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Vegetation response to clearing of exotic invasive plants along the Sabie River, South Africa

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CHAPTER 1

INTRODUCTION

The intention of this project is to evaluate the Reconstruction and Development Program's Working for Water Program, in terms of the impact made to the plant community and in the degree of success in removing selected exotic species.

There are two broad aims of the study. Firstly, to determine the effects of invasion intensity and clearing of exotic plants on soil seed bank composition, vegetation structure, plant species diversity, habitat characteristics and species composition. Secondly, to determine the effective soil seed bank of *Solanum mauritianum* and *Acacia mearnsii* through time. Due to the extensive spread of *S. mauritianum* within the communities observed, additional investigations into the spread and persistence of this species were also done.

The literary topics identified to be pertinent to the study were as follows: Disturbance theory - definitions, intermediate disturbance hypothesis and implications of clearing and exotic species in "natural" environments. Plant species diversity and species richness - measurements and definitions. Vegetation regeneration - types/modes of vegetation regeneration and the role of these in vegetation recovery, dispersal of individuals and successional implications for plant communities. These three topics are inter-linked at a number of levels, but for simplicity only direct relationships will be reviewed.

1.1 Disturbance in Plant Communities

1.1.1 Defining Disturbance

Two features characterize all natural communities at all scales of community structure. Firstly, communities are dynamic systems, and secondly all are spatially heterogeneous (Sousa 1984). Disturbance is a major source of temporal and spatial heterogeneity in the structure and dynamics of natural communities, and an agent of natural selection in the evolution of plant life histories. The type, duration and intensity of a disturbance have direct consequences for community structure and function. This is due to the important influence on ecosystem level processes that disturbances have, such as primary and secondary production, biomass accumulation, energetics, and nutrient cycling (Bormann & Likens 1979; Boerner 1982; Sprugel 1984; Vitousek 1984). Disturbances also have consequences at each hierarchical

level, and inclusion of each level is vital in order to understand disturbance as both a natural, and human induced phenomenon (Rykiel 1985; Pickett *et al*. 1989; Dovie *et al.* 2004). A universally applicable definition of diversity would thus have to: a) identify the entity disturbed, b) distinguish change in the object that is indeed a disturbance, and change that is not, and c) distinguish between the direct and indirect consequences of disturbance (Pickett *et al.* 1989). Many definitions of disturbance do not satisfy all these requirements, and consequently many debates still exist today on the full definition of disturbance.

Even so, the definition of disturbance most preferred is as follows: "A disturbance is the discrete, punctuated killing, displacement, or damaging of one or more individuals (or colonies) that directly or indirectly creates an opportunity for new individuals (or colonies) to become established" (Sousa, 1984). Disturbance may change the state of the dynamic system (community), which may be augmented by further levels of disturbance, in effect an additive disturbance event. The situation seen along the Sabie River is an example of this, where the presence of exotic invasive species in communities constitutes a disturbance, even "prior" to another disturbance such as clearing. Another disturbance factor to be considered is the condition of the community (level of disturbance) prior to the recorded disturbance event(s). This can be defined as the ambient disturbance level, and may lead to confusion when analyzing a monitored disturbance event such as clearing. This can be partially accounted for by identifying areas with minimal outside influences, for example human induced impacts such as grazing, firewood collection, and invasion by exotic species (Mentis & Ellery 1994).

Another factor in the understanding of disturbance is the type or disturbance regime being observed. Disturbance may be characterized as:

(1) Aerial extent - size of disturbed area;

(2) Magnitude - a) Intensity: a measure of strength of disturbing force;

b) Severity: measure of the damage caused by the disturbing force;

(3) Frequency - number of disturbances per unit time:

a) Random point frequency;

b) Regional frequency;

(4) Predictability - measured by the variance of the mean time between disturbances;

(5) Rotation rate - mean time required to disturb the entire area in question (Sousa 1984).

The above classification of the components of a disturbance event is useful, not only in identifying the spatial scale of the disturbance, but also the temporal scale. The disturbance of clearing exotic species

could be characterized according to Sousa (1984), as (1) large, (2) both intense and severe, (3) occur at a regional frequency of 1 - 2 years, (4) occur at a predictable regular interval, and (5) have a reasonably long rotation time. On the other hand, invasion by exotic plant species would be (1) large, (2) not as intense or severe as clearing, (3 & 4) occur at predictable and regular intervals, and (5) occur on a continual time scale. This indicates that clearing of exotic plant species would have a large effect on the overall disturbance to the community in the short term. Invasion by exotic species however, may have the same magnitude of disturbance, but occur over a longer time frame.

1.1.2 Implications of disturbance to community diversity and structure

Generally, high levels of disturbance may result in loss of community diversity and structure (Petraitis *et al.* 1989; Breytenbach 1991). Typically, it has been shown that community function becomes less stable with a loss in community diversity (Shugart & Seagle 1985; Petraitis *et al.* 1989; Tilman & Downing 1994).

Other complicating factors are involved in community function such as vegetation structure, which has been shown to play an important role in the stability and diversity of plant communities (Shugart & Seagle 1985). A loss in vegetation height classes has been observed to result in the loss of under canopy species that require shade. In forest ecosystems, shade tolerance is the primary criterion used for arranging tree species into a competitive hierarchy (Horn 1971; Keddy & MacLellan 1990). The removal of this hierarchy by exotic species invasion, or the removal of exotic species, could result in a loss of species from the community. According to Tilman & Downing (1994), this also results in a loss in stability of the community and further susceptibility to the effects of disturbance.

