskop	Hazeyview
Sabie	0.44	0.58
Graskop		0.53
1000 m^2	Graskop	Hazeyview
Sabie	0.42	0.50
Graskop		0.50
(c) Herbs		
1 m^2	Graskop	Hazeyview
Sabie	0.59	0.63
Graskop		0.65
10 m^2	Graskop	Hazeyview
Sabie	0.58	0.59
Graskop		0.65
100 m^2	Graskop	Hazeyview
Sabie	0.54	0.46
Graskop		0.46
1000 m^2	Graskop	Hazeyview
Sabie	0.59	0.57
Graskop		0.56

(d) Grasses		
1 m^2	Graskop	Hazeyview
Sabie	0.73	0.70
Graskop		0.67
10 m^2	Graskop	Hazeyview
Sabie	0.62	0.76
Graskop		0.74
100 m^2	Graskop	Hazeyview
Sabie	0.54	0.55
Graskop		0.48
1000 m^2	Graskop	Hazeyview
Sabie	0.62	0.65
Graskop		0.65

The Sabie, Graskop and Hazeyview regions were not very similar in terms of the tree, shrub and herbaceous species (Table 3.5). These three regions were between 54 – 76% similar in terms of the grass species (Table 3.5).

Species complementarity (the Marczewski-Steinhaus (MS) distance)

(a) Biome comparison of total plant species: grassland and savanna biomes

Table 3.6. Species complementarity (mean ± 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.

Quadrat Size	Species Complementarity
1 m^2	0.58
10 m^2	0.54
100 m^2	0.64
1000 m^2	0.60

Complementarity describes the difference between areas in terms of the species they support. Therefore, the higher the complementarity, the less species the two areas have in common. The grassland and savanna biomes were between approximately 50 – 60% different in terms of the species composition (Table 3.6).

(b) Regional comparison of total plant species: Sabie (grassland), Graskop (grassland) and Hazeyview (savanna)

Table 3.7. Species complementarity (mean ± 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.

1 m^2	Graskop	Hazeyview
Sabie	0.60	0.59
Graskop		0.55
10 m^2	Graskop	Hazeyview
Sabie	0.62	0.60
Graskop		0.56
100 m^2	Graskop	Hazeyview
Sabie	0.67	0.67
Graskop		0.66
1000 m^2	Graskop	Hazeyview
Sabie	0.64	0.62
Graskop		0.62

The Sabie, Graskop and Hazeyview regions were between 55 – 67% different in terms of the species composition (Table 3.7).

(c) Biome comparison of tree, shrub, herbaceous, and grass and sedge growth forms: grassland and savanna biomes

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.

Growth Form	Quadrat Size	Species Complementarity
Trees	1 m^2	0.54
	10 m^2	0.61
	100 m^2	0.59
	1000 m^2	0.60
Shrubs	1 m^2	0.66
	10 m^2	0.61
	100 m^2	0.57
	1000 m^2	0.62
Herbs	1 m^2	0.57
	10 m^2	0.54
	100 m^2	0.71
	1000 m^2	0.61
Grasses	1 m^2	0.48
	10 m^2	0.35
	100 m^2	0.65
	1000 m^2	0.52

The grassland and savanna biomes had less tree, shrub and herbaceous species in common, than grass species (Table 3.8).

(d) Regional comparison of tree, shrub, herbaceous, and grass and sedge growth forms: Sabie (grassland), Graskop (grassland) and Hazeyview (savanna)

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.

(a) Trees		
1 m^2	Graskop	Hazeyview
Sabie	0.62	0.65
Graskop		0.42
10 m^2	Graskop	Hazeyview
Sabie	0.67	0.74
Graskop		0.65
100 m^2	Graskop	Hazeyview
Sabie	0.69	0.76
Graskop		0.58
1000 m^2	Graskop	Hazeyview
Sabie	0.79	0.67
Graskop		0.63
(b) Shrubs		
1 m^2	Graskop	Hazeyview
Sabie	0.66	0.70
Graskop		0.67
10 m^2	Graskop	Hazeyview
Sabie	0.69	0.68
Graskop		0.62
100 m^2	Graskop	Hazeyview
Sabie	0.72	0.60
Graskop		0.64
1000 m^2	Graskop	Hazeyview
Sabie	0.73	0.67
Graskop		0.68
(c) Herbs		
1 m^2	Graskop	Hazeyview
Sabie	0.58	0.55
Graskop		0.52
10 m^2	Graskop	Hazeyview
Sabie	0.59	0.58
Graskop		0.52
100 m^2	Graskop	Hazeyview
Sabie	0.63	0.70
Graskop		0.71
1000 m^2	Graskop	Hazeyview
Sabie	0.58	0.60
Graskop		0.62
(d) Grasses		
1 m^2	Graskop	Hazeyview
Sabie	0.43	0.46

Graskop		0.50
10 m^2	Graskop	Hazeyview
Sabie	0.56	0.39
Graskop		0.41
100 m^2	Graskop	Hazeyview
Sabie	0.63	0.62
Graskop		0.69
1000 m^2	Graskop	Hazeyview
Sabie	0.56	0.52
Graskop		0.52

The Sabie and Hazeyview regions had the lowest percentage of tree species in common, whereas the Graskop and Hazeyview regions had the highest (Table 3.9). The Sabie and Graskop regions had the lowest percentage of shrub species in common, whereas the Graskop and Hazeyview regions had the highest (Table 3.9). The Sabie and Hazeyview regions had the lowest percentage (only slightly though) of herbaceous species in common, whereas the Graskop and Hazeyview regions had the highest (only slightly though) (Table 3.9). The Sabie and Graskop regions had the lowest percentage of grass species in common, whereas the Sabie and Hazeyview regions had the highest (Table 3.9).

3.4.3 Overstorey aerial cover

(a) Biome comparison: grassland and savanna biomes

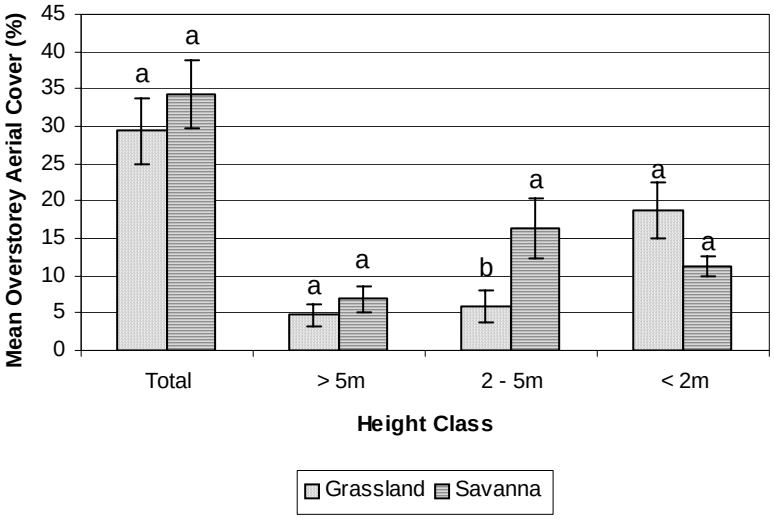


Figure 3.21. Percentage aerial cover of alien vegetation (mean ± S.E.) from the 1000 m^2 plots in the grassland and savanna biomes. Columns with different superscript letters within the same height class are significantly different using t-tests (for independent-samples) ($P < 0.05$). N = 20 for all height classes; *d.f.* = 38.

In total, the plots in the savanna had a greater (but not significantly greater) aerial cover of alien plants than those in the grassland (Figure 3.21; Appendix 5 for probability values). The plots in the savanna had a greater aerial cover of trees > 5 m

(but not significantly greater) and between 2 and 5 m (significantly greater), whereas those in the grassland had a greater aerial cover of shrubs < 2 m (but not significantly greater) (Figure 3.21; Appendix 5 for probability values).

(b) Regional comparison: Sabie (grassland), Graskop (grassland) and Hazeyview (savanna)

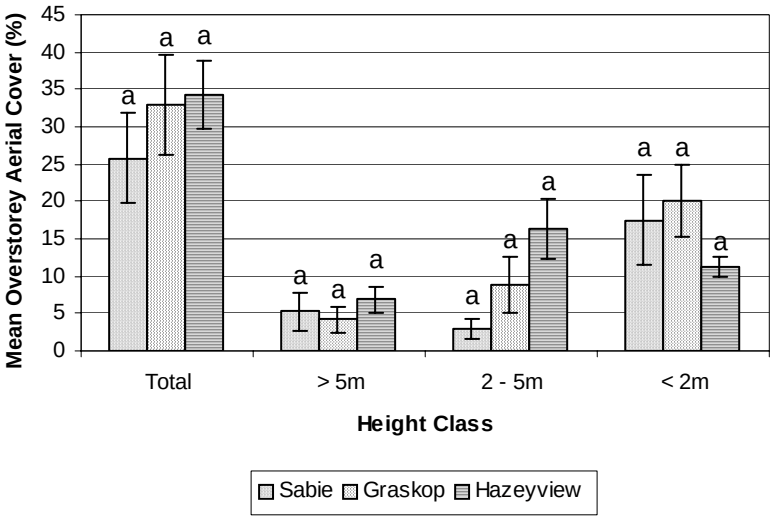


Figure 3.22. Percentage aerial cover of alien vegetation (mean ± S.E.) from the 1000 m^2 plots in the Sabie (grassland), Graskop (grassland) and Hazeyview (savanna) regions. Columns with different superscript letters within the same height class are significantly different using Tukey's honest significant 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.

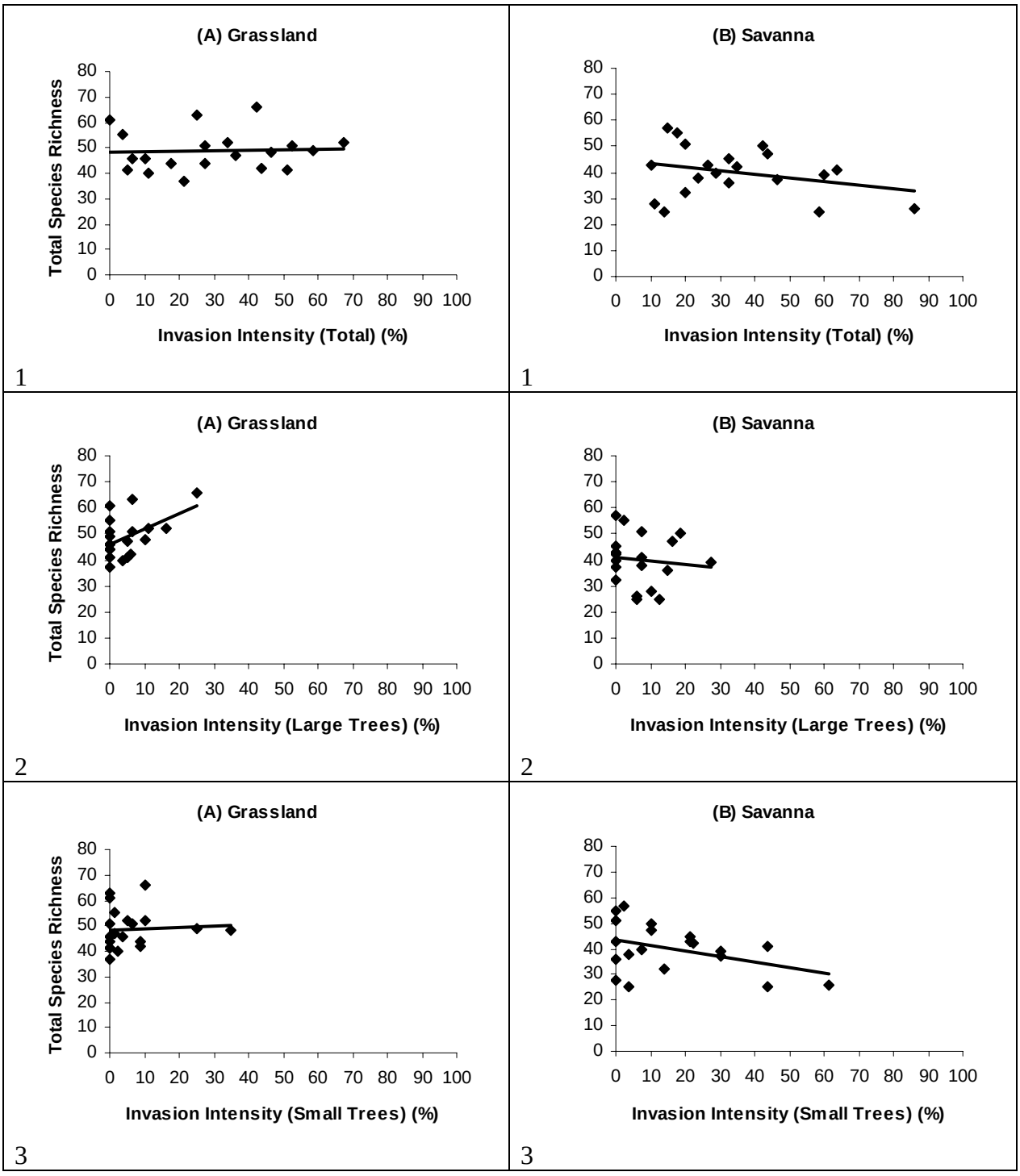
In total, plots in the Hazeyview region had the greatest aerial cover of alien plants, while those in the Sabie region had the lowest (Figure 3.22). The aerial cover of alien plants > 5 m and between 2 and 5 m, were also the greatest in the Hazeyview region. Plots in the Graskop region, on the other hand, had the greatest aerial cover of alien plants < 2 m, while those in the Hazeyview region had the lowest. However, the total aerial cover, as well as the aerial cover of the different height classes, was not significantly different between all three regions (Appendix 6 for probability values).

3.4.4 Linear regression analyses of the percentage aerial cover of woody alien plants (invasion intensity), and plant species richness and diversity measures

The total percentage aerial cover of woody alien plants, i.e. of large trees (> 5 m), small trees (2 – 5 m), and saplings and shrubs (< 2 m), was used as a measure of invasion intensity. Linear regression analyses were then performed whereby the relationship between the invasion intensity (independent variable) and various species richness and diversity measures (dependent variables) were determined. Linear regression analyses were also performed whereby the relationship between the aerial cover of the large alien trees (independent variable), small alien trees (independent variable), as well as alien saplings and shrubs (independent variable), and various species richness and diversity measures (dependent variables) were determined.

Total plant species richness

(a) Biome comparison: grassland and savanna biomes



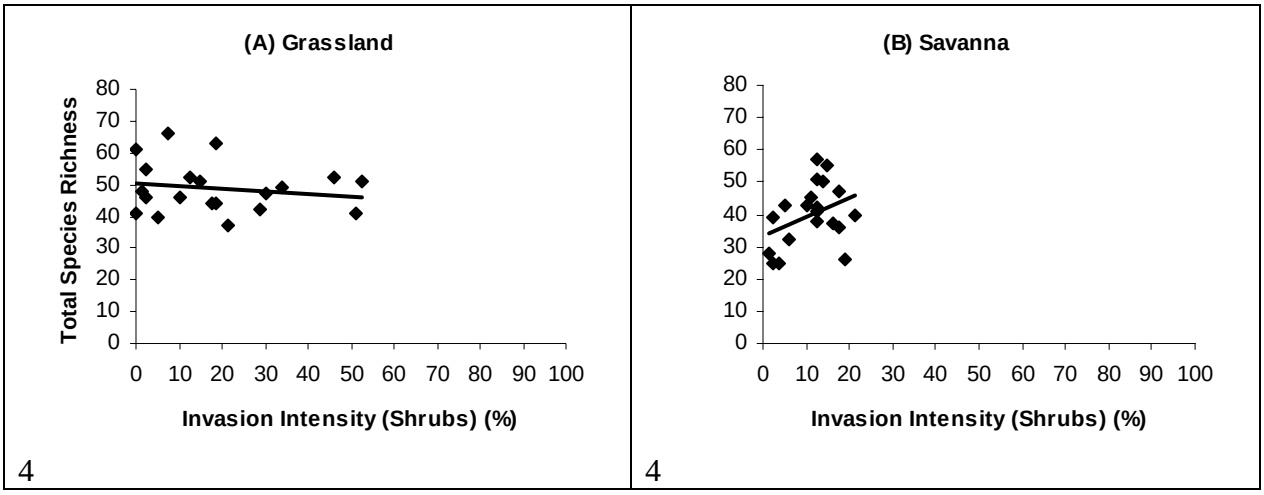
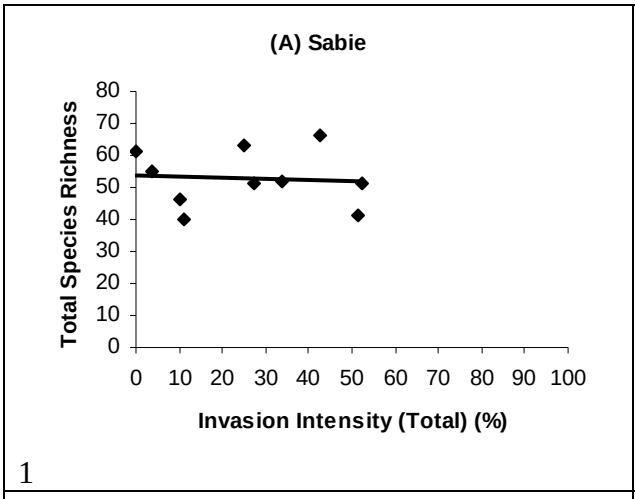


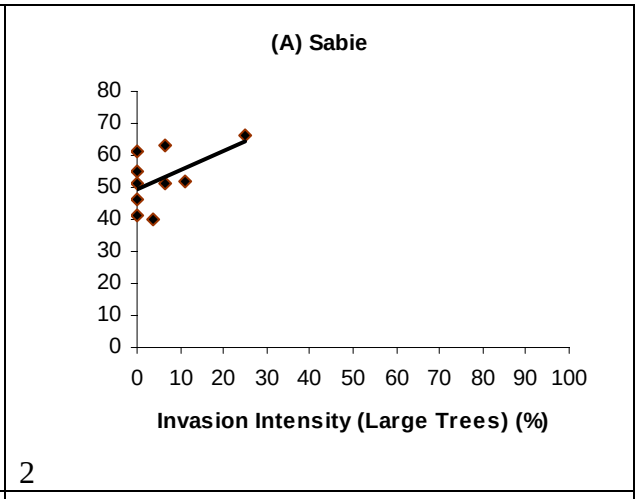
Figure 3.23. The linear relationship between total plant species richness (at the 1000 m^2 scale) and 1) total invasion intensity (% aerial cover of large alien trees, small alien trees and alien shrubs); 2) invasion intensity – aerial cover (%) of large alien trees; 3) invasion intensity – aerial cover (%) 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 ($P > 0.05$).

In the grassland, the total species richness increased slightly as the total invasion intensity and the invasion intensity of small trees increased (Figure 3.23 (1A)(3A)); it also increased as the invasion intensity of large trees increased (Figure 3.23 (2A)); and decreased slightly as the invasion intensity of shrubs increased (Figure 3.23 (4A)). In the savanna, the total species richness decreased as the total invasion intensity, and the invasion intensity of large and small trees, increased (Figure 3.23 (1B)(2B)(3B)); whereas the total species richness increased as the invasion intensity of shrubs increased (Figure 3.23 (4B)). The linear relationship between the two biomes indicates that the two data sets were similar.

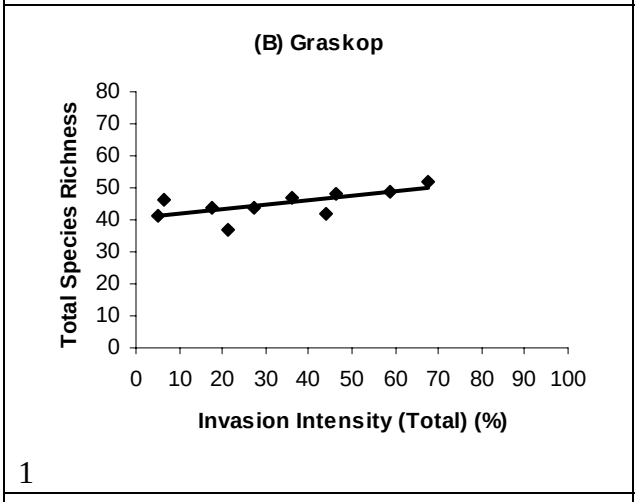
(b) Regional comparison: Sabie (grassland), Graskop (grassland) and Hazeyview (savanna)


(A) Sabie
Total Species Richness
Invasion Intensity (Total) (%)

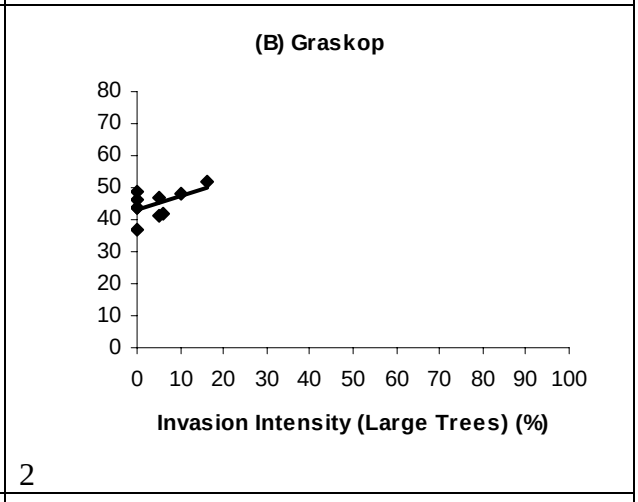
1


(A) Sabie
Invasion Intensity (Large Trees) (%)

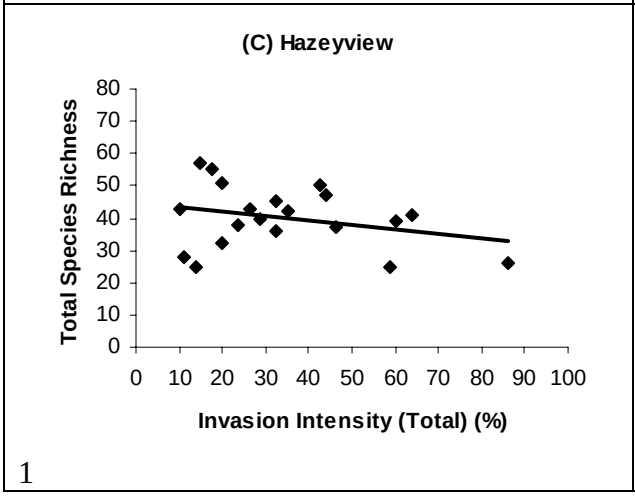
2


(B) Graskop
Total Species Richness
Invasion Intensity (Total) (%)

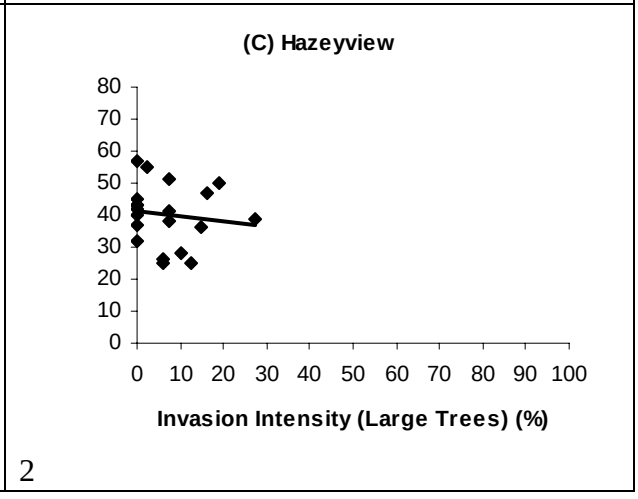
1


(B) Graskop
Invasion Intensity (Large Trees) (%)

2


(C) Hazeyview
Total Species Richness
Invasion Intensity (Total) (%)

1


(C) Hazeyview
Invasion Intensity (Large Trees) (%)

2

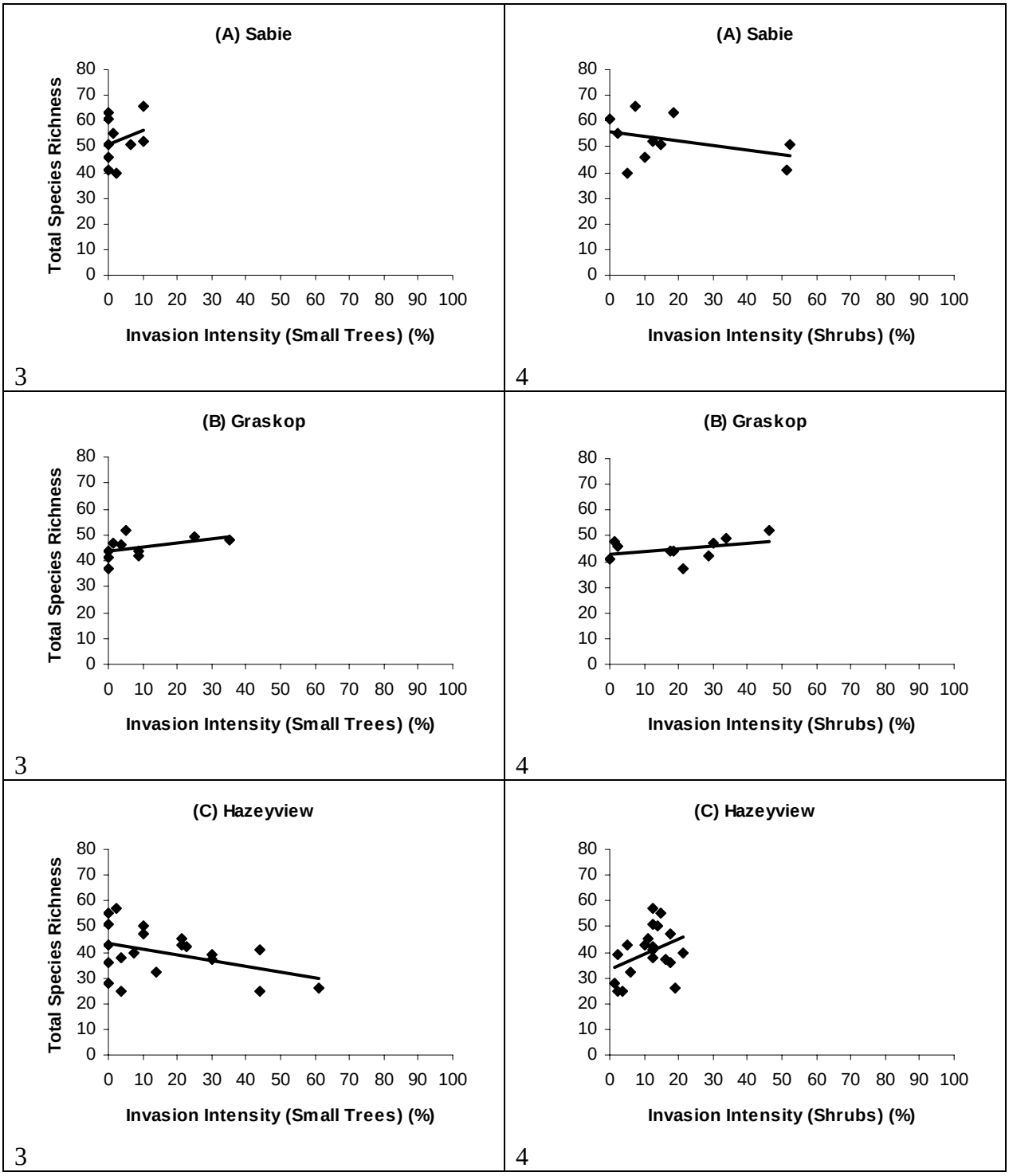


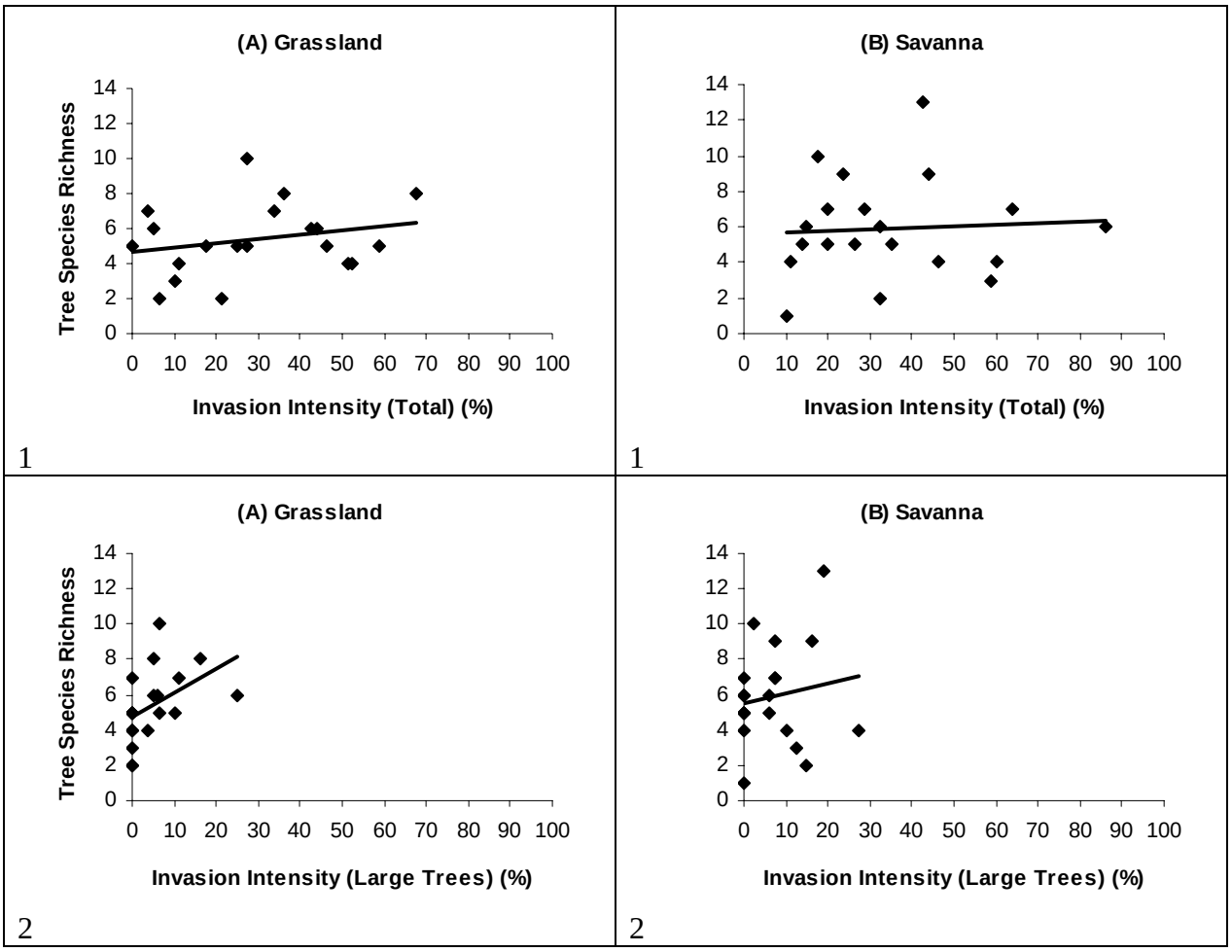
Figure 3.24. The linear relationship between total plant species richness (at the 1000 m^2 scale) and 1) total invasion intensity (% aerial cover of large alien trees, small alien trees and alien shrubs); 2) invasion intensity – aerial cover (%) of large alien trees; 3) invasion intensity – aerial cover (%) 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) ($P < 0.05$).

In the Sabie region, the total species richness decreased slightly as the total invasion intensity increased (Figure 3.24 (1A)). The total species richness increased as the invasion intensity of large and small trees increased (Figure 3.24 (2A)(3A)), and decreased as the invasion intensity of shrubs increased (Figure 3.24 (4A)). In the Graskop region, the total species richness increased as the total invasion intensity, as well as the invasion intensity of large and small trees, and shrubs, increased (Figure 3.24 (1B)(2B)(3B)(4B)). In the Hazeyview region, the total species richness decreased as the total invasion intensity, and the invasion intensity of large and small trees, increased (Figure 3.24 (1C)(2C)(3C)). The total species richness increased as the invasion intensity of shrubs increased (Figure 3.24 (4C)). The linear relationships between the three regions indicate that only the data sets between Sabie and Hazeyview (Figure 3.24 (3A and 3C)) were significantly different.

Tree species richness

(a) Biome comparison: grassland and savanna biomes



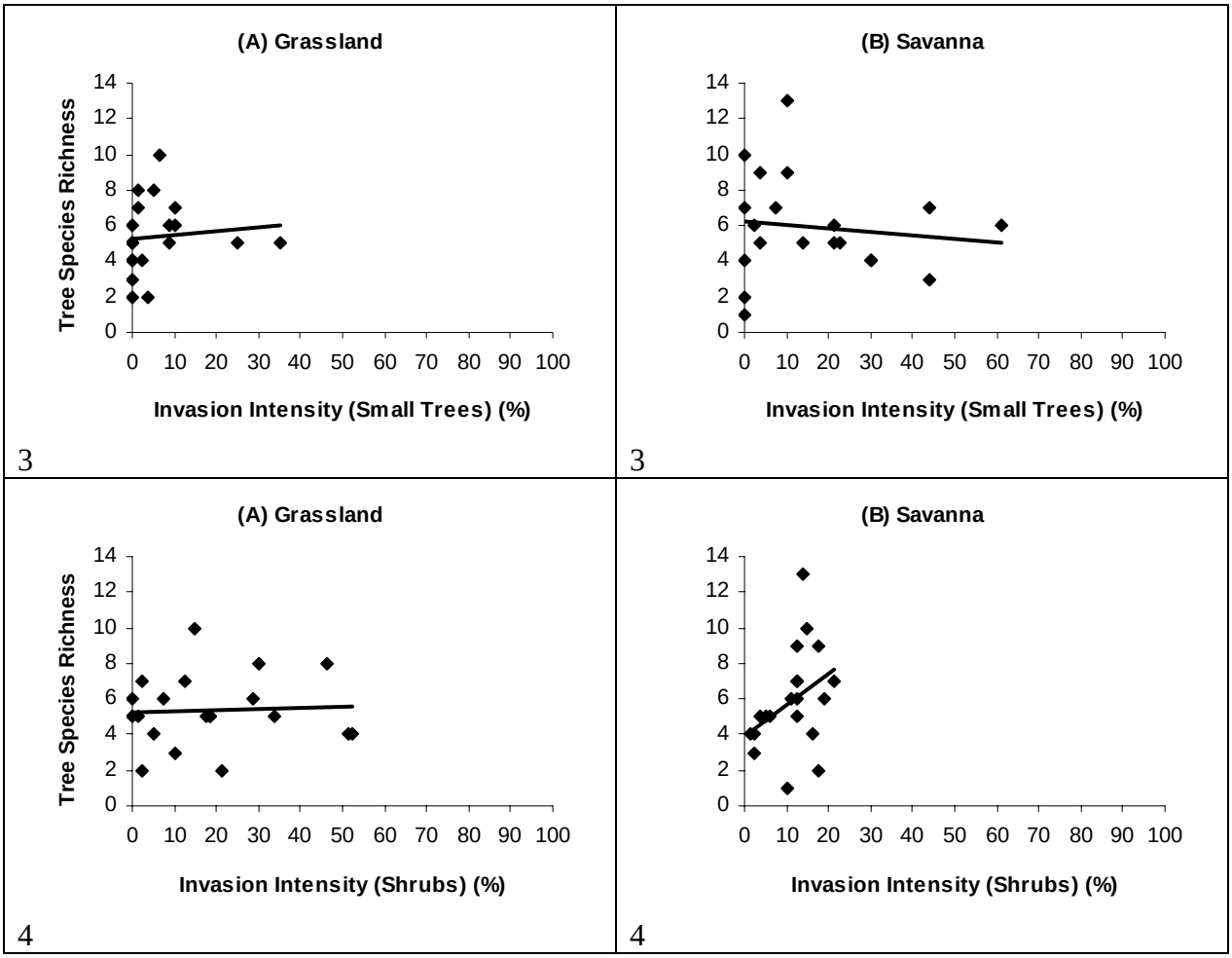
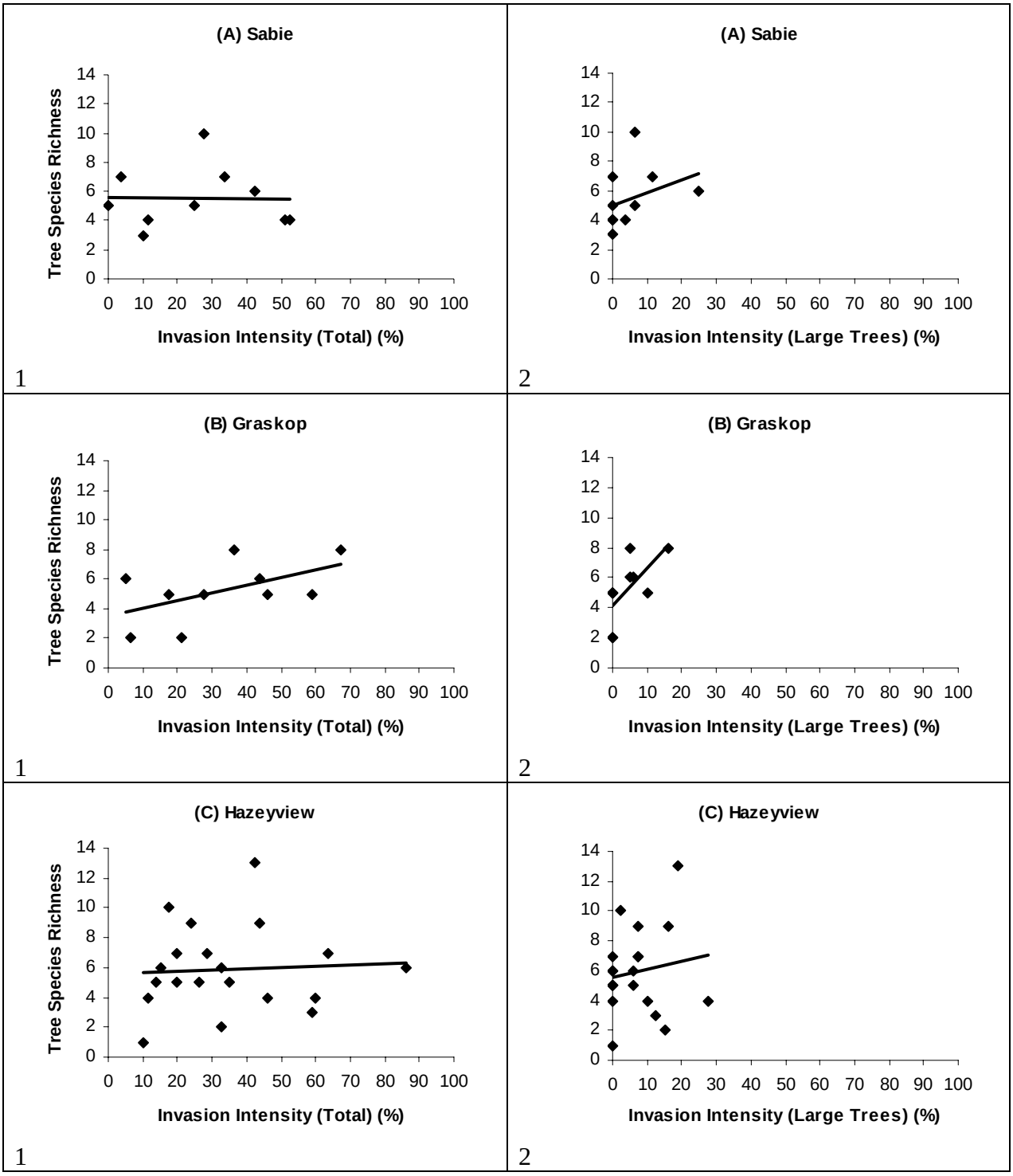


Figure 3.25. The linear relationship between tree species richness (at the 1000 m^2 scale) and 1) total invasion intensity (% aerial cover of large alien trees, small alien trees and alien shrubs); 2) invasion intensity – aerial cover (%) of large alien trees; 3) invasion intensity – aerial cover (%) 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 $r^2 = 0.06$, $y = 0.03x + 4.61$ 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 ($P > 0.05$).

In the grassland, the tree species richness increased as the total invasion intensity, as well as the invasion intensity of large and small trees, increased (Figure 3.25 (1A)(2A)(3A)). The tree species richness increased only slightly as the invasion intensity of the shrubs increased (Figure 3.25 (4A)). In the savanna, the tree species richness increased very slightly as the total invasion intensity increased (Figure 3.25 (1B)). The tree species richness increased as the invasion intensity of large trees and shrubs increased (Figure 3.25 (2B)(4B)), and decreased as the invasion intensity of small trees increased (Figure 3.25 (3B)). The linear relationship between the two biomes indicates that the two data sets were similar.

(b) Regional comparison: Sabie (grassland), Graskop (grassland) and Hazeyview (savanna)



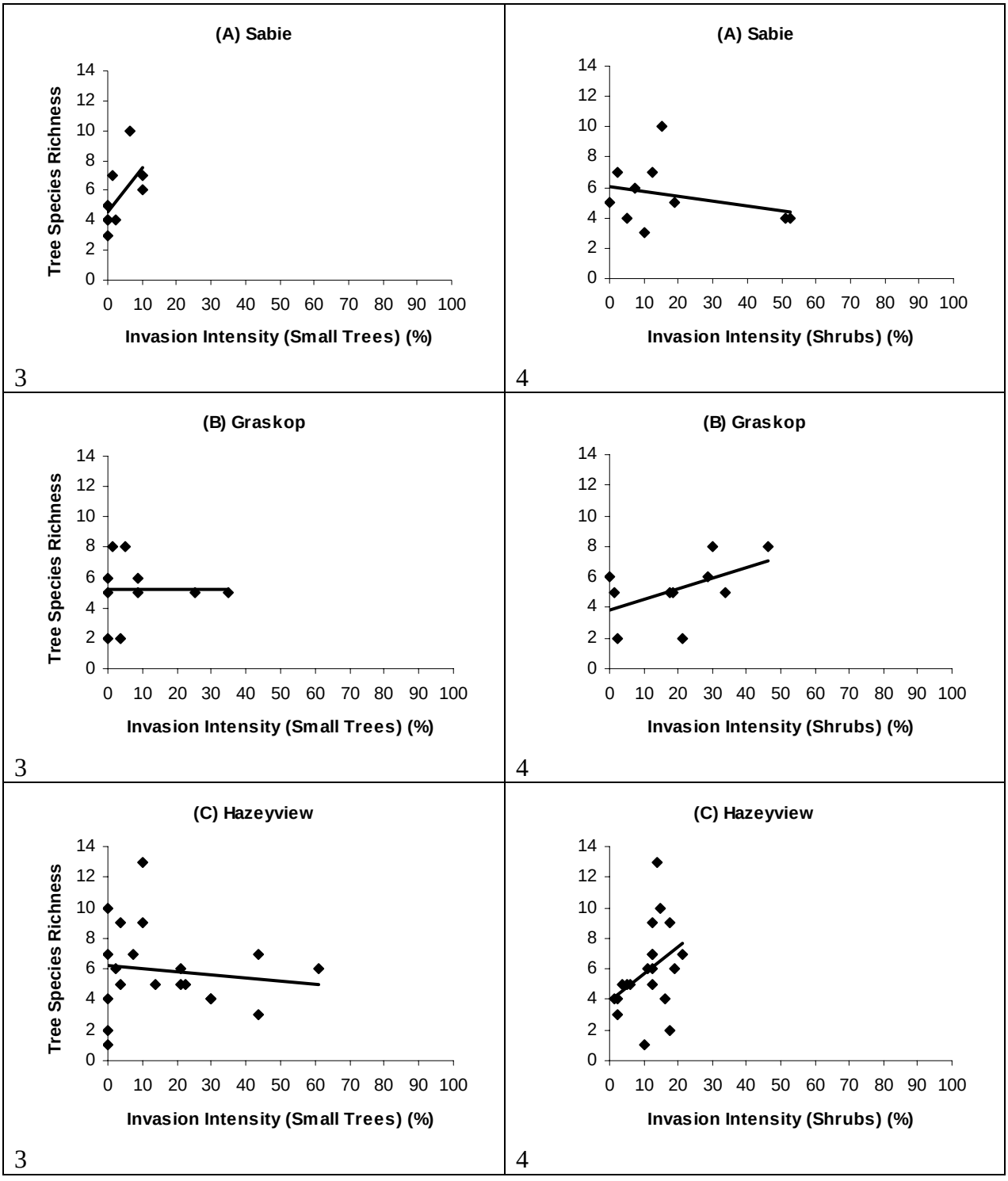


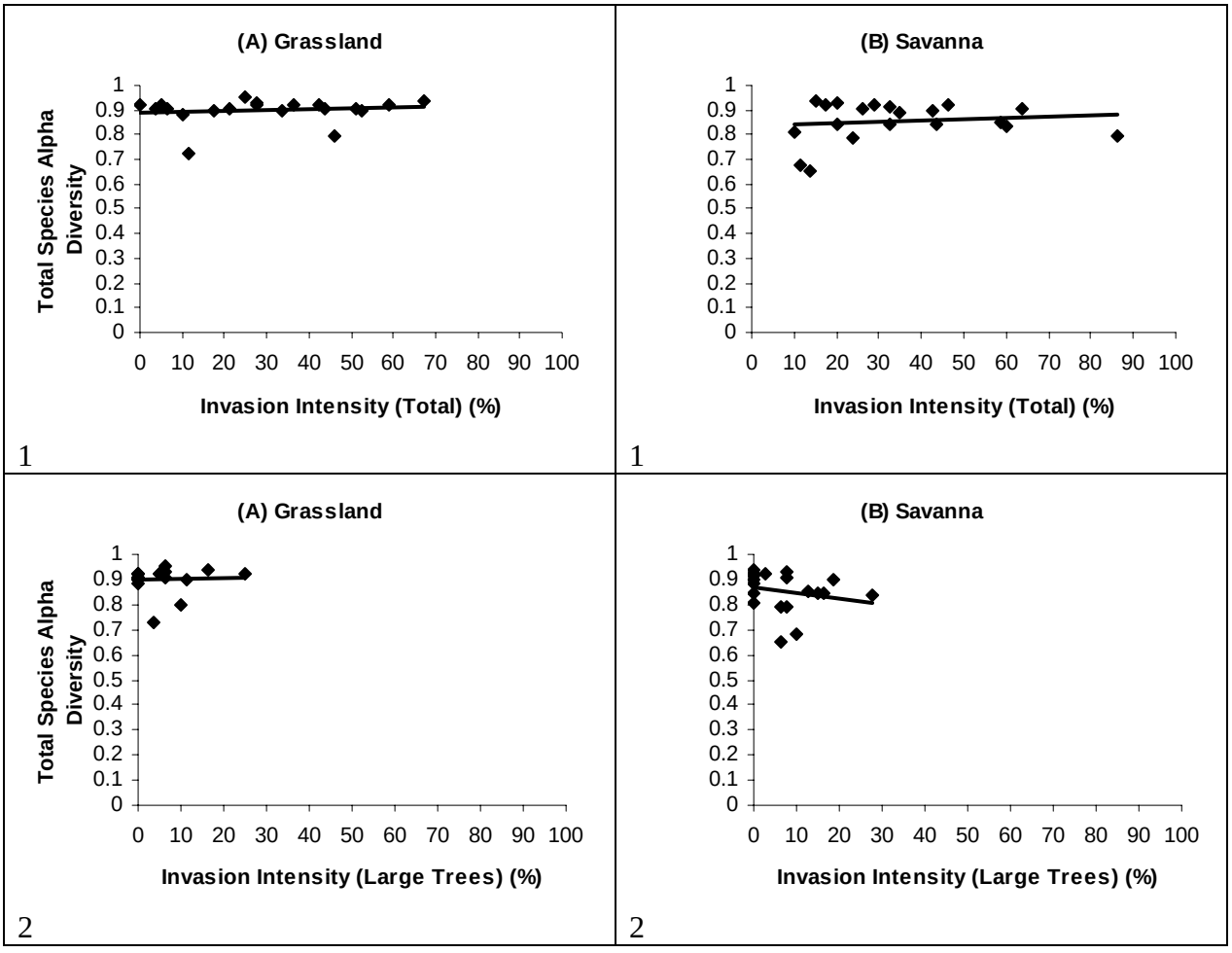
Figure 3.26. The linear relationship between tree species richness (at the 1000 m^2 scale) and 1) total invasion intensity (% aerial cover of large alien trees, small alien trees and alien shrubs); 2) invasion intensity – aerial cover (%) of large alien trees; 3) invasion intensity – aerial cover (%) 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 $r^2 = 0.001$, $y = -0.003x + 5.57$, (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 $r^2 =$

$3x10^{-6}$, 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) ($P < 0.05$).

In the Sabie region, the tree species richness remained unchanged with increasing total invasion intensity (Figure 3.26 (1A)). However, the tree species richness increased with increasing invasion intensity of large and small trees (Figure 3.26 (2A)(3A)), and decreased with increasing invasion intensity of shrubs (Figure 3.26 (4A)). In the Graskop region, the tree species richness increased with increasing total invasion intensity, as well as the invasion intensity of large trees and shrubs (Figure 3.26 (1B)(2B)(4B)). The tree species richness remained unchanged with increasing invasion intensity of small trees (Figure 3.26 (3B)). In the Hazeyview region, the tree species richness increased slightly with increasing total invasion intensity (Figure 3.26 (1C)). The tree species richness increased with increasing invasion intensity of large trees and shrubs (Figure 3.26 (2C) (4C)), and decreased with increasing invasion intensity of small trees (Figure 3.26 (3C)). Only the data sets between Sabie and Hazeyview (Figure 3.26 (3A and 3C)) were significantly different.

Simpson's index of diversity (alpha diversity) for total plant species

(a) Biome comparison: grassland and savanna biomes



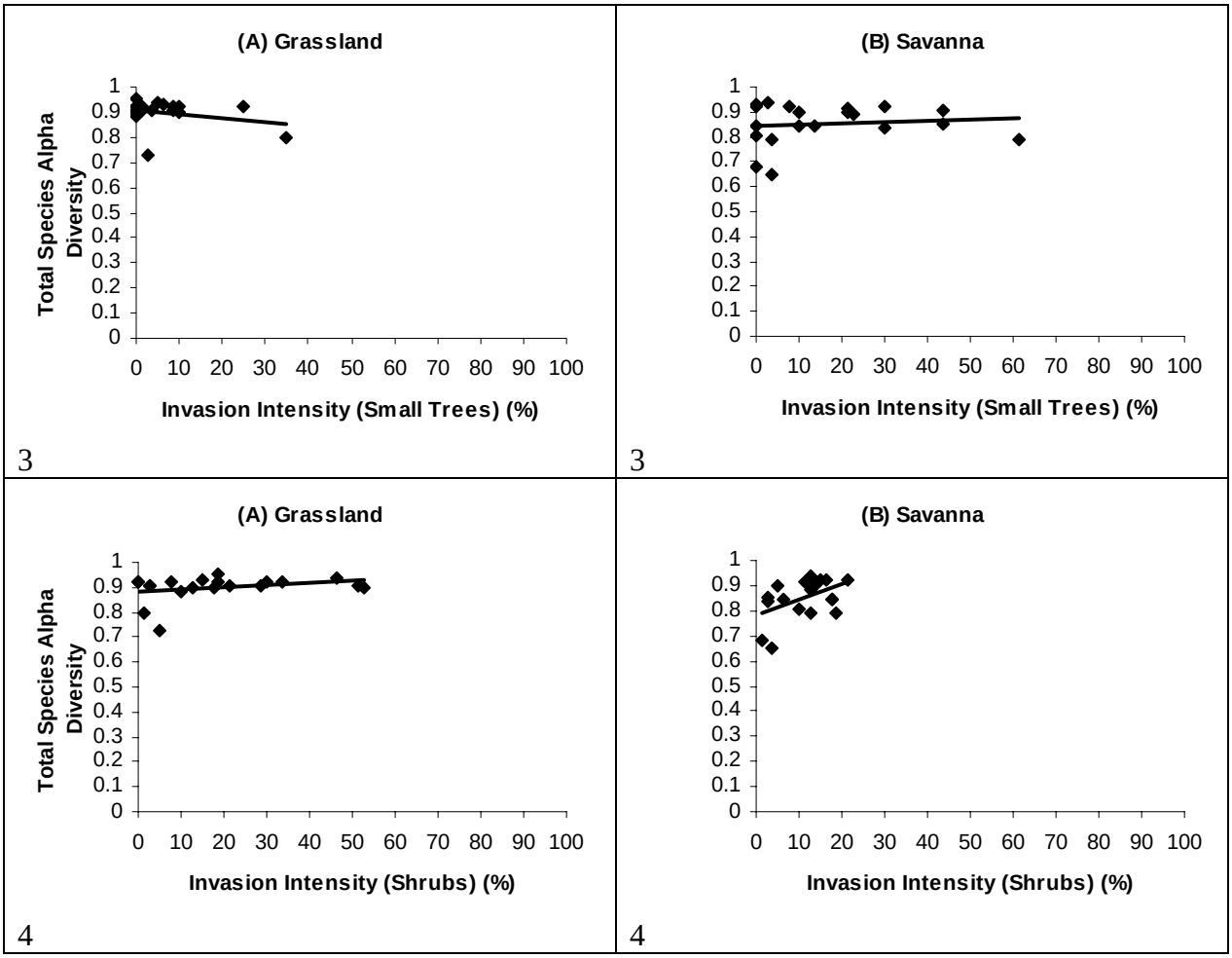
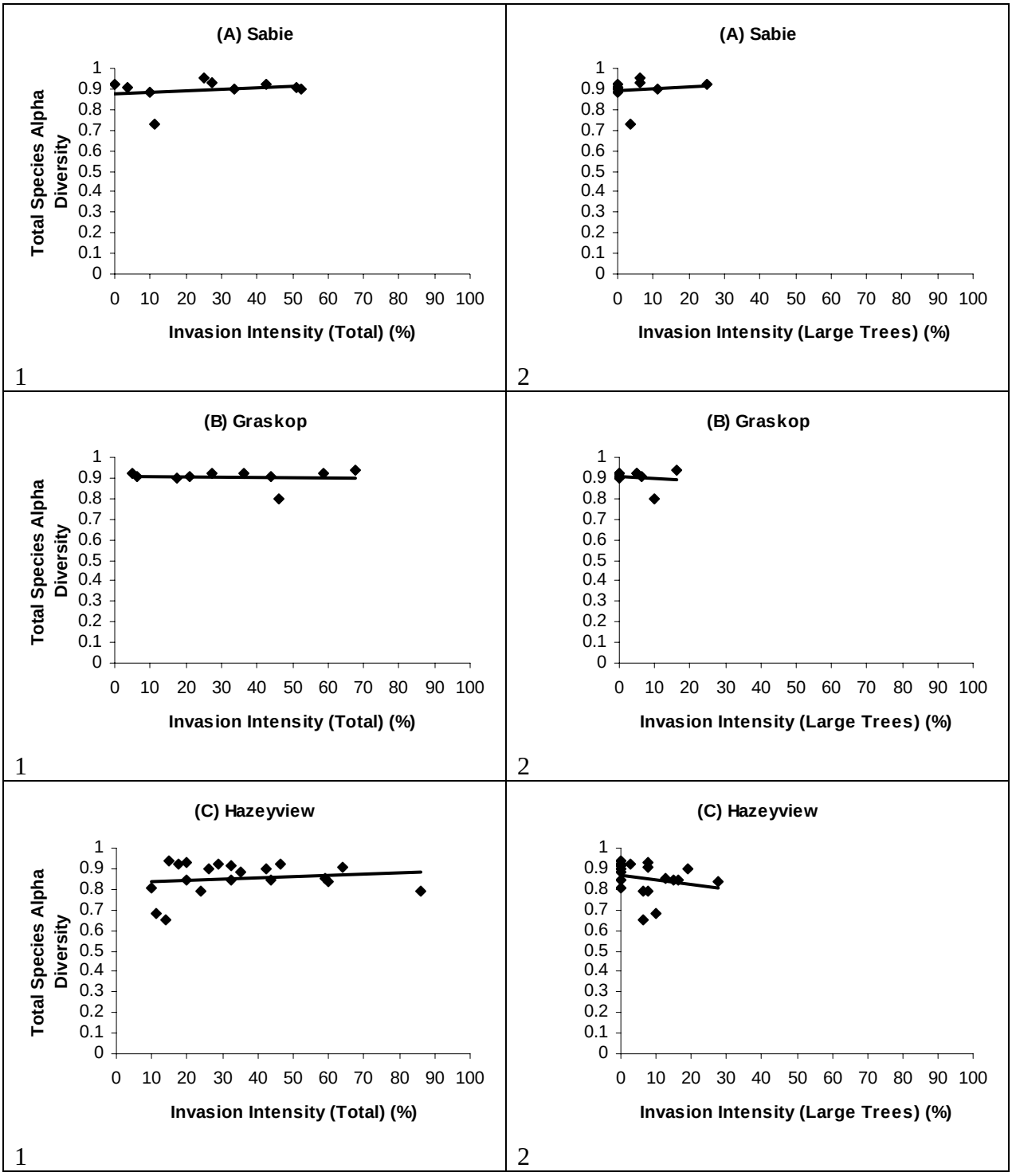


Figure 3.27. The linear relationship between total plant species Simpson's index of diversity (alpha diversity) (at the 100 m^2 scale) and 1) total invasion intensity (% aerial cover of large alien trees, small alien trees and alien shrubs); 2) invasion intensity – aerial cover (%) of large alien trees; 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 $r^2 = 0.02$, $y = 0.0003x + 0.89$ 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 ($P > 0.05$).

In the grassland biome, there was only a very slight increase in the total species alpha diversity with increasing total invasion intensity, and invasion intensity of large trees and shrubs (Figure 3.27 (1A)(2A)(4A)). There was a slight decrease in the total species alpha diversity with increasing invasion intensity of small trees (Figure 3.27 (3A)). In the savanna, there was only a very slight increase in the total species alpha diversity with increasing total invasion intensity and invasion intensity of small trees (Figure 3.27 (1B)(3B)). The total species alpha diversity decreased with increasing invasion intensity of large trees (Figure 2.27 (2B)), and increased with increasing invasion intensity of shrubs (Figure 3.27 (4B)). The linear relationship between the two biomes indicates that the two data sets were similar.

(b) Regional comparison: Sabie (grassland), Graskop (grassland) and Hazeyview (savanna)



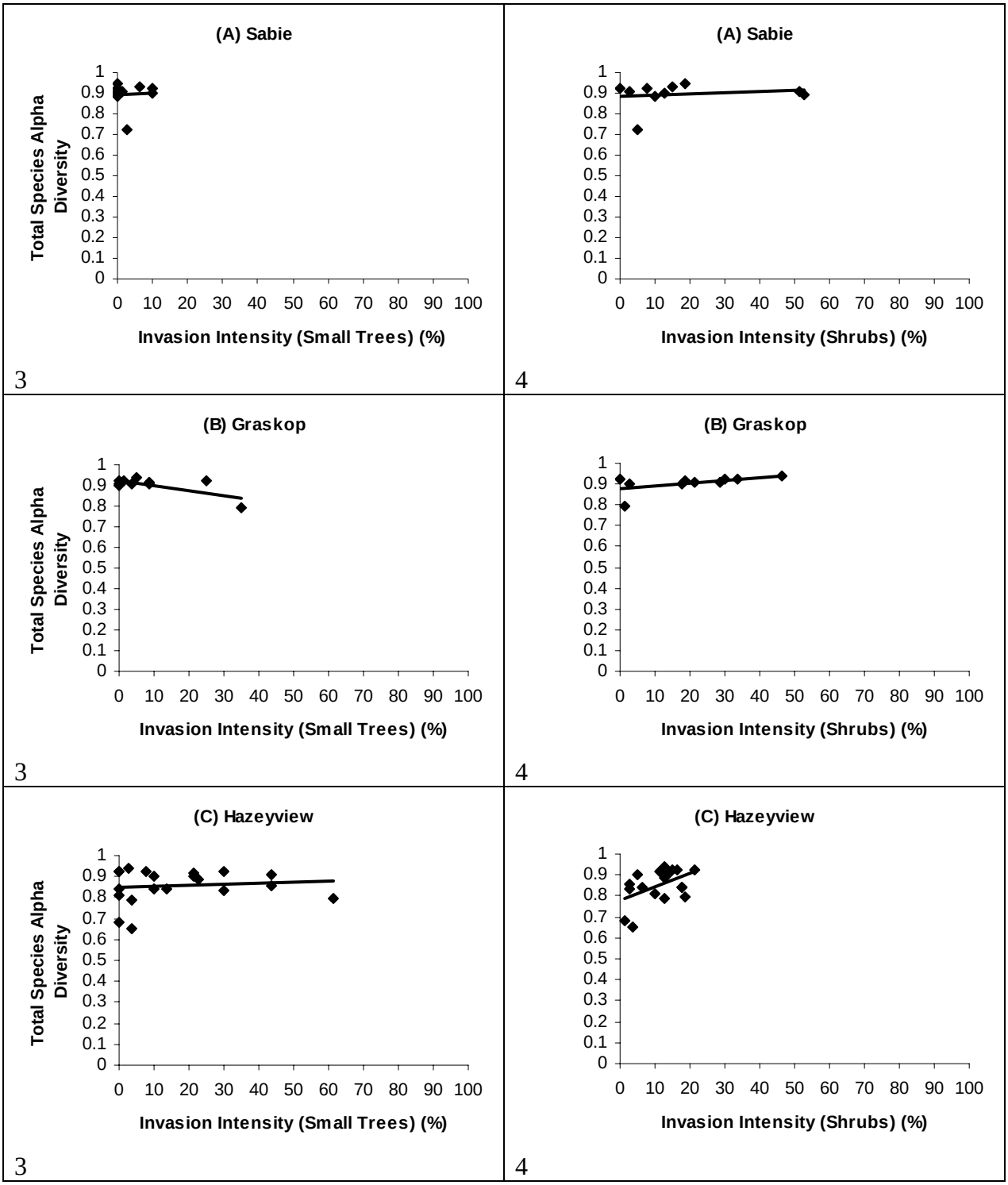
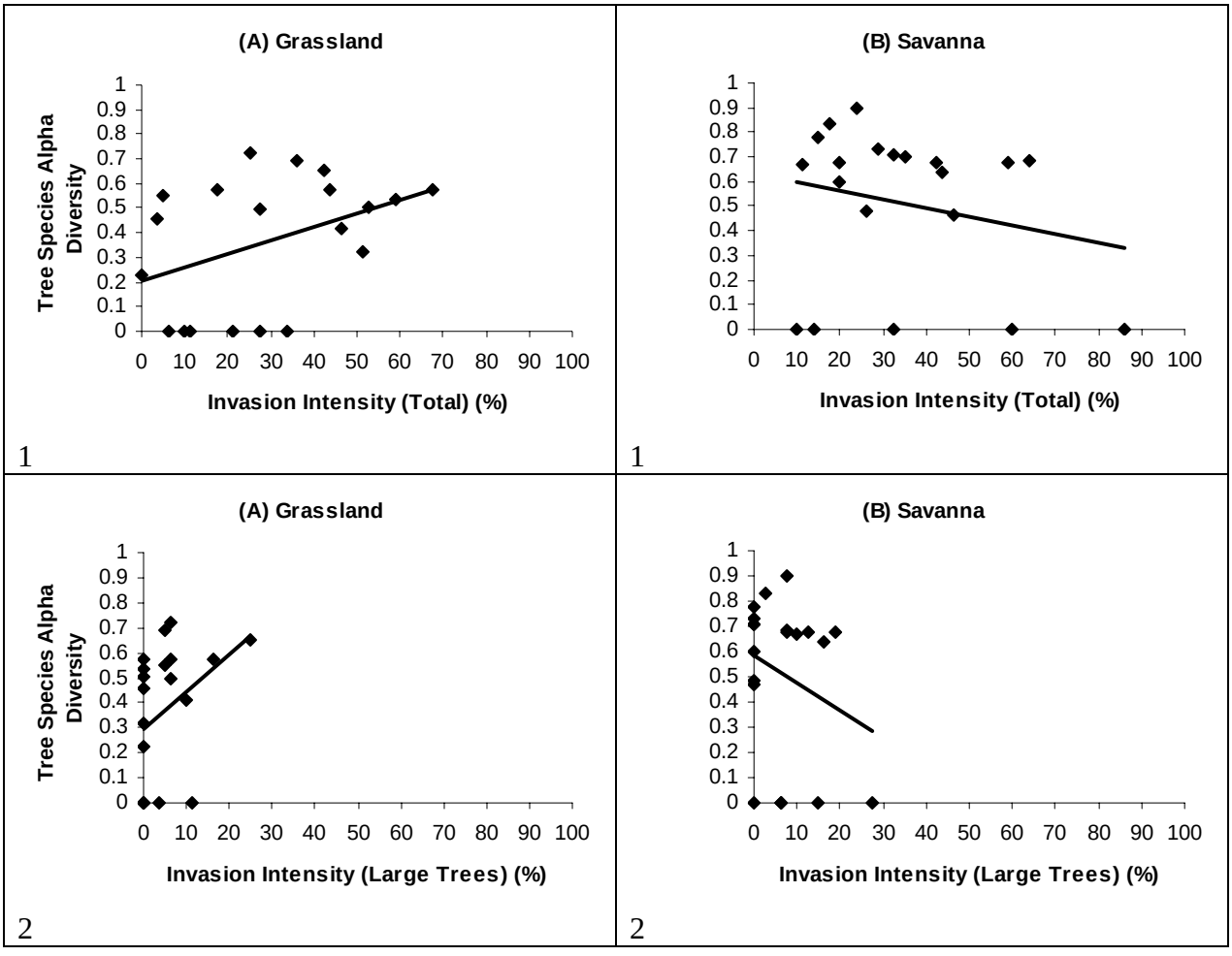


Figure 3.28. The linear relationship between total plant species Simpson's index of diversity (alpha diversity) (at the 100 m^2 scale) and 1) total invasion intensity (% aerial cover of large alien trees, small alien trees and alien shrubs); 2) invasion intensity – aerial cover (%) of large alien trees; 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 $r^2 = 0.06$, $y = 0.001x + 0.87$, (B) is $r^2 = 0.002$, $y = -8x10^{-6}x + 0.91$ 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 ($P > 0.05$).

In the Sabie region, there was only a very slight increase in the total species alpha diversity with increasing total invasion intensity, as well as the invasion intensity of large and small trees, and shrubs (Figure 3.28 (1A)(2A)(3A)(4A)). In the Graskop region, there was a very slight decrease in the total species alpha diversity with increasing total invasion intensity and the invasion intensity of large trees (Figure 3.28 (1B)(2B)). There was a decrease in the total species alpha diversity with increasing invasion intensity of small trees (Figure 3.28 (3B)), and an increase with increasing invasion intensity of shrubs (Figure 3.28 (4B)). In the Hazeyview region, there was a very slight increase in the total species alpha diversity with increasing total invasion intensity and the invasion intensity of small trees (Figure 3.28 (1C)(3C)). There was a very slight decrease in the total species alpha diversity with increasing invasion intensity of large trees (Figure 3.28 (2C)), and an increase with increasing invasion intensity of shrubs (Figure 3.28 (4C)). The linear relationships between the three regions indicate that the three data sets were similar.

Simpson's index of diversity (alpha diversity) for tree species
(a) Biome comparison: grassland and savanna biomes



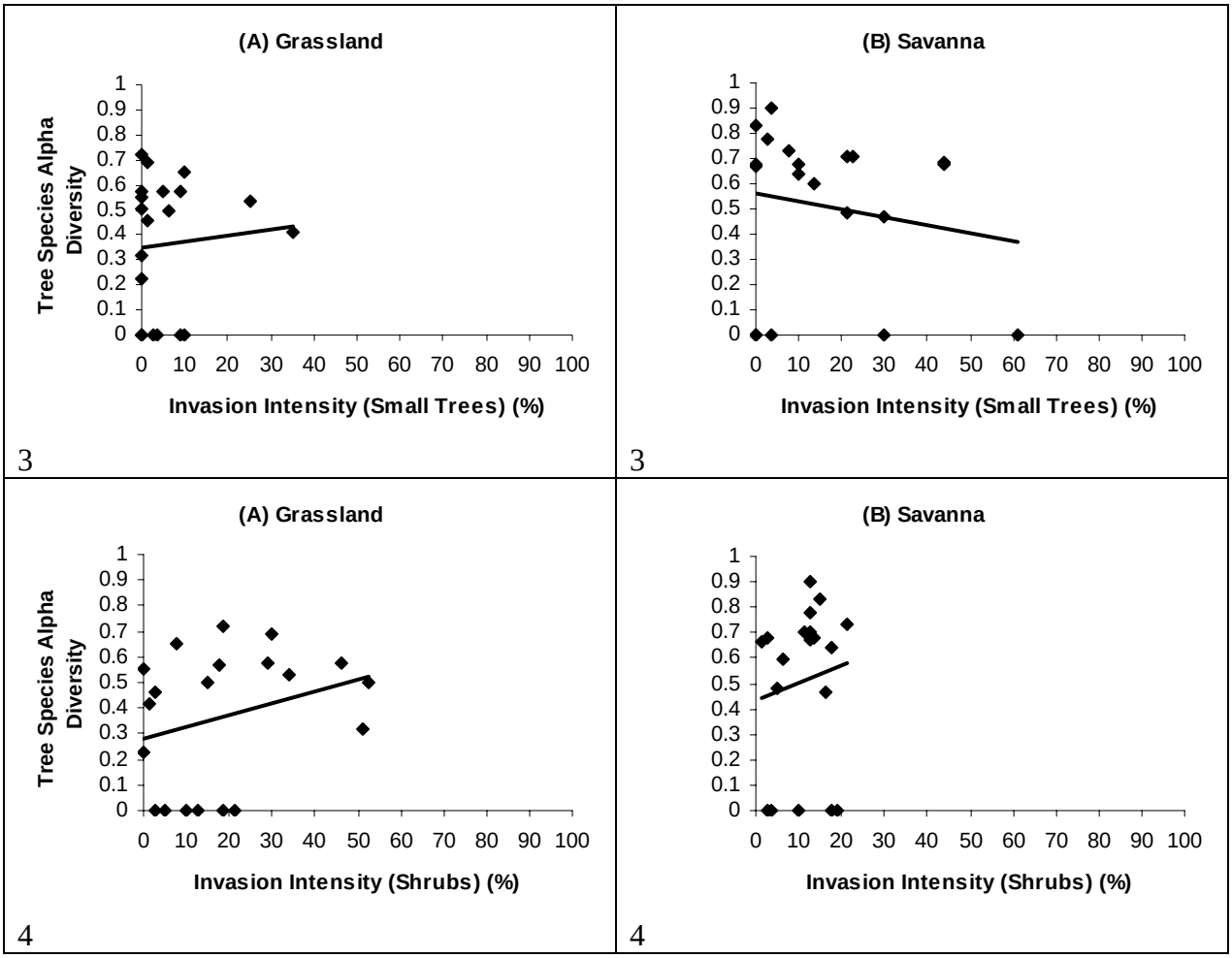
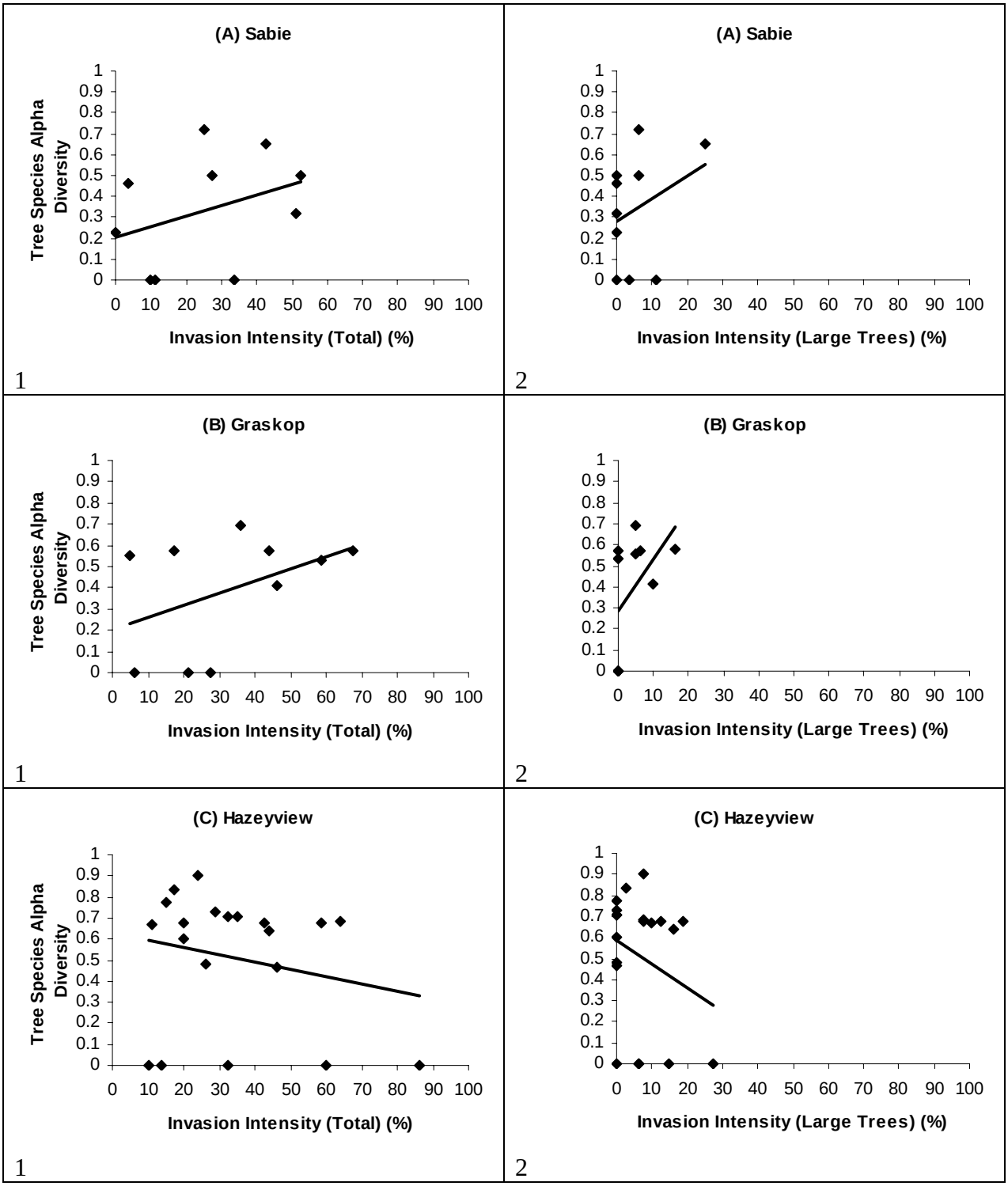


Figure 3.29. The linear relationship between tree species Simpson's index of diversity (alpha diversity) (at the 100 m^2 scale) and 1) total invasion intensity (% aerial cover of large alien trees, small alien trees and alien shrubs); 2) invasion intensity – aerial cover (%) of large alien trees; 3) 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 $r^2 = 0.17$, $y = 0.01x + 0.20$ 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 ($P > 0.05$).

