Effects of treatment on *Lantana camara* (L.) and the restoration potential of riparian seed banks in cleared areas of the Victoria Falls World Heritage Site, Livingstone, Zambia

Michael Nang'alelwa

Thesis presented in fulfilment of the requirements for the degree of Master of Science, Botany Department

Rhodes University

Project Supervisor: Dr. S. Vetter

December 2010

Declaration

I, the undersigned, hereby declare that the work contained in this thesis is my own original work and that I have not previously in its entirety or in part submitted it at any university for a degree

Signature…………………………...   Date…………………………

Table of Contents

List of tables

List of appendices

List of figures

Acknowledgements

I am grateful to my supervisor Dr. S. Vetter for her guidance during my study. I also acknowledge the partial sponsorship received from the UNEP/GEF Project *Removing Barriers to Invasive Plant Management in Africa* (RIBPMA). I thank my workmates on the RBIPMA Project at Victoria Falls; Bonna Zulu, Brian Malambo, Gaddafi Muchindu, Charity Moomba, Joseph Mwanza, Weinwright Muyembi, Arnold Bowa and Peter Mwale for their dedicated assistance in the field.

I thank Mphande Sichamba of the Forest Herbarium in Kitwe, Norman Stewart and Evelyn Roe of the Northwest Naturalists Society, Livingstone, Helen Pickering of England and Mike Bingham of Lusaka for their help with identification of plant species in the research sites. Trumber Jura, Phillip Gonde, Joshua Magaya and Cecillia Ncube of Zimbabwe Parks and Wildlife Management Authority in Victoria Falls town are thanked for their help with fieldwork and plant identification. Russell Young of Maramba River Lodge is thanked for his keen interest in my work and allowing access to his property for research.

I thank Dean Pitt and Simon Tembo of Sun International for use of the hotel grounds for the seed bank experiments while Top Turf Ltd is thanked for the seed trays and other nursery equipment used during the study. Alfred Kashweka and Collins Kabyema of NHCC helped with research facilities and equipment, while Joseph Lishomwa provided sacks for the erection of the seed traps. My colleagues, Muyumbwa Ndiyoi and Simbangala Simbangala helped with formatting of the document and editing of the maps.

I owe my wife Mitred and our children, Lishebo and Mwangala, my sister Sikopo and niece, Muzione, deep gratitude for their patience and understanding on the many occasions I had to be away from home on account of my studies. I dedicate this thesis to my parents, Sikopo and Mwangala Nang'alelwa (MHSRIP) for all the love and encouragement given in the formative years of my life. Finally, I wish to thank God for having made it all possible.

Summary

The exotic plant *Lantana camara* L. has invaded the riparian areas of the Victoria Falls World Heritage Site in Livingstone, southern Zambia, threatening native plant communities which support populations of species of special concern. I trialled the mechanical control method of manual uprooting and 3 different herbicides applied through paint brushing of an imazapyr concentrate at 250g. l^{-1}, spraying on cut stumps with metsulfron methyl at 600g.l^{-1}, and foliar spraying on re-emergent lantana foliage with glyphosate at a dosage of 166g. l^{-1} in July 2008 in 20 100m^2 treatment plots, 5 invaded control plots and 5 uninvaded controls.

Follow-up treatments for re-sprouting lantana stumps and emerging seedlings were undertaken in June 2009. I measured effectiveness of the methods using adult lantana mortality in June 2009 and lantana seedling density in the different treatment plots during the follow-up exercise. The cost of the various methods and human labour applied were compared across the four treatments at initial clear and at follow-up.

All treatments recorded a high adult lantana mortality rate, though there were no significant differences in lantana adult mortality amongst the treatments. Overall, uprooting had the highest adult mortality, followed by imazapyr, metsulfron and lastly glyphosate. Germination of lantana seedlings after clearing was high for all treatments but with no significant differences occurring between the treatments. Both adult lantana mortality and seedling density were however significantly different from the control. With labour included, chemical costs were far higher relative to uprooting, though uprooting costs were the highest when it came to the follow-up because of the emerging seedlings and some resprouting stumps.

The effects of mechanical and chemical treatments on vegetation composition in the cleared areas were also assessed in order to detect any non-target and medium term effects of treatments. Contrary to expectation, none of the chemicals showed any significant effects on vegetation composition in the short and medium-term and no significant differences were found in plant species richness, diversity and seedling density between invaded and uninvaded plots at baseline, in October 2008 and in September 2009.

In order to determine potential for unaided vegetation recovery in the riparian areas of the study site after lantana clearing, I conducted an investigation of soil seed banks and seed rain using 60 seed bank samples measuring 1800m³ collected from 30 invaded and uninvaded plots. Using the seedling emergence method, 1, 991 seedlings belonging to 66 species representing 27 families germinated from the seed bank. Sedges (Cyperaceae family) were the most abundant taxa in the seed banks from invaded areas, followed by *Ageratum conyzoides*, lantana, *Triumfetta annua* and *Achyranthes aspera* which also occurred in the uninvaded soil seed banks. The seed banks from uninvaded plots were dominated by the grass *Oplismenus hirtellus.* Overall, species richness, diversity and seedling density from seed banks in invaded areas did not differ significantly from seed bank in uninvaded areas and there was a low similarity in species composition when above ground vegetation was compared to seed banks from invaded and uninvaded areas.

It would appear if natural regeneration occured from the current seed bank in disturbed areas, future vegetation would largely comprise of short lived, early successional species in the short term as the seed bank is dominated by non-native herbaceous weedy species. From the seed traps investigating seed rain, a total of 27 species numbering 623 individual seeds were found in the thirty 1m² seedtraps distributed in invaded and uninvaded areas at the five sites, over an intermittent period of three months. Lantana had the highest monthly arrival rate in the seed traps followed by *Phoenix reclinata* and *Ricinus communis*. The number of species with invasive potential found in the seed traps located in invaded areas was more than that found in seed traps under native vegetation cover by far.

Considerable forest remnants still occur around the invaded sites, and these could serve as an important source for long-term natural re-establishment of native vegetation if seed availability by animals and wind dispersal continues, while the re-invasion of lantana is prevented by ongoing follow-ups and futher clearing of lantana invaded areas. It is concluded that while uprooting and other treatments are effective in the control of lantana, its successful control in the Victoria Falls World Heritage Site will require extensive clearing to keep it from reinvading infested areas after clearing as shown by the seed rain data. The high seedling density of lantana in the seed banks and in the cleared areas shows the need for ongoing follow-up in order to deplete soil stored seed banks. There is need for longer term research to establish what the exact follow-up requirements are in order to contain lantana re-infestation and create favourable micro-sites for native species to establish. It is predicted that ongoing lantana control in the cleared plots will most likely initiate long-term community recovery.