Not all disturbances are detrimental to ecosystem function, however. Disturbances that change vegetation structure also allow “new” species to enter the community through increasing the heterogeneity of the habitat (Stalmans *et al.* 2001) and hence altering the regeneration properties of the community and the environment. Some of these “new” species may be detrimental to ecosystem function, further disturbing the community (Geldenhuys *et al.* 1986; Hanley & Goulson 2003), but intermediate levels of disturbance may also allow for regeneration of previously dominant species, introducing "new" cohorts into the population (Shugart & Seagle 1985; Everard *et al.* 1995). Hence disturbance, depending on its frequency, extent and intensity can play either a destructive or a regenerative role in plant communities.

1.2 Invasion of plant communities by exotic plants: a source of disturbance

The relatively limited degree of understanding of the processes involved in the invasion of South African ecosystems by introduced vegetation prevents any useful generalizations being made at this stage (Cowling *et al.* 1989). A number of studies on the processes involved in invasion and spread of exotic species have however, been done (Higgins *et al.* 1997; Higgins & Richardson 1998).

One factor is clear, dispersal is crucial. The dynamic relationships between dissemination and animal vectors is complex and needs to be better understood (Harper 1977, Higgins *et al.* 1997). There is however, sufficient evidence that even for major weeds, clearly quantifiable and predictable relationships between habitat factors and invasion may be obtained. Determining these relationships in the South African context could provide an important means of evaluating introduced plants in terms of potential spread and control. The patterns of success and failure in persistence and spread among introduced plants points clearly to the governing role of biotic interactions, disruption of which is often needed for invasion (Harper 1977).

1.2.1 Definitions and classification of exotic and weed species

Definitions of weed and exotic species

A weed may be defined as “any plant considered undesirable, unattractive or troublesome, or one growing where it is not wanted” (Oxford dictionary 1965). In comparison, an invasive species may be defined as, “a weed that is a threat to the survival of natural vegetation” (Oxford dictionary 1965), and introduced species as, “those species translocated by man” (Kruger *et al.* 1991).

Exotic species are familiar plants in our environment, which are seen, consciously and unconsciously, infesting lawns, roadsides, ditches, waterways, croplands, rangelands and forests (Anderson 1982). In general, exotic species adversely affect the use, economic value, and aesthetic aspects of the areas they infest. Exotic species are controversial plants however, as they can have either positive or negative impacts. For example, exotic species can comprise the first stage of plant succession where the native vegetation has been disturbed or removed (Anderson 1982). This is both a problem during removal of exotics, and a solution considering the protection the vegetation cover provides against erosion in high rainfall areas.

Human intervention in the natural ecology of an area however, is very disruptive to the dynamic and mutually dependant system of interrelated plant and animal life. Often, "original" plant species disappear, and are replaced by other species, which are more adept to persisting in the new environment (Anderson

1982). More often than not, these are exotic species, which are able to regenerate faster than indigenous species.

Invasive plant classification

The characteristics of alien or exotic plants have long been observed as indicators of invasion potential or risk of invasion. Two fields of invasion biology, historical and modern, exist. The former uses distribution patterns of species to assess the extent to which taxa have invaded. The modern field uses the characteristics of taxa that have become invasive to classify species (Richardson *et al.* 1990; Frean *et al.* 1998). Either of these can be used to assess whether taxa are likely to become invasive if they are introduced to an area, whether for commercial or other purposes (Frean *et al.* 1998).

For example, based on the historical method of classification, many invader plants have been identified as to their origin (Wells *et al.* 1986). Using this information it was determined that 45.8% of exotic species in South Africa originated from Europe and Asia, while only 26.2% originated from South America (Wells *et al.* 1986). This is supported by the fact that the majority of colonization, which was aided by humans, took place from trade between the east and the west in the 1600s and 1700s. The remaining 28% of exotic species in South Africa come from around the remainder of the world including the north Americas and Australia.

The modern method, using species characteristics as indicators to predict invasion success allows species not yet introduced into the environment to be identified as possible invasive species. This then allows for preventative measures to be put in place to prevent the introduction of high risk species into the community.

Both the historical and modern fields are complementary, allowing species to be classified into problematic and non-problematic groups, based on their impacts on the environment and potential to become invader species. A study on exotic invasive species in KwaZulu-Natal Province, South Africa, illustrates this technique whereby a number of species were ranked in importance on the extent of their distribution, potential extent of distribution, difficulty of control, rate of spread and ecological impacts on the environment (MacDonald & Jarman 1985). This was done for a number of land uses (silviculture, conservation, agriculture, etc.) and resulted in a better understanding of which species were problematic and under what conditions.

1.2.2 Entry of exotic plant species into the South African environment

Invasion processes

There are a number of characteristics that play an important role in the introduction and spread of exotic species and their persistence in the environment. These characteristics are as follows: seed dispersal mechanisms; seed ecology; breeding systems; rates of growth; ability to resprout; germination requirements; environmental tolerances; susceptibility to disease; and comparative ecology of invasive species with respect to species which are likely to replace them after control methods have been implemented. Each of these characteristics plays a role in each stage of the invasion process. There are several identified stages in the invasion process however, these being divided into introduction, naturalization, facilitation, spread, species interactions and stabilization (Kruger *et al.* 1991; Cronk & Fuller 1995).