In the grassland, the tree species alpha diversity increased with increasing total invasion intensity, as well as the invasion intensity of large and small trees, and shrubs (Figure 3.29 (1A)(2A)(3A)(4A)). In the savanna, the tree species alpha diversity decreased with increasing total invasion intensity, as well as the invasion intensity of large and small trees (Figure 3.29 (1B)(2B)(3B)). The tree species alpha diversity increased with increasing invasion intensity of shrubs (Figure 3.29 (4B)). The linear relationship between the two biomes indicates that the two data sets were similar.

(b) Regional comparison: Sabie (grassland), Graskop (grassland) and Hazeyview (savanna)



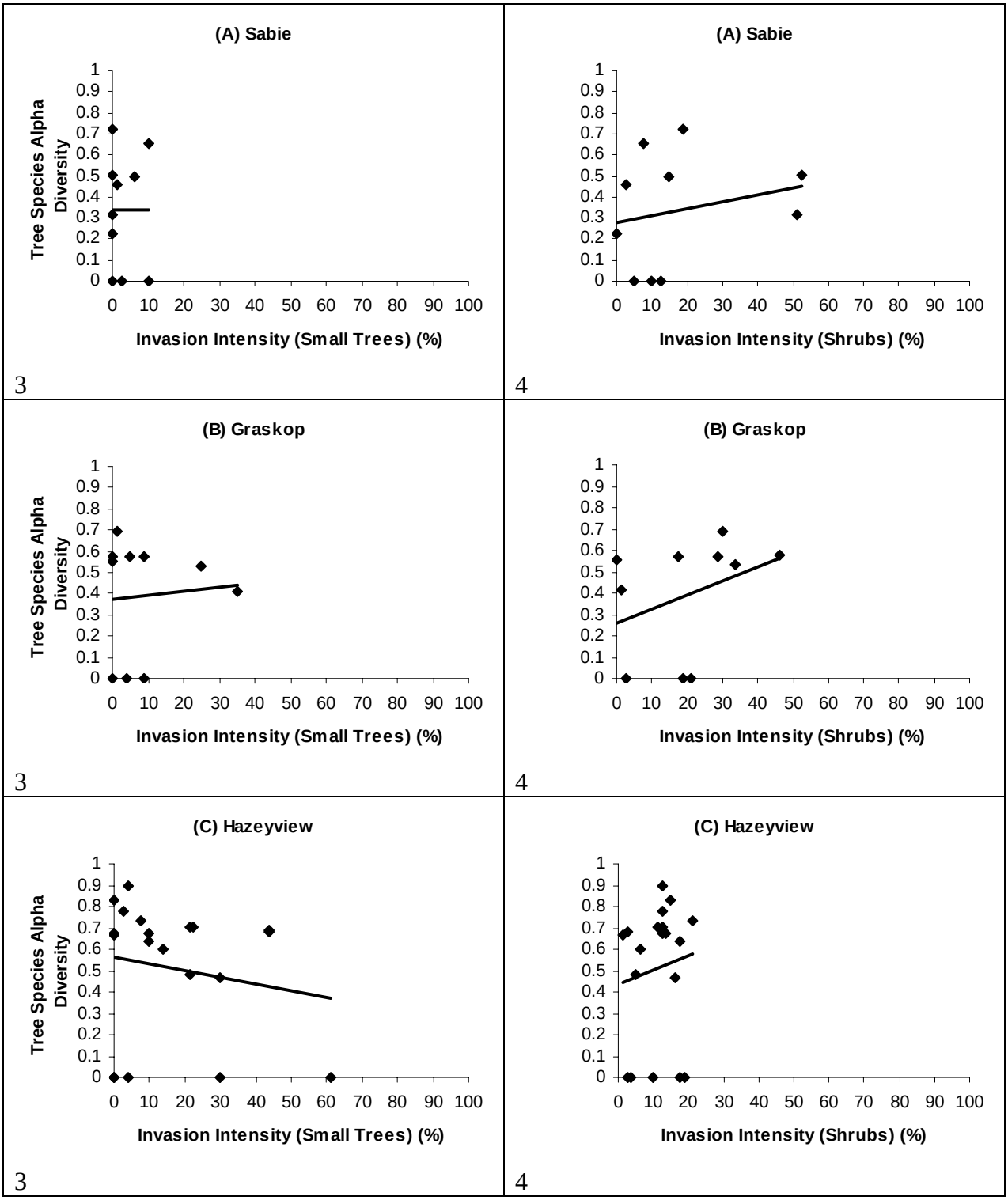


Figure 3.30. The linear relationship between tree species Simpson's index of diversity (alpha diversity) (at the 100 m^2 scale) and 1) total invasion intensity (% aerial cover of large alien trees, small alien trees and alien shrubs); 2) invasion intensity – aerial cover (%) of large alien trees; 3) 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 $r^2 = 0.13$, $y = 0.01x + 0.21$, (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 $r^2 = 6x10^{-6}$, 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 ($P > 0.05$).

In the Sabie region, the tree species alpha diversity increased with increasing total invasion intensity, as well as the invasion intensity of large trees and shrubs (Figure 3.30 (1A)(2A)(4A)). The tree species alpha diversity remained unchanged with increasing invasion intensity of small trees (Figure 3.30 (3A)). In the Graskop region, the tree species alpha diversity increased with increasing total invasion intensity, as well as the invasion intensity of large and small trees, and shrubs (Figure 3.30 (1B)(2B)(3B)(4B)). In the Hazeyview region, the tree species alpha diversity decreased with increasing total invasion intensity, as well as the invasion intensity of large and small trees (Figure 3.30 (1C)(2C)(3C)). The tree species alpha diversity increased with increasing invasion intensity of shrubs (Figure 3.30 (4C)). The linear relationships between the three regions indicate that the three data sets were similar.

3.4.5 Linear regression analyses of the indigenous and alien plant species richness

(a) For all 40 plots

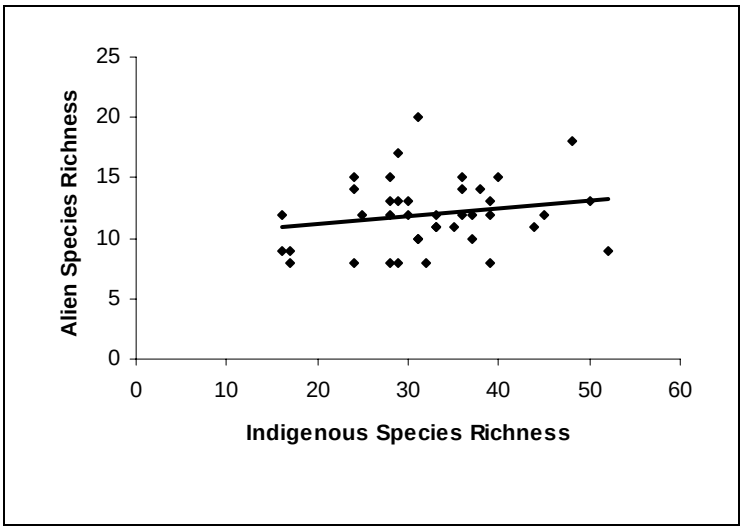


Figure 3.31. The linear relationship between the total indigenous and alien plant species richness (r^2 = 0.04). The linear relationship is y = 0.06x + 9.83.

There was a slight positive regression relationship between indigenous and alien species richness (Figure 3.31).

(b) Biome comparison: grassland and savanna biomes

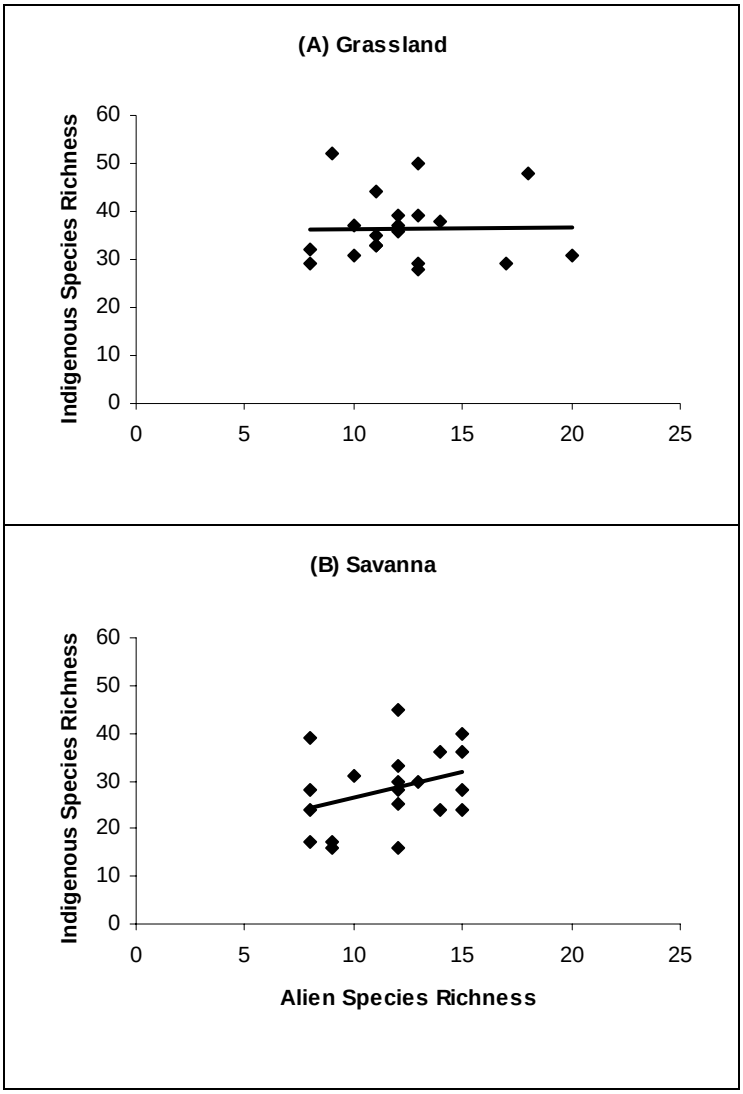


Figure 3.32. The linear relationship between the indigenous and alien plant species richness for plots in the (A) grassland biome ($r^2 = 5x10^{-6}$, y = 0.02x + 36.3) and (B) savanna biome ($r^2 = 0.12$, y = 1.08x + 15.7). The slopes of these regression lines were not significantly different ($P > 0.05$).

In the grassland, the indigenous species richness remained unchanged with increasing alien species richness (Figure 3.32 (A)). In the savanna, the indigenous species richness increased with increasing alien species richness (Figure 3.32 (B)). The linear relationship between the two biomes indicates that the two data sets were similar.

(c) Regional comparison: Sabie (grassland), Graskop (grassland) and Hazeyview (savanna)

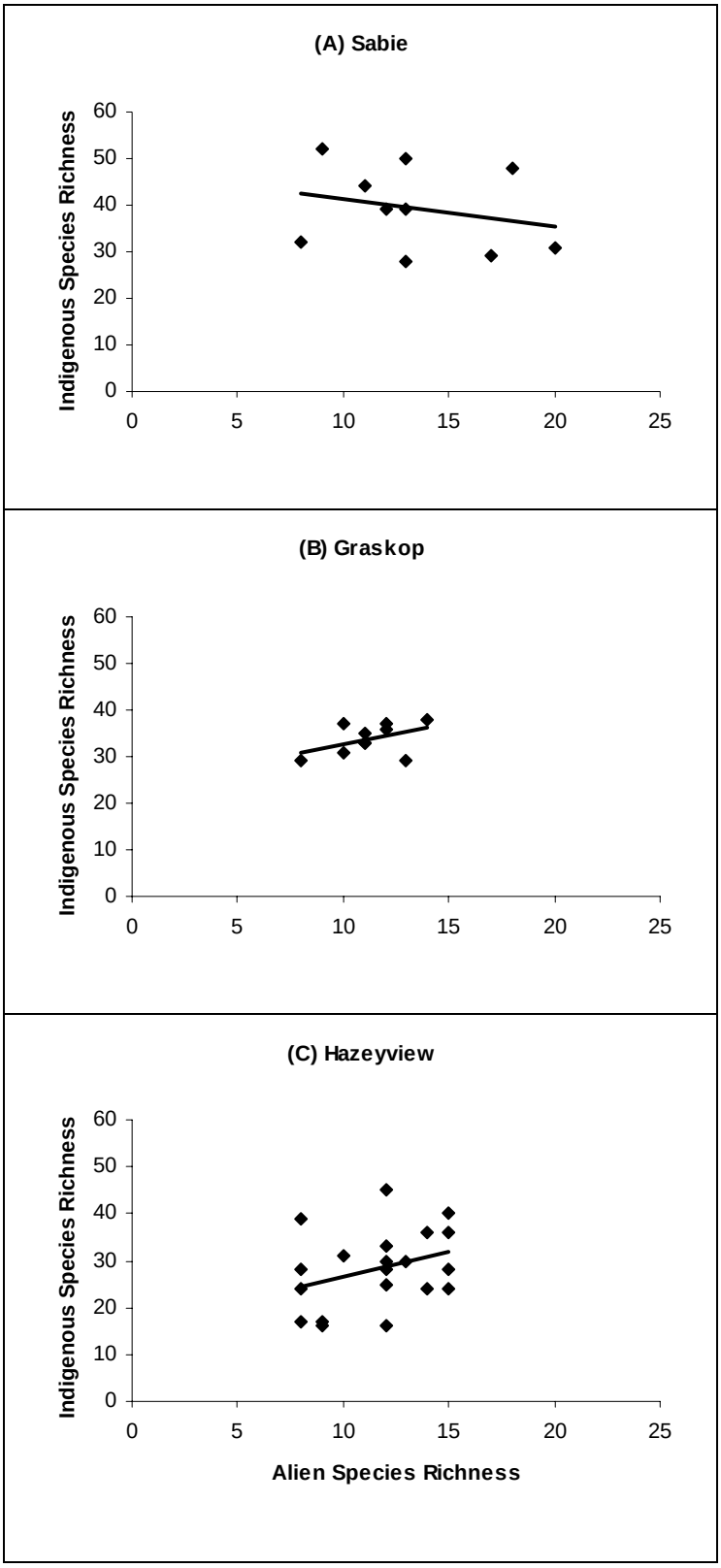


Figure 3.33. The linear relationship between the indigenous and alien plant species richness for plots in the (A) Sabie ($r^2 = 0.06$, $y = -0.59x + 47.06$), (B) Graskop ($r^2 = 0.20$, $y = 0.88x + 24$) and (C) Hazeyview ($r^2 = 0.12$, $y = 1.08x + 15.71$) regions. The slopes of these regression lines were not significantly different ($P > 0.05$), except between Graskop and Hazeyview ($P < 0.05$).

In the Sabie region, the indigenous species richness decreased with increasing alien species richness (Figure 3.33 (A)), whereas in the Graskop and Hazeyview regions, the indigenous species richness increased with increasing alien species richness (Figure 3.33 (B)(C)). The linear relationships between the three regions indicate that only the data sets between Graskop and Hazeyview were significantly different.

(d) Growth form comparison: tree, shrub, herbaceous and grass growth forms

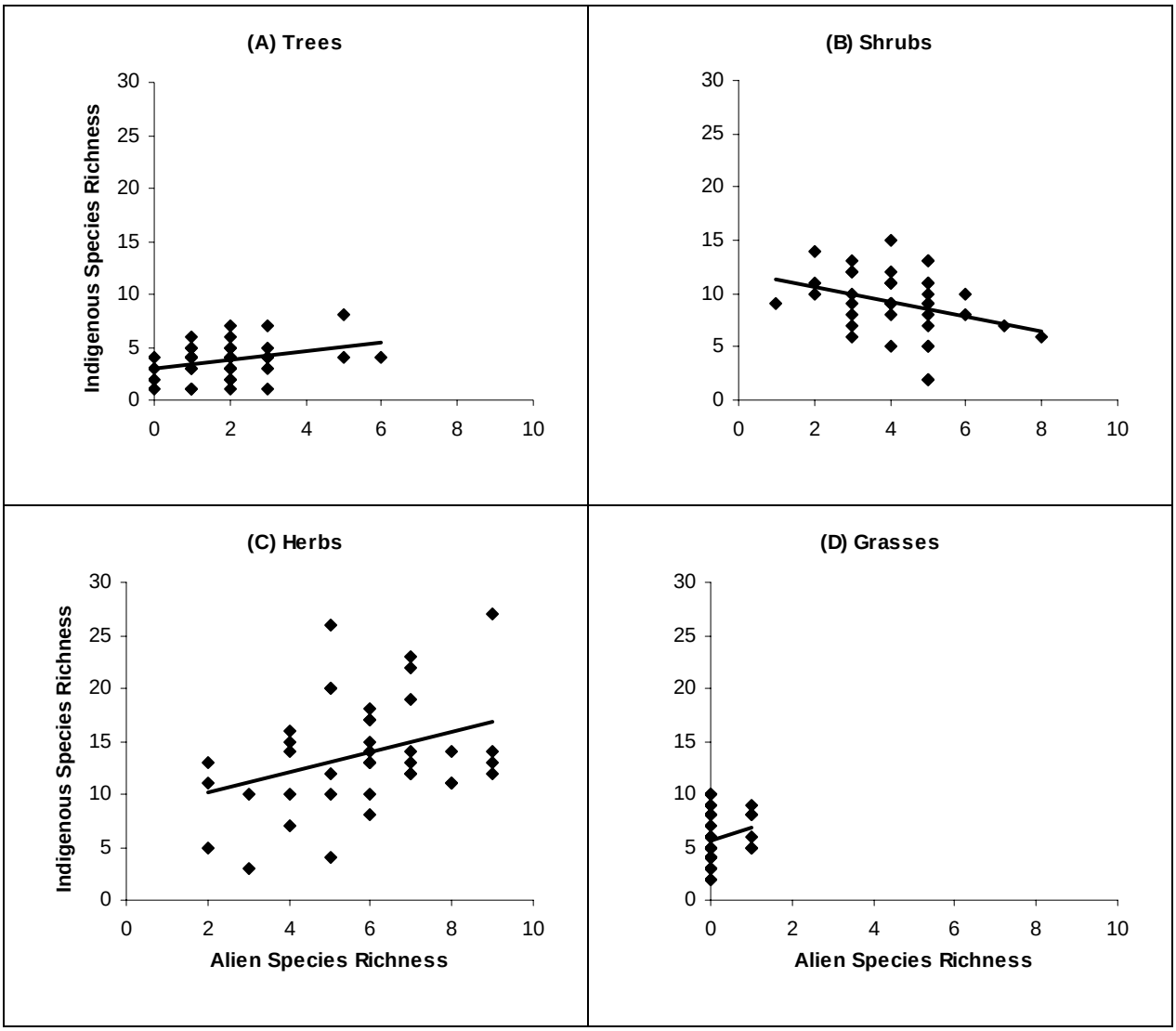


Figure 3.34. The linear relationship between the (A) indigenous and alien tree species richness ($r^2 = 0.10$, $y = 0.39x + 3.02$), (B) indigenous and alien shrub species richness ($r^2 = 0.11$, $y = -0.71x + 12.10$), (C) indigenous and alien herbaceous species richness ($r^2 = 0.12$, $y = 0.95x + 8.28$) 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 ($P > 0.05$).

The indigenous tree, herbaceous and grass species richness increased as the alien tree, herbaceous and grass species richness increased (Figure 3.34 (A)(C)(D)). The indigenous shrub species richness decreased with increasing alien shrub species

richness (Figure 3.34 (B)). The linear relationships between the growth forms indicate that the data sets were similar.

3.4.6 Detrended correspondece analysis (DCA) of the indigenous and alien plant species composition between the grassland and savanna plots, in 2005

A multivariate statistical analysis was done using the unimodal, indirect gradient analysis (unconstrained) method (DCA) in CANOCO. The analysis was done on the species data and the grassland and savanna plots in order to determine if there were any relationships between the species and the plots.

Table 3.10. Summary of the detrended correspondence analysis (DCA).

Axes	1	2	3	4	Total inertia
Eigenvalues:	0.715	0.423	0.311	0.268	8.842
Lengths of gradient:	5.786	3.798	2.931	2.588	
Cumulative % variance of species data:	8.1	12.9	16.4	19.4	
Sum of all eigenvalues:					8.842

The gradient length is another way of determining the beta diversity in community composition (the extent of species turnover) along the individual independent gradients (ordination axes) (Leps and Smilauer, 2003). Because the length of the longest gradient was > 4, the use of the unimodal method was appropriate (Leps and Smilauer, 2003). The longest gradient was axis 1, which explained about 8% of the total species variability, whereas the other axes explained a lot less.

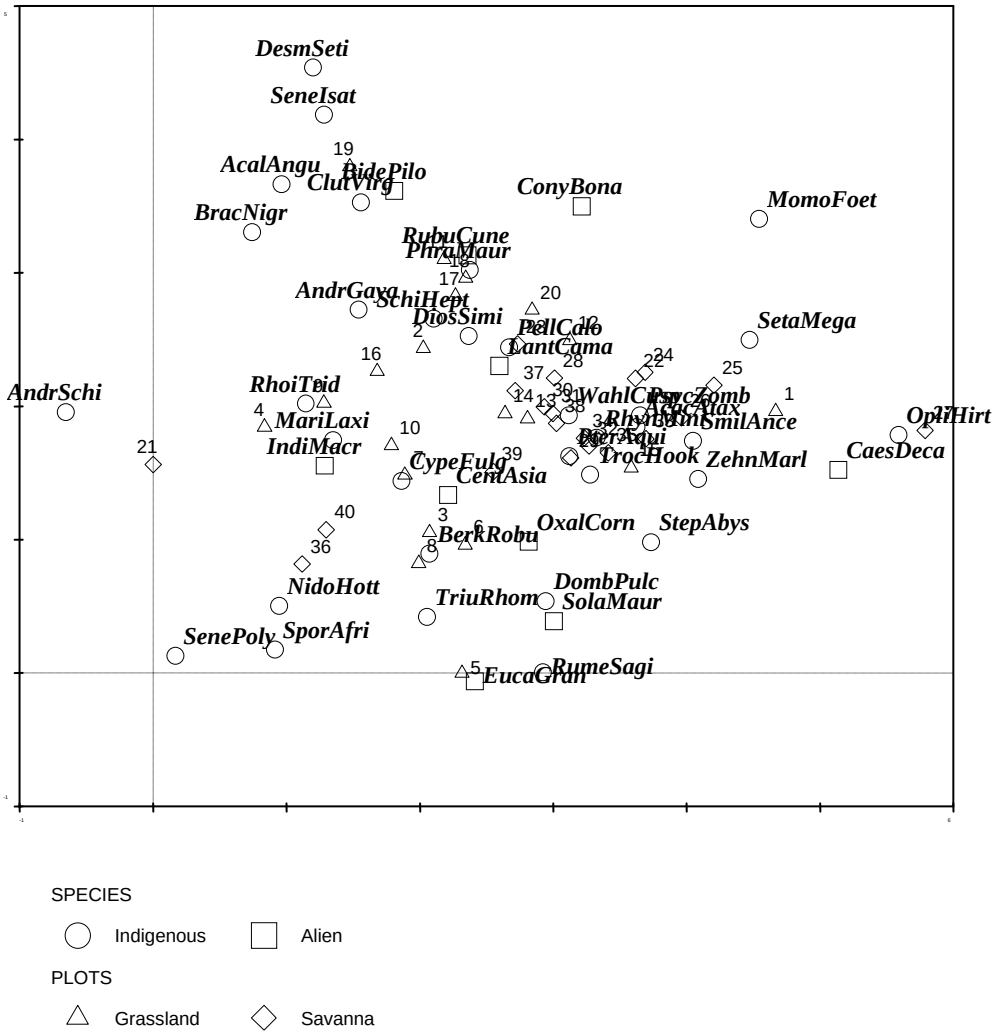


Figure 3.35. Detrended correspondence analysis (DCA) of plant species (with a weight of 10 – 100%) in the 40 plots at the 100 m^2 scale, in 2005. Plots were categorised into grassland and savanna, and species into indigenous and alien. Species are labeled by the first four letters of the generic name and the first four letters of the specific name (refer to Appendix 2 for species names).

The general distribution (Figure 3.35) suggests that there was a continuous variation of species composition in the whole data set. Therefore, no distinct vegetation types were found grouped together in the data set. Most of the savanna plots lay near each other, which indicated that they were more similar in terms of the composition of co-occurring species than the grassland plots. This might be partially due to the savanna plots coming from a single region (Hazeyview) compared with the grassland plots being split between two regions (i.e. Sabie and Graskop).

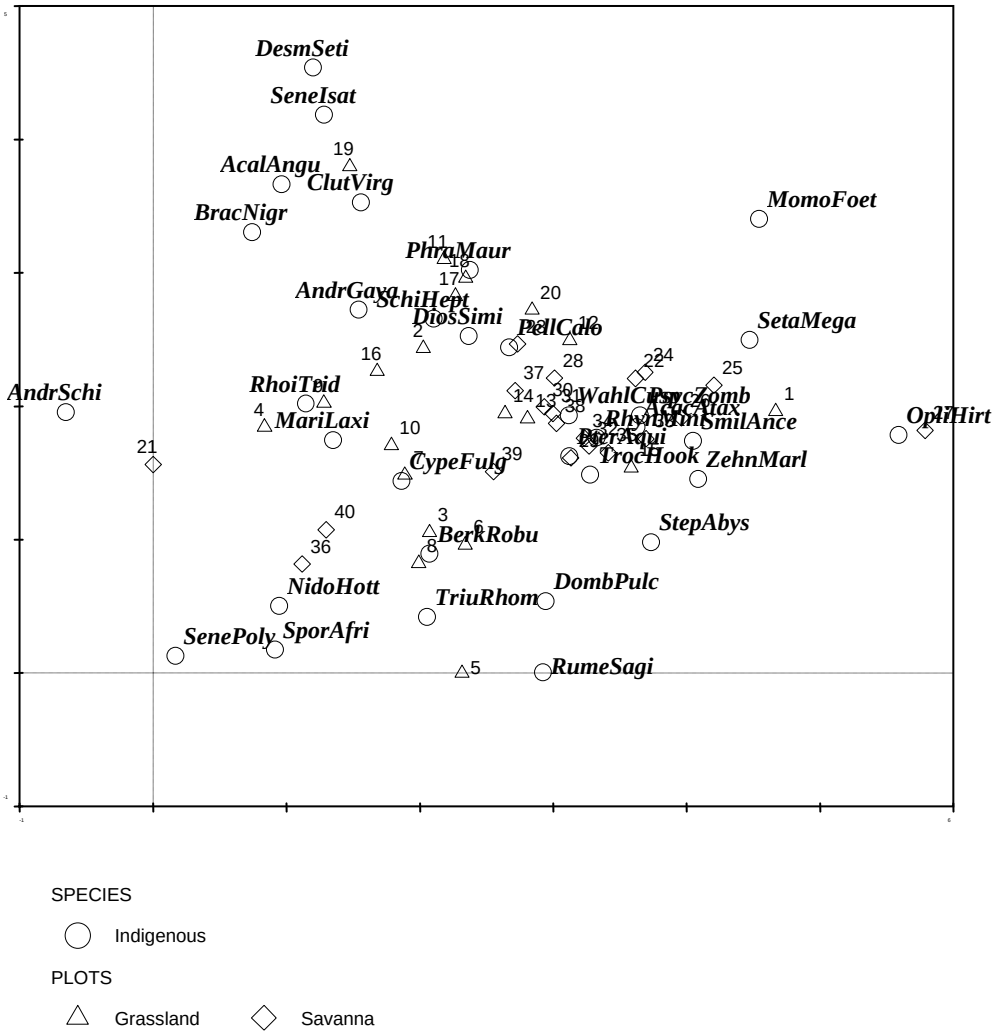


Figure 3.36. Detrended correspondence analysis (DCA) of plant species in the 40 plots at the 100 m^2 scale, in 2005. Only the indigenous species are shown (with a weight of 10 – 100%). Plots were categorised into grassland and savanna. Species are labeled by the first four letters of the generic name and the first four letters of the specific name (refer to Appendix 2 for species names).

An inspection of the distribution of the indigenous species from Figure 3.36, suggests that the occurrence of the species was not specific to either the grassland or savanna biome. This therefore indicates that the biomes were generally very similar in terms of the indigenous species composition.

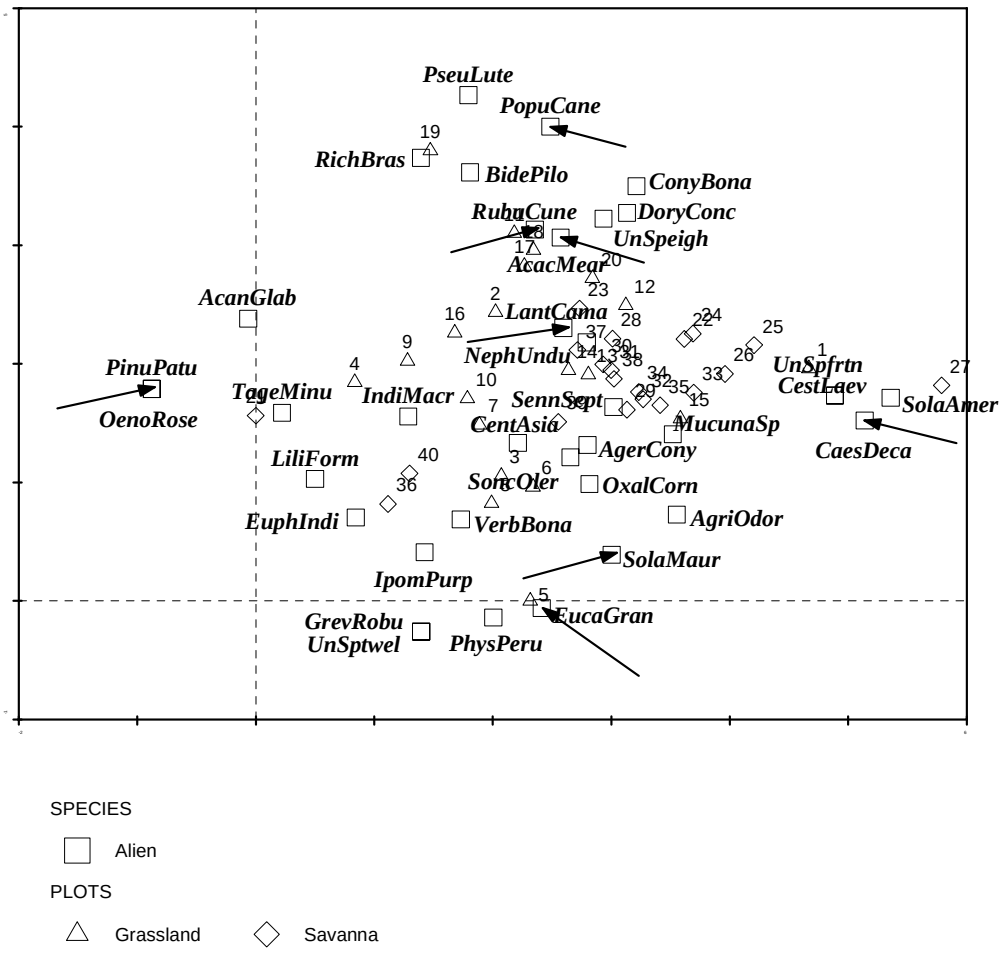


Figure 3.37. Detrended correspondence analysis (DCA) of plant species in the 40 plots at the 100 m^2 scale, in 2005. Only the alien species are shown (all of them). Plots were categories into grassland and savanna. Species are labeled by the first four letters of the generic name and the first four letters 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).

The declared weeds and invaders in Figure 3.37 consists of the category 1 species *Lantana camara*, *Rubus cuneifolius* and *Solanum mauritianum*, and the category 2 species *Caesalpinia decapetala*, *Populus x canescens*, *Acacia mearnsii*, *Eucalyptus grandis* and *Pinus patula*. *L. camara* had a strong association with plots 12 and 13, *R. cuneifolius* had a strong association with plot 18 and *S. mauritianum* had a strong association with plot 8. *C. decapetala* had a strong association with plot 15, *P. canescens* had a strong association with plot 20, *A. mearnsii* had a strong association with plot 23, *E. grandis* was strongly associated with plots 5 and 6, and *P. patula* was strongly associated with plot 21. This indicates that these species occurred with a higher (relative) abundance than species further away from these plots. However, the very low proportion of the variance explained by these ordinations also indicates that they don't really reflect the results that well and so it is not surprising that there are no clear communities coming out or little in the way of interesting trends.

3.5 Discussion

3.5.1 Total plant species richness and diversity

The plots in the grassland biome were separated geographically to a large degree, i.e. ten plots in the Sabie region (which was at the highest altitude) and ten plots in the Graskop region which was at the second highest altitude). Hence the two regions were analysed separately in order to determine if there were any differences in the species richness and diversity between them.

A total of 282 species were found in the study area along the Sabie River. Of this total, 222 (79%) were indigenous and 60 (21%) were alien. A cumulative total of 222 species in all 40 plots were present in the grassland biome and 171 in the savanna biome. Hence the grassland was almost 20% more species rich than the savanna. A total of 112 (39% of the total species of 282) were common to both biomes, with 86 indigenous species (30%) and 26 alien species (9%) in common. At each quadrat scale, the species richness and alpha diversity (Simpson's index of diversity) was significantly higher in the grassland than in the savanna biome. The Sabie region had the greatest species richness (a cumulative total of 178 species in all 40 plots), followed by the Graskop region (124 species) and then the Hazeyview region, which was in the savanna biome and at the lowest altitude (171 species). At each quadrat scale, the species richness was greatest in the Sabie region, followed by the Graskop region, and then the Hazeyview region, which had a species richness that was significantly lower than that in the Sabie region. Thus, it was the Sabie region that accounted for the significantly higher species richness in the grasslands relative to the savanna sites. On the other hand, the Graskop region had the highest alpha diversity, thus resulting in the significantly higher alpha diversity in the grassland. Within regions of roughly similar climate, heterogeneity in topography or soils is often correlated with plant species diversity (Sarr *et al.*, 2005). In this case, the higher altitude regions were more species rich and diverse. The beta diversity (Sorenson's coefficient of community), as well as the species complementarity (the Marczewski-Steinhaus (MS) distance), also indicated that the biomes (as well as the regions) were not very similar in terms of species composition.

The overall beta diversity between the grassland and savanna biomes of the Sabie River riparian community (i.e. 0.57), was slightly higher than patterns of beta diversity between non-riverine grasslands and savannas in southern Africa. According to Cowling *et al.* (1991), Sorenson's coefficient for the grassland and savanna biomes indicates a 41-50% similarity, which is higher than other pair-wise biome comparisons of similarity, which all yield Sorenson's coefficient of less than 30%. The reason why the upper and lower reaches (i.e. grassland and savanna biomes) of the Sabie River riparian community had a slightly higher beta diversity, may be because this riverine environment essentially supports a riparian forest/woodland (rather than reflecting the species typically found in the adjoining (more upland) grasslands and savannas), and thus the plant community was fairly uniform along the Sabie River.

Even though the grassland biome was significantly more diverse than the savanna biome, the study area along the Sabie River had a high overall alpha diversity, i.e. approximately 0.8-0.9 (at the 1000 m^2 scale). This is similar to non-

riverine biome-scale patterns of diversity in southern Africa. According to Scholes (1997), the plant species richness of southern African savannas at a whole-biome scale is high relative to other southern African biomes, and is second only to the fynbos biome. Southern African savannas contain 40 –100 species per 1000 m^2, which is not significantly different from other southern African biomes (Whittaker *et al.*, 1984; Cowling *et al.*, 1991). In this study, the savanna biome contained 40 species per 1000 m^2, which is at the lower part of the 40 –100 species range. A possible reason for this lower species richness may be due to fire being excluded or reduced from the Sabie River riparian community due to the structural characteristics of the riparian community rendering it less flammable than the surrounding vegetation (Holmes *et al.*, 2005). Fires are a natural part of savanna ecosystems, and can act as a germination cue for many species with soil-stored seeds that may not otherwise be present in the community (Hughes and Vitousek, 1993). This minimises germination prior to a fire and maximizes germination following fire, thus increasing their chance of survival, which can thus increase the species richness. Another reason could be because the Sabie River riparian environment essentially supports a riparian forest/woodland, and, according to Cowling *et al.* (1991), southern African forests are not particularly rich in species. Southern African grasslands are also considered rich in terms of plant species – even richer than the fynbos at a 1000 m^2 scale (Cowling *et al.*, 1991). According to Cowling *et al.* (1991), southern African grasslands contain 82 species per 1000 m^2. In this study, the grassland biome contained 48 species per 1000 m^2, which is much lower. Once again, reasons for this may be attributed to fires being reduced or excluded from the Sabie River riparian community, and because this community essentially supports a riparian forest/woodland.

On a global scale, the alpha diversity of southern African vegetation does not differ markedly from that in equivalent biomes elsewhere (Cowling *et al.*, 1991). However, according to Cowling *et al.* (1991), southern African savannas (at the 1000 m^2 scale) have marginally higher species richness than tropical Australian savannas, but much lower richness than the extremely high richness of the cerrado savannas in Brazil (230 species per 1000 m^2) (Eiten, 1978).

The savanna plots were more similar in terms of the composition of co-occurring species than the grassland plots. This might partially be due to the savanna plots coming from a single region (Hazeyview) compared with the grassland plots being split between two regions (i.e. Sabie and Graskop). Even though the grassland was more rich and diverse in terms of species than the savanna, the biomes were very similar in terms of the indigenous and alien species composition. The biomes and regions were also similar in terms of the overall relative abundances of plant species (the species evenness (Simpson's measure of evenness) was approximately the same in both biomes and in all three regions).

3.5.2 Invasion intensity, i.e. percentage aerial cover of woody alien plants

The difference in the species richness and diversity of the two biomes could be due to the invasion intensity, i.e. percentage aerial cover of woody alien plants, tending to be higher in the savanna. It was found that the savanna biome (and therefore Hazeyview region) had a greater (but not significantly greater) aerial cover of alien plants than the grassland biome. The savanna also had a greater aerial cover of plants > 5 m in height (but not significantly greater) and between 2 and 5 m in

height (significantly greater), whereas the grassland had a greater aerial cover of plants < 2 m in height (but not significantly greater) (with the Graskop region having a greater aerial cover than the Sabie region).

In the study areas, the alien tree species with the greatest invasion intensity (i.e. the greatest density) was *Eucalyptus grandis* (Saligna gum) (which dominated the > 5 m height class) and the alien shrub species were *Rubus cuneifolius* (American bramble), *Lantana camara* (Lantana) and *Solanum mauritianum* (Bugweed) (which dominated the 2 – 5 m height class). These alien trees and shrubs generally have a taller and fuller aerial cover than the indigenous species and usually outgrow them (in growth rate and height) (Garner, 2005). Many of the indigenous species are typically light seeking and may be shaded out if the alien species upper canopy is extensive (Henderson and Wells, 1986). These alien trees also modify the habitat by their high litter cover (Shugart and Seagle, 1985; Reinhart and Vandevoort, 2006). Because the savanna was dominated by these taller alien species, the indigenous species that usually form the upper canopy may have been overtopped, and the smaller growth forms may have been shaded out, by the taller- and faster-growing alien species, thus reducing the overall species richness in the savanna. This shading out effect is also reflected in the growth form composition, which showed that the savanna had a higher proportion of trees, and a lower proportion of shrubs, herbaceous plants and grasses (whereas the grassland had a higher proportion of shrubs, herbaceous plants and grasses, and a lower proportion of trees).

The reason why the savanna tended to have a higher degree of invasion intensity could be due to its position lower in the catchment relative to the grasslands. Areas lower down in the river receive seeds, and probably other propagules as well, of invasive species that are transported from the upper catchments (Le Maitre *et al.*, 2000). Many riparian invasions came about through the introduction of invading species into the upper catchments, which have subsequently spread rapidly downstream (Le Maitre *et al.*, 2000).

Another reason why the savanna tended to have a higher degree of invasion intensity could be attributed to the species composition and dominant vegetation type in each biome. The savanna biome is dominated by hemicryptophytes (defined as perennial plants, generally herbaceous, with the renewal buds at or, more often, close to ground level, but seldom exceeding 0.1 m in height (Rutherford and Westfall, 1994)) and phanerophytes (defined as perennial plants, usually woody, with the average height of the renewal buds > 0.7 m above ground level, and because plant height is usually greater than the average height of renewal buds, the average plant height is seldom < 1.0 m (Rutherford and Westfall, 1994)). However, these are generally respectively known as grasses and trees. The graminoids (grasses) have a continuous layer and the woody tree or shrub understorey layer is discontinuous (Walker and Noy-Meir, 1982; Scholes, 1997). On the other hand, the grassland biome is characterised by a strong dominance of hemicryptophytes of the Poaceae (Rutherford and Westfall, 1994). Therefore, the higher dominance of phanerophytes in the savanna may have contributed to the higher degree of invasion intensity in this biome.

3.5.3 Relationship between total plant species richness and diversity, and invasion intensity

In the savanna, trees usually establish only upon disturbance of the graminoid layer (Archer, 1990) since, in undisturbed grass swards, tree seed germination and seedling success is constrained by abiotic and biotic controls (Stock *et al.*, 1997). When a disturbance does take place and trees are able to establish, they alter local micro-climates and patterns of nutrient cycling, which can facilitate further invasion by trees and often leads to the development of closed woodlands (Walker, 1985). The morphological and physiological effects of the taller growing tree species include the shading out of indigenous species, which can reduce species richness. This decrease in the total species richness with increasing total invasion intensity was found in the Hazeyview (savanna) region. On the other hand, there was a very slight increase in the total species alpha diversity with increasing total invasion intensity. Therefore, the alien tree species may have added (but only very slightly) to the total species alpha diversity.

In the Sabie region, the total species richness decreased slightly as the total invasion intensity increased, whereas in the Graskop region, the total species richness increased as the total invasion intensity increased. This resulted in the total species richness increasing slightly in the grassland as the total invasion intensity increased. Therefore, the invasion of the aliens has so far had less of an affect on the grassland compared with the savanna community. This could be due to the fact that because smaller growth forms inherently dominate grasslands, any seedlings of alien plants would have to compete with this already well-established plant community for resources such as light, water and nutrients. Not many aliens therefore manage to grow into large trees, and those that do, have little affect on the indigenous plant community. There was also a very slight increase in the total species alpha diversity with increasing total invasion intensity in the grassland, thus indicating once again that the alien tree species may have added slightly to the total species alpha diversity.

3.5.4 Relationship between indigenous and alien plant species richness

The two most prominent conceptual models of plant community invasibility are the diversity-resistance hypothesis (Elton, 1958) and the resource-enrichment hypothesis (Davis *et al.*, 2000). The diversity-resistance hypothesis builds on assumptions about niche overlap and competitive exclusion to argue that, all else being equal, communities with high indigenous diversity are less invasible (Elton, 1958); i.e. higher plant species richness and/or diversity should enhance community resistance to alien plant invasions (the hypothesis of this study). The resource-enrichment hypothesis (which is also known as the fluctuating-resource hypothesis) assumes that alien species are resource-limited and that communities become more susceptible to invasion whenever there is an increase in unused resources, such as after a disturbance (*Davis et al.*, 2000); i.e. an increase in nutrient availability will increase invasion success. Both hypotheses assume that the success of alien species is dependent on resource availability, either directly (resource-enrichment) or indirectly due to competition with indigenous species having similar niches (diversity-resistance) (Gilbert and Lechowicz, 2005). In the savanna (and therefore Hazeyview region), the indigenous species richness increased with increasing alien species richness. On the other hand, in the grassland, the indigenous species richness

remained unchanged with increasing alien species richness, which was a result of the indigenous species richness decreasing with increasing alien species richness in the Sabie region, and increasing with increasing alien species richness in the Graskop region. These different patterns in the correlations between the indigenous and alien species richness of the grassland and savanna biomes resulted in a slight overall positive correlation between the indigenous and alien species richness.

Other studies have also shown positive correlations between the indigenous and alien plant species richness. For example, in a California riparian system, the most diverse natural assemblages were the most invaded by alien plants (Levine, 2000). Levine (2000) states that the positive correlations may have resulted from a simple response of indigenous and alien species to environmental conditions. In addition, factors other than diversity influence invasions, such as disturbance, propagule pressure (which is a composite measure of the number of individuals released into a region to which they are not native (Lockwood *et al.*, 2005)), and species composition (Levine, 2000). Lonsdale (1999) also found that communities richer in indigenous species had more alien species. Lonsdale's reason for this was that alien species richness responds to greater habitat diversity in the same positive way that indigenous species richness does, and thus alien and indigenous richness are positively correlated without a causal link. Gilbert and Lechowicz (2005) also found that numbers of indigenous and alien species were positively correlated. They found that both indigenous and alien species richness increased with soil pH and decreased along a gradient of increasing nitrate availability. This therefore indicated that environmental conditions favouring indigenous species richness also favour alien species richness (Shea and Chesson, 2002), and that competitive interactions among natives do not set an upper limit to local diversity and communities can still accommodate additional species without loss of natives (Gilbert and Lechowicz, 2005). Meiners *et al.* (2002) also noted that species richness of natives and aliens were positively correlated, showing no effects of alien invasion on indigenous species richness. However, when alien plants made up a large proportion of the total cover of a plot, they observed reductions in the community richness. Therefore, restoration efforts should be focused on controlling species that have the potential to dominate local plant communities. In the study areas of this study, the alien tree and shrub species with the greatest densities (and also probably corresponding invasion intensities) 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), and *Lilium formosanum* (St. Joseph's lily) (218). Thus, focus should be on controlling these species first.

There are also studies that have found negative correlations between the indigenous and alien plant species richness. These negative relationships indicate that biotic resistance to invasions can in fact operate in natural systems, if only at local scales (Ortega and Pearson, 2005). For example, Fox and Fox (1986) found that sites that were rich in indigenous species had a reduced incidence of alien species. This relationship was attributed to better resource utilization in species-rich communities, which prevents alien species becoming established (McIntyre *et al.*, 1988).

Reasons why both positive and negative correlations between the indigenous and alien species richness have been found in studies, is due to differences in the types of alien species – some aliens are "weak" invaders and some are "strong" invaders. According to Ortega and Pearson (2005), the majority of alien species that establish within indigenous communities appear to be weak invaders that coexist with indigenous species as minor community components. However, there are crucial subsets of alien species that are strong invaders that are able to attain community dominance and thus dramatically impact on the indigenous species, thereby altering pre-invasion patterns (Ortega and Pearson, 2005). When strong invaders dominate the natural community, relationships between indigenous and alien species may be negative at local scales because of the dominating impact of the alien invaders on the indigenous community (Ortega and Pearson, 2005). As stated previously, there was a negative correlation between the indigenous and alien species richness in the Sabie region and therefore the hypothesis that higher plant species richness and/or diversity should enhance community resistance to alien plant invasions, is not rejected. This negative correlation in the Sabie region may have been as a result of a few strong invaders dominating the community – amongst the densest alien species (> 500 plants/ha) in the Sabie region, were two alien tree species (*Eucalyptus grandis* and *Agrimonia odorata*) and five alien shrub species (*Rubus cuneifolius, Solanum mauritianum*, *Lantana camara*, *Indigofera macrophylla* and *Lilium formosanum*).

On the other hand, when invaders occur primarily at low abundances (as either weak invaders or as strong invaders in early phases of establishment), the local-scale relationship between the indigenous and alien species richness is positive (Ortega and Pearson, 2005). In the Graskop and Hazeyview regions, there was a positive correlation between the indigenous and alien species richness, and therefore the hypothesis that higher plant species richness and/or diversity should enhance community resistance to alien plant invasions, is rejected. In these regions, there were relatively fewer dominating alien species (in comparison with the Sabie region); i.e. amongst the densest alien species (> 500 plants/ha) in the Graskop region, were five alien shrub species (*Lantana camara*, *Rubus cuneifolius*, *Caesalpinia decapetala*, *Indigofera macrophylla* and *Populus x canescens*), while in the Hazeyview region there were three alien shrub species (*Rubus cuneifolius*, *Solanum mauritianum* and *Lantana camara*). Thus, this may have resulted in the positive correlation between the indigenous and alien species richness in the Graskop and Hazeyview regions.

3.5.5 Species richness and diversity of tree, shrub, herbaceous, grass and sedge growth forms

Of the 282 species found, 121 species (43%) were herbs, 82 (29%) were shrubs, 46 (16%) were trees, and 33 (12%) were grasses. At each quadrat scale (in both biomes), the herbaceous species richness and diversity was the highest, followed by the shrub, grass and tree species richness and diversity. The exception to this pattern was found at the 100 m^2 and 1000 m^2 scales, where there were more trees than grasses in the savanna biome. This point is expected due to the larger sizes of trees and shrubs relative to herbaceous plants and hence the requirement for larger plot sizes in order to sample them adequately.

The indigenous species richness of each growth form was significantly higher than the alien species richness of each growth form. Twenty-seven (45%) of the 60

alien species found were herbaceous, 17 (28%) were shrubs, 15 (25%) were trees, and 1 (2%) was a grass. Therefore, more than half (53%) of the alien species were trees and shrubs. While invasive alien plant species of all growth forms can have major impacts upon the indigenous plant community, invasive alien trees are among the most damaging species, owing to their ability to become structurally dominant (Panetta and Sparkes, 2001). This was shown by the evenness of the growth forms – trees were found to have the lowest evenness, followed by the shrubs and herbs, while the grasses had the highest evenness. Therefore, there were a few alien tree species that were dominating the community, unlike the other growth forms, which had a higher proportion of species that were equally abundant. Once alien trees dominate, they can spread rapidly into the riparian zones, eventually forming dense thickets that are difficult and expensive to eradicate (Dye and Poulter, 1995b). These trees also greatly reduce surface water runoff, and evapotranspiration by these plant communities is markedly greater than by the indigenous plant communities (Dye *et al.*, 2001; Everson *et al.*, 2001).

The most dominant alien trees and shrubs in the study areas were *Eucalyptus grandis, Agrimonia odorata, Rubus cuneifolius*, *Lantana camara, Solanum mauritianum, Indigofera macrophylla* and *Caesalpinia decapetala*. The problem with Lantana and Bramble is that they form very dense thickets in the lower canopy and are often intertwined with the indigenous vegetation, which makes them very difficult to locate. These plants also have strong regenerative capabilities, which are often facilitated by the disturbance caused by clearing (Witkowski and Wilson, 2000). These factors make the removal of these species very difficult. The Gum and Bugweed also have strong regenerative capabilities. Resprouting individuals of these species have exceptionally fast growth rates, which are seldom surpassed by the indigenous vegetation (MacDonald and Jarman, 1985). A consequence of this is that more follow-up clearings will be needed by WfW in order to reduce the re-invasion by these species. However, the previously cleared and regenerating individuals will be smaller in size and more difficult to locate in the dense vegetation. Therefore, the follow-up clearings may be difficult. With time, however, the indigenous vegetation may slowly become dominant again, due to the successional sequence of the community being reset. Because the alien species that had strong regenerative capabilities were the ones that increased in invasion intensity over time, the life-history characteristics of species could be used used to predict which species are likely to become successful invaders.

Clearing of invasive species functions as a disturbance, which will in essence reset the successional sequence of the vegetation (Mentis and Ellery, 1994). In early phases of recovery from plant invasions, the first plants to establish are herbaceous plants, followed by an increased abundance of indigenous woody plants (Sousa, 1984). This change in species composition as a result of the removal of alien species, results in a change in the availability of resources required by plants such as light, water and nutrients (Canham and Marks 1985; Luken, 1990). There is increased soil moisture, soil temperature and improved substrate quality, which stimulates nitrogen mineralization and increases nitrogen pool sizes, and consequently increases short-term nitrogen availability (Agrawal and Tiwari, 1987; Matson *et al.*, 1987). The first plants to establish after the removal of alien plants should thus encounter a greater availability of resources, improving the probability of survival and establishment in the community. The initial colonizer's competitive advantage and consequent

dominance could inhibit establishment by other species as succession proceeds and resources become more limited (Hughes and Vitousek, 1993). In this way, the indigenous community could slowly become dominant again. A period of many years will be required to regain the same successional stage that was present prior to the disturbance. This dominant, well-adapted indigenous community would usually be expected to have a marked competitive advantage over newly arriving species that are adapted to different habitats and resource availabilities (Vermeij and Dudley, 2000). Thus, this could result in the indigenous community being more resistant to alien invasions, and therefore the number of follow-up treatments could be reduced.

3.5.6 Species richness and diversity of tree, shrub, herbaceous, grass and sedge growth forms in the grassland and savanna biomes

Grasslands are characterised by a strong dominance of hemicryptophytes of the Poaceae (Rutherford and Westfall, 1994). On the other hand, savannas are characterised by vegetation with a herbaceous, usually graminoid, layer with an upper layer of woody plants, which can vary from widely spaced to 75% canopy cover (Edwards, 1983). This was reflected by the species richness and alpha diversity of the different growth forms in the biomes – the grassland biome had a significantly higher shrub, herbaceous and grass species richness (in total and indigenous) and diversity (with the Sabie region containing more shrub, herbaceous and grass species than the Graskop region), whereas the savanna biome (and therefore Hazeyview region) had a higher (but not significantly higher) tree species richness (in total and indigenous) and diversity. On the other hand, the grassland contained more (but not significantly more) alien tree, shrub and grass species, whereas the savanna contained more (but not significantly more) alien herbaceous species. In terms of species overlap, 46 herbaceous species (16%), 32 shrub species (11%), 18 tree species (6.4%) and 16 grass species (5.6%) of the total species of 282, were common to both biomes. The lower richness and diversity of the shrubs, herbs and grasses in the savanna may be related to the higher invasion intensity in this biome, i.e. the taller growing alien trees may have shaded out the smaller growth forms.

The beta diversity, as well as the species complementarity, also indicated that the biomes were not that similar in terms of tree, shrub, herbaceous and grass species, except the grass species at the 10 m^2 scale where there was a 79% similarity between the biomes. The tree and grass species similarities between the biomes were slightly higher than the herbaceous and shrub species similarities; therefore there were more differences in the shrub and herbaceous species than the tree and grass species between the biomes. The Sabie, Graskop and Hazeyview regions were not very similar in terms of tree, shrub, herbaceous and grass species, except grass species at the 10 m^2 scale, where there was a 76% similarity between the Sabie and Hazeyview regions. Even though the biomes and regions were different in growth form compositions, the abundance of each growth form was similar between the biomes and regions. The only significant difference was in the shrub species (at the 1 m^2 scale), which had an evenness significantly lower in the savanna (and therefore Hazeyview region). This means that the savanna had a few shrub species that were significantly dominating the community.

3.5.7 Relationship between species richness and diversity of tree, shrub, herbaceous, grass and sedge growth forms, and invasion intensity

In the savanna (and therefore Hazeyview region), the tree species richness increased very slightly as the total invasion intensity increased. On the other hand, the tree species alpha diversity decreased with increasing total invasion intensity. It is expected that there would be a strong positive relationship between the tree species richness and invasion intensity, as the more tree species (alien) there are, the greater the aerial cover (and hence invasion intensity). However, because the savanna plots were dominated by only a few alien tree species that had relatively large aerial covers, any more alien tree species found would not have added to the aerial cover, and hence with more alien tree species, the invasion intensity remained unchanged. In the Sabie region, the tree species richness remained unchanged with increasing total invasion intensity, whereas in the Graskop region, the tree species richness increased with increasing total invasion intensity. This resulted in the tree species richness increasing in the grassland as the total invasion intensity increased. This indicates that many of the tree species that were found in this biome, were alien; and thus the more tree species found, the greater the invasion intensity. This was reflected in the tree species alpha diversity increasing with increasing total invasion intensity.

3.5.8 The effect of quadrat size on plant species richness measures

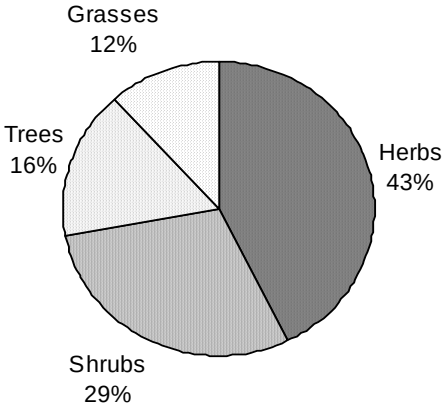
As the quadrat size increased, the species richness increased. Therefore, the size of the quadrat used affected the species richness that was measured. This was to be expected because as sampling effort increases, more individuals are encountered and more species are likely to be recorded (Hayek and Buzas, 1997).

3.5.9 Edge effects on plant species richness measures

Because each modified Whittaker nested plot was situated parallel between the river and the plantation dirt (unsealed) road, the effects of these "edges" were analysed. It was found that the roadsides of the plots had a greater total species richness than the riversides (in both the grassland and savanna biomes, with the roadside and riverside of the grassland plots being more species rich than those of the savanna plots)). It was also found that the roadsides of the plots had a greater alien species richness than the riversides. This may be explained by the 'intermediate disturbance hypothesis' (Connell, 1978). This hypothesis states that all communities are composed of early seral species that colonize quickly after disturbance and late seral species that increase in abundance and dominance through time (Connell, 1978). Optimal diversity occurs, therefore, when disturbance is sufficiently frequent to limit dominance while allowing complete time for colonization by all species (Connell, 1978). Thus in the Sabie riparian zone, the forestry roads have a higher degree of disturbance relative to that of the river. The forestry roads allow easier access of cars and trucks used by the forestry companies during their operations, which can alter conditions and therefore allow easier access of other vectors of plant dispersal. The roadsides can also retain reserves of propagules for future invasion following disturbance for some species of alien plants (Parendes and Jones, 2000). The reason why alien plants may tend to favour the roadsides, is that roadsides have higher light conditions and bare soil (compared to the riversides which have low light conditions from greater tall tree cover), which favours alien plant establishment (Pauchard and Alaback, 2004). Fortunately, most alien plant species growing along roadsides are incapable of colonizing less disturbed natural environments, as they are weedy species with short life cycles and high reproductive rates (Pauchard and Alaback, 2004).

Roadsides, however, still may serve as starting points from which some species spread from the edges to the interiors of pristine or naturally disturbed environments.

3.6 Conclusions



TOTAL OF 282 PLANT SPECIES

222 species in Grassland (178 in Sabie, 124 in Graskop)

171 species in Savanna (Hazeyview)

222 (79%) Indigenous

60 (21%) Alien

		Grassland	Savanna
Species richness ($1000m^2$):	Total	48.8 ± 1.8^a	40.0 ± 2.1^b
	Trees	5.4 ± 0.4^a	5.9 ± 0.6^a
	Shrubs	14.2 ± 0.5^a	12.5 ± 0.7^a
	Herbs	22.4 ± 1.2^a	16.7 ± 1.3^b
	Grass	6.8 ± 0.5^a	5.0 ± 0.5^b
Alpha diversity ($100m^2$)		0.90 ± 0.01^a	0.85 ± 0.02^b
Species evenness ($100m^2$)		0.52 ± 0.03^a	0.51 ± 0.03^a
Beta diversity ($1000m^2$)		0.57	
Species complementarity ($1000m^2$)		0.60	
Total aerial cover of woody aliens		$29.4 \pm 4.5\%^a$	$34.4 \pm 4.6\%^a$

Figure 3.38. Summary diagram of the most important results from chapter 3.

There are several important conclusions that can be made (Figure 3.38). Firstly, it is concluded that the grassland biome was more rich and diverse in terms of species than the savanna biome. In the grassland, the Sabie region had the highest species richness whereas the Graskop region had the highest species diversity. The difference in the species richness and diversity between the biomes may have been partially due to the higher degree of invasion intensity in the savanna, which may have reduced the species richness and diversity in this biome. Because the savanna was lower in the catchment relative to the grassland, the savanna plots probably received more seeds and propagules of invasive species than the grasslands. This may have resulted in the higher invasion intensity in the savanna reach of the river.

It is recommended that the WfW control program should initially concentrate on the upper parts of the catchment first, i.e. the grassland area (and all the way up the catchment) so that the lower savanna areas are not re-invaded from propagules upstream. The overall beta diversity between the biomes, as well as the species complementarity, indicated that the biomes were not very similar in terms of species composition. On the other hand, the species evenness was very similar between the biomes, and thus the biomes were similar in terms of the overall relative abundances of plant species.

Overall, the study area along the Sabie River had a high alpha diversity, i.e. approximately 0.8-0.9 (at the 100 m^2 scale). This diversity is similar to non-riverine biome-scale patterns of diversity in southern Africa (Whittaker *et al.*, 1984; Cowling *et al.*, 1991; Scholes, 1997). However, even though the diversity along the Sabie River was high and a large proportion (79%) of the species were indigenous, alien species were still being found (21% of the total), more than half of which were shrubs and trees. This shows that the WfW clearing operations have clearly not been succeeding in removing or controlling the infestations of woody alien plants. This may be a consequence of some plants, that should have been cut, being missed during the clearing operations, but also through many of the cut stems surviving and resprouting, and new seedlings establishing from seed banks. More follow-up treatments are therefore needed in order to reduce the number of resprouting alien plants. Currently, follow-up clearings are taking place about a year after the initial clearings, with further follow-up clearings taking place about eight months later. It is recommended that the frequency of the follow-up clearings should increase to about four, spread over three years. These follow-up clearings should occur in the growing season, when it is clearly apparent whether regrowth is occurring or not.

The Sabie riverine growth form composition consisted of 43% herbaceous species, 29% shrub species, 16% tree species and 12% grass species. The grassland had higher proportions of shrub, herbaceous and grass species, whereas the savanna had a higher proportion of tree species. This difference in the growth form composition between the biomes is probably due to the inherent dominant growth forms found in each biome, as well as the higher invasion intensity in the savanna shading out a higher proportion of the smaller growth forms.

In the savanna, the total species richness decreased with increasing total invasion intensity, which may be a result of the morphological and physiological effects of the taller growing tree species shading out the indigenous species, thus reducing the species richness. On the other hand, in the grassland, the total species

richness increased slightly with increasing total invasion intensity, thus indicating it may have been more resistant to the invasion of the aliens compared with the savanna, and thus the hypothesis that higher plant species richness and/or diversity should enhance community resistance to alien plant invasions, was not rejected (the grassland was significantly more diverse than the savanna).

Both negative and positive correlations between the indigenous and alien species richness were found, which is likely to be a result of different types of invaders, strong or weak, predominating in the different regions. The Sabie region had two alien tree species (*Eucalyptus grandis* and *Agrimonia odorata*) and five alien shrub species (i.e. *Rubus cuneifolius, Solanum mauritianum, Lantana camara, Indigofera macrophylla* and *Lilium formosanum*) that dominated the community, which may have resulted in the negative correlation between the indigenous and alien species richness. On the other hand, there were relatively fewer dominating alien species (in comparison with the Sabie region) in the Graskop and Hazeyview regions; i.e. the Graskop region had five dominating alien shrub species (*Lantana camara, Rubus cuneifolius, Caesalpinia decapetala, Indigofera macrophylla* and *Populus x canescens*), while the Hazeyview region had three dominating alien shrub species (*Rubus cuneifolius, Solanum mauritianum* and *Lantana camara*). This low dominance of alien tree and shrub species in these regions may therefore have resulted in the positive correlation between the indigenous and alien species richness. The problem with these species is that they are strong resprouters, and are therefore not being effectively removed by the WfW clearing operations. Therefore, these species that have the potential to dominate the local plant communities (especially in the Sabie region) should be focused upon in the WfW clearing operations. This will help to reduce costs and increase ease of the clearing.

Finally, it was found that the roadsides of the plots were more species rich (in total and of aliens) than the riversides. Thus, roads could be an additional contributing factor to the spread of some of the aliens in the riverine areas; therefore this factor also needs to be taken into account in the WfW clearing programme.

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

4.1 Abstract

The impacts of the Working for Water (WfW) alien plant clearing programme, as well as the invasion of alien plants, on changes in the plant species composition, diversity and vegetation structure of riparian ecosystems on the Sabie River between 1996 and 2005, was investigated. The Sabie River traverses through both the grassland and savanna biomes, and this long-term study used essentially the same 40 modified Whittaker nested plots at both time periods. 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).

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 species richness 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 m^2 scale) was 24.1 ± 1.0 (S.E.) 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 the greatest increase was for category 1, 2 and 3 weed species over time, namely 25 in 1996 to 50 in 2005, a 50% increase. Although mean alpha diversity (Simpson's index of diversity) was higher in 2005 (0.9 ± 0.01 compared to only 0.3 ± 0.03 in 1996 (at the 100 m^2 scale); $P < 0.001$), overall beta diversity (Sorenson's coefficient of community) 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. Once again, the lack of any overall relationship between the 1996 and 2005 alpha diversities between the different treatments, indicates that the original treatments of the 1996/1997 study did not persist over time, except for differences between the biomes. The growth form composition was very similar between the years, i.e. in 1996, 17% of the species were trees, 27% shrubs, 43% herbaceous and 12% grasses; whereas in 2005, 16% were trees, 29% shrubs, 42% herbaceous and 11% grasses. The invasion intensity (i.e. percentage aerial cover of woody alien plants) was also similar between the years, i.e. 30.0 ± 4.6% in 1996 and 31.9 ± 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 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 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 ± 4.1% in 1996 to 5.8 ± 1.2% in 2005 (P = 0.02), and (b) those between 2 – 5 m tended to decrease from 13.3 ± 2.8% in 1996 to 11.1 ± 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 ± 1.0% in 1996 to 15.0 ± 2.1% in 2005 (P < 0.001). This therefore showed that the WfW clearing programme is succeeding, to some extent, in removing most the larger alien plants but not in controlling the regenerating plants, which recover through post-clearing resprouting and/or newly established seedlings. More focus should therefore be placed on the few dominant alien species that were not being effectively removed due to their resprouting potentials. In 1996, post-clearing resprouting was a significant issue for *Eucalyptus grandis* and *Solanum mauritianum*. The frequency of follow-up treatments also needs to increase in order to reduce the extent of recovery through resprouting from cut stems and seedlings establishing from the soil seed bank. It is recommended that the frequency of the follow-up clearings should increase to about four, spread over three years (currently, follow-up clearings are taking place about a year after the initial clearings, with further follow-up clearings taking place about eight months later). These follow-up clearings should occur in the growing season, when it is clearly apparent whether regrowth is occurring or not.

4.2 Introduction

4.2.1 Impacts of alien plant invasions and subsequent clearing

Alien plant invasions are a problem of global significance. Invasive alien plants can decrease biodiversity (particularly of indigenous species) by out-competing the indigenous plants for essential resources, including space, light, water and nutrients (Arriaga *et al.*, 2004). These invasive plants can also reduce water flow and impact negatively on the economy (Le Maitre *et al.*, 2004). Controlling the alien plant infestations, i.e. reducing the invasion intensity of the alien plants, will have many benefits, not only to the environment, but to society as well. Thus, the removal of these alien plants is of the utmost importance.

There are many benefits of controlling invasive alien species, such as an increased water flow and the creation of “gaps” allowing indigenous species to establish and/or regenerate. The ultimate success of a clearing program such as WfW, depends to a large extent upon a functional cover of vegetation (indigenous) being restored following the alien plant removal (Holmes, 2002). Failure to restore the area adequately would risk the re-invasion by the same alien plant species or secondary alien species (Holmes, 2002).

Even though there are many benefits of clearing invasive plants, the clearing in itself tends to result in greatly increased levels of disturbance to the affected community. This increased disturbance caused by the removal process may result directly in the loss of community diversity and structure (Breytenbach, 1991; Petraitis *et al.*, 1989). This is because alien species quickly colonize after a disturbance and may dominate during early succession and alter the establishment conditions (Bellingham *et al.*, 2005). Therefore, there is a need for long-term observations in the assessment of vegetation restoration in areas that have been disturbed by clearing of invasive species.

4.2.2 The Working for Water (WfW) alien plant clearing programme

Since the WfW programme began in 1995, invasive alien plants have been cleared from riparian areas in Mpumalanga and the rest of the country. A large proportion of the Sabie River flows through forest plantations, which have reduced the flow of the river quite dramatically over the years (Le Maitre *et al.*, 2002). Because of this flow reduction and because the Sabie River catchment is important from the ecotourism perspective, WfW has done extensive clearing along this river since 1995 and continues to do so. WfW used to fell all alien trees and shrubs, and then treat the stumps of the coppicing species with herbicide; the felled material was either removed from the river corridor or burnt in slash stacks (Holmes *et al.*, 2005). The current method is to use frilling or ring barking to kill the larger trees (> 200 mm basal diameter) as felling and timber removal is too expensive (Holmes *et al.*, 2005).

Approximately two years after the WfW programme began, a study was conducted in 1996/1997, which assessed the impacts of the invasive plant species clearing and invasion on the Sabie riverine ecosystem (Garner, 2005). The 1996/1997 study was then compared to this 2005 study in order to assess the Sabie riparian vegetation recovery in response to the WfW clearing. The aim of this chapter was to assess how the WfW alien plant clearing (and any subsequent further alien plant invasions post-clearing) affected the plant species composition, diversity and vegetation structure of the Sabie River over time, i.e. from 1996 to 2005.

4.2.3 Objectives and hypothesis

The objectives of this chapter were to:

1) Compare the alien and indigenous plant species composition of the Sabie River riparian vegetation between 1996 and 2005.
2) Compare the alien and indigenous plant species diversity (alpha and beta) of the Sabie River riparian vegetation between 1996 and 2005.
3) Compare the vegetation structure of the Sabie River riparian vegetation between 1996 and 2005.
4) Use the information from objectives 1-3 to assess the effectiveness of the WfW clearing over time, i.e. from 1996 to 2005. Note: “effectiveness” can be assessed in various ways, such as determining whether there is an increase in indigenous species richness and/or a decrease in alien species richness. In this study it also includes determining whether there is a reduction in the invasion intensity (defined as the percentage aerial cover of woody alien plants) after clearing.

It is hypothesized that higher plant species richness and/or diversity should enhance community resistance to alien plant invasions, in both 1996 and 2005. It is important to note that the invasion intensity was used as a measure of the degree of alien plant invasions.

4.3 Materials and methods

4.3.1 Experimental design

In 1996/1997, 40 permanent modified Whittaker nested plots were first surveyed along the Sabie River and several variables were measured, such as the plant species composition, diversity and vegetation structure, as well as environmental variables (Garner, 2005). Three different experimental treatments, i.e. (A) high altitude (grassland) versus low altitude (savanna) plots (=biome), (B) high invaded versus low invaded plots (=invasion intensity) and (C) cleared versus uncleared plots (=clearing), were assessed. These data were collected at one point in time, i.e. from October 1996 to the end of February 1997, across the three treatments, and were compared using various statistical analyses. In terms of the present study, field work was undertaken later in the growing season, from the 14th February to the 6th April 2005, using the same 40 modified Whittaker nested plots positioned as close as possible to the original 1996/1997 plots. The positioning of the plots could not exactly match that of the previous study because the floods of 2000 had removed all the concrete-embedded corner markers that were used to "permanently" mark the plots (Garner, 2005). The floods of 2000 also resulted in considerable changes to river morphology, with considerable erosion of the banks, and so plots could not always be in exactly the same place as before. The same three experimental treatments were used, i.e. (A) biome, (B) invasion intensity and (C) clearing, based on the historical 1996/1997 situation. However, because WfW had been clearing alien plants over the last eight years, i.e. from 1996/1997 to 2005, there were no 2005 uncleared plots as all of the plots had been cleared to some degree, and therefore the 'clearing' treatment was different. In addition, alien plants had invaded the 40 plots to a similar extent over the last eight years, and therefore most of the plots had a similar extent of invasion. Therefore, the 'invasion intensity' category also differed. The 2005 data were compared across the same three treatments, as the plot designations in terms of the three treatments were still the same as those of 1996/1997, despite the changes over time. In addition, the changes over the last eight to nine years (i.e. 1996/1997 versus 2005) were analysed. In a sense, these analyses were done to also test if there was any remaining legacy of the original treatments, as tested by Garner (2005) in 1996/1997, within the plots in 2005.

Within each biome, i.e. the high altitude, grassland biome and the low altitude, savanna biome, plots of different degrees of invasion intensity were chosen subjectively in 1996/1997 (Garner, 2005). The following categories were used: (a) a low to moderate invasion (0-50% of alien vegetation aerial cover); and (b) a high invasion (50-100% of alien vegetation aerial cover). Therefore, each biome contained plots of 'high invasion' and 'low invasion'. For each 'invasion intensity' treatment, ten modified Whittaker nested plots were completed (Figures 2.8 (Chapter 2) and 4.1). Therefore, each 'biome' treatment contained 20 plots, giving a total of 40 modified Whittaker nested plots (Figures 2.8 (Chapter 2) and 4.1). For each 'invasion intensity' treatment, plots were chosen that had been cleared of alien plants, as well as

uncleared plots. Therefore, each 'invasion intensity' treatment consisted of 'cleared' and 'uncleared' plots. For each 'clearing' treatment, five modified Whittaker nested plots were completed (Figures 2.8 (Chapter 2) and 4.1). Hence, based on the three "treatments" (biome, invasion intensity and clearing), each of which were set at two levels, there were a total of eight different experimental categories (or treatment combinations), with each containing five plots (Figures 2.8 (Chapter 2) and 4.1).