CHAPTER 1

GENERAL INTRODUCTION AND LITERATURE REVIEW

Biological invasions and their impacts

Invasive Alien Species (IAS) are defined by the Convention on Biological Diversity (CBD) as "species, subspecies or lower taxa (including any part, gametes, seeds, eggs or propagules of such species) introduced outside their natural past or present distribution and whose introduction and/ or spread threatens biological diversity" (UNEP, 2004). Invasive Alien Species are a threat to biodiversity through their proliferation and spread, displacing or killing native flora and fauna and thus affecting ecosystem services. They have since been recognised as important agents of global environmental change (Vitousek *et al*., 1996) and as the second greatest known threat to global biodiversity after direct anthropogenic habitat destruction and landscape fragmentation (Drake *et al*., 1989; UNEP, 2004; Sharma *et al*., 2005). Invasion of native communities by exotic species has been among the most difficult ecological problems of recent years (Sharma *et al*., 2005) and the economic impact of these invasions is a major concern throughout the world (Pimentel *et al*., 2000).

Invasive Alien Species (IAS) alter ecosystem structure and function and affect the abundance and diversity of resident vegetation of natural communities (Weiss and Noble, 1984; Macdonald *et al*., 1989; Vitousek, 1990; Cronk and Fuller, 1995; Gurevitch and Padilla, 2004). They may also adversely affect plant species diversity by displacing mature vegetation or limiting juvenile recruitment (Yurkonis *et al*., 2005). The mechanisms limiting resident species recruitment in invaded communities include competition for resources such as light, nutrient and space (Tilman, 1987; Davis *et al*, 2000) as well as non resource mediated interference, such as allelopathy (Achhireddy and Singh, 1984; Gentle and Duggin, 1997; Lwando - Tembo, 2008).

According to Lonsdale (1999) invasion of an environment by new species is driven by three principal factors: the number of propagules entering the new environment (propagule pressure), the inherent characteristics of the new species, and the susceptibility of the environment to new invasions. Some of the reasons that lead to invasibility of an environment include the region's climate, the environment's disturbance regime, and the competitive ability of the native species (Lonsdale, 1999). There are several other factors ascribed to the success of invasions, including release of such exotic species from their coevolved natural pests and predators in the new environment (Lake and Leishman, 2004).

Several hypotheses have been proposed to explain why some communities are more prone to invasion than others, but results from field studies have been too inconsistent to establish one common theory. Owing to this Davis *et al.* (2000) propose that a plant community becomes more susceptible to invasion whenever there is an increase in the amount of unused resources. This theory is based on an assumption that invading species will require resources such as light, nutrients and water to be readily available for them to succeed. With reduced competition intensity from resident species, a new species will have higher chances of successfully invading a community (Davis *et al*., 2000).

Disturbance, described as a disruption of population, community or ecosystem structure which results in changed resource availability (White and Pickett, 1985) is one of the leading factors that predispose natural environments to invasion (Davis *et al*., 2000, Tickner *et al*., 2001) as it can damage some of the native vegetation, reducing light, water and nutrient uptake. An increase in resource availability arises if use of a resource by resident species declines, or if an increase in resource availability occurs at a pace faster than the resident species can assimilate (Davis *et al.*, 2000). In the case of the Victoria Falls area, the disturbance prone characteristics of the invaded riparian areas enhance the possibilities of invasion success.

Normally, a range of quantitative procedures are used to assess weed impacts on natural communities, including multi-site comparisons, weed removal and weed addition procedures (Adair and Groves, 1998; D' Antonio *et al*., 1998), though direct impacts of weeds on species are difficult to establish due to the correlative nature of the procedure (Weiss and Noble, 1984; Daehler and Strong, 1994; Adair and Groves, 1998). But in any case, weed removal studies provide strong evidence of impacts of invasive aliens on native species because changes in species diversity and abundance following clearing can be directly assessed. By monitoring community structure changes to native species populations consequent to control of invasive aliens, studies looking at clearing of invasive alien plants can reveal weed impact mechanisms such as recruitment limitation (D'Antonio *et al*., 1998). However, clearing activities will always have residual effects like altered soil nutrient composition, soil compaction, root disturbance, trampling and other variant effects of different control methods (Adair and Groves, 1998; D' Antonio *et al*., 1998; Zavaleta *et al*., 2001; Mason and French, 2007) limiting their usefulness.

In areas where invasive alien plants have been cleared, increased species diversity has been reported, for example, following control of the invasive bunchgrass *Schizachyprium condensatum* in the Hawaii Volcanoes National Park (D' Antonio *et al*., 1998). However, the opposite response has also been demonstrated for native communities following removal of some weeds, such as *Asparagus asparagoides* in southern Australia (Turner and Virtue, 2006), showing clearly that removal of the target invasive plant alone does not necessarily initiate resident species recovery. In fact, the process of invasive alien control itself has the potential of significantly disturbing natural communities, differentially influencing the composition of regenerating species and facilitating secondary weed invasion (Yelenik *et al*., 2004; Turner and Virtue, 2006; Mason and French, 2007).

This makes it important that other than merely investigating the effects of a plant invader; the effects of its control on native vegetation should also be assessed. Only then can appropriate and effective management procedures be developed to mitigate the adverse effects of the invader and promote community recovery.

Biological invasions and riparian areas

Gurnell (1995) described the term 'riparian' to mean the entire area of interaction between aquatic and terrestrial environments including the river channel, its banks and the contemporary flood plain. The spatial extent of the riparian zone is not easy to delineate precisely as its heterogeneity is expressed in an array of life-history strategies and successional patterns, with the functional attributes depending on community composition as well as the environmental setting (Naiman and Decamps, 1997) leading to differing descriptions among researchers. Disproportional to their minor extent in most landscapes, riparian ecosystems are important for the delivery of key services, especially water supply, flood conveyance and biodiversity conservation (Naiman and Decamps, 1997). Riparian ecosystems are also essential for the delivery of other vital services such as food provision, propagule dispersal, control of evapo-transpiration and water temperature, filtering of sediments, stabilization of stream banks and support of faunal communities, forming vital links between terrestrial and aquatic ecosystems (Naiman *et al*., 1993; Goodson *et al*., 2001; Galatowitsch and Richardson, 2005).

Riparian zones are characteristically diverse mosaics of landforms, communities and environments within the larger landscape (Naiman and Decamps, 1997) and contain high species richness (De Ferrari and Naiman, 1994). One of the factors responsible for the high species richness of riparian areas is that regular floods decrease competitive interactions, and periodically return portions of riparian community to early successional stages, leading to the creation of diverse microhabitats.