The first stage, or introduction of plants into a community, involves the translocation of living material by humans from one area to another, either unintentionally or intentionally. Once introduced, an invasive plant must become established beyond the site of initial introduction to form large self-sustaining populations in natural or semi-natural vegetation (Cronk & Fuller 1995). Facilitation means that a naturalized plant species may remain rare unless facilitated in some manner to spread (i.e. by a pollinator, disturbance, etc.). If the spread of the exotic plant species has been facilitated, the rate of spread depends on it's intrinsic growth and reproduction rates as well as the nature of the invaded habitat, including the presence of suitable 'safe sites' (Harper 1977) for reproduction. Efficiency of establishment and seed dispersal distance have been noted as important for rate of spread (Cronk & Fuller 1995).

The outcome of interactions with other species is important, and will determine if the exotic species "fit in" (passive) or "repel"(active) indigenous pollinators, consumers and competitors. This establishes the effect the species will have on ecosystem processes, community composition and vegetation structure. Stabilization of a community after invasion and/or clearing may occur through time, but this often results in a single or near single species stand or community (Dean 1985; Cronk & Fuller 1995). This may result in an unstable ecosystem, which could be more prone to the ill effects of disturbance.

Deliberate introduction of exotic plants

Many forms of introduction of "new" species may occur in the environment, but the main source of introduction of exotic plant species results from human intrusion. Many plants introduced into the South African environment by humans have served a purpose, and will continue to do so, both economically and

environmentally in the future. This is demonstrated by the silvicultural industry, where the majority of timber species were deliberately introduced and of exotic origin.

The risk of invasion by a species introduced for a given use is a complex function of several factors, one of which may be the extent to which a species is favored for such a purpose (i.e. forestry). Exotic plant species used in silviculture in South Africa have been propagated extensively, and a number of variants have been selected for their high productivity within the South African environment. Deliberate introduction of species has been found to favor a proportionately higher rate of successful establishment (de Winter *et al.* 1978; Kruger *et al.* 1991), both for intended use, and in terms of unwanted invasion. When considering this and the number of introduced species, the problem of invasion and risk of invasion as a form of disturbance to South African ecosystems becomes evident.

At least 400 species of trees and shrubs, both indigenous and exotic, were successfully cultivated in South Africa in the early 1980s (Poynton 1984), and even greater numbers at the present. This was about 40% of the native tree and shrub flora found in South Africa at the time, as calculated by de Winter *et al.* (1978). What is interesting however, is why most of these introduced species have not spread. Although bio-climatic matching aids successful introduction, it does not necessarily result in invasive spread (Kruger *et al*. 1986). Hence of the over 170 species that have been introduced into South Africa in the past two centuries (Poynton 1979 & 1984), few rank high on any invasion list (Henderson & Musil 1984; Macdonald & Jarman 1984; 1985). About 25% of the species introduced tend to spread (Poynton 1984), and are problematic only in or around plantations (Le Roux 1980).

Deliberate introduction may have other side effects besides the spread of the species (Dye & Jarmain 2004). Deliberate propagation of exotic species may modify the habitat in such a manner as to facilitate the dispersal and establishment of other exotic invader species. These "other exotic species" may be present by chance or be introduced by other means. In KwaZulu-Natal, a number of problematic invader species are escapees of timber plantations (MacDonald & Jarman 1985). Timber plantations tend to form seed source centers, especially for species that are dispersed by birds (eg. *S. mauritianum*) (Dean 1985). It follows that areas adjacent to plantations are subject to high invasion risk (MacDonald & Jarman 1985).

1.2.3 Invasion history in South Africa and its implications for invasion pressure

Although there are inadequacies in the historical record and in the coverage of introductions, a considerable amount of data is available on the introduction of plants into South Africa which are human

driven (Le Maitre *et al*. 2004). Historically, southern Africa has been subjected to a two-directional invasion of exotic plants; (1) via northern Africa and (2) via coastal ports. The northern Africa source of invasion relates to pre-modern man and can be considered minor to the invasion contributions made by the second source of exotic plants, the coastal ports, over the last 200 years. About 50% of invasive species identified belong to four families of which, by 1910, half originated from Asia and Europe (Henderson & Wells 1986; Wells *et al*. 1986). Since then, South America has supplied more exotic species. Most of these invasive exotic plants were cultivated at one time or another (Wells *et al*. 1986). Ports however, have been the *foci* of colonization and therefore plant invasion, and historically have the longest history of introduction to southern African ecosystems (Wells *et al*. 1986).

The impacts of a plant invasion may vary according to the duration and history of invasion (Nel *et al.* 2004). In South Africa exotic plant invasions are still relatively recent, with almost all human related introductions being less than two hundred years old, and mostly less than a hundred years old. This may be an important factor when evaluating the restoration of invaded areas. Many studies illustrate however, that the impact of invasion and the ability to remove and restore indigenous communities may not be related to the age of the invasion but rather dependant on other physiological variables making the establishment of indigenous vegetation equally difficult (Mentis & Ellery 1994; Robertson *et al.* 2003).

If however, the age of the invasive stand were the dominating factor, the extent of the impact by exotic plant species would also be related to the species and extent of habitat modification that they impose through time. This concept is called infection pressure, and indicates the potential of a species to become problematic with increasing time in a new habitat (Mentis & Ellery 1994). An analysis of the information on species of *Eucalyptus, Acacia* and *Pinus* in Poynton (1984) together with the dates of introduction taken from seed-stock records and other sources, indicated a real increase in the incidence of invasion with time since introduction (Poynton, 1984). Many of the areas invaded today are near to or in areas initially invaded by exotic species, and although most plant invasions in South Africa are relatively "young", species within the region have been naturalized for over 100 years in some instances. This is important when considering the regeneration of vegetation in cleared areas, as many of these areas are surrounded by plantations and have a history of invasion by exotic species.