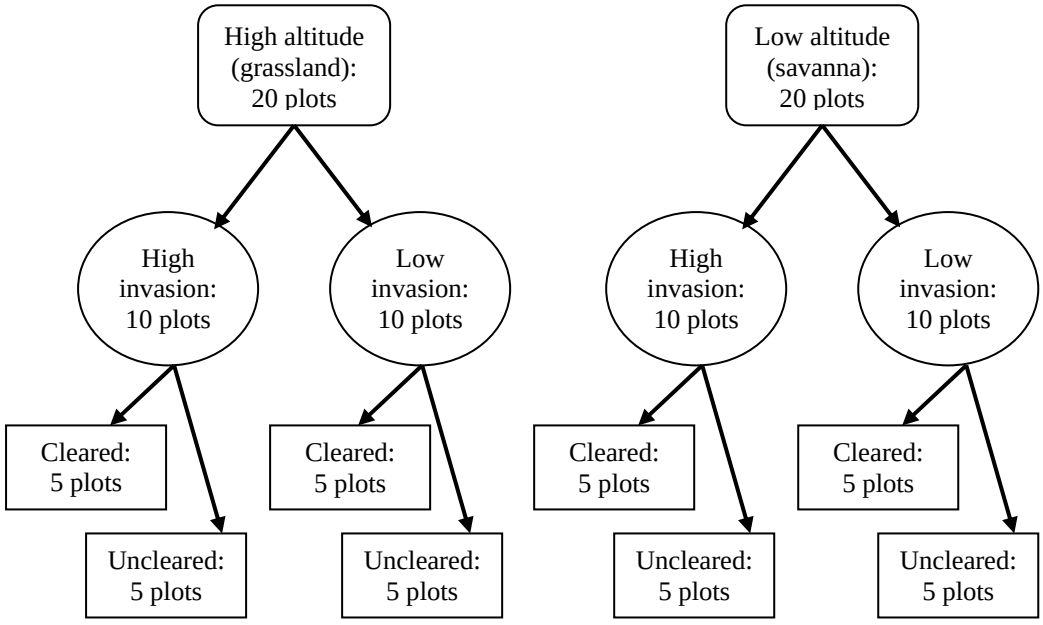


Figure 4.1. Flow diagram of the experimental layout of the plots, showing the three different experimental treatments, i.e. high altitude (grassland) versus low altitude (savanna) plots (biome), high invaded versus low invaded plots (invasion intensity) and cleared versus uncleared plots (clearing). These categorizations were made in 1996/1997 and are used again in 2005, despite all the changes over time.

4.3.2 Field sampling

The field sampling of both studies were very similar and the data collected from the 1996 study was compared with the data from this study of 2005 (refer to Chapter 3 for the field sampling methods).

4.3.3 Data analyses

Plant species richness

For both studies, the total plant species richness was determined at each quadrat scale, i.e. 1 m^2, 10 m^2, 100 m^2 and 1000 m^2, and for each growth form, i.e. (a) trees, which were defined as multi- or single stemmed perennial woody plants with a distinct upper crown, that remained erect unassisted and were ≥ 2 m in height (Van Wyk and Van Wyk, 1997); (b) shrubs, which were defined as multi- or single stemmed perennial woody plants that arose from or near the ground and remained erect unassisted with a maximum height of less than 2 m (they differed from trees in that they were smaller and did not have a trunk) (Van Wyk and Van Wyk, 1997); (c) herbaceous vegetation, which was defined as plants whose stems were not woody;

and (d) grasses and sedges. For both studies, the total species richness was also determined for each biome (grassland and savanna), and for each of the eight experimental categories of the three different experimental treatments, i.e. (1) grassland, high invaded, cleared plots; (2) grassland, high invaded, uncleared plots; (3) grassland, low invaded, cleared plots; (4) grassland, low invaded, uncleared plots; (5) savanna, high invaded, cleared plots; (6) savanna, high invaded, uncleared plots, (7) savanna, low invaded, cleared plots; and (8) savanna, low invaded, uncleared plots (Figure 4.1). The indigenous and alien species richness was determined at the 1000 m^2 quadrat scale for each biome for both studies. Total species richness, as well as (a) tree, (b) shrub, (c) herbaceous, and (d) grass and sedge species richness (for all 40 plots), were statistically compared between 1996 and 2005 (at the 1 m^2, 10 m^2, 100 m^2 and 1000 m^2 quadrat scale) using t-tests (for independent-samples). The species richness values of the two biomes (of the different years) were also compared using t-tests (for independent-samples). The species richness values of the three different experimental treatments (within and between the years) were then compared using three-way analysis of variances (ANOVA's) and Tukey's honest significant difference (HSD) tests, a three-way analysis of covariance (ANCOVA) (with the 1996 data as the co-variate), and t-tests (for independent-samples). The programme STATISTICA (1999 edition) was used for the statistical analyses. Data were checked for normality, and were transformed if not.

Plant species diversity

In 1996 and 2005, Simpson's index of diversity was used as a measure of the alpha diversity and Sorenson's coefficient of community was used as a measure of the beta diversity. Simpson's index of diversity for both years was calculated for total species as well as (a) tree, (b) shrub, (c) herbaceous, and (d) grass and sedge species in each of the 40 plots. These values were then meaned to give an overall measure in each biome, as well as in each of the eight experimental categories of the three different experimental treatments. Simpson's index of diversity was calculated at the 1 m^2, 10 m^2 and 100 m^2 scales. Because this index uses species abundance data, it could not be calculated for the 1000 m^2 quadrat scale, as only species presence/absence data was collected at this scale. Simpson's index of diversity at each quadrat scale was then compared statistically between the years (in all 40 plots) using t-tests (for independent-samples). Simpson's index of diversity was also compared between the biomes of the different years using t-tests (for independent-samples). Simpson's index of diversity of each of the eight experimental categories of the three different treatments (within and between the years) was then compared using three-way ANOVA's and Tukey's HSD tests, a three-way ANCOVA (with the 1996 data as the co-variate), and t-tests (for independent-samples). Sorenson's coefficient of community was calculated at the 1 m^2, 10 m^2, 100 m^2 and 1000 m^2 quadrat scales. Sorenson's coefficient of community was calculated for all pair-wise comparisons of each of the 40 plots in 1996 and 2005, and for all pooled plots of the eight experimental categories of the three different experimental treatments (between the years) (i.e. five plots pooled for each experimental category).

Overstorey aerial cover

In both years, the percentage aerial cover of woody alien plants was calculated for each height class, i.e. (a) large trees (> 5 m in height), (b) small trees (between 2 –

5 m in height), and (c) saplings and shrubs (between 1 – 2 m in height), and in total. Plants less than 1 m in height were excluded (not specifically sampled). The percentage aerial cover data were meaned for plots in 1996 and 2005, and statistically compared using t-tests (for independent-samples). The percentage aerial cover data were also then meaned for plots in each of the eight experimental categories of the three different experimental treatments (for both years), and compared using three-way ANOVA's and Tukey's HSD tests, a three-way ANCOVA (with the 1996 data as the co-variate), and t-tests (for independent-samples). These analyses were done for each of the height classes, and in total.

The percentage aerial cover of woody alien plants was used as a measure of invasion intensity. Linear regression analyses were then performed and compared between 1996 and 2005, whereby the relationships between the invasion intensity (independent variable) and various species richness and species diversity measures (dependent variables) were determined.

4.4 Results

4.4.1 Plant species richness

Plant species composition

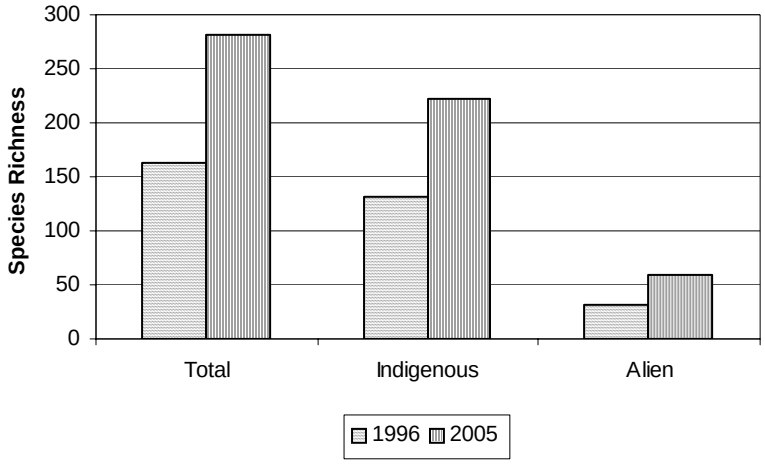


Figure 4.2. Total, indigenous and alien plant species of each of the 40 1000 m^2 plots, in 1996 and 2005, along the Sabie River.

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.

Species	1996	2005	Percentage increase from 1996 to 2005	Number of species common between 1996 and 2005
TOTAL	163	282	42%	62
Indigenous	132 (81%)	222 (79%)	41%	46
Alien	31 (19%)	60 (21%)	48%	16
Herbaceous	71 (44%)	121(43%)	41%	18
Shrub	44 (27%)	82 (29%)	46%	20
Tree	28 (17%)	46 (16%)	39%	19
Grass	20 (12%)	33 (12%)	39%	5
Weed	25 (15%)	50 (18%)	50%	20

In 1996, a total of 163 species were found in the study area along the Sabie River, whereas 282 species were found in 2005 (Figure 4.2; Table 4.1). Therefore, there was an increase of 42% in the total species richness over time (Table 4.1). Of the 163 species found in 1996, 132 (81% of the total) were indigenous and 31 (19%) were alien. In 2005, 222 (79%) were indigenous and 60 (21%) were alien. Therefore, there was an increase in the total number of indigenous and alien species over time ($P < 0.001$). However, even though there was an increase of 41% in the indigenous species richness and 48% in the alien species richness, the proportion of indigenous and alien species remained approximately the same over time (Table 4.1).

From the list of plant species in 1996 (Appendix 4), the herbaceous species richness was the greatest (71 species (44% of the total)), followed by the shrubs (44 species (27%)), trees (28 species (17%)), and grasses (20 species (12%)) (Table 4.1). The proportion of species of each growth form in 1996 was similar to that in 2005 (Appendix 3), where 121 (43% of the total) of the total species were herbaceous, 82 (29%) were shrubs, 46 (16%) were trees, and 33 (12%) were grasses (Table 4.1). Thus, even though the total species richness increased over time (i.e. an increase of 42%), the proportion of species within each growth form remained approximately the same ($P = 0.97$) (Table 4.1). The most dramatic change over time was in the weed species richness. In 1996, there were 25 weed species (15%), whereas in 2005, there were 50 weed species (18%). Therefore, there was an increase of 50% in the weed species richness over time (Table 4.1).

There was a total 62 species common between the years, 46 of which were indigenous and 16 alien (Table 4.1). Of these 62 species, 20 were shrubs, 19 trees, 18 herbaceous, and 5 grasses (Table 4.1). There were 20 weed species common between the years (Table 4.1). A list of the species that have been lost since 1996 is given in Appendix 4. A total of 101 species have been lost, 50% of which are herbaceous, 20% shrubs, 15% grasses, and 15% trees.

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).

Species	Grassland		Savanna		Percentage increase from 1996 to 2005	
	1996	2005	1996	2005	Grassland	Savanna
TOTAL	140	222	106	171	40%	38%
Indigenous	111(79%)	176(79%)	89 (84%)	132(77%)	37%	32%
Alien	29 (21%)	46 (21%)	17 (16%)	39 (23%)	37%	56%
Herbaceous	64 (46%)	100(45%)	38 (36%)	67 (39%)	36%	43%
Shrub	36 (26%)	64 (29%)	33 (31%)	50 (29%)	44%	34%
Tree	21 (15%)	31 (11%)	21 (20%)	32 (19%)	32%	34%
Grass	19 (13%)	27 (12%)	14 (13%)	22 (13%)	30%	36%
Weed	24 (17%)	37 (17%)	18 (17%)	30 (17%)	35%	40%

In 1996, there were a total of 140 species in the grassland and 106 species in the savanna, whereas in 2005, there were a total 222 species in the grassland and 171 species in the savanna (Table 4.2). Therefore, the grassland remained more species rich than the savanna over time. There was a greater increase in the total species richness, as well as the indigenous and shrub species richness in the grassland compared to the savanna over time (Table 4.2). On the other hand, there was a greater increase in the alien, herbaceous, tree, grass and weed species richness in the savanna compared to the grassland over time (Table 4.2). The most dramatic change over time was in the alien species richness in the savanna, which increased by 56% (Table 4.2).

Total plant species richness

(a) Year comparison: 1996 and 2005

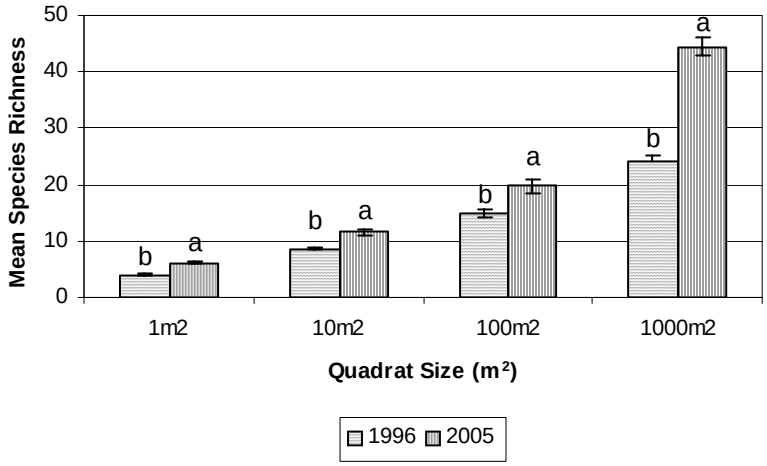


Figure 4.3. Total plant species richness (mean ± S.E.) for all 40 plots in 1996 and 2005, at the 1 m^2, 10 m^2, 100 m^2 and 1000 m^2 quadrat scales. Columns with different superscript letters within the same quadrat size are significantly different using t-tests (for independent-samples) ($P < 0.05$). N = 40 for quadrat scales; *d.f.* = 78.

At all quadrat scales, the species richness was significantly greater in 2005 (Figure 4.3; Appendix 12 for probability values).

(b) Biome comparison between 1996 and 2005: grassland and savanna biomes

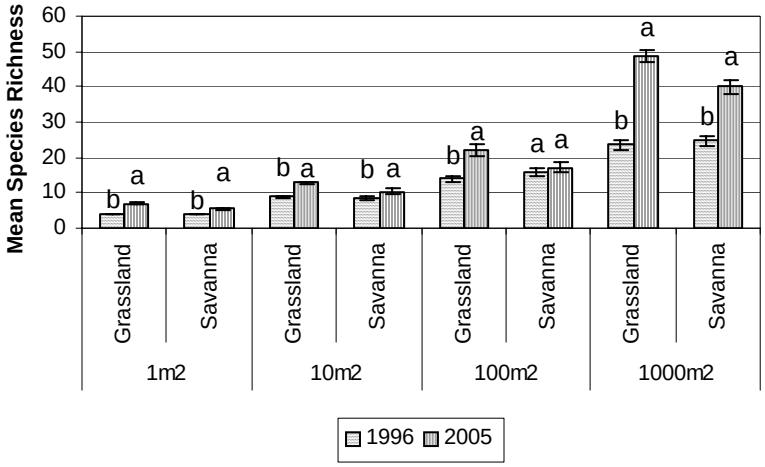


Figure 4.4. Total plant species richness (mean ± S.E.) for plots in the grassland and savanna biomes in 1996 and 2005, at the 1 m^2, 10 m^2, 100 m^2 and 1000 m^2 quadrat scales. Columns with different superscript letters within the same quadrat size and biome are significantly different using t-tests (for independent-samples) ($P < 0.05$). N = 20 for all quadrat scales and biomes; *d.f.* = 38.

At all quadrat scales, the species richness of both biomes was significantly greater in 2005, except at the 100 m^2 scale in the savanna where there was no significant difference between the species richness of 1996 and 2005 (Figure 4.4; probability values are given in Appendix 13).

(c) Treatment comparison in 1996 and 2005: (A) biome, (B) invasion intensity and (C) clearing

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).

Quadrat Size	High Altitude (Grassland)				Low Altitude (Savanna)			
	High Invasion		Low Invasion		High Invasion		Low Invasion	
	Cleared	Uncleared	Cleared	Uncleared	Cleared	Uncleared	Cleared	Uncleared
1996								
$1m^2$	$4.0\pm0.7_b^{ab}$	$2.8\pm0.1_b^{b}$	$4.6\pm0.2_b^{a}$	$4.4\pm0.4_b^{ab}$	$3.6\pm0.2_a^{ab}$	$3.7\pm0.3_b^{ab}$	$4.3\pm0.5_a^{ab}$	$4.2\pm0.3_a^{ab}$
$10m^2$	$8.9\pm0.5_b^{a}$	$8.3\pm1.3_b^{a}$	$8.9\pm0.5_b^{a}$	$9.4\pm1.0_a^{a}$	$6.7\pm0.5_a^{a}$	$9.3\pm0.5_a^{a}$	$7.8\pm1.1_a^{a}$	$9.9\pm0.8_a^{a}$
$100\ m^2$	$12.8\pm1.9_b^{ab}$	$11.8\pm1.7_a^{b}$	$16.2\pm1.8_b^{ab}$	$15.6\pm1.5_a^{ab}$	$13.8\pm1.0_a^{ab}$	$11.6\pm0.5_b^{b}$	$20.0\pm2.2_a^{a}$	$17.6\pm2.2_a^{ab}$
$1000m^2$	$20.4\pm2.5_b^{bcd}$	$19.0\pm2.2_b^{d}$	$31.2\pm2.7_b^{a}$	$23.6\pm1.1_b^{ad}$	$22.4\pm1.9_b^{ad}$	$18.8\pm1.1_b^{d}$	$28.6\pm2.3_b^{ac}$	$28.8\pm2.2_a^{ab}$
2005								
$1m^2$	$6.5\pm0.6_a^{a}$	$6.9\pm0.8_a^{a}$	$6.9\pm0.5_a^{a}$	$7.1\pm0.4_a^{a}$	$5.0\pm0.7_a^{a}$	$5.6\pm0.5_a^{a}$	$5.9\pm0.5_a^{a}$	$5.6\pm1.0_a^{a}$
$10m^2$	$14.2\pm0.9_a^{a}$	$12.2\pm0.8_a^{ab}$	$13.8\pm0.7_a^{a}$	$10.8\pm1.0_a^{ab}$	$8.1\pm1.7_a^{b}$	$12.1\pm1.3_a^{ab}$	$9.8\pm1.4_a^{ab}$	$11.2\pm1.2_a^{ab}$
$100m^2$	$24.2\pm2.7_a^{a}$	$17.8\pm3.6_a^{a}$	$26.2\pm3.7_a^{a}$	$20.6\pm1.9_a^{a}$	$16.0\pm2.5_a^{a}$	$16.8\pm2.1_a^{a}$	$17.4\pm3.3_a^{a}$	$18.4\pm4.0_a^{a}$
$1000m^2$	$52.4\pm4.31_a^{a}$	$48.0\pm1.9_a^{a}$	$51.4\pm4.4_a^{a}$	$43.4\pm2.1_a^{a}$	$38.4\pm5.0_a^{a}$	$39.2\pm2.3_a^{a}$	$40.0\pm4.2_a^{a}$	$42.4\pm5.9_a^{a}$

When the plots were divided into the eight different experimental categories of the three different experimental treatments, the species richness was higher (sometimes significantly) in 2005 (Table 4.3; probability values are given in Appendix 15). An important point to note is that the plots in the 'uncleared' category in 1996 can be used as the control plots, as no clearing had been done previously in these plots. Therefore, the effect of WfW clearing on the environment can be assessed. In most of the uncleared plots over time, the total species richness increased significantly (Table 4.3).

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 $P < 0.05$.

Year	Quadrat Size	BIOME	INVIN	CLEAR	BIOME* INVIN	BIOME* CLEAR	INV* CLEAR	BIOME* INVIN* CLEAR	Co-variate
(a) 1996	$1m^2$	0.971	**0.003**	0.184	0.385	0.196	0.468	0.295	
	$10\ m^2$	0.444	0.237	0.056	0.798	**0.047**	0.798	0.496	
	$100\ m^2$	0.181	**$3x10^{-5}$**	0.208	0.307	0.538	0.967	0.902	
	$1000m^2$	0.460	**$7x10^{-7}$**	0.043	0.893	0.348	0.686	0.099	
(b) 2005	$1m^2$	**0.005**	0.443	0.613	0.843	0.947	0.583	0.708	
	$10\ m^2$	**0.005**	0.760	0.903	0.428	**0.003**	0.275	0.625	
	$100\ m^2$	**0.026**	0.374	0.247	0.836	0.120	0.909	0.945	
	$1000m^2$	**0.004**	0.944	0.425	0.368	0.180	0.862	0.651	
(c) 1996 and 2005	$1m^2$	**0.005**	0.253	0.794	0.965	0.873	0.676	0.583	0.327
	$10\ m^2$	**0.007**	0.683	0.948	0.449	**0.009**	0.270	0.679	0.588
	$100\ m^2$	**0.012**	0.894	0.410	0.632	0.084	0.916	0.971	0.137
	$1000m^2$	**0.004**	0.607	0.611	0.380	0.229	0.902	0.814	0.501

In 1996, no significant differences were found in the species richness between the grassland and savanna plots, as well as the cleared and uncleared plots (Table 4.4 (a)). However, the low invaded plots were significantly more species rich (Table 4.4). In 2005, there was no significant difference in the species richness between high and low invaded plots, as well as cleared and uncleared plots (Table 4.4 (b)). However, the plots (at all scales) of the grassland were significantly more species rich than the savanna (Table 4.4 (b)). There was a significant interaction between the biome and clearing treatments at the 10 m^2 scale in both years. Therefore, at the 10 m^2 scale, the value for the biomes (for both years) is dependent on whether it is cleared or not. In 1996, the uncleared plots generally had a higher species richness than the cleared plots, in both biomes. In the grassland in 2005, the species richness was higher in the cleared plots, whereas in the savanna, the species richness was higher in the uncleared plots.

There was a significant change in the species richness of the biomes over time (Table 4.4 (c)). In 1996, the species richness was greater in the savanna plots, whereas in 2005 it was greater in the grassland plots. There was significant interaction between the biome and clearing treatments in the ANCOVA. This pattern was the same as the pattern for the 2005 and 1996 ANOVA's. This means that there is virtually no effect of the 1996 pattern on the outcome in 2005. This is supported by

the fact that none of the *P* – values for the covariate, i.e. 1996 values, are significant; therefore, there is no clear overall relationship between the 2005 and 1996 data.

Species richness (tree, shrub, herbaceous, and grass and sedge growth forms)

(a) Year comparison: 1996 and 2005

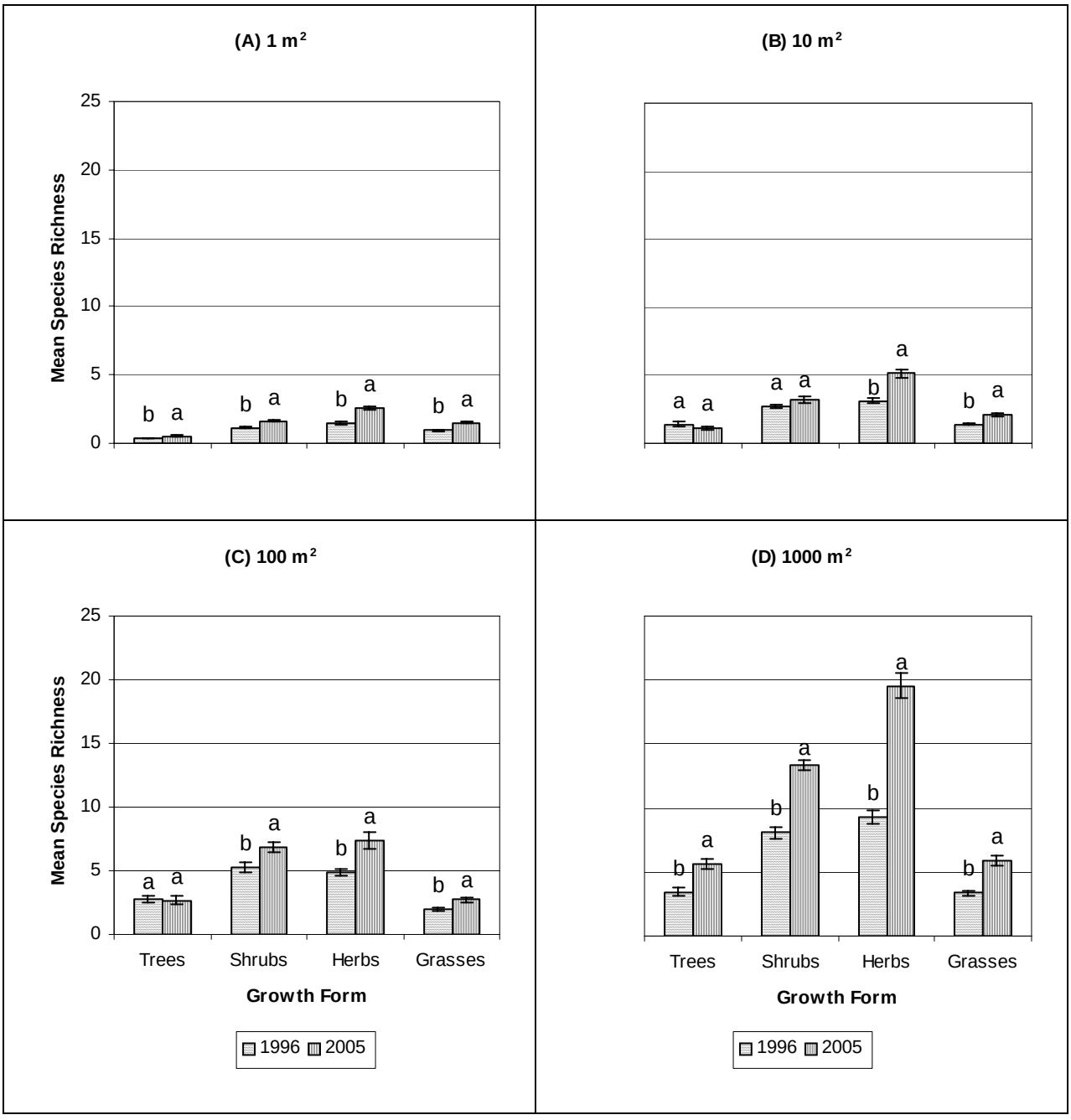


Figure 4.5. Species richness (mean ± S.E.) for (a) tree, (b) shrub, (c) herbaceous, and (d) grass and sedge growth forms in all 40 plots in 1996 and 2005, at the (A) 1 m^2, (B) 10 m^2, (C) 100 m^2 and (D) 1000 m^2 quadrat scales. Columns with different superscript letters within the same growth form are significantly different using t-tests (for independent-samples) ($P < 0.05$). N = 40 for all growth forms and quadrat scales; *d.f.* = 78.

At all quadrat scales, the species richness of each growth form was significantly greater in 2005 (except at the 10 m^2 and 100 m^2 scales, where the tree species richness was greater (but not significantly) in 1996, and at the 10 m^2 scale, where the shrub species richness was greater (but not significantly) in 2005) (Figure 4.5; probability values are given in Appendix 14).

(b) Treatment comparison in 1996 and 2005: (A) biome, (B) invasion intensity and (C) clearing

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).

Quadrat Size	High Altitude (Grassland)				Low Altitude (Savanna)			
	High Invasion		Low Invasion		High Invasion		Low Invasion	
	Cleared	Uncleared	Cleared	Uncleared	Cleared	Uncleared	Cleared	Uncleared
1996								
$1m^2$	$0.1\pm0.1a^{b}$	$0.3\pm0.1_b^{ab}$	$0.2\pm0.1_a^{ab}$	$0.4\pm0.1_a^{ab}$	$0.4\pm0.1_a^{ab}$	$0.4\pm0.1_a^{ab}$	$0.6\pm0.2_a^{a}$	$0.5\pm0.1_a^{ab}$
$10m^2$	$0.8\pm0.5_a^{a}$	$1.2\pm0.1_a^{a}$	$0.8\pm0.3_a^{a}$	$1.2\pm0.6_a^{a}$	$1.3\pm0.2_a^{a}$	$1.6\pm0.3_a^{a}$	$2.0\pm0.4_a^{a}$	$2.3\pm0.6_a^{a}$
$100\ m^2$	$0.6\pm0.2_b^{b}$	$2.6\pm0.7_a^{ab}$	$2.4\pm0.8_a^{ab}$	$2.2\pm0.8_a^{ab}$	$2.4\pm0.5_a^{ab}$	$2.6\pm0.2_a^{ab}$	$5.0\pm0.8_a^{a}$	$4.2\pm0.7_a^{a}$
$1000m^2$	$1.0\pm0.6_b^{c}$	$3.2\pm0.2_b^{abc}$	$3.2\pm0.8_b^{abc}$	$2.8\pm0.6_a^{bc}$	$2.4\pm0.8_a^{bc}$	$3.4\pm0.5_a^{abc}$	$5.2\pm0.7_a^{abc}$	$6.2\pm1.0_a^{a}$
2005								
$1m^2$	$0.6\pm0.2_a^{a}$	$0.8\pm0.2_a^{a}$	$0.6\pm0.2_a^{a}$	$0.3\pm0.1_a^{a}$	$0.5\pm0.2_a^{a}$	$0.6\pm0.1_a^{a}$	$0.6\pm0.8_a^{a}$	$0.3\pm0.1_a^{a}$
$10m^2$	$1.4\pm0.3_a^{a}$	$1.1\pm0.4_a^{a}$	$0.9\pm0.2_a^{a}$	$0.5\pm0.2_a^{a}$	$0.9\pm0.3_a^{a}$	$1.4\pm0.4_a^{a}$	$1.5\pm0.7_a^{a}$	$1.2\pm0.3_a^{a}$
$100m^2$	$2.6\pm0.5_a^{a}$	$1.8\pm0.9_a^{a}$	$2.8\pm0.6_a^{a}$	$1.6\pm0.6_a^{a}$	$4.2\pm1.5_a^{a}$	$3.0\pm0.7_a^{a}$	$2.4\pm1.0_a^{a}$	$2.8\pm1.2_a^{a}$
$1000m^2$	$5.2\pm0.7_a^{a}$	$5.8\pm0.9_a^{a}$	$6.4\pm1.0_a^{a}$	$4.0\pm0.8_a^{a}$	$6.8\pm1.9_a^{a}$	$4.8\pm0.4_a^{a}$	$5.4\pm1.2_a^{a}$	$6.6\pm1.4_a^{a}$

There was no significant difference in the tree species richness of the plots of the different experimental categories at all quadrat scales between 1996 and 2005, except between the grassland, high invaded, uncleared plots at the 1 m^2 scale, the grassland, high invaded, cleared plots at the 100 m^2 scale, and the grassland, high invaded, cleared and uncleared plots, and the grassland, low invaded, cleared plots at the 1000 m^2 scale, which all had a significantly greater tree species richness in 2005 (Table 4.5; probability values are given in Appendix 16).

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. *d.f.* = 1,32 for all main effects and interaction terms. Bold text indicates $P < 0.05$.

Year	Quadrat Size	BIOME	INVIN	CLEAR	BIOME* INVIN	BIOME* CLEAR	INVIN* CLEAR	BIOME* INVIN* CLEAR
1996	$1m^2$	**0.006**	0.122	0.513	0.793	0.242	0.361	0.513
	$10\ m^2$	**0.012**	0.254	0.254	0.254	0.869	0.999	0.999
	$100\ m^2$	**0.001**	**0.005**	0.519	0.138	0.201	0.091	0.519
	$1000m^2$	**0.001**	**0.001**	0.058	0.058	0.918	0.187	0.187
2005	$1m^2$	0.585	0.166	0.436	0.533	0.876	0.057	0.938
	$10\ m^2$	0.326	0.530	0.653	0.183	0.420	0.420	0.530
	$100\ m^2$	0.181	0.453	0.296	0.453	0.652	0.652	0.453
	$1000m^2$	0.490	0.950	0.416	0.753	0.753	0.950	0.058

In 1996, the savanna plots had a significantly higher tree species richness at all quadrat scales (Table 4.6). At the 100 m^2 and 1000 m^2 scales, the tree species richness was significantly higher in the low invaded plots (Table 4.6). However, there was no significant difference in the tree species richness between the high and low invaded plots at the 1 m^2 and 10 m^2 scales, as well as the cleared and uncleared plots at all quadrat scales (even though this was almost significant) (Table 4.6). In 2005, there was no significant difference in the tree species richness between the grassland and savanna plots, the high and low invaded plots, and cleared and uncleared plots (Table 4.6).

Table 4.7. Shrub 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).

Quadrat Size	High Altitude (Grassland)				Low Altitude (Savanna)			
	High Invasion		Low Invasion		High Invasion		Low Invasion	
	Cleared	Uncleared	Cleared	Uncleared	Cleared	Uncleared	Cleared	Uncleared
1996								
$1m^2$	$1.4\pm0.4_a^a$	$0.8\pm0.2_b^a$	$1.0\pm0.1_b^a$	$1.2\pm0.3_a^a$	$0.7\pm0.1_a^a$	$1.1\pm0.3_a^a$	$1.4\pm0.1_a^a$	$1.5\pm0.2_a^a$
$10m^2$	$2.8\pm0.2_a^a$	$2.1\pm0.6_a^a$	$2.7\pm0.5_a^a$	$3.3\pm0.6_a^a$	$2.1\pm0.4_a^a$	$2.8\pm0.3_a^a$	$2.4\pm0.2_a^a$	$3.5\pm0.3_a^a$
$100\ m^2$	$4.8\pm0.9_b^{ab}$	$3.4\pm0.4_b^b$	$5.6\pm0.7_a^{ab}$	$6.0\pm1.4_a^{ab}$	$4.8\pm0.9_a^{ab}$	$3.8\pm0.7_a^{ab}$	$8.0\pm1.5_a^a$	$5.8\pm0.9_a^{ab}$
$1000m^2$	$7.2\pm1.2_b^a$	$6.0\pm1.2_b^a$	$10.4\pm0.5_b^a$	$8.2\pm0.8_b^a$	$7.8\pm0.7_a^a$	$6.4\pm0.8_b^a$	$9.2\pm1.5_a^a$	$9.2\pm1.7_a^a$
2005								
$1m^2$	$1.8\pm0.2_a^{abc}$	$2.4\pm0.2_a^a$	$2.2\pm0.2_a^{ab}$	$1.7\pm0.2_a^{abc}$	$1.4\pm0.3_a^{abc}$	$1.1\pm0.2_a^c$	$1.4\pm0.1_a^{abc}$	$1.2\pm0.3_a^{bc}$
$10m^2$	$4.4\pm0.8_a^a$	$3.3\pm0.5_a^a$	$4.3\pm0.6_a^a$	$3.1\pm0.2_a^a$	$2.1\pm0.6_a^a$	$3.3\pm0.3_a^a$	$2.2\pm0.6_a^a$	$2.8\pm0.5_a^a$
$100m^2$	$9.0\pm1.0_a^a$	$7.6\pm1.2_a^a$	$7.6\pm0.7_a^a$	$7.8\pm0.6_a^a$	$5.6\pm0.8_a^a$	$6.0\pm0.9_a^a$	$5.4\pm1.3_a^a$	$6.0\pm1.6_a^a$
$1000m^2$	$15.4\pm1.5_a^a$	$14.4\pm0.8_a^a$	$13.4\pm0.7_a^a$	$13.6\pm0.4_a^a$	$13.2\pm2.3_a^a$	$12.6\pm1.1_a^a$	$13.0\pm1.2_a^a$	$11.2\pm1.2_a^a$

At the 1 m^2, 10 m^2 and 100 m^2 scales, there was no significant difference between the shrub species richness of the plots of the different experimental categories between 1996 and 2005, except between the grassland, high invaded, uncleared plots and the grassland, low invaded, cleared plots (at the 1 m^2 scale), and the grassland, high invaded, cleared and uncleared plots (at the 100 m^2 scale), which all had a significantly higher shrub species richness in 2005 (Table 4.7; probability values are given in Appendix 16). At the 1000 m^2 scale, the shrub species richness was significantly higher in all of the grassland plots in 2005, as well as the savanna,

high invaded, uncleared plots (Table 4.7; probability values are given in Appendix 16).

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. *d.f.* = 1,32 for all main effects and interaction terms. Bold text indicates $P < 0.05$.

Year	Quadrat Size	BIOME	INVIN	CLEAR	BIOME* INVIN	BIOME* CLEAR	INVIN* CLEAR	BIOME* INVIN* CLEAR
1996	$1m^2$	0.579	0.102	0.805	0.115	0.199	0.424	0.091
	$10\ m^2$	0.933	0.084	0.159	0.933	0.117	0.159	0.451
	$100\ m^2$	0.349	**0.004**	0.134	0.515	0.427	0.828	0.281
	$1000m^2$	0.800	**0.004**	0.135	0.704	0.528	0.899	0.449
2005	$1m^2$	**$5x10^{-6}$**	0.848	0.524	0.408	0.374	0.132	0.081
	$10\ m^2$	**0.005**	0.653	0.748	0.949	**0.012**	0.653	0.748
	$100\ m^2$	**0.005**	0.640	0.947	0.738	0.463	0.548	0.640
	$1000m^2$	0.065	0.226	0.376	0.738	0.656	0.999	0.505

In 1996, there was no significant difference in the shrub species richness (at all quadrat scales) between the grassland and savanna biomes, the high and low invaded plots (only at the 1 m^2 and 10 m^2 scales), and the cleared and uncleared plots (Table 4.8). The low invaded 100 m^2 and 1000 m^2 plots had a significantly higher shrub species richness (Table 4.8). In 2005, there was no significant difference in the shrub species richness between the grassland and savanna plots (only at the 1000 m^2 scale), high and low invaded plots (at all quadrat scales), and the cleared and uncleared plots (at all quadrat scales) (Table 4.8). At the 1 m^2, 10 m^2 and 100 m^2 quadrat scales, the shrub species richness was significantly higher in the grassland plots (Table 4.8). There was a significant interaction between the biome and clearing treatments for the shrub species richness in 2005 at the 10 m^2 scale (Table 4.8). Therefore, the value for the biomes is dependent on whether it is cleared or not. In the grassland, the shrub species richness was higher in the cleared plots, whereas in the savanna, it was higher in the uncleared plots.

Table 4.9. Herbaceous 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).

Quadrat Size	High Altitude (Grassland)				Low Altitude (Savanna)			
	High Invasion		Low Invasion		High Invasion		Low Invasion	
	Cleared	Uncleared	Cleared	Uncleared	Cleared	Uncleared	Cleared	Uncleared
1996								
$1m^2$	$1.7\pm0.3_b^{ab}$	$0.9\pm0.1_b^{b}$	$2.4\pm0.1_a^{a}$	$2.2\pm0.5_a^{ab}$	$1.2\pm0.1_a^{b}$	$1.1\pm0.1_b^{b}$	$1.4\pm0.3_a^{ab}$	$1.3\pm0.2_a^{b}$
$10m^2$	$4.0\pm0.7_a^{a}$	$4.0\pm0.8_a^{a}$	$3.7\pm0.7_b^{a}$	$3.5\pm0.5_a^{a}$	$2.1\pm0.2_a^{a}$	$3.2\pm0.5_a^{a}$	$1.9\pm0.5_b^{a}$	$2.6\pm0.5_a^{a}$
$100\ m^2$	$5.0\pm1.0_a^{a}$	$4.0\pm0.6_a^{a}$	$6.2\pm0.9_a^{a}$	$4.8\pm0.4_a^{a}$	$4.4\pm0.7_a^{a}$	$3.6\pm0.6_a^{a}$	$5.2\pm0.7_a^{a}$	$5.8\pm1.5_a^{a}$
$1000m^2$	$8.6\pm1.4_b^{ab}$	$7.4\pm1.4_b^{b}$	$13.4\pm1.9_b^{a}$	$9.4\pm0.8_b^{ab}$	$8.6\pm1.3_a^{ab}$	$6.4\pm0.6_b^{b}$	$10.4\pm1.2_a^{ab}$	$9.8\pm1.0_a^{ab}$
2005								
$1m^2$	$2.8\pm0.3_a^{a}$	$2.5\pm0.5_a^{a}$	$3.0\pm0.2_a^{a}$	$3.3\pm0.3_a^{a}$	$1.8\pm0.3_a^{a}$	$2.6\pm0.2_a^{a}$	$2.3\pm0.5_a^{a}$	$2.5\pm0.6_a^{a}$
$10m^2$	$6.0\pm0.9_a^{a}$	$5.8\pm1.0_a^{a}$	$6.4\pm0.8_a^{a}$	$5.0\pm1.1_a^{a}$	$3.3\pm1.0_a^{a}$	$5.7\pm1.1_a^{a}$	$4.2\pm0.3_a^{a}$	$4.7\pm0.9_a^{a}$
$100m^2$	$9.4\pm1.6_a^{a}$	$6.4\pm2.0_a^{a}$	$11.6\pm2.6_a^{a}$	$7.4\pm1.4_a^{a}$	$4.2\pm0.9_a^{a}$	$5.8\pm0.8_a^{a}$	$7.4\pm1.4_a^{a}$	$7.0\pm1.8_a^{a}$
$1000m^2$	$24.8\pm2.6_a^{a}$	$22.0\pm1.2_a^{a}$	$23.8\pm3.3_a^{a}$	$19.0\pm2.2_a^{a}$	$13.4\pm1.7_a^{a}$	$17.8\pm1.5_a^{a}$	$17.8\pm3.1_a^{a}$	$17.6\pm3.7_a^{a}$

At the 1 m^2, 10 m^2 and 100 m^2 scales, there was no significant difference in the herbaceous species richness of the plots of the different experimental categories between 1996 and 2005, except between the grassland, high invaded, cleared and uncleared plots, and the savanna, high invaded, uncleared plots (at the 1 m^2 scale), and the grassland, low invaded, cleared plots, and the savanna, low invaded, cleared plots (at the 10 m^2 scale), which all had a significantly higher herbaceous species richness in 2005 (Table 4.9; probability values are given in Appendix 16). At the 1000 m^2 scale, the herbaceous species richness of all of the grassland plots were significantly higher in 2005, as well as of the savanna, high invaded, uncleared plots (Table 4.9; probability values are given in Appendix 16).

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. *d.f.* = 1,32 for all main effects and interaction terms. Bold text indicates $P < 0.05$.

Year	Quadrat Size	BIOME	INVIN	CLEAR	BIOME* INVIN	BIOME* CLEAR	INVIN* CLEAR	BIOME* INVIN* CLEAR
1996	$1m^2$	**0.003**	**0.001**	0.810	**0.023**	0.213	0.398	0.502
	$10\ m^2$	**0.002**	0.327	0.327	0.999	0.223	0.711	0.902
	$100\ m^2$	0.680	**0.046**	0.288	0.680	0.367	0.680	0.460
	$1000m^2$	0.317	**0.002**	**0.031**	0.655	0.503	0.737	0.223
2005	$1m^2$	**0.029**	0.237	0.365	0.630	0.347	0.986	0.296
	$10\ m^2$	0.050	0.849	0.621	0.909	0.094	0.243	0.790
	$100\ m^2$	**0.034**	0.116	0.211	0.800	0.083	0.501	0.866
	$1000m^2$	**0.003**	0.978	0.638	0.261	0.110	0.364	0.719

In 1996, the grassland plots had a significantly higher herbaceous species richness (at the 1 m^2 and 10 m^2 scales), whereas at the 100 m^2 and 1000 m^2 scales, there was no significant difference (Table 4.10). At all quadrat scales (except the 10 m^2 scale), the low invaded plots had a significantly higher herbaceous species richness (Table 4.10). There was no significant difference in the species richness between the cleared and uncleared plots, except at the 1000 m^2 scale where cleared plots were significantly richer in terms of herbaceous species (Table 4.10). In 2005, the grassland plots had a significantly higher herbaceous species richness (except at the 10 m^2 scale, although this was almost significantly higher in the grassland) (Table 4.10). There was no significant difference in the herbaceous species richness between

the high and low invaded plots, and the cleared and uncleared plots (Table 4.10). There was a significant interaction between the biome and invasion intensity treatments for herbaceous species richness in 1996 at the 1 m^2 scale (Table 4.10). Therefore, the herbaceous species richness of the biomes is dependent on whether there is a high or low invasion of alien plants in the plots. In both biomes, the low invaded plots had a higher herbaceous species richness.

Table 4.11. Grass and sedge 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).

Quadrat Size	High Altitude (Grassland)				Low Altitude (Savanna)			
	High Invasion		Low Invasion		High Invasion		Low Invasion	
	Cleared	Uncleared	Cleared	Uncleared	Cleared	Uncleared	Cleared	Uncleared
1996								
$1m^2$	$0.9\pm0.2_a^a$	$0.8\pm0.2_b^a$	$0.9\pm0.2_a^a$	$0.6\pm0.3_b^a$	$1.3\pm0.2_a^a$	$1.0\pm0.1_b^a$	$0.9\pm0.3_a^a$	$0.9\pm0.2_a^a$
$10m^2$	$1.3\pm0.1_b^a$	$1.0\pm0.3_a^a$	$1.7\pm0.2_a^a$	$1.4\pm0.2_b^a$	$1.2\pm0.3_a^a$	$1.7\pm0.1_a^a$	$1.5\pm0.5_a^a$	$1.5\pm0.3_a^a$
$100\ m^2$	$2.4\pm0.5_a^a$	$1.8\pm0.4_a^a$	$2.0\pm0.6_a^a$	$2.4\pm0.4_b^a$	$2.2\pm0.5_a^a$	$1.6\pm0.2_a^a$	$1.8\pm0.6_a^a$	$1.8\pm0.6_a^a$
$1000m^2$	$3.6\pm0.7_b^a$	$2.4\pm0.2_b^a$	$4.2\pm0.4_b^a$	$3.2\pm0.6_b^a$	$3.6\pm0.8_a^a$	$2.4\pm0.4_b^a$	$3.8\pm0.6_a^a$	$3.6\pm0.5_b^a$
2005								
$1m^2$	$1.4\pm0.2_a^a$	$1.3\pm0.1_a^a$	$1.3\pm0.1_a^a$	$1.9\pm0.2_a^a$	$1.4\pm0.1_a^a$	$1.4\pm0.1_a^a$	$1.6\pm0.1_a^a$	$1.7\pm0.3_a^a$
$10m^2$	$2.4\pm0.4_a^a$	$2.0\pm0.5_a^a$	$2.2\pm0.2_a^a$	$2.2\pm0.3_a^a$	$1.8\pm0.1_a^a$	$1.8\pm0.2_a^a$	$2.1\pm0.2_a^a$	$2.5\pm0.7_a^a$
$100m^2$	$3.2\pm0.5_a^{ab}$	$2.0\pm0.5_a^b$	$4.2\pm0.7_a^a$	$3.8\pm0.2_a^{ab}$	$2.0\pm0.5_a^b$	$2.0\pm0.3_a^b$	$2.2\pm0.6_a^{ab}$	$2.6\pm0.3_a^{ab}$
$1000m^2$	$7.0\pm1.3_b^a$	$5.8\pm1.2_a^a$	$7.8\pm1.0_a^a$	$6.6\pm0.7_a^a$	$5.0\pm0.6_a^a$	$4.0\pm0.6_a^a$	$3.8\pm0.8_a^a$	$7.0\pm1.1_a^a$

At the 1 m^2, 10 m^2 and 100 m^2 scales, there was no significant difference in the grass and sedge species richness of the plots of the different experimental categories between 1996 and 2005, except between the grassland, high invaded, uncleared plots, the grassland, low invaded, uncleared plots, and the savanna, high invaded, uncleared plots (at the 1 m^2 scale), the grassland, high invaded, cleared plots, and the grassland, low invaded, uncleared plots (at the 10 m^2 scale), and the grassland, low invaded, uncleared plots (at the 100 m^2 scale), which all had a significantly higher grass and sedge species richness in 2005 (Table 4.11; probability values are given in Appendix 16). At the 1000 m^2 scale, the grass and sedge species richness of all of the grassland plots were significantly higher in 2005, as well as of the savanna, high invaded, uncleared plots, and the savanna, low invaded, uncleared plots (Table 4.11; probability values are given in Appendix 16).

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. *d.f.* = 1,32 for all main effects and interaction terms. Bold text indicates $P < 0.05$.

Year	Quadrat Size	BIOME	INVIN	CLEAR	BIOME* INVIN	BIOME* CLEAR	INVIN* CLEAR	BIOME* INVIN* CLEAR
1996	$1m^2$	0.138	0.375	0.248	0.452	0.837	0.999	0.340
	$10\ m^2$	0.513	0.242	0.895	0.361	0.155	0.513	0.513
	$100\ m^2$	0.395	0.999	0.570	0.776	0.776	0.259	0.776
	$1000m^2$	0.999	0.075	**0.024**	0.999	0.603	0.437	0.603
2005	$1m^2$	0.871	0.059	0.200	0.935	0.375	0.130	0.420
	$10\ m^2$	0.554	0.326	0.999	0.326	0.431	0.431	0.999
	$100\ m^2$	**0.002**	**0.010**	0.367	0.137	0.137	0.367	0.762
	$1000m^2$	**0.009**	0.211	0.941	0.941	0.093	0.124	0.124

In 1996, there was no significant difference in the grass and sedge species richness between the grassland and savanna plots, the high and low invaded plots, and the cleared and uncleared plots, except for cleared plots at the 1000 m^2 scale, which had a significantly higher grass and sedge species richness than uncleared plots (Table 4.12). In 2005, the grass and sedge species richness was significantly higher in the grassland plots (at the 100 m^2 and 1000 m^2 scales). The grass and sedge species richness of the low invaded plots were significantly richer (only at the 100 m^2 scale). There was no significant difference in the grass and sedge species richness between the cleared and uncleared plots (Table 4.12).

4.4.2. Plant species diversity

Simpson's index of diversity (1-D)

(a) Year comparison: 1996 and 2005

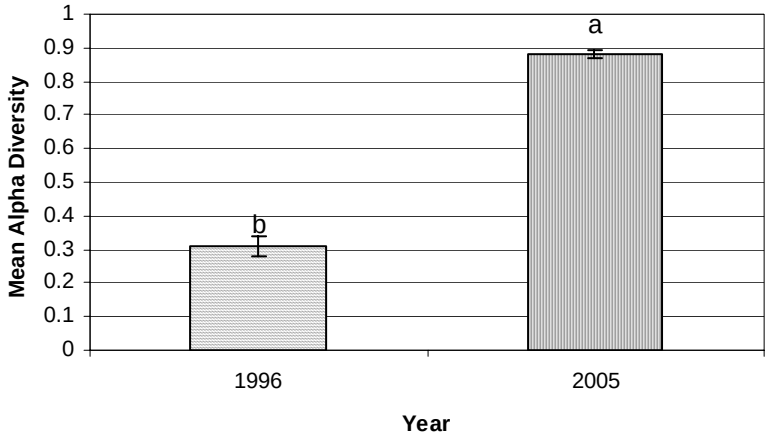


Figure 4.6. Simpson's index of diversity (alpha diversity) (mean ± S.E.) for total plant species for all 40 plots in 1996 and 2005, at the 100 m^2 quadrat scale. Columns with different superscript letters are significantly different using t-tests (for independent-samples) ($P < 0.05$). N = 40 for each year; *d.f.* = 78.

The alpha diversity at the 100 m^2 scale was significantly greater in 2005 ($P < 0.001$) (Figure 4.6).

(b) Biome comparison between 1996 and 2005: grassland and savanna biomes

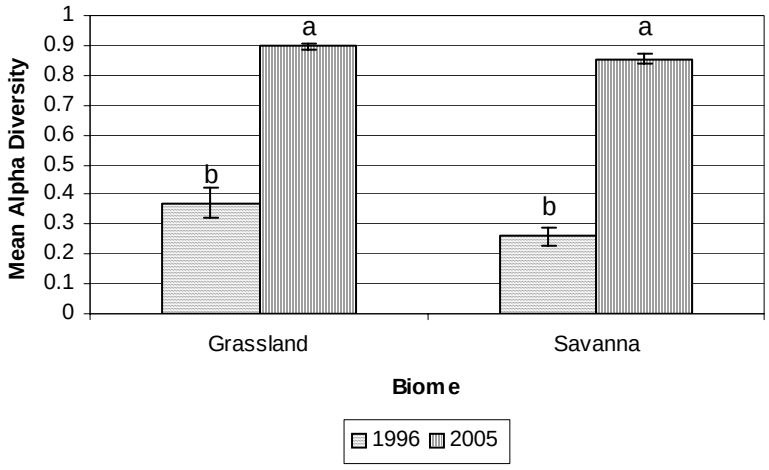


Figure 4.7. Simpson's index of diversity (alpha diversity) (mean ± S.E.) for total plant species for plots in the grassland and savanna biomes in 1996 and 2005, at the 100 m^2 quadrat scale. Columns with different superscript letters within the same biome are significantly different using t-tests (for independent-samples) ($P < 0.05$). N = 20 for each biome; *d.f.* = 38.

In both years, the alpha diversity was greater in the grassland (Figure 4.7). 2005 had a significantly greater alpha diversity than 1996 in both biomes ($P < 0.001$ for both biomes) (Figure 4.7).

(c) Treatment comparison in 1996 and 2005: (A) biome, (B) invasion intensity and (C) clearing

Table 4.13. Total plant species Simpson's index of diversity (alpha diversity) (mean ± 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).

High Altitude (Grassland)				**Low Altitude (Savanna)**			
High Invasion		**Low Invasion**		**High Invasion**		**Low Invasion**	
Cleared	**Uncleared**	**Cleared**	**Uncleared**	**Cleared**	**Uncleared**	**Cleared**	**Uncleared**
1996							
$0.50\pm0.11_b^a$	$0.52\pm0.11_b^a$	$0.19\pm0.03_b^b$	$0.27\pm0.05_b^{ab}$	$0.37\pm0.07_b^{ab}$	$0.28\pm0.02_b^{ab}$	$0.14\pm0.03_b^b$	$0.24\pm0.05_b^{ab}$
2005							
$0.88\pm0.04_a^a$	$0.88\pm0.02_a^a$	$0.91\pm0.01_a^a$	$0.91\pm0.004_a^a$	$0.83\pm0.04_a^a$	$0.88\pm0.02_a^a$	$0.84\pm0.05_a^a$	$0.86\pm0.03_a^a$

The alpha diversity of the 100 m^2 plots of the different experimental categories was significantly higher in 2005 (Table 4.13; Appendix 15 for probability values). It can be said that the WfW clearing had a positive effect on the diversity of the total species over time, as the control 'uncleared' plots in 1996 had a significantly lower alpha diversity that those plots of 2005.

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 (*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 $P < 0.05$.

Year	BIOME	INVIN	CLEAR	BIOME* INVIN	BIOME* CLEAR	INVIN* CLEAR	BIOME* INVIN* CLEAR	Co-variate
(a) 1996	**0.021**	**$9x10^{-6}$**	0.587	0.123	0.664	0.171	0.486	
(b) 2005	0.054	0.603	0.446	0.400	0.481	0.689	0.692	
(c) 1996 and 2005	**0.034**	0.854	0.397	0.579	0.529	0.873	0.783	0.345

In 1996, the grassland and high invaded plots (for both biomes) had a significantly higher alpha diversity; however, there were no significant differences between the cleared and uncleared plots (Table 4.14 (a)). In 2005, there was no significant difference in the alpha diversity between the grassland and savanna plots (although this was almost significant, with the grassland plots having a higher diversity), the high and low invaded plots, and the cleared and uncleared plots (Table 4.14 (b)). There was a significant change in the alpha diversity of the biomes over time (Table 4.14 (c)), i.e. the alpha diversity (of both biomes) was much higher in 2005 than that in 1996. The *P* – value for the covariate, i.e. 1996 value, is not significant; therefore, there is little or no relationship between the 2005 and 1996 alpha diversities.

Sorenson's coefficient of community (CC)

(a) Treatment comparison in 1996 and 2005: (A) biome, (B) invasion intensity and (C) clearing

Sorenson's coefficient of community is a measure of the beta diversity and indicates how similar two communities are in terms of the species they support. In 1996, the plots in the eight different experimental categories of the three different experimental treatments were not very similar in terms of species composition, whereas in 2005, the beta diversity was higher (Table 4.15). In each of the eight experimental categories of the three different experimental treatments, the species similarity between 1996 and 2005 was very low.

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.

				High Altitude								**Low Altitude**							
				High Invasion				**Low Invasion**				**High Invasion**				**Low Invasion**			
				Cleared		**Uncleared**		**Cleared**		**Uncleared**		**Cleared**		**Uncleared**		**Cleared**		**Uncleared**	
				1996	**2005**	**1996**	**2005**	**1996**	**2005**	**1996**	**2005**	**1996**	**2005**	**1996**	**2005**	**1996**	**2005**	**1996**	**2005**
High Altitude	**High Invasion**	**Cleared**	**1996**		**0.09**	0.29	0.06	0.32	0.08	0.28	0.03	0.48	0.09	0.37	0.08	0.27	0.07	0.28	0.13
			2005			0.17	0.53	0.19	0.59	0.12	0.52	0.13	0.40	0.13	0.44	0.18	0.49	0.15	0.47
		Uncleared	**1996**				**0.12**	0.50	0.12	0.40	0.08	0.45	0.16	0.30	0.15	0.40	0.12	0.48	0.12
			2005					0.13	0.45	0.06	0.50	0.09	0.35	0.09	0.47	0.09	0.45	0.08	0.43
	Low Invasion	**Cleared**	**1996**						**0.13**	0.40	0.10	0.49	0.15	0.37	0.22	0.47	0.13	0.46	0.15
			2005							0.07	0.48	0.07	0.32	0.07	0.36	0.12	0.40	0.09	0.50
		Uncleared	**1996**								**0.08**	0.44	0.14	0.29	0.11	0.47	0.09	0.33	0.09
			2005									0.06	0.30	0.06	0.45	0.11	0.47	0.07	0.49
Low Altitude	**High Invasion**	**Cleared**	**1996**										**0.11**	0.47	0.15	0.47	0.09	0.51	0.09
			2005											0.14	0.45	0.25	0.38	0.27	0.37
		Uncleared	**1996**												**0.15**	0.49	0.09	0.49	0.18
			2005													0.17	0.57	0.19	0.52
	Low Invasion	**Cleared**	**1996**														**0.12**	0.62	0.21
			2005															0.11	0.63
		Uncleared	**1996**																**0.13**
			2005																

4.4.3 Overstorey aerial cover

(a) Year comparison: 1996 and 2005

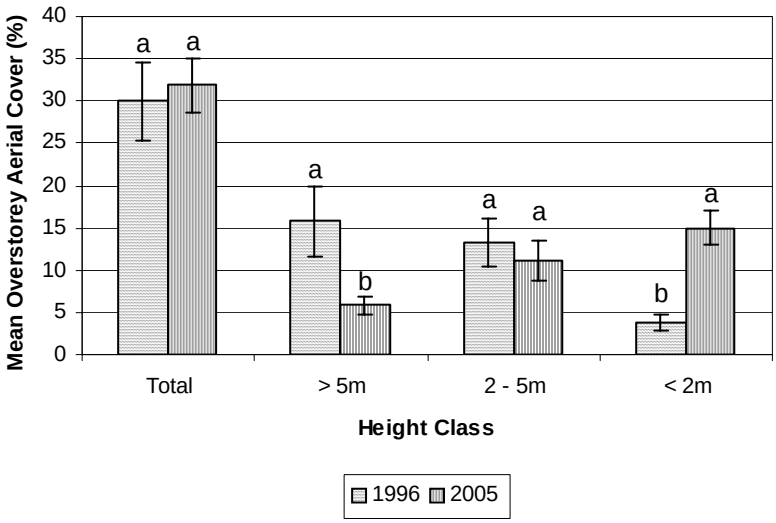


Figure 4.8. Percentage aerial cover of alien vegetation (mean ± S.E.) for all 40 plots in 1996 and 2005. Columns with different superscript letters within the same height class are significantly different using t-tests (for independent-samples) ($P < 0.05$). N = 40 for all height classes; *d.f.* = 78.

In total, the alien vegetation aerial cover was greater in 2005, but not significantly (Figure 4.8; Appendix 12 for probability values). The aerial cover of alien plants > 5 m and between 2 and 5 m in height was greater (significantly for > 5 m) in 1996, whereas the aerial cover of plants < 2 m in height was significantly greater in 2005 (Figure 4.8; Appendix 12 for probability values).

(b) Biome comparison between 1996 and 2005: grassland and savanna biomes

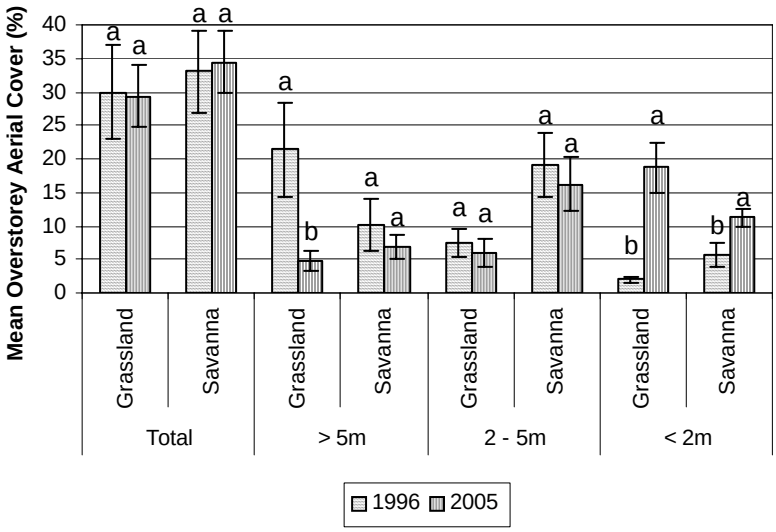


Figure 4.9. Percentage aerial cover of alien vegetation (mean ± S.E.) for plots in the grassland and savanna biomes in 1996 and 2005. Columns with different superscript letters within the same height class and biome are significantly different using t-tests

(for independent-samples) ($P < 0.05$). N = 20 for each height class and biome; *d.f.* = 38.

In both years, the overstorey aerial cover was greater in the savanna for all height classes, except the > 5 m height class in 1996 and the < 2 m height class in 2005 (Figure 4.9). In the grassland, the aerial cover in 1996 was greater, except for plants < 2 m in height, which had a significantly greater aerial cover in 2005 (Figure 4.9; probability values are given Appendix 13). In total, and for plants < 2 m in height, the alien vegetation aerial cover in the savanna in 2005 was greater, whereas the aerial cover of plants > 5 m and between 2 and 5 m in height was greater in 1996 (Figure 4.9; probability values are given Appendix 13).

(c) Treatment comparison in 1996 and 2005: (A) biome, (B) invasion intensity and (C) clearing

Table 4.16. Percentage aerial cover of alien vegetation (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 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).

% Alien Vegetation Aerial Cover	High Altitude (Grassland)				Low Altitude (Savanna)			
	High Invasion		Low Invasion		High Invasion		Low Invasion	
	Cleared	Uncleared	Cleared	Uncleared	Cleared	Uncleared	Cleared	Uncleared
1996								
Total	$21.1\pm11.8_a^b$	$72.2\pm7.5_a^a$	$3.3\pm1.1_b^b$	$11.0\pm3.8_a^b$	$29.1\pm8.0_a^b$	$69.1\pm11.2_a^a$	$10.9\pm3.7_a^b$	$23.0\pm6.6_a^b$
> 5m	$12.7\pm11.4_a^b$	$67.1\pm8.9_a^a$	$0.8\pm0.8_a^b$	$5.2\pm3.2_a^b$	$0.8\pm0.5_b^b$	$28.0\pm11.9_a^b$	$4.2\pm4.2_a^b$	$7.3\pm3.2_a^b$
2 –5 m	$6.2\pm2.7_a^b$	$18.1\pm6.3_a^b$	$1.3\pm0.8_a^b$	$4.3\pm1.8_a^b$	$14.7\pm3.7_a^b$	$45.5\pm12.4_a^a$	$3.4\pm1.8_a^b$	$12.8\pm3.6_a^b$
< 2 m	$3.0\pm1.7_a^b$	$2.1\pm1.3_a^b$	$1.3\pm0.4_a^b$	$1.5\pm0.4_a^b$	$13.9\pm5.4_a^a$	$4.1\pm1.8_a^{ab}$	$3.4\pm2.1_b^{ab}$	$1.7\pm0.9_b^b$
2005								
Total	$25.0\pm9.2_a^a$	$40.3\pm9.3_b^a$	$28.5\pm8.5_a^a$	$23.8\pm9.7_a^a$	$38.3\pm7.8_a^a$	$37.0\pm7.2_b^a$	$27.3\pm9.7_a^a$	$35.0\pm13.1_a^a$
> 5m	$3.0\pm1.3_a^a$	$8.8\pm2.7_b^a$	$6.3\pm4.8_a^a$	$1.0\pm1.0_a^a$	$11.5\pm3.3_a^a$	$5.5\pm5.5_a^a$	$4.2\pm1.7_a^a$	$6.2\pm2.5_a^a$
2 –5 m	$0.8\pm0.5_a^a$	$11.8\pm6.1_a^a$	$3.5\pm2.0_a^a$	$7.5\pm4.7_a^a$	$17.3\pm7.5_a^a$	$23.3\pm3.1_a^a$	$11.0\pm8.3_a^a$	$13.5\pm11.9_a^a$
< 2 m	$21.2\pm9.4_a^a$	$19.8\pm8.0_a^a$	$18.8\pm8.5_a^a$	$15.3\pm6.3_a^a$	$9.5\pm3.2_a^a$	$8.2\pm2.5_a^a$	$12.0\pm2.8_a^a$	$15.3\pm1.3_a^a$

There were no significant differences in the total percentage aerial cover of alien vegetation of the plots of the different experimental categories, between 1996 and 2005, except between the grassland and savanna high invaded, uncleared plots (higher in 1996), and between the grassland, low invaded, cleared plots (higher in 2005) (Table 4.16; see Appendix 15 for probability values). There was also no significant difference in the percentage aerial cover of the large (< 5 m) and small (2 – 5 m) trees of the plots of the different experimental categories, between 1996 and 2005, except between the grassland, high invaded, uncleared plots (higher in 1996), and the savanna, high invaded, cleared plots (higher in 2005) (Table 4.16; Appendix 15 for probability values). There was no significant difference in the percentage aerial cover of shrubs (< 2 m) of the plots of the different experimental categories, between 1996 and 2005, except between the savanna, low invaded, cleared and uncleared plots (higher in 2005) (Table 4.16; Appendix 15 for probability values).

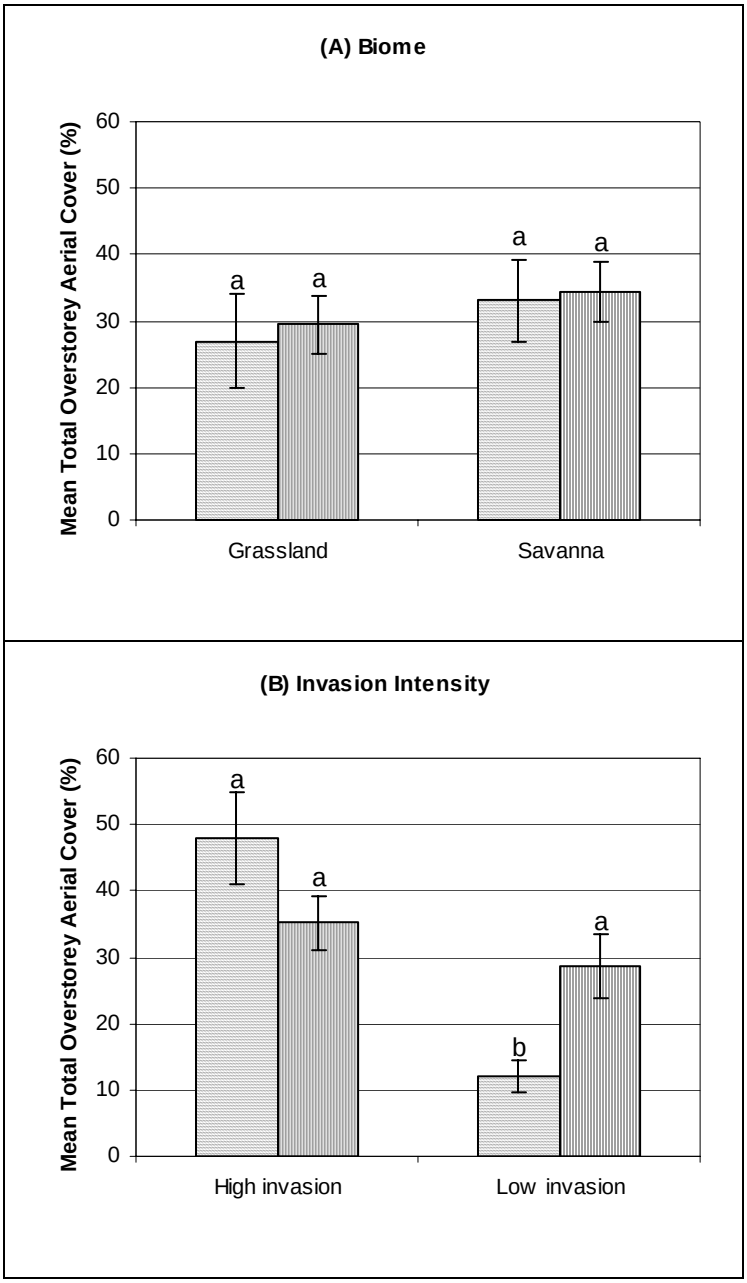
Table 4.17. Percentage aerial cover of alien vegetation probability values for: ((a) and (b)) three-way ANOVA's between the three different experimental treatments, i.e. (A) biome (BIOME), (B) invasion intensity (INVIN) and (C) clearing (CLEAR), for plots in 1996, and for plots in 2005 (*d.f.* = 1,32); 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 $P < 0.05$.

Year	Height Class	BIOME	INVIN	CLEAR	BIOME* INVIN	BIOME* CLEAR	INV* CLEAR	BIOME* INVIN* CLEAR	Co-variate
(a) 1996	Total	0.259	**$1x10^{-8}$**	**$1x10^{-6}$**	0.493	0.753	**0.002**	0.472	
	> 5 m	**0.028**	**$6x10^{-6}$**	**$8x10^{-6}$**	**0.007**	0.159	**$7x10^{-5}$**	0.199	
	2 – 5 m	**0.005**	**$3x10^{-5}$**	**0.001**	0.109	0.107	0.058	0.420	
	< 2 m	**0.026**	**0.027**	0.074	0.115	0.108	0.165	0.293	
(b) 2005	Total	0.462	0.339	0.531	0.999	0.881	0.684	0.288	
	> 5 m	0.363	0.236	0.702	0.827	0.627	0.747	**0.046**	
	2 – 5 m	**0.032**	0.350	0.212	0.437	0.727	0.572	0.852	
	< 2 m	0.088	0.882	0.861	0.340	0.686	0.885	0.705	
(c) 1996 and 2005	Total	0.451	0.440	0.548	0.980	0.873	0.649	0.287	0.829
	> 5 m	0.130	0.875	0.165	0.321	0.959	0.486	0.102	0.084
	2 – 5 m	**0.025**	0.221	0.141	0.333	0.918	0.425	0.947	0.416
	< 2 m	0.098	0.812	0.936	0.329	0.647	0.943	0.751	0.787

In 1996, the total alien vegetation aerial cover was significantly greater in the high invaded, uncleared plots; however there was no significant difference between the grassland and savanna plots (Table 4.17 (a)). The aerial cover of plants > 5 m was significantly greater in the grassland, high invaded, uncleared plots (Table 4.17 (a)). The aerial cover of plants between 2 – 5 m was significantly greater in the savanna, high invaded, uncleared plots (Table 4.17 (a)). The aerial cover of plants < 2 m was significantly greater in the grassland, low invaded plots; however, there was no significant difference between the cleared and uncleared plots (although this was almost significant, with the cleared plots having a greater aerial cover) (Table 4.17 (a)). In 2005, there was no significant difference in the aerial cover in total, and in each height class, between the grassland and savanna plots, the high and low invaded plots, and the cleared and uncleared plots (Table 4.17 (b)). Only the aerial cover of plants between 2 – 5 m was significantly greater in the savanna plots (Table 4.17 (b)).

There was a significant change in the aerial cover of plants between 2 – 5 m in the biomes over time (Table 4.17 (c)). The aerial cover of the 2 – 5 m plants was greater in 2005, in both biomes. In 1996, there was a significant interaction between the biome and invasion intensity treatments for the aerial cover of plants > 5 m (Table 4.17 (a)). This means that, in 1996, the aerial cover of large trees in the biomes is dependent on the invasion intensity – the plots that had a high invasion, had a greater aerial cover of plants > 5 m. In 1996, there was also a significant interaction between the invasion intensity and clearing treatments for total aerial cover, as well as the aerial cover of plants > 5 m (Table 4.17 (a)). Therefore, the values for the invasion intensity is dependent on whether the plots are cleared or not – the uncleared plots of both high and low invasion had a greater aerial cover than the cleared plots. In 2005, there was a significant interaction between the biome, invasion intensity and clearing treatments for the aerial cover of plants > 5 m (Table 4.17 (b)). This means that the values for the biomes is dependent on whether the plots are cleared or not, and whether there is a high or low invasion in the plots. None of the *P* – values for the co-

variate are significant (Table 4.17 (c)), therefore there is little or no clear overall relationship between the 2005 and 1996 data.