However, without exception, riparian zones worldwide are complex, disturbance mediated systems with high susceptibility to invasion by invasive alien plants. This is because they are exposed to periodic natural phenomena such as floods, dynamic nutrient levels and hydrology, water aided dispersal of propagules, and the role of stream banks as a reservoir for propagules of both indigenous and exotic species (Planty-Tabbachi *et al*., 1996; Galatowitsch and Richardson, 2005). For example, spread of invasive plants to new foci in areas with patchy suitable habitat requires long distance transport of propagules, and linear habitats such as river margins can be very efficient in enabling such movement (Ellenberg, 1988; Pysek and Prach, 1993). In relation to this, Macdonald and Frame (1988) argued that the control of *Lantana camara* and *Melia azedarach*, which had heavily infested riparian vegetation in the Kruger National Park of South Africa, was difficult because of continued reinvasion from upstream sources. Their position in lower lying areas in the landscape and their utilization by large herbivores and humans, exacerbate their susceptibility to alien plant invasion (Witkowski and O' Connor, 1996; Beater *et al*., 2008).

Plant invaders of riparian ecosystems have been shown to modify plant-pollinator interactions (Vranjic *et al*., 2000) and inhibit the recruitment of resident native species by preventing seedling establishment and growth (Yurkonis *et al*., 2005; Bjerknes *et al*., 2007). They are also implicated in the displacement of resident species through direct below and above ground competition for resources such as space, water, nutrients and light (Walck *et al*., 1999; Vila and Weiner, 2004), modifying or engineering ecosystem processes and the physical resources of the recipient community, such as sedimentation, nutrient cycling and disturbance regimes (D' Antonio and Vitousek, 1992; Mack and D' Antonio, 1998). The eventual outcomes of these effects are reduced native species richness and abundance, and altered species assemblages in infested areas. Other ecosystem effects of invasive alien species, particularly the woody invasives of the South African grasslands and fynbos, are the reduction of stream flow and altered sedimentation where aliens 'choke up' stream channels resulting into later floods which cause erosion and other damage (Anon, 2007; Le Maitre *et al*., 2002).

Clearing invasive alien species in riparian areas

From the foregoing, it has been established that invasive alien plants negatively impact on structure and function of ecosystems, and several studies in the past affirm this (e.g. Witkowski and Mitchell, 1987; Vitousek, 1990; Witkowski and Wilson, 2001). Clearing efforts aimed at addressing alien species usually lead to further disturbance, in proportion to the duration and severity of the invasion (Holmes *et al*., 2005).

Mechanical and chemical methods are among the most commonly used interventions for the control of invasive aliens in riparian ecosystems. In the South African fynbos, various forms of mechanical clearing which include the fell only method and felling accompanied by application of herbicides on cut stumps of resprouting species have been used by the Working for Water (WfW) project (Galatowitsch and Richardson, 2005; Holmes, 2008). The other method that has been used is the fell and remove; where large wood (>50mm diameter) is removed (Galatowitsch and Richardson, 2005; Holmes, 2008). The fell and remove method differs from the fell only method as cleared brush is removed in the former, whereas in the latter, the cleared brush is left lying on the ground in cleared areas. Other methods include the fell and burn, where the resultant slash is burnt after drying out for several months, and the ‘kill standing method’ where large trees are killed by ring barking or frilling by applying herbicide into the cambium layer (Galatowitsch and Richardson, 2005; Holmes *et al*., 2008).

Subsequent to clearing, previously affected areas are normally followed up with hand pulling or re-application of herbicides on surviving stumps and seedlings. Some of the main factors to consider when choosing a method for use in riparian ecosystems, particularly in protected natural areas, is the environmental acceptability of the method, its effectiveness in controlling the target plant, its potential effects on non-target native species, and the related costs.

Recovery of riparian ecosystems after clearing invasive aliens

An analysis of the impacts of alien invasions and recovery potential in South African riparian ecosystems identifies both biotic and abiotic obstacles to restoration at local reach and catchment scale (Holmes *et al*., 2005). In highly transformed catchments, clearing interventions at the reach scale (defined as a short river length), may not succeed if important constraints at the catchment scale are not addressed (Richardson *et al*., 2007). Issues such as altered flow regimes and inappropriate land uses in catchments can lead to protracted recovery of riparian ecosystems (Holmes *et al*., 2008). Often, alien species recolonize previously invaded areas after clearing and become dominant during early successional stages, altering conditions for seedling establishment of native species (Bellingham *et al*., 2005). Many of the most problematic invader species have persistent seed banks, posing a serious challenge to restoration efforts.

Poor recruitment of riparian species following alien plant clearing may result from unsuitable germination or establishment conditions. A lag phase is usually expected prior to the re-emergence of indigenous species in previously heavily invaded sites as a result of possible indigenous propagule inadequacy (Beater *et al*., 2008) and also a lack of suitable micro-sites for establishment ensuing from reach-scale alterations caused by alien plants (Galatowitsch and Richardson, 2005). Where dense to closed alien stands have existed for a long time, there is a likelihood that thresholds, whereby ecosystems no longer have the capacity to recover without human intervention after clearing, will have been reached. Recovery in such situations may require either vegetation reintroduction or modification of the physical environment (Whisenant, 1999). Further, there has been little knowledge of the specific regeneration requirements of plants in the Savanna and Grassland Biomes, including riparian trees (Witkowski and Garner, 2001) but Morris *et al*., (2008) sheds some light on the response of indigenous vegetation to clearing of invasive alien species in riparian areas of the Kruger National Park of South Africa.

Restoration of degraded riparian ecosystems in such situations hinges on the processes influencing diversity levels and the pathways by which plant species colonize sites. Downstream dispersal of vegetative propagules or seeds by water from intact riparian vegetation patches is one important pathway. Seed dispersal by wind or animal vectors along the riparian corridor and from adjacent terrestrial vegetation can also play a key role, as may *in situ* soil stored seed banks. The drawback is the effect of proximity to disturbed areas on seed bank size (Young, 1985). Numerous studies show that lack of seed dispersal, particularly of animal-dispersed seed, in highly transformed catchments where few natural refugia remain may be a primary limiting factor to forest recovery in large disturbed areas (Kolb, 1993; Nepstad *et al*., 1996; Zimmerman *et al*., 2000).

Globally, many restoration projects are underway to address changes to riparian ecosystem structure and functioning caused by alien plant invasions for various reasons. In South Africa, for instance, restoration of hydrological flows in rivers to deliver water benefits to humans is the primary concern of the alien removal projects as the main invader trees of riparian areas consume more water than indigenous riparian plants, reducing catchment water yield (Prinsloo and Scott, 1999; Le Maitre e*t al*., 2002). The other reasons are threats posed to biodiversity and reduced productivity of the land (Anon, 2007).

In the instances above and in many situations elsewhere, there is need to set a realistic goal of returning the riparian zone to a vegetation stand representative of the native riparian ecosystem, dominated by indigenous species. However, it should be realised that for some dense to closed alien stands, it may be unrealistic to restore the vegetation to a pre-invasion reference state in terms of species composition and diversity within a short time frame of 5-10 years (Holmes *et al*., 2008). Subsequent to clearing, the expectation is that as soon as native structural components have re-established, species diversity and composition will embark on a trajectory towards reference community, albeit over a long time (Holmes *et al*., 2008).