1.2.4 Differential invasion within the ecosystems/biomes of South Africa

Using the number of invasive plant species recorded as a measure of the extent of invasions in South Africa, Wells *et al.* (1983) concluded that aquatic ecosystems were the most severely affected, with stream

bank ecosystems second, and the terrestrial habitats of the winter rainfall region third. Macdonald & Jarman (1985) deemed the riverine habitat the most susceptible to invasion in KwaZulu-Natal, and Rutherford & Westfall (1994) identified the eastern escarpment of southern Africa as an overall area susceptible to invasion. This is supported by the fact that this area occupies a small proportion of the total land surface in South Africa, but has been invaded by as many as 261 species (151 herbaceous perennials and 112 trees, shrubs and climbers) (Wells *et al.* 1980; Henderson & Wells 1986).

One of the reasons for increased exotic invasion of riverine environments, is the frequency of disturbance within these ecosystems (MacDonald 1983; Henderson & Musil 1984; Gubb 1985 in Henderson & Wells 1986). In the South African silvicultural zones, this increased invasion can be multiplied, as these areas are closely associated with timber plantations, which provide a source of invasive species (Le Roux 1980; MacDonald & Jarman 1985). Under "natural" conditions however, the reasons for riverine habitats being susceptible to invasion is the dispersal mechanisms, namely water & avian, present within the ecosystem (MacDonald & Richardson 1986). Invasive species make use of these dispersal mechanisms and become established when disturbance to the community occurs. This has been observed for *Acacia* species, where distribution along watercourses has been documented (MacDonald & Richardson 1986). Species dependant on avian dispersal also distribute along water courses, but dispersal is dependent on a water source and vegetation that provides roosting opportunities (MacDonald & Richardson 1986).

1.2.5 Impacts of exotic plant invasions on communities

The impacts of exotic invasive species can be defined as any change to ecosystem, community or population processes caused by exotic species once it has entered the landscape. Processes within communities which are adversely affected, such as species turnover and establishment, are considered important for the continuing function of the community. Robinson & Edgemon (1988) suggested that species richness values were idiosyncratic and determined to a considerable degree by historical patterns of invasion. The most obvious impact of exotic species invasion in both the grassland and savanna biomes comes from the partial to complete replacement of indigenous communities, thereby reducing species richness and altering the appearance and character of the landscape (Henderson & Wells 1986). For example, on the eastern escarpment silvicultural zone the increased woody element has formed thickets altering infiltration of water and light to ground level (Henderson & Wells 1986). Changes to the fire regime by an increased fuel load, but with a reduction in ground cover, has resulted in fewer fires of greater intensity (Henderson & Wells 1986). This has resulted in a further loss in species and a reduction in plant diversity.

Other environmental modifications also occur with introductions of exotic plants, such as decreased soil and surface water run-off (Van Wilgen & Richardson 1985) and increased fuel load and fire frequency and/or intensity (Van Wilgen & Richardson 1985; Scott & Van Wyk 1990; Scott & Schulze 1992). Not only do the above physical alterations to the environment occur, but biological agents can also alter the environment, as *Acacia* invasions in the Fynbos have shown by increasing the rate of nutrient cycling (Witkowski 1991a,b; 1994). The above factors should all be taken into consideration when evaluating the impacts of exotic species invasion on communities.

1.3 Clearing of exotic species from plant communities

1.3.1 Exotic species control

Weed control encompasses those practices whereby weed infestations are reduced, but not necessarily eliminated (Anderson 1982). The degree of weed control obtained is dependant on the characteristics of the weed(s) involved, and the effectiveness of the control method(s) used. Eradication is the ideal form of weed control, but is rarely obtained in practice. In order to increase the effectiveness of any weed control programme, an integrated approach is normally utilized. An integrated control mechanism involves two or more of the five basic weed-control techniques, namely: prevention, biological, cultural, mechanical and chemical (Anderson 1982). Integrated weed control is not a new practice and has been utilized by farmers and range managers for many years.

Unfortunately many of these weed control methods are not totally species specific, and result in the disturbance or removal of indigenous plant species as well as the targeted species. The least specific weed-control techniques are that of chemical control, especially if it is not managed correctly. Chemical control requires the dispensation of chemicals into the environment. The method of dispensation and the chemicals used are both important in determining the specificity of the treatment and hence the degree of disturbance (Anderson 1982). Physical control techniques constitute a disturbance, both creating an opportunity for re-establishment of exotic species and damaging indigenous vegetation present within the treated area. Physical control techniques may also contribute to soil erosion by removing vegetation from sloped areas (especially areas under high invasion intensity). Biological control needs careful research into organism specificity (Olckers 2004). Often however, it is observed too late that the biological control agents can adapt to other hosts. It appears that there is no solution to the disturbances imposed by exotic species control. The only option is to reduce application and maintain a high degree of specificity and control when applying these techniques.

1.3.2 Motivation for clearing of exotic plant species

Some plantation and range management practices (especially clear-cut harvesting with intensive site-preparation and range improvement through chopping and discing) conjure vivid images of ecosystem destruction (Lewis *et al*. 1988). The Conservation of Resources Act makes provision for control over the utilization of natural agricultural resources in order to promote the conservation of soil, water resources and vegetation. This includes the control of weeds and invader plants (Section 5- The prohibition of the spread of invasive plants; Part II. Weeds and invader plants) (Henderson *et al.* 1987). This act was administered by the directorate of soil production, of the Department of Agriculture and Water Supplies (Henderson *et al.*1987), but currently the Department of Water Affairs and Forestry has taken over this role.