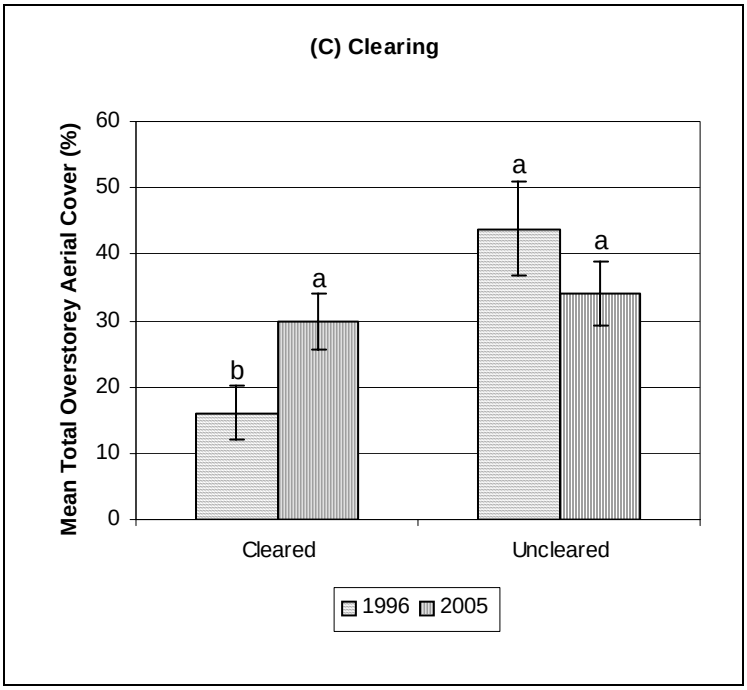


Figure 4.10. Total percentage aerial cover of alien vegetation (mean ± S.E.) for plots of the three different experimental treatments in 1996 and 2005, i.e. grassland and savanna (= biome), high and low invasion (= invasion intensity), and cleared and uncleared (= clearing). Columns with different superscript 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.

There was no significant difference in the total percentage aerial cover of alien vegetation in the grassland, savanna, high invaded, and uncleared plots between 1996 and 2005 (Figure 4.10; probability values are given in Appendix 18). However, there were significant differences in the low invaded and cleared plots between the years (with the 2005 plots having a greater aerial cover) (Figure 4.10; probability values are given in Appendix 18), thus indicating that the original (1996) invasion intensity and clearing treatments did not persist over time.

4.4.4 Linear regression analyses of the percentage aerial cover of woody alien plants (invasion intensity), and plant species richness and diversity measures

The percentage aerial cover of woody alien plants was used as a measure of invasion intensity. Linear regression analyses were then performed whereby the relationship between invasion intensity (independent variable) and various species richness and species diversity measures (dependent variables) were determined. This was done for both 1996 and 2005.

Total plant species richness

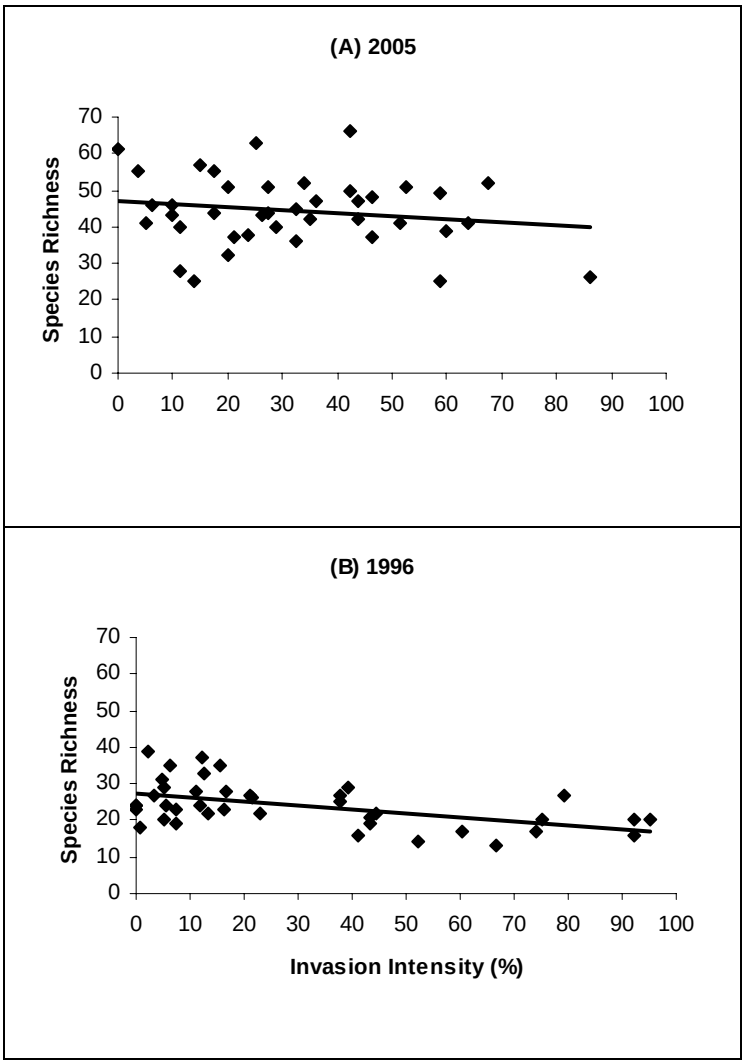


Figure 4.11. The linear relationship between total plant species richness (at the 1000 m^2 scale) and invasion intensity (% aerial cover of woody alien plants) for each of the 40 plots in (A) 2005 (r^2 = 0.03) and (B) 1996 (r^2 = 0.26). The linear regression relationship for (A) is y = -0.09 + 47.15, and for (B) is y = -0.11x + 27.33. The slopes of these regression lines were significantly different ($P < 0.05$).

In both years, there was a decrease in total species richness with an increase in invasion intensity (Figure 4.11). The linear relationship between the two years indicates that the two data sets were significanlty different.

Tree species richness

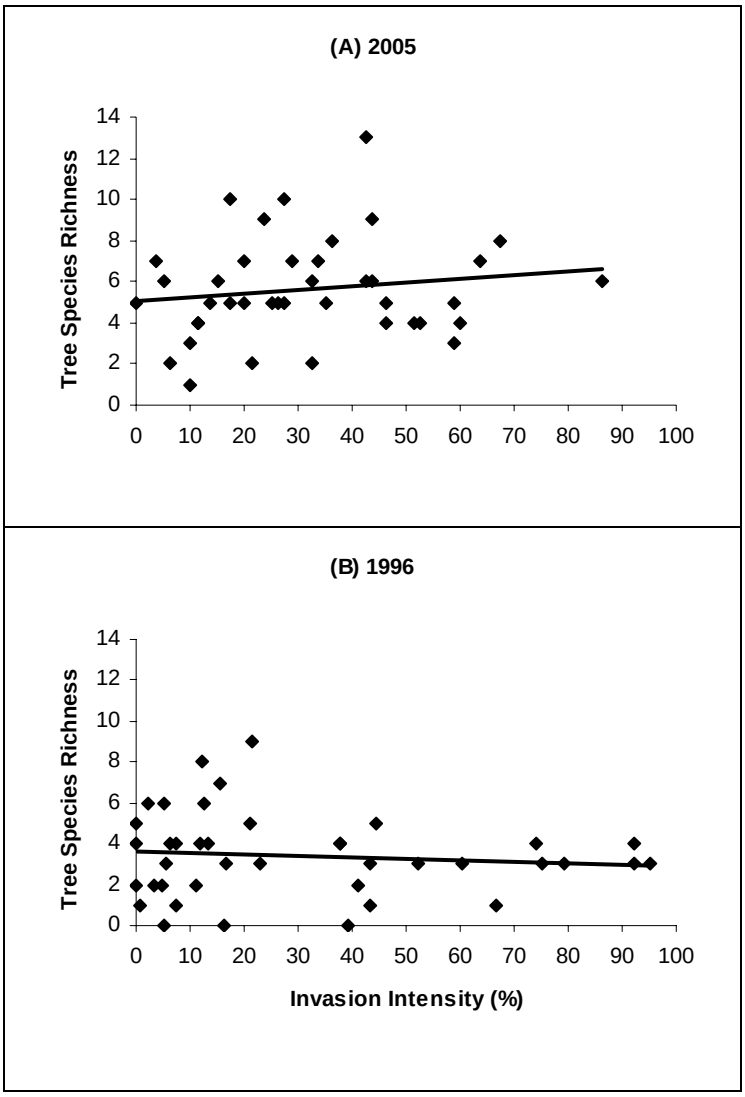


Figure 4.12. The linear relationship between tree species richness (at the 1000 m^2 scale) and invasion intensity (% aerial cover of woody alien plants) for each of the 40 plots in (A) 2005 (r^2 = 0.02) and (B) 1996 (r^2 = 0.01). The linear regression relationship for (A) is y = 0.02x + 5.05 and for (B) is y = -0.01x + 3.66. The slopes of these regression lines were significantly different ($P < 0.05$).

With an increase in invasion intensity, there was an increase in tree species richness in 2005 (Figure 4.12 (A)), and a slight decrease in tree species richness in 1996 (Figure 4.12 (B)). The linear relationship between the two years indicates that the two data sets were signicantly different.

Simpson's index of diversity (alpha diversity) for total plant species

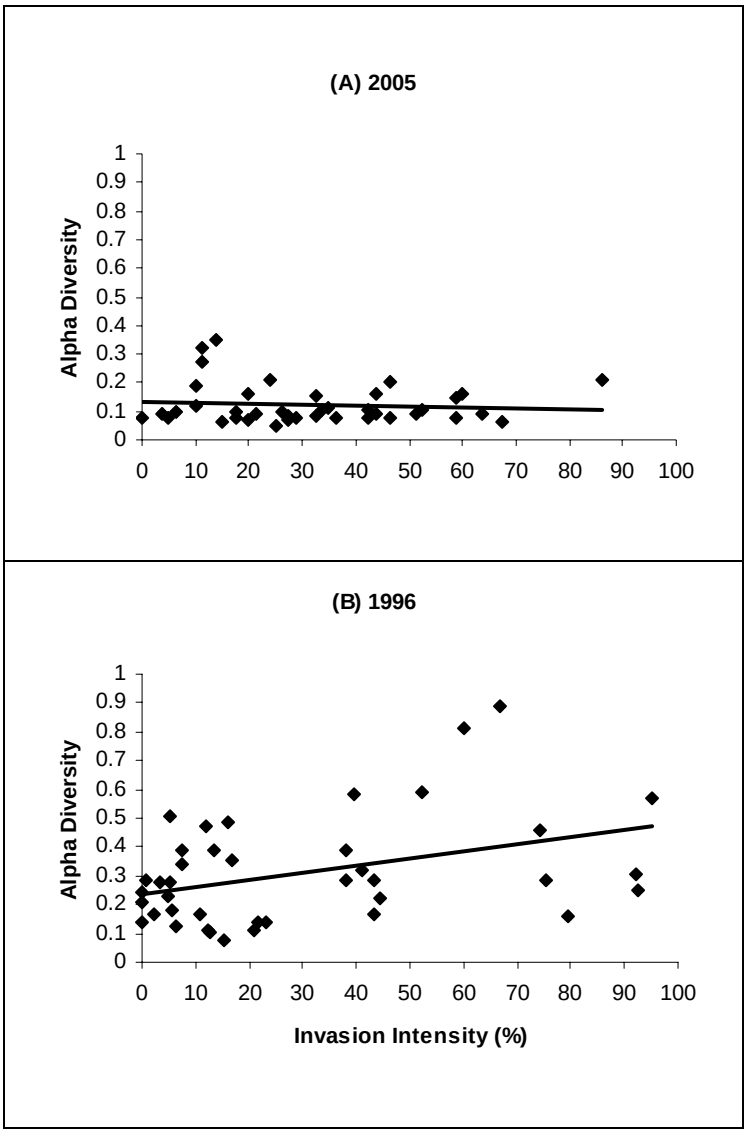


Figure 4.13. The linear relationship between Simpson's index of diversity (plant alpha diversity) (at the 100 m^2 scale) and invasion intensity (% aerial cover of woody alien plants) for each of the 40 plots in (A) 2005 ($r^2 = 0.01$) and (B) 1996 ($r^2 = 0.14$). The linear regression relationship for (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 ($P < 0.05$).

With increasing invasion intensity, the total alpha diversity in 2005 decreased very slightly (Figure 4.13 (A)), whereas in 1996 the total alpha diversity increased (Figure 4.13 (B)). The linear relationship between the two years indicates that the two data sets were significantly different.

4.4.5 Linear regression analyses of the percentage aerial cover of woody alien plants (invasion intensity) in 1996 and 2005

Invasion intensity of all 40 plots in 1996 and 2005

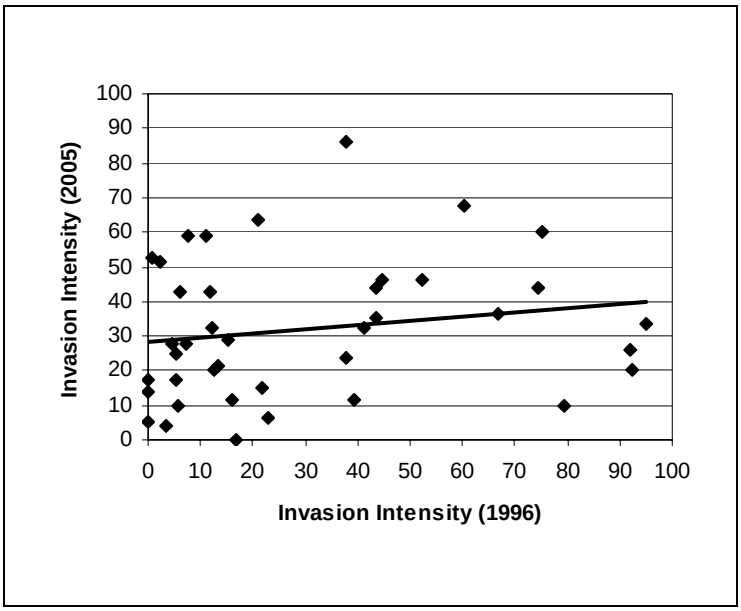
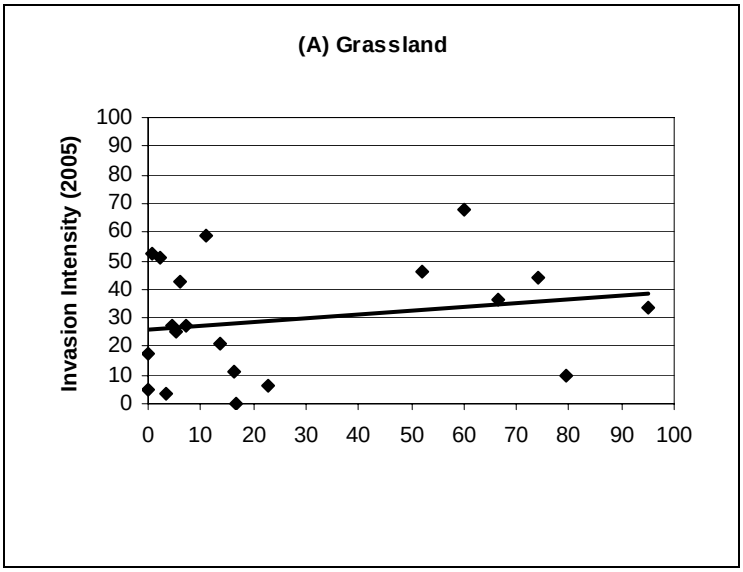


Figure 4.14. The linear relationship between the invasion intensity (% aerial cover of woody alien plants) in 1996 and the invasion intensity in 2005 (for each of the 40 plots) ($r^2 = 0.03$). The linear regression relationship is $y = 0.12x + 28.18$.

There was a very weak positive linear relationship between the invasion intensity of all 40 plots in 1996 and 2005 (Figure 4.14).

Invasion intensity of the grassland and savanna plots in 1996 and 2005



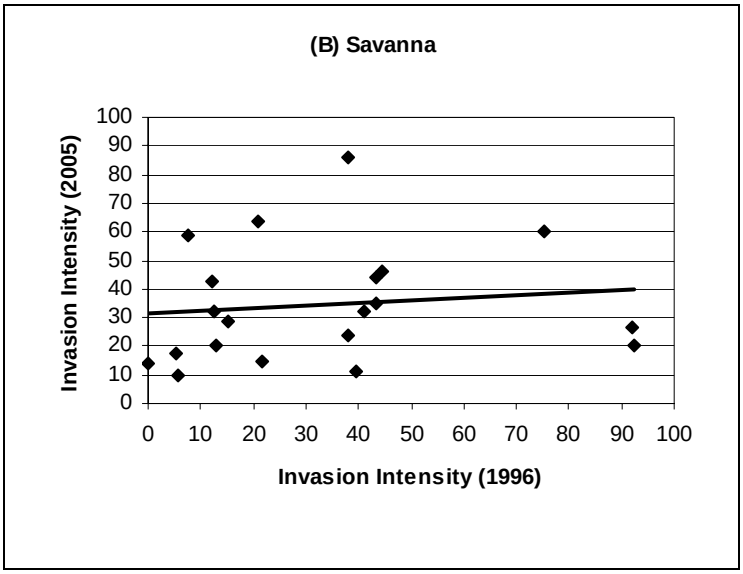
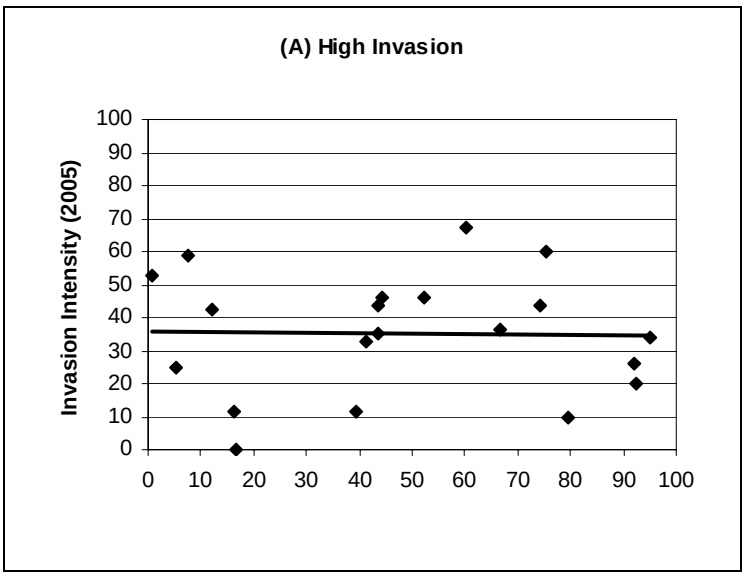


Figure 4.15. The linear relationship between the invasion intensity (% aerial cover of woody alien plants) in 1996 and the invasion intensity in 2005, for plots in the (A) grassland biome ($r^2 = 0.04$) and (B) savanna biome ($r^2 = 0.02$). The linear regression relationship for (A) is $y = 0.13x + 25.80$ and for (B) is $y = 0.09x + 31.31$. The slopes of these regression lines were not significantly different ($P > 0.05$).

In both biomes, there was a positive linear relationship between the invasion intensity in 1996 and that of 2005 (Figure 4.15). The linear relationship between the two biomes indicates that the two data sets were similar.

Invasion intensity of the high and low invaded plots in 1996 and 2005



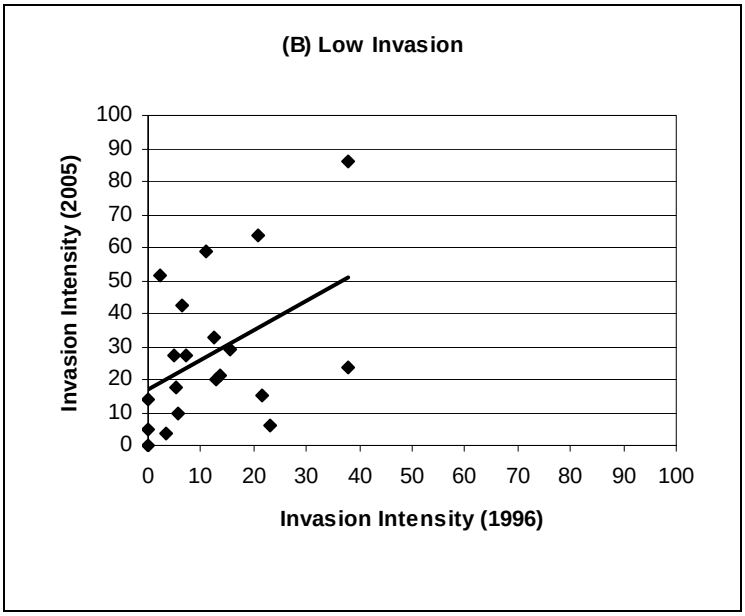
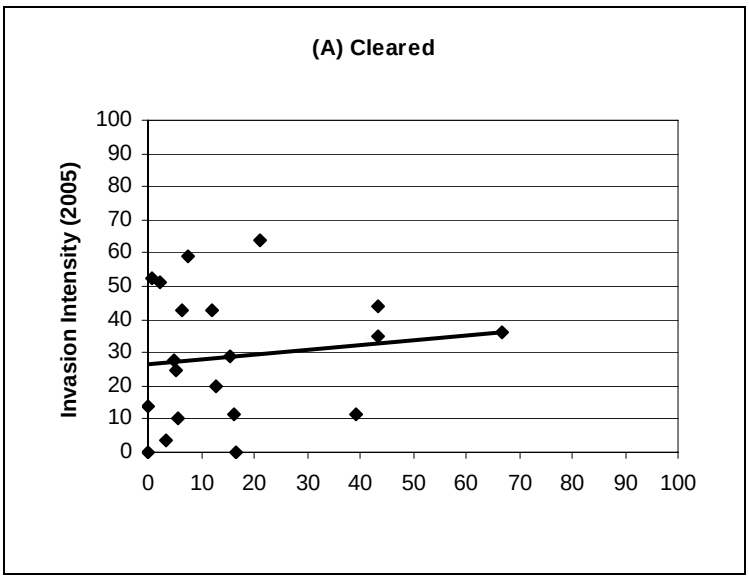


Figure 4.16. The linear relationship between the invasion intensity (% aerial cover of woody alien plants) in 1996 and the invasion intensity in 2005, for plots with a (A) high invasion ($r^2 = 2x10^{-5}$) and (B) low invasion ($r^2 = 0.20$). The linear regression relationship for (A) is $y = -0.01x + 35.55$ and for (B) is $y = 0.89x + 16.98$. The slopes of these regression lines were not significantly different ($P > 0.05$).

There was no linear relationship between the invasion intensity of 1996 and 2005 of the plots with a high invasion (Figure 4.16(A)). On the other hand, there was a positive linear relationship between the invasion intensity of 1996 and 2005 of the plots with a low invasion (Figure 4.16(B)). The linear relationship between the two invasion intensities indicates that the two data sets were similar.

Invasion intensity of the cleared and uncleared plots in 1996 and 2005



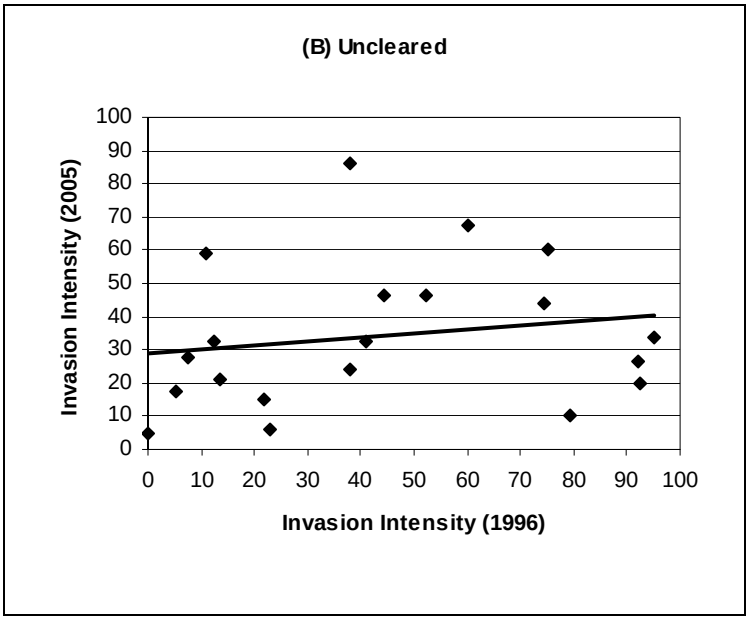


Figure 4.17. The linear relationship between the invasion intensity (% aerial cover of woody alien plants) in 1996 and the invasion intensity in 2005, for plots that are (A) cleared ($r^2 = 0.02$) and (B) uncleared ($r^2 = 0.03$). The linear regression relationship for (A) is $y = 0.14x + 26.63$ and for (B) is $y = 0.12x + 28.69$. The slopes of these regression lines were not significantly different ($P > 0.05$).

In both cleared and uncleared plots, there was a positive linear relationship between the invasion intensity in 1996 and 2005 (Figure 4.17).

4.5 Discussion

4.5.1 Total plant species richness and diversity

In 1996, a cumulative total of 163 species were found in the study area along the Sabie River (with 140 species in the grassland and 106 species in the savanna), whereas 282 species were found in 2005 (with 222 species in the grassland and 171 species in the savanna). Therefore, there was an increase of 42% in the total species richness over time, with the grassland remaining more species rich than the savanna (this may be a result of the invasion intensity remaining higher in the savanna over time). There were a total of 62 species common between the years, with 101 species being lost since 1996. Species richness (in total and of the grassland and savanna biomes, at all quadrat scales) and alpha diversity (in total and of the grassland and savanna biomes, at the 100 m^2 scale) were significantly higher in 2005. The overall beta diversity indicated that there was a very low plant community similarity between the plots of the two years. The beta diversity also showed that there was a lower plant community similarity between the plots in 1996, than between the plots in 2005. Of the 163 species found in 1996, 132 (81% of the total) were indigenous and 31 (19%) alien, and in 2005, 222 (79%) were indigenous and 60 (21%) alien. Therefore, there was an increase in the total number of indigenous and alien species over time ($P < 0.001$). However, even though there was an increase of 41% in the indigenous species richness and 48% in the alien species richness, the proportion of indigenous and alien species remained approximately the same over time ($P = 0.62$).

The clearing of alien plants by WfW may have allowed new species to establish due to reducing the dominance of vigorous alien species, and hence allowing less competitive species a better chance of establishing and persisting, and these species added to the total species richness and diversity. The clearing in itself acted as a disturbance, which may have stimulated a number of more early successional and weedy species to establish. This may be explained by the 'intermediate disturbance hypothesis' (Connell, 1978). This hypothesis states that all communities are composed of early seral species that colonize quickly after disturbance and late seral species that increase in abundance and dominance through time (Connell, 1978). Optimal diversity occurs, therefore, when disturbance is sufficiently frequent to limit dominance while allowing complete time for colonization by all species (Connell, 1978). High diversity is promoted by intermediate disturbances ensuring a mixture of pioneer, intermediate and late successional stages (Johst and Hutn, 2005). Intermediate intensity disturbances are also believed to create variability in resources, such as light and soil moisture, that are especially crucial for species establishment (Sarr *et al.*, 2005). Therefore, the significantly higher total species richness and diversity seen in 2005 may be a result of higher levels of disturbance over the years, from both floods and WfW clearing. A study found that maximum species richness was maintained in habitats of intermediate (moderate to moderately high) disturbance regimes, whereas relatively undisturbed communities tended to be poorer in species (McIntyre *et al.*, 1988).

Studies have shown that increased disturbance of plant communities (such as the clearing operations) can also increase the invasibility of plant communities (Burke and Grime, 1996; Zobel *et al.*, 2000; Suding and Goldberg, 2001). Therefore, the increase in the alien species richness and diversity over time may be a result of the disturbance created by the WfW clearing operations. Disturbance generally facilitates plant invasions by creating vacant niches (i.e. bare soil or reduced vegetative cover) for germination and emergence (Suding and Goldberg, 2001; Setterfield *et al.*, 2005). Disturbances can also result in the reduced uptake of resources by the indigenous community, which creates fluctuations in the resources (Gross *et al.*, 2005). Davis *et al.* (2000) have proposed that resource fluctuations are important in promoting invasion.

A factor that could explain the persistence of the dominant aliens over time is the regeneration potentials of these plants. Resprouting allows a species to persist in a site after a wide range of disturbances (Vesk and Westoby, 2004). Resprouting ability depends upon the anatomy of the plants, pre-disturbance size, disturbance intensity, disturbance frequency, soil fertility and water availability (Mlambo and Mapaure, 2006). As discussed in chapter 3, the problem lies with some of the dominant alien species, i.e. *Eucalyptus grandis* (Saligna gum), *Rubus cuneifolius* (American bramble), *Lantana camara* (Lantana) and *Solanum mauritianum* (Bugweed), which all have strong regenerative capabilities. These coppicing individuals have exceptionally fast growth rates, which are seldom surpasses by the indigenous vegetation, and the disturbance caused by the clearing often facilitates the regeneration of these individuals (Witkowski and Wilson, 2000). Therefore, it is difficult to prevent the re-invasion of these species. The regeneration potential of aliens is usually related to their large soil seed banks. Species with seeds already in the disturbed environment have an advantage over species that are some distance away as they do not have the delay of dispersal. Therefore, it is important to consider

the soil seed bank structure in order to determine the regeneration and species structure of the community after a disturbance.

The soil seed banks were not assessed in this study as an extensive analysis of the seed banks was conducted in 1996 (Garner, 2005). Garner (2005) found that the soil seed banks in the Sabie riverine community were limited in their species richness and were dominated by propagules of four species – two aliens (*Eucalyptus grandis* and *Solanum mauritianum*), one indigenous shrub (*Clutia monticola*) and one indigenous herb (*Ipomoea* sp.). The study also showed that the invasive species propagules increased with invasion intensity (Garner, 2005). A solution to reducing the frequency of re-invasions would be to focus on the dominant species during the clearing operations, as well as increase the frequency of the follow-up treatments, which may eventually allow the indigenous community to re-establish itself and slowly become dominant again, thus making the community more resistant to these invasions. This dominant, well-adapted indigenous community would usually be expected to have a marked competitive advantage over newly arriving species that are adapted to different habitats and resource availabilities (Vermeij and Dudley, 2000). Thus, this could result in the indigenous community being more resistant to alien invasions, and therefore the number of follow-up treatments could eventually be reduced.

The most dramatic change over time was in the weed species richness. In 1996, there were 25 weed species (15% of the total), whereas in 2005, there were 50 weed species (18%). Hence, there was an increase of 50% in the weed species richness over time. A factor that could explain this increase over time is the flood event of February 2000. Studies have shown that areas on rivers that receive the greatest flooding disturbance tend to have the greatest proportion of alien species (Decamps *et al.*, 1995; Hood and Naiman, 2000). This is because floods disturb river-banks and re-route water courses, providing recruitment sites for invading plants with water-borne propagules (Rowntree, 1991). Also, when historical flooding patterns are changed in intensity or frequency, the likelihood of invasions in riparian zones is increased (Sher *et al.*, 2002). A large proportion of the existing species may have been removed by the 2000 flood – a total of 101 species have been lost since 1996, 50% of which are herbaceous, 20% shrubs, 15% grasses, and 15% trees. Thus, this may have contributed to the difference in the total species richness and diversity between the two years. The assumption that the flood removed a large proportion of the existing species is also based on the fact that all of the concrete-embedded markers that were used to mark the plots in 1996 (Garner, 2005) were no longer in the ground (or possibly some might be buried) (it was assumed that they were washed away by the flood). According to Richter and Stromberg (2005), flood disturbance is one process that can maintain high levels of biodiversity in riparian ecosystems, by creating spatial and temporal heterogeneity and allowing for co-existence of plants with a variety of life-history strategies. Thus, the higher species richness and diversity in 2005 may be a response to the 2000 flood event.

The disturbance of the 2000 flood would have reset the successional stage of the Sabie River riparian environment, so that the 2005 community was probably in a more early successional stage, whereas the 1996 community would have been in a more mature stage. Studies have shown that invasive species richness and abundance declines with successional stage, i.e. there are fewer invaders in late than early-

successional plant communities (Ramakrishnan and Vitousek, 1989; Rejmanek, 1989; Blumenthal *et al.*, 2003). Because the competitive ability of dominant species often increases with successional stage, while levels of available resources decline, late-successional plant communities may be more difficult to invade than early successional communities (Blumenthal *et al.*, 2005). This suggests that late-successional plant communities may be relatively more resistant to invasion compared to early successional communities (Blumenthal *et al.*, 2003). This may therefore explain the lower species richness of aliens in 1996, as this plant community was probably in a more mature successional stage than the 2005 community.

A factor that must be taken into account when comparing the 1996 and 2005 data, is that in each year, the data was collected by a different person. Studies have shown that vegetation sampling precision may be influenced by different observers, and that the effect of different observers is an important contributor to variability in the data set (Kercher *et al.*, 2003). Therefore, some of the differences in the results between the 1996 and 2005 studies may be because of the different observers. In addition, the field work and data collection for the 1996/1997 study took place from October 1996 to the end of February 1997, and for the 2005 study from the 14th February 2005 to the 6th April 2005. Therefore, there was a slight difference in the seasonality of sampling between the two years. A higher proportion of plants were probably flowering or fruiting later in the season and hence in the 2005 study period, and thus the identification of the species may have been made easier and therefore more species were observed, and fewer missed. Hence, the higher species richness and diversity in 2005 may be partially due to this difference in the sampling periods.

Another reason why there was a lower species richness and diversity in 1996, may be due to the severe drought of 1991/1992. This drought reduced the flow in the Sabie River on the Mozambique border to previously unrecorded low discharges, measured in the Kruger National Park, of only 0.33 m^3s^{-1} (Weeks *et al.*, 1996). During droughts many species may show a more patchy distribution and therefore appear to become locally extinct, but gradually return when higher rainfall returns. Even though the 1996 study took place four years after this drought, the plant community may have still been in the recovery stages.

Treatment effects (i.e. (A) biome, (B) invasion intensity and (C) clearing)

In 1996, the low invaded plots were significantly more species rich, whereas the high invaded plots were significantly more diverse. Therefore the invasion intensity treatment had a significant effect on the plant community. In 2005, there was no significant effect of these original (1996/1997) clearing and invasion intensity treatments on the community. This shows that, over time, the plots of the different invasion intensity and clearing treatments had been cleared, as well as invaded, to approximately the same extent, and therefore these original treatments did not persist over time. The only significant treatment effect was between the biomes – the grassland plots were significantly more species rich and diverse than the savanna plots. Even though the two biomes are a treatment from a statistical sense, they are inherently different, unlike the clearing and invasion intensity treatments.

Significant interactions were found between the biome and clearing treatments at the 10 m^2 scale for both ANOVA's of the 1996 and 2005, as well as the ANCOVA.

Therefore, the values for the biome were dependent on whether clearing had been done or not. Because the 1996 community was probably in a mature successional stage (as the flood of 2000 had not yet occurred), and because clearing had not been done before in some of the plots, the disturbance created by the clearing had a significant effect on this plant community.

The ANCOVA showed that there was a significant change in the species richness and alpha diversity of the biomes over time. In 1996, the species richness was greater in the savanna plots, whereas in 2005 it was greater in the grassland plots; and the alpha diversity (of both biomes) was much greater in 2005. The ANCOVA also indicated that there was virtually no relationship between the 1996 and 2005 species richness and alpha diversity. A possible reason for this could be because the 1996 plant community was probably in a more mature successional stage than the 2005 community, which was in a more early successional stage due to the 2000 flood event resetting the successional trajectory of the Sabie River riparian environment. Thus, there was litte or no clear overall relationship between the 1996 and 2005 plant communities.

4.5.2 Species richness of tree, shrub, herbaceous, grass and sedge growth forms

In 1996, the herbaceous species richness was the greatest (71 species (44% of the total)), followed by the shrubs (44 species (27%)), trees (28 species (17%)) and grasses (20 species (12%)). The proportion of species of each growth form in 1996 was similar to that in 2005, where 121 (43%) of the total species were herbaceous, 82 (29%) were shrubs, 46 (16%) were trees and 33 (12%) were grasses. Thus, even though the species richness of each growth form increased significantly over time (i.e. an increase of 41% of herbaceous species, 46% of shrub species, 39% of tree species and 39% of grass species), the proportion of species within each growth form remained approximately the same ($P = 0.97$). Therefore there was little change in the growth form composition over time.

Treatment effects (i.e. (A) biome, (B) invasion intensity and (C) clearing)

In 1996, the tree species richness was significantly affected by the biome and invasion intensity treatments, and the shrub species richness by the invasion intensity treatments, i.e. the tree species richness was higher in the savanna, low invaded plots, and the shrub species richness was higher in the low invaded plots. The herbaceous species richness was significantly affected by all three treatments – the richness was higher in the grassland, low invaded, cleared plots. There was no significant effect of the biome and invasion intensity treatments on the grass species richness; however it was significantly affected by the clearing treatment, i.e. the richness was higher in the cleared plots. Reasons for the significant biome treatment effect on the trees and herbaceous vegetation may be due to the grassland and savanna being inherently different in terms of the growth form composition. The invasion intensity had a significant effect on most of the growth forms possibly due to the shading effects of the aerial cover of the woody alien plants (the invasion intensity) on the plant community, i.e. shading out of smaller growth forms and overtopping of indigenous vegetation in the upper canopy.

In 2005, there was no significant effect of the biome, invasion intensity and clearing treatments on the tree species richness. On the other hand, there was a significant difference between the biomes on the shrub, herbaceous and grass species richness, i.e. the grassland biome was richer in terms of these species. The invasion intensity treatment had a significant effect on the grass species richness – the low invaded plots were richer. The significant difference between the biomes on most of the growth form compositions may once again be due to the grassland and savanna biomes being inherently different in terms of these growth forms. The reason why there was no significant effect of invasion intensity and clearing treatments on the growth forms (except grasses) may be because the plots had been cleared and invaded to a similar extent over time.

4.5.3 Invasion intensity, i.e. percentage aerial cover of woody alien plants

One of the primary goals of the WfW programme is to reduce the invasion intensity of the woody alien plants. Therefore, it is expected that the invasion intensity would decrease over time due to the clearing. However, this study showed that the clearing made little difference to the total invasion intensity. In fact, the total invasion intensity actually increased in 2005, but not significantly. This increase in invasion intensity over time is also indicated by the very weak positive linear relationship between the invasion intensity of the 40 plots, as well as the grassland and savanna plots, in 1996 and 2005. Therefore, the WfW programme is not achieving its primary aim of controlling woody alien plants. However, the data did show that there was a significantly higher aerial cover of alien plants > 5 m and between 2 and 5 m in height (not significant) in 1996 (represented in the past largely by *Eucalyptus* spp.), whereas there was a significantly higher aerial cover of plants < 2 m in 2005. These results indicate that WfW are clearing away most of the larger woody plants. However, the significantly higher invasion intensity of the smaller growth forms over time indicates that the regeneration of these woody plants is significant. Therefore, even though the control programme is initially successful in clearing the alien trees, the current follow-up clearings are not enough to control the coppicing individuals. It is therefore recommended that follow-up clearings are undertaken more often and/or different clearing methods are used to prevent/reduce the regeneration of the aliens. It is important to note that alien plants < 1 m in height were excluded in both the 1996 and 2005 studies (not specifically sampled), which was probably an error. Therefore, the density of the re-invading aliens is an underestimate as there were many individuals of < 1 m that were not being counted, but were still there. It is therefore recommended that in future follow-up studies, these small individuals should be counted in the 1 m^2 and 10 m^2 quadrats in order to get a full estimate of the re-invading alien plants.

Because of the higher invasion intensity of large and small trees in 1996, indigenous species that usually form the upper canopy may have been overtopped, and smaller growth forms may have been shaded out, by the taller- and faster-growing alien plants. This is because competition for light is one of the primary mechanisms for change following alien invasions, resulting in shading of indigenous plants by the invasive alien plants (Standish *et al.*, 2001). The higher invasion intensity of large and small trees may have also prevented any new species from establishing in the community. This may have reduced the total species richness and diversity in 1996 (relative to that of 2005).

In the grassland biome, the total invasion intensity remained approximately the same over time. However, the invasion intensity of plants > 5 m and between 2 and 5 m in height decreased (significantly for > 5 m) over time. Therefore, WfW are managing to clear away most of the larger woody alien plants. However, the invasion intensity of smaller growth forms (< 2 m) increased significantly over time, therefore indicating that the regeneration of the alien plants is significant. Similar patterns were seen in the savanna biome, i.e. the invasion intensity of large and small trees decreased over time, whereas that of smaller growth forms increased significantly over time. However, in this biome, the total invasion intensity increased over time (although not significantly). A reason for this could be due to the savanna plots being situated lower in the catchment relative to the grassland plots – areas lower down in the river receive more seeds, and probably other propagules as well, of invasive species that are transported from the upper catchments (Le Maitre *et al.*, 2000). Therefore, it is recommended that the grassland plots (and all the way up the catchment) are cleared first so that the savanna plots are not re-invaded from propagules upstream.

Treatment effects (i.e. (A) biome, (B) invasion intensity and (C) clearing)

In 1996, the total aerial cover of woody plants, as well as the aerial cover of trees > 5 m and between 2 – 5 m, was significantly affected by the invasion intensity and clearing treatments, i.e. the percentage aerial cover was higher in the high invaded, uncleared plots. The total invasion intensity was not affected by the biome treatment, whereas the > 5 m and < 2 m aerial covers were higher in the grassland and the 2 – 5 m aerial cover was higher in the savanna. The < 2 m aerial cover was also significantly affected by the invasion intensity treatment (higher in the low invaded plots) and almost significantly affected by the clearing treatment (higher in the cleared plots). Because the invasion intensity is a measure of the aerial cover of woody alien plants, the invasion intensity treatment would have significantly affected the aerial cover. The clearing treatment had a significant effect as the clearing process involves the removal of alien plants, which thereby reduces the aerial cover of the plants.

In 2005, there was no significant effect of the three treatments on the aerial cover in total, and of each height class. Once again, this could be due to the plots being cleared and invaded to similar extents over time, i.e. the high and low invasion intensity categories, as well as the cleared and uncleared categories, were essentially the same in 2005.

The ANCOVA showed that there was a significant change in the aerial cover of plants between 2 – 5 m of the biomes over time (the aerial cover was higher in 2005). The ANCOVA also indicated that there was virtually no relationship in the percentage aerial cover of alien vegetation between 2005 and 1996. A possible reason for this is could again be attributed to the 1996 community being in a more mature successional stage, whereas the 2005 community was probably in an earlier successional stage, due to the flood of 2000 resetting the Sabie River riparian environment.

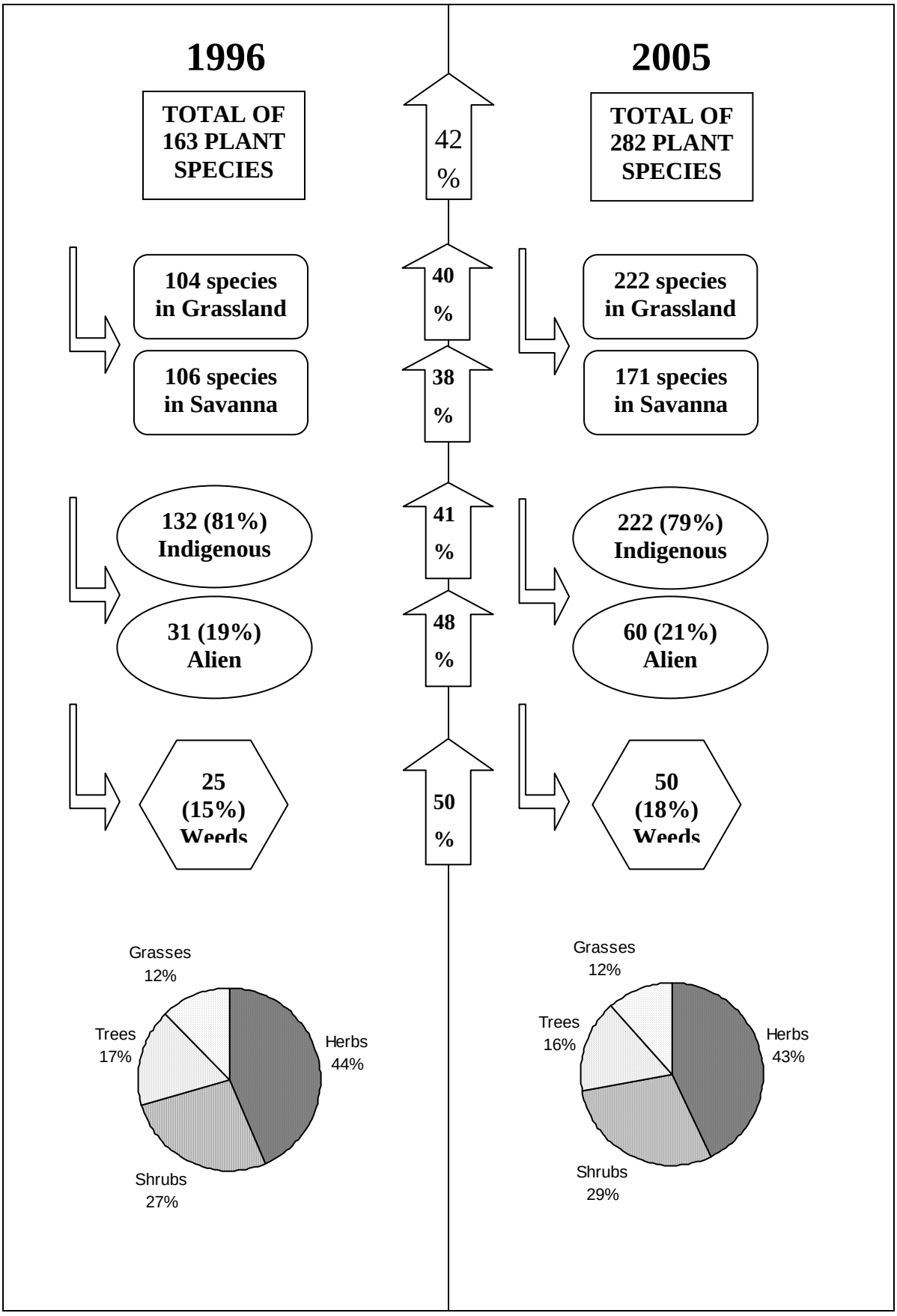
From the linear regressions of the treatments between 1996 and 2005, it was found that there was no relationship between the invasion intensity of the high-invaded plots of 1996 and 2005. Therefore, there was a difference in the high-

invaded plots over time. This could be due to the decrease in invasion intensity of large and small trees, and the increase in invasion intensity of smaller growth forms, over time. On the other hand, there was a positive linear relationship between the invasion intensity of the low-invaded plots of 1996 and 2005. Therefore, there was little change in the low-invaded plots over time. Because these plots initially had a low invasion of alien plants, it was easier to clear them. It was also easier to maintain the clearing of the alien plants in these low invaded plots over time (compared to the plots that were initially very densely invaded with alien plants). In both cleared and uncleared plots, there was a very slight positive linear relationship between the invasion intensity in 1996 and 2005, thus indicating that there was a slight difference in these plots over time. This is due to the fact that WfW have been clearing these plots to a similar extent over time, and hence there are now no "uncleared" plots left.

4.5.4 Relationship between total plant species richness and diversity, and invasion intensity

In both years, the total species richness decreased with increasing invasion intensity. The morphological and physiological effects of the taller growing trees include the shading out of the shorter growth forms, as well as the overtopping of the indigenous species in the upper canopy, which may have resulted in the reduction in species richness. In 2005, there was a slight decrease in the total alpha diversity with increasing invasion intensity, which again may be a result of the invading trees excluding smaller growth forms, which may have reduced the diversity. In 1996, however, there was an increase in the total alpha diversity with increasing invasion intensity. This may have been due to the invading trees adding to the richness of this relatively species-poor community. The decrease in the species richness with increasing invasion intensity indicates that both the 1996 and 2005 plant communities were not that resistant to the invasion of alien plants. Furthermore, because the 2005 plant community was significantly more species rich and diverse than the 1996 community, the hypothesis that higher plant species richness and/or diversity should enhance community resistance to alien plant invasions, is rejected.

4.6 Conclusions



		1996	2005
Species richness ($1000m^2$):	Total	24.1 ± 1.0^b	44.4 ± 1.5^a
	Trees	3.4 ± 0.3^b	5.6 ± 0.4^a
	Shrubs	8.1 ± 0.4^b	13.4 ± 0.4^a
	Herbs	9.3 ± 0.5^b	19.5 ± 1.0^a
	Grass	3.4 ± 0.2^b	5.9 ± 0.4^a
Alpha diversity ($100m^2$)		0.3 ± 0.03^b	0.9 ± 0.01^a
Beta diversity ($100m^2$)		Between 0.08 and 0.15	
Total aerial cover of woody aliens		$30.0 \pm 4.6\%^a$	$31.9 \pm 3.2\%^a$

Figure 4.18. Summary diagram of the most important results from chapter 4.

There are several important conclusions that can be made (Figure 4.17). Species richness and alpha diversity were significantly higher in 2005, with an increase of 42% in the total species richness over time. The overall beta diversity between the two years was very low, indicating a small overall change in species composition, despite the increase in species richness. The indigenous species richness increased by 41% and the alien species richness by 48% (however the proportion of indigenous and alien species remained approximately the same over time). In both years, the herbaceous species richness was the greatest, followed by the shrub, tree and grass species. Thus, even though the species richness of each growth form increased significantly over time, the proportion of species within each growth form remained approximately the same. Therefore there was little change in the growth form composition over time.

The increase in the species richness and diversity over time may be due to several reasons. The clearing of alien plants by WfW may have allowed new species to establish due to reducing the dominance of vigorous alien species, and hence allowing less competitive species a better chance of establishing and persisting. The clearing in itself acted as a disturbance, which may have stimulated a number of more early successional and weedy species to establish, thus resulting in an increase in the total species richness and diversity (which can be explained by the 'intermediate disturbance hypothesis'). Increased disturbance (such as the clearing operations) can also increase the invasibility of plant communities. Therefore, the increase in the alien species richness and diversity over time may be a result of the disturbance created by the WfW clearing operations.

A factor that could explain the persistence of the dominant aliens over time is the regeneration potentials of these plants. The dominant alien species of the Sabie River riparian environment were *Eucalyptus grandis*, *Rubus cuneifolius*, *Lantana camara* and *Solanum mauritianum*, which all have strong regenerative capabilities; therefore, it is difficult to prevent the re-invasion of these species. It is recommended that the dominant alien species are focused on during the clearing operations in order to help reduce the frequency of re-invasions. Increasing the frequency of the follow-up treatments would also help to reduce the frequency of re-invasions. Over time, the indigenous community may eventually re-establish itself and slowly become dominant again, thus making the community more resistant to these invasions, and therefore the number of follow-up treatments could eventually be reduced.

The most dramatic change over time was in the weed species richness, which increased by 50%. This dramatic increase may be a result of the flood event of February 2000. This very major disturbance may have resulted in the increased proportion of alien species, possibly due to recruitment sites being provided for the invading plants with water-borne propagules. The disturbance of the 2000 flood would have reset the successional stage of the Sabie River riparian environment, so that the 2005 community was probably in a more early successional stage, whereas the 1996 community would have been in a more mature stage. Late-successional plant communities may be relatively more resistant to invasion compared to early successional communities; hence this may partially explain the lower alien species richness in 1996, as this plant community was probably in a more mature successional stage than the 2005 community. Because the 2000 flood may have resulted in the dramatic increase in the weed species richness over time, one could predict, in a comparison of road edge and riparian plots, that there would be a greater change in the river plots.

Some of the differences in the results between the 1996 and 2005 studies may be because of the different observers. There was also a slight difference in the seasonality of sampling between the two years; therefore the difference between the 1996 and 2005 data may also be partially due to the difference in the sampling periods. Another reason why there was a lower species richness and diversity in 1996, may be due to the severe drought of 1991/1992. During droughts many species may show a more patchy distribution and therefore appear to become locally extinct, but gradually return when higher rainfall returns, and even though the 1996 study took place 4 years after this drought, this plant community may still have been in the recovery stages.

The total invasion intensity (i.e. percentage aerial cover of woody alien plants) tended to be slightly higher in 2005 compared to 1996, but not significantly, despite all the WfW clearing in the intervening years. Therefore, the WfW programme is not achieving its primary aim of controlling alien woody plants. However, there was a significantly higher aerial cover of large (> 5 m in height) and intermediate-sized (2 – 5 m) alien trees (not significant) in 1996, whereas there was a significantly higher aerial cover of smaller alien shrubs/trees (< 2 m in height) in 2005. Therefore WfW are clearing away most of the larger woody alien plants. However, the significantly higher invasion intensity of the smaller growth forms over time indicates that the regeneration of these woody plants, which recover through post-clearing resprouting and/or newly established seedlings, is significant. Therefore, even though the control programme is initially successful in clearing the alien trees, the current follow-up clearings are not enough to control the regenerating individuals. It is recommended that follow-up clearings are undertaken more often and/or different clearing methods are used to prevent/reduce the regeneration of the aliens. Because alien plants < 1 m in height were excluded (not specifically sampled) in both the 1996 and 2005 studies, it is recommended that in future follow-up studies, these small individuals should be counted in the 1 m^2 and 10 m^2 quadrats in order to get a full estimate of the densities of the re-invading alien plants.

When comparing the invasion intensity between the three original "treatments" of the 1996/1997 study over time, namely (A) biome (grassland versus savanna), (B) invasion intensity (high (> 50%) versus low (< 50%)), and (C) clearing

(cleared versus uncleared), the invasion intensity of the 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). This is of significance as it shows that the cleared plots in 1996 regained their former pre-clearing (presumably) invasion intensity.

In the grassland biome, the total invasion intensity remained approximately the same over time, whereas in the savanna biome, it increased (although not significantly). This may have been due to the savanna plots being situated lower in the catchment relative to the grassland plots – areas lower down in the river receive more seeds, and probably other propagules as well, of invasive species that are transported from the upper catchments (Le Maitre *et al.*, 2000). It is recommended that the grassland plots (and all the way up the catchment) are cleared first so that the savanna plots are not re-invaded from propagules upstream.

In both years, the total species richness decreased with increasing invasion intensity, which may be a result of the morphological and physiological effects of the taller growing tree species shading out smaller growth forms and overtopping the indigenous species, thus reducing the species richness. These decreases in the species richness with increasing invasion intensity, indicates that both the 1996 and 2005 plant communities were not that resistant to the invasion of alien plants. Furthermore, because the 2005 plant community was significantly more species rich and diverse than the 1996 community, the hypothesis that higher plant species richness and/or diversity should enhance community resistance to alien plant invasions, was rejected.

Finally, of the original "treatments" of the 1996/1997 study, namely (A) biome, (B) invasion intensity and (C) clearing, 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. Therefore, the 1996 and 2005 plant communities in the corresponding plots were quite different, suggesting that the Sabie River riparian plant community has changed considerably over time, and this change has been largely a consequence of alien plant invasions.

CHAPTER 5:

RELATING PLANT SPECIES COMPOSITION, DIVERSITY AND VEGETATION STRUCTURE TO ENVIRONMENTAL FEATURES ON THE SABIE RIVER, SOUTH AFRICA, FROM 1996 TO 2005

5.1 Abstract

The impacts of the invasive alien plant clearing by Working for Water (WfW) (and the alien plant invasion itself) on the riparian environment of the Sabie River (which traverses through both the grassland and savanna biomes), was 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), and various soil chemical and physical properties. The response was compared between the grassland and savanna biomes, and between 1996 and 2005. The effects of the WfW clearing was assessed using 40 modified Whittaker nested plots. 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).

Exposed soil, litter and grass covers tended to be slightly higher in the savanna (14.4 ± 1.6% (S.E.); 43.5 ± 3.0%; 21.8 ± 1.7% respectively) than in the grassland (12.1 ± 2.5%; 43.2 ± 4.2%; 20.1 ± 2.3% respectively) (P = 0.43, 0.96 and 0.56 respectively). Rock and herbaceous covers were higher in the grassland (4.3 ± 1.6% and 20.3 ± 1.7% respectively) than in the savanna (0.8 ± 0.2% and 19.5 ± 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 be a response to the slightly higher invasion intensity in the savanna (34.4 ± 4.6%) compared to the grassland (29.4 ± 4.5%) (P = 0.44). 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 ± 0.2% versus 3.3 ± 0.4%; P = 0.01) and total nitrogen (0.3 ± 0.02% versus 0.2 ± 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 proportion of the available nutrients than in 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 ± 0.1 kg/cm^2) (but not significantly) than those of the savanna sites (0.7 ± 0.1 kg/cm^2) (P = 0.43), and the savanna plots were on significantly steeper ground (12.8 ± 1.7º) than the grassland plots (4.8 ± 1.1º) (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.

Exposed soil, rock and litter covers were higher in 2005 (13.3 ± 1.5%; 2.5 ± 0.8%; 43.3 ± 2.5% respectively) than in 1996 (2.1 ± 0.5%; 0.9 ± 0.3%; 16.4 ± 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 ± 2.8% and 32.8 ± 2.6% respectively) than in 2005 (20.0 ± 1.4% and 20.9 ± 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 (31.9 ± 3.2%) than in 1996 (30.0 ± 4.6%). 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 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.

5.2 Introduction

5.2.1 Effects of alien plant invasions on the environment

The invasion of alien species and their subsequent removal, affects all aspects of an ecosystem. One of the most damaging effects of alien plant invasions is the disruption to entire ecosystem processes. Alien plants can change nutrient resources within biogeochemical cycles, trophic resources within food webs, physical resources such as living space, sediment, light, or water (Vitousek, 1990), and disturbance regimes (D'Antonio and Meyerson, 2002; Gordon, 1998). Once species have changed ecosystem processes, positive feedbacks can increase the resistance of the system in its degraded state and make it resilient to restoration efforts (Hobbs and Harris, 2001; Scheffer, 2001). These positive feedbacks also reinforce and accelerate damaging processes, leading to irreversible vegetation change once a site's capacity for self-repair has been exceeded (Rietkerk and Van de Koppel, 1997). Therefore it is important to remove the alien species before they have had time to change ecosystem processes beyond a critical point or threshold.

Invasive species affect nutrient cycles by altering soil processes, which may create changes that have the potential to radiate through the ecosystem. Highly disturbed areas are often highly acidic and may be low in macronutrients, such as nitrogen, phosphorus and potassium, as well as various micronutrients (Mack *et al.*, 2000; Ehrenfeld *et al.*, 2001; Evans *et al.*, 2001; Scott *et al.*, 2001; Holl and Cairns, 2002). Many studies have found relationships between changes in species richness and nutrient availability. It has been found that species richness is low at low nutrient levels, increases to a peak at intermediate levels and declines more gradually at high nutrient levels (Pausas and Austin, 2001). The reasons for this pattern are that few species are able to tolerate extreme conditions of nutrient deficiency, and that as resources increase, more species can survive and hence species richness rises. At higher nutrient levels, a few highly competitive species become dominant, suppressing other species, thus causing a decline in species richness.

Invasions also increase fuel loads and fire frequencies, to which key indigenous species are not adapted (Van Wilgen and Richardson, 1985; Scott and Van Wyk, 1990; Scott and Schulze, 1992; Mack *et al.*, 2000). The increased intensity of fires makes them more difficult to control, and damages soils through heating and combustion of the organic matter which, in turn, can result in water repellency and severe soil erosion (DeBano and Rice, 1973; Giovannini and Lucchesi, 1983; Scott and Van Wyk, 1990, 1992; Scott *et al.*, 1998b; Euston-Brown, 2000; Scott *et al.*, 2000), which can increase the risk of severe flooding. The severe fires also kill seeds in the soil and sprouting plant species (Richardson and Van Wilgen, 1986; Holmes *et al.*, 2000).

The susceptibility of a community to invasion will be influenced by the supply of resources and the uptake of those resources (Davis *et al.* 2000). This is because a plant community with unused resources such as water, nutrients, space, or light, will become more susceptible to invasion, and any factor that makes resources more available, e.g. a wet spell, the input of nutrients or the removal of a species, will promote invasion by new species.

5.2.2 Effects of alien plant clearing on the environment

Impacts of removing invasive alien species include enhancing available surface and underground water, preventing the loss of biodiversity, reducing fire hazard, stabilizing catchment areas and preventing erosion. With the removal of alien species, the availability of resources reaches a peak soon afterwards (Canham and Marks, 1985). There is increased soil moisture, soil temperature and improved substrate quality, which stimulate nitrogen mineralization and nitrogen pool sizes, and consequently increase short-term nitrogen availability (Daubenmire, 1968; Hobbs and Schimel, 1984; Agrawal and Tiwari, 1987; Matson *et al.*, 1987). The first plants to establish after a disturbance should encounter a greater availability of resources, improving the probability of survival and establishment in the community. The initial colonizer's competitive advantage and consequent dominance could inhibit establishment by other species as succession proceeds and resources become more limited (Hughes and Vitousek, 1993).

5.2.3 Effects of flooding on the riparian vegetation

Very heavy rainfall in February 2000 resulted in a severe flood over Mpumalanga and Limpopo provinces, as well as Zimbabwe and Mozambique. This 2000 flood was termed a Large Infrequent Disturbance (LID) event due to the infrequent nature of this type of event (Heritage *et al*., 2001). In general, riparian plant species require bare, wet surfaces for establishment, which are generated by large floods (Scott *et al.*, 1997). Most opportunities for recruitment of plant propagules occur after floods when the availability of establishment sites is greatly increased, and the dispersal of propagules in water may have a major role in structuring the flora (Johansson *et al.*, 1996). The 2000 flood resulted in a major change in the vegetation distribution along the Sabie River in the Kruger National Park (KNP). Using transects across the river, Leroy (2003) showed that the flood reduced the number of woody species occurrences and woody plant density per transect. Leroy (2003) also found an increase in the herbaceous and grass species richness (Leroy, 2003). The number of alien species along the river increased quite considerably, which was expected as the flood brought in large quantities of propagules from the surrounding catchment (Leroy, 2003). Along the Sabie River in the upper catchments outside of the KNP, Garner (2005) found that the soil seed banks in the community were limited in their species richness and were dominated by propagules of four species – two aliens (*Eucalyptus grandis* and *Solanum mauritianum*), one indigenous shrub (*Clutia monticola*) and one indigenous herb (*Ipomoea* sp.). Therefore, these species would have been expected to have arrived from the upper catchment. The flood also caused a greater decrease in indigenous plant density compared with alien plant density, with the alien woody species showing a significant increase in species richness (Leroy, 2003).

5.2.4 Aim, objectives and hypothesis

In the 10 year period from 1995 to 2005, WfW has been clearing invasive alien plants along the Sabie River, which included the study areas. The upper catchment of the Sabie River traverses through the grassland biome, whereas the lower catchment occurs in the savanna biome. Approximately two years after the WfW programme began, a study was conducted in 1996/1997, which assessed the impacts of the invasive alien species invasion and subsequent clearing on the Sabie riverine ecosystem (Garner, 2005). The data from the 1996/1997 study was then compared with the data from this 2005 study, in order to assess the Sabie River riparian vegetation recovery in response to the WfW clearing.

The overall aim of this chapter was to investigate the relationship between the Sabie River riparian environment (i.e. ground cover, and soil chemical and physical properties) and the invasion of alien plant species and their removal. The objectives of this chapter were to:

1) Measure and compare the cover of exposed soil, rock, litter, herbaceous vegetation (except graminoids) and grass between the grassland and savanna biomes in 2005.
2) Compare the cover of exposed soil, rock, litter, herbaceous vegetation and grass between 1996 and 2005.
3) Measure and compare various soil chemical and physical properties of the grassland and savanna biomes in 2005.

4) Compare various soil chemical and physical properties between 1996 and 2005.
5) Use the information from objectives 1-4 to assess the effectiveness of the WfW clearing over time, i.e. from 1996 to 2005. Note: "effectiveness" can be assessed in various ways, such as determining whether there is an increase in indigenous species richness and/or a decrease in alien species richness. In this study it also includes determining whether there is a reduction in the invasion intensity (defined as the percentage aerial cover of woody alien plants) after clearing.

It is hypothesized 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, and in both 1996 and 2005. It is important to note that the invasion intensity was used as a measure of the degree of alien plant invasions.

5.3 Materials and methods

5.3.1 Experimental design

In 1996/1997, 40 permanent modified Whittaker nested plots were first surveyed along the Sabie River and several variables were measured, such as the plant species composition, diversity and vegetation structure, as well as a range of environmental variables (Garner, 2005). Three different experimental treatments, i.e. (A) high altitude (grassland) versus low altitude (savanna) plots (=biome), (B) high invaded versus low invaded plots (=invasion intensity) and (C) cleared versus uncleared plots (=clearing), were assessed. In terms of the present study, field work was undertaken from the 14th February to the 6th April 2005, using the same 40 modified Whittaker nested plots positioned as close as possible to the original 1996/1997 plots. The same three experimental treatments were used, i.e. (A) biome, (B) invasion intensity and (C) clearing, based on the historical 1996/1997 situation. The 2005 data were compared across the same three treatments, despite the changes from the invasion and subsequent clearing of alien plants over time. Each biome contained plots of 'high invasion' and 'low invasion'. For each 'invasion intensity' treatment, ten modified Whittaker nested plots were completed (Figures 2.8 (Chapter 2) and 4.1 (Chapter 4)). Therefore, each 'biome' treatment contained 20 plots, giving a total of 40 modified Whittaker nested plots (Figures 2.8 (Chapter 2) and 4.1 (Chapter 4)). Each 'invasion intensity' treatment consisted of 'cleared' and 'uncleared' plots. For each 'clearing' treatment, five modified Whittaker nested plots were completed (Figures 2.8 (Chapter 2) and 4.1 (Chapter 4)). Hence, based on the three "treatments" (biome, invasion intensity and clearing), each of which were set at two levels, there was a total of eight different experimental categories (or treatment combinations), with each containing five plots (Figures 2.8 (Chapter 2) and 4.1 (Chapter 4)). Refer to Chapter 4 for more detailed notes on the experimental design.

5.3.2 Field sampling

The field sampling of both studies were very similar and the data collected from the 1996 study was compared with the data from this study of 2005 (refer to Chapter 3 for the field sampling methods).

Descriptive variables

For each plot, the co-ordinates, altitude (m.a.s.l.), landscape context, slope steepness (º), aspect and position relative to the river, i.e. north, south, etc., were determined. The co-ordinates and altitude were determined from GPS readings (Garmin GPS V). The slope steepness, aspect and position relative to the river were all determined using a compass with a built-in clinometer (Brunton Prismatic Compass). The landscape context was determined by observing what the surrounding land-use was – in all 40 plots it was close to *Eucalyptus* plantations.

Ground cover

Within each modified Whittaker nested plot, the ten 1 m^2 quadrats were used to determine the ground cover. Each quadrat was marked out using a rigid steel quadrat of 0.5 x 2 m. A visual estimation of percentage cover was determined for each of (a) exposed soil, (b) rock, (c) litter, (d) herbaceous vegetation and (e) grass.

Soil

In the 1996 study (Garner, 2005), a large number of soil features were obtained from each of the 40 modified Whittaker nested plots, from both the A horizon (0 – 10 cm depth) and B horizon (10 – 20 cm depth), such as soil organic matter, soil pH, texture, minerals and trace elements. As many of these soil characteristics would probably not have changed much over the last eight years, only those variables that were more likely to have changed, were re-measured. Only the A horizon was assessed in 2005, as it was expected that any possible changes would be more strongly indicated here, rather than in the B horizon. Soil samples were taken from the 1000 m^2 plot by carefully removing the litter layer and sampling the A horizon (i.e. 0 – 10 cm depth) using a trowel. Four samples were collected from corners of each plot, and then bulked. Soil compaction (kg/cm^2) was then measured using a hand held penetrometer, with 50 measurements taken per plot, which were randomly distributed.

The soil samples were sent to The Soil Fertility and Analytical Services Section of the KwaZulu-Natal Department of Agriculture and Environmental Affairs at Cedara for analysis of bulk density (g/ml), exchangeable acidity (cmolc/l), total cations (cmolc/l), acid saturation (%), pH (in KCl, potassium chloride), clay (%), soil organic matter (SOM) (%), total nitrogen (N) (%), phosphate (PO_4^{3-}) (mg/l), exchangeable potassium (K) (mg/l), exchangeable calcium (Ca) (mg/l), exchangeable magnesium (Mg) (mg/l), total zinc (Zn) (mg/l), total manganese (Mn) (mg/l) and total copper (Cu) (mg/l) (refer to Appendix 19 for laboratory methodologies).

5.3.3 Data analyses

Slope steepness

The steepness of the slopes of the grassland and savanna plots was statistically compared using t-tests (for independent-samples). The steepness of the slopes of the Sabie, Graskop and Hazeyview regions were then statistically compared using one-way analysis of variances (ANOVA's), along with Tukey's honest significant

difference (HSD) tests. The programme STATISTICA (1999 edition) was used for the statistical analyses, and data were checked for normality, and transformed if not.

Ground cover

The percentage cover of (a) exposed soil, (b) rock, (c) litter, (d) herbaceous vegetation and (e) grass, was compared between plots in the grassland and savanna biomes, as well as between plots in the Sabie, Graskop and Hazeyview regions. These values were statistically compared using t-tests (for independent-samples) between the biomes and one-way ANOVA's, along with Tukey's honest significant difference (HSD) tests, between the three regions. The ground cover for 2005 was then compared to that of 1996 using t-tests (for independent-samples). The ground cover of each of the eight experimental categories of the three different treatments (within and between the years) was then compared using three-way ANOVA's and Tukey's HSD tests, a three-way analysis of covariance (ANCOVA) (with the 1996 data as the co-variate), and t-tests (for independent-samples). The interaction between biomes and times (for each ground cover variable) was then determined by a two-way ANOVA.

Soil

The soil results were statistically analysed to compare between the plots in the grassland and savanna biomes, as well as between the plots in the three regions, namely Sabie, Graskop and Hazeyview. They were statistically compared using t-tests (for independent-samples) between the biomes and one-way ANOVA's and Tukey's HSD tests between the three regions. The pH of 1996 and 2005 were then compared using t-tests (for independent-samples). The pH of each of the eight experimental categories of the three different treatments (within and between the years) was then compared using three-way ANOVA's and Tukey's HSD tests, and t-tests (for independent-samples). The interaction between biomes and times (for pH) was then determined by a two-way ANOVA.

Linear regressions

The percentage aerial cover of woody alien plants was used as a measure of invasion intensity. Linear regression analyses were then performed whereby the relationships between invasion intensity (independent variable) and litter cover and soil organic matter (dependent variables) were determined for the grassland and savanna biomes; the Sabie, Graskop and Hazeyview regions; and 1996 and 2005. Different methods were used to calculate the soil organic matter contents in 1996 and 2005, i.e. in 1996 the muffle furnace was used, whereas in 2005 near infrared spectroscopy was used. Thus, the soil organic matter contents of the different years could not be compared directly; therefore these results were regressed against one another to determine if there was a relationship.

Multivariate statistical analyses on environmental variables

Multivariate analyses were done on the environmental data using the multivariate package CANOCO (Leps and Smilauer, 2003). Analyses were done to determine if there was any association between the plots and the environmental

variables. The linear, indirect gradient analysis method, principal component analysis (PCA), was used because there was a single response variable with no predictors. Environmental variables included PO_4^{3-}, K, Ca, Mg, Zn, Mn, Cu, organic C, total N, acidity, cations, acid saturation, pH, altitude, slope, compaction, and the percentage cover of exposed soil, rock, litter, herbaceous vegetation and grass, as well as the invasion intensity (i.e. percentage aerial cover of woody alien plants).

Multivariate statistical analyses on environmental variables and species data

Multivariate statistical analyses were also done using both the species data and the environmental variables to determine the plots' associations with the species composition and the environmental variables. Firstly, the unimodal, indirect gradient analysis (unconstrained) method, correspondence analysis (CA) was used, which summarized the distributional properties of the species. This method was used because there was a single response variable (i.e. the species) with no predictors available. The unimodal, direct gradient analysis (constrained) method, canonical correspondence analysis (CCA) was then used because there were predictors available for a set of response variables. The ordination diagrams of the CA and CCA were then compared. Species abundance data from the 100 m^2 quadrat from each of the 40 plots were used in the analyses. During the CCA, a simpler model was built by performing Monte Carlo permutation tests. These tests determined which of the environmental variables were the most important ones, i.e. which environmental variables sufficiently explained the species composition patterns.

5.4 Results

5.4.1 Slope steepness

Biome comparison: grassland and savanna biomes (in 2005)

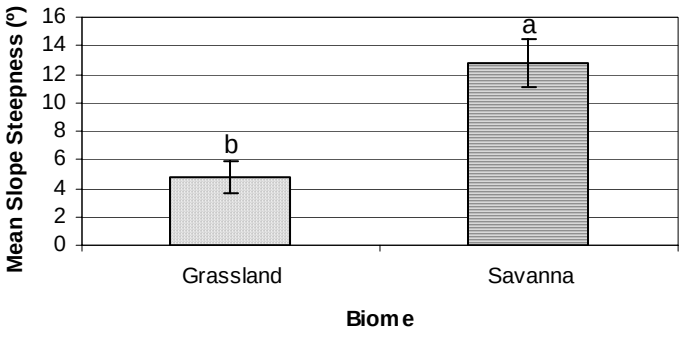


Figure 5.1. Degree of slope steepness (mean ± S.E.) of plots in the grassland and savanna biomes in 2005. Columns with different superscript letters are significantly different using t-tests (for independent-samples) ($P < 0.05$). N = 20 for each biomes; *d.f.* = 38.

The plots of the savanna biome were significantly steeper than those of the grassland biome ($P < 0.001$) (Figure 5.1).

Regional comparison: Sabie (grassland), Graskop (grassland) and Hazeyview (savanna) (in 2005)

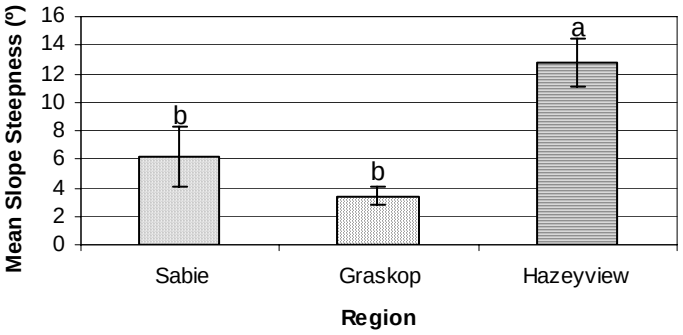


Figure 5.2. Degree of slope steepness (mean ± S.E.) of plots in the Sabie (grassland), Graskop (grassland) and Hazeyview (savanna) regions in 2005. Columns with different superscript letters are significantly different using Tukey's honest significant difference (HSD) tests ($P < 0.05$). N = 10 for Sabie and Graskop, and 20 for Hazeyview; *d.f.* = 2,37.