Seed bank ecology of riparian areas

The ultimate goal of rehabilitation in disturbed or degraded sites is to return the lost functions of ecosystems. In this context, a comprehensive understanding of the role of seed banks can be an important aid for designing post clearing rehabilitation projects (Richter and Stromberg, 2005; Fourie, 2008; Vosse *et al*., 2008).

The seed bank is defined as 'a reserve of viable seeds, fruits, propagules and other reproductive plant structures in the soil' (Poiani and Johnson, 1989) and includes seeds present both above and below the soil surface (Thompson and Grime, 1979) that are capable of replacing adult plants (Baker, 1989). Very little is known about the vertical or lateral movement of seeds in seed banks, especially in riparian systems (Goodson *et al*., 2001). Much research has been done on the movement of seed by animals (Milton and Hall, 1981; Fenner, 1985; Holmes, 1990a) which all play a role in the spatial distribution of seeds within certain areas, but the dominant transport medium for seeds in the riparian environment remains water (Danvind and Nilsson, 1997; Goodson *et al*., 2001).

Seed banks are an important component for natural regeneration (van der Valk and Pederson, 1989). Seed banks can also provide an insight into the history of lost vegetation after it is destroyed or disturbed by fire, overgrazing, drought, flooding or invasion by alien plants. It has been shown that seed density is usually greatest near the surface, as this is where recent accretion takes place, with density declining rapidly with an increase in depth (Milton and Hall, 1981; Fenner, 1985; Holmes, 1990a). This however may not be the case in riparian systems where there are certain processes, such as deposition and erosion due to flooding, which affect the distribution with depth and the composition of seed banks (Goodson *et al*., 2001).

A good comprehension of seed bank composition and dynamics can be used to predict post clearing recruitment and vegetation composition in a disturbed environment cleared of invasive alien plants. Seed bank data will also reveal information on species composition, relative abundance of recently recruited species, and the potential distribution of each species in regenerating vegetation (Welling *et al*., 1988). By analysing the compositional data of the seed banks and comparing it to the above ground vegetation, we can tell which species are lacking from the seed bank, and whether any undesirable species are present which may be consequently established.

It is important to understand to what extent riparian seed banks and seed rain contribute to the recovery of riparian ecosystems cleared of invasive alien species. Some of the key issues that determine the capacity of seed bank-led recovery are propagule input into an ecosystem, which in turn depends on dispersal mechanisms of seed and other plant propagules into degraded habitats. The *in situ* distribution of propagules and availability of suitable growth conditions is also of importance.

There are many issues that can affect the capacity of the soil seed bank as a definite 'tool' for the recovery of riparian forest ecosystems, particularly in areas that have been under the invasion of invasive alien plants for a long period. For example, seed loss can negatively affect seed banks in riparian areas if losses are not balanced with gains with various factors being responsible for the loss of seed. The larger proportion of the seed bank will probably die *in situ* (Harper, 1977) and losses from the seed bank will continue to occur through predation, germination, deep burial, attacks by pathogens, physiological death, decay (microbial action) and dispersal to other parts (Harper, 1977; Fenner, 1985, Holmes and Moll, 1990). In most cases, the seeds remain dormant until conditions are favourable for germination, though this is highly unlikely in a tropical, moist riparian zone such as the Victoria Falls where susceptibility to pathogen attack is bound to be fairly high. Further, the process of seed deposition into the soil is not well understood.

The number of viable buried seeds of each species at any given time is largely dependent on the balance between 'gains' and 'losses' (Fenner and Thompson, 2005). A gain in seed numbers by a species occurs largely as a result of seed shed in the environment, which is influenced by the plants' abundance and seed production, and the proportion of seeds which become buried in the soil. Both gains and losses are affected by past and present environmental and management conditions, and how these interact with the species (Fenner and Thompson, 2005).

One major question of seed ecology in riparian areas is whether the seed size and shape has a major bearing on seed persistence. It appears that in most cases, larger seeded species decay at faster rates than smaller seeded ones (Thompson, 1987). In a study of 97 species of the British flora, Thompson (1993) demonstrated that the majority of persistent seeds in the soil tended to be small and compactly shaped, while transient seeds were comparatively larger, and more flattened or elongated. Venable and Brown (1988) suggested that smaller seeds had greater dormancy due to ease of burial, were more numerous and more widely dispersed than larger seeds. Predation pressure is further seen to substantially reduce soil survivorship in larger seeds (Fenner, 1983; Thompson, 1987). However, work by Leishman and Westoby (1998) shows distinct patterns in Australian flora which do not relate seed size and shape to persistence as in the case of British flora. The relationship between seed size and persistence in the seed bank may be largely an effect of life history, with ruderal species generally having smaller seeds than late successional species.

Several studies have shown that early successional species are typically seed bank forming (Thompson, 1992; Warr *et al*., 1993; Thompson, 1993, Goodson *et al*., 2001). Long-lived species have relatively short-lived seed banks while short-lived species have persistent seed banks, leading to their over representation in the seed bank in comparison to their parent plants (Goodson *et al*., 2001). This is because long lived species can continue producing seed over a longer period as compared to short lived species (Goodson *et al*., 2001). Such reproductive strategies are partly responsible for the observed difference between species present in the seed bank and in the overlying vegetation (Goodson *et al*., 2001).

Late successional communities, such as climax forests, often have relatively few viable buried seeds (Donelan and Thompson, 1980; Galatowitsch and Richardson, 2005) although new seed inputs may occur following the opening of gaps in the canopy or undergrowth. In almost all cases, seeds have irregular, clustered spatial distributions, dictated by both biological and environmental factors (Thompson, 1978). Thompson (1992) and (1993) proposed a three category soil seed bank classification based on seed longevity, which included transient seeds (seeds that are viable for a maximum of 1 year); short term-persistent (with a viability longer than 1 year but less than 5 years) and long term persistent seeds (whose viability is at least 5 years).

Much work on seed banks has been done in soils of temperate and tropical forest ecosystems, desert and alpine grasslands and tidal and non-tidal wetlands in Europe and North America (Hopfensperger, 2007). In recent years, with the increased attention on invasive alien species, several works have been published which focus on the terrestrial components of seed banks within the fynbos region (Holmes, 2002; Holmes and Newton, 2004; Vosse, 2006; Fourie, 2008). Studies on riparian seedbanks have also been undertaken in the savannas of South Africa (Witkowski and Garner, 2000), Canary Islands (Arevalo *et al*., 2000), Ethiopia (Kebrom and Tesfaye, 2000) and China (Du *et al*., 2007). However, no research has focused specifically on the riparian seed banks of the sub tropical savanna biomes of Sub Saharan Africa.