In addition to the legal ramifications of exotic species control, it has been calculated that invasive species consume large quantities of water from the environment, and that clearing of these species would result in increased water availability. In addition, clearing of exotic species would increase water supply at a cheaper cost per litre than piping from other sources, or construction of dams (Bosch & Hewlett 1982; Le Maitre *et al*. 1996; Van Wilgen *et al.* 1996). Thus, water gained by clearing justifies the cost of the clearing operations. Besides this, the environmental benefits of exotic species removal (Van Wilgen *et al.* 1996), such as increased plant diversity, corridor formation (island biogeography theory) (MacArther & Wilson 1967), decreased soil erosion, and increased aesthetic and eco-tourism value are also attractive motivators. Hence, clearing of exotic species from riverine corridors has both economic (direct and indirect) and environmental benefits to serve as motivation.

The Working for Water Programme also offers other benefits. One of these is the increased income to the rural communities of the region (Magadlela & Mdzeke 2004). This programme plays an integral part in the Reconstruction and Development Programme (RDP), by offering a means of reducing poverty.

1.3.3 Clearing of exotic plant species in Mpumalanga and the Sabie River Catchment

The Reconstruction and Development Programme (RDP) have undertaken clearing of exotic invasive species in South Africa. At the time of the study the RDP Working for Water Programme was in the "active clearing" phase of the project (1995 - 98 in Mpumalanga Province). This was planned to be streamlined down to the "follow up" phase, which would continue for up to twenty years (Coetzee 1996; K. Asmal *pers. comm.* 1996). At the time of the study, the RDP Working for Water Programme was removing a

predetermined list of exotic invasive species (Table 1.1.) from river catchment areas. This has recently changed to include the category 1 to 3 declared plants (Appendix 1.), which are plant species, which have been declared Weeds and Alien Invader Plants in South Africa in terms of the Regulations pertaining to the Conservation of Agricultural Resources Act 43 of 1983 as amended. This list is even more extensive for the lower catchment areas (Foxcroft *et al.* 2003). For more information, please see the website for Weeds and Invasive Plants in South Africa at http://www.agis.agric.za/agisweb/wip.htm.

Weed species are broken up into three categories of aggressiveness and application:

- **Category 1 Plants.** This is the strictest category. These plants may not occur on any land or inland water surface other than in a biological control reserve. Except for the purposes of establishing a biological control reserve, one may not plant, maintain, multiply or propagate such plants, import or sell or acquire propagating material of such plants except with the written exception of the executive officer.

- **Category 2 Plants.** These are plants with a commercial application and may only be grown in demarcated areas (or biological control reserves). See the Government Gazette listed below for details relating to demarcated areas. Other provisions of category 1 apply.

- **Category 3 Plants**. The regulations regarding these plants are the same as for category 1, except that plants already in existence at the time of the commencement of these regulations are exempt, unless they occur within 30 m of a 1:50 year flood line of river, stream etc.

Exotic vegetation identified as falling into the Mpumalanga RDP Working for Water Programme species removal list was being removed in a 30 m strip (minimum) defined as the riparian zone, found on both sides of rivers, streams and other water bodies (A. Poulter *pers. comm.* 1996). Clearing of invasive species using mechanical means (felling or ringbarking), and chemical herbicide application such as Roundup and Chopper have and are currently being used for the control of exotic plant invasions (RDP Water Conservation Pamphlet- Working for Water 1996).

1.4 Plant species diversity

1.4.1 Definitions of species diversity

The literature on the measurement of species diversity is voluminous with many definitions of diversity available (Solomon 1979; Patil & Taillie 1982). Species diversity has traditionally been equated with the number of species (species richness) or species density when species are quantified in relation to the area

from which the sample was taken (Whittaker 1972; Mueller-Dombois & Ellenberg 1974). Species diversity may also be divided into two components: species richness and species evenness (Pielou 1977; Smith & Wilson 1996). Diversity measures attempt to include both species richness/composition and species evenness into a single entity (Pielou 1977; Ludwig & Reynolds 1988; Smith & Wilson 1996). It has been recognized however, that a lack of knowledge of the properties of the various diversity indices has been a limitation to their ecological usefulness (Alato 1981).

1.4.2 Diversity measures

Development of diversity indices

Many conservation and environmental groups have, through time, suggested a need for the assessment of the effects of human practices such as the control of exotic species, firewood collection and grazing on species diversity. The ease of biodiversity measurement has lead to the development of a variety of indices of species diversity, among them the more popular Shannon's index, Simpson's index, Jaccard's coefficient and Hill's diversity numbers (Kempton & Wedderburn 1978; Lewis *et al.* 1988). The statistical determination of species diversity, and hence biodiversity, became a controversial issue due to indices differing in the emphasis placed on either "species richness" or "species evenness" (Huston 1994).

Subsequent studies however, have shown that issues in sampling design are of more consequence to the abovementioned measure of diversity. Issues such as scale, sampling technique and what type of data (abundance value) collected are of importance when measuring diversity (Whittaker 1972; Bond 1989; Cowling *et al.* 1989; Walker 1989). This has led ecologists to research and recognize the independently controlled components of species diversity rather than just the index (Whittaker 1972; Bond 1989; Walker 1989; Hobbs 1992).