The plots of the Hazeyview region were significantly steeper than those of the Sabie and Graskop regions, even though the Sabie plots had steeper slopes than the Graskop plots (Figure 5.2; probability values are given in Appendix 6).

5.4.2 Ground cover

Biome comparison: grassland and savanna biomes (in 2005)

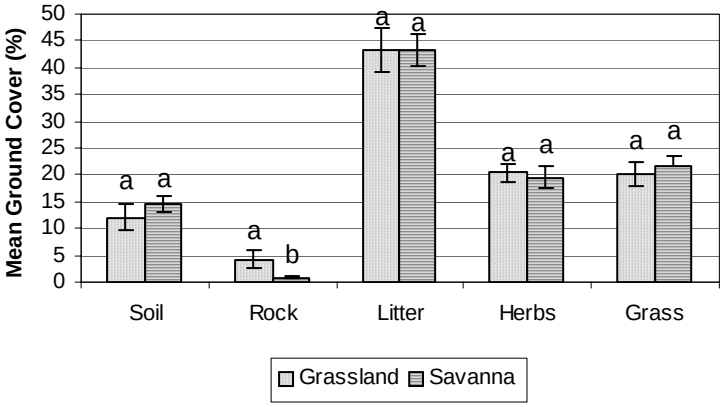


Figure 5.3. Percentage ground cover estimates (mean ± S.E.) of (a) exposed soil, (b) rock, (c) litter, (d) herbaceous vegetation and (e) grass from plots in the grassland and savanna biomes in 2005. Columns with different superscript letters within the same ground cover variable are significantly different using t-tests (for independent-samples) ($P < 0.05$). N = 20 for all ground cover variables; *d.f.* = 38.

Litter ground cover was the greatest, followed by grass and herbaceous covers, and then exposed soil and rock covers (Figure 5.3). The savanna had a higher cover

of exposed soil, litter and grass, whereas the grassland had a higher cover of rock and herbs (Figure 5.3). However, only rock cover was significantly different between the biomes (Appendix 5 for probability values).

Regional comparison: Sabie (grassland), Graskop (grassland) and Hazeyview (savanna) (in 2005)

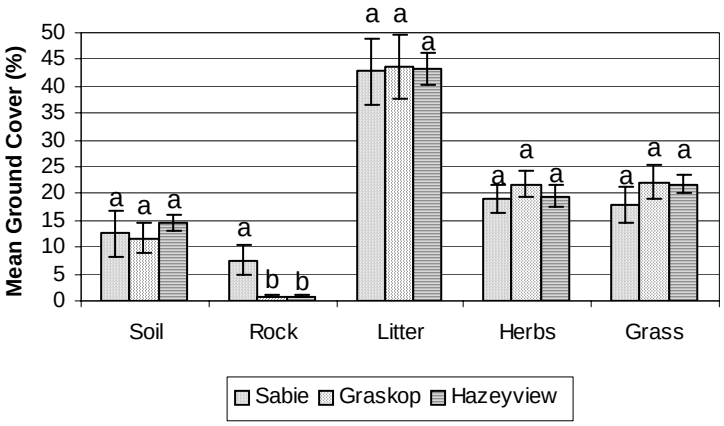


Figure 5.4. Percentage ground cover estimates (mean ± S.E.) of (a) exposed soil, (b) rock, (c) litter, (d) herbaceous vegetation and (e) grass from plots in the Sabie (grassland), Graskop (grassland) and Hazeyview (savanna) regions in 2005. Columns with different superscript letters within the same ground 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.

The Graskop region had the highest litter, herbaceous and grass cover, whereas the Sabie region had the lowest (Figure 5.4). The Hazeyview region had the highest exposed soil cover and the Graskop region had the lowest (Figure 5.4). However, there was no significant difference in these ground cover variables between the regions. The only significant difference was in rock cover, which was significantly higher in the Sabie region, which accounted for higher rock cover in the grassland than savanna (Appendix 6 for probability values).

Year comparison: 1996 and 2005

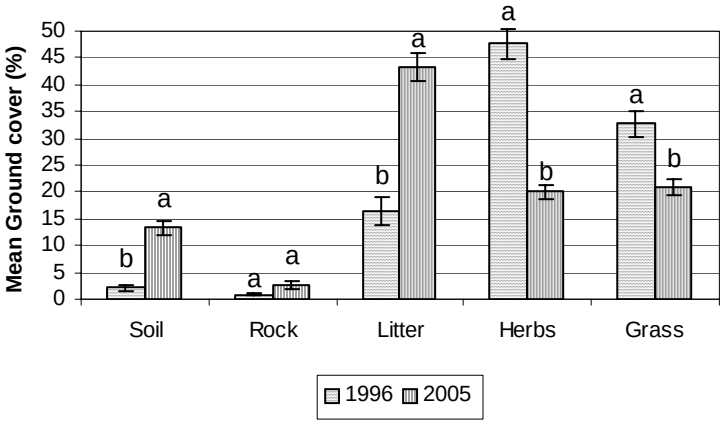


Figure 5.5. Percentage ground cover estimates (mean ± S.E.) of (a) exposed soil, (b) rock, (c) litter, (d) herbaceous vegetation and (e) grass from all 40 plots along the Sabie River, in 1996 and 2005. Columns with different superscript letters within the same ground cover variable are significantly different using t-tests (for independent-samples) ($P < 0.05$). N = 40 for each ground cover variable; *d.f.* = 78.

In 1996, the cover of herbs and grasses were significantly greater than in 2005, whereas exposed soil, rock (not significant) and litter covers were significantly greater in 2005 (Figure 5.5; probability values in Appendix 12).

Treatment comparison in 1996 and 2005: (A) biome, (B) invasion intensity and (C) clearing

Table 5.1. Percentage ground cover estimates (mean ± 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).

% Ground Cover	High Altitude (Grassland)				Low Altitude (Savanna)			
	High Invasion		Low Invasion		High Invasion		Low Invasion	
	Cleared	Uncleared	Cleared	Uncleared	Cleared	Uncleared	Cleared	Uncleared
1996								
Soil	$0.9\pm0.5_a^a$	$0\pm0_b^a$	$3.5\pm1.3_a^a$	$0.3\pm0.2_b^a$	$1.5\pm1.3_b^a$	$4.2\pm 2.6_a^a$	$4.2\pm2.6_b^a$	$2.2\pm0.9_b^a$
Rock	$0.3\pm0.3_a^a$	$0\pm0_a^a$	$2.0\pm1.2_a^a$	$0.6\pm0.4_a^a$	$1.2\pm1.2_a^a$	$1.5\pm 1.2_a^a$	$0.1\pm0.1_a^a$	$1.3\pm1.2_a^a$
Litter	$19.9\pm4.3_a^{ab}$	$42.2\pm12.0_a^a$	$5.1\pm2.0_b^b$	$8.9\pm4.5_b^b$	$11.3\pm4.7_b^b$	$20.4\pm8.8_b^{ab}$	$10.4\pm2.8_b^b$	$12.7\pm5.5_b^b$
Herbs	$59.3\pm5.9_a^{ab}$	$30.9\pm5.8_a^b$	$48.3\pm8.8_a^{ab}$	$51.4\pm6.7_a^{ab}$	$39.6\pm5.3_a^b$	$34.4\pm 6.1_a^b$	$68.5\pm6.2_a^a$	$51.9\pm6.4_a^{ab}$
Grass	$19.6\pm4.0_a^{ab}$	$26.9\pm9.1_a^{ab}$	$41.1\pm9.1_a^{ab}$	$38.8\pm4.9_a^{ab}$	$46.4\pm3.9_a^a$	$39.5\pm8.1_a^{ab}$	$16.8\pm2.2_a^b$	$31.9\pm5.2_a^{ab}$
2005								
Soil	$13.2\pm5.9_a^a$	$5.4\pm1.2_a^a$	$13.4\pm6.5_a^a$	$16.4\pm4.5_a^a$	$12.6\pm2.1_a^a$	$10.0\pm1.7_a^a$	$15.4\pm3.2_a^a$	$19.8\pm3.8_a^a$
Rock	$10.0\pm5.2_a^a$	$0.6\pm0.4_a^a$	$5.2\pm2.6_a^a$	$1.2\pm0.4_a^a$	$0.6\pm0.4_a^a$	$0.8\pm0.2_a^a$	$0.8\pm0.6_a^a$	$1.0\pm0.5_a^a$
Litter	$42.8\pm10.3_a^a$	$56.8\pm3.4_a^a$	$42.2\pm9.5_a^a$	$31.0\pm6.4_a^a$	$49.4\pm3.1_a^a$	$52.6\pm4.9_a^a$	$32.6\pm7.1_a^a$	$39.2\pm4.4_a^a$
Herbs	$17.6\pm2.2_b^a$	$19.2\pm2.9_a^a$	$22.0\pm5.5_b^a$	$22.8\pm3.1_b^a$	$12.2\pm3.2_b^a$	$17.0\pm2.7_b^a$	$27.8\pm4.1_b^a$	$21.2\pm4.7_b^a$
Grass	$16.4\pm4.5_a^a$	$18.0\pm4.6_a^a$	$17.2\pm3.6_b^a$	$28.6\pm4.7_a^a$	$25.2\pm3.7_b^a$	$19.6\pm3.6_a^a$	$23.4\pm3.6_a^a$	$18.8\pm3.0_a^a$

Exposed soil and litter covers were significantly higher in 2005 than in 1996, in most experimental categories (Table 5.1; Appendix 15 for probability values). Herbaceous cover was significantly higher in 1996 than in 2005 in most experimental categories (Table 5.1; Appendix 15 for probability values). There was no significant difference in rock cover over time and grass cover was only significantly higher in 1996 in the grassland, low invaded, cleared plots and the savanna, high invaded, cleared plots (Table 5.1; Appendix 15 for probability values).

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 $P < 0.05$.

Year	Ground Cover	BIOME	INVIN	CLEAR	BIOME* INVIN	BIOME* CLEAR	INV* CLEAR	BIOME* INVIN* CLEAR	Co-variate
(a) 1996	Soil	0.079	0.423	0.423	0.603	0.241	0.095	0.571	
	Rock	0.518	0.871	0.935	0.131	0.152	0.746	0.468	
	Litter	0.252	**0.003**	**0.046**	**0.036**	0.430	0.167	0.524	
	Herbs	0.786	**0.005**	**0.013**	**0.040**	0.745	0.360	**0.026**	
	Grass	0.638	0.829	0.469	**$4x10^{-5}$**	0.846	0.511	0.088	
(b) 2005	Soil	0.419	**0.046**	0.796	0.904	0.570	0.131	0.743	
	Rock	**0.025**	0.522	**0.034**	0.439	**0.025**	0.365	0.365	
	Litter	0.958	**0.005**	0.507	0.841	0.712	0.254	0.137	
	Herbs	0.747	**0.012**	0.955	0.267	0.690	0.252	0.318	
	Grass	0.547	0.436	0.804	0.219	**0.046**	0.340	0.436	
(c) 1996 and 2005	Soil	0.568	0.061	0.870	0.859	0.674	0.108	0.795	0.528
	Rock	**0.022**	0.510	**0.036**	0.340	**0.048**	0.344	0.319	0.419
	Litter	0.942	**0.007**	0.409	0.972	0.782	0.215	0.127	0.542
	Herbs	0.708	0.074	0.618	0.503	0.646	0.194	0.599	0.292
	Grass	0.534	0.451	0.773	0.232	0.050	0.330	0.530	0.722

In 1996, no significant differences were found in the percentage cover of exposed soil, rock and grass between the grassland and savanna plots, the high and low invaded plots, as well as the cleared and uncleared plots (Table 5.2 (a)). There were no significant differences in litter and herbaceous covers between the grassland and savanna plots; however, the high invaded plots had a significantly higher litter and herbaceous cover, the uncleared plots had a significantly higher litter cover, and the cleared plots had a significantly higher herbaceous cover (Table 5.2 (a)). In 1996, there were significant biome by invasion intensity interactions for litter, herbaceous and grass covers. This means that the value for the biomes is dependent on whether there is a high or low invasion intensity in the plots. Litter cover was higher in the high invaded plots (for both biomes). Herbaceous cover was higher in the low invaded plots (for both biomes). Grass cover in the grassland was higher in the low invaded plots, and in the savanna in the high invaded plots. There were significant interactions between the biome, invasion intensity and clearing treatments for herbaceous cover. Therefore, the value for the biomes is dependent on whether there is high or low invasion in the plots, and whether the plots are cleared or not.

In 2005, no significant differences were found in the percentage cover of exposed soil, litter and herbaceous vegetation between the grassland and savanna plots, and cleared and uncleared plots (Table 5.2 (b)). However, the low invaded plots had a significantly higher percentage cover of exposed soil and herbs, whereas the high invaded plots had a significantly higher percentage cover of litter (Table 5.2 (b)). There was no significant difference in grass cover between the grassland and savanna biomes, the high and low invaded plots, and the cleared and uncleared plots (Table 5.2 (b)). There was also no significant difference in rock cover between the high and low invaded plots, but the grassland and cleared plots had a significantly higher rock cover (Table 5.2 (b)). Significant interactions were found between the biome and clearing treatments for rock and grass covers (Table 5.2 (b)). Thus, the value for the biomes is dependent of whether the plots are cleared or not. Rock cover was higher in the cleared plots (for both biomes), and grass cover was higher in the uncleared plots (in the grassland) and cleared plots (in the savanna).

There was a significant change in rock cover of the biomes and clearing treatments over time (Table 5.2 (c)). This is due to rock cover being significantly higher in a few of the grassland, cleared plots in 2005. There was also a significant change in litter cover of the invasion intensity treatment over time (Table 5.2 (c)), i.e. litter cover was higher in both invasion categories in 2005. None of the *P* – values for the covariate, i.e. 1996 values, are significant, therefore indicating that there is virtually no relationship between the 2005 and 1996 data.

Interaction between biomes and times

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 $P < 0.05$.

Ground Cover	YEAR	BIOME	YEAR*BIOME
Soil	**< 0.001**	0.174	0.885
Rock	0.058	0.079	**0.027**
Litter	**< 0.001**	0.503	0.461
Herbs	**< 0.001**	0.950	0.741
Grass	**< 0.001**	0.523	0.943

There were significant differences in exposed soil, litter, herbaceous and grass covers over time, whereas rock cover did not change significantly over time (Table 5.3). There was a significant interaction between the year and biome treatments for rock cover (Table 5.3). Therefore, the value for the years is dependent on which biome it is. This was a result of rock cover being significantly higher in some of the grassland plots in 2005.

5.4.3 Soil

Biome comparison: grassland and savanna biomes (in 2005)

(a) Soil organic matter (SOM)

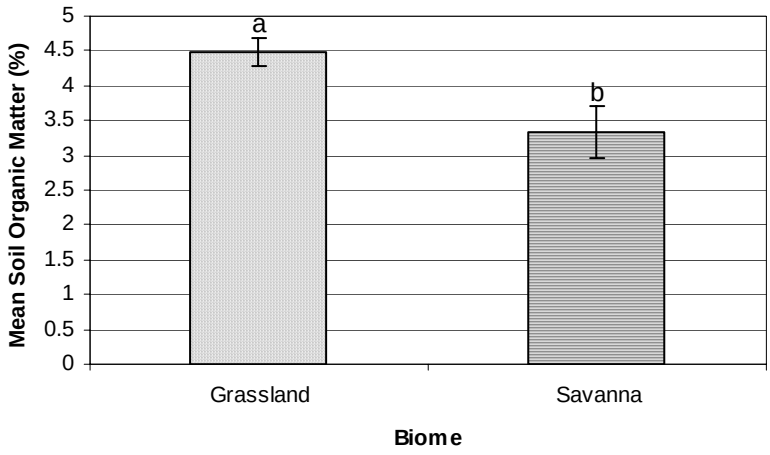


Figure 5.6. Percentage of soil organic matter (mean ± S.E.) for plots in the grassland and savanna biomes in 2005. Columns with different superscript letters are significantly different using t-tests (for independent-samples) ($P < 0.05$). N = 20 for each biome; *d.f.* = 38.

The SOM was significantly higher in the grassland ($P = 0.012$) (Figure 5.6).

(b) Total nitrogen (N)

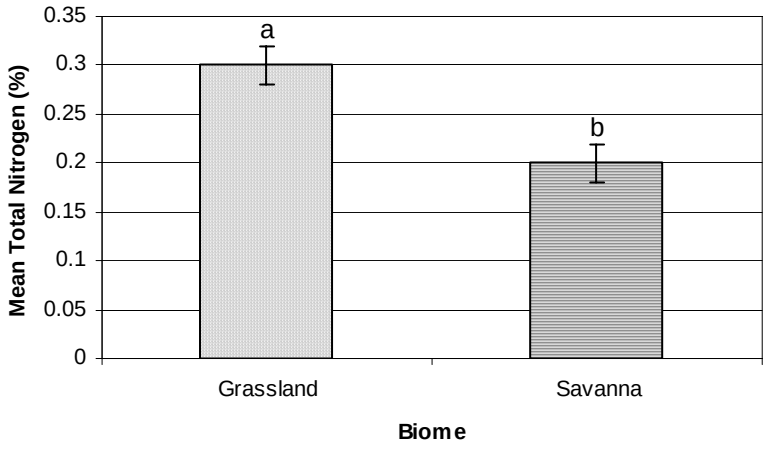


Figure 5.7. Percentage of total nitrogen (mean ± S.E.) for plots in the grassland and savanna biomes in 2005. Columns with different superscript letters are significantly different using t-tests (for independent-samples) ($P < 0.05$). N = 20 for each biome; *d.f.* = 38.

The total N was significantly greater in the grassland ($P = 0.029$) (Figure 5.7).

(c) pH

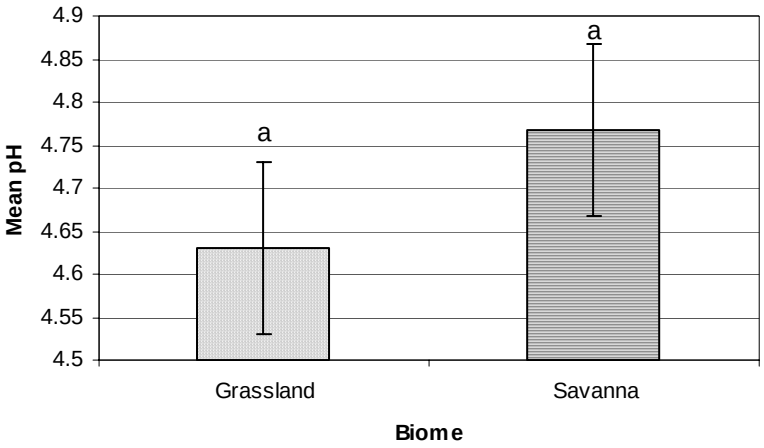


Figure 5.8. pH (mean ± S.E.) for plots in the grassland and savanna biomes in 2005. Columns with different superscript letters are significantly different using t-tests (for independent-samples) ($P < 0.05$). N = 20 for each biome; *d.f.* = 38.

The savanna tended to have a slightly higher (but not significantly) pH than the grassland ($P = 0.342$) (Figure 5.8).

(d) Soil elements

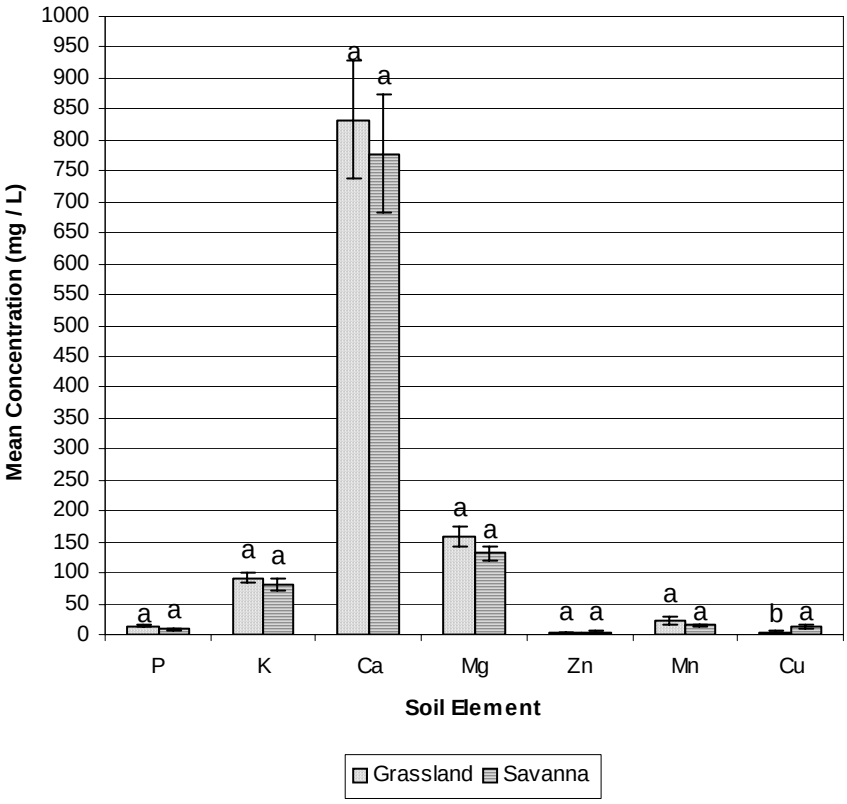


Figure 5.9. Concentration of soil elements (mg/L) (mean ± S.E.) for plots in the grassland and savanna biomes in 2005. Soil elements include phosphate (indicated as

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.

The most abundant element, of those measured, was Ca, followed by Mg and K; the remaining elements were found in much smaller amounts (Figure 5.9). The grassland had higher concentrations of all the elements except for Cu and Zn, which tended to be higher in the savanna. There were no statistical differences in the concentrations of the elements between the biomes, except for Cu (probability values in Appendix 5).

(e) Soil compaction

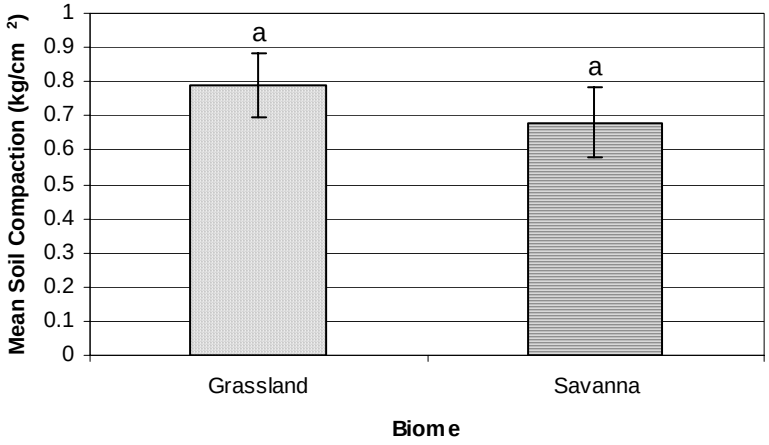


Figure 5.10. Soil compaction (mean ± S.E.) of plots in the grassland and savanna biomes in 2005. Columns with different superscript letters are significantly different using t-tests (for independent-samples) ($P < 0.05$). N = 20 for each biome; *d.f.* = 38.

The soils of the grassland biome were more compacted (but not significantly) than the soils of the savanna biome ($P = 0.429$) (Figure 5.10).

Regional comparison: Sabie (grassland), Graskop (grassland) and Hazeyview (savanna) (in 2005)

(a) Soil organic matter

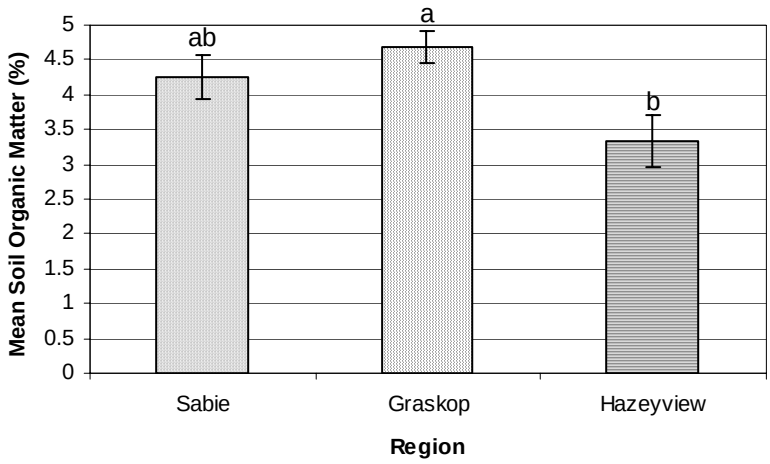


Figure 5.11. Percentage of soil organic matter (mean ± S.E.) for plots in the Sabie (grassland), Graskop (grassland) and Hazeyview (savanna) regions in 2005. Columns with different superscript letters are significantly different using Tukey's honest significant difference (HSD) tests ($P < 0.05$). N = 10 for Sabie and Graskop, and 20 for Hazeyview; *d.f.* = 2,37.

The SOM tended to be the highest in the Graskop region and the lowest in the Hazeyview region (Figure 5.11), with Hazeyview tending to have a significantly lower percentage than Graskop (Appendix 6 for probability values).

(b) Total nitrogen

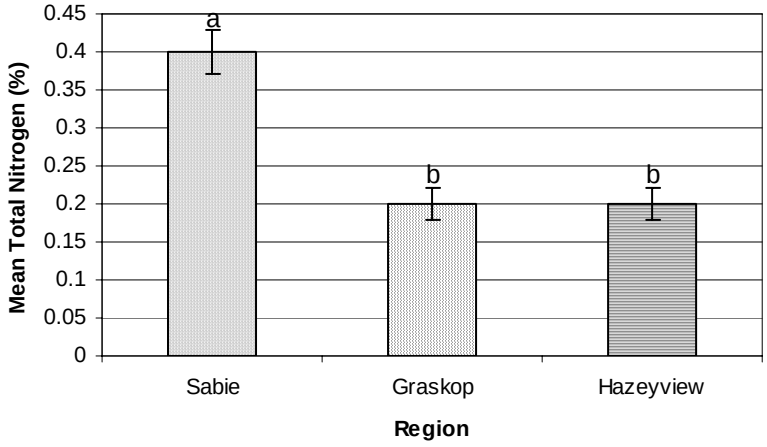


Figure 5.12. Percentage of total nitrogen (mean ± S.E.) for plots in the Sabie (grassland), Graskop (grassland) and Hazeyview (savanna) regions in 2005. Columns with different superscript letters are significantly different using Tukey's honest significant difference (HSD) tests ($P < 0.05$). N = 10 for Sabie and Graskop, and 20 for Hazeyview; *d.f.* = 2,37.

The total N was significantly greater in the Sabie than in the other regions (Figure 5.12; Appendix 6 for probability values).

(c) pH

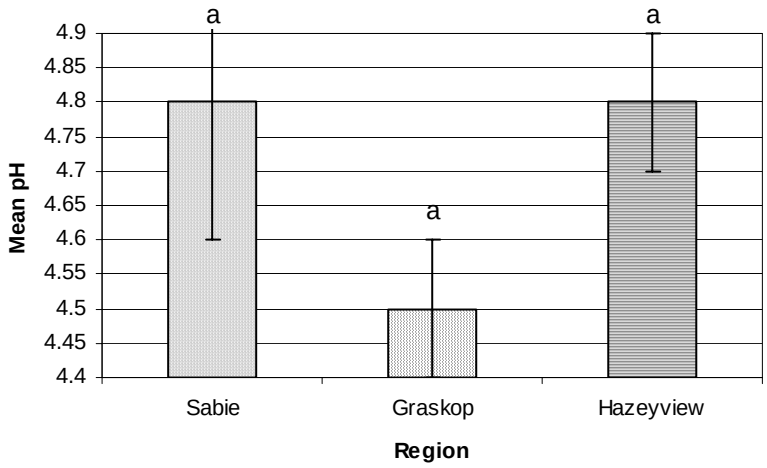


Figure 5.13. pH (mean ± S.E.) for plots in the Sabie (grassland), Graskop (grassland) and Hazeyview (savanna) regions in 2005. Columns with different superscript letters are significantly different using Tukey's honest significant difference (HSD) tests ($P < 0.05$). N = 10 for Sabie and Graskop, and 20 for Hazeyview; *d.f.* = 2,37.

The pH was the lowest (but not significantly) in the Graskop region and the same in the Sabie and Hazeyview regions (Figure 5.13; Appendix 6 for probability values).

(d) Soil elements

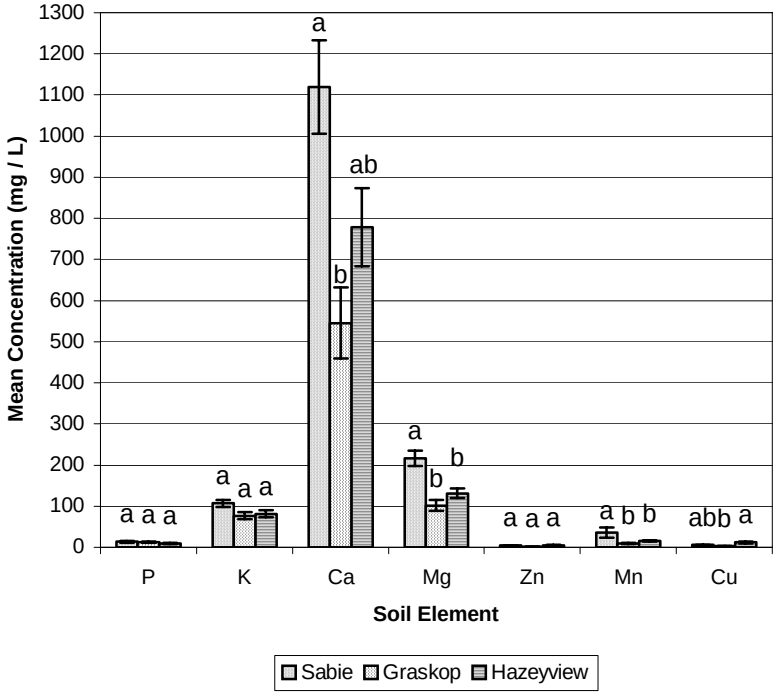


Figure 5.14. Concentration of soil elements (mg/L) (mean ± S.E.) for plots in the Sabie (grassland), Graskop (grassland) and Hazeyview (savanna) regions in 2005.

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.

The Sabie region tended to have the highest concentrations of all the elements except Cu and Zn, which were the highest in the Hazeyview region, and the Graskop region tended to have the lowest concentrations of all the elements, except P, which was the lowest in the Hazeyview region (Figure 5.14). Therefore, the higher (often significantly) concentrations of elements in the soils found in the Sabie region, accounted for the grassland having higher concentrations of most of the elements than the savanna (Appendix 6 for probability values).

(e) Soil compaction

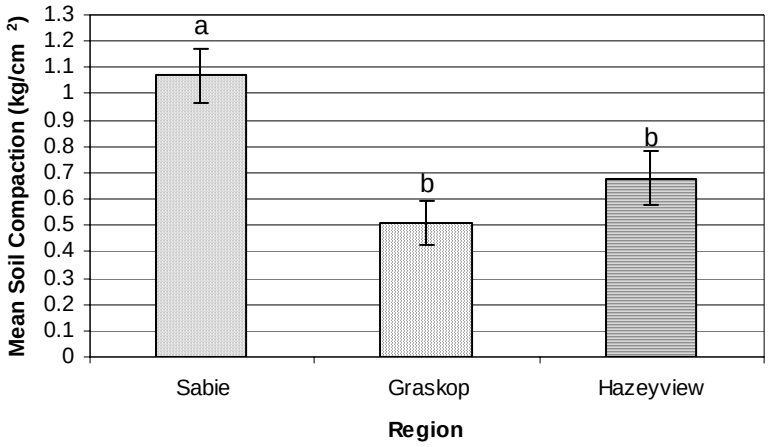


Figure 5.15. Soil compaction (mean ± S.E.) for plots in the Sabie (grassland), Graskop (grassland) and Hazeyview (savanna) regions in 2005. Columns with different superscript letters are significantly different using Tukey's honest significant difference (HSD) tests ($P < 0.05$). N = 10 for Sabie and Graskop, and 20 for Hazeyview; *d.f.* = 2,37.

The soils of the Sabie region were significantly more compacted compared to the Graskop and Hazeyview soils (Figure 5.15; probability values are given in Appendix 6).

Year comparison: 1996 and 2005

(a) pH

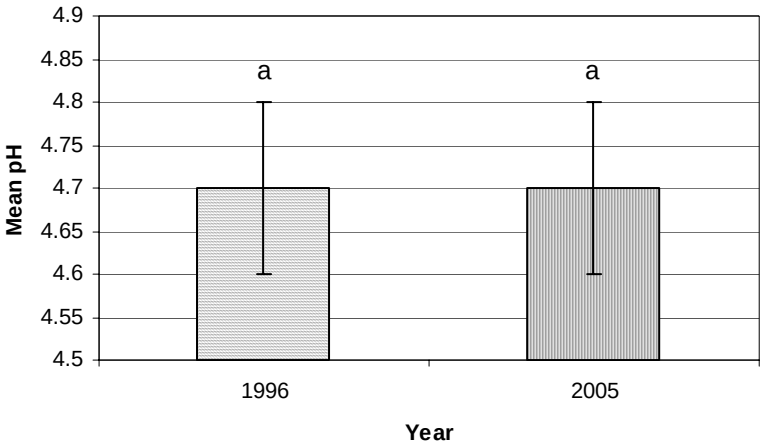


Figure 5.16. pH (mean ± S.E.) for all 40 plots in 1996 and 2005, along the Sabie River. Columns with different superscript letters are significantly different using t-tests (for independent-samples) ($P < 0.05$). N = 40 for each year; *d.f.* = 78.

The pH remained unchanged over time, i.e. from 1996 to 2005 ($P = 0.989$) (Figure 5.16).

Treatment comparison in 1996 and 2005: (A) biome, (B) invasion intensity and (C) clearing

Table 5.4. Soil pH (mean ± 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).

Year	High Altitude (Grassland)				Low Altitude (Savanna)			
	High Invasion		Low Invasion		High Invasion		Low Invasion	
	Cleared	Uncleared	Cleared	Uncleared	Cleared	Uncleared	Cleared	Uncleared
1996	$4.7\pm0.2_a^a$	$4.6\pm0.4_a^a$	$4.7\pm0.2_a^a$	$4.5\pm0.1_a^a$	$5.1\pm0.3_a^a$	$4.9\pm0.2_a^a$	$4.7\pm0.2_a^a$	$4.4\pm0.1_a^a$
2005	$5.0\pm0.3_a^a$	$4.5\pm0.1_a^a$	$4.6\pm0.2_a^a$	$4.4\pm0.1_a^a$	$4.9\pm0.2_a^a$	$4.7\pm0.2_a^a$	$4.7\pm0.2_a^a$	$4.8\pm0.2_a^a$

There was no significant difference in the pH over time in each of the eight experimental categories of the three different experimental treatments (Table 5.4; probability values are given in Appendix 15).

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 $P < 0.05$.

Year	BIOME	INVINT	CLEAR	BIOME* INVIN	BIOME* CLEAR	INVIN* CLEAR	BIOME* INVIN* CLEAR
1996	0.364	0.123	0.342	0.255	0.736	0.797	0.889
2005	0.340	0.258	0.194	0.422	0.323	0.206	0.820

No significant differences were found in the pH between the grassland and savanna plots, the high and low invaded plots, and the cleared and uncleared plots for both 1996 and 2005 (Table 5.5).

Interaction between biomes and times

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 $P < 0.05$.

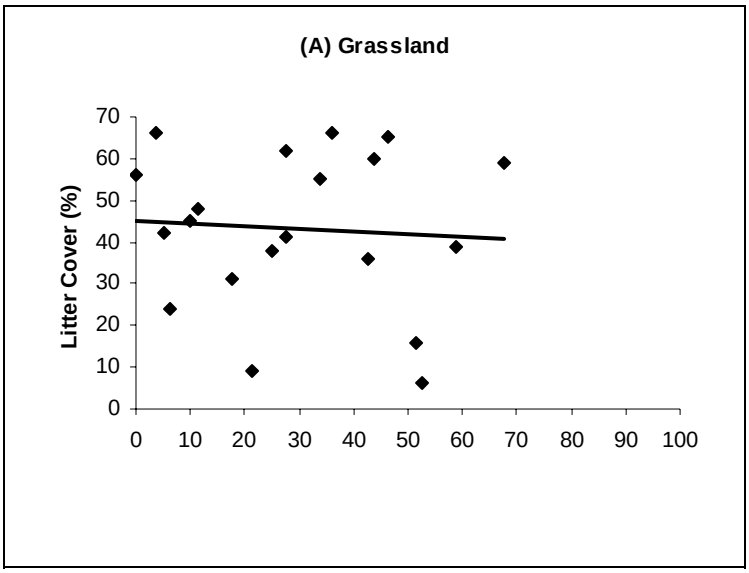
	YEAR	**BIOME**	**YEAR*BIOME**
pH	0.989	0.185	0.963

There was no significant difference in the pH over time (Table 5.6). The pH of the grassland and savanna biomes also did not change significantly over time (Table 5.6).

5.4.4 Linear regression analyses of the percentage aerial cover of woody alien plants (invasion intensity), and litter cover and soil organic matter

Biome comparison: grassland and savanna biomes (in 2005)

(a) Litter cover



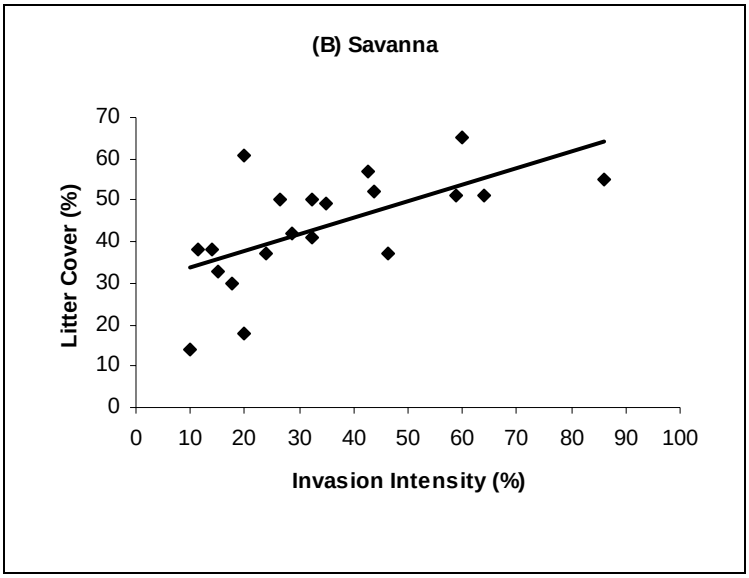
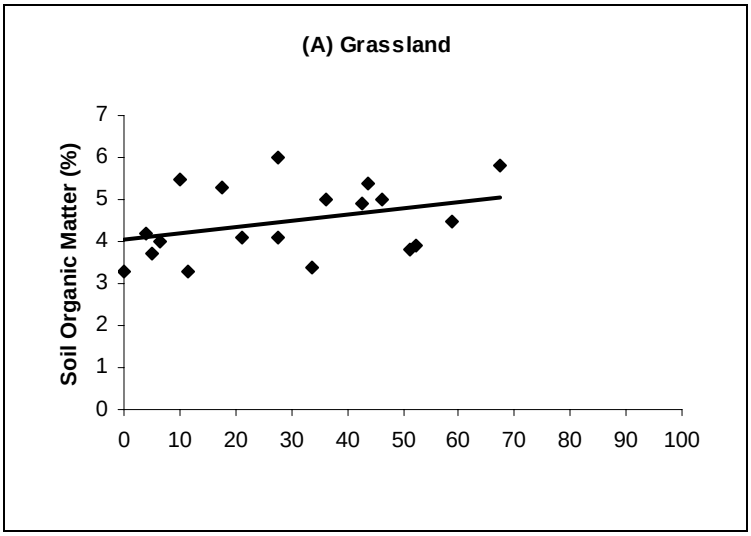


Figure 5.17. The linear relationship between percentage litter cover and invasion intensity (% aerial cover of woody alien plants) for plots in the (A) grassland biome (r^2 = 0.004) and (B) savanna biome (r^2 = 0.38) in 2005. The linear regression relationship for (A) is y = -0.06x + 44.93 and for (B) is y = 0.40x + 29.64. The slopes of these regression lines were not significantly different ($P > 0.05$).

In the grassland, there was a slight decrease in litter cover with increasing invasion intensity (5.17 (A)), whereas in the savanna, there was an increase in litter cover with increasing invasion intensity (Figure 5.17 (B)). The linear relationship between the two biomes indicates that the two data sets were similar.

(b) Soil organic matter



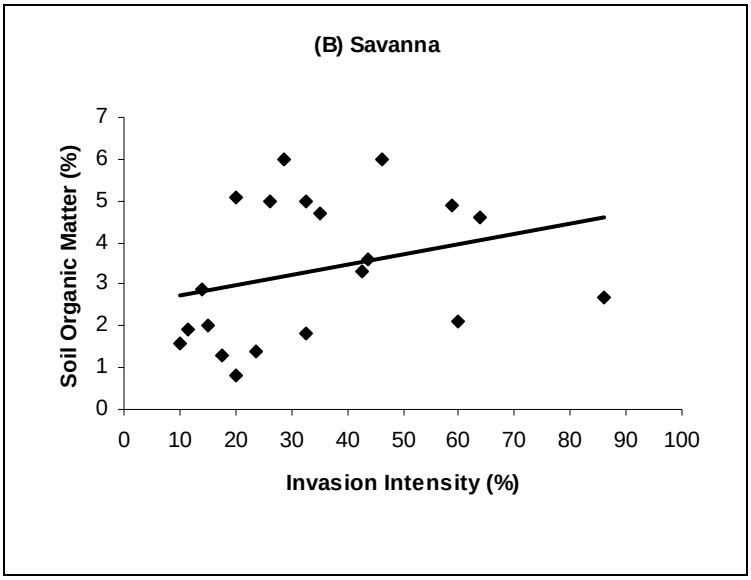
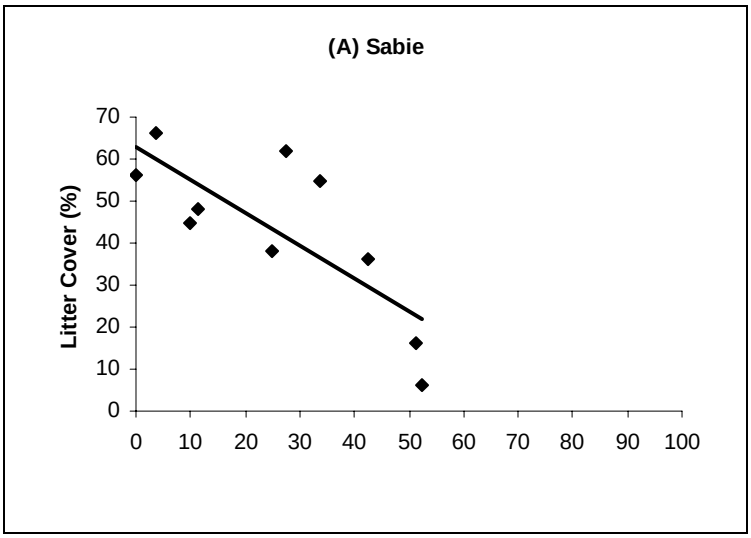


Figure 5.18. The linear relationship between percentage of soil organic matter and invasion intensity (% aerial cover of woody alien plants) for plots in the (A) grassland biome ($r^2 = 0.13$) and (B) savanna biome ($r^2 = 0.09$) in 2005. The linear regression relationship for (A) is $y = 0.02x + 4.04$ and for (B) is $y = 0.02x + 2.50$. The slopes of these regression lines were not significantly different ($P > 0.05$).

In both biomes, there was an increase in SOM with increasing invasion intensity (Figure 5.18). The linear relationship between the two biomes indicates that the two data sets were similar.

Regional comparison: Sabie (grassland), Graskop (grassland) and Hazeyview (savanna) (in 2005)

(a) Litter cover



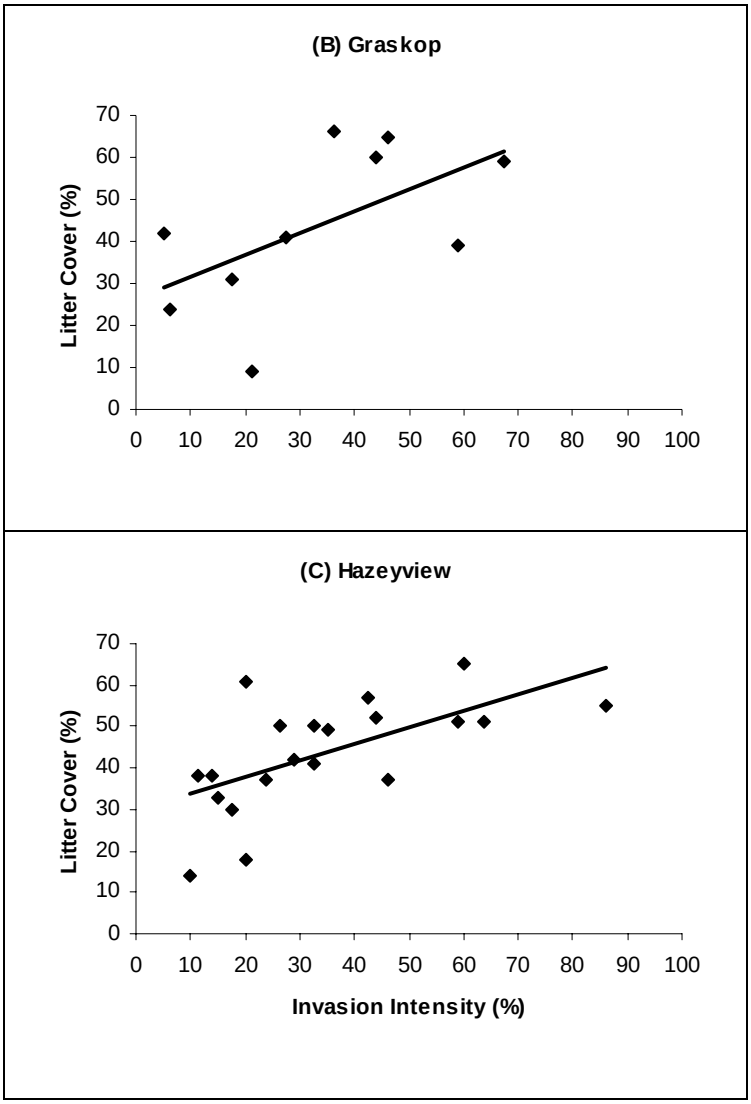


Figure 5.19. The linear relationship between percentage litter cover and invasion intensity (% aerial cover of woody alien plants) for plots in the (A) Sabie ($r^2 = 0.60$), (B) Graskop ($r^2 = 0.34$) and (C) Hazeyview ($r^2 = 0.38$) regions in 2005. The linear regression relationship for (A) is $y = -0.79x + 63.04$, 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 ($P > 0.05$).

In the Sabie region, there was a decrease in litter cover with increasing invasion intensity (Figure 4.19 (A)), whereas in the Graskop and Hazeyview regions there was an increase in litter cover with increasing invasion intensity (Figure 5.19 (B)(C)). The linear relationships between the three regions indicate that the three data sets were similar.

(b) Soil organic matter

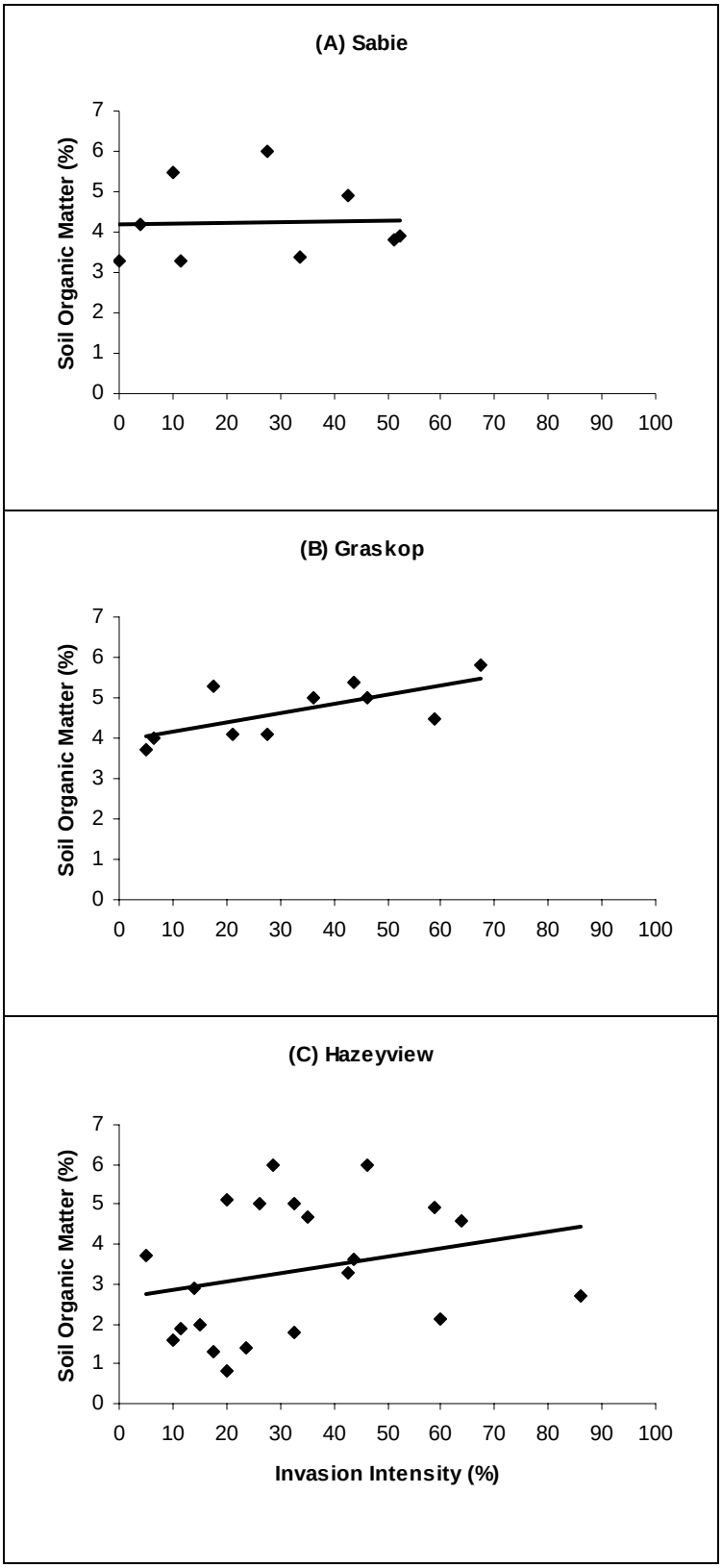


Figure 5.20. The linear relationship between percentage of soil organic matter and invasion intensity (% aerial cover of woody alien plants) for plots in the (A) Sabie (r^2 = 0.001), (B) Graskop (r^2 = 0.47) and (C) Hazeyview (r^2 = 0.07) regions in 2005. The linear regression relationship for (A) is 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 ($P > 0.05$).

In the Sabie region, there was a very slight increase in SOM with increasing invasion intensity (Figure 5.20 (A)). With increasing invasion intensity, there was an increase in SOM in the Graskop and Hazeyview regions (Figure 5.20 (B)(C)). The linear relationships between the three regions indicate that the three data sets were similar.

Year comparison: 1996 and 2005

(a) Litter cover

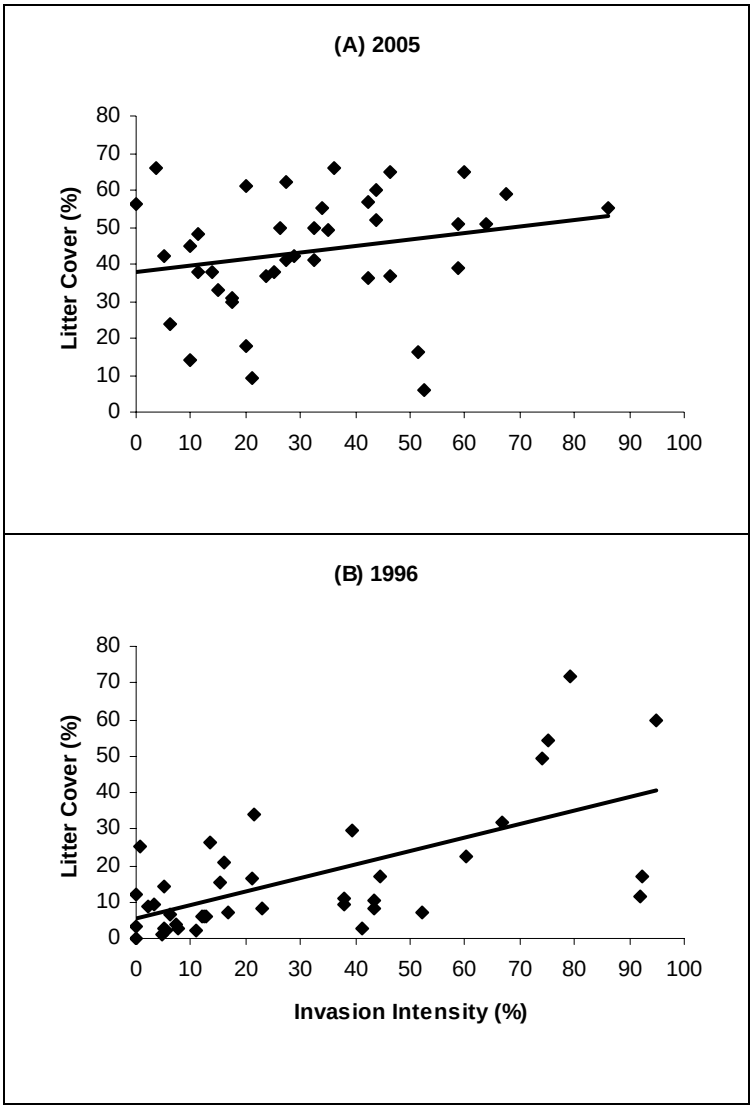


Figure 5.21. The linear relationship between percentage litter cover and invasion intensity (% aerial cover of woody alien plants) for each of the 40 plots in (A) 2005 ($r^2 = 0.05$) and (B) 1996 ($r^2 = 0.41$). The linear regression relationship for (A) is y = 0.17x + 37.78 and for (B) is y = 0.37x + 5.22. The slopes of these regression lines were significantly different ($P < 0.05$).

With increasing invasion intensity, there was an increase in litter cover in both years (Figure 5.21). The linear relationship between the two years indicates that the two data sets were significantly different.

(b) Soil organic matter

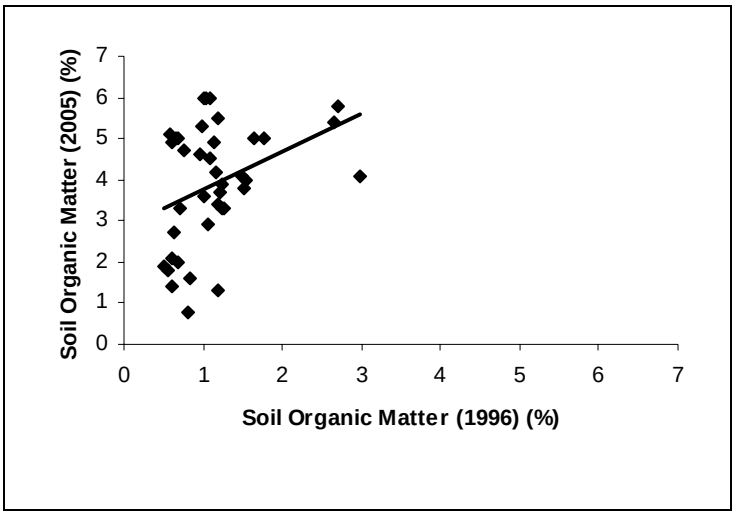


Figure 5.22. The linear relationship between percentage of soil organic matter in each of the 40 plots in 1996 and 2005 ($r^2 = 0.13$). The linear regression relationship is $y = 0.92x + 2.85$.

There was a positive linear relationship between soil organic matter percentage in 1996 and 2005 (Figure 5.22).

5.4.5 Principal component analysis (PCA) of the environmental variables between the grassland and savanna plots, in 2005

A multivariate statistical analysis was done using CANOCO and the linear, indirect gradient analysis (unconstrained) method (PCA). The analysis was done on the environmental variables and the grassland and savanna plots in order to determine if there was any association between these variables and the plots.

Table 5.7. Summary of the principal component analysis (PCA) of the environmental variables, and the grassland and savanna plots.

Axes	1	2	3	4	Total variance
Eigenvalues:	0.904	0.078	0.007	0.005	1.000
Cumulative % variance of species data:	90.4	98.2	98.8	99.3	
Sum of all eigenvalues:					1.000

The eigenvalues (which measure the importance of the ordination axes (Leps and Smilauer, 2003)) indicate that Axis 1 explained a high proportion (90.4%) of the variability of the environmental variables (Table 5.7). This indicates that the data set was governed primarily by the first axis.

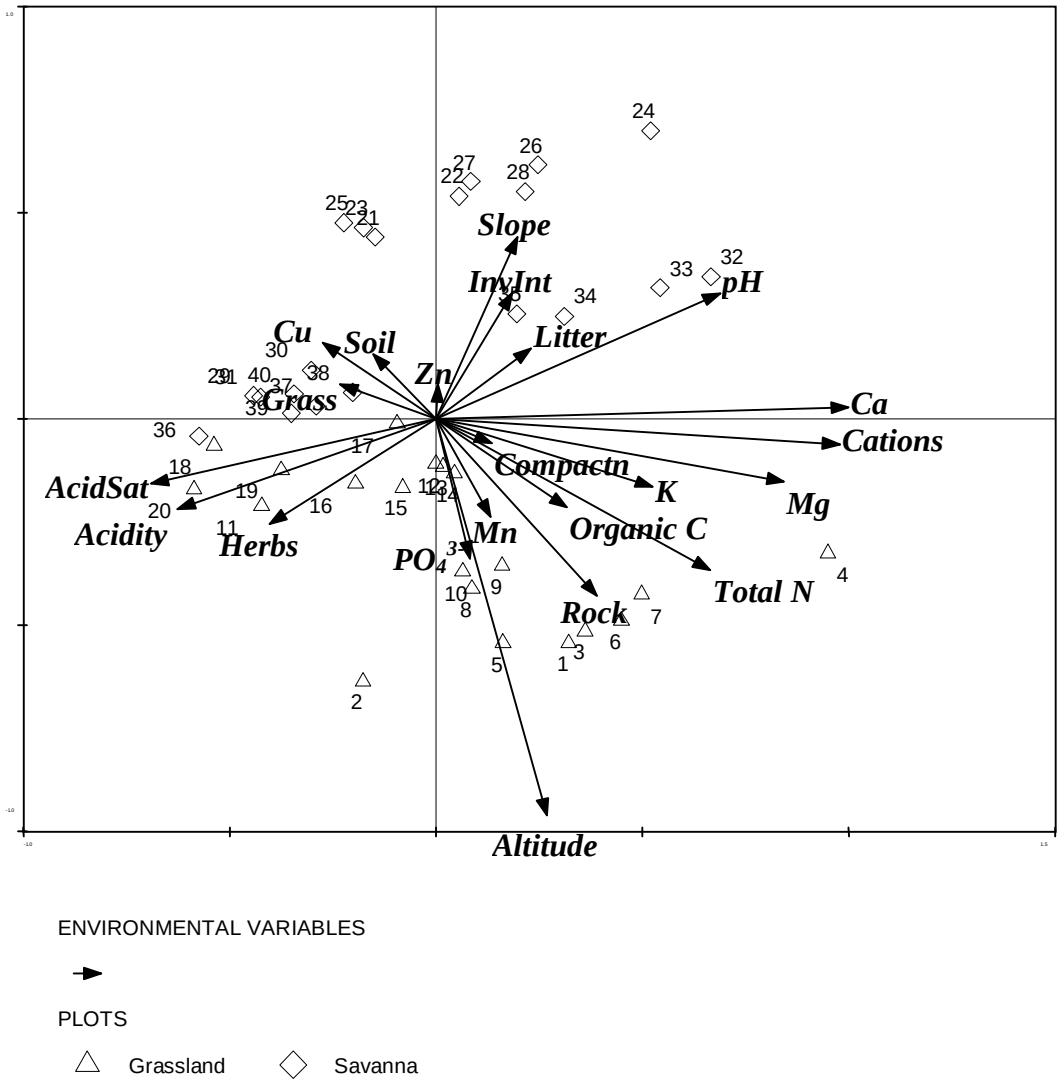


Figure 5.23. Principal component analysis (PCA) of the environmental variables of the 40 plots, in 2005. Plots were categorised into grassland and savanna. Environmental variables include phosphate (PO_4^{3-}), exchangeable potassium (K), calcium (Ca), and magnesium (Mg), total zinc (Zn), manganese (Mn), 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).

There was a separation of the grassland and savanna plots according to altitude, i.e. the grassland plots (1-20) were at higher altitudes than the savanna plots (21-40) (Figure 5.23). Axis 1, which accounts for most of the variation, is a soil pH/fertility gradient, largely based on the soil acidity, with corresponding changes in the cation concentrations. Plots with more acidic soils had a lower concentration of cations, possibly due to more leaching taking place. The grassland plots were slightly more associated with acidic soils (i.e. pH of 4.6 ± 0.1 compared to 4.8 ± 0.1 in the savanna). It was the Graskop plots that contributed most to the overall lower pH in the grassland, as this region had a pH of 4.5 ± 0.1, whereas the Sabie region had a pH of 4.8 ± 0.2.

Herbaceous cover, which is more positively associated with the grassland (20.3 ± 1.7%) rather than the savanna plots (19.5 ± 2.2%), is also correlated with the more acidic soils. Rock cover is also more associated with the grassland (4.3 ± 1.6%) than the savanna plots (0.8 ± 0.2%). On the other hand, grass, exposed soil and litter covers are more associated with the savanna (21.8 ± 1.7%; 14.4 ± 1.6%; 43.5 ± 3.0% respectively) rather than the grassland plots (20.1 ± 2.3%; 12.1 ± 2.5%, 43.2 ± 4.2% respectively). Litter cover is positively correlated with invasion intensity, which is also more associated with the savanna plots (i.e. 34.4 ± 4.6% compared to 29.4 ± 4.5% in the grassland). This is because an increase in alien vegetation cover (i.e. invasion intensity) tends to result in an increase in litter cover due to the alien woody plants generally having a higher vegetative biomass than the indigenous plants. Steeper slopes (which are positively correlated with invasion intensity and litter cover) are more associated with the savanna (12.8 ± 1.7º) than the grassland plots (4.8 ± 1.1º). There was no strong association of soil compaction with any of the plots. This is because soil compaction was generally similar between the biomes (i.e. 0.8 ± 0.1 kg/cm^2 in the grassland and 0.7 ± 0.1 kg/cm^2 in the savanna).

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

Multivariate statistical analyses were done using CANOCO and the unimodal, indirect gradient analysis (unconstrained) method (CA), as well as the unimodal, direct gradient analysis (constrained) method (CCA). Analyses were done on the indigenous and alien species composition, the environmental variables, and the grassland and savanna plots in order to determine if there was any association between the species composition and the environmental variables amongst the plots.

In unconstrained ordinations, any variable that best explains the species composition is searched for (and this variable is taken as the ordination axis), and in constrained ordinations, the ordination axes are weighted sums of environmental gvariables (Leps and Smilauer, 2003). The CA and CCA are complementary; therefore both methods were used and compared with each other. The CA was calculated first to ensure that the main part of the variability in species composition was not missed (Leps and Smilauer, 2003). The CCA was then calculated to ensure that the part of the variability that was related to the measured environmental variables was not missed (Leps and Smilauer, 2003). Therefore, in CCA, the main part of the biological variability explained by the environmental variables is not missed out, whereas the main part of the variability that is not related to the measured environmental variables could be missed out (Leps and Smilauer, 2003).

During the CCA, a simpler model was built by performing Monte Carlo permutation tests. These tests determined which of the environmental variables were the most important ones, i.e. which environmental variables sufficiently explained the species composition patterns. The CCA was then performed again, using only the significant environmental variables. It is important to note that the CCA ordination diagrams with the environmental variables were based purely on their effects on the species composition; therefore they were not exactly the same as the PCA ordination diagrams of only the environmental variables (Leps and Smilauer, 2003).

Table 5.8. Summary of the correspondence analysis (CA) of the indigenous and alien plant species, and the grassland and savanna plots.

Axes	1	2	3	4	Total inertia
Eigenvalues:	0.715	0.594	0.526	0.481	8.842
Cumulative % variance of species data:	8.1	14.8	20.8	26.2	
Sum of all eigenvalues:					8.842

The eigenvalues indicate that Axis 1 explained a relatively high proportion (71.5%) of the variability of the species distribution (Table 5.8). This indicates that the data set was governed primarily by the first axis.

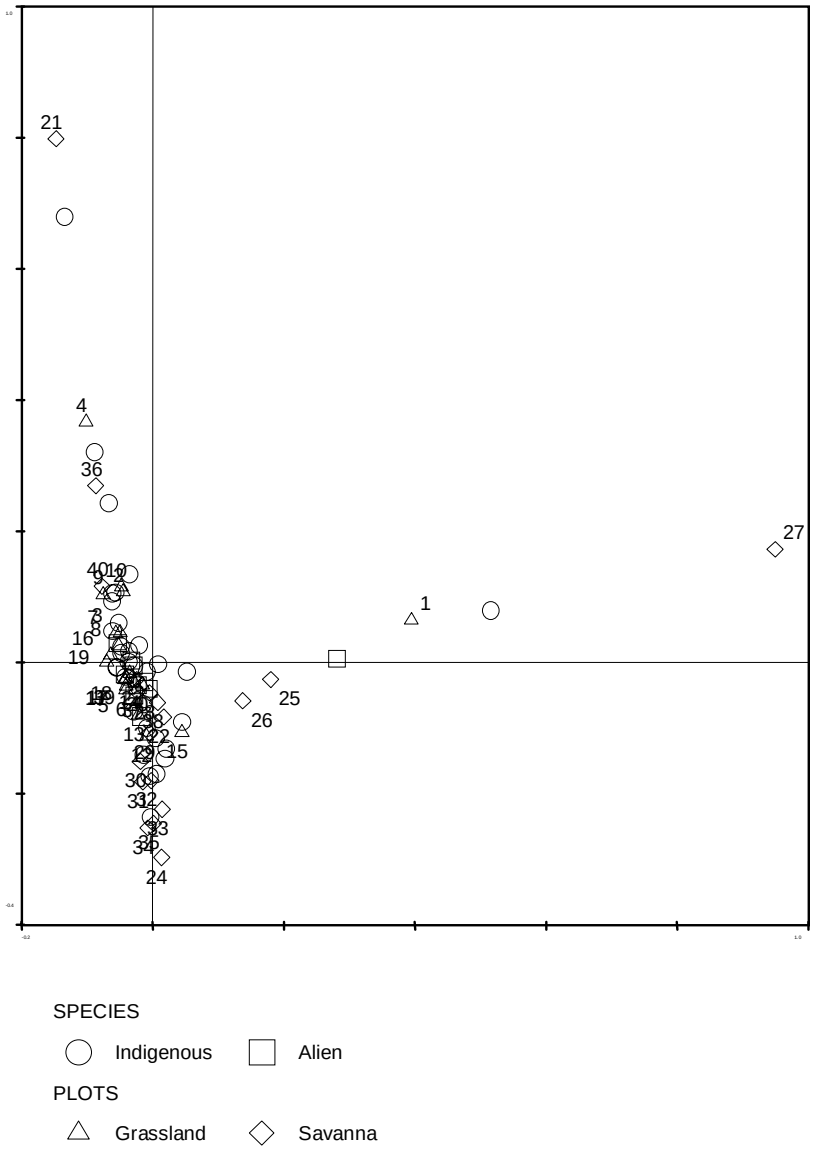


Figure 5.24. Correspondence analysis (CA) of the plant species of the 40 plots, in 2005. Plots were categorised into grassland and savanna, and species into indigenous and alien. Only those species with a weight range of 10-100% were included, i.e. the less abundant species were not included. For clarity, the species labels were not included.

From the distribution pattern of the species in Figure 5.24, it can be seen that there is an 'arch effect'. This is a result of the positions of the samples on the second (vertical) axis being strongly (but not linearly) dependent on their positions on the first (horizontal) axis (Leps and Smilauer, 2003). Two of the plots (21 and 27) are outliers; therefore the abundances of the species, as well as the types of species, are very different in these plots (in comparison with the other plots).

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 $P < 0.05$.

Marginal Effects			**Conditional Effects**				
Variable	**Var.N**	**Lambda 1**	**Variable**	**Var.N**	**Lambda A**	***P***	***F***
Slope steepness	16	0.47	**Slope steepness**	16	0.47	**0.002**	2.14
Altitude	15	0.44	**Altitude**	15	0.39	**0.002**	1.82
Rock cover	19	0.40	**Organic C**	9	0.33	**0.002**	1.55
Soil pH	14	0.35	**Exposed soil cover**	18	0.33	**0.022**	1.58
Compaction	17	0.34	**Soil pH**	14	0.33	**0.030**	1.56
Mn	7	0.34	Mn	7	0.32	0.056	1.59
Organic C	9	0.33	Compaction	17	0.25	0.068	1.28
Total N	10	0.33	Litter cover	20	0.26	0.094	1.28
Cations	12	0.33	Grass cover	22	0.26	0.080	1.33
Mg	5	0.33	Total N	10	0.23	0.166	1.19
Litter cover	20	0.32	Invasion intensity	23	0.23	0.236	1.14
Ca	4	0.32	Herbaceous cover	21	0.22	0.260	1.14
Invasion intensity	23	0.31	Rock cover	19	0.24	0.124	1.29
Exposed soil cover	18	0.30	Mg	5	0.20	0.420	1.01
Grass cover	22	0.29	K	3	0.19	0.504	1.00
Herbaceous cover	21	0.29	Cations	12	0.18	0.536	0.96
PO_4^{3-}	2	0.28	PO_4^{3-}	2	0.18	0.556	0.92
Cu	8	0.27	Acid saturation	13	0.18	0.568	0.91
Acid saturation	13	0.26	Ca	4	0.21	0.362	1.10
K	3	0.24	Acidity	11	0.24	0.214	1.28
Acidity	11	0.24	Cu	8	0.15	0.776	0.76
Zn	6	0.17	Zn	6	0.14	0.762	0.71

Monte Carlo permutation tests were performed in order to build a simpler model (with fewer explanatory variables), but one that still sufficiently explained the species composition patterns (Leps and Smilauer, 2003). The marginal effects (i.e. the independent effect of each environmental variable (Leps and Smilauer, 2003))

indicates that the slope steepness of the plot was the most important factor for species composition, followed by the altitude, rock cover and soil pH (Table 5.9). The conditional effects (i.e. the effect that each variable brings in addition to all the variables already selected (Leps and Smilauer, 2003)) indicates that the slope steepness, altitude, organic C, exposed soil cover and soil pH were the only variables that qualified for the final model when the 0.05 probability threshold for entry of a variable was adopted (Table 5.9). This final selection of environmental variables shows that this was a sufficient set of predictors, and that further addition of variables did not significantly improve the fit (Leps and Smilauer, 2003). Because certain environmental variables were closely correlated, for example the organic C and total N, the conditional effect of total N decreased dramatically after the organic C variable was selected, as only one of these variables was needed in the final model. Therefore, even though some environmental variables (that had close correlations with the included variables) were not included in the final model, the effect of these variables was not negligible.

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.

Axes	1	2	3	4	Total inertia
Eigenvalues:	0.511	0.403	0.364	0.288	8.842
Species – environment correlations:	0.949	0.951	0.901	0.891	
Cumulative % variance –					
of species data:	5.8	10.3	14.5	17.7	
of species – environment relation:	27.7	49.5	69.2	84.9	
Sum of all eigenvalues					8.842
Sum of all canonical eigenvalues					1.845

The eigenvalues indicate that the first axis explained about 51% of the variability in the data, and the second axis explained about 40% (Table 5.10). There was a close correlation between the environmental variables and the species composition (Table 5.10).

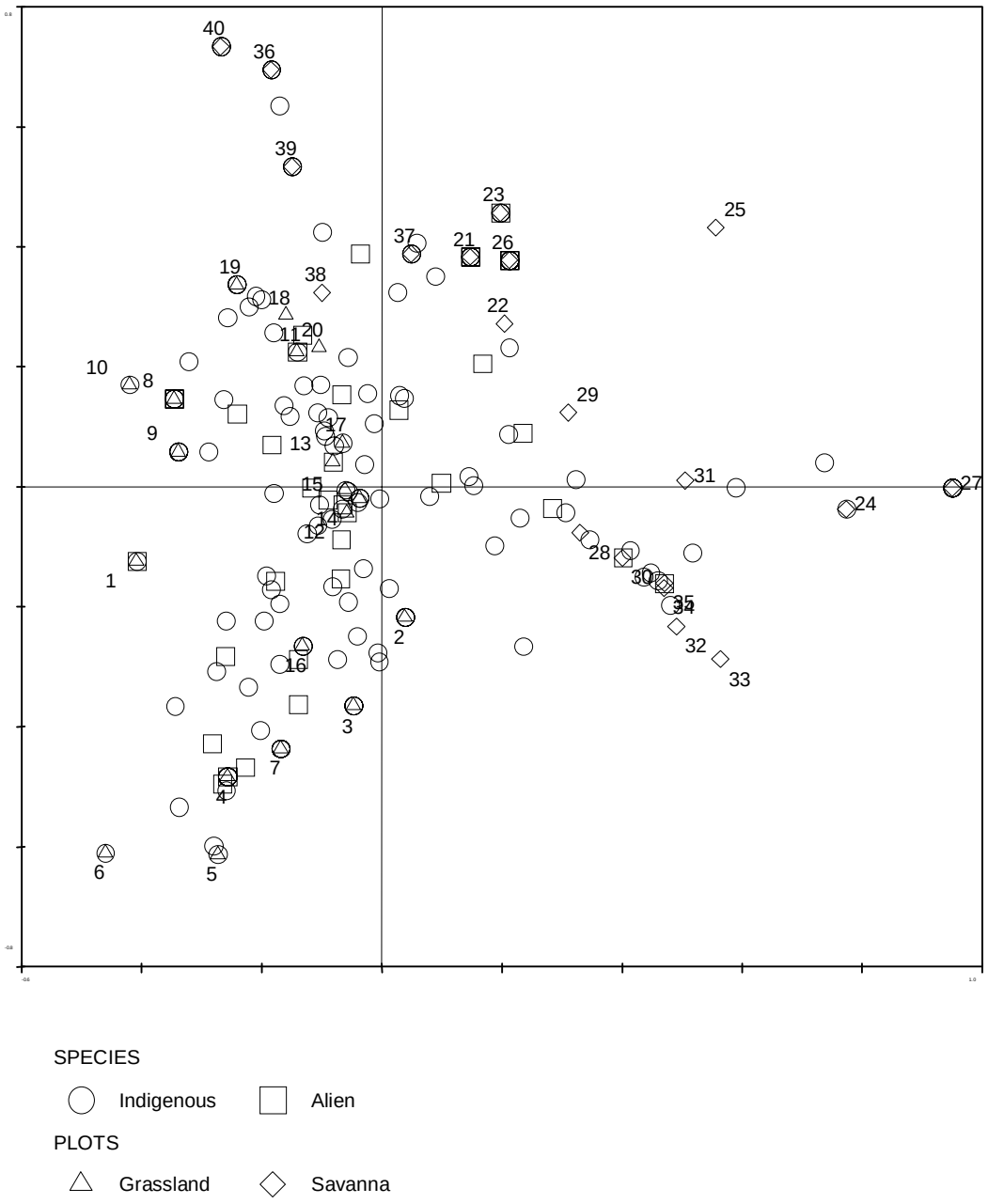


Figure 5.25. Canonical correspondence analysis (CCA) of the plant species and environmental variables, within the 40 plots (in 2005). Environmental variables are not shown in this ordination diagram, only the species (all of them), which were categorised into alien and indigenous. For clarity, species labels were not included.