A low correspondence of species present in the seed bank and the above-ground vegetation has been reported in grasslands (Thompson, 1987; Bakker, 1989) though not in all cases as found by Dessaint *et al*. (1997) and Bossuyt and Hermy (2004). However, in forest ecosystems, the seed bank and above-ground compositions have been found to have very low similarity (Rico-Gray and Garcia-Franco, 1992; Yorks *et al*., 2000 and Gashaw *et al*., 2002) while wetland seed banks appear to be of intermediate similarity with above ground vegetation (Hopfensperger, 2007). Fourie (2008) and Vosse *et al* (2008) found differences in riparian seed banks and above ground vegetation in fynbos, with seed banks dominated by early successional species. According to Goodson (2001) this can be partly attributed to the reproductive strategies of the species concerned. Some species are known to produce many short lived seeds, while others produce very few or no seeds at all and rely on vegetative propagation and asexual growth. Such contrasts can be attributed to the successional cycle of plant communities whereby the seed bank can be representative of species and vegetation types that are no longer observed in the current vegetation. In forest habitats, for example, seed bank species may represent early successional species that can no longer survive in the shaded habitat of a dense forest, but are still present in the soil seed bank (Warr *et al*., 1993).

The primary reproductive characteristics of riparian plants are a result of selected trade-offs between sexual and asexual reproduction, timing of dormancy, timing of seed dispersal, seed dispersal mechanisms, seed size and longevity. Many riparian plants have specialized seed dispersal strategies that optimize propagule dispersal with the onset of the flooding season (Leck, 1989). Hydrochory (dispersal by water) is utilized by many riparian species. Some species additionally use vegetative reproduction, whereby segments of the roots or stems are broken off during flood or disturbance and may successfully re-root if they become lodged at a suitable site (Goodson *et al*., 2001; Tickner *et al*., 2001). In addition, it is important to note that not all species are always represented in the seed bank. It is encouraging that studies conducted in the riparian habitats of the fynbos (Vosse *et al*., 2008; Fourie, 2008) show that with the use of appropriate clearing and post clearing management strategies, seed banks in those areas can facilitate ecosystem recovery in the long term.

The Lantana camara invasion in the Victoria Falls riparian area

Lantana camara L. (hereafter lantana) is a major weed in many regions of the palaeotropics where it invades natural and agricultural ecosystems (Thomas and Ellison, 1999). It has been cited as one of the world's ten worst weeds (IUCN, 2004; Lwando-Tembo, 2008) and is classified as a noxious plant in Zambia under the Noxious Weeds Act No 233 of 1949. This Act defines noxious weeds as "aquatic or terrestrial plants, that when translocated into a new area and freed from controls over their spread, explode into growth to such an extent that they suppress all other plant species" (ECZ, 2004a).

Lantana has invaded the riparian zone of the Victoria Falls World Heritage Site ecosystem covering an extent of 524 ha (Masocha and Ndaimani, 2010). The riparian forest in front of the Falls (hereafter rainforest), riparian areas upstream and the gorges downstream of the Falls are the most affected. The riparian patch in front of the Victoria

Falls is referred to as the rainforest because it is perpetually wet during the rainy months and for a period of four months thereafter as a result of the incessant mist from the waterfalls.

The lantana invasion in the Victoria Falls area is linked to human and wildlife disturbance as it occurs in mosaic patches in riparian forest gaps where forest canopy cover has been lost due to destruction of vegetation by humans, wildlife or natural mortality (pers. obs., 2007; Masocha and Ndaimani, 2010). It is also linked to previous construction work of trails and viewing platforms within the core tourism area. Construction materials and equipment were stockpiled in open forest patches leading to disturbance of these areas. Wastelands, major migration routes and dispersal corridors for megafauna such as elephant and hippo along the river banks and on islands of the Zambezi have also become invaded by lantana (pers. obs., 2007; Masocha and Ndaimani, 2010).

The riparian woodland and rainforest of the Victoria Falls are floristically rich areas containing 140 species of trees and tall shrubs, 50 species of sub-shrubs and 150 species of herbs (Fanshawe, 1975). When understorey plants such as grasses, sedges, ferns and climbers are taken into account, the total is over 400 recorded plant species (Fanshawe, 1975). There are also several endemic plants, which are limited to the rainforest, including herbs like *Rotala cataractae*, *Gladiolus unguiculatus*, *Sebea pentandra*, *Loberlia kirkii* and the rare fern *Cheilanthes farinosa* (Fanshawe, 1975).

Further, the rainforest is an area of great biodiversity importance not only for its unique combination of plants (species dependent on relatively high moisture in a surrounding area of relatively low and very seasonal rainfall) but for the fact that it has a set of species of both plants and animals that are representative of the lower altitude parts of Southern Africa in the centre of the African Plateau (UNEP, 2004). For this reason, the riparian belts of the Zambezi, its tributaries, seasonal streams and islands on the Zambezi are recognized as sensitive habitats (Meynell *et al*., 1996). Much of this unique assemblage is threatened by lantana as it spreads in the rainforest across the face of the falls, in the fringing forest and the surrounding woodlands.

Considering that the lantana infestation in the site is concentrated along rivers and seasonal streams (Masocha and Ndaimani, 2010), there is a risk that these critical habitats will ultimately be degraded. The relationship between moist areas and lantana invasion is also evident on the Zimbabwean side of the Zambezi River (Chimbalanga *et al*., 2005), suggesting that other than disturbance, moisture availability and soil type are the two other major drivers of the lantana invasion in the Victoria Falls area (pers. obs., 2007; Masocha and Ndaimani, 2010). This invasion is steadily altering the structure of the vegetation around and below the falls, and is thus expected to affect the flora and fauna of this unique area. This concern is based on the argument that native species are usually outcompeted by invading species with a host of negative ecological results at ecosystem, community and population level (Lake and Leishman, 2004).

In warm, moist areas such as the Victoria Falls, lantana often becomes dominant in regenerating pastures. Lantana typically forms dense thickets, suppressing less competitive native vegetation and seedlings through shading (Swarbrick *et al*., 1995). Lantana dominance may also adversely affect the richness of some soil faunal assemblages. Cummings (2007) reported a reduced presence of several functional groups of ant species in lantana-dominated vegetation in comparison to adjacent natural communities, and concluded that this probably related to both initial disturbance events and the structure of lantana-dominated vegetation that followed. Lantana is also thought to be allelopathic (Achhireddy and Singh, 1984; Swarbrick *et al*., 1995; Day *et al*., 2003; Lwando-Tembo, 2008) and an Australian field trial (Gentle and Duggin, 1997b), provides support for this.

Fensham *et al.* (1994) document declines in plant species richness with increasing levels of lantana infestation of dry rainforest, and accumulation of heavy fuel loads along boundaries between savanna woodland and dry rainforest, which lead to significant canopy tree loss and edge erosion in the latter, with lantana dominating the area of lost dry rainforest and rendering it prone to further fires. Swarbrick *et al.* (1995) present summary data from Alcova (1987) showing a large decline of at least 70% in inferred recruitment (number of native tree and shrub saplings present) in lantana-infested areas of eucalypt woodland compared to lantana-free areas. Lantana infestations are very persistent and can block the natural succession of plant communities (Lamb, 1991). While lantana infestations usually increase in wetter years, they do not recede during dry years (Waterhouse, 1970). The mortality rate among mature lantana plants in their naturalized range is very low (Sahu and Panda, 1998).