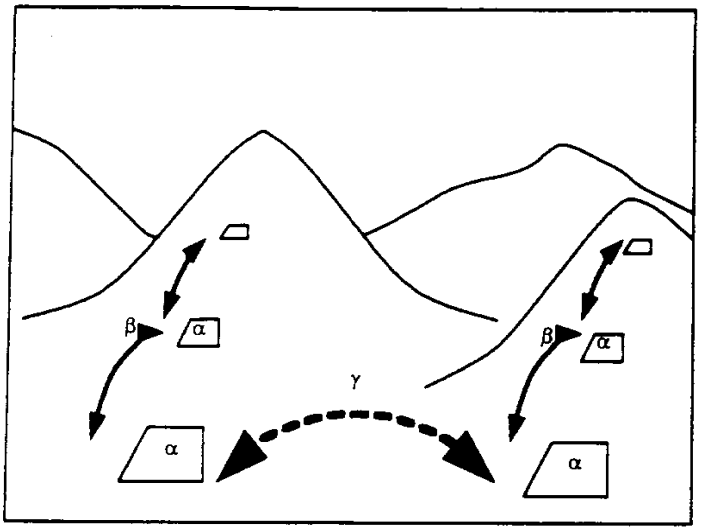


Figure 1.1. The three components of species diversity. α=species richness within a habitat, β=species turnover between habitats, γ=species turnover within habitats between geographic regions (after Bond, 1989)

Scale is important, and the scales at which diversity is measured can be summarized into alpha, beta and gamma diversities (Bond 1989). The number of species that occur within a community or habitat is termed alpha diversity, which can be measured using the conventional indices such as the Shannon index (Cowling *et al*. 1989). Alpha diversity is usually determined at the 0.1 ha scale, and is called point diversity at the 1 m^2 scale (Cowling *et al*. 1994). Beta diversity is measured as the turnover of species from one habitat to the next (Figure 1.1.). Regions that have similar species compositions within each of their communities will have low beta diversity. The turnover of species from one geographical region to the next however, is termed gamma diversity (Figure 1.1.). Gamma diversity is synonymous to delta diversity, described by Whittaker (1972). Since geographical gradients incorporate some degree of environmental and thus habitat changes, it is difficult to separate the beta and gamma components of diversity (Cowling *et al*. 1989). The division of diversity into these components however, allowed some recognition of the different scales of diversity that occur within the environment.

Table 1.1. List of invasive exotic species targeted for clearing in the riverine areas of Mpumalanga Province (A. Poulter 1996[1]). Stars (*) indicate the weed category number of the species (Appendix 1).

SCIENTIFIC NAME	COMMON NAME
Acacia mearnsii De Wild	Black Wattle **
Acacia melanoxylon R. Br.	Blackwood **
Caesalpinia decapetala (Roth) Alston	Mauritius Thorn *
Eucalyptus spp.	Including all gum species **
Jacaranda mimosifolia D. Don.	Jacaranda ***
Lantana camara L.	Lantana, Tickberry *
Ligustrum vulgare L.	Common Privet ***
Melia azedarach L.	Syringa ***
Morus alba L.	Mulberry ***
Passiflora edulis Sims.	Granadilla
Pinus spp.	Including all pine species **
Populus spp.	Including all poplar species **
Quercus acutissima Carr.	Bristle Oak
Ricinus communis L.	Castor Oil Plant **
Rubus cuneifolius Pursh.	American Bramble *
Salix babylonica L.	Weeping Willow **
Sesbania punicea (Cav) Benth.	Red Sesbania *
Solanum mauritianum Scop.	Bugweed *

1.4.3 Measurement of plant species diversity

Attempts at addressing the problems in experimental design, and the measurement of species diversity have only recently been undertaken. Several recent textbooks have focused on the importance of diversity and its measurement, but none contain precise methodologies to measure it (Stohlgren *et al.* 1995). Lamont *et al.* (1995) discussed the approaches to be used in assessment in order to improve experimental design. In this study it was found that quadrat size significantly affects the measurement of alpha diversity, and that in order to obtain a more realistic measure, larger quadrats must be used (Kwiatkowska & Symonides 1986).

One of the methods used to determine the optimum quadrat size, is the nested quadrat approach (Mueller-Dombois & Ellenberg 1974). The most popular of these approaches is that of the Whittaker nested plot (Stohlgren *et al.* 1995). The nested plot approach allows for: (a) evaluation of the influence of spatial scale on local species richness patterns; (b) better comparisons of community richness than singe scale methods provide (Whittaker 1977); and (c) the development of species area curves to estimate larger scale richness patterns (Shmida 1984, Cowling 1994). The most attractive attributes of the Whittaker nested plot design are that it provides: (a) a standardized approach to quantify species richness and diversity in different plant communities; and (b) insights on the effects of quadrat size when determining species-area relationships (Pielou 1977; Stohlgren *et al.* 1995). Attribute (a) has become a vital aspect of species diversity measurement, as β and γ diversity measures require a standardized approach if data is to be comparable. A number of flaws have been noted in the original Whittaker nested plot design, such as differences in plot shape at different scales, and the effects of this in non-homogeneous vegetation. The area covered by different shapes of quadrat may bias sampling, the extent of which is dependent on the vegetation type. For example, a square plot may be dominated by a single characteristic of the environment i.e. a single tree in a grassland. In contrast, a rectangular quadrat would include more environmental heterogeneity.

Plot size and spatial auto-correlation by overlaying plots can also be a problem (Stohlgren *et al.* 1995). The modified-Whittaker nested plot design, proposed by Stohlgren *et al.* (1995), attempts to amend these faults, and provides a more realistic plot design to measure species richness and diversity.