The distribution of the species in the CCA ordination diagram (Figure 5.25) is different to that in the CA ordination diagram (Figure 5.24). Hence, the environmental variables that were measured do not sufficiently explain the species composition patterns, and therefore other additional environmental variables should have been included. It is not obvious what these additional variables should be, and the tremendous disturbance that the sites have experienced due to the 2000 flood and the WfW clearing may have resulted in transient vegetation dynamics which results in a poor correlation with the measured environmental variables.

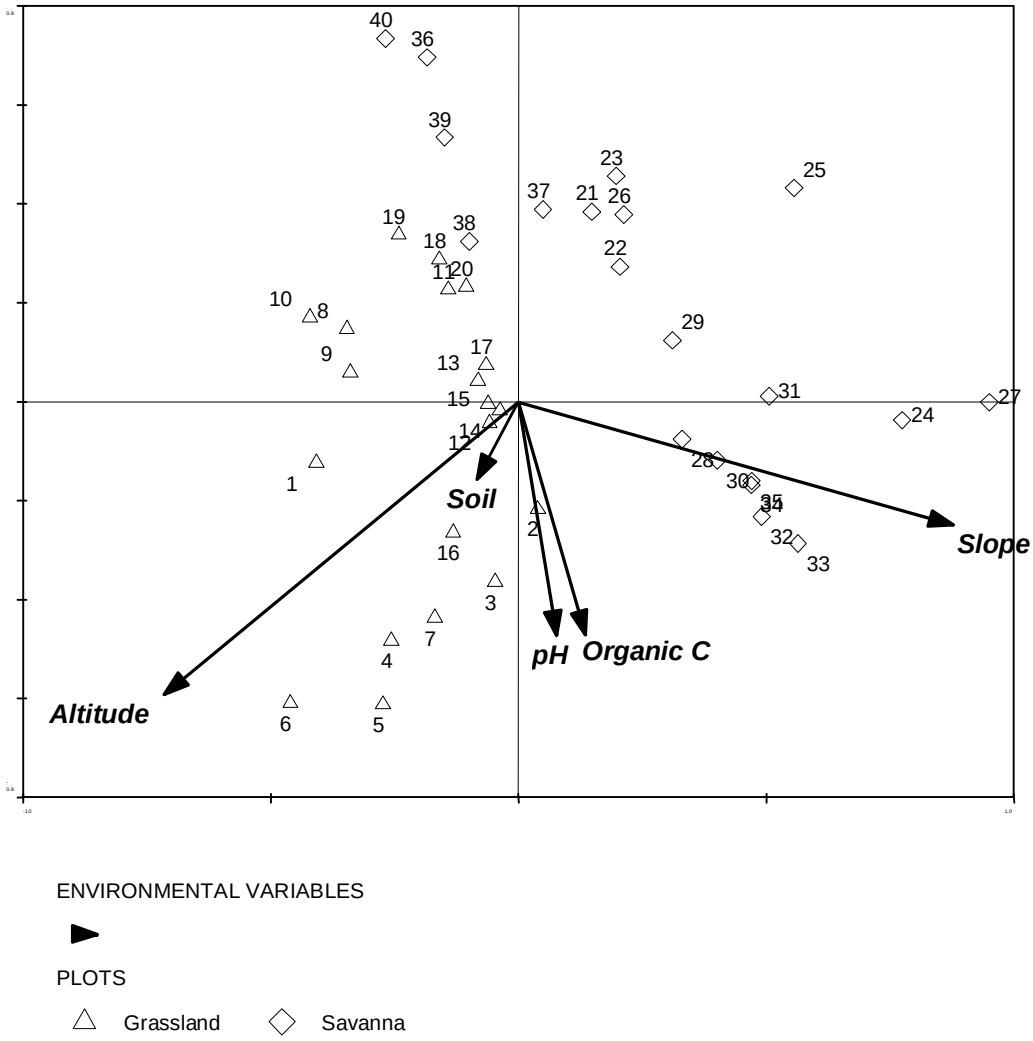


Figure 5.26. Canonical correspondence analysis (CCA) of the plant species and environmental variables, within the 40 plots (in 2005). Only environmental variables and plots (which were categorised into grassland and savanna) are shown in this ordination diagram. Only those environmental variables that 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.

There was a clear separation of the grassland and savanna plots, with the grassland plots (1-20) occurring at higher altitudes than the savanna plots (21-40) (Figure 5.26). There was a further separation of the grassland plots according to altitude, with the Sabie plots (1-10) occurring at higher altitudes than the Graskop plots (11-20). The savanna plots were more associated with steeper slopes (12.8 ± 1.7º) compared to the grassland (4.8 ± 1.1º). The Sabie (grassland) and Hazeyview (savanna) plots had the highest soil pH (4.8 ± 0.2 in Sabie and 4.8 ± 0.1 in Hazeyview), whereas the Graskop plots had the lowest soil pH (4.5 ± 0.1). Soil pH and organic carbon (=fertility) are positively highly correlated. The grassland plots were more associated with higher fertility (organic C content of 4.5 ± 0.2%), whereas the savanna plots were more associated with lower fertility (3.3 ± 0.4%).

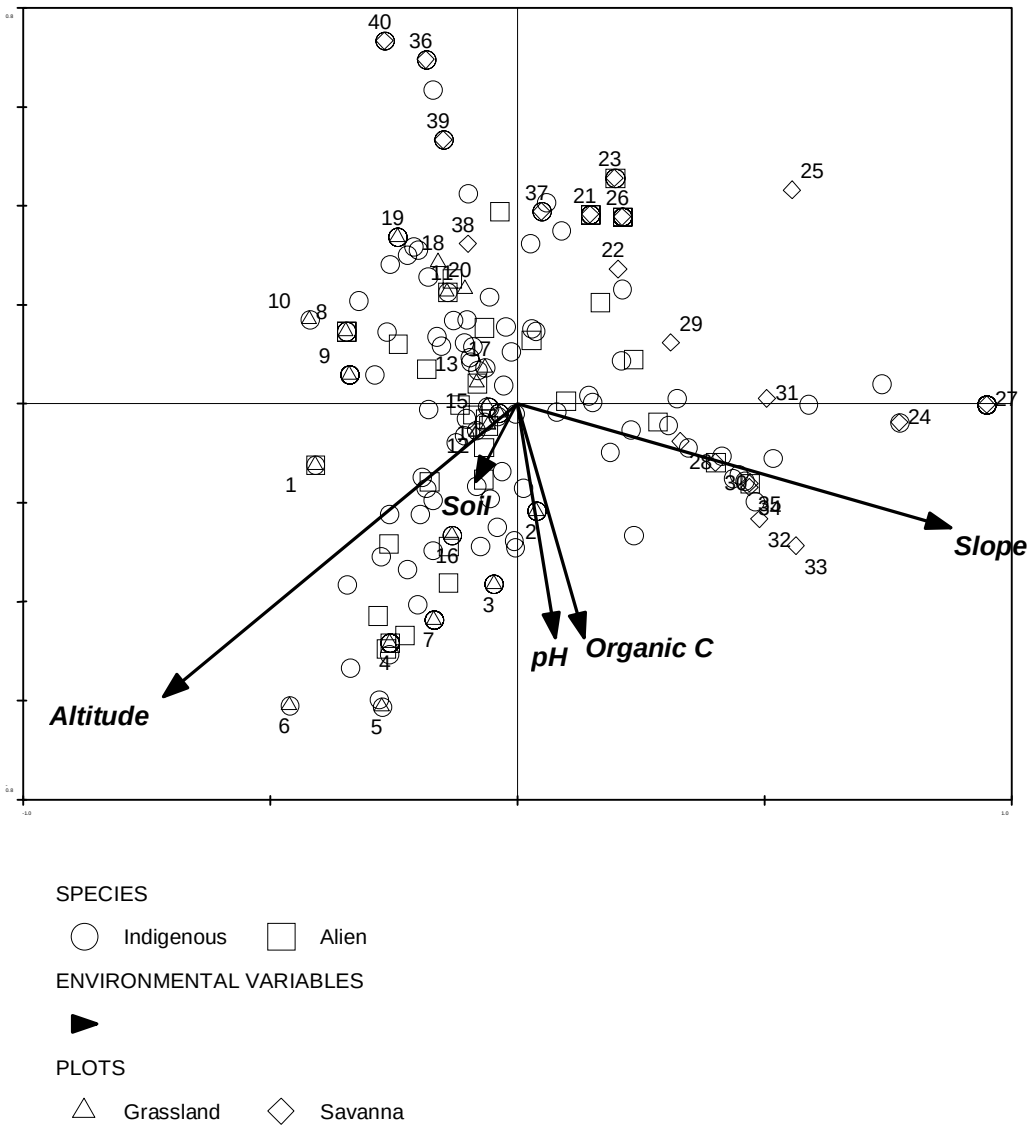
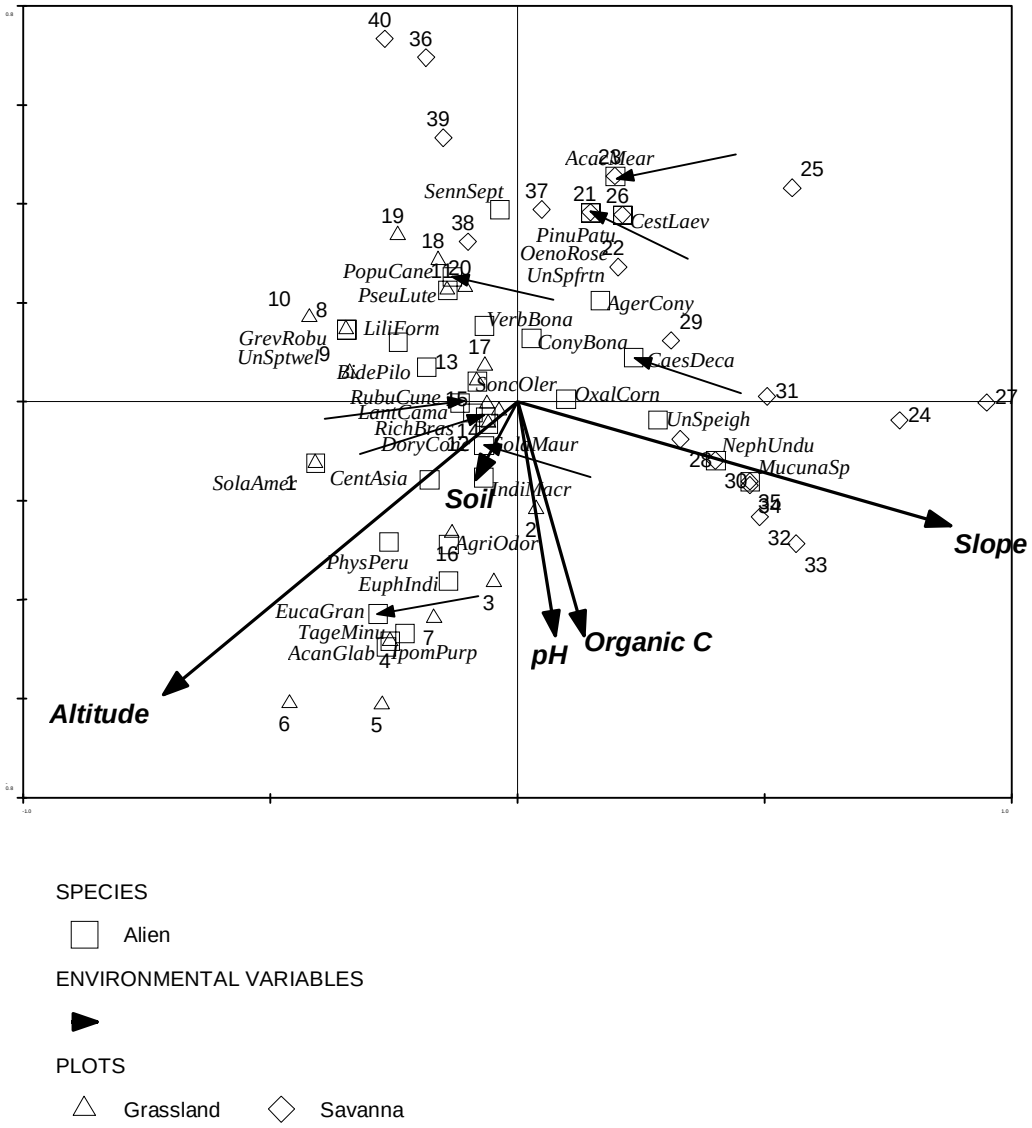


Figure 5.27. Canonical correspondence analysis (CCA) of the plant species and environmental variables, within the 40 plots (in 2005). Only those environmental variables that significantly explained the species composition patterns were included in the CCA, namely slope steepness (Slope), altitude, organic 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.

There is continuous variation in the species composition of the whole data set, and there is therefore no distinction between the indigenous and alien species (Figure 5.27). This suggests that the grassland and savanna biomes were generally very similar in terms of indigenous and alien species composition. In order to see the distribution of the category 1 and 2 weed species, only the alien species were included in the ordination diagram shown in Figure 5.28.



SPECIES

Alien

ENVIRONMENTAL VARIABLES

PLOTS

Grassland Savanna

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).

The declared weeds and invaders shown in Figure 5.28 consisted of the category 1 species *Lantana camara*, *Rubus cuneifolius* and *Solanum mauritianum*, and the category 2 species *Caesalpinia decapetala*, *Populus x canescens*, *Acacia mearnsii*, *Eucalyptus grandis* and *Pinus patula*. The category 1 species all occurred in the middle of the ordination diagram, which suggests that these species were not strongly influenced by any of the environmental variables; thus they occurred in most of the plots (percentage occurrence in the 40 plots of *R. cuneifolius* was 70%; of *S. mauritianum* was 58%; and of *L. camara* was 50%). The category 2 species,

Eucalyptus grandis and *Caesalpinia decapetala*, were found in both biomes; however they tended to have higher occurrences in the savanna (percentage occurrence, in the savanna, of *E. grandis* and *C. decapetala* was 35% and 20% respectively (compared to 20% and 15% in the grassland)). *Acacia mearnsii* and *Pinus patula* occurred only in the savanna (percentage occurrence of 5% for both species). *Populus x canescens* occurred only in the grassland, with an occurrence of 10%.

5.5 Discussion

5.5.1 The effects of alien plant invasion and subsequent clearing on the ground cover in the grassland and savanna biomes in 2005

Litter cover

An increase in alien vegetation cover resulted in an increase in litter cover. This may be because alien woody plants have a higher vegetative biomass than indigenous plants (which was found in the 1996 study (Garner, 2005)). Furthermore, if the deposition of litter is greater than the rate of decomposition, this could lead to an accumulation of litter on the soil surface (Stout *et al.*, 1979). Litter cover prevents evaporation from the soil and increases soil moisture content, and hence may be better for seed germination and establishment. In this 2005 study, litter cover dominated the ground cover of the plots (43.3 ± 2.5%). The soils of the savanna tended to have higher litter cover (but not significantly higher) (43.5 ± 3.0%) than the grassland (43.2 ± 4.2%) ($P = 0.96$). The reason for this reach of the river having slightly more litter is related to the invasion intensity being slightly higher in the savanna (i.e. 34.4 ± 4.6% versus 29.4 ± 4.5% in the grassland; $P = 0.44$). This was further illustrated by the univariate and multivariate analyses, which showed that invasion intensity and litter cover were positively correlated.

In the Hazeyview (savanna) and Graskop (grassland) regions, there was an increase in litter cover with increasing invasion intensity. An increase in alien vegetation cover can result in an increase in litter cover due to alien woody plants generally having a higher vegetative biomass than indigenous plants (which was found in the 1996 study (Garner, 2005)). Therefore, the higher the invasion intensity (i.e. aerial cover of woody alien plants), the higher the litter cover. Both the Hazeyview and Graskop regions had higher invasion intensities (34.4 ± 4.6% and 33.02 ± 6.7% respectively) than the Sabie region (25.8 ± 6.1%), which had litter cover that decreased with increasing invasion intensity.

Vegetation cover

In 2005, grass and herbaceous covers in the plots were 20.9 ± 1.4% and 20.0 ± 1.4% respectively. With increasing invasion intensity, the cover of smaller growth forms decreases. This is probably a result of the taller growing alien woody plants shading out the herbaceous vegetation. In the savanna, there was a slightly lower (but not significantly) herbaceous cover (19.5 ± 2.2%) than the grassland (20.3 ± 1.7%) ($P = 0.76$), which could be attributed to the invasion intensity tending to be higher in the savanna. Grass cover tended to be slightly higher (but not significantly) in the savanna (21.8 ± 1.7%) than in the grassland (20.1 ± 2.3%) ($P = 0.56$). The canonical

correspondence analysis (CCA) showed that herbaceous cover, which was more associated with the grassland plots, was correlated with more acidic soils.

Exposed soil

When there is no vegetation cover, the soil is open to erosion and compaction (Van Outshoorn, 1992). The input of organic matter in bare soils is lowered which ultimately results in nutrient deficiencies (Theng, 1980). Also, with no vegetation cover, there is nowhere for seeds to deposit, thus the burial and persistence of seeds in a soil seed bank is affected (Garner and Witkowski, 1997). In this study, the percentage of exposed soil was relatively low (13.3 ± 1.5%). It was found that the savanna had a greater (but not significantly) cover of exposed soil (14.4 ± 1.6%) than the grassland (12.1 ± 2.5%) (P = 0.43), with the Sabie (grassland) region having a greater cover (12.6 ± 4.3%) than the Graskop (grassland) region (11.6 ± 2.8%).

The higher exposed soil cover in the savanna is also related to litter cover being higher in this biome. Litter cover is not as stable as grass or herbaceous cover, and surface water runoff in high rainfall areas washes away litter. The results therefore imply that modifications by invasions (i.e. a reduction in grass and herbaceous covers, which are then replaced by increased litter and exposed soil), can lead to an increased risk of soil erosion. According to Cowling *et al.* (1976), local soil erosion increases in areas densely invaded by alien trees, as the ground cover that provides surface stability (grass and herbaceous vegetation) is excluded by the alien canopy. The canonical correspondence analysis (CCA) showed that exposed soil cover was one of the most important variables associated with species composition.

Rock cover and slope steepness

When a large cover of rocks is found, many aspects of the environment are adversely affected. Rock cover can increase the surface runoff of water thereby altering the hydrodynamics of the community. The presence of rocks can also prevent plants from establishing and alters the vegetation composition of the community. Steeper slopes generally tend to have a higher cover of rock, due to increased soil erosion. In this 2005 study, the overall rock cover was relatively low (2.5 ± 0.8%). However, it was found that the grassland soils had a significantly higher rock cover (4.3 ± 1.6%) than the savanna soils (0.8 ± 0.2%) (P = 0.04). This difference was probably a result of the Sabie (grassland) region having a significantly higher rock cover (7.6 ± 2.8%) than both the Graskop (grassland) (0.9 ± 0.3%) and Hazeyview (savanna) (0.8 ± 0.2%) regions. It would therefore have been expected that the slopes of the Sabie plots were steeper than those of Graskop and Hazeyview (because steeper slopes tend to have higher rock cover). However, the plots of the Hazeyview region were significantly steeper (12.8 ± 1.7º) than those of the Sabie (6.2 ± 2.1º) and Graskop (3.4 ± 0.6º) regions. The canonical correspondence analysis (CCA) showed that steeper slopes were correlated with invasion intensity and litter cover – the savanna plots, which were steeper, indeed had a higher invasion intensity (34.4 ± 4.6%) and litter cover (43.5 ± 3.0%) than the grassland (29.4 ± 4.5% and 43.2 ± 4.2% respectively). The CCA also showed that the steepness of the slope was one of the most important variables associated with species composition.

It is concluded that 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, is 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.

5.5.2 The effects of alien plant invasion and subsequent clearing on the soil environment in the grassland and savanna biomes in 2005

The availability of essential nutrients, such as nitrogen, carbon and phosphorus, controls many aspects of local ecosystem function (Peverill *et al.*, 1999), and invasion and subsequent clearing of alien species affects the concentration of nutrients in the soil. Nutrient availability and productivity have been recognized as important determinants of plant community organization and structure (Fynn and O'Connor, 2005). Nitrogen availability affects the outcome of species competition and consequently controls the development, persistence and decline of plant communities in many areas (Schaffers, 2000). Plant growth may depend almost entirely on the release of phosphorus from dead organic matter. Highly disturbed areas are often highly acidic and may be low in nutrients. Soil organic matter is essential to the functioning of terrestrial ecosystems and is the most important indicator of sustainability in a system. This is because it functions as a source of inorganic nutrients to plants, as a substrate for micro-organisms, as an ion exchange material because of its negative charge, as a factor in soil aggregation and root development, and as a factor in soil and water conservation.

The biomes did not differ significantly in soil pH (grassland pH: 4.6 ± 0.1; savanna pH: 4.8 ± 0.1; $P = 0.34$). However, the canonical correspondence analysis (CCA) showed that soil pH was one of the variables that was most associated with species composition. The shallower grassland soils were generally more fertile than the deeper savanna soils, i.e. higher organic matter (4.5 ± 0.2% versus 3.3 ± 0.4%; $P = 0.01$) and total nitrogen content (0.3 ± 0.02% versus 0.2 ± 0.02%; $P = 0.03$), with the Graskop (grassland) soils having the highest organic matter content and the Sabie (grassland) soils having the highest total nitrogen content. From the CCA, the organic carbon content was found to be an important variable associated with species composition.

The concentrations of most of the nutrients were also higher in the grassland. The grasslands had higher concentrations of exchangeable calcium, magnesium and potassium, total manganese and phosphate (832.4 ± 95.6 mg/l; 159.1 ± 17.1 mg/l; 92.0 ± 6.8 mg/l; 22.8 ± 6.7 mg/l; 13.4 ± 1.4 mg/l respectively) than the savanna (777.7 ± 95.0 mg/l; 131.3 ± 12.0 mg/l; 81.5 ± 9.0 mg/l; 15.9 ± 1.4 mg/l; 9.4 ± 1.4 mg/l respectively), with the Sabie (grassland) region having the highest concentrations, and the Graskop (grassland) region having the lowest concentrations. Therefore, the highest (often significantly) concentrations of these elements in the soils of the Sabie region, accounted for the grasslands having higher concentrations of these elements than the savanna. On the other hand, the savanna had higher concentrations of total copper and zinc (12.0 ± 2.7 mg/l and 4.7 ± 1.1 mg/l respectively) than the grassland (4.5 ± 0.4 mg/l and 2.9 ± 0.5 mg/l respectively). However, there were no statistical

differences in the concentrations of the elements between the biomes, except for total copper, which was significantly higher in the savanna ($P = 0.01$), with the phosphate being almost significantly higher in the grassland ($P = 0.06$). The CCA showed that there was a pH/fertility gradient present, which was largely based on soil acidity, with corresponding changes in the cation concentrations. Plots with more acidic soils tended to have lower concentrations of cations – this was reflected in the Graskop (grassland) soils having the lowest pH (4.5 ± 0.1) and concentrations of nutrients, and the Sabie (grassland) soils having the highest pH (4.8 ± 0.2) and concentrations of nutrients. This may have been due to more leaching taking place in the presumably wetter Graskop soils (even though both these regions occurred in the grassland biome, they were separated geographically to a large degree, with the Sabie plots occurring at higher altitudes than the Graskop plots).

Because the savanna tended to have a higher invasion intensity of large and small alien trees than the grassland, litter cover was higher in the savanna. With high litter cover, a large proportion of available nutrients in the ecosystem is "caught" here and can only be made available by the decomposition of leaf litter (Alhamd *et al.*, 2004). The rate of litter decomposition has been found to be associated with carbon and nitrogen contents (Alhamd *et al.*, 2004). Rate limiting factors for decomposition include anaerobic conditions (Theng, 1980), unfavourable pH (Theng, 1980), high salt concentrations (Theng, 1980), excessive moisture (Denslow, 1987), temperature (Jenny and Raychaudhuri, 1960), bacterial population (Young, 1976) and nutrient status (Theng, 1980). Some of the savanna plots illustrated the rate-limiting factor of low nutrient status. Another reason why the grassland soils may have been more fertile is due to slower rates of soil organic matter decomposition in the slightly cooler (higher altitude) grassland regions, thus resulting in higher concentrations of nutrients in the soil. According to Scholes and Walker (1993), the organic matter content of savanna soils is generally low due to the high temperatures, which leads to a high rate of organic matter decomposition. On the other hand, organic matter tends to accumulate in the topsoil of grasslands (Scholes and Walker, 1993).

The soils of the grassland sites tended to be more compacted (0.8 ± 0.1 kg/cm^2) (but not significantly) than those of the savanna sites (0.7 ± 0.1 kg/cm^2) ($P = 0.43$), and the savanna plots were on significantly steeper ground (12.8 ± 1.7^{o}) than those of the grassland (4.8 ± 1.1^{o}) ($P < 0.001$), which may have also contributed to lower fertility through greater leaching and erosion losses. When the soil compaction of the three regions was compared, the soils of the Sabie (grassland) region tended to be significantly more compacted (1.1 ± 0.1 kg/cm^2) than those of the Graskop (grassland) (0.5 ± 0.1 kg/cm^2) and Hazeyview (savanna) (0.7 ± 0.1 kg/cm^2) regions. However, the canonical correspondence analysis (CCA) showed that there was no strong association of soil compaction with any of the plots, which was due to soil compaction being similar between the biomes.

In both biomes (and all three regions), soil organic matter content increased with increasing invasion intensity. This may be a simple consequence of the already established relationship in this study between invasion intensity and litter cover, and as the litter is broken down into smaller fragments, it becomes incorporated into soil organic matter. Thus, higher invasion intensity corresponds with higher litter deposition (as the leaf biomass is higher), resulting in more soil organic matter.

The grassland plots occur at higher altitudes than the savanna plots, with the Sabie (grassland) plots occurring at higher altitudes than the Graskop (grassland) plots. The CCA showed that altitude was one of the most important variables correlated with the species composition.

5.5.3 The influence of the biomes and environmental variables on the indigenous and alien plant species composition in 2005

From the canonical correspondence analysis (CCA), there appears to be no distinct communities of species separating out between the biomes and regions. Even though the high altitude plots occur in the grassland biome and the low altitude plots occur in the savanna biome, the Sabie River riparian environment essentially supports a riverine forest/woodland. Therefore, the species composition of the riparian environment is fairly uniform throughout the study area.

The category 1 species, *Lantana camara*, *Rubus cuneifolius* and *Solanum mauritianum*, were not strongly influenced by any of the environmental variables; thus they occurred in most of the plots (percentage occurrence in the 40 plots of *R. cuneifolius* was 70%; of *S. mauritianum* was 58%; and of *L. camara* was 50%). Thus, these species are predicted to invade both the grassland and savanna reaches of the Sabie River to similar extents. All of these species have strong regenerative capabilities, and once in an area, they spread rapidly. Thus, the WfW clearing treatments should focus on these species that have the potential to dominate the community.

The category 2 species, *Eucalyptus grandis* and *Caesalpinia decapetala*, were found in both biomes; however they tended to have higher occurrences in the savanna (percentage occurrence of *E. grandis* and *C. decapetala* in the savanna, was 35% and 20% respectively (compared to 20% and 15% respectively in the grassland)). Thus, the invasiveness of these species is predicted to be higher in the savanna. Other category 2 species, i.e. *Acacia mearnsii* and *Pinus patula*, only occurred in the savanna (percentage occurrence of 5% for both species). *Populus x canescens* (category 2) only occurred in the grassland, with an occurrence of 10%. WfW can use these predictions and occurrences of invasiveness of the different species to help them prioritise where the clearing efforts should be focused.

5.5.4 The effects of alien plant invasion and subsequent clearing on the environment over time, i.e. from 1996 to 2005

Soil pH remained unchanged over time (soils in 1996 and 2005 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. 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 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 clearing operations also removed a significant proportion of the vegetation, and disturbed much that remained, thus modifying the environment. However, the flood and clearing operations did not have a significant effect on rock cover, as this did not change significantly over time. The clearings may have also increased litter cover due to the fact that clearing deposits a large amount of dead vegetation matter (litter). However, this was not found in 1996, where litter cover tended to be higher in uncleared plots (Garner, 2005). The increase in litter cover over time may therefore have been due to the slightly higher invasion intensity in 2005 (invasion intensity and litter cover were found to be correlated). It is concluded that the hypothesis that the lower the degree of alien plant invasion, the higher the understorey vegetation cover, in both 1996 and 2005, is not rejected, as the plots in 1996 tended to have a lower degree of alien plant invasion (although not significant), a higher cover of herbaceous vegetation, and corresponding lower covers of exposed soil and litter.

With increasing invasion intensity (i.e. percentage aerial cover of woody alien plants), there was an increase in litter cover in both the 1996 and 2005 data. This is due to alien vegetation tending to have a higher vegetative biomass (in comparison with indigenous plants). Therefore, the higher the invasion intensity, the higher the litter cover. There was a positive linear relationship between the soil organic matter percentages in 1996 and 2005, despite the different analytical methods used, and hence this suggests that there was little change in the soil organic matter over time, or at least that the general rank order remained essentially the same. Thus, overall, the invasion and subsequent clearing of aliens has only had a small effect on the organic matter content of the Sabie River riparian environment.

Treatment effects (i.e. (A) biome, (B) invasion intensity and (C) clearing)

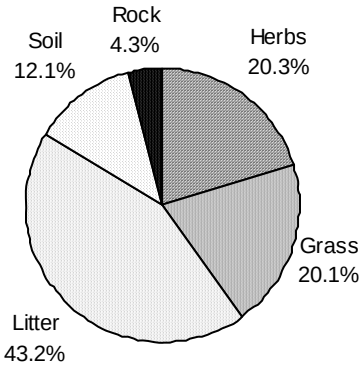
In 1996, biome, invasion intensity and clearing treatments had no significant effect on the cover of exposed soil, rock and grass. Biome also had no significant effect on the cover of litter and herbs; however, both covers were higher in the high invaded plots, with litter cover being higher in the uncleared plots and herbaceous cover being higher in the cleared plots. In 2005, biome and clearing treatments had no significant effect on any of the ground cover variables, expect for rock cover (which was significantly higher in the grassland and cleared plots). The invasion intensity treatment, however, did have a significant effect on all the ground cover variables (except for rock and grass covers) – soil and herbaceous covers were higher in the low invaded plots, and litter cover was higher in the high invaded plots.

The ANCOVA showed that there was a significant change in rock cover of the biomes and clearing treatments over time, which was due to rock cover being significantly higher in a few of the grassland, cleared plots in 2005. There was also a significant change in litter cover of the invasion intensity treatment over time, i.e. litter cover was higher in both invasion categories in 2005. The ANCOVA also indicated that there was virtually no relationship between the 2005 and 1996 ground cover variables. A possible reason for this is that the 2000 flood removed a high proportion of the smaller growth forms, thus resulting in a high proportion of exposed soil and rock. Therefore, the ground cover variables between the two years were very different. This was further illustrated by the two-way ANOVA (biome versus time), which indicated that there were significant differences between most of the ground

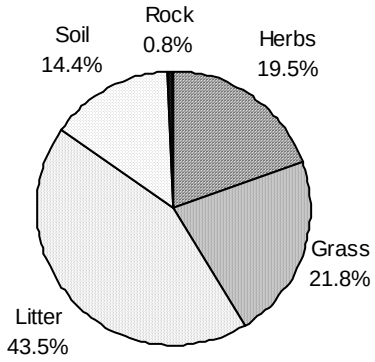
cover variables over time. The pH was not significantly affected by the different biome, invasion intensity and clearing treatments in both years.

5.6 Conclusions

Grassland

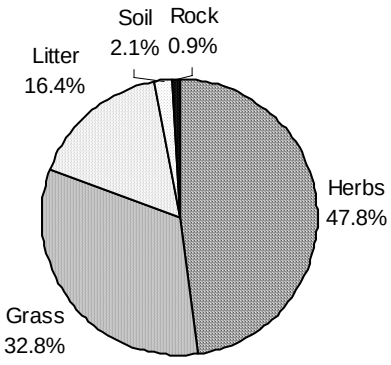


Savanna



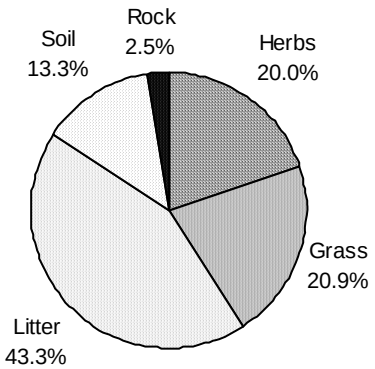
	Grassland	Savanna
Slope steepness	$4.8 \pm 1.1^{o\ b}$	$12.8 \pm 1.7^{o\ a}$
Soil compaction	0.8 ± 0.1 kg/cm$^{2\ a}$	0.7 ± 0.1 kg/cm$^{2\ a}$
pH	4.6 ± 0.1^{a}	4.8 ± 0.1^{a}
Soil organic matter	$4.5 \pm 0.2\%^{a}$	$3.3 \pm 0.4\%^{b}$
Total nitrogen	$0.3 \pm 0.02\%^{a}$	$0.2 \pm 0.02\%^{b}$
Nutrients	Higher concentration	Lower concentration

1996



pH: 4.7 ± 0.1^{a}

2005



pH: 4.7 ± 0.1^{a}

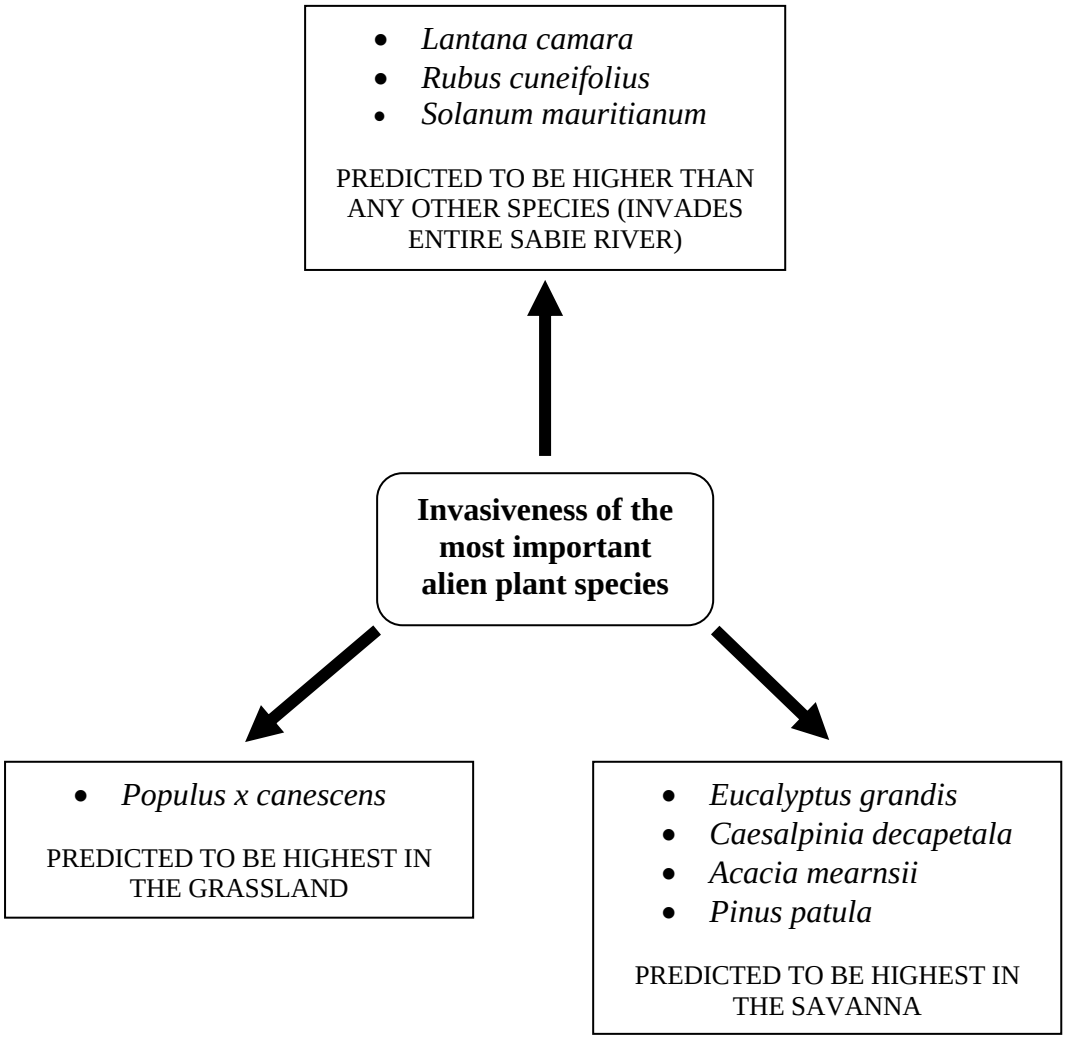


Figure 5.29. Summary diagram of the most important results from chapter 5.

5.6.1 Grassland and savanna biomes (in 2005)

There are several important conclusions that can be made (Figure 5.29). In terms of ground cover in 2005, exposed soil, litter and grass covers tended to be slightly higher in the savanna, whereas rock and herbaceous covers tended to be slightly higher in the grassland. These patterns in ground covers may be due to the invasion intensity being slightly higher in the savanna compared to the grassland. With increasing invasion intensity, the cover of smaller growth forms decreases due to the taller growing alien woody plants shading out the herbaceous vegetation; therefore the savanna had a lower cover of herbaceous vegetation. The invasion intensity and litter cover are positively correlated – an increase in alien vegetation cover results in an increase in litter cover due to alien woody plants generally having a higher vegetative biomass than indigenous plants, and resulting in higher levels of litter fall and hence a greater litter layer cover (and mass). Therefore, the higher invasion intensity in the savanna resulted in a higher litter cover in this biome. The higher exposed soil cover in the savanna is also related to litter cover being higher in this biome. Litter cover is not as stable as grass or herbaceous cover and surface

water runoff in high rainfall areas washes away litter. The results therefore imply that modifications by invasions (i.e. a reduction in grass and herbaceous covers, which are then replaced by increased litter and exposed soil), can lead to an increased risk of soil erosion. The higher invasion intensity in the savanna also leads to an increase in exposed soil due to the alien canopy excluding (through relatively dense shading) the ground cover (grass and herbaceous) vegetation that provides the surface stability. The difference in rock cover between the biomes was due to a few of the Sabie (grassland) plots having a significantly higher rock cover than both the Graskop (grassland) and Hazeyview (savanna) regions.

The biomes did not differ significantly in soil pH. The shallower grassland soils were generally more fertile than the deeper savanna soils, i.e. higher organic matter and total nitrogen content, with the Graskop (grassland) soils having the highest organic matter content and the Sabie (grassland) soils having the highest total nitrogen content. The concentrations of most of the nutrients were also higher in the grassland. Specifically, the grassland had higher concentrations of exchangeable calcium, magnesium and potassium, total manganese, and phosphate than the savanna, with the Sabie (grassland) region having the highest concentrations and the Graskop (grassland) region having the lowest concentrations. Therefore, the highest concentrations (often significantly) of these elements in the soils of the Sabie region, accounted for the grassland having higher concentrations of these elements compared with the savanna. On the other hand, the savanna had higher concentrations of total copper and zinc than the grassland.

Because the savanna tended to have a higher invasion intensity of large and small alien trees than the grassland, litter cover was higher in the savanna. With high litter cover, a large proportion of available nutrients in the community may have been immobilized and would then only become available by decomposition of the leaf litter and soil organic matter. Another reason why the grassland soils may have been more fertile is due to slower rates of soil organic matter decomposition in the slightly cooler (higher altitude) grassland regions, thus resulting in higher concentrations of nutrients in the soil. The soils of the grassland sites tended to be more compacted (but not significantly) than those of the savanna sites, and the savanna plots were on significantly steeper ground, which may have also contributed to lower fertility through greater leaching and erosion losses. The soils of the Sabie (grassland) region tended to be significantly more compacted than those of the Graskop (grassland) and Hazeyview (savanna) regions. However, the canonical correspondence analysis (CCA) showed that there was no strong association of the soil compaction with any of the plots, which was due to the soil compaction being relatively similar in both biomes.

In both biomes (and all three regions), soil organic matter content increased with increasing invasion intensity. This may be a simple consequence of the already established relationship in this study between invasion intensity and litter cover, and as the litter is broken down into smaller fragments, it becomes incorporated into soil organic matter. Thus, higher invasion intensity corresponds with higher litter deposition (as the leaf biomass is higher), resulting in more soil organic matter.

The canonical correspondence analysis (CCA) 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. Altitude was clearly important as the grassland plots occur at higher altitudes than the savanna plots, with the Sabie (grassland) plots occurring at slightly higher altitudes than the Graskop (grassland) plots. It was also found that steeper slopes were positively correlated with invasion intensity and litter cover – the savanna plots (which were on steeper ground) had a higher invasion intensity and litter cover than the grassland plots. The CCA also showed that there was a pH/fertility gradient, which was largely based on the soil acidity, with corresponding changes in the cation concentrations. Plots with more acidic soils tended to have lower concentrations of cations – this was reflected in the Graskop (grassland) soils having the lowest pH and concentrations of nutrients, and the Sabie (grassland) soils having the highest pH and concentrations of nutrients. This may have been due to more leaching taking place in the presumably wetter Graskop soils (even though both these regions occurred in the grassland biome, they were separated geographically to a large degree, with the Sabie plots occurring at higher altitudes than the Graskop plots).

From the canonical correspondence analysis (CCA), there appears to be no distinct communities of species separating out between the biomes and regions. Even though the high altitude plots occur in the grassland biome and the low altitude plots occur in the savanna biome, the Sabie River riparian environment essentially supports a riverine forest/woodland. Therefore, the species composition of the riparian environment is fairly uniform throughout the study area.

The category 1 species, *Lantana camara*, *Rubus cuneifolius* and *Solanum mauritianum*, are predicted to have the highest invasion intensity as they invade the entire Sabie River, i.e. they are not specific to either biome. All of these species have strong regenerative capabilities, and once in an area, they spread rapidly. Thus, the WfW clearing treatments should focus on these species that have the potential to dominate the community. The invasiveness of the category 2 species, *Eucalyptus grandis*, *Caesalpinia decapetala*, *Acacia mearnsii* and *Pinus patula*, is predicted to be higher in the savanna. The invasiveness of *Populus x canescens* (category 2), is predicted to be higher in the grassland. WfW can use these predictions of invasiveness of the different species to help them prioritise where the clearing efforts should be focused.

5.6.2 Change over time (from 1996 to 2005)

Soil pH remained unchanged over time, 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. Exposed soil, rock (not significant) and litter covers were significantly higher in 2005, whereas herbaceous and grass covers were significantly higher in 1996. 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 clearing operations also removed a significant proportion of the vegetation, and disturbed much that remained, thus modifying the environment. The increase in litter cover over time may have been due to the slightly higher invasion intensity in 2005 (as invasion intensity and litter cover are positively correlated, as discussed previously).

With increasing invasion intensity (i.e. percentage aerial cover of woody alien plants), there was an increase in litter cover in both the 1996 and 2005 data. This is due to alien vegetation tending to have a higher vegetative biomass (in comparison with indigenous plants). Therefore, the higher the invasion intensity, the higher the litter cover. There was a positive linear relationship between the soil organic matter percentages in 1996 and 2005, despite the different analytical methods used, and hence this suggests that there was little change in the soil organic matter over time, or at least that the general rank order remained essentially the same. Thus, overall, the invasion and subsequent clearing of aliens has only had a small effect on the organic matter content of the Sabie River riparian environment.

CHAPTER 6:

SUMMARY OF RESULTS, GENERAL CONCLUSIONS AND RECOMMENDATIONS

6.1 Summary of the rationale of the study

Southern Africa is severely affected by alien invasions, resulting in the transformation of large areas, as well as many negative impacts on the economy, in sectors such as health, agriculture, water supply and tourism (Macdonald, 1989). However, one of the biggest threats of alien plant invasions is to biodiversity (Randall, 1996). Clearing infestations of invading alien plants will have many benefits, which include increasing the available surface and underground water, preventing the loss of biodiversity, reducing fire hazard, stabilizing catchment areas and preventing erosion (Le Maitre *et al.*, 2002).

This study took place along the Sabie River catchment in the Mpumalanga province of South Africa. This catchment is important from both economic and eco-tourism perspectives. However, the Sabie River riparian ecosystem has been severely affected by invasive alien plants. As a result, the Working for Water (WfW) alien plant clearing programme has been clearing alien plants along this river over the past 10 years (i.e. from 1995 to 2005). The WfW programme was initiated in 1995 by the Department of Water Affairs and Forestry (DWAF) in response to the massive threat posed by invasive alien woody plants to ecosystems, and has a primary aim of increasing water supplies (by controlling woody alien plants). Other aims of this programme include enhancing social development and maintaining biodiversity over the long-term (via the restoration of indigenous ecosystems).

This study also forms part of a national project in which targets for ecosystem repair in riparian ecosystems in the fynbos, grassland and savanna biomes will be developed. This study will develop targets for the grassland and savanna biomes as the Sabie River traverses through both these biomes. Ecosystem recovery studies assess the degree of repair that has occurred as a result of alien clearing, based on suitable benchmarks, and an analysis of the information then clarifies whether biotic or abiotic thresholds in the environment have been passed (Whisenant, 1999). It can then be determined whether biotic or abiotic components need to be manipulated in order to facilitate the recovery of the indigenous community, which then facilitates the development of achievable targets for ecosystem repair. The national ecosystem repair project developed key questions relating to the ecosystem repair in the three biomes, and this study will aim to answer these questions in relation to the grassland and savanna biomes, and any relevant gaps in our knowledge or understanding will be identified and prioritised.

6.2 Summary of the aims, objectives and hypotheses

Several aims, objectives and hypotheses were proposed at the initiation of this study.

6.2.1 Aims

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 response to the clearing of alien plants by WfW. 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, such as determining whether there is an increase in indigenous species richness and/or a decrease in alien species richness, in this study it also includes determining whether there is a reduction in the invasion intensity (defined as the percentage aerial cover of woody alien plants) after clearing. More specifically, the aims were to:

1) Assess how the WfW alien plant clearing (and any subsequent further alien plant invasions post-clearing) affected the plant species composition, diversity and vegetation structure along riparian corridors on the Sabie River in both the grassland and savanna biomes, in 2005 (Chapter 3).
2) Assess how the WfW alien plant clearing (and any subsequent further alien plant invasions post-clearing) affected the plant species composition, diversity and vegetation structure of the Sabie River over time, i.e. from 1996 to 2005 (Chapter 4).
3) Investigate the relationship between the Sabie River riparian environment (i.e. ground cover, and soil chemical and physical properties) and the invasion of alien plant species and their removal (Chapter 5).

These aims were was accomplished using two fundamental approaches, i.e. by resurveying existing permanent plots that were established and first sampled in 1996/1997 (Garner, 2005) to assess riparian vegetation recovery, and by observing the effects of alien plant species invasion and clearing on plant species diversity and composition, vegetation structure and habitat characteristics.

6.2.2 Objectives

There were three main results chapters (i.e. 3, 4 and 5) that set out to achieve the objectives.

Chapter 3 focused on the comparison between the grassland and savanna biomes in 2005. The objectives were to:

1) Determine the alien and indigenous plant species composition of the Sabie River riparian vegetation in both the grassland and savanna biomes in 2005, and compare them.
2) Determine the alien and indigenous plant species diversity (alpha and beta), species evenness and species complementarity of the Sabie River riparian vegetation in both the grassland and savanna biomes in 2005, and compare them.
3) Determine the vegetation structure of the Sabie River riparian vegetation in both the grassland and savanna biomes in 2005, and compare them.
4) Use the information from objectives 1-3 to assess the effectiveness of the WfW clearing. As stated previously, "effectiveness" can be assessed in various ways, such as determining whether there is an increase in indigenous species richness and/or a decrease in alien species richness. In this study it

also includes determining whether there is a reduction in the invasion intensity (defined as the percentage aerial cover of woody alien plants) after clearing.

Chapter 4 focused on the comparison between the 1996 and 2005 Sabie River riparian plant communities. The objectives were to:

1) Compare the alien and indigenous plant species composition of the Sabie River riparian vegetation between 1996 and 2005.
2) Compare the alien and indigenous plant species diversity (alpha and beta) of the Sabie River riparian vegetation between 1996 and 2005.
3) Compare the vegetation structure of the Sabie River riparian vegetation between 1996 and 2005.
4) Use the information from objectives 1-3 to assess the effectiveness of the WfW clearing over time, i.e. from 1996 to 2005.

Chapter 5 focused on the comparison of the Sabie River riparian environment (i.e. the ground cover, and soil chemical and physical properties) between the grassland and savanna biomes in 2005, as well as between 1996 and 2005. The objectives were to:

1) Measure and compare the cover of exposed soil, rock, litter, herbaceous vegetation (except graminoids) and grass between the grassland and savanna biomes in 2005.
2) Compare the cover of exposed soil, rock, litter, herbaceous vegetation and grass between 1996 and 2005.
3) Measure and compare various soil chemical and physical properties of the grassland and savanna biomes in 2005.
4) Compare various soil chemical and physical properties between 1996 and 2005.
5) Use the information from objectives 1-4 to assess the effectiveness of the WfW clearing over time, i.e. from 1996 to 2005.

6.2.3 Hypotheses

There were two main hypotheses that were put forward. It is important to note that the invasion intensity (i.e. percentage aerial cover of woody alien plants) was used as a measure of the degree of alien plant invasions. These hypotheses stated that:

1) Higher plant species richness and/or diversity should enhance community resistance to alien plant invasions, in both the grassland and savanna biomes (Chapter 3), and in both 1996 and 2005 (Chapter 4).
2) 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, and in both 1996 and 2005 (Chapter 5).

6.3 Summary of the most important results

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).

The grassland biome was significantly more species rich at the 1000 m^2 scale (48.8 ± 1.8) and diverse at the 100 m^2 scale (Simpson's index of alpha diversity of 0.90 ± 0.01) than the savanna biome (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). In the grassland, at the 1000 m^2 scale, the Sabie region had the highest species richness (52.6 ± 2.8) whereas the Graskop region had the highest species diversity (0.90 ± 0.01). At the 1000 m^2 scale, the overall beta diversity (Sorenson's coefficient of community) between the biomes was 0.57 and the species complementarity (Marczewski-Steinhaus distance) was 0.60, thus indicating that the biomes were not very similar in terms of species composition. On the other hand, the species evenness (Simpson' measure of evenness) (at the 100 m^2 scale) was very similar between the biomes (0.52 ± 0.03 in the grassland and 0.51 ± 0.03 in the savanna; P = 0.74), thus indicating that the biomes were similar in terms of the overall relative abundances of plant species.

The difference in the species richness and diversity between the biomes may have been partially due to the higher degree of invasion intensity in the savanna (total woody alien plant aerial cover of 34.4 ± 4.6% compared to 29.4 ± 4.5% in the grassland; P = 0.44), which may have reduced the species richness and diversity in this biome. Because the savanna was lower in the catchment relative to the grassland, the savanna plots probably received more seeds and propagules of invasive species than the grassland.

Overall, the study area along the Sabie River had a high alpha diversity, i.e. approximately 0.8-0.9 (at the 100 m^2 scale). This diversity is similar to non-riverine biome-scale patterns of diversity in southern Africa (Whittaker *et al.*, 1984; Cowling *et al.*, 1991; Scholes, 1997). However, even though the diversity along the Sabie River was high and a large proportion (79% of a total of 282 species) was indigenous, alien species were still being found (21%), more than half of which were trees and shrubs. This shows that the WfW clearing operations have clearly not been succeeding in removing or controlling the infestations of woody alien plants. This may be a consequence of some plants, that should have been cut, being missed during the clearing operations, but also through many of the cut stems surviving and resprouting, and new seedlings establishing from seed banks.

The Sabie riverine growth form composition consisted of 43% herbaceous species, 29% shrub species, 16% tree species and 12% grass species. The grassland had higher proportions of shrub, herbaceous and grass species, whereas the savanna had a higher proportion of tree species. This difference in the growth form composition between the biomes is probably due to the inherent dominant growth forms found in each biome, as well as the higher invasion intensity in the savanna shading out a higher proportion of the smaller growth forms.

The grassland community appeared to be more resistant to the invasion of alien plants compared to the savanna community, possibly as a result of the grassland being more diverse. This was shown, when comparing the results between the plots in 2005, by the total species richness increasing slightly with increasing total invasion intensity in the grassland. On the other hand, the total species richness decreased with increasing total invasion intensity in the savanna, which may be a result of the morphological and physiological effects of the taller growing tree species shading out

the smaller growth forms and overtopping the indigenous species in the upper canopy. Thus, the hypothesis that higher plant species richness and/or diversity should enhance community resistance to alien plant invasions, was not rejected as the grassland was significantly more diverse than the savanna and appeared to be more resistant to alien plant invasions.

Both negative and positive correlations between the indigenous and alien species richness were found, which is likely to be a result of different types of invaders, strong or weak, predominating in the different regions. The Sabie region had two alien tree species (*Eucalyptus grandis* and *Agrimonia odorata*) and five alien shrub species (i.e. *Rubus cuneifolius, Solanum mauritianum, Lantana camara, Indigofera macrophylla* and *Lilium formosanum*) that dominated the community, which may have resulted in the negative correlation between the indigenous and alien species richness. On the other hand, there were relatively fewer dominating alien species (in comparison with the Sabie region) in the Graskop and Hazeyview regions; i.e. the Graskop region had five dominating alien shrub species (*Lantana camara, Rubus cuneifolius, Caesalpinia decapetala, Indigofera macrophylla* and *Populus x canescens*), while the Hazeyview region had three dominating alien shrub species (*Rubus cuneifolius, Solanum mauritianum* and *Lantana camara*). This low dominance of alien tree and shrub species in these regions may therefore have resulted in the positive correlation between the indigenous and alien species richness. The problem with these species is that they are strong resprouters, and are therefore not being effectively removed by the WfW clearing operations.

Finally, it was found that the roadsides of the plots were more species rich (in total and of aliens) than the riversides. Thus, roads could be an additional contributing factor to the spread of some of the aliens in the riverine areas and also needs to be taken into account in the WfW clearing operations.

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).

Total species richness (cumulative total for the 40 plots) increased from 163 species in 1996, to 282 in 2005 (42% increase). Mean species richness (at the 1000 m^2 scale) was 24.1 ± 1.0 in 1996 and 44.4 ± 1.5 in 2005 ($P < 0.001$). Mean alpha diversity was also significantly higher in 2005 (0.9 ± 0.01 compared to only 0.3 ± 0.03 in 1996 (at the 100 m^2 scale); $P < 0.001$). The overall beta diversity over time (a change from 1996 to 2005) was relatively low (between 0.08 and 0.15), indicating a small overall change in species composition, despite the increase in species richness. There were a total of 62 species common between the years, with 101 species being lost since 1996. Of the total of 163 species in 1996, 132 (81%) were indigenous and 31 (19%) alien, and of the 282 species in 2005, 222 (79%) were indigenous and 60 (21%) alien. Therefore, the indigenous species richness increased by 41% and the alien species richness by 48% (however the proportion of indigenous and alien species remained approximately the same over time).

Trees increased from 28 species in 1996 to 46 in 2005 (39% increase), shrubs from 44 to 82 (46% increase), herbaceous from 71 to 121 (41% increase), and grasses from 20 to 33 (39% increase). However, the growth form composition was very

similar between the years, i.e. in 1996, 17% of the species were trees, 27% shrubs, 43% herbaceous and 12% grasses; whereas in 2005, 16% were trees, 29% shrubs, 42% herbaceous and 11% grasses. Thus, even though the species richness of each growth form increased significantly over time, the proportion of species within each growth form remained approximately the same. The most dramatic change over time was in the weed species richness (category 1, 2 and 3 weed species), which increased by 50%.

The increase in the species richness and diversity over time may be due to several reasons. The clearing of alien plants by WfW may have allowed new species to establish due to reducing the dominance of vigorous alien species, and hence allowing less competitive species a better chance of establishing and persisting. The clearing in itself acted as a disturbance, which may have stimulated a number of more early successional and weedy species to establish. Increased disturbance (such as the clearing operations) can also increase the invasibility of plant communities. Therefore, the increase in the alien species richness and diversity over time may be a result of the disturbance created by the WfW clearing operations.

A factor that could explain the persistence of the dominant aliens over time is the regeneration potentials of these plants. As stated previously, the dominant alien species of the Sabie River riparian environment were *Eucalyptus grandis*, *Rubus cuneifolius*, *Lantana camara* and *Solanum mauritianum*, which all have strong regenerative capabilities; therefore, it is difficult to prevent the re-invasion of these species. The dramatic increase in the weed species richness over time may be a result of the flood event of February 2000. This very major disturbance may have resulted in the increased proportion of alien species, possibly due to recruitment sites being provided for the invading plants with water-borne propagules. The disturbance of the 2000 flood would have reset the successional stage of the Sabie River riparian environment, so that the 2005 plant community was probably in a more early successional stage, whereas the 1996 plant community would have been in a more mature stage. Late-successional plant communities may be relatively more resistant to invasion compared to early successional communities; hence this may partially explain the lower alien species richness in 1996.

Some of the differences in the results between the 1996 and 2005 studies may be because of the different observers. Studies have shown that vegetation sampling precision may be influenced by different observers, and that the effect of different observers is an important contributor to variability in the data set (Kercher *et al.*, 2003). In addition, the field work and data collection for the 1996/1997 study took place from October 1996 to the end of February 1997, and for the 2005 study from the 14th February 2005 to the 6th April 2005. Therefore, there was a slight difference in the seasonality of sampling between the two years. A higher proportion of plants were probably flowering or fruiting later in the season and hence in the 2005 study period, and thus the identification of the species may have been made easier and therefore more species were observed, and fewer missed. Hence, the higher species richness and diversity in 2005 may be partially due to this difference in the sampling periods. Another reason why there was a lower species richness and diversity in 1996, may have been due to the severe drought of 1991/1992. This drought reduced the flow in the Sabie River on the Mozambique border to previously unrecorded low discharges, measured in the Kruger National Park, of only 0.33 m^3s^{-1} (Weeks *et al.*,

1996). During droughts many species may show a more patchy distribution and therefore appear to become locally extinct, but gradually return when higher rainfall returns. Even though the 1996 study took place four years after this drought, this plant community may have still been in the recovery stages.

The total invasion intensity (i.e. percentage aerial cover of woody alien plants) tended to be slightly higher in 2005 compared to 1996, but not significantly (30.0 ± 4.6% in 1996 and 31.9 ± 3.2% in 2005; $P = 0.73$), despite all the WfW clearing in the intervening years. Because of this similar invasion intensity, as well as the similar growth form composition between the years, 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 in height (respresented in the past largely by *Eucalyptus* spp.) decreased from 15.8 ± 4.1% in 1996 to 5.8 ± 1.2% in 2005 ($P = 0.02$), and (b) those between 2 and 5 m in height decreased from 13.3 ± 2.8% in 1996 to 11.1 ± 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 ± 1.0% in 1996 to 15.0 ± 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 woody alien plants, but not in controlling the regenerating plants, which recover through post-clearing resprouting and/or newly established seedlings.

When comparing the invasion intensity between the three original "treatments" of the 1996/1997 study over time, namely (A) biome (grassland versus savanna), (B) invasion intensity (high (> 50%) versus low (< 50%)), and (C) clearing (cleared versus uncleared), the invasion intensity of the 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 ($P = 0.03$). This is of significance as it shows that the cleared plots in 1996 regained their former pre-clearing (presumably) invasion intensity.

In the grassland biome, the total invasion intensity remained approximately the same over time, whereas in the savanna biome, it increased (although not significantly). This may have been due to the savanna plots being situated lower in the catchment relative to the grassland plots (and hence a sink for upstream alien plant propagules).

In both years, the total species richness decreased with increasing invasion intensity, which may be a result of the morphological and physiological effects of the taller growing tree species shading out smaller growth forms and overtopping the indigenous species, thus reducing the species richness. These decreases in the species richness with increasing invasion intensity, indicates that both the 1996 and 2005 plant communities were not that resistant to the invasion of alien plants. Furthermore, because the 2005 plant community was significantly more species rich and diverse than the 1996 community, the hypothesis that higher plant species richness and/or diversity should enhance community resistance to alien plant invasions, was rejected.

Finally, of the original "treatments" of the 1996/1997 study, namely (A) biome, (B) invasion intensity and (C) clearing, 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 species richness when analysed by ANCOVA. Therefore, the 1996 and 2005 plant communities in the corresponding plots were quite different.

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).

Grassland and savanna biomes (in 2005)

In terms of ground cover in 2005, exposed soil, litter and grass covers tended to be slightly higher in the savanna (14.4 ± 1.6%; 43.5 ± 3.0%; 21.8 ± 1.7% respectively) than in the grassland (12.1 ± 2.5%; 43.2 ± 4.2%; 20.1 ± 2.3% respectively) (P = 0.43, 0.96 and 0.56 respectively). Rock and herbaceous covers tended to be higher in the grassland (4.3 ± 1.6% and 20.3 ± 1.7% respectively) than in the savanna (0.8 ± 0.2% and 19.5 ± 2.2% respectively), but only rock cover was significantly different (P = 0.04) (P = 0.76 for herbaceous cover). These patterns in ground covers may have been related to the invasion intensity being slightly higher in the savanna compared to the grassland. Thus, 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 plant invasion (although not significant), a higher cover of herbaceous vegetation, and corresponding lower covers of exposed soil and litter.

With increasing invasion intensity, the cover of smaller growth forms decreases due to the taller growing alien woody plants shading out the herbaceous vegetation; therefore the savanna had a lower cover of herbaceous vegetation. The invasion intensity and litter cover are positively correlated – an increase in alien vegetation cover results in an increase in litter cover due to alien woody plants generally having a higher vegetative biomass than indigenous plants, and resulting in higher levels of litter fall and hence a greater litter layer cover (and mass). Therefore, the higher invasion intensity in the savanna resulted in a higher litter cover in this biome. The higher exposed soil cover in the savanna is also related to litter cover being higher in this biome. Litter cover is not as stable as grass or herbaceous cover, and surface water runoff in high rainfall areas washes away litter. The results therefore imply that modifications by invasions (i.e. a reduction in grass and herbaceous covers, which are then replaced by increased litter and exposed soil), can lead to an increased risk of soil erosion. The higher invasion intensity in the savanna also leads to an increase in exposed soil due to the alien canopy excluding (through relatively dense shading) the ground cover (grass and herbaceous) vegetation that provides the surface stability. The difference in rock cover between the biomes was due to a few of the Sabie (grassland) plots having a significantly higher rock cover than both the Graskop (grassland) and Hazeyview (savanna) regions.

The grassland and savanna biomes did not differ significantly in soil pH (grassland pH: 4.6 ± 0.1; savanna pH: 4.8 ± 0.1; P = 0.34). However, the shallower grassland soils were generally more fertile than the deeper savanna soils, i.e. higher

organic matter (4.5 ± 0.2% versus 3.3 ± 0.4%; P = 0.01) and total nitrogen (0.3 ± 0.02% versus 0.2 ± 0.02%; P = 0.03), with the Graskop (grassland) soils having the highest organic matter content and the Sabie (grassland) soils having the highest total nitrogen content. The concentrations (mg/l) of most of the nutrients were also higher in the grassland. Specifically, the grassland had higher concentrations of exchangeable calcium, magnesium and potassium, total manganese, and phosphate than the savanna, with the Sabie (grassland) region having the highest concentrations and the Graskop (grassland) region having the lowest concentrations. Therefore, the highest concentrations (often significantly) of these elements in the soils of the Sabie region, accounted for the grassland having higher concentrations of these elements compared with the savanna. On the other hand, the savanna had higher concentrations of total copper and zinc than the grassland.

Because the savanna tended to have a higher invasion intensity of large and small alien trees than the grassland, litter cover was higher in the savanna. With high litter cover, a large proportion of available nutrients in the community may have been immobilized and would then only become available by decomposition of the leaf litter and soil organic matter. Another reason why the grassland soils may have been more fertile is due to slower rates of soil organic matter decomposition in the slightly cooler (higher altitude) grassland regions, thus resulting in higher concentrations of nutrients in the soil. The soils of the grassland sites tended to be more compacted (0.8 ± 0.1 kg/cm^2) (but not significantly) than those of the savanna sites (0.7 ± 0.1 kg/cm^2) (P = 0.43), and the savanna plots were on significantly steeper ground (12.8 ± 1.7º) than the grassland plots (4.8 ± 1.1º) (P < 0.001), which may have also contributed to lower fertility in the savanna through greater leaching and erosion losses. The soils of the Sabie (grassland) region tended to be significantly more compacted (1.1 ± 0.1 kg/cm^2) than those of the Graskop (grassland) (0.5 ± 0.1 kg/cm^2) and Hazeyview (savanna) regions (0.7 ± 0.1 kg/cm^2). However, the canonical correspondence analysis (CCA) showed that there was no strong association of the soil compaction with any of the plots, which was due to the soil compaction being relatively similar in both biomes.

In both biomes (and all three regions), soil organic matter content increased with increasing invasion intensity. This may be a simple consequence of the already established relationship in this study between invasion intensity and litter cover, and as the litter is broken down into smaller fragments, it becomes incorporated into soil organic matter. Thus, higher invasion intensity corresponds with higher litter deposition (as the leaf biomass is higher), resulting in more soil organic matter.

The canonical correspondence analysis (CCA) 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. Altitude was clearly important as the grassland plots occur at higher altitudes than the savanna plots, with the Sabie (grassland) plots occurring at slightly higher altitudes than the Graskop (grassland) plots. It was also found that steeper slopes were positively correlated with invasion intensity and litter cover – the savanna plots (which were on steeper ground) had a higher invasion intensity and litter cover than the grassland plots. The CCA also showed that there was a pH/fertility gradient, which was largely based on the soil acidity, with corresponding changes in the cation concentrations. Plots with more acidic soils tended to have lower concentrations of

cations – this was reflected in the Graskop (grassland) soils having the lowest pH and concentrations of nutrients, and the Sabie (grassland) soils having the highest pH and concentrations of nutrients. This may have been due to more leaching taking place in the presumably wetter Graskop soils (even though both these regions occurred in the grassland biome, they were separated geographically to a large degree, with the Sabie plots occurring at higher altitudes than the Graskop plots).

From the canonical correspondence analysis (CCA), there appears to be no distinct communities of species separating out between the biomes and regions. Even though the high altitude plots occur in the grassland biome and the low altitude plots occur in the savanna biome, the Sabie River riparian environment essentially supports a riverine forest/woodland. Therefore, the species composition of the riparian environment is fairly uniform throughout the study area.

The CCA also indicated that the category 1 species, *Lantana camara*, *Rubus cuneifolius* and *Solanum mauritianum*, were not strongly influenced by any of the environmental variables; thus they occurred in most of the plots (percentage occurrence in the 40 plots of *R. cuneifolius* was 70%; of *S. mauritianum* was 58%; and of *L. camara* was 50%). Thus, these species are predicted to have the highest invasion intensity as they invade the entire Sabie River, i.e. they are not specific to either biome. All of these species have strong regenerative capabilities, and once in an area, they spread rapidly. The category 2 species, *Eucalyptus grandis* and *Caesalpinia decapetala*, were found in both biomes; however they tended to have higher occurrences in the savanna (percentage occurrence of *E. grandis* and *C. decapetala* in the savanna, was 35% and 20% respectively (compared to 20% and 15% respectively in the grassland)). Thus, the invasiveness of these species is predicted to be higher in the savanna. Other category 2 species, i.e. *Acacia mearnsii* and *Pinus patula*, only occurred in the savanna (percentage occurrence of 5% for both species). *Populus x canescens* (category 2) only occurred in the grassland, with an occurrence of 10%.

Change over time (from 1996 to 2005)

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. Exposed soil, rock (not significant) and litter covers were significantly higher in 2005 (13.3 ± 1.5%; 2.5 ± 0.8%; 43.3 ± 2.5% respectively) than in 1996 (2.1 ± 0.5%; 0.9 ± 0.3%; 16.4 ± 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 ± 2.8% and 32.8 ± 2.6% respectively) than in 2005 (20.0 ± 1.4% and 20.9 ± 1.4% respectively) ($P < 0.001$ for herbaceous and grass covers). Hence, 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 tended to have a lower degree of alien plant invasion (although not significant), a higher cover of herbaceous vegetation, and corresponding lower covers of exposed soil and litter.

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 over time may have been due to the slightly higher invasion intensity in 2005 (as invasion intensity and litter cover are positively correlated, as discussed previously).

With increasing invasion intensity, there was an increase in litter cover in both the 1996 and 2005 data. This is due to alien vegetation tending to have a higher vegetative biomass (in comparison with indigenous plants). Therefore, the higher the invasion intensity, the higher the litter cover. There was a positive linear relationship between the soil organic matter percentages in 1996 and 2005, despite the different analytical methods used, and hence this suggests that there was little change in the soil organic matter over time, or at least that the general rank order remained essentially the same. Thus, overall, the invasion and subsequent clearing of aliens has only had a small effect on the organic matter content of the Sabie River riparian environment.

6.4 Key questions relating to the ecosystem repair of the grassland and savanna biomes

The key questions developed by the national ecosystem repair project relating to the ecosystem repair in the biomes, were:

1) *"What level of ecosystem repair has been achieved in each of the different situations studied?"*
   The Sabie River riparian environment is essentially in a similar state to what is was in 1996. Evidence for this includes a similar growth form composition of species, a similar proportion of indigenous and alien species, as well as similar invasion intensities (i.e. percentage aerial cover of woody alien plants) over time. Thus, it can be concluded that little or no ecosystem repair has been achieved along the Sabie River.

2) *"Are the thresholds derived from ecological theory applicable in practice?"*
   a) In what situations have biotic thresholds been passed?"
   Amongst the tree and shrub species with the greatest densities (i.e. > 500 plants/ha) in the grassland biome, were ten indigenous species and five alien species (Figure 6.1). Therefore, a higher proportion of indigenous tree and shrub species were dominating the community. However, the densest species by far were two alien species, i.e. *Lantana camara* and *Rubus cuneifolius*. Both of these species have strong resprouting abilities and once in an area, they spread rapidly. Therefore, because the grassland community was dominated by these two alien species, biotic thresholds of the grassland reach of the Sabie River riparian ecosystem may have been passed. However, with frequent follow-up clearings by WfW, the density of these dominant alien species could be reduced.

   Amongst the tree and shrub species with the greatest densities (i.e. > 500 plants/ha) in the savanna biome, were eight indigenous species and three alien species (Figure 6.2). Therefore, this biome also had a higher proportion of

indigenous tree and shrub species dominating the community. However, unlike the grassland biome, the densest species were indigenous. Thus, biotic thresholds of the savanna reach of the Sabie riparian ecosystem may not have been passed. However, even though the most dominant species (in terms of density) were indigenous, the invasion intensity (i.e. percentage aerial cover of woody alien plants) may have had a more significant effect in the savanna, as these sites had lower total species richness and diversity. If WfW does not follow a rigid schedule of frequent follow-up clearing treatments, the density of the alien species could increase, and this could possibly exacerbate the effects that the high invasion intensity has on the riparian community in this biome. It is important to note, however, that density (i.e. plants/ha) does not have to increase for invasion intensity to increase as the same plants can just grow bigger in size (each of them), and the overall adverse affect (measured as percentage canopy cover here) will increase. Thus, it it important to take into account both the density and percentage canopy cover of the dominant species when determining whether biotic thresholds have been passed.

b) *In what situations have abiotic thresholds been passed?"*
The abiotic (i.e. hydrological and geomorphological) components of the Sabie River riparian ecosystem were not looked at in this study. Therefore, it cannot be determined whether abiotic thresholds have been passed. This is a possible future area of research.

3) *"What is achievable in each of the different situations studied?"*
This study showed that the WfW clearing operations are successful, to some extent, in removing the bulk of the alien plant biomass, but the programme fails to control the resprouting individuals, especially in the grassland biome. However, with a rigid schedule of frequent subsequent clearing treatments, the density of the alien plants could be reduced over time, which would eventually allow the indigenous community to become dominant, thus increasing its resistance to alien plant invasions.

4) "What could be improved?"
Several recommendations are given to WfW to help them improve the programme's success in controlling woody alien plants along the Sabie River (refer to section 6.5).

5) "Have any important ecosystem drivers or keystone species (to facilitate recovery) been identified?"
Important ecosystem drivers or keystone species were not identified in this study, as this was not focused upon. This could be a possible future area of research.