Lantana is reported to have contributed towards the depletion of indigenous plant species and biodiversity in general on the Zimbabwean side of the Zambezi River which forms the southernmost part of the Victoria Falls World Heritage Site (Chimbalanga *et al*., 2005). It is believed the allelopathic properties of lantana have contributed to the elimination of grasses and other understorey flora leading to loss of ground cover and inevitable soil erosion. Recent surveys of the lantana invasion which dates back over 30 years in the Victoria Falls World Heritage Site in Zimbabwe, have established that 2.82km² of riparian forest and islands is invaded by lantana on the Zimbabwean side (Chimbalanga *et al*., 2005), representing an invasion of about 10% of the total habitat (State of Conservation Report, 2010).

History of lantana invasion and control in the Victoria Falls World Heritage Site

Lantana is believed to have been introduced into Zambia in the late 1800's as an ornamental plant and groundcover to halt erosion (Morton, 1994). According to Lottyniemi (1982) it was soon recognised as a pest when it was found overrunning rangeland and forest plantations. However, there is very limited data available on the invasion history of lantana in the Victoria Falls/Mosi-oa-Tunya National Park area in the literature. Fanshawe (1975) was among the earlier botanists who noted the presence and spread of lantana at the bottom of the Boiling Pot below the Falls. By 1996 it was recognised that the lantana invasion was a major threat to the biodiversity of the area (Meynell *et al.*, 1996). Though there are no official records concerning its establishment, I assume that like in most other cases worldwide, its main mode of introduction in the riparian zones and surrounding areas was human transportation and subsequent spread in the Victoria Falls area has mainly been through bird dispersal. Its extent and density has increased over the years, leading to the current problematic situation.

Several efforts dating back to the 1950s have been made to control lantana since it was identified as a threat to the Victoria Falls ecosystem (Victoria Falls Trust, 1962). In 1988, the National Heritage Conservation Commission (NHCC), a government body directly responsible for the management of the Victoria Falls World Heritage Site, initiated lantana control experiments using mechanical control and the herbicide glyphosate in an area north of the Maramba River (NHCC, 1992; NHCC, 1993). Though the trials were reported to be successful (NHCC, 1992; NHCC, 1993), they were not sustained and no reliable documentation of the activities undertaken exists.

Zambia Wildlife Authority (ZAWA), managers of the adjacent Mosi-oa-Tunya National Park also set up experimental plots where chemical control was attempted. These trials were futile because no long term monitoring or follow up mechanisms were put in place. The Wildlife Environmental Conservation Society of Zambia (WECSZ) and Environmental Clubs from local schools have also participated in mass lantana clearing activities in the past. The main control method in these efforts has always been mechanical removal involving cutting and uprooting of lantana, with some intermittent use of herbicides. Maramba River Lodge, private tour operators in the Victoria Falls World Heritage Site conducted chemical trials at a small scale using glyphosate on lantana colonies within their premises (Russell Young, pers. comm, 2007) but discontinued the activity without an evaluation of its success.

The largest scale of chemical use was the lantana clearing exercise carried out by Sun International in 2001. The whole of the Eastern Cataract, including a forested gorge immediately below the waterfalls called the ‘Boiling Pot’ and islands within the fenced area of the Victoria Falls were cleared of lantana and the chemical Access (active ingredient picloram) topically applied on cut stems. This project should have offered the most useful data concerning the efficacy of picloram to permit a possible upscale to the entire invaded area. However no records of lantana response to this chemical were kept and no monitoring was undertaken to establish its effects on lantana and the response of indigenous species after clearing. No follow-up treatments were applied and all these cleared areas have since been recolonised by lantana.

This was largely due to the absence of a clear management plan for the activities and also the lack of coordinated and well identified monitoring parameters. For instance, no follow-up action was undertaken despite high vegetative regeneration of lantana in all cleared areas. The consequences of a viable and persistent lantana seed-bank in the soil were not dealt with, nor were the soil erosion problems that resulted on the steep gorges where the dominant vegetation cover (of lantana) had been removed. Lantana stems easily coppice and dense stands re-establish over a few years period. Therefore, the erratic nature of these control activities allowed lantana to recolonize the previously invaded areas, returning to its pre-clearing extent and density.

Similar efforts to address the lantana invasion have been ongoing on the Zimbabwean side as well. The first major efforts at lantana control were between 1975 and 1980. Clearing activities were discontinued in the years between 1980 and 1999, allowing the invasion to proliferate during this period of neglect (Chimbalanga *et al*., 2005). However, since 1999 lantana control activities have been ongoing with collaboration between Zimbabwe Parks and Wildlife Management Authority (ZPMWA) and a non-governmental organization called Environment Africa. The lantana control methods on the Zimbabwean side have so far focused on uprooting, and the situation has come under control in a fenced area of rainforest opposite the falls, though the islands upstream and gorges downstream of the Falls remain invaded.

Over the past five decades, lantana has continued to pose a serious threat to the biodiversity of the Victoria Falls World Heritage Site. The main challenge to its sustainable control has been the sporadic nature of the control activities, its dense soil seed banks capable of rapid re-infestation of cleared areas and the steepness of the invaded gorges which hinder control activities downstream of the Falls. There has also been no consensus on the most appropriate lantana control methods, in terms of the effectiveness of the method at control of the target plant, possible impacts on the native ecosystem and the costs associated with these clearing operations. Owing to the global significance of the Victoria Falls World Heritage Site, and the long standing problem of lantana invasion as discussed above, the area was nominated as one of the Pilot Sites for implementation of an international project called *Removing Barriers to Invasive Plant*

Management in Africa (RBIPMA) which is sponsored by the United Nations Environment Programme (UNEP), the Global Environment Facility (GEF) and the Government of Zambia.

The Commonwealth Agricultural Research Bureau (CABI) and the World Conservation Union (IUCN) are the lead executing agencies. At national level, the Environmental Council of Zambia (ECZ) is the executing agency. The project aims to conserve globally important habitats and species in the Victoria Falls World Heritage Site through the control of *Lantana camara* and *Eichhornia crassipes*. Much work has concentrated on investigating appropriate methods for the control of lantana and water hyacinth as in this study which focuses on lantana invasion in the area.

Aims of the study

Globally, there are a number of treatments indicated for the control of invasive alien species, including lantana. These include mechanical, chemical and biological control methods. These various treatments have been tried in different countries, with varied results in terms of effectiveness at killing the target plant, recolonisation by the same invader and the costs for undertaking the treatment. To a large extent, the non-target effects of such treatments remain relatively unknown, as are the effects of the treatments on vegetation composition after clearing.