1.4.4 The nested plot technique

In the past, the nested plot technique involved the use of sampling areas employing plots that increase in size from a usually small quadrat size (Mueller-Dombois & Ellenberg 1974), then enlarging the area following a log distribution pattern with the smallest plot size being 1 m² (log1 = 0), and increasing at one unit intervals (i.e. log10 = 1; log100 = 2; log1000 = 3). A number of modifications to the nested plot technique are possible (Westfall *et al*. 1983). Apart from the standard nested plot used by Whittaker and many other authors (Ward *et al.* 1993), with standard plot sizes of 1, 5, 10, 100 and 1000 m² (Naveh & Whittaker 1979; Whittaker *et al*. 1979; Ward *et al*. 1993), other plot sizes have also been used to study diversity and species richness (Naveh & Whittaker 1979; Westfall *et al*. 1983; Van der Moezel & Bell 1989).

The Whittaker nested plot sampling method consists of a number quadrats of unequal sizes situated within a larger quadrat. Quadrat sizes within the Whittaker nested plot range from a 1 m x 1 m square to a 2 m x 5 m rectangle to a 10 m x 10 m square, and then back to a 20 m x 50 m rectangular plot (Table 1.2.). The modified Whittaker nested plot designed by Stohlgren *et al.* (1995) alters the size of the nested plots to maintain the same overall shape of the greater quadrat and hence minimize variation between plot size being caused by differing edge effects at each scale of the nested plot (Table 1.2.)

Table 1.2. Dimensions of plots and subplots in various nested vegetation sampling designs. A comparison of the original Whittaker nested plot with the modified-Whittaker nested plot.

Dimensions	Whittaker Method	Modified-Whittaker Method
Ten 1 m^2 sub-plots	1 m x 1 m (contiguous, clustered)	0.5 m x 2 m (systematic, outer perimeter not contiguous)
Two 10 m^2 subplots	2 m x 5 m (contiguous, overlapping)	5 m x 2 m (systematic, outer perimeter non-overlapping)
One 100 m^2 sub-plots	10 m x 10 m (overlapping)	5 m x 20 m (centred, non-overlapping)
One 1000 m^2 plot	20 m x 50 m (overlapping)	50 m x 20 m (overlapping)
Source:	Shmida (1984)	Stohlgren *et al*. (1995)

1.5 Vegetation regeneration after disturbance

Riparian ecosystems are dynamic and the current state of vegetation extremely fragile (Sousa 1984). They experience periodic flooding, erosion, silting and a variety of biotic and abiotic stresses like grazing, scraping, agriculture, waste and sewage disposal and discharge of effluent. With these disturbances comes the need for regeneration of the plant species within the community. The rate and pattern of reestablishment following a disturbance depends on the following elements:

(1) The morphological and reproductive traits of the species present;

(2) The reproductive biology of the species not present on the site when the disturbance occurred, but those that have occupied it previously (resulting in a seed bank) or those that occur within dispersal distance of it;

(3) Characteristics of the disturbed patch which includes a) the intensity and severity of the disturbance, b) its size and shape, c) its location and degree of isolation of sources of colonists, d) the heterogeneity of its internal environment and e) the time required for open patch creation (Sousa 1984).

1.5.1 Mechanisms of vegetation regeneration

Resprouting after disturbance

Many species resprout, coppice and extend via stoloniferous growth (Pate *et al.* 1990; Enright & Lamont 1993; Lamont & Witkowski 1993). These species have the advantage over obligate re-seeder species because vegetative growth generally occurs from an original individual, which may or may not have been damaged by disturbance (Enright & Lamont 1993). This means access to resources, that germinant individuals would not have. Many exotic species have the ability to resprout in this manner, thus giving these species the opportunity to explore disturbances to a greater extent, hence facilitating their proliferation within a disturbed community (Luoga *et al*. 2004).

Seed production/sexual reproduction

Seeds are the principal means by which weed species regenerate, allowing species to re-colonize and invade new areas. A single weed plant species commonly produces vast numbers of seeds, typically these eventually constitute an extensive seed bank, and hence regeneration potential (Kruger *et al.* 1991; Witkowski & Wilson 2001; Witkowski 2002). The number of seeds produced per plant is related to the mean weight per seed. The lighter the seeds, the more seeds produced per plant. Where natural vegetation is disturbed, it is apparent that the first plants to appear are weeds and that most of these plants arise from seeds either lying dormant in the soil or recently dispersed to the site (Anderson 1982).

Storage of seed propagules in the environment

Any attempt to understand the population dynamics of a species must include factors that affect the fecundity of that species (Smith 1990). The spatial pattern of a species, and its population size and density, depend on the dispersibility of its seed, the pattern and degree of seed germination and seed and seedling mortality (Smith 1990). Thus, no investigation of the population biology of a plant species or community is complete without an understanding of its population dynamics during the seed stage of the life cycle. The extent to which persistent seed banks influence community function and diversity is largely unknown

(Kalisz 1991; Tybirk *et al.* 1994). What is known however, is that the spatial distribution, and the extent of such a regenerative property, has a major role to play (Witkowski & Garner 2000). The extent of the effect is dependant on the size of the seed bank, degree of persistence and the number of propagules that grow to maturity (Milton 1980; Kalisz 1991; Garner & Witkowski 1997).

Re-invasion from seed banks raises the question of seed persistence in the soil as seed dormancy could be considered a form of long-term dispersal (Dean *et al*. 1986). It is recognized that species which dominate the seed bank have an advantage when disturbance creates regeneration opportunities (Bond & Slingsby 1984). There is evidence that compositional gradients in the seed bank and above-ground vegetation are highly correlated (Looney & Gibson 1995). Thus, in certain situations, invasive species with the greatest number of viable seeds in the seed bank could become the dominant vegetation, eventually replacing the indigenous vegetation (Dean *et al*. 1986).