6) *"What are the realistic goals for the different situations, particularly in relation to vegetation type, river order and level of ecosystem degradation?"*
A realistic goal for the grassland biome would be to reduce the density of the two most dominant species (*Lantana camara* (2925 plants/ha) and *Rubus cuneifolius* (2760)) to levels below that of the dominant indigenous species (i.e. to levels below 2100 plants/ha, but preferably to much lower levels still). In both biomes, a realistic goal would be to reduce the percentage aerial cover

of the woody alien plants (invasion intensity) to about 10% or less. Currently, the invasion intensity in the grassland is approximately 30% and in the savanna 35%. Both of these goals can be achieved by increasing the frequency of the WfW follow-up clearings.

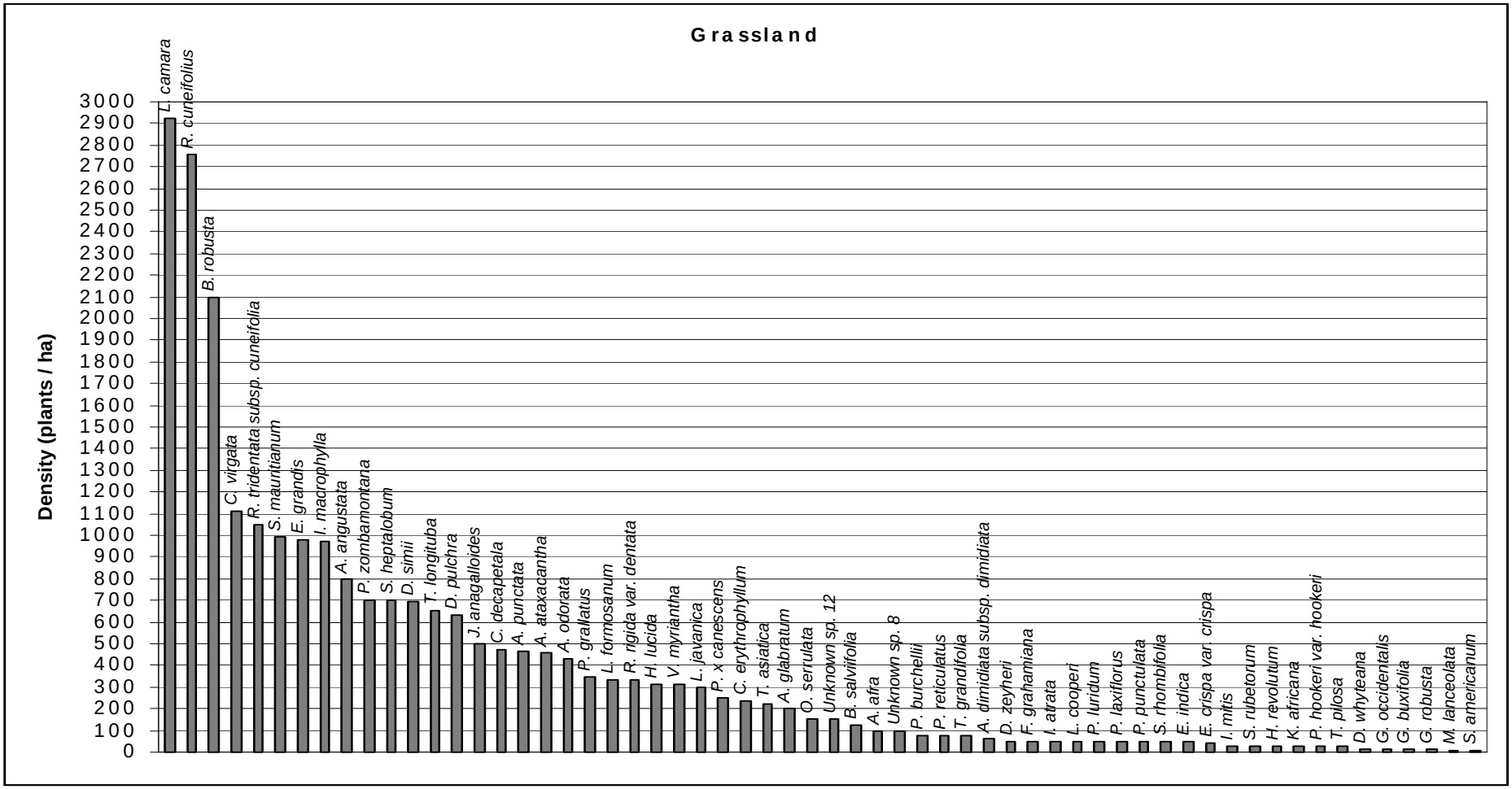


Figure 6.1. The total density (plants/ha) of indigenous and alien tree and shrub species at the 0.01 ha scale (i.e. 100 m^2), along the Sabie River in the grassland biome (species names and invasive status are given in Appendix 3).

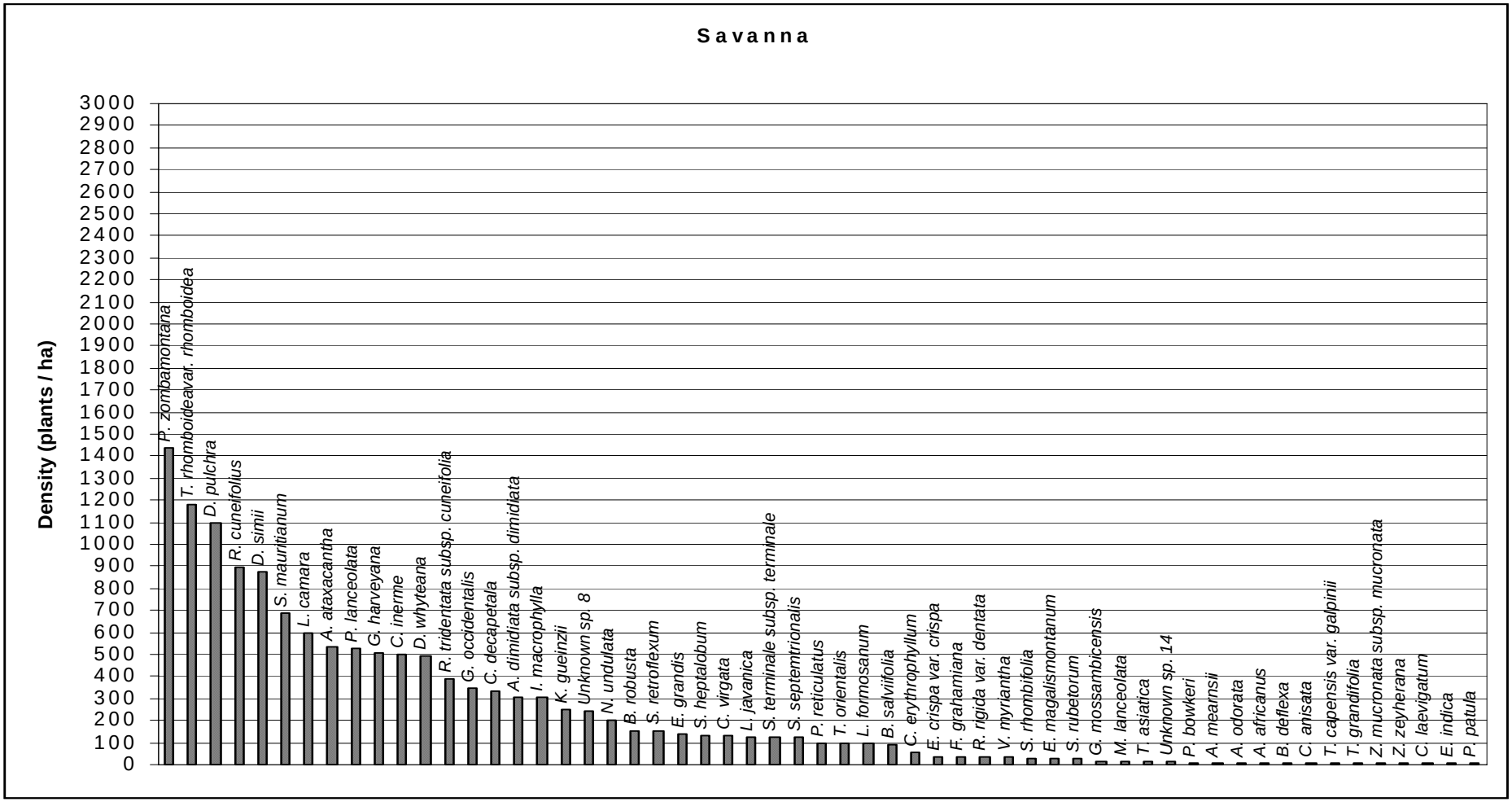


Figure 6.2. The total density (plants/ha) of indigenous and alien tree and shrub species at the 0.01 ha scale (i.e. 100 m^2), along the Sabie River in the savanna biome (species names and invasive status are given in Appendix 3).

6.5 Recommendations to WfW

Even though the WfW alien plant clearing programme is successful, to some extent, in removing alien woody plants along the Sabie River, it is not succeeding in controlling many of the species, due to both prolific resprouting from cut stems and also seedlings establishing from a soil seed bank. Therefore, various recommendations are made to WfW in order to assist them in improving the control of these alien plants.

1) Follow-up monitoring should be undertaken immediately after the initial clearings in order to check that the clearing has been done well and then improve if necessary.

2) Follow-up clearings need to be undertaken more often in order to reduce the extent of recovery of the alien plants through resprouting from cut stems and seedlings establishing from the soil seed bank. Currently, follow-up clearings are taking place about a year after the initial clearings, with further follow-up clearings taking place about eight months later. It is recommended that the frequency of the follow-up clearings should increase to about four, spread over three years. These follow-up clearings should occur in the growing season, when it is clearly apparent whether regrowth is occurring or not. Unless WfW follows this more rigid schedule of frequent subsequent clearing treatments, the subsequent alien species establishment will result in an even larger invasion problem for the Sabie River riparian ecosystem.

3) WfW should initially concentrate on the upper parts of the catchment first, i.e. the grassland area (and all the way up the catchment) to minimise dispersal of propagules from upstream, so that the lower savanna areas are not continuously re-invaded.

4) The species that have the potential to dominate the local plant communities (i.e. that have the greatest invasion intensities) should be focused upon in the WfW clearing operations. Along the Sabie River, the alien tree and shrub species with the greatest densities (in both the grassland and savanna biomes combined) 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, as well as reduce costs and increase ease of the clearing. This would eventually allow the indigenous community to re-establish itself and slowly become dominant again, thus making the community more resistant to these invasions; therefore the number of follow-up clearings could eventually be reduced.

5) WfW should use the predictions of invasiveness of the different category 1 and 2 species to help them prioritise where the clearing efforts should be focused.

6) Other, more effective, ways of controlling the key resprouting alien species needs to be implemented. For example, cutting the stems closer to the ground, and taking more care in painting the stumps with herbicide (Garner, 2005).

7) Clearing should be integrated with other measures such as biocontrol and restorative plantings of key riparian indigenous species. Biocontrol agents should be released on as many of the key alien species as possible (listed above) at these sites along the Sabie River, which are now extremely well characterised sites, and would therefore be excellent for further monitoring of both ecosystem repair and the impacts of biocontrol agents on these alien invasive weeds.

6.6 Future areas of research

From this study, various areas of research have been identified.

1) Future studies similar to this 2005 study and the 1996 study, need to continue to take place in order to determine the even longer-term effects of the invasion and subsequent clearing of alien plants along the Sabie River. However, in future follow-up studies, alien plants < 1 m in height should also be counted in the 1 m^2 and 10 m^2 quadrats in order to get a full estimate of the densities of the re-invading alien plants. These small alien plants were excluded (not specifically sampled) in both the 1996 and 2005 studies (which was probably an error), and therefore the density of the re-invading aliens is an underestimate as there were many individuals of < 1 m that were not being counted, but were still there.

2) One of the recommendations to WfW is to implement other ways of controlling the dominant alien species. Therefore, a future area of research would be to determine the influence of different clearing treatments on the recovery of the riparian vegetation.

3) In order to determine the best clearing methods, research would also be needed to understand fully the consequences of the key alien species that invade riparian zones.

4) The abiotic (i.e. hydrological and geomorphological) components of the Sabie River riparian ecosystem were not looked at in this study. Therefore, the importance of these abiotic factors in relation to the recovery of riparian vegetation after the invasion of alien plants, needs to be researched.

5) The important ecosystem drivers or keystone species that facilitate riparian vegetation recovery needs to be identified.

6) On a larger scale, research is needed to determine the effects of removing indigenous woody plants from riparian ecosystems versus the effects of removing alien woody plants from the same setting. In other words, is the water “saved” as a result of alien plant species being cleared greater than the water “saved” if indigenous forests were cleared?

In a recent South African review article on riparian zones (Holmes *et al.*, 2005), several areas of research were identified. These included:

a) Researching the extent to which propagule supply and microsite conditions inhibit vegetation recovery.

b) Researching the relative importance of dispersing vegetative propagules, dispersing seeds and soil-stored seed banks in vegetation dynamics after the invasion by alien plants.

c) Researching the potential negative effects of herbicides on amphibians and other fauna (Webb and Erskine, 2005).

d) Researching the biophysical impacts of standing dead trees (and later fallen trees), in the riparian zones.

6.7 Final concluding points

The overall species diversity along the Sabie River (in 2005) was high, and was similar to non-riverine biome-scale patterns of diversity in southern Africa, whereas the overall species richness was slightly lower, which may have been because the Sabie River riparian environment essentially supports a riparian forest/woodland, rather than the surrounding (more upland) grasslands and savannas. The species richness and diversity of the 2005 plant community was significantly higher than the 1996 plant community. However, the proportion of indigenous and alien species, as well as the growth form composition, remained approximately the same over time. Because of this, and because alien plant cover and species richness were still high in 2005 (more than half of which were shrubs and trees), the WfW clearing operations have clearly not been succeeding in removing or controlling the infestations of woody alien plants. This may be a consequence of some plants, that should have been cut, being missed during the clearing operations, but also through many of the cut stems surviving and resprouting, and new seedlings establishing from seed banks. The most dramatic change over time was in the weed species richness (category 1, 2 and 3 weed species), which increased by 50%. Of the original "treatments" of the 1996/1997 study, namely (A) biome, (B) invasion intensity and (C) clearing, 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. This suggests that the Sabie River riparian plant community has changed considerably over time, and this change has been largely a consequence of alien plant invasions.

The total invasion intensity tended to be slightly higher (but not significantly) in 2005 compared to 1996; thus, once again, this indicates that the WfW clearing efforts are not succeeding in the primary aim of controlling aliens, particularly woody alien species. However, there was a large decrease in the aerial cover of large (> 5 m in height) and intermediate-sized (2 – 5 m) alien trees, which was balanced by a considerable increase in the aerial cover of the smaller alien shrubs/trees (< 2 m in height). Therefore, 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.

Both the 1996 and 2005 plant communities were not that resistant to the invasion of alien plants, as the total species richness decreased with increasing invasion intensity in both years, which may be a result of the morphological and physiological effects of the taller growing tree species shading out smaller growth forms and overtopping the indigenous species.

The differences in the 1996 and 2005 plant communities may be due to several reasons. The clearing of alien plants by WfW may have allowed new species to establish due to reducing the dominance of vigorous alien species, and hence allowing less competitive species a better chance of establishing and persisting. The clearing in itself acted as a disturbance, which may have stimulated a number of more early successional and weedy species to establish. Increased disturbance (such as the clearing operations) can also increase the invasibility of plant communities. Therefore, the increase in the alien species richness and diversity over time may be a result of the disturbance created by the WfW clearing operations. The 1996 sampling period followed a severe drought in 1991/1992, thus this may have also resulted in the lower species richness and diversity in 1996. Some of the differences in the results between the 1996 and 2005 data may be because of different observers in both studies, as well as the slight difference in the seasonality of sampling between the two years.

The flood event of February 2000 would have also contributed to the dramatic increase in the weed species richness, possibly due to recruitment sites being provided for the invading plants with water-borne propagules. This major disturbance would have reset the successional stage of the Sabie River riparian environment, so that the 2005 community was probably in a more early successional stage, whereas the 1996 community would have been in a more mature stage. Late-successional plant communities may be relatively more resistant to invasion compared to early successional communities; hence this may explain the lower alien species richness in 1996. The 2000 flood cleared a large proportion of the vegetation, resulting in much greater rates of erosion and deposition of soils, and hence the exposed soil, rock (not significant) and litter covers were significantly higher in 2005, whereas the herbaceous and grass covers were significantly higher in 1996. The WfW clearing operations also removed a significant proportion of the vegetation, and disturbed much that remained, thus modifying the environment. Soil pH remained unchanged over time, 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.

When comparing the grassland and savanna biomes in 2005, it was found that the grassland biome was significantly more species rich and diverse. The biomes were similar in terms of the overall relative abundances of plant species, but not in terms of the species composition. The difference in the species richness and diversity between the biomes may have been partially due to the higher (but not significantly higher) degree of invasion intensity in the savanna, which may have reduced the species richness and diversity in this biome. Because the savanna was lower in the catchment relative to the grassland, the savanna plots probably received more seeds and propagules of invasive species than the grassland. Over time, the invasion intensity remained approximately the same in the grassland, whereas it increased (although not significantly) in the savanna. The higher proportions of shrub,

herbaceous and grass species in the grassland, and the higher proportion of tree species in the savanna, is probably due to the inherent dominant growth forms found in each biome, as well as the higher invasion intensity in the savanna shading out a higher proportion of the smaller growth forms. The grassland community appeared to be more resistant to the invasion of alien plants compared to the savanna community, possibly as a result of the grassland being more diverse.

The slightly higher exposed soil, litter and grass covers in the savanna, and the slightly higher rock and herbaceous covers in the grassland, may have been related to the invasion intensity being slightly higher in the savanna compared to the grassland. With increasing invasion intensity, the cover of smaller growth forms decreases due to the taller growing alien woody plants shading out the herbaceous vegetation. Furthermore, an increase in alien vegetation cover may result in an increase in litter cover due to alien woody plants generally having a higher vegetative biomass than indigenous plants, and resulting in higher levels of litter fall and hence a greater litter layer cover (and mass). The higher invasion intensity in the savanna can also lead to an increase in exposed soil due to the alien canopy excluding (through relatively dense shading) the ground cover (grass and herbaceous) vegetation that provides the surface stability.

The shallower grassland soils were generally more fertile than the deeper savanna soils, even though there was no significant difference in soil pH. With high litter cover (as seen in the savanna biome), a large proportion of available nutrients in the community may have been immobilized and would then only become available by decomposition of the leaf litter and soil organic matter. Another reason why the grassland soils may have been more fertile is due to slower rates of soil organic matter decomposition in the slightly cooler (higher altitude) grassland region, thus resulting in higher concentrations of nutrients in the soil. The soils of the grassland sites tended to be more compacted (but not significantly) than those of the savanna sites, and the savanna plots were on significantly steeper ground, which may have also contributed to lower fertility through greater leaching and erosion losses. 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.

Along the Sabie River (in 2005), the alien tree and shrub species with the greatest densities were *Rubus cuneifolius, Lantana camara, Solanum mauritianum, Indigofera macrophylla, Eucalyptus grandis, Caesalpinia decapetala, Agrimonia odorata, Lilium formosanum,* and *Populus x canescens*. The Sabie (grassland) region had more tree and shrub species dominating the community, compared with the Graskop (grassland) and Hazeyview (savanna) regions, which may have resulted in the negative correlation between the indigenous and alien species richness in the Sabie region (compared to the positive correlations in the other regions). The category 1 species, *L. camara, R. cuneifolius* and *S. mauritianum*, were not strongly influenced by any of the environmental variables, and thus occurred in most of the plots. Therefore, these species are predicted to have the highest invasion intensity as they invade the entire Sabie River, i.e. they are not specific to either biome. The re-invasion and persistence of the dominant alien species over time may be due to the

regeneration potentials of these species, thus making it difficult for the WfW clearing operation to control them.

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. By following the various recommendations suggested in section 6.5, the effectiveness of the WfW programme along the Sabie River may be greatly improved. However, there is still much that needs to be researched (refer to section 6.6), which will greatly improve our understanding of the impacts and controls of alien invasive species along riparian corridors, as well as how to improve the restoration of riparian communities.

CHAPTER 7:

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CHAPTER 8:

APPENDICES

Appendix 1. Study plot locations, altitudes and co-ordinates of the 2005 plots.

Plot No.	Region	Biome	Co-ordinates	Altitude
1	Sabie	Grassland	S 25° 08’ 09.8” E 30° 41’ 02.0”	1 166 m
2	Sabie	Grassland	S 25° 08’ 08.3” E 30° 41’ 03.2”	1 151 m
3	Sabie	Grassland	S 25° 08’ 06.4” E 30° 41’ 05.7”	1 163 m
4	Sabie	Grassland	S 25° 08’ 01.9” E 30° 41’ 20.5”	1 153 m
5	Sabie	Grassland	S 25° 08’ 02.5” E 30° 41’ 21.5”	1 153 m
6	Sabie	Grassland	S 25° 08’ 01.7” E 30° 41’ 22.9”	1 159 m
7	Sabie	Grassland	S 25° 07’ 54.9” E 30° 41’ 27.1”	1 134 m
8	Sabie	Grassland	S 25° 07’ 32.1” E 30° 42’ 09.7”	1 090 m
9	Sabie	Grassland	S 25° 07’ 32.0” E 30° 42’ 15.1”	1 085 m
10	Sabie	Grassland	S 25° 07’30.9” E 30° 42’ 16.6”	1 080 m
11	Graskop	Grassland	S 24° 56’ 54.6” E 30° 53’ 16.4”	987 m
12	Graskop	Grassland	S 24° 56’ 54.7” E 30° 53’ 17.9”	995 m
13	Graskop	Grassland	S 24° 56’ 55.1” E 30° 53’ 23.5”	996 m
14	Graskop	Grassland	S 24° 56’ 55.8” E 30° 53’ 25.6”	1 005 m
15	Graskop	Grassland	S 24° 56’ 56.4” E 30° 53’ 27.7”	1 002 m
16	Graskop	Grassland	S 24° 57’ 18.6” E 30° 54’ 31.5”	984 m
17	Graskop	Grassland	S 24° 57’ 18.1” E 30° 54’ 34.4”	942 m
18	Graskop	Grassland	S 24° 57’ 17.9” E 30° 54’ 35.4”	924 m
19	Graskop	Grassland	S 24° 57’ 16.2” E 30° 54’ 43.7”	955 m
20	Graskop	Grassland	S 24° 57’ 16.1” E 30° 54’ 44.0”	956 m
21	Hazeyview	Savanna	S 25° 03’ 44.7” E 30° 54’ 27.1”	783 m
22	Hazeyview	Savanna	S 25° 03’ 45.0” E 30° 54’ 25.2”	766 m
23	Hazeyview	Savanna	S 25° 03’ 44.4” E 30° 54’ 28.7”	779 m
24	Hazeyview	Savanna	S 25° 03’ 45.7” E 30° 54’ 21.2”	760 m

25	Hazeyview	Savanna	S 25° 03’ 46.7” E 30° 54’ 15.9”	774 m
26	Hazeyview	Savanna	S 25° 03’ 46.6” E 30° 54’ 15.2”	766 m
27	Hazeyview	Savanna	S 25° 03’ 44.6” E 30° 54’ 12.1”	763 m
28	Hazeyview	Savanna	S 25° 03’ 46.2” E 30° 54’ 28.6”	781 m
29	Hazeyview	Savanna	S 25° 04’ 32.6” E 30° 50’ 30.5”	886 m
30	Hazeyview	Savanna	S 25 °04’ 34.4” E 30° 50’ 26.4”	879 m
31	Hazeyview	Savanna	S 25° 04’ 34.4” E 30° 50’ 25.7”	892 m
32	Hazeyview	Savanna	S 25° 04’ 36.6” E 30° 50’ 21.3”	903 m
33	Hazeyview	Savanna	S 25° 04’ 36.9” E 30° 50’ 20.0”	899 m
34	Hazeyview	Savanna	S 25° 04’ 38.9” E 30° 50’ 15.5”	900 m
35	Hazeyview	Savanna	S 25° 04’ 39.7” E 30° 50’ 13.5”	883 m
36	Hazeyview	Savanna	S 25° 04’ 47.4” E 30° 49’ 33.5”	913 m
37	Hazeyview	Savanna	S 25° 04’ 47.8” E 30° 49’ 32.6”	906 m
38	Hazeyview	Savanna	S 25° 04’ 49.2” E 30° 49’ 31.3”	912 m
39	Hazeyview	Savanna	S 25° 04’ 50.2” E 30° 49’ 30.6”	917 m
40	Hazeyview	Savanna	S 25° 04’ 52.2” E 30° 49’ 30.2”	902 m

Appendix 2. Codes used for species names in the multivariate statistical analyses.

Species Name (Indigenous)	Species Code
Acacia ataxacantha	AcacAtax
Acalypha angusta	AcalAngu
Acalypha ornata	AcalOrna
Acalypha punctata	AcalPunc
Acalypha villicaulis	AcalVill
Aerva leucura	AervLeuc
Allophyllus africanus	AlloAfri
Andropogom gayanus var. *gayanus*	AndrGaya
Andropogon schirensis	AndrSchi
Apodytes dimidiata subsp. *dimidiata*	ApodDimi
Artemisia afra	ArteAfra
Asclepias fruticosa	AsclFrut
Berkheya robusta	BerkRobu
Brachiaria deflexa	BracDefl
Brachiaria nigropedata	BracNigr
Buddleja salviifolia	BuddSalv
Canthium inerme	CantIner
Ceratotheca triloba	CeraTril
Chamaecrista mimosoides	ChamMimo
Cissampelos torulosa	CissToru

Clausena anisata	ClauAnis
Clutia virgata	ClutVirg
Combretum erythrophyllum	CombEryt
Commelina eckloniana	CommEckl
Conostomium natalense var. *glabrum*	ConoNata
Crocosmia paniculata	CrocPani
Crossandra greenstockii	CrosGree
Cyanotis lapidosa	CyanLapi
Cynoglossum lanceolatum	CynoLanc
Cynoglossum sp.	CynoglSp
Cyperus fulgens	CypeFulg
Cyphia elata var. *elata*	CyphElat
Cyphostemma simulans	CyphSimu
Cyphostemma woodii	CyphWood
Desmodium setigerum	DesmSeti
Diospyros simii	DiosSimi
Diospyros whyteana	DiosWhyt
Dombeya pulchra	DombPulc
Dovyalis zeyheri	DovyZeyh
Elytraria acanlis	ElytAcan
Englerophytum magalismontanum	EnglMaga
Eriosema psoraleoides	ErioPsor
Euclea crispa var. *crispa*	EuclCris
Flemingia grahamiana	FlemGrah
Geranium baurianum	GeraBaur
Grewia occidentalis	GrewOcci
Gymnosporia buxifolia	GymnBuxi
Gymnosporia harveyana	GymnHarv
Gymnosporia mossambicensis	GymnMoss
Halleria lucida	HallLuci
Helichrysum mariepscopicum	HeliMari
Helichrysum umbraculigerum	HeliUmbr
Helinus integrifolius	HeliInte
Heliotropium ciliatum	HeliCili
Hermannia althaeoides	HermAlth
Hyparrhenia dregeana	HypaDreg
Hypericum revolutum	HypeRevo
Ilex mitis	IlexMiti
Impatiens hochstetteri	ImpaHoch
Indigofera atrata	IndiAtra
Indigofera swaziensis var. *perplexa*	IndiPerp
Indigofera swaziensis var. *swaziensis*	IndiSwaz
Justicia anagalloides	JustAnag
Keetia gueinzii	KeetGuen
Kiggelaria africana	KiggAfri
Knowltonia transvaalensis var. *transvaalensis*	KnowTran
Ledebouria cooperi	LedeCoop
Lippia javanica	LippJava
Loudetia simplex	LoudSimp
Maesa lanceolata	MaesLanc
Mariscus congestus	MariCong
Mariscus laxiflorus	MariLaxi
Mohria caffrorum var. *caffrorum*	MohrCaff
Momordica foetida	MomoFoet
Moraea huttonii	MoraHutt
Nidorella auriculata	NidoAuri
Nidorella hottentotica	NidoHott
Ochna serrulata	OchnSerr

Oldenlandia affinis subsp. *fugax*	OldeAffi
Oplismenus hirtellus	OpliHirt
Pachystigma bowkeri	PachBowk
Pavetta lanceolata	PaveLanc
Pavonia burchellii	PavoBurc
Pelargonium luridum	PelaLuri
Pellaea calomelanos var. *calomelanos*	PellCalo
Phragmites mauritianus	PhraMaur
Phyllanthus reticulates	PhylReti
Phymaspermum athanasioides	PhymAtha
Plectranthus grallatus	PlecGral
Plectranthus laxiflorus	PlecLaxi
Polygala albida var. *albida*	PolyAlbi
Protasparagus asparagoides	ProtAspa
Protasparagus setaceus	ProtSeca
Pseudarthria hookeri var. *hookeri*	PseuHook
Psiadia punctulata	PsiaPunc
Psychotria zombamontana	PsycZomb
Pteridium aquilinum	PterAqui
Rhoicissus tridentate subsp. *cuneifolia*	RhoiTrid
Rhus rigida var. *dentata*	RhusRigi
Rhynchosia minima var. *prostrata*	RhynMini
Rumex sagittatus	RumeSagi
Schistostephium heptalobum	SchiHept
Senecio ilicifolius	SeneIlic
Senecio isatidioides	SeneIsat
Senecio polyodon var. *polyodon*	SenePoly
Setaria megaphylla	SetaMega
Setaria sphacelata var. *sericea*	SetaSpha
Sida rhombifolia	SidaRhom
Smilax anceps	SmilAnce
Solanum retroflexum	SolaRetr
Solanum rubetorum	SolaRube
Solanum terminale subsp. *terminale*	SolaTerm
Spermacoce natalensis	SperNata
Sporobolus africanus	SporAfri
Sporobolus pyramidalis	SporPyra
Stephania abyssinica var. *tomentella*	StepAbys
Sutera floribunda	SuteFlor
Tetraselago longituba	TetrLong
Thelypteris dentata	ThelDent
Thunbergia natalensis	ThunNata
Toddalia asiatica	ToddAsia
Trema orientalis	TremOrie
Tricalysia capensis var. *galpinii*	TricCape
Trichopteryx dregeana	TricDreg
Trimeria grandifolia	TrimGran
Triumfetta pilosa	TriuPilo
Triumfetta rhomboidea var. *rhomboidea*	TriuRhom
Trochomeria hookeri	TrocHook
Unknown sp. 1	UnSpone
Unknown sp. 2	UnSptwo
Unknown sp. 3	UnSpthre
Unknown sp. 4	UnSpfour
Unknown sp. 6	UnSpsix
Vernonia myriantha	VernMyri
Wahlenbergia cuspidata	WahlCusp
Zehneria marlothii	ZehnMarl

Ziziphus mucronata subsp. *mucronata*	ZiziMucr
Ziziphus zeyherana	ZiziZeyh
Species Name (Alien)	**Species Code**
Acacia mearnsii	AcacMear
Acanthospermum glabratum	AcanGlab
Ageratum conyzoides	AgerCony
Agrimonia odorata	AgriOdor
Bidens pilosa	BidePilo
Caesalpinia decapetala	CaesDeca
Centella asiatica	CentAsia
Cestrum laevigatum	CestLaev
Conyza bonariensis	ConyBona
Doryopteris concolor	DoryConc
Eucalyptus grandis	EucaGran
Euphorbia indica	EuphIndi
Grevillea robusta	GrevRobu
Indigofera macrophylla	IndiMacr
Ipomoea purpurea	IpomPurp
Lantana camara	LantCama
Lilium formosanum	LiliForm
Mucuna sp.	MucunaSp
Nephrolepis undulata	NephUndu
Oenothera rosea	OenoRose
Oxalis corniculata	OxalCorn
Physalis peruviana	PhysPeru
Pinus patula	PinuPatu
Populus x canescens	PopuCane
Pseudognaphalium luteo-album	PseuLute
Richardia brasiliensis	RichBras
Rubus cuneifolius	RubuCune
Senna septemtrionalis	SennSept
Solanum americanum	SolaAmer
Solanum mauritianum	SolaMaur
Sonchus oleraceus	SoncOler
Tagetes minuta	TageMinu
Unknown sp. 8	UnSpeigh
Unknown sp. 12	UnSptwel
Unknown sp. 14	UnSpfrtn
Verbena bonariensis	VerbBona

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).

SPECIES	NAMING AUTHORITIES	FAMILY	ALIEN/ INDIGENOUS	INVASIVE STATUS	GRASSLAND		SAVANNA
					Sabie	Graskop	Hazeyview
Grass and sedge species							
Andropogon gayanus var. *gayanus*	Kunth	Poaceae	Indigenous		1	1	1
Andropogon schirensis	A. Rich.	Poaceae	Indigenous		1	1	1
Bothriochloa bladhii	(Retz.) S.T. Blake	Poaceae	Indigenous		0	1	0
Brachiaria deflexa	(Schumach.) C.E. Hubb. ex Robyns	Poaceae	Indigenous	Can be problematic	0	0	1
Brachiaria nigropedata	(Fical. & Hiern) Stapf	Poaceae	Indigenous		1	0	1
Crocosmia aurea var. *pauciflora*	(Pappe ex Hook) Planch, (Milne-Redhead) De Vos	Iridaceae	Indigenous		0	0	1
Crocosmia paniculata	(Klatt) Goldbl.	Iridaceae	Indigenous		1	1	1
Cyperus alternifolius	L.	Cyperaceae	Indigenous		1	0	1
Cyperus esculentus	L.	Cyperaceae	Alien	Weed	1	1	1
Cyperus fulgens	C.B.Cl.	Cyperaceae	Indigenous		1	1	1
Cyperus rupestris var. *rupestris*	Kunth	Cyperaceae	Indigenous		0	0	1
Cyperus sp.	Unknown	Cyperaceae	Indigenous		1	0	0
Hyparrhenia dregeana	(Nees) Stapf	Poaceae	Indigenous		1	0	1
Kyllinga erecta	Schumach.	Cyperaceae	Indigenous	Can be problematic	1	0	1
Loudetia simplex	(Nees) C.E. Hubb	Poaceae	Indigenous		1	0	0

Mariscus congestus	(Vahl) C.B. Cl.	Cyperaceae	Indigenous		1	0	0
Mariscus laxiflorus	Turril.	Cyperaceae	Indigenous		1	1	1
Moraea huttonii	(Bak) Oberm	Iridaceae	Indigenous		1	0	0
Oplismenus hirtellus	(L.) Beauv.	Poaceae	Indigenous		1	1	1
Phragmites mauritianus	Kunth	Poaceae	Indigenous	Can be problematic	1	1	1
Schoenoplectus corymbosus	(Roth. ex Roem. & Schult) J. Raynal	Cyperaceae	Indigenous		1	0	0
Setaria megaphylla	(Steud.) Dur. & Schinz	Poaceae	Indigenous	Weed	1	1	1
Setaria sphacelata var. *sericea*	(Schumach.) Moss. (Stapf) Clayton	Poaceae	Indigenous	Weed	0	1	1
Sporobolus africanus	(Poir.) Robyns & Tournay	Poaceae	Indigenous	Weed	1	1	1
Sporobolus fimbriatus var. *fimbriatus*	(Trin.) Nees	Poaceae	Indigenous	Weed	0	0	1
Sporobolus pyramidalis	Beauv.	Poaceae	Indigenous	Weed	1	1	1
Trichopteryx dregeana	Nees	Poaceae	Indigenous		0	1	0
Unknown sp. 1	Unknown	Cyperaceae	Indigenous		0	0	1
Unknown sp. 2	Unknown	Poaceae	Indigenous		1	1	0
Unknown sp. 3	Unknown	Poaceae	Indigenous		1	0	0
Unknown sp. 4	Unknown	Poaceae	Indigenous		1	0	0
Unknown sp. 5	Unknown	Poaceae	Indigenous		0	0	1
Unknown sp. 6	Unknown	Cyperaceae	Indigenous		1	0	0
Total number of grass and sedge species: 33 (12%)					**24**	**15**	
					27		**22**
Herbaceous species							
Acalypha ornate	Hochst. ex A. Rich.	Euphorbiaceae	Indigenous		1	1	0
Acalypha villicaulis	Hochst.	Euphorbiaceae	Indigenous		0	0	1
Acanthospermum australe	(Loefl.) Kuntze	Asteraceae	Alien	Weed	1	0	0
Acanthospermum glabratum	(DC.) Willd.	Asteraceae	Alien		1	0	0
Achyranthes aspera	L.	Amaranthaceae	Alien	Special effect weed (category 1) – competitive, irritant	0	0	1
Adenia gummifera	(Harv.) Harms	Passifloraceae	Indigenous		0	0	1
Aerva leucura	Moq.	Amaranthaceae	Indigenous		1	1	1
Agathisanthemum bojeri subsp. *bojeri*	Klotzsch	Rubiaceae	Indigenous		0	0	1

Ageratum conyzoides	L.	Asteraceae	Alien	Special effect weed (category 1) – competitive, poisonous	1	1	1
Asclepias fruticosa	L.	Asclepiadaceae	Indigenous		0	1	0
Asclepias physocarpa	(E. Mey.) Schltr.	Asclepiadaceae	Indigenous	Weed	0	1	0
Bidens pilosa	L.	Asteraceae	Alien	Weed	1	1	1
Centella asiatica	(L.) Urban	Apiaceae	Alien		1	1	1
Centella virgata	(L.f.) Drude	Apiaceae	Indigenous		1	1	1
Ceratotheca triloba	(Bernh.) Hook. f.	Pedaliaceae	Indigenous	Weed	1	0	1
Chamaecrista mimosoides	(L.) Greene	Fabaceae	Indigenous		1	1	1
Cirsium vulgare	(Savi) Ten	Asteraceae	Alien	Special effect weed (category 2) – competitive, irritant	1	0	0
Cissampelos torulosa	E. Mey ex Harv.	Menispermaceae	Indigenous		1	0	1
Clematis brachiata	Thunb.	Ranunculaceae	Indigenous		1	0	0
Coccinia palmata	(Sond.) Cogn.	Cucurbitaceae	Indigenous		1	0	0
Coccinia sessilifolia	(Sond.) Cogn.	Cucurbitaceae	Indigenous		1	1	0
Commelina eckloniana	Kunth	Commelinaceae	Indigenous		1	1	1
Conostomium natalense var. *glabratum*	(Hochst.) Brem., Brem.	Rubiaceae	Indigenous		1	1	1
Conyza bonariensis	(L.) Cronq.	Asteraceae	Alien	Weed	1	1	1
Conyza chilensis	Spreng.	Asteraceae	Alien		1	0	1
Conyza ulmifolia	(Burm. f.) Kuntze	Asteraceae	Indigenous		1	0	0
Crossandra greenstockii	S. Moore	Acanthaceae	Indigenous		1	0	0
Cuscuta campestris	Yunck.	Convolvulaceae	Alien	Special effect weed – smothering, parasitic	0	0	1
Cyanotis lapidosa	E. Phillips	Commelinaceae	Indigenous		1	0	0
Cynoglossum lanceolatum	Forssk.	Boraginaceae	Indigenous	Weed	1	0	0
Cynoglossum sp.	Unknown	Boraginaceae	Indigenous		1	0	0
Cyphia elata var. *elata*	Harv.	Lobeliaceae	Indigenous		1	0	1
Cyphostemma simulans	(C.A.Sm.)Wild&Drumm.	Vitaceae	Indigenous		0	0	1
Cyphostemma woodii	(Gilg&Brandt) Descoings	Vitaceae	Indigenous		1	0	1
Desmodium setigerum	(E. Mey.) Benth. ex Harv.	Fabaceae	Indigenous		1	1	1
Dicliptera heterostegia	Presl ex Nees	Acanthaceae	Indigenous		0	1	0
Dicoma macrocephala	DC.	Asteraceae	Indigenous		1	0	1
Doryopteris concolor	(Langsd. & Fisch.) Kuhn	Adiantaceae	Alien		1	1	0

Elytraria acanlis	(L.f.) Lindau	Acanthaceae	Indigenous		1	1	1
Eriosema cordatum	E. Mey	Fabaceae	Indigenous		1	0	0
Eriosema psoraleoides	(Lam.) G. Don	Fabaceae	Indigenous		1	1	1
Fadogia homblei	De Wild.	Rubiaceae	Indigenous		0	1	0
Geranium baurianum	Knuth.	Geraniaceae	Indigenous		1	1	1
Helichrysum mariepscopicum	Hilliard	Asteraceae	Indigenous		0	1	1
Helichrysum umbraculigerum	Less.	Asteraceae	Indigenous		1	1	1
Helinus integrifolius	(Lam.) Kuntze	Rhamnaceae	Indigenous		0	0	1
Heliotropium ciliatum	Kaplan	Boraginaceae	Indigenous		0	0	1
Hermannia althaeoides	Link	Sterculiaceae	Indigenous		0	0	1
Hibiscus engleri	A. Schum.	Malvaceae	Indigenous		1	0	0
Hypochoeris radicata	L.	Asteraceae	Alien	Weed	1	0	0
Impatiens hochstetteri	Warb.	Balsaminaceae	Indigenous		1	0	0
Indigofera swaziensis var. *perplexa*	H. Bol., (N.E. Br.) Gillet	Fabaceae	Indigenous		1	0	0
Indigofera swaziensis var. *swaziensis*	H. Bol	Fabaceae	Indigenous		0	0	1
Ipomoea purpurea	(L.) Roth	Convolvulaceae	Alien	Special effect weed (category 3) – competitive	1	0	0
Ipomoea sp.	Unknown	Convolvulaceae	Alien	Weed	1	0	0
Knowltonia transvaalensis var. *transvaalensis*	Szyszyl.	Ranunculaceae	Indigenous		0	1	0
Laggera crispate	(Vahl) Hepper & J.R.I. Wood	Asteraceae	Indigenous		1	1	0
Lunathyrium japonicum	(Thunb.) Kurata	Athyriaceae	Indigenous		1	0	0
Mohria caffrorum var. *caffrorum*	(L.) Desv.	Schizaeaceae	Indigenous		1	1	0
Momordica foetida	Schumach.	Cucurbitaceae	Indigenous		1	1	1
Mucuna sp.	Unknown	Fabaceae	Alien		0	0	1
Nidorella auriculata	DC.	Asteraceae	Indigenous		0	0	1
Nidorella hottentotica	DC.	Asteraceae	Indigenous		1	1	1
Oenothera rosea	L'Her. ex Aiton.	Onagraceae	Alien	Weed (category 3)	0	0	1
Oldenlandia affinis subsp. *fugax*	(Roem. & Schult.) DC., (Vatke) Verdc.	Rubiaceae	Indigenous		1	1	1

Oldenlandia herbacea var. *herbacea*	(L.) Roxb.	Rubiaceae	Indigenous		0	1	0
Oxalis corniculata	L.	Oxalidaceae	Alien	Weed	1	1	1
Pechuel-Loeschea leubnitziae	(Kontzelo Hoffm.)	Asteraceae	Indigenous		0	0	1
Pellaea calomelanos var. *calomelanos*	(Swartz) Link	Adiantaceae	Indigenous		1	1	1
Persicaria attenuata subsp. *africana*	(R. Br.) Sojak, K. L. Wilson	Polygonaceae	Indigenous		1	0	1
Phymaspermum acerosum	(DC.) Kallersjo	Asteraceae	Indigenous		1	0	0
Phymaspermum athanasioides	(S. Moore) Kallersjo	Asteraceae	Indigenous		0	0	1
Physalis peruviana	L.	Solanaceae	Alien		1	0	1
Polygala albida var. *albida*	Schinz	Malpighiaceae	Indigenous		1	0	1
Protasparagus asparagoides	(L.) W. Wight	Asparagaceae	Indigenous		1	1	1
Protasparagus cooperi	(Bak.) Oberm. comb. nov.	Asparagaceae	Indigenous		0	1	1
Protasparagus falcatus	(L.) Oberm. comb. nov.	Asparagaceae	Alien		0	0	1
Protasparagus minutiflorus	(Kunth) Oberm. comb. nov.	Asparagaceae	Indigenous		1	0	0
Protasparagus setaceus	(Kunth) Oberm. comb. nov.	Asparagaceae	Indigenous		0	1	1
Protasparagus virgatus	(Bak.) Oberm. comb. nov.	Asparagaceae	Indigenous		1	1	0
Pseudognaphalium luteo-album	(L.) Hilliard & Burtt, L.	Asteraceae	Alien	Weed	0	1	0
Pteridium aquilinum	(L.) Kuhn	Dennstaedtiaceae	Indigenous	Weed	1	1	1
Ranunculus multifidus	Forssk.	Ranunculaceae	Indigenous		0	0	1
Rhoicissus tomentosa	(Lam.) Wild&Drummond	Vitaceae	Indigenous		0	0	1
Rhynchosia minima var. *prostrata*	(L.) DC., (Harv.) Meikle	Fabaceae	Indigenous		1	1	1
Rhynchosia totta var. *totta*	(Thunb.) DC.	Fabaceae	Indigenous		1	0	0
Richardia brasiliensis	Gomes	Rubiaceae	Alien	Weed	1	1	1
Rumex sagittatus	Thunb.	Polygonaceae	Indigenous		1	1	1
Selaginella kraussiana	(Kunze) A. Braun	Selaginellaceae	Indigenous		1	1	0
Senecio coronatus	(Thunb.) Harv.	Asteraceae	Indigenous		1	0	0
Senecio digitalifolius	DC.	Asteraceae	Indigenous		1	0	0
Senecio helminthioides	(Sch. Bip.) Hilliard.	Asteraceae	Indigenous		0	0	1
Senecio ilicifolius	Thunb.	Asteraceae	Indigenous	Weed	1	1	1

Senecio isatidioides	Pgill. & C.A. Sm.	Asteraceae	Indigenous		0	1	0
Senecio polyodon var. *polyodon*	DC.	Asteraceae	Indigenous		1	1	1
Senecio poseideonis	Hilliard & Burtt	Asteraceae	Indigenous		0	0	1
Smilax anceps	Meisn.	Smilacaceae	Indigenous		1	1	1
Sonchus oleraceus	L.	Asteraceae	Alien	Weed	1	1	0
Spermacoce natalensis	Hochst.	Rubiaceae	Indigenous		1	0	0
Spermacoce senensis	(Klotzsch) Hiern	Rubiaceae	Indigenous		1	1	0
Stachys natalensis var.*natalensis*	Hochst.	Lamiaceae	Indigenous		0	1	0
Stephania abyssinica var. *tomentella*	(Dill. & Rich.) Walp.	Menispermaceae	Indigenous		1	1	1
Striga elegans	Benth.	Scrophulariaceae	Indigenous		0	1	0
Sutera calycina	(Benth.) Kuntze	Scrophulariaceae	Indigenous		0	0	1
Sutera floribunda	(Benth.) Kuntze	Scrophulariaceae	Indigenous		0	1	0
Tagetes minuta	L.	Asteraceae	Alien	Weed	1	0	1
Tephrosia longipes subsp. *longipes*	Meisn.	Fabaceae	Indigenous		0	1	0
Tephrosia multijuga	R.G.N. Young	Fabaceae	Indigenous		1	0	0
Thalictrum rhynchocarpum	Dill. & Rich.	Ranunculaceae	Indigenous		1	0	0
Thelypteris dentata	(Forssk.) E. St. John	Thelypteridaceae	Indigenous		1	0	0
Thunbergia natalensis	Hook.	Acanthaceae	Indigenous		1	1	0
Trochomeria hookeri	Harw.	Cucurbitaceae	Indigenous		1	0	1
Unknown sp. 10	Unknown	Unknown	Alien		1	0	0
Unknown sp. 11	Unknown	Unknown	Alien		0	1	0
Unknown sp. 15	Unknown	Unknown	Alien		0	1	0
Verbena bonariensis	L.	Verbenaceae	Alien	Weed	1	1	1
Veronica anagallis-aquatica	L.	Scrophulariaceae	Indigenous		1	0	0
Wahlenbergia cuspidata	Brehmer	Campanulaceae	Indigenous		1	1	1
Wahlenbergia grandiflora	A.DC.	Campanulaceae	Indigenous		1	0	0
Wahlenbergia squamifolia	V. Brehm	Campanulaceae	Indigenous		1	1	1
Zehneria marlothii	(Cogn.) R.&A. Fernandes	Cucurbitaceae	Indigenous		1	1	1
Total number of herbaceous species: 121 (43%)					**83**	**59**	
					100		**67**
Shrub species							

Abutilon fruticosum	Guill. &Perr.	Malvaceae	Indigenous		0	0	1
Acalypha angusta	Sond.	Euphorbiaceae	Indigenous		1	1	0
Acalypha punctata	Meisn.	Euphorbiaceae	Indigenous		1	0	0
Adenopodia spicata	(E. Mey) Presl	Mimosaceae	Indigenous		1	0	0
Artemisia afra	Jacq. ex Willd.	Asteraceae	Indigenous		1	0	0
Asplenium aethiopicum	(Burm) Becherer	Aspleniaceae	Alien		0	0	1
Berkheya carlinopsis subsp. *magalismontana*	Welw. ex O. Hoffm., (H. Bolus) Roessl.	Asteraceae	Indigenous		1	0	0
Berkheya robusta	Bohnen ex Roessl.	Asteraceae	Indigenous		1	1	1
Berkheya setifera	DC.	Asteraceae	Indigenous		0	0	1
Caesalpinia decapetala	(Roth) Alston	Caesalpiniaceae	Alien	Weed (category 2) – transformer	1	1	1
Canna indica	L.	Cannaceae	Alien	Weed – potential transformer	0	0	1
Canthium inerme	(L.f.) Kunze	Rubiaceae	Indigenous		0	0	1
Clausena anisata	(Willd.) Hook.f. ex Benth.	Rutaceae	Indigenous		0	1	1
Cliffortia erectisepala	Weim.	Rosaceae	Indigenous		0	1	0
Cliffortia linearifolia	Eckl. & Zeyh.	Rosaceae	Indigenous		0	0	1
Clutia virgata	Pax & K. Hoffm.	Euphorbiaceae	Indigenous		1	1	1
Colocasia esculenta	(L.) Schott	Araceae	Alien		1	0	0
Crotalaria brachycarpa	(Benth.) Burt & Davy	Fabaceae	Indigenous		1	0	0
Crotalaria mucronata	Desv.	Fabaceae	Indigenous		0	1	0
Diospyros galpinii	(Hiern) De Winter	Ebenaceae	Indigenous		0	1	0
Diospyros simii	(Kuntze) De Winter	Ebenaceae	Indigenous		0	1	1
Diospyros whyteana	(Hiern) F. White	Ebenaceae	Indigenous		0	1	1
Dovyalis zeyheri	(Sond.) Warb.	Flacourtiaceae	Indigenous		1	0	0
Euclea crispa var. *crispa*	(Thunb.) Guerke	Ebenaceae	Indigenous		0	1	1
Euclea divinorum	Hiern	Ebenaceae	Indigenous		1	0	1
Euphorbia indica	Lam.	Euphorbiaceae	Alien		1	0	1
Flemingia grahamiana	Wight & Arn.	Fabaceae	Indigenous		1	0	1
Gymnosporia buxifolia	(L.) Szyszyl.	Celastraceae	Indigenous		1	0	0
Gymnosporia harveyana	Loes.	Celastraceae	Indigenous		0	0	1
Gymnosporia mossambicensis	(Klotzsch) Blakelock	Celastraceae	Indigenous		0	0	1
Heteropyxis natalensis	Harv.	Heteropyxidaceae	Indigenous		0	0	1
Hypericum aethiopicum subsp.	Thunb., (Bred.) N.K.B.	Hypericaceae	Indigenous		1	0	0

sonderi							
Hypericum natalense	Woody & Evans	Clusiaceae	Indigenous		0	1	0
Hypericum revolutum	Vahl	Clusiaceae	Indigenous		1	0	0
Indigofera atrata	N. E. Br.	Fabaceae	Indigenous		0	1	0
Indigofera macrophylla	Schum. & Thonn.	Fabaceae	Alien	Weed	1	1	1
Justicia anagalloides	(Nees) T. Anderson	Acanthaceae	Indigenous		1	0	0
Keetia queinzii	(Sond.) Bridson	Rubiaceae	Indigenous		0	0	1
Kniphofia linearifolia	Bak.	Asphodelaceae	Indigenous		0	1	0
Lantana camara	L.	Verbenaceae	Alien	Invader (category 1) – transformer	1	1	1
Ledebouria cooperi	(Hook. f.) Jessop	Liliaceae	Indigenous		1	1	0
Leonotis ocymifolia var. *raineriana*	(Burm. f.) Iwarsson, Iwarsson	Lamiaceae	Indigenous	Weed	1	0	0
Lilium formosanum	A. Wallace	Liliaceae	Alien	Invasive and special effect weed (category 3) – competitive	1	0	1
Lippia javanica	(Burm. f.) Spreng.	Verbenaceae	Indigenous		1	1	1
Monanthotaxis caffra	(Sond.) Verdc.	Annonaceae	Indigenous		0	0	1
Mundulea sericea	(Willd.) A. Chev.	Fabaceae	Indigenous		0	0	1
Nephrolepis undulata	(Afz. ex Sw.) J. Sim	Davalliaceae	Alien		0	0	1
Ochna serrulata	(Hochst.) Walp.	Ochnaceae	Indigenous		0	1	0
Pavetta lanceolata	Eckl.	Rubiaceae	Indigenous		0	0	1
Pavonia burchellii	(DC.) R.A. Dyer	Malvaceae	Indigenous		1	0	0
Pelargonium luridum	(Andr.) Sweet	Geraniaceae	Indigenous		0	1	0
Phyllanthus parvulus	Sond.	Euphorbiaceae	Indigenous		0	0	1
Phyllanthus reticulatus	Poir.	Euphorbiaceae	Indigenous		1	1	1
Phytolacca octandra	L.	Phytolaccaceae	Alien	Weed (category 1)	1	0	1
Plectranthus grallatus	Briq.	Lamiaceae	Indigenous		0	1	1
Plectranthus hadiensis var. *tomentosus*	(Forssk.) Schweinf. ex Sprenger, (Benth.) Codd	Lamiaceae	Indigenous		1	0	0
Plectranthus laxiflorus	Benth.	Lamiaceae	Indigenous		1	0	0
Plectranthus praetermissus	Codd.	Lamiaceae	Indigenous		0	0	1
Populus x canescens	(Ait.) Sm.	Salicaceae	Alien	Invader (category 2) – transformer	0	1	0

Psiadia punctulata	(DC.) Oliv. & Hiern ex Vatke	Asteraceae	Indigenous		1	0	0
Rhoicissus tridentata subsp. *cuneifolia*	(L.f.) Wild & Drummond, (Ecl. & Zeyh.)	Vitaceae	Indigenous		1	1	1
Rhus rigida var. *dentata*	Mill., (Engl.) Moffett	Anacardiaceae	Indigenous		1	1	1
Rubus cuneifolius	Pursh	Rosaceae	Alien	Invader (category 1)	1	1	1
Schistostephium heptalobum	(DC.) Oliv. & Hiern	Asteraceae	Indigenous		1	1	1
Sida rhombifolia	L.	Malvaceae	Indigenous	Weed	1	0	1
Solanum americanum	Mill.	Solanaceae	Alien		1	0	0
Solanum mauritianum	Scop.	Solanaceae	Alien	Weed (category 1) – transformer	1	1	1
Solanum nigrum	L.	Solanaceae	Alien	Can be problematic	1	0	1
Solanum retroflexum	Dun.	Solanaceae	Indigenous		1	0	1
Solanum rubetorum	Dunal	Solanaceae	Indigenous		1	0	1
Solanum terminale subsp. *terminale*	Forsk.	Solanaceae	Indigenous		0	0	1
Tetraselago longituba	(Rolfe) Hilliard & Burtt	Selaginaceae	Indigenous		1	1	0
Toddalia asiatica	(L.) Lam.	Rutaceae	Indigenous		1	0	1
Tragia sp.	Unknown	Euphorbiaceae	Indigenous		0	0	1
Trema orientalis	(L.) Blume	Celtidaceae	Indigenous		0	1	1
Trimeria grandifolia	(Hochst.) Warb.	Flacourtiaceae	Indigenous		0	1	1
Triumfetta pilosa	Roth	Malvaceae	Indigenous	Weed	1	1	0
Triumfetta rhomboidea var. *rhomboidea*	Jacq.	Malvaceae	Indigenous	Weed	0	1	1
Unknown sp. 7	Unknown	Fabaceae	Alien		1	0	0
Unknown sp. 12	Unknown	Unknown	Alien		1	0	0
Vernonia adoensis var. *kotschyana*	Sch. Bip. ex Walp.	Asteraceae	Indigenous		1	0	1
Vernonia myriantha	Hook. f.	Asteraceae	Indigenous		1	1	1
Total number of shrub species: 82 (29%)					**47**	**34**	
					64		**50**
Tree species							
Acacia ataxacantha	DC.	Mimosaceae	Indigenous		0	1	1
Acacia mearnsii	De Wild.	Mimosaceae	Alien	Invader (category 2) –	1	0	1

				transformer			
Acacia melanoxylon	R. Br.	Mimosaceae	Alien	Invader (category 2) – transformer	1	0	0
Agrimonia odorata	Mill.	Rosaceae	Alien	Weed (category 3)	1	1	1
Allophyllus africanus	Beuv.	Sapindaceae	Indigenous		0	0	1
Apodytes dimidiata subsp. *dimidiata*	E. Mey. ex Arn.	Icacinaceae	Indigenous		0	1	1
Bowkeria cymosa	MacOwan	Scrophulariaceae	Indigenous		1	0	0
Brachylaena transvaalensis	E. Phillips & Schweick	Asteraceae	Indigenous		1	0	1
Buddleja auriculata	Benth.	Buddlejaceae	Indigenous		1	0	0
Buddleja pulchella	(L.) Lam.	Buddlejaceae	Indigenous		0	1	0
Buddleja salviifolia	N.E. Br.	Buddlejaceae	Indigenous		1	1	1
Carya illinoensis	(Wangenh.) K. Koch	Juglandaceae	Alien		0	0	1
Cassinopsis ilicifolia	(Hochst.) Kuntze	Icacinaceae	Indigenous		1	0	0
Cestrum laevigatum	Schlechtd.	Solanaceae	Alien	Weed – transformer	0	0	1
Cinnamomum camphora	(T. Nees & Eberm.)	Lauraceae	Alien	Weed – transformer	0	0	1
Combretum erythrophyllum	(Burch.) Sond.	Combretaceae	Indigenous		0	1	1
Dalbergia armata	E. Mey	Fabaceae	Indigenous		0	0	1
Dissotis canescens	(E. Mey ex Graham) Hook. f.	Melastomataceae	Indigenous		1	0	1
Dombeya pulchra	N. E. Br.	Sterculiaceae	Indigenous		1	1	1
Englerophytum magalismontanum	Krause	Sapotaceae	Indigenous		0	0	1
Erythrina humeana	Spreng.	Fabaceae	Indigenous		0	1	0
Eucalyptus grandis	(Hill ex Maiden)	Myrtaceae	Alien	Invader (category 2) – transformer	1	1	1
Ficus sur	Forssk.	Moraceae	Indigenous		0	0	1
Grevillea robusta	Cunn. ex R. Br.	Proteaceae	Alien	Invader (category 3) – potential transformer	1	0	0
Grewia occidentalis	L.	Tiliaceae	Indigenous		1	0	1
Halleria lucida	L.	Scrophulariaceae	Indigenous		1	1	1
Ilex mitis	(L.) Radlk.	Aquifoliaceae	Indigenous		1	0	0
Kiggelaria africana	L.	Flacourtiaceae	Indigenous		0	1	0
Maesa lanceolata	Forssk.	Myrsinaceae	Indigenous		1	1	1

Manihot esculenta	Crantz	Euphorbiaceae	Alien		1	0	0
Ocotea kenyensis	(Chiov.) Robyns & R. Wilczek	Lauraceae	Indigenous		0	0	1
Pachystigma bowkeri	Robyns	Rubiaceae	Indigenous		0	0	1
Pappea capensis	Eckl. & Zeyh.	Sapindaceae	Indigenous		1	0	0
Pinus patula	Schltdl. & Cham.	Pinaceae	Alien	Invader (category 2) – transformer	1	0	1
Pseudarthria hookeri var. *hookeri*	Wight & Arn.	Fabaceae	Indigenous		1	1	1
Psychotria zombamontana	(Kuntze) Petit	Rubiaceae	Indigenous		1	1	1
Senna septemtrionalis	(Viv.) Irwin & Barneby	Caesalpiniaceae	Alien	Invader and special effect weed – competitive	0	0	1
Tarchonanthus trilobus var. *galpinii*	DC. (Hutch & E. Phillips) Paiva	Asteraceae	Indigenous		1	0	0
Tricalysia capensis var. *galpinii*	(Meisn. ex Hochst.) Sim, (Schinz) Robbrecht.	Rubiaceae	Indigenous		0	0	1
Unknown sp. 8	Unknown	Fabaceae	Alien		1	1	1
Unknown sp. 9	Unknown	Unknown	Alien		0	0	1
Unknown sp. 13	Unknown	Rutaceae	Alien		0	1	1
Unknown sp. 14	Unknown	Unknown	Alien		0	0	1
Vitex zeyheri	Sond.	Lamiaceae	Indigenous		1	0	0
Ziziphus mucronata subsp. *mucronata*	Willd.	Rhamnaceae	Indigenous		0	0	1
Ziziphus zeyherana	Sond.	Rhamnaceae	Indigenous		0	0	1
Total number of tree species: 46 (16%)					**24**	**16**	
					31		**32**
TOTAL NUMBER OF ALIENS: 60 (21%) **TOTAL NUMBER OF INDIGENOUS: 222 (79%)**					**178**	**124**	
TOTAL NUMBER OF SPECIES: 282					**222**		**171**

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).

SPECIES	NAMING AUTHORITIES	FAMILY	ALIEN/ INDIGENOUS	INVASIVE STATUS	GRASSLAND	SAVANNA
Grass and sedge species						
Bothriochloa radicans	(Lehm) A. Camus	Poaceae	Indigenous		0	1
Brachiaria deflexa	(Schumach.) C.E. Hubb.	Poaceae	Indigenous	Can be problematic	1	1
Cymbopogon validus	(Stapf) Stapf ex Burtt	Poaceae	Indigenous		1	0
Cyperus esculentus	L.	Cyperaceae	Alien	Weed	1	1
Hemarthria altissima	L.	Poaceae	Indigenous		1	0
Hyparrhenia dichroa	(Steud.) Stapf	Poaceae	Indigenous		1	1
Ischaemum fasciculatum	L.	Poaceae	Indigenous		1	1
Kyllinga erecta	L.	Cyperaceae	Indigenous	Can be problematic	1	1
Mariscus congestus	(Vahl) C.B. Cl.	Cyperaceae	Indigenous		1	1
Panicum aequinerve	Nees	Poaceae	Indigenous		1	0
Panicum maximum	Jacq.	Poaceae	Indigenous		1	0
Paspalum urvillei	Steud.	Poaceae	Alien		1	1
Pennisetum macrourum	Leeke	Poaceae	Indigenous		1	1
Phragmites australis	(Cav.) Steud.	Poaceae	Indigenous		1	1
Setaria incrassata	(Steud.) Dur. & Shinz.	Poaceae	Indigenous		1	1
Setaria megaphylla	(Hochst.) Hack.	Poaceae	Indigenous	Weed	1	1
Sorghum bicolour	L.	Poaceae	Indigenous		1	1
Sporobolus consimilis	Fresen	Poaceae	Indigenous		1	0
Themeda triandra	Forssk.	Poaceae	Indigenous		1	0
Unknown sp.	Unknown	Poaceae	Indigenous		1	1
Total number of grass and sedge species: 20 (12%)					**19**	**14**
Herbaceous species						
Acalyphya caperonioides	Baill.	Euphorbiaceae	Indigenous		1	0

Acalypha viliicaulis	Hochst.	Euphorbiaceae	Indigenous		1	1
Achyranthes aspera	L.	Amaranthaceae	Alien	Special effect weed (category 1) – competitive, irritant	1	1
Adenocline acuta	(Thunb.) Baill	Euphorbiaceae	Indigenous		1	0
Adiantum poiretii	Wikstr.	Adiantaceae	Alien		1	0
Anomatheca laxa	(Thunb.) Goldbl.	Iridaceae	Indigenous		1	0
Anthospermum welwitschii	Hiern	Rubiaceae	Indigenous		1	1
Asclepias physocarpa	(E. Mey.) Schltr.	Asclepiadaceae	Indigenous	Weed	1	0
Bidens pilosa	L.	Asteraceae	Alien	Weed	1	1
Cheilanthes viridus	(Forssk.) Swartz	Adiantaceae	Indigenous		1	1
Chenopodium schraderianum	Schult.	Chenopodiaceae	Alien		1	1
Convolvulus arvensis	L. Field	Convolvulaceae	Alien	Weed (category 1)	1	1
Conyza aegyptiaca	(L.) Ait.	Asteraceae	Alien		1	0
Conyza albida	Spreng	Asteraceae	Indigenous		1	1
Corchorus asperifolius	Burch.	Tiliaceae	Alien		1	1
Cucumis zeyheri	Sond.	Cucurbitaceae	Indigenous		1	1
Cynoglossum lanceolatum	Forssk.	Boraginaceae	Indigenous	Weed	1	1
Desmodium repandum	(Vahl) DC.	Fabaceae	Indigenous		1	0
Dietes iridioides	(L.) Sweet ex Klatt	Iridaceae	Indigenous		0	1
Eriosema pauciflorum	Notzsch	Fabaceae	Indigenous		1	1
Eriosema psoraleoides	(Lam.) G. Dom.	Fabaceae	Indigenous		1	0
Foeniculum vulgare	Mill.	Apiaceae	Alien		1	0
Gladiolus dalenii	Van Geel	Iridaceae	Indigenous		1	1
Helichrysum acutatum	DC.	Asteraceae	Indigenous		1	0
Helichrysum revolutum	(Thunb.) Less.	Asteraceae	Indigenous		0	1
Helichrysum ruderale	Hilliard & Burtt	Asteraceae	Indigenous		1	0
Helichrysum rugulosum	Less.	Asteraceae	Indigenous		0	1
Helichrysum sp.	Mill.	Asteraceae	Indigenous		1	1
Hydrocotyle americana	L.	Apiaceae	Indigenous		1	1
Hypoestes forskaolii	(Vahl) R. Br.	Acanthaceae	Indigenous		0	1
Hypoxis rigidula	Bak.	Hypoxidaceae	Indigenous		1	0
Hypoxis sp.	L.	Hypoxidaceae	Indigenous		1	0
Indigofera swaziensis	H. Bol.	Fabaceae	Indigenous		1	1

Ipomoea pes-caprae	(L.) R. Br.	Convolvulaceae	Indigenous		0	1
Ipomoea purpurea	(L.) Roth	Convolvulaceae	Alien	Special effect weed (category 3) – competitive	1	0
Lagenaria siceraria	(Malina) Standl.	Cucurbitaceae	Indigenous		1	0
Medicago hispida	Gaertn.	Fabaceae	Alien		1	0
Mentha longifolia	(L.) Hudson	Lamiaceae	Indigenous		1	0
Myrsiphyllum volubile	(Thunb.) Oberm.	Liliaceae	Indigenous		1	0
Nepeta cataria	L.	Lamiaceae	Indigenous		1	1
Oxalis corniculata	L.	Oxalidaceae	Alien	Weed	1	0
Oxalis latifolia	H.B.K.	Oxalidaceae	Indigenous		1	1
Passiflora edulis	L.	Passifloraceae	Indigenous		1	1
Passiflora sp.	L.	Passifloraceae	Alien	Weed (category 1)	1	1
Pentodon pentandrus	(Schumach. & Thonn.) Vatke	Rubiaceae	Indigenous		1	1
Physalis angulata	L.	Solanaceae	Alien		1	0
Protasparagus cooperi	(Bak.)	Asparagaceae	Indigenous		1	0
Protasparagus exuvialis	(Burch.) Oberm.	Asparagaceae	Indigenous		1	0
Pseudarthria hookeri	Wright & Arn.	Fabaceae	Indigenous		1	1
Pseudognaphalium luteo-album	(L.) Hilliard & Burtt.	Asteraceae	Alien	Weed	1	0
Pteridium aquilinum	(L.) Kuhn	Dennstaedtiaceae	Indigenous	Weed	1	1
Rhynchosia galpinii	Bak. f.	Fabaceae	Indigenous		0	1
Rhynchosia hirta	(Andr.) Meikle & Verde.	Fabaceae	Indigenous		1	1
Rumohra adiantiformis	(G. Farst.) Ching	Polypodiaceae	Indigenous		1	1
Scadoxus multiflorus	(Martyn) Raf.	Amarillidaceae	Indigenous		1	0
Selago transvaalensis	Rolfe	Selaginaceae	Indigenous		1	0
Senecio affinis	DC.	Asteraceae	Indigenous		1	0
Senecio conrathii	N.E. Br.	Asteraceae	Indigenous		1	0
Senecio coronatus	(Thunb.) Harv.	Asteraceae	Indigenous		1	1
Senecio graminifolius	(Thunb.) DC.	Asteraceae	Indigenous		1	1
Senecio poseideonis	Hilliard & Burtt.	Asteraceae	Indigenous		1	0
Senecio quinquelobus	(Thunb.) DC.	Asteraceae	Indigenous		1	0
Senecio serratuloides	DC.	Asteraceae	Indigenous		1	0
Senna septemtrionalis	(Viv) Irwin & Barneby	Fabaceae	Alien	Invader and special effect weed –	0	1

				competitive		
Smilax anceps	Willd.	Smilaceae	Indigenous		1	1
Solanum nigrum	L.	Solanaceae	Alien	Can be problematic	1	0
Solanum sisymbrifolium	Lam.	Solanaceae	Alien	Weed (category 1)	1	0
Stephania abyssinica	(Dill. & Rich) Walp.	Menispermaceae	Indigenous		1	1
Thelypteris pozoi	(Lag.) Morton	Thelypteridaceae	Indigenous		1	1
Thunbergia natalensis	Hook.	Thunbergiaceae	Indigenous		1	1
Wahlenbergia undulata	(L.f.) A. DC.	Campanulaceae	Indigenous		1	0
Total number of herbaceous species: 71 (44%)					**64**	**38**
Shrub species						
Ageratum houstonianum	Mill.	Asteraceae	Alien	Weed (category 1)	1	0
Antidesma venosum	E, Mey. ex Tul.	Euphorbiaceae	Indigenous		0	1
Artemisia afra	Jacq. ex Willd.	Asteraceae	Indigenous		1	0
Brachylaena discolor	(Phill. & Schweick) J. Paiva	Asteraceae	Indigenous		0	1
Caesalpinia decapetala	(Roth) Alston	Caesalpiniaceae	Alien	Weed (category 2) – transformer	1	1
Cassinopsis ilicifolia	(Hochst.) Kuntze	Icacinaceae	Indigenous		1	1
Clausena anisata	(Willd.) Hook. f. ex Benth	Rutaceae	Indigenous		1	0
Cliffortia linearifolia	Eckl. & Zeyh.	Rosaceae	Indigenous		1	0
Clutia affinis	Sond.	Euphorbiaceae	Indigenous		1	1
Clutia monticola	S. Moore	Euphorbiaceae	Indigenous		1	0
Dalbergia armata	E. Mey.	Fabaceae	Indigenous		1	1
Diospyros galpinii	(Hiern) De Winter	Ebenaceae	Indigenous		1	1
Diospyros lycipioides	Desf.	Ebenaceae	Indigenous		0	1
Diospyros whyteana	(Hiern) F. White	Ebenaceae	Indigenous		0	1
Endostemon obtusifolius	(E. Mey. ex Benth) N.E. Br.	Lamiaceae	Indigenous		1	1
Englerophytum magalismontanum	(Sond.) Heine & J.H. Hemsl.	Sapotaceae	Indigenous		1	1
Euclea crispa	(Thunb.) Guerke	Ebenaceae	Indigenous		1	1
Euclea natalensis	DC.	Ebenaceae	Indigenous		1	1
Flemingia grahamiana	Wight & Arn.	Fabaceae	Indigenous		0	1
Gymnosporia mossambicensis	(Klotzsch) Blakelock	Celastraceae	Indigenous		1	1
Hymenodictyon parvifolium	Oliv.	Rubiaceae	Indigenous		0	1
Indigofera daleoides	Benth. ex Harv.	Fabaceae	Indigenous		1	0
Keetia gueinzii	(Sond.) Bridson	Rubiaceae	Indigenous		1	1

Lantana camara	L.	Verbenaceae	Alien	Invader (category 1) – transformer	1	1
Leonotis sp.	(Pers.) R. Br.	Lamiaceae	Indigenous		1	0
Leucosidea sericea	Eckl. & Zeyh.	Rosaceae	Indigenous		1	0
Lippia javanica	(Burm. f.) Spreng.	Verbenaceae	Indigenous		1	1
Maesa lanceolata	Forssk.	Myrsinaceae	Indigenous		0	1
Maytenus polyacantha	(Sond.) Marais	Celastraceae	Indigenous		1	1
Passerina filiformis	L.	Thymelaeaceae	Indigenous		1	1
Pavetta gracilifolia	Brem.	Rubiaceae	Indigenous		0	1
Pavonia burchellii	(DC.) R.A. Dyer	Fabaceae	Indigenous		1	0
Plectranthus laxiflorus	Benth.	Lamiaceae	Indigenous		1	1
Plectranthus oertendahlii	Th. Fr. Jr.	Lamiaceae	Indigenous		1	1
Rhamnus prinoides	L' Herit.	Rhamnaceae	Indigenous		1	0
Rhoicissus torminalis	(Lam.) Wild & Drum.	Vitaceae	Indigenous		1	1
Rhoiscissus tridentata subsp. *cuneifolia*	(L.f.) Wild & Drum.	Vitaceae	Indigenous		1	1
Rhus dentata	Thunb.	Anacardiaceae	Indigenous		1	1
Rhus discolor	E. Mey. ex Sond.	Anacardiaceae	Indigenous		1	1
Rubus cuneifolius	Pursh	Rosaceae	Alien	Invader (category 1)	1	1
Solanum mauritianum	Scop.	Solanaceae	Alien		1	1
Toddalia asiatica	(L.) Lam.	Rutaceae	Indigenous		1	1
Trimeria grandifolia	(Hochst.) Warb.	Flacourtiaceae	Indigenous		1	0
Verbena bonariensis	L.	Verbenaceae	Alien	Weed	1	1
Total number of shrub species: 44 (27%)					**36**	**33**
Tree species						
Acacia ataxacantha	DC. Benth.	Mimosaceae	Indigenous		1	1
Acacia mearnsii	De Wild.	Mimosaceae	Alien	Invader (category 2) – transformer	1	1
Acacia pycnantha	Benth.	Mimosaceae	Alien	Invader (category 1)	1	1
Apodytes dimidiata subsp. *dimidiata*	E. Mey. ex Arn.	Icacinaceae	Indigenous		1	1
Breonadia salicina	(Vahl) Hepper & Wood	Rubiaceae	Indigenous		1	0
Buddleja loricata	Leeuwenberg	Loganiaceae	Indigenous		1	1
Buddleja salviifolia	(L.) Lam.	Loganiaceae	Indigenous		1	1
Cephalanthus natalensis	Oliv.	Rubiaceae	Indigenous		0	1

Combretum celastroides	Welw. ex Laws.	Combretaceae	Indigenous		0	1
Combretum fragrans	Holfm.	Combretaceae	Indigenous		1	1
Combretum kraussii	Hochst.	Combretaceae	Indigenous		1	1
Cussonia paniculata	Eckl. & Zeyh.	Araliaceae	Indigenous		1	0
Cyathea dregei	Kunze	Cyatheaceae	Indigenous		1	1
Dombeya rotundifolia	(Hochst.) Plunch	Sterculiaceae	Indigenous		1	0
Eucalyptus grandis	W. Hill. ex Maiden	Myrtaceae	Alien	Invader (category 2) – transformer	1	1
Ficus sur	Forssk.	Moraceae	Indigenous		1	0
Grevillea robusta	A. Cunn. ex R. Br.	Proteaceae	Alien	Invader (category 3) – potential transformer	1	0
Grewia occidentalis	L.	Tiliaceae	Indigenous		1	1
Halleria lucida	L.	Scrophulariaceae	Indigenous		0	1
Ilex mitis	(L.) Radlh.	Aquifoliaceae	Indigenous		1	0
Pinus patula	Schlechtd. & Cham.	Pinaceae	Alien	Invader (category 2) – transformer	1	1
Prunus persica	(L.) Batsch	Rosaceae	Indigenous		0	1
Rawsonia lucida	Harv. & Sond.	Flacourtiaceae	Indigenous		1	1
Sequoia sempervirens	(Taxod.)	Taxodiaceae	Alien		1	0
Syzygium cordatum	Hochst.	Myrtaceae	Indigenous		0	1
Tricalysia capensis	(Meisn. ex Hochst.) Sim	Polypodiaceae	Indigenous		1	1
Zanthoxylum davyi	(Verdoorn) Waterm.	Rutaceae	Indigenous		0	1
Ziziphus mucronata	Willd.	Rhamnaceae	Indigenous		0	1
Total number of tree species: 28 (17%)					**21**	**21**
TOTAL NUMBER OF ALIENS: 31 (19%) **TOTAL NUMBER OF INDIGENOUS: 132 (81%)** **TOTAL NUMBER OF SPECIES: 163**					**140**	**106**

Appendix 5. Statistical *P*-values for t-tests (for independent-samples) for differences in several tested variables between the grassland and savanna biomes. *d.f.* = 38. Bold text indicates $P < 0.05$.