After the implementation of clearing activities, the success of the project is usually measured by how well the ecosystem reverts to its pre-invasion status. Though pre-invasion conditions are usually difficult to determine, species richness, diversity and native species seedling density are sometimes used as indicators for success or otherwise. In most cases, the post clearing species composition is an attribute of the seed banks in cleared areas, and seed input through seed rain. However, seed bank and seed rain potential in invaded areas are difficult to estimate in the absence of empirical evidence and no studies to this effect had previously been undertaken in the Victoria Falls area.

Therefore, this study focused on mechanical and chemical treatments using different herbicides and herbicide concentrations as well as uprooting. The treatments applied for the control of lantana in this study were manual uprooting, where lantana brush was cut and the remaining stump dug out using a mattock, and three herbicide treatments. The chemical treatments involved application of Glyphosate at the rate of $144g.l^{1}.ha^{-1}$ on re-emergent lantana foliage a month after slashing, the application of a concentrate of imazapyr at $250g.l^{1}.ha^{-1}$ on lantana cut stump immediately after cutting and the application of metsulfron methyl at a rate of $600g.l^{1}.ha^{-1}$ on cut stump using a 5 l hand held sprayer. The concentrations used for the treatments were based on advice from the suppliers of the chemicals (TSS, 2008).

The study comprised of three main aims: Firstly, I investigated the effectiveness of the four different methods of lantana control on lantana adult mortality subsequent to treatment. I also evaluated the effects of different treatments on post clearing lantana seedling density and the costs involved in lantana control in terms of chemical procurement and labour in order to determine the relative costs of each method. I predicted that chemical control would be more effective in controlling lantana compared to the uprooting method. This was due to the fact that as a resprouting species, mechanical control of lantana is perceived to be ineffective and time-consuming. I also expected that the glyphosate treatment would be less time consuming as compared to the other treatments as it only involved slashing of lantana brush at the initial clearing, followed by spraying of regrowth at a later stage. I further assessed the management costs related to the various control operations and the preferred methods for future implementation (Chapter 3).

Secondly, I investigated the effect of lantana on species richness, diversity and composition at baseline and the effects of treatment on non target species 48 weeks after clearing lantana in invaded areas. I assessed species composition, richness, abundance and diversity in the post clearing period and made comparisons across the four treatments. I predicted that chemical treatments would reduce species richness, diversity and cover of non target species whereas uprooting would stimulate seed germination in cleared areas. This is discussed in Chapter 4.

Thirdly, I investigated the potential of post clearing natural vegetation recovery based on the seed bank and seed rain in the project area. I examined the composition, richness, diversity and density of seed banks and seed rain from invaded and univaded areas and compared the seed bank species composition and richness to above ground vegetation across invaded and uninvaded areas. I predicted that seed banks and seed rain in uninvaded areas would have higher species richness and diversity than in invaded areas. This is covered in Chapter 5. The synthesis and discussion of main findings and their implications for management of lantana in the Victoria Falls area is found in Chapter 6.

CHAPTER 2

STUDY AREA AND EXPERIMENTAL SET UP

Study Area

This study was conducted in the Victoria Falls World Heritage Site, a smaller enclave within the larger Mosi-oa-Tunya National Park in Southern Zambia (see Fig 1). It is 3,900 ha in size, forming about 59 % of the Mosi-oa-Tunya National Park, and is an area of high conservation value, registered on the UNESCO list of World Heritage properties since December 1989 (NHCC, 2008). The Victoria Falls are located on the Zambezi River at around 17^{o} 55'S, 25^{o} 51'E. The altitude at the top of the Falls is about 875m above sea level and the waters descend a maximum of 108m over an edge 1,708m wide across the Zambia–Zimbabwe border (Nalumino, 1997). The Victoria Falls are the main tourist attraction in Zambia, receiving close to 1,000,000 visitors a year and making a substantial contribution to the country's tourism industry (NHCC, 2008).

Shalwindi (undated) reports that the predominant natural habitat in the Victoria Falls World Heritage Site is woodland (Meynell *et al.*, 1996). Further, Shalwindi (2000) states that according to the 1:50,000 LANDSAT imagery and vegetation map of Zambia, four main vegetation types are observed in the Victoria Falls World Heritage Site, namely mopane woodland, mixed scrubland, riparian forest and swamp vegetation. An even closer analysis of this woodland reveals six main types as per Meynell *et al*., (1996) with segments of Kalahari and Baikiea woodlands being the two additional forest types.

The Victoria Falls World Heritage Site and Mosi-oa-Tunya National Park provide habitat to the typical southern and central African types of vertebrates with some species of concern such as the White Rhino *Ceratotherium simum* and the rare Taita Falcon *Falco fasciinucha*. In recent years, the increased number of grazers and elephant populations have led to a major change in woody biomass in the area. The area is declared an Important Bird Area (IBA) because of its high diversity of bird species.