Re-colonization of disturbed areas

Re-invasion of areas cleared of exotic species may occur in a number of different ways, namely propagation from seed banks (aerial or soil), vegetative growth (resprouting from original root stock or from cuttings), and dispersal of seed propagules from outside. All three of these mechanisms are important, as clearing of exotic individuals disturbs the surrounding vegetation creating a “window of opportunity” for plant establishment and the opportunity to re-colonize or colonize areas previously unoccupied.

In disturbed areas there is a greater probability of colonization by “new species”, both indigenous and exotic (Geldenhuys *et al.* 1986). Hence, the clearing of exotic species, a disturbance event, may lead to invasion by other species or re-invasion by the same species at even higher densities. Clearing also offers opportunities for "new" indigenous species to become established in areas where they were previously excluded.

Unfortunately weed species generally re-colonize the cleared areas first. This could be attributed to the annual seed production of invasive exotic species, which usually exceeds that of indigenous vegetation (Rutherford *et al.* 1991). Their rapid growth is often associated with structural (height) advantages (Rutherford *et al.* 1991), which can lead to “shading out” of indigenous vegetation. Thus there is a need to determine the success of clearing operations on exotic species, both in terms of preventing direct re-invasion by resprouting, and determining the extent of re-colonization by exotic and indigenous vegetation through seed. There are however, few studies that deal with exotic species clearing, particularly at the

community level. It is important to understand this negative aspect of exotic species removal, as re-invasion of disturbed areas after clearing may be more detrimental to the ecosystem than the initial invasion.

1.5.2 Succession in disturbed plant communities

In early phases of recovery from plant invasion, the changes in diversity and abundance of herbaceous plants is the quickest, followed by the increased abundance of indigenous woody plants such as shrubs and trees (Connell & Slayter 1977; Mentis & Ellery 1994). An increase in holistic diversity can therefore be expected after clearing of exotic species (Sousa 1984). In essence, the clearing disturbance resets the successional sequence of the community (Denslow 1987; Mentis & Ellery 1995). A number of years will be required however, to regain the same successional stage that was present prior to the clearing disturbance, and species composition may be altered in the post cleared community. Hence the need for long term studies of vegetation restoration/regeneration in areas that have been disturbed by human activities.

1.6 Motivation for the assessment of exotic species removal

One of the aims of conservation is to manage the environment in order to maintain biotic diversity and to ensure that ecosystem processes continue to function. This is often difficult to translate into management actions (Van Wilgen *et al*. 1994). To complicate this, there are several approaches to the "weighting" of species in order to calculate biodiversity. Systematists have generally been more concerned with compositional diversity, suggesting that biodiversity is synonymous with species diversity, while ecologists have become interested in functional diversity, shifting the emphasis from the conservation of species to the maintenance of ecosystem processes. As our understanding of the links between ecosystem function and biodiversity is rudimentary, managers often opt for the actions that benefit well studied individual species (Western 1992; Van Wilgen *et al*. 1994). There must be a movement away from this approach if there is to be an effective management of the ecosystem as a whole.

With this in mind, the motivation for assessment of clearing operations was considered twofold. Firstly, based on the question of whether the Mpumalanga Province Working for Water Programme has been successful in eradicating exotic species from the riverine environment and preventing re-establishment of invasive vegetation. Secondly, to determine if clearing operations have disturbed the riverine ecosystem in such a manner as to alter its function, structure and diversity. This last point has numerous implications in

terms of a holistic approach to ecosystem management, and key community characteristics affected by invasion and clearing, such as loss of species, ecosystem aesthetic properties, community composition, changes in soil properties, hydrology, erosion and species reproduction. The study was also needed in order to locate problem areas in the clearing programme's strategy and application, which have resulted in poor clearing efficiency such as persistent exotic species and the determination of the extent of disturbance to the indigenous vegetation. In order to fully understand and assess the process of vegetation recovery after exotic species removal, and the modifications caused by "invasion intensity" on vegetation composition, the role of key species (mostly exotic) must also be analyzed, together with vegetation structure and regeneration potential.

With this motivation in mind, a number of objectives were set out in order to assess the disturbance of invasion and exotic species clearing on indigenous vegetation. The objectives of this study were as follows:

1. To determine the environmental modifications that occurs with exotic species invasion and the effects of clearing (Chapter 3).
2. To determine growth form diversity as a function of degree of invasion (Chapter 4).
3. To determine vegetation growth form diversity after exotic species clearing as a function of degree of prior invasion (Chapter 4).
4. To determine the effects of invasion and clearing on vegetation structure (Chapter 4).
5. Determine the seed bank persistence of two of the major invasive species, *Solanum mauritianum* and *Acacia mearnsii* (Chapter 4 & 5).
6. To determine soil seed banks of woody species (indigenous and exotic) as a function of the degree of invasion prior to and after clearing (Chapter 5).
7. Compare seed bank composition with woody plant species composition prior to clearing (Chapter 5).
8. To determine species richness and diversity as a function of degree of invasion prior to clearing (Chapter 6).
9. To determine species richness and diversity after exotic species clearing and as a function of prior invasion intensity (Chapter 6).

These objectives can be logically grouped together to fall under the following chapters which will be used in the thesis: (1) The impacts of invasion and clearing on the environment (Chapter 3); (2) Changes in vegetation structure in response to invasion and clearing (Chapter 4); (3) The effects of invasion and clearing of exotic species on soil seed banks (Chapter 5); and (4) Changes in species richness and diversity in response to invasion and clearing (Chapter 6).