Tested Variable		*P* – value
Total species richness	1 m^2	**0.003**
	10 m^2	**0.008**
	100 m^2	**0.023**
	1000 m^2	**0.003**
Total alpha diversity	1 m^2	**0.011**
	10 m^2	**0.004**
	100 m^2	**0.042**
Total species Evenness	1 m^2	0.108
	10 m^2	0.442
	100 m^2	0.744
% Alien vegetation aerial cover	Total	0.440
	> 5 m	0.364
	2 – 5 m	**0.026**
	< 2 m	0.068
Ground cover	Soil	0.425
	Rock	**0.037**
	Litter	0.961
	Herbaceous	0.761
	Grass	0.557
Soil element	Phosphate	0.055
	Potassium	0.358
	Calcium	0.687
	Magnesium	0.192
	Zinc	0.157
	Manganese	0.317
	Copper	**0.009**

Appendix 6. Statistical *P*-values for one-way ANOVA analyses for differences in several tested variables between the Sabie (grassland), Graskop (grassland) and Hazeyview (savanna) regions. *d.f.* = 2,37. Bold text indicates $P < 0.05$.

Tested Variable		Sabie*Graskop	Sabie*Hazeyview	Graskop*Hazeyview
Total species richness	1 m^2	0.174	0.244	**0.002**
	10 m^2	0.593	**0.020**	0.219
	100 m^2	0.419	**0.028**	0.450
	1000 m^2	0.119	**0.001**	0.283
Total alpha diversity	1 m^2	0.119	0.519	**0.004**
	10 m^2	0.988	0.060	**0.041**
	100 m^2	0.948	0.296	0.160
Total species evenness	1 m^2	0.919	0.278	0.520
	10 m^2	0.288	0.969	0.289
	100 m^2	0.166	0.709	0.378
% Alien vegetation aerial cover	Total	0.708	0.524	0.983
	> 5 m	0.949	0.841	0.631
	2 – 5 m	0.638	0.053	0.369

	< 2 m	0.899	0.425	0.193
Ground cover	Soil	0.969	0.866	0.713
	Rock	**0.006**	**0.001**	0.998
	Litter	0.994	0.994	0.999
	Herbaceous	0.790	0.991	0.806
	Grass	0.543	0.521	0.991
Soil element	Phosphate	0.923	0.177	0.362
	Potassium	0.139	0.149	0.939
	Calcium	**0.005**	0.062	0.262
	Magnesium	**$2x10^{-5}$**	**0.001**	0.319
	Zinc	0.323	0.933	0.117
	Manganese	**0.013**	**0.032**	0.694
	Copper	0.746	0.182	**0.031**
Slope		0.596	**0.032**	**0.002**
Soil organic matter		0.769	0.226	**0.038**
Total nitrogen		**0.002**	**$5x10^{-5}$**	0.999
pH		0.363	0.999	0.263
Soil compaction		**0.007**	**0.034**	0.492

Appendix 7. Statistical *P*-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. *d.f.* = 38. Bold text indicates $P < 0.05$.

Tested Variable	**Growth Form**	**Quadrat Size**	***P* – value**
Species richness	Trees	1 m^2	0.589
		10 m^2	0.313
		100 m^2	0.164
		1000 m^2	0.482
	Shrubs	1 m^2	**$5x10^{-6}$**
		10 m^2	**0.005**
		100 m^2	**0.003**
		1000 m^2	0.054
	Herbs	1 m^2	**0.025**
		10 m^2	**0.045**
		100 m^2	**0.037**
		1000 m^2	**0.002**
	Grasses	1 m^2	0.876
		10 m^2	0.538
		100 m^2	**0.004**
		1000 m^2	**0.011**
Alpha diversity	Trees	1 m^2	0.477
		10 m^2	0.801
		100 m^2	0.125
	Shrubs	1 m^2	**0.002**
		10 m^2	**0.014**
		100 m^2	**0.024**
	Herbs	1 m^2	0.124
		10 m^2	0.197

		100 m^2	**0.011**
	Grasses	1 m^2	0.937
		10 m^2	0.177
		100 m^2	**0.046**
Species evenness	Trees	1 m^2	0.369
		10 m^2	0.397
		100 m^2	0.630
	Shrubs	1 m^2	**0.001**
		10 m^2	0.578
		100 m^2	0.072
	Herbs	1 m^2	0.093
		10 m^2	0.875
		100 m^2	0.260
	Grasses	1 m^2	0.913
		10 m^2	0.125
		100 m^2	0.155

Appendix 8. Statistical *P*-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. *d.f.* = 2,37. Bold text indicates $P < 0.05$.

Tested Variable	**Growth Form**	**Quadrat Size**	**Sabie* Graskop**	**Sabie* Hazeyview**	**Graskop* Hazeyview**
Species richness	Trees	1 m^2	0.849	0.991	0.732
		10 m^2	0.991	0.736	0.644
		100 m^2	0.899	0.351	0.649
		1000 m^2	0.961	0.909	0.749
	Shrubs	1 m^2	0.999	**0.002**	**0.002**
		10 m^2	0.590	**0.013**	0.164
		100 m^2	0.978	**0.026**	**0.045**
		1000 m^2	0.483	0.068	0.607
	Herbs	1 m^2	0.476	0.441	**0.036**
		10 m^2	0.943	0.165	0.312
		100 m^2	0.141	**0.015**	0.764
		1000 m^2	0.246	**0.002**	0.196
	Grasses	1 m^2	0.072	0.328	0.474
		10 m^2	0.659	0.574	0.999
		100 m^2	0.258	**0.004**	0.251
		1000 m^2	0.099	**0.004**	0.556
Alpha diversity	Trees	1 m^2	0.699	0.993	0.549
		10 m^2	0.803	0.986	0.836
		100 m^2	0.916	0.304	0.559
	Shrubs	1 m^2	0.997	**0.030**	**0.037**
		10 m^2	0.954	0.078	0.154
		100 m^2	0.976	0.124	0.194
	Herbs	1 m^2	0.595	0.754	0.168
		10 m^2	0.780	0.325	0.779
		100 m^2	0.979	0.072	0.115
	Grasses	1 m^2	0.178	0.592	0.510

		10 m^2	0.987	0.462	0.570
		100 m^2	0.999	0.224	0.242
Species evenness	Trees	1 m^2	0.582	0.985	0.394
		10 m^2	0.664	0.979	0.462
		100 m^2	0.999	0.922	0.917
	Shrubs	1 m^2	0.995	**0.021**	**0.016**
		10 m^2	0.820	0.994	0.704
		100 m^2	0.771	0.153	0.517
	Herbs	1 m^2	0.974	0.295	0.423
		10 m^2	0.984	0.999	0.972
		100 m^2	0.578	0.934	0.296
	Grasses	1 m^2	0.665	0.911	0.827
		10 m^2	0.967	0.347	0.505
		100 m^2	**0.014**	**0.013**	0.909

Appendix 9. Statistical *P*-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. *d.f.* = 38. Bold text indicates $P < 0.05$.

Growth Form	Total	Indigenous	Alien
Trees	0.482	0.205	0.210
Shrubs	0.054	0.190	0.725
Herbs	**0.002**	**$2x10^{-5}$**	0.809
Grasses	**0.011**	**0.013**	0.389

Appendix 10. Statistical *P*-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. *d.f.* = 2,27 for Sabie and Graskop, and 2,57 for Hazeyview. Bold text indicates $P < 0.05$.

Species Richness	Growth Form	Sabie*Graskop	Sabie*Hazeyview	Graskop*Hazeyview
Total	Trees	0.961	0.909	0.749
	Shrubs	0.483	0.068	0.607
	Herbs	0.246	**0.002**	0.196
	Grasses	0.099	**0.004**	0.556
Indigenous	Trees	0.962	0.444	0.630
	Shrubs	0.925	0.427	0.690
	Herbs	0.198	**$3x10^{-5}$**	**0.046**
	Grasses	0.132	**0.005**	0.533
Alien	Trees	0.686	0.725	0.980
	Shrubs	0.303	0.147	0.980
	Herbs	0.775	0.979	0.826
	Grasses	0.437	0.334	0.999

Appendix 11. Statistical *P*-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. *d.f.* = 39 for total plots, *d.f.* = 19 for savanna, grassland and Hazeyview plots, and *d.f.* = 9 for Sabie and Graskop plots. Bold text indicates $P < 0.05$.

Total Species Richness			
Quadrat Size	***P* – value**		
	Total		
1 m^2	**0.001**		
10 m^2	0.068		
	Grassland	**Savanna**	
1 m^2	0.123	**$5x10^{-5}$**	
10 m^2	0.169	0.247	
	Sabie	**Graskop**	**Hazeyview**
1 m^2	0.537	0.146	**$5x10^{-5}$**
10 m^2	0.641	0.169	0.247
Alien Species Richness			
Quadrat Size	***P* – value**		
	Total		
1 m^2	**$4x10^{-7}$**		
10 m^2	**0.007**		
	Grassland	**Savanna**	
1 m^2	0.097	**$2x10^{-7}$**	
10 m^2	0.337	**0.005**	
	Sabie	**Graskop**	**Hazeyview**
1 m^2	0.441	0.093	**$2x10^{-7}$**
10 m^2	0.487	0.544	**0.005**

Appendix 12. Statistical *P*-values for t-tests (for independent-samples) for differences in several tested variables between 1996 and 2005. *d.f.* = 78. Bold text indicates $P < 0.05$.

Tested Variable		***P* – value**
Total species richness	1 m^2	**$1x10^{-8}$**
	10 m^2	**$2x10^{-7}$**
	100 m^2	**0.001**
	1000 m^2	**$8x10^{-19}$**
% Alien vegetation aerial cover	Total	0.733
	> 5 m	**0.021**
	2 – 5 m	0.547
	< 2 m	**$5x10^{-7}$**
Ground cover	Soil	**$3x10^{-11}$**
	Rock	0.067
	Litter	**$2x10^{-11}$**
	Herbaceous	**$2x10^{-14}$**
	Grass	**$2x10^{-5}$**

Appendix 13. Statistical *P*-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. *d.f.* = 38. Bold text indicates $P < 0.05$.

Tested Variable		***P* – value**	
		Grassland	**Savanna**
Total species richness	1 m^2	**$1x10^{-8}$**	**$1x10^{-5}$**
	10 m^2	**$1x10^{-8}$**	**0.028**
	100 m^2	**$7x10^{-6}$**	0.436
	1000 m^2	**$2x10^{-14}$**	**$4x10^{-7}$**
% Alien vegetation aerial cover	Total	0.767	0.861
	> 5 m	**0.025**	0.456
	2 – 5 m	0.609	0.650
	< 2 m	**$8x10^{-6}$**	**0.018**

Appendix 14. Statistical *P*-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. *d.f.* = 78. Bold text indicates $P < 0.05$.

Growth Form	**Quadrat Size**	***P* – value**
Trees	1 m^2	**0.032**
	10 m^2	0.170
	100 m^2	0.817
	1000 m^2	**$4x10^{-6}$**
Shrubs	1 m^2	**$3x10^{-5}$**
	10 m^2	0.077
	100 m^2	**0.004**
	1000 m^2	**$5x10^{-14}$**
Herbs	1 m^2	**$1x10^{-8}$**
	10 m^2	**$3x10^{-7}$**
	100 m^2	**$5x10^{-5}$**
	1000 m^2	**$4x10^{-15}$**
Grasses	1 m^2	**$1x10^{-8}$**
	10 m^2	**$1x10^{-6}$**
	100 m^2	**0.005**
	1000 m^2	**$7x10^{-9}$**

Appendix 15. Statistical *P*-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. *d.f.* = 8. Bold text indicates $P < 0.05$. Note H = High altitude (i.e. grassland)/High invasion; L = Low altitude (i.e. savanna)/Low invasion; C = Cleared; and U = Uncleared.

	Experimental Category							
	HHC	**HHU**	**HLC**	**HLU**	**LHC**	**LHU**	**LLC**	**LLU**
Total species richness								
$1m^2$	**0.019**	**0.001**	**0.004**	**0.002**	0.069	**0.008**	0.055	0.214
$10m^2$	**0.001**	**0.032**	**$3x10^{-5}$**	0.345	0.455	0.072	0.286	0.390
$100m^2$	**0.008**	0.169	**0.040**	0.078	0.431	**0.040**	0.532	0.867
$1000m^2$	**$2x10^{-5}$**	**$9x10^{-7}$**	**0.004**	**$3x10^{-6}$**	**0.018**	**$5x10^{-6}$**	**0.045**	0.063
Alpha diversity								
$100m^2$	**0.010**	**0.010**	**$8x10^{-10}$**	**$2x10^{-7}$**	**0.001**	**$1x10^{-9}$**	**$2x10^{-7}$**	**$7x10^{-7}$**
% Alien vegetation aerial cover								
Total	0.801	**0.028**	**0.019**	0.256	0.435	**0.042**	0.153	0.438
> 5 m	0.425	**$2x10^{-5}$**	0.298	0.244	**0.012**	0.126	0.993	0.801
2 – 5 m	0.082	0.492	0.321	0.531	0.768	0.121	0.395	0.958
< 2 m	0.093	0.060	0.076	0.061	0.506	0.210	**0.040**	**$2x10^{-6}$**
Ground cover								
Soil	0.074	**0.002**	0.175	**0.007**	**0.002**	0.105	**0.025**	**0.002**
Rock	0.098	0.172	0.292	0.182	0.648	0.435	0.271	0.883
Litter	0.074	0.271	**0.005**	**0.022**	**$2x10^{-5}$**	**0.013**	**0.020**	**0.005**
Herbs	**$2x10^{-5}$**	0.109	**0.034**	**0.006**	**0.003**	**0.031**	**0.001**	**0.005**
Grass	0.611	0.409	**0.040**	0.173	**0.004**	0.054	0.163	0.061
Soil characteristic								
pH	0.360	0.788	0.722	0.350	0.677	0.412	0.971	0.190

Appendix 16. Statistical *P*-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. *d.f.* = 8. Bold text indicates $P < 0.05$. Note H = High altitude (i.e. grassland)/High invasion; L = Low altitude (i.e. savanna)/Low invasion; C = Cleared; and U = Uncleared.

Quadrat Size	**Experimental Category**							
	HHC	**HHU**	**HLC**	**HLU**	**LHC**	**LHU**	**LLC**	**LLU**
Trees								
1 m^2	0.074	**0.049**	0.100	0.568	0.613	0.421	0.999	0.353
10 m^2	0.305	0.817	0.803	0.335	0.291	0.710	0.552	0.169
100 m^2	**0.008**	0.503	0.700	0.565	0.279	0.608	0.086	0.349
1000 m^2	**0.002**	**0.019**	**0.040**	0.273	0.062	0.058	0.885	0.823
Shrubs								
1 m^2	0.363	**0.001**	**$4x10^{-5}$**	0.193	0.087	0.911	0.886	0.426
10 m^2	0.097	0.144	0.083	0.773	0.999	0.272	0.744	0.248
100 m^2	**0.013**	**0.011**	0.071	0.273	0.518	0.084	0.217	0.914
1000 m^2	**0.002**	**$5x10^{-5}$**	**0.008**	**$3x10^{-5}$**	0.052	**0.002**	0.082	0.362
Herbs								
1 m^2	**0.023**	**0.010**	0.050	0.072	0.138	**$1x10^{-5}$**	0.168	0.108
10 m^2	0.114	0.197	**0.034**	0.241	0.264	0.074	**0.007**	0.075
100 m^2	0.050	0.278	0.088	0.111	0.865	0.059	0.202	0.618
1000 m^2	**$6x10^{-5}$**	**$5x10^{-6}$**	**0.024**	**0.003**	0.058	**$1x10^{-5}$**	0.054	0.074
Grasses								

1 m^2	0.114	**0.022**	0.159	**0.008**	0.617	**0.039**	0.070	0.080
10 m^2	**0.039**	0.093	0.115	**0.035**	0.067	0.681	0.273	0.205
100 m^2	0.291	0.740	0.053	**0.014**	0.771	0.347	0.641	0.242
1000 m^2	**0.045**	**0.028**	**0.011**	**0.005**	0.191	**0.046**	0.999	**0.019**

Appendix 17. Statistical *P*-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. *d.f.* = 1,32. Bold text indicates $P < 0.05$. Note H = High altitude (i.e. grassland)/High invasion; L = Low altitude (i.e. savanna)/Low invasion; C = Cleared; and U = Uncleared.

	Experimental Category								
		HHC	**HHU**	**HLC**	**HLU**	**LHC**	**LHU**	**LLC**	**LLU**
Total species richness: 1996									
1 m^2	**HHC**		0.357	0.943	0.997	0.994	0.998	0.999	0.999
	HHU			**0.036**	0.098	0.818	0.738	0.133	0.191
	HLC				0.999	0.556	0.649	0.999	0.994
	HLU					0.818	0.884	0.999	0.999
	LHC						0.999	0.884	0.943
	LHU							0.934	0.973
	LLC								0.999
	LLU								
10 m^2	**HHC**		0.999	0.999	0.999	0.565	0.999	0.979	0.988
	HHU			0.999	0.979	0.861	0.988	0.999	0.861
	HLC				0.999	0.565	0.999	0.979	0.988
	HLU					0.312	0.999	0.861	0.999
	LHC						0.357	0.979	0.143
	LHU							0.896	0.999
	LLC								0.620
	LLU								
100 m^2	**HHC**		0.999	0.846	0.937	0.999	0.999	0.088	0.503
	HHU			0.608	0.760	0.990	0.999	**0.034**	0.273
	HLC				0.999	0.972	0.555	0.760	0.999
	HLU					0.995	0.712	0.608	0.990
	LHC						0.983	0.203	0.760
	LHU							**0.028**	0.236
	LLC								0.972
	LLU								
1000 m^2	**HHC**		0.999	**0.017**	0.955	0.997	0.999	0.133	0.116
	HHU			**0.005**	0.767	0.938	0.999	**0.047**	**0.040**
	HLC				0.198	0.087	**0.004**	0.985	0.991
	HLU					0.999	0.728	0.687	0.644
	LHC						0.918	0.431	0.391
	LHU							**0.040**	**0.034**
	LLC								0.999
	LLU								
Total species richness: 2005									

1 m^2	**HHC**		0.999	0.999	0.999	0.654	0.959	0.992	0.964
	HHU			0.999	0.999	0.418	0.830	0.933	0.841
	HLC				0.999	0.418	0.830	0.933	0.841
	HLU					0.309	0.722	0.861	0.735
	LHC						0.997	0.978	0.996
	LHU							0.999	0.999
	LLC								0.999
	LLU								
10 m^2	**HHC**		0.915	0.999	0.438	**0.014**	0.894	0.155	0.592
	HHU			0.973	0.987	0.220	0.999	0.812	0.998
	HLC				0.592	**0.026**	0.963	0.245	0.745
	HLU					0.708	0.992	0.998	0.999
	LHC						0.245	0.963	0.553
	LHU							0.842	0.999
	LLC								0.987
	LLU								
100 m^2	**HHC**		0.812	0.999	0.989	0.563	0.680	0.762	0.876
	HHU			0.533	0.998	0.999	0.999	0.999	0.999
	HLC				0.894	0.295	0.393	0.475	0.622
	HLU					0.960	0.986	0.995	0.999
	LHC						0.999	0.999	0.999
	LHU							0.999	0.999
	LLC								0.999
	LLU								
1000 m^2	**HHC**		0.993	0.999	0.757	0.248	0.314	0.390	0.651
	HHU			0.999	0.991	0.695	0.777	0.848	0.974
	HLC				0.848	0.332	0.410	0.495	0.757
	HLU					0.986	0.995	0.999	0.999
	LHC						0.999	0.999	0.996
	LHU							0.999	0.999
	LLC								0.999
	LLU								
Tree species richness: 1996									
1 m^2	**HHC**		0.961	0.992	0.753	0.753	0.425	**0.042**	0.350
	HHU			0.999	0.999	0.999	0.961	0.350	0.928
	HLC				0.992	0.992	0.883	0.225	0.824
	HLU					0.999	0.999	0.674	0.997
	LHC						0.999	0.674	0.997
	LHU							0.928	0.999
	LLC								0.961
	LLU								
10 m^2	**HHC**		0.997	0.999	0.997	0.990	0.881	0.502	0.235
	HHU			0.997	0.999	0.999	0.997	0.881	0.607
	HLC				0.997	0.990	0.881	0.502	0.235
	HLU					0.999	0.997	0.881	0.607
	LHC						0.999	0.937	0.711
	LHU							0.997	0.937
	LLC								0.999

	LLU								
100 m^2	**HHC**		0.392	0.524	0.662	0.524	0.392	**0.001**	**0.009**
	HHU			0.999	0.999	0.999	0.999	0.189	0.662
	HLC				0.999	0.999	0.999	0.123	0.524
	HLU					0.999	0.999	0.078	0.392
	LHC						0.999	0.123	0.524
	LHU							0.189	0.662
	LLC								0.987
	LLU								
1000 m^2	**HHC**		0.334	0.334	0.582	0.826	0.236	**0.003**	**$3x10^{-5}$**
	HHU			0.999	0.999	0.990	0.999	0.452	0.067
	HLC				0.999	0.990	0.999	0.452	0.067
	HLU					0.999	0.998	0.236	**0.025**
	LHC						0.965	0.105	**0.009**
	LHU							0.582	0.105
	LLC								0.965
	LLU								
Tree species richness: 2005									
1 m^2	**HHC**		0.996	0.999	0.876	0.999	0.999	0.999	0.876
	HHU			0.996	0.467	0.931	0.996	0.998	0.467
	HLC				0.876	0.999	0.999	0.999	0.876
	HLU					0.987	0.876	0.842	0.999
	LHC						0.999	0.999	0.987
	LHU							0.999	0.876
	LLC								0.842
	LLU								
10 m^2	**HHC**		0.999	0.983	0.728	0.983	0.999	0.999	0.999
	HHU			0.999	0.955	0.999	0.999	0.996	0.999
	HLC				0.996	0.999	0.983	0.955	0.999
	HLU					0.996	0.728	0.615	0.903
	LHC						0.983	0.955	0.999
	LHU							0.999	0.999
	LLC								0.999
	LLU								
100 m^2	**HHC**		0.999	0.999	0.994	0.922	0.999	0.999	0.999
	HHU			0.994	0.999	0.611	0.983	0.999	0.994
	HLC				0.983	0.960	0.999	0.999	0.999
	HLU					0.514	0.960	0.999	0.983
	LHC						0.983	0.865	0.960
	LHU							0.999	0.999
	LLC								0.999
	LLU								
1000 m^2	**HHC**		0.999	0.994	0.994	0.969	0.999	0.999	0.985
	HHU			0.999	0.942	0.998	0.998	0.999	0.999
	HLC				0.789	0.999	0.969	0.998	0.999
	HLU					0.639	0.999	0.985	0.717
	LHC						0.904	0.985	0.999
	LHU							0.999	0.942

	LLC								0.994
	LLU								
Shrub species richness: 1996									
1 m^2	**HHC**		0.620	0.911	0.999	0.463	0.991	0.999	0.999
	HHU			0.999	0.889	0.999	0.972	0.580	0.389
	HLC				0.995	0.991	0.999	0.889	0.735
	HLU					0.771	0.999	0.999	0.987
	LHC						0.911	0.425	0.262
	LHU							0.987	0.931
	LLC								0.999
	LLU								
10 m^2	**HHC**		0.930	0.999	0.989	0.930	0.999	0.997	0.930
	HHU			0.968	0.475	0.999	0.930	0.999	0.287
	HLC				0.968	0.968	0.999	0.999	0.869
	HLU					0.475	0.989	0.788	0.999
	LHC						0.930	0.999	0.287
	LHU							0.997	0.930
	LLC								0.585
	LLU								
100 m^2	**HHC**		0.967	0.999	0.986	0.999	0.995	0.304	0.995
	HHU			0.742	0.560	0.967	0.999	**0.037**	0.653
	HLC				0.999	0.999	0.886	0.653	0.999
	HLU					0.986	0.742	0.821	0.999
	LHC						0.995	0.304	0.995
	LHU							0.073	0.821
	LLC								0.742
	LLU								
1000 m^2	**HHC**		0.994	0.471	0.998	0.999	0.999	0.901	0.901
	HHU			0.129	0.849	0.940	0.999	0.471	0.471
	HLC				0.849	0.712	0.211	0.994	0.994
	HLU					0.999	0.940	0.998	0.998
	LHC						0.985	0.985	0.985
	LHU							0.633	0.633
	LLC								0.999
	LLU								
Shrub species richness: 2005									
1 m^2	**HHC**		0.622	0.937	0.999	0.843	0.315	0.919	0.581
	HHU			0.998	0.384	0.052	**0.005**	0.081	**0.018**
	HLC				0.777	0.201	**0.028**	0.283	0.081
	HLU					0.966	0.540	0.989	0.811
	LHC						0.984	0.999	0.999
	LHU							0.953	0.999
	LLC								0.998
	LLU								
10 m^2	**HHC**		0.839	0.999	0.696	0.089	0.839	0.117	0.452
	HHU			0.894	0.999	0.772	0.999	0.839	0.998
	HLC				0.772	0.117	0.894	0.153	0.532
	HLU					0.894	0.999	0.936	0.999

	LHC						0.772	0.999	0.983
	LHU							0.839	0.998
	LLC								0.993
	LLU								
100 m^2	**HHC**		0.979	0.979	0.991	0.327	0.482	0.262	0.482
	HHU			0.999	0.999	0.872	0.957	0.810	0.957
	HLC				0.999	0.872	0.957	0.810	0.957
	HLU					0.810	0.922	0.735	0.922
	LHC						0.999	0.999	0.999
	LHU							0.999	0.999
	LLC								0.999
	LLU								
1000 m^2	**HHC**		0.999	0.947	0.969	0.915	0.762	0.873	0.295
	HHU			0.999	0.999	0.997	0.969	0.993	0.626
	HLC				0.999	0.999	0.999	0.999	0.915
	HLU					0.999	0.999	0.999	0.873
	LHC						0.999	0.999	0.947
	LHU							0.999	0.993
	LLC								0.969
	LLU								
Herbaceous species richness: 1996									
1 m^2	**HHC**		0.322	0.386	0.842	0.842	0.642	0.979	0.947
	HHU			**0.002**	**0.015**	0.985	0.999	0.869	0.931
	HLC				0.994	**0.021**	**0.008**	0.064	**0.043**
	HLU					0.121	0.056	0.293	0.215
	LHC						0.999	0.999	0.999
	LHU							0.990	0.998
	LLC								0.999
	LLU								
10 m^2	**HHC**		0.999	0.999	0.998	0.293	0.972	0.189	0.661
	HHU			0.999	0.998	0.293	0.972	0.189	0.661
	HLC				0.999	0.504	0.998	0.357	0.865
	HLU					0.661	0.999	0.504	0.948
	LHC						0.865	0.999	0.998
	LHU							0.737	0.995
	LLC								0.987
	LLU								
100 m^2	**HHC**		0.990	0.971	0.999	0.999	0.936	0.999	0.997
	HHU			0.605	0.997	0.999	0.999	0.971	0.803
	HLC				0.936	0.803	0.399	0.990	0.999
	HLU					0.999	0.971	0.999	0.990
	LHC						0.997	0.997	0.936
	LHU							0.880	0.605
	LLC								0.999
	LLU								
1000 m^2	**HHC**		0.997	0.157	0.999	0.999	0.913	0.969	0.997
	HHU			**0.035**	0.945	0.997	0.999	0.692	0.871
	HLC				0.347	0.157	**0.009**	0.692	0.478

	HLU					0.999	0.692	0.999	0.999
	LHC						0.913	0.969	0.997
	LHU							0.347	0.549
	LLC								0.999
	LLU								
Herbaceous species richness: 2005									
1 m^2	**HHC**		0.999	0.999	0.990	0.556	0.999	0.970	0.998
	HHU			0.987	0.865	0.865	0.999	0.999	0.999
	HLC				0.999	0.360	0.994	0.880	0.980
	HLU					0.148	0.907	0.602	0.832
	LHC						0.814	0.984	0.894
	LHU							0.999	0.999
	LLC								0.999
	LLU								
10 m^2	**HHC**		0.999	0.999	0.994	0.453	0.999	0.859	0.971
	HHU			0.999	0.998	0.548	0.999	0.917	0.989
	HLC				0.958	0.285	0.999	0.694	0.890
	HLU					0.890	0.999	0.998	0.999
	LHC						0.597	0.997	0.958
	LHU							0.940	0.994
	LLC								0.999
	LLU								
100 m^2	**HHC**		0.901	0.980	0.988	0.371	0.785	0.988	0.968
	HHU			0.371	0.999	0.980	0.999	0.999	0.999
	HLC				0.632	0.062	0.245	0.632	0.524
	HLU					0.867	0.997	0.999	0.999
	LHC						0.997	0.867	0.929
	LHU							0.997	0.999
	LLC								0.999
	LLU								
1000 m^2	**HHC**		0.993	0.999	0.736	0.057	0.527	0.527	0.492
	HHU			0.999	0.989	0.276	0.934	0.934	0.917
	HLC				0.877	0.106	0.703	0.703	0.669
	HLU					0.768	0.999	0.999	0.999
	LHC						0.917	0.917	0.934
	LHU							0.999	0.999
	LLC								0.999
	LLU								
Grass species richness: 1996									
1 m^2	**HHC**		0.999	0.999	0.994	0.790	0.999	0.999	0.999
	HHU			0.998	0.999	0.668	0.994	0.999	0.999
	HLC				0.933	0.950	0.999	0.999	0.999
	HLU					0.332	0.886	0.976	0.976
	LHC						0.976	0.886	0.886
	LHU							0.999	0.999
	LLC								0.999
	LLU								
10 m^2	**HHC**		0.992	0.961	0.999	0.999	0.961	0.999	0.999

	HHU			0.590	0.961	0.999	0.590	0.883	0.883
	HLC				0.992	0.883	0.999	0.999	0.999
	HLU					0.999	0.992	0.999	0.999
	LHC						0.883	0.992	0.992
	LHU							0.999	0.999
	LLC								0.999
	LLU								
100 m^2	**HHC**		0.988	0.999	0.999	0.999	0.940	0.988	0.988
	HHU			0.999	0.988	0.999	0.999	0.999	0.999
	HLC				0.999	0.999	0.999	0.999	0.999
	HLU					0.999	0.940	0.988	0.988
	LHC						0.988	0.999	0.999
	LHU							0.999	0.999
	LLC								0.999
	LLU								
1000 m^2	**HHC**		0.761	0.993	0.999	0.999	0.761	0.999	0.999
	HHU			0.293	0.962	0.761	0.999	0.600	0.761
	HLC				0.887	0.993	0.293	0.999	0.993
	HLU					0.999	0.962	0.993	0.999
	LHC						0.761	0.999	0.999
	LHU							0.600	0.761
	LLC								0.999
	LLU								
Grass species richness: 2005									
1 m^2	**HHC**		0.999	0.999	0.422	0.999	0.999	0.995	0.889
	HHU			0.999	0.375	0.999	0.999	0.991	0.855
	HLC				0.331	0.999	0.999	0.984	0.817
	HLU					0.522	0.422	0.855	0.991
	LHC						0.999	0.999	0.942
	LHU							0.995	0.889
	LLC								0.999
	LLU								
10 m^2	**HHC**		0.992	0.999	0.999	0.927	0.927	0.999	0.999
	HHU			0.999	0.999	0.999	0.999	0.999	0.972
	HLC				0.999	0.992	0.992	0.999	0.999
	HLU					0.992	0.992	0.999	0.999
	LHC						0.999	0.999	0.852
	LHU							0.999	0.852
	LLC								0.992
	LLU								
100 m^2	**HHC**		0.606	0.789	0.982	0.606	0.606	0.789	0.982
	HHU			**0.038**	0.146	0.999	0.999	0.999	0.982
	HLC				0.999	**0.038**	**0.038**	0.077	0.257
	HLU					0.146	0.146	0.257	0.606
	LHC						0.999	0.999	0.982
	LHU							0.999	0.982
	LLC								0.999
	LLU								

1000 m^2	**HHC**		0.984	0.999	0.999	0.800	0.348	0.273	0.999
	HHU			0.800	0.999	0.999	0.871	0.800	0.984
	HLC				0.984	0.434	0.116	0.085	0.999
	HLU					0.925	0.526	0.434	0.999
	LHC						0.994	0.984	0.800
	LHU							0.999	0.348
	LLC								0.273
	LLU								
Total species alpha diversity: 1996									
100 m^2	**HHC**		0.999	**0.035**	0.214	0.833	0.260	**0.009**	0.122
	HHU			**0.025**	0.163	0.757	0.200	**0.006**	0.089
	HLC				0.989	0.530	0.978	0.999	0.999
	HLU					0.951	0.999	0.851	0.999
	LHC						0.971	0.229	0.851
	LHU							0.798	0.999
	LLC								0.951
	LLU								
Total species alpha diversity: 2005									
100 m^2	**HHC**		0.999	0.997	0.996	0.945	0.999	0.985	0.999
	HHU			0.998	0.997	0.937	0.999	0.981	0.999
	HLC				0.999	0.611	0.997	0.756	0.912
	HLU					0.594	0.996	0.741	0.903
	LHC						0.942	0.999	0.999
	LHU							0.983	0.999
	LLC								0.999
	LLU								
% Alien vegetation aerial cover: 1996									
Total	**HHC**		**0.001**	0.707	0.978	0.995	**0.002**	0.978	0.999
	HHU			**$1x10^{-5}$**	**$2x10^{-5}$**	**0.007**	0.999	**$2x10^{-5}$**	**0.002**
	HLC				0.996	0.267	**$2x10^{-5}$**	0.996	0.597
	HLU					0.687	**$3x10^{-5}$**	0.999	0.946
	LHC						**0.015**	0.685	0.999
	LHU							**$3x10^{-5}$**	**0.003**
	LLC								0.945
	LLU								
> 5 m	**HHC**		**$2x10^{-5}$**	0.925	0.994	0.925	0.777	0.988	0.999
	HHU			**$1x10^{-5}$**	**$1x10^{-5}$**	**$1x10^{-5}$**	**0.008**	**$1x10^{-5}$**	**$2x10^{-5}$**
	HLC				0.999	0.999	0.145	0.999	0.998
	HLU					0.999	0.323	0.999	0.999
	LHC						0.145	0.999	0.998
	LHU							0.273	0.442
	LLC								0.999
	LLU								
2 – 5 m	**HHC**		0.778	0.998	0.999	0.951	**$4x10^{-5}$**	0.999	0.987
	HHU			0.384	0.625	0.999	**0.022**	0.552	0.997
	HLC				0.999	0.654	**$2x10^{-5}$**	0.999	0.797
	HLU					0.867	**$3x10^{-5}$**	0.999	0.948
	LHC						**0.007**	0.814	0.999

	LHU							**$2x10^{-5}$**	**0.004**
	LLC								0.916
	LLU								
< 2 m	**HHC**		0.999	0.999	0.999	**0.040**	0.999	0.999	0.999
	HHU			0.999	0.999	**0.021**	0.998	0.999	0.999
	HLC				0.999	**0.011**	0.987	0.998	0.999
	HLU					**0.013**	0.993	0.999	0.999
	LHC						0.087	0.053	**0.015**
	LHU							0.999	0.995
	LLC								0.999
	LLU								
% Alien vegetation aerial cover: 2005									
Total	**HHC**		0.943	0.999	0.999	0.973	0.984	0.999	0.995
	HHU			0.986	0.916	0.999	0.999	0.976	0.999
	HLC				0.999	0.995	0.998	0.999	0.999
	HLU					0.956	0.973	0.999	0.989
	LHC						0.999	0.991	0.999
	LHU							0.996	0.999
	LLC								0.999
	LLU								
> 5 m	**HHC**		0.909	0.996	0.999	0.589	0.999	0.999	0.996
	HHU			0.999	0.691	0.999	0.996	0.973	0.999
	HLC				0.941	0.941	0.999	0.999	0.999
	HLU					0.327	0.974	0.996	0.942
	LHC						0.887	0.753	0.939
	LHU							0.999	0.999
	LLC								0.999
	LLU								
2 – 5 m	**HHC**		0.928	0.999	0.995	0.632	0.257	0.950	0.859
	HHU			0.985	0.999	0.999	0.911	0.999	0.999
	HLC				0.999	0.808	0.412	0.991	0.956
	HLU					0.961	0.682	0.999	0.998
	LHC						0.998	0.997	0.999
	LHU							0.881	0.961
	LLC								0.999
	LLU								
< 2 m	**HHC**		0.999	0.999	0.996	0.861	0.789	0.956	0.996
	HHU			0.999	0.999	0.925	0.872	0.983	0.999
	HLC				0.999	0.955	0.916	0.993	0.999
	HLU					0.997	0.990	0.999	0.999
	LHC						0.999	0.999	0.997
	LHU							0.999	0.990
	LLC								0.999
	LLU								
Ground cover: 1996									
Soil	**HHC**		0.999	0.913	0.999	0.999	0.733	0.761	0.998
	HHU			0.705	0.999	0.996	0.465	0.494	0.962
	HLC				0.761	0.978	0.999	0.999	0.998

	HLU					0.998	0.524	0.555	0.978
	LHC						0.878	0.896	0.999
	LHU							0.999	0.971
	LLC								0.978
	LLU								
Rock	**HHC**		0.999	0.856	0.999	0.995	0.919	0.999	0.995
	HHU			0.728	0.999	0.974	0.818	0.999	0.974
	HLC				0.890	0.998	0.999	0.775	0.998
	HLU					0.998	0.942	0.999	0.998
	LHC						0.999	0.984	0.999
	LHU							0.856	0.999
	LLC								0.984
	LLU								
Litter	**HHC**		0.245	0.720	0.915	0.977	0.999	0.961	0.992
	HHU			**0.006**	**0.016**	**0.032**	0.276	**0.025**	**0.047**
	HLC				0.999	0.997	0.678	0.999	0.989
	HLU					0.999	0.891	0.999	0.999
	LHC						0.967	0.999	0.999
	LHU							0.946	0.987
	LLC								0.999
	LLU								
Herbs	**HHC**		0.068	0.929	0.965	0.344	0.156	0.968	0.990
	HHU			0.552	0.457	0.989	0.999	**0.005**	0.338
	HLC				0.999	0.958	0.791	0.374	0.999
	HLU					0.918	0.704	0.463	0.999
	LHC						0.999	**0.046**	0.836
	LHU							**0.015**	0.573
	LLC								0.594
	LLU								
Grass	**HHC**		0.991	0.268	0.415	0.086	0.352	0.999	0.862
	HHU			0.747	0.885	0.389	0.836	0.948	0.999
	HLC				0.999	0.999	0.999	0.154	0.964
	HLU					0.988	0.999	0.258	0.994
	LHC						0.995	**0.044**	0.734
	LHU							0.212	0.987
	LLC								0.701
	LLU								
Ground cover: 2005									
Soil	**HHC**		0.869	0.999	0.999	0.999	0.999	0.999	0.940
	HHU			0.854	0.551	0.909	0.992	0.661	0.228
	HLC				0.999	0.999	0.999	0.999	0.949
	HLU					0.998	0.949	0.999	0.999
	LHC						0.999	0.999	0.909
	LHU							0.979	0.683
	LLC								0.994
	LLU								
Rock	**HHC**		0.055	0.726	0.086	0.055	0.064	0.064	0.074
	HHU			0.766	0.999	0.999	0.999	0.999	0.999

	HLC				0.867	0.766	0.803	0.803	0.836
	HLU					0.999	0.999	0.999	0.999
	LHC						0.999	0.999	0.999
	LHU							0.999	0.999
	LLC								0.999
	LLU								
Litter	**HHC**		0.806	0.999	0.908	0.996	0.964	0.955	0.999
	HHU			0.772	0.145	0.993	0.999	0.201	0.576
	HLC				0.928	0.994	0.950	0.967	0.999
	HLU					0.522	0.323	0.999	0.986
	LHC						0.999	0.631	0.955
	LHU							0.418	0.838
	LLC								0.996
	LLU								
Herbs	**HHC**		0.999	0.989	0.972	0.966	0.999	0.528	0.997
	HHU			0.999	0.997	0.877	0.999	0.720	0.999
	HLC				0.999	0.577	0.977	0.950	0.999
	HLU					0.480	0.950	0.977	0.999
	LHC						0.982	0.089	0.674
	LHU							0.457	0.992
	LLC								0.906
	LLU								
Grass	**HHC**		0.999	0.999	0.386	0.760	0.999	0.909	0.999
	HHU			0.999	0.561	0.896	0.999	0.976	0.999
	HLC				0.471	0.835	0.999	0.950	0.999
	HLU					0.999	0.739	0.980	0.652
	LHC						0.971	0.999	0.941
	LHU							0.997	0.999
	LLC								0.990
	LLU								
pH: 1996									
	HHC		0.999	0.999	0.999	0.899	0.997	0.999	0.995
	HHU			0.999	0.999	0.854	0.992	0.999	0.998
	HLC				0.999	0.895	0.996	0.999	0.995
	HLU					0.621	0.922	0.999	0.999
	LHC						0.999	0.888	0.482
	LHU							0.996	0.836
	LLC								0.996
	LLU								
pH: 2005									
	HHC		0.689	0.795	0.408	0.999	0.916	0.914	0.998
	HHU			0.999	0.999	0.856	0.999	0.999	0.961
	HLC				0.998	0.925	0.999	0.999	0.987
	HLU					0.601	0.982	0.983	0.798
	LHC						0.982	0.981	0.999
	LHU							0.999	0.999
	LLC								0.999
	LLU								

Appendix 18. Statistical *P*-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. *d.f.* = 38. Bold text indicates $P < 0.05$.

Treatment		***P* – value**
BIOME	Grassland	0.766
	Savanna	0.861
INVASION INTENSITY	High invasion	0.122
	Low invasion	**0.004**
CLEARING	Cleared	**0.025**
	Uncleared	0.265

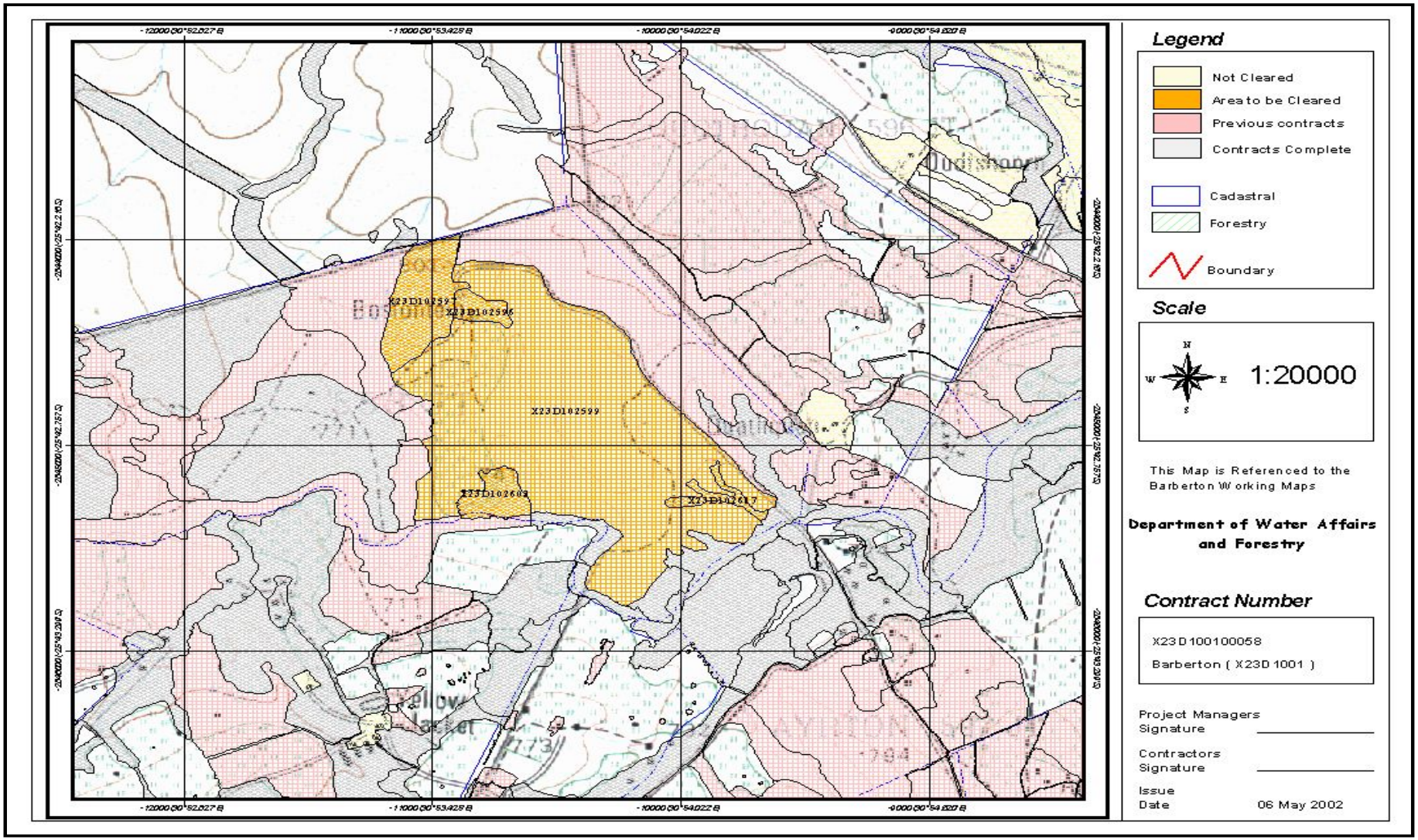
Appendix 19. Methodology used by the Soil Fertility and Analytical Services Section of the KwaZulu-Natal Department of Agriculture and Environmental Affairs at Cedara for soil sample analyses (Manson and Roberts, 2000).

Soil samples were spread onto drying trays and dried at room temperature. Once the soil was dry, samples were crushed using rubber belts and the soil was then passed through a 1 mm sieve. Once the soil samples had been dried and milled, the density was measured. Samples were then placed into trays that contained 11, 70 ml PVC cups. Nine of the cups were each filled with one of the unknown soil samples, one with a standard soil sample for quality control and one blank. Dispensers and diluter/dispensers were used to dispense aliquots of extractant or reagent to three samples at a time.

Organic carbon and clay contents were determined utilizing near-infrared spectroscopy. Organic carbon was also determined using the Walkley-Black procedure (Allison 1965), which measures the readily oxidizable organic carbon. Total nitrogen was analyzed by the Automated Dumas dry combustion method using a LECO CNS 2000 (Matejovic 1996). Weighed soil samples were deposited into ceramic crucibles containing 0.5 g vanadium pentoxide (a combustion catalyst). The crucibles were placed in a horizontal furnace, and burned in a stream of oxygen at 1350 °C. Nitrogen was determined as N_2 in a thermal conductivity cell. Effective cation exchange capacity was calculated as the sum of extractable Ca, Mg, K and acidity. For pH in KCl, 10 ml of soil was placed in each PVC cup and 25 ml of one molar KCl added. The suspension was stirred at 400 r.p.m. for 5 minutes using a multiple stirrer. The suspension was allowed to stand for 30 minutes before the pH was measured using a gel-filled combination glass electrode while stirring. For calcium, magnesium and acidity, 2.5 ml of soil were placed in each PVC cup and 25 ml of 1 molar KCl solution was added. The suspension was stirred at 400 r.p.m. for 10 minutes using a multiple stirrer. The extracts were filtered using Whatman No. 1 filter paper. Five millilitres of the filtrate was diluted with 20 ml of 0.0356 molar $SrCl_2$. Calcium and Mg were determined by atomic absorption. Extractable acidity was determined by diluting 10 ml of the filtrate with 10 ml of de-ionized water containing 2 to 4 drops of phenolphthalein, and titrating with 0.005 molar NaOH. For extractable phosphorus and potassium, the extracting solution consisted of 0.25 molar NH_4CO_3, 0.01 molar Na_2 EDTA, 0.01 molar NH_4F and 0.05 g/l Superfloc adjusted to pH8 with a concentrated ammonia solution. Twenty-five milliliters of this solution were added to 2.5 ml of soil. The suspension was stirred at 400 r.p.m. for 10 minutes

using a multiple stirrer. The extracts were filtered using Whatman No.1 filter paper. Phosphorus was determined on a 2 ml aliquot of filtrate using a modification of the Murphy and Riley (1962) molybdenum blue procedure (Hunter 1975). Potassium was determined by atomic absorption on a 5 ml aliquot of the filtrate after dilution with 20 ml de-ionised water.

Appendix 20. Example of a Working for Water (WfW) clearing contract (for the Barbeton area).



Project **Barberton**

Treatment Area ID: **X23D100100058**

WORKING FOR WATER

Part D (Page 1.1)
Attached as Part D of the Quotation

ENVIRONMENTAL FACTORS

(Affecting Adjusted Persondays [APD] on page2)

NBALID	Approx. Flat Area	Slope	Slp_Area	AI UFC	AI Ht Obst Veg	AI Dens Obst Veg	AI %	Walk Time (min)	Treatment
X23D102596	2.72	0	2.72	Easy	Knee High	Slight	0.00	25	Initial Treatment
X23D102597	13.55	0	13.55	Easy	Knee High	Slight	0.00	40	Initial Treatment
X23D102603	5.07	0	5.07	Easy	Knee High	Slight	0.00	25	Initial Treatment
X23D102617	2.53	0	2.53	Easy	Knee High	Slight	0.00	25	1st follow-up
X23D102599	119.68	0	119.68	Easy	Chest High	Slight	16.67	45	Initial Treatment
TOTAL	143.55 ha		143.55 ha						

KEY

Nbalid	= Identity number for NBAL	UFC	= Under Foot Conditions
AI	= Acessibility Index	Ht Obst Veg	= Height of Obstructive Vegetation
Walk Time	= Walk time (one way)	Dens Obst Veg	= Density of Obstructive Vegetation

Project Manager's Initials

Contractor's Initials

Project **Barberton**

Treatment Area ID: **X23D100100058**

WORKING FOR WATER

Part D (Page 2.2)
Attached as Part D of the Quotation

DESCRIPTION OF WORK *(as marked on attached map)*

NBALID	Species	Age	Density	Method	Herbicide	Rate	Total Herb.	UPD	APD	Area	PD/ha
X23D102596	Syringa	x	10	cut-stump trtment		0	00.00	4.6	5.2	2.72	1.9
X23D102596	Jacaranda	x	v	frill	Chopper	8	00.65	0.0	0.0	2.72	0.0
X23D102596	White Mulberry	x	v	frill		0	00.00	1.1	1.2	2.72	0.4
X23D102596	Bugweed	x	v	cut-stump trtment	Chopper	1	00.08	0.6	0.6	2.72	0.2
X23D102596	Lantana	x	5	cut-stump trtment	Chopper	2	00.27	0.9	1.1	2.72	0.4

Project **Barberton**

Treatment Area ID: **X23D100100058**

WORKING FOR WATER

Part D (Page 2.3)
Attached as Part D of the Quotation

DESCRIPTION OF WORK *(as marked on attached map)*

NBALID	Species	Age	Density	Method	Herbicide	Rate	Total Herb.	UPD	APD	Area	PD/ha
X23D102599	Guava	x	4	cut-stump trtment	Chopper	6	28.72	43.1	53.0	119.68	0.4
X23D102599	White Mulberry	y	1	cut-stump trtment		0	00.00	12.0	14.7	119.68	0.1
X23D102599	Eucalypts	a	2	frill	Chopper	12	28.72	35.9	44.2	119.68	0.4
X23D102599	Lantana	a	5	cut-stump trtment	Chopper	2.5	14.96	47.9	58.9	119.68	0.5
X23D102599	Jacaranda	a	3	frill	Chopper	12	43.08	28.7	35.4	119.68	0.3
X23D102599	Syringa	a	5	cut-stump trtment		0	00.00	47.9	58.9	119.68	0.5
X23D102599	Granadilla spp	x	1	cutting or slashing		0	00.00	12.0	14.7	119.68	0.1
TOTAL								330.1	397.7	143.55	2.8

Estimated Herbicide: Chopper = 185.56 litres Actual Herbicide: Chopper = _____

Persondays Initial	= 389.53	Area Initial	= 141.02	APD / Ha Initial	= 2.8
Persondays Foll Up	= 8.13	Area Foll Up	= 2.53	APD / Ha Foll Up	= 3.2

KEY

Nbalid = Identity number for NBAL
Rate = Litres of Product per closed hectare
PD/ha = Persondays per hectare
UPD = Unadjusted Persondays
APD = Adjusted Persondays

Project Manager's Initials

Contractor's Initials

Project: **GP Apies Rivier IDT**

Treatment Area ID: **A23D100100041**

WORKING FOR WATER

Part D (Page 3.3)
Attached as Part D of the Quotation

To be completed by the Project Manager

DETAILED DESCRIPTION OF THE WORK AND METHOD *(How the site is to look afterwards, special methods, exclusions etc)*	SPECIAL SITE CONDITIONS AND PRECAUTIONS *(i.e. access times and routes, fire, sanitation, hazards)*

ADDITIONAL WORK

Description of additional work	Additional Persondays	Area Manager Authorisation

OWNERSHIP OF MATERIAL

WFW Contractor Landowner Other _____

Project Manager's Initials	Contractor's Initials

Appendix 21. Example of a Working for Water (WFW) worker's contract.

WORKING FOR WATER PROGRAMME

CONTRACT OF EMPLOYMENT

BETWEEN

CONTRACTOR
Name:
Address:
ID:

AND

WORKER
Name:
Details
ID:

1. I am pleased to confirm that you have been appointed to work on a task based employment contract within a Special Public Works Programme (SPWP) project. Within this contract you will undertake numerous groups of tasks.

2. This contract must be read in conjunction with the standard terms and conditions of employment on SPWP attached.

3. The project where you will be employed is located at …….

4. The contract will start on …….

5. You must be aware that this contract is a limited term contract and not a permanent job. The contract may be terminated for one of the following reasons:

   a) If the contractor does not get additional contracts from the SPWP.
   b) Funding for the programme in your area comes to an end.
   c) You repeatedly do not perform in terms of the tasks set out in your work programme.
   d) You have worked a maximum of 24 months within a 60 month cycle.

6 You will be employed within the team as a …… .

7 While you are working you will report to ……

8 Payment

   a) You will be paid a fixed amount of R…… for completing a fixed amount of work .
   b) The amount of work required for the agreed rate of pay will vary from task to task. You will be informed at the beginning of each task or group of tasks how

much work you are expected to complete per day.

c) You will only be paid for work completed.
d) You will be paid the amount for the number of days quoted in the contract even if you finish the work before the time or after the estimated date of completion.
e) A contractor must pay you the production bonus (the extra days if the work is finished early) if you have completed your share of tasks.
f) The contractor will be paid within 30 days after the work is completed. You will be paid within 5 days of the contractor being paid.

9 In addition to the conditions above all the terms and conditions of employment on SPWP apply to your employment. If you breach any of these terms you contract may be terminated.

Signatures:

Signed on this day …… of …….. 2000

Contractor: …….. Date: …….

Worker: …….. Date. ……..

Witness: …….. Date: ……..

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.

Plot number	Region	Biome	Cleared prior to 1996 study	Clearing history provided by WfW:			Herbicides	Comments
				Initial (completion)	Follow-up			
1	Sabie	Grassland	Yes	31/01/2003	26/03/2004	30/11/2004	Chopper, mamba, garlon, blue dye	Biocontrol upstream, good tributaries
2	Sabie	Grassland	Yes	N/A	N/A	N/A	As above	No comment
3	Sabie	Grassland	Yes	N/A	N/A	N/A	As above	Biocontrol upstream, good tributaries
4	Sabie	Grassland	Yes	N/A	N/A	N/A	As above	No comment
5	Sabie	Grassland	Yes	N/A	N/A	N/A	As above	No comment
6	Sabie	Grassland	Yes	N/A	N/A	N/A	As above	No comment
7	Sabie	Grassland	Yes	31/01/2003	26/03/2004	30/11/2004	As above	Biocontrol upstream, good tributaries
8	Sabie	Grassland	Yes	N/A	N/A	N/A	As above	No comment
9	Sabie	Grassland	No	N/A	N/A	N/A	As above	No comment
10	Sabie	Grassland	No	N/A	N/A	N/A	As above	No comment
11	Graskop	Grassland	No	N/A	N/A	N/A	As above	Blue swallow breeding site
12	Graskop	Grassland	No	N/A	N/A	N/A	As above	Sunlight, Phasaphasa, Motitsi Rivers
13	Graskop	Grassland	Yes	18/09/2003	18/05/2004	N/A	As above	Sunlight, Phasaphasa, Motitsi Rivers
14	Graskop	Grassland	No	N/A	N/A	N/A	As above	No comment
15	Graskop	Grassland	No	N/A	N/A	N/A	As above	Sunlight, Phasaphasa, Motitsi Rivers
16	Graskop	Grassland	No	N/A	N/A	N/A	As above	No comment
17	Graskop	Grassland	Yes	27/08/2004	N/A	N/A	As above	Sunlight, Phasaphasa, Motitsi Rivers
18	Graskop	Grassland	No	27/08/2004	N/A	N/A	As above	Sunlight, Phasaphasa, Motitsi Rivers
19	Graskop	Grassland	No	N/A	N/A	N/A	As above	No comment

20	Graskop	Grassland	No	N/A	N/A	N/A	As above	No comment
21	Hazeyview	Savanna	Yes	N/A	N/A	N/A	As above	No comment
22	Hazeyview	Savanna	Yes	N/A	08/02/2002	17/01/2003	As above	No comment
23	Hazeyview	Savanna	No	N/A	N/A	N/A	As above	Cleared downstream in the past 3 months (Dec '04 – Jan '05)
24	Hazeyview	Savanna	Yes	N/A	N/A	N/A	As above	No comment
25	Hazeyview	Savanna	No	N/A	N/A	N/A	As above	No comment
26	Hazeyview	Savanna	Yes	N/A	N/A	N/A	As above	Cleared downstream in the past 3 months (Dec '04 – Jan '05)
27	Hazeyview	Savanna	Yes	N/A	N/A	N/A	As above	No comment
28	Hazeyview	Savanna	No	N/A	N/A	N/A	As above	Cleared downstream in the past 3 months (Dec '04 – Jan '05)
29	Hazeyview	Savanna	Yes	N/A	N/A	N/A	As above	No comment
30	Hazeyview	Savanna	No	N/A	N/A	N/A	As above	No comment
31	Hazeyview	Savanna	No	N/A	N/A	N/A	As above	No comment
32	Hazeyview	Savanna	No	N/A	N/A	N/A	As above	No comment
33	Hazeyview	Savanna	No	N/A	N/A	N/A	As above	No comment
34	Hazeyview	Savanna	Yes	N/A	N/A	N/A	As above	No comment
35	Hazeyview	Savanna	Yes	N/A	N/A	N/A	As above	Cleared downstream in the past 3 months (Dec '04 – Jan '05)
36	Hazeyview	Savanna	Yes	N/A	08/02/2002	17/01/2003	As above	No comment
37	Hazeyview	Savanna	Yes	N/A	N/A	N/A	As above	No comment
38	Hazeyview	Savanna	No	N/A	N/A	N/A	As above	No comment
39	Hazeyview	Savanna	No	N/A	N/A	N/A	As above	No comment
40	Hazeyview	Savanna	No	N/A	N/A	N/A	As above	No comment

Appendix 23. Details of the contractual engagement of Working for Water (WfW) with the landowners.

WORKING FOR WATER PROGRAMME
REQUEST FOR CLEARING ASSISTANCE
Part 1 - PROPERTY INFORMATION

TITLE DEED NUMBER:

SURVEYOR GENERAL REFERENCE NUMBER:

PROPERTY NAME

PHYSICAL ADDRESS OF PROPERTY

Code

X-COORDINATE (LONGITUDE) OF PROPERTY (Deg/Min/Sec)

D D M M S S **E**

Y-COORDINATE (LATITUDE) OF PROPERTY (Deg/Min/Sec)

D D M M S S **S**

Part 2 – LAND USER INFORMATION

SURNAME OF LAND USER

FULL NAMES OF LAND USER

ID NO./PASSPORT NO./BUSINESS REGISTRATION NO.

PHYSICAL ADDRESS OF LAND USER

Code

POSTAL ADDRESS OF LAND USER (*if different from above)*

Code

TELEPHONE NUMBERS OF LAND USER:

Work: *Code:* *No:* **Home:** *Code:* *No:*

Cell:

Email

Are you the land owner**?** Yes ☐ No ☐ *If no, please complete land owner details.*

SIGNATURE OF APPLICANT DATE

For office use only:
Questionnaire ID Number:

WORKING FOR WATER PROGRAMME
Part 3 – LAND OWNER INFORMATION

Are you a registered water user with the Department of Water Affairs and Forestry?
Yes ☐ No ☐ *If yes, state your water user registration number below.*

WATER USER REGISTRATION NUMBER: ☐☐☐☐☐☐☐☐

Complete details below only if different from land user information

SURNAME OF LAND OWNER

FULL NAMES OF LAND OWNER

ID NO./PASSPORT NO./BUSINESS REGISTRATION NO.

PHYSICAL ADDRESS OF LAND OWNER

Code

POSTAL ADDRESS OF LAND OWNER (*if different from above)*

Code

TELEPHONE NUMBERS OF LAND OWNER:

Work: *Code:* *No:* **Home:** *Code:* *No:*

Cell:

Email

SIGNATURE OF APPLICANT DATE

WORKING FOR WATER PROGRAMME
Part 4 – INVASIVE ALIEN PLANT INFORMATION

Section 1 –Complete this table for the area of the property on which invasive alien plants grow. If there is more than one area, copy this page and complete a separate page for each additional area)

Description of area (e.g. south of house, along river)	
List species occurring in this Area	
Approx. Area (Hectares)	

Section 2 - Complete this table for each species that has been listed in Section 1 above. If there are more than two species copy this page and complete a separate page/s for the additional species

Species Name:	
Density (e.g. scattered, dense)	
Maturity (young, seedling, mature)	
Dominant Land-use in area	
Are the plants grown for a purpose? (e.g. woodlot, shade)	
Future control steps for new growth and what steps will be taken to prevent spreading?	
Do you have a license to grow this species? If yes, provide details	
To be cleared? If no, provide details	
Restrictions regarding treatment methods	

Species Name:	
Density (e.g. scattered, dense)	
Maturity (young, seedling, mature)	
Dominant Land-use in area	
Are the plants grown for a purpose? (e.g. woodlot, shade)	
Future control steps for new growth and what steps will be taken to prevent spreading?	
Do you have a license to grow this species? If yes, provide details	
To be cleared? If no, provide details	
Restrictions regarding treatment methods	

SIGNATURE OF APPLICANT

DATE

WORKING FOR WATER PROGRAMME
Part 5 – CLEARING INFORMATION
(Only complete part 5 if the alien species are to be cleared)

PROPOSED LAND USER CONTRIBUTION

RESTRICTIONS REGARDING HERBICIDE USAGE ON PROPERTY

RESTRICTIONS REGARDING ACCESS TO PROPERTY

OTHER RESTRICTIONS/SPECIAL ARRANGEMENTS

OWNERSHIP OF CLEARED MATERIAL

DECLARATION

I have completed Part 1, Part 2, Part 3, Part 4 and Part 5.

I understand that by completing this form and submitting it to the Working for Water programme, the Working for Water programme is not obliged to render assistance with the clearing work.
I confirm that if this application for clearing assistance is successful, this documentation will form the terms of a binding agreement between the Working for Water programme and myself.

I know and understand the contents of Part 6.

I hereby accept that if assistance with clearing is granted to me it will be rendered in accordance with these conditions which will be binding on me

_____ _____

SIGNATURE OF APPLICANT DATE

FOR OFFICIAL USE ONLY:

Approved / Not approved: _____
Date received: _____ **Treatment number: _____**
Date treatment commenced: _____ **Date treatment ended: _____**
Name of WFW Officer: _____ **Future Inspection date: _____**

WORKING FOR WATER PROGRAMME
Part 6 - WFW STANDARD CONDITIONS FOR CLEARING INVADING ALIEN PLANTS ON PRIVATE LAND

Section 1:

FULL NAME OF LAND USER:

WATER USER REGISTRATION NUMBER:

DEED OF TRANSFER NUMBER

SURVEYOR GENERAL REFERENCE NUMBER:

FARM NAME AND ADDRESS/STREET ADDRESS OF PROPERTY:

This document must be signed on each page by the Applicant. It forms part of the Application for Clearing Assistance and must be submitted with the completed Part, Part 2, Part 3, Part 4 and Part 5 to the office of the Working for Water Programme, in the region in which the property is located.

If this document is not signed and submitted with the other Parts forming the Application for Clearing Assistance the application will NOT be considered.

1. In these conditions the terms "land user" carries the same meaning as in the Conservation of Agricultural Resource, 43 of 1983 and means the land owner or any person with a real or personal right to the land or a person who has the right to cut or remove trees or wood from the land.

2. Upon receipt of the Application for Clearing Assistance the Working for Water Programme will assess the Application and decide whether or not it is prepared to give assistance and, if so, to what extent.

If the Working for Water Programme is prepared to assist directly with the clearing work,

3. The application will be approved by the Regional Programme Leader of the Working for Water Programme and will be lodged with the regional office.

4. The land user will be notified that the application has been approved and a binding contract will be deemed to exist between the land user and the Working for Water Programme.

5. A representative of the Working for Water Programme will prepare a Plan for Clearing for each area of the Property.
   PLEASE NOTE: Where the Working for Water Programme is to assist with the clearing, the Working for Water Programme will not itself undertake the clearing work. It will engage independent contractors to do the work on behalf of the land user.

6. A representative of the Working for Water Programme will determine the costs of the clearing work in accordance with the standard tendering procedures of the Working for Water Programme as well as the dates upon which any contributions by the land user are to be made.

   Please note that once revised regulations 15 and 16 relating to weeds and invader plants have been promulgated in terms of the Conservation of Agricultural Resources Act, No 43 of 1983:
   - **All plants listed as Category 1 in terms of those revised regulations must be removed.**
   - **If plants that are listed as Category 2 in terms of those revised regulations are to be left, the land user must apply in accordance with the revised regulations to have the area in which they are grown demarcated for this purpose. In addition, the land owner must apply for registration as a water user (in terms of the National Water Act, 36 of 1998).**

SIGNATURE OF APPLICANT **DATE**

7. The Working for Water Programme representative will conduct an inspection of the land with the land user to determine the general condition of the land with regard to fencing, litter, erosion, quality of roads and any other aspects that may be affected by the clearing work.

8. The Working for Water Programme will then, in its absolute discretion but in good faith, determine the terms and conditions under which the clearing work is to be undertaken by Independent Contractors and payment is to be made to them. The Working for Water Programme will negotiate and, in accordance with its standard procurement procedures, conclude agreements with Independent Contractors to undertake the clearing works on these terms and conditions.

9. Should the clearing work on the land not commence within 6 (six) months of the land user being notified that the Working for Water Programme is prepared to assist with the clearing, the contract between the Working for Water Programme and the land user will be deemed to be null and void.

In the course of the clearing works,

10. The Working for Water Programme will be responsible for all negotiations and dealings with the Independent Contractors and workers employed by the Independent Contractor, to the extent that this may be necessary.

11. The land user must take all reasonable precautions to prevent injury to persons doing clearing work on the land other than injuries that would normally be associated with the carrying out of clearing work.

12. The Working for Water Programme and its employees or agents will not be liable for any acts or omissions done in good faith in the execution of the assistance.

13. The land user indemnifies the Working for Water Programme from all claims from whatsoever cause arising resulting from the execution of the assistance except where those claims arise from the fraudulent actions of the Working for Water Programme, its employees or agents.

14. The representative of the Working for Water Programme will notify the land user of any burning activity that the Working for Water Programme views to be desirable as part of the clearing work. The land user must supervise and take responsibility for any burning that may be undertaken as part of clearing work and will be responsible for any damage sustained as a result of such burning.

15. Once a substantial part of the area has been cleared, the representative of the Working for Water Programme will notify the land user of a date on which a joint inspection with the land user will take place to determine the adequacy of clearing work undertaken prior to the inspection.

16. The land user must attend all joint inspections of which the land user is notified. In the event of the land user failing to attend any inspection despite having prior notice thereof, the land user shall abide by any conclusions reached by the Working for Water Programme pursuant to such an inspection.

17. If, after any inspection, the parties agree that the clearing work in an area is incomplete and that further work is required to complete the task, the representative of the Working for Water Programme will notify the Independent Contractor accordingly.

18. The land user must co-operate with the representative of the Working for Water Programme and must ensure that all contributions to be made by the land user are made timeously.

19. If the assistance by the Working for Water Programme is terminated as a result of the land user failing to perform properly or timeously the land user will refund to the Working for Water Programme the costs incurred by the Working for Water Programme in providing assistance to the land user.

When the clearing work has been completed,

20. The Working for Water Programme will notify the land user of completion.

21. The representative of the Working for Water Programme will also notify the land user of a date for a joint inspection to determine the effectiveness of the work undertaken.

22. If the representative of the Working for Water Programme is of the view that the work has been completed to an acceptable standard the clearing work will be deemed to be completed and will advise the land user accordingly.

23. The representative of the Working for Water Programme will then advise the land user of the dates by which the land user must do further work to clear the land of any recurrence of invading alien plants.

24. If the land user is dissatisfied with the work, the land user shall notify the Working for Water Programme within 14 days of completion of the cause of dissatisfaction. If the land user fails to give such a notification to the Working for Water Programme the work will be deemed to have been done in accordance with these conditions of clearing and to the full satisfaction of the land user.

25. The land user must ensure that further clearing work is done by the dates determined by the representative of the Working for Water Programme and that thereafter the land is maintained in a condition where invading alien plants are effectively controlled.

26. **Should the land user thereafter fail to maintain the property in a state where invading alien plants are controlled the Working for Water Programme shall be entitled to recover from the land user ALL costs incurred in rendering this assistance and carrying out clearing work in terms of it.**

27. Unless otherwise agreed with the Working for Water Programme, should the land user cultivate or otherwise develop the cleared land within three years of the completion of the clearing work in terms of these conditions the land user must compensate the Working for Water Programme for all costs incurred by the Working for Water Programme in rendering this assistance.

28. The land user must notify the Working for Water Programme in writing of any claims that the land user may have arising from the implementation of this agreement, within 30 (thirty) days of completion of the clearing work.

29. Any disputes between the Working for Water Programme and the land user relating to the implementation of these Conditions for Clearing which they are not able to resolve amongst themselves must be referred for mediation with seven days of the other party being notified of the dispute. If the dispute is still unresolved after twenty-one days of the other party being notified of the dispute either party may refer it for arbitration by an arbitrator either agreed to by the parties or appointed by the president of the General Council of the Bar, in accordance with procedures to be determined by the Arbitrator. These procedures must have as their objective the expedited resolution of the dispute. The findings of the Arbitrator will be final and binding.

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SIGNATURE OF APPLICANT