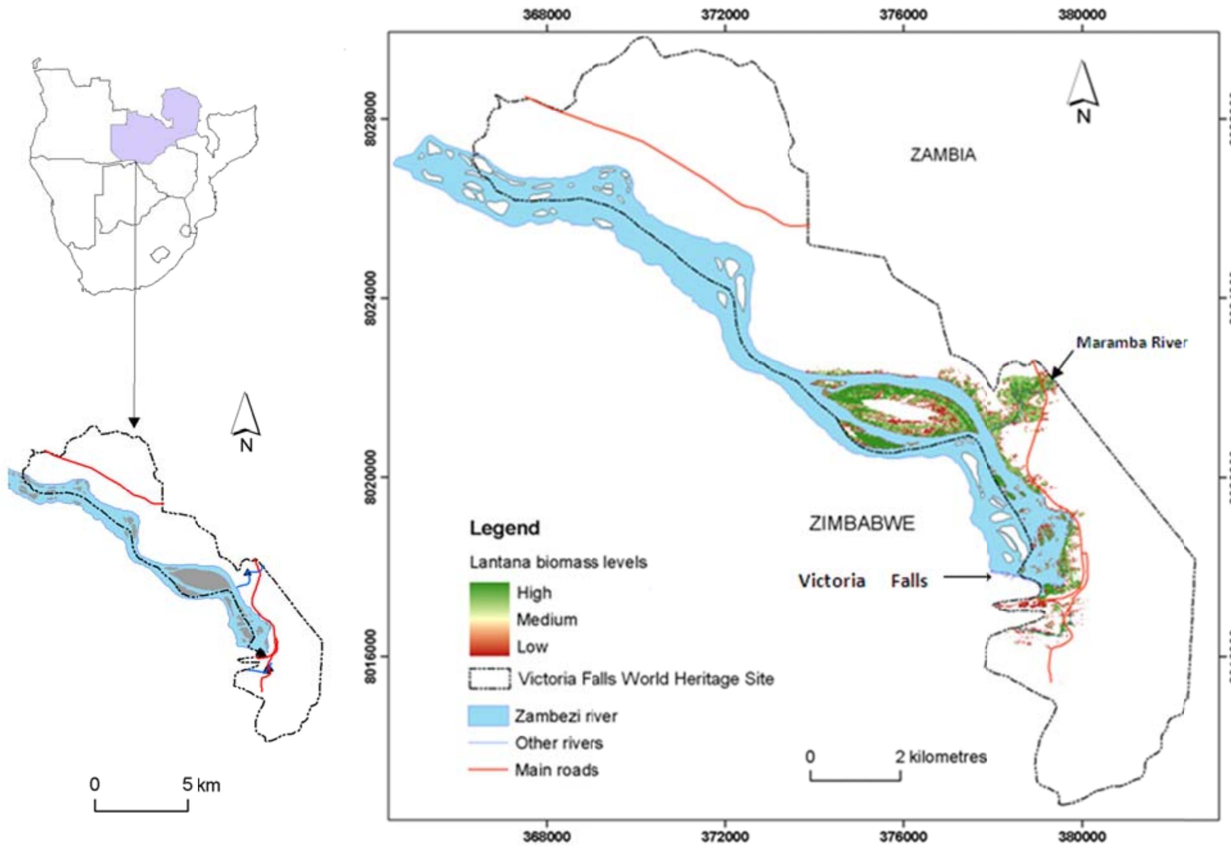

Figure 1. Map showing the distribution and biomass of lantana in the riparian areas of the Victoria Falls World Heritage Site. Uninvaded areas are white whereas those in green and brown have high and low *L. camara* biomass respectively. (Masocha and Ndaimani, 2010). River flow is north to south and the course of the Zambezi below the Victoria Falls follows the World Heritage Site boundary.

The climate is sub-tropical, hot and arid, with a marked seasonal variation (Meynell *et al*., 1996). The hot season runs from September to October and through to the onset of the rains. The main rainy season runs from October-November to March-April with an annual rainfall of about 750mm, with the rainfall highest from January to March. During this period, maximum daily temperatures average between 27-32° C (Meynell *et al*., 1996). Thereafter the months of April/May constitute the post rainy season before the cool dry season between June and August (Meynell *et al*., 1996). The temperatures are highest in October (mean maximum 33.9° C) and lowest in June (mean minimum 6.4° C).

The Study Species

Lantana (*Lantana camara* L. *sens. lat.*, family Verbenaceae), is a perennial woody shrub that is native to the tropical and sub-tropical Americas (Henderson *et al*., 1987; Thomas and Ellison, 1999) thriving in a wide range of climatic conditions (Holm *et al*., 1977 in Thomas and Ellison, 1999). It has become naturalised in many countries of the world, including Zambia. It is a profusely branching, scrambling aromatic shrub attaining 2-4 (up to 8) m in height, with square-sectioned, often prickly cane-like stems. The leaves are opposite, ovate, often toothed, 2-6 (up to 10) cm long. Flowers are 20-40 together in clustered compact heads 2-3 cm diameter.

The alkaloid rich leaves are unpalatable to most herbivorous animals and are poisonous to some (Morton, 1994). Flower colour is variable, ranging from cream and yellow to orange, red, pink, and mauve with flowers usually opening yellow and changing colour as a signal to pollinators (Mohan Ram and Mathur, 1984). Flowering occurs through most months of the year in the Victoria Falls area of Zambia, and especially from November with the onset of the rains to May (Fig 2). The fruit is a single-seeded 'berry' (drupe) 4-8 mm diameter, fleshy and purplish-black when ripe. Some variants are non-fruiting. There are many detailed descriptions of the plant (see Swarbrick *et al*., 1998 and Parsons and Cuthbertson, 2001).

Figure 2. Lantana shoots flowering in the Victoria Falls rainforest. Unripe lantana seed is seen to the right (Photograph by Evelyn Roe June 2009)

Lantana is an 'aggregate species', or 'species complex'. It has several natural variants across its presumed native range in the tropical Americas, and in addition some hundreds of horticultural varieties have been developed around the world, numbering over 650 varieties (Howard, 1969; Smith and Smith, 1982). Lantana typically occurs where there is a moderate to high summer rainfall and well-drained sloping sites, mainly preferring fertile organic soils, but also capable of surviving on siliceous sands and sandstone-derived soils of moderate depth if other conditions, especially year-round moisture, are suitable. Lantana does not tolerate water logging, salinity, prolonged drought, dense shading by overstorey species, frequent or severe frosts, or winter temperatures with prolonged periods below 5° C (Stirton, 1977; Cilliers, 1983).

Lantana readily invades disturbed sites and communities and so various types of habitats are susceptible to lantana invasion. In communities with a naturally dense canopy, lantana colonisation may be heavily dependent on, and limited to, disturbance zones, edges, and canopy breaks as is the case in the Victoria Falls World Heritage Site. There is a strong correlation between lantana establishment and disturbance (Stock and Wild, 2002; Stock, 2004) with critical factors being disturbance-mediated increases in light and available soil nutrients (Gentle and Duggin, 1998). It is known that high light conditions are a prerequisite for lantana seed germination and early growth (Gentle and Duggin, 1997b; Duggin and Gentle, 1998) and seedlings do not usually survive beneath parent bushes. In open forests and woodlands, with suitable soils and moisture, lantana often becomes a dominant understory species.

Seed dispersal is primarily by fruit-eating birds and to a lesser degree by foxes, monkeys and other vertebrate foragers (Clifford and Drake, 1985; Sharma *et al*., 1988; Wells and Stirton, 1988; Bisht and Bhatnagar, 1979; Day *et al*., 2003). In the Victoria Falls area, Chacma baboons (*Papio ursinus*) and Vervet monkey (*Cercopithecus aethiopus*) have been observed eating lantana fruit, lending credence to an assertion that they are among local dispersers of the plant. Seed longevity in the soil is not well documented, but 50% seed viability after 6 months of dry shelf-storage has been recorded and seeds are considered to remain viable for several years under natural conditions (CRC Weed Management, 2003).

Germination rates are reportedly increased by removal of fruit pulp, as occurs with passage through bird gut (Day *et al*., 2003, CRC Weed Management, 2003) and by warm temperatures, light, and high soil moisture. It has been observed that germination rate of lantana is low under both laboratory and field conditions (Spies, 1983-84; Graaff, 1986; 1987; Sahu and Panda, 1998) with estimates of 4-20% (Graaff 1986; 1987) and 44.5% (Duggin and Gentle, 1998), but as fruits may set at rates of up to several thousand m^{-2} there may be a considerable soil seed bank to perpetuate lantana infestation as a single plant can produce up to 12,000 fruit each year (NHT, 2004). Graaff (1987) suggested that the low germination rate was due to seed dormancy and/or low seed viability, while Spies (1983-84) proposed that the meiotic instability of lantana might produce low germination rates. Germination rates increased from 10 per cent to 46 per cent when the fleshy pulp was manually removed from the seed. This higher germination rate was found to be comparable to that obtained from seeds collected from the faeces of wild birds. Seed germination may occur at any time of the year given sufficient soil moisture, with most seed germination after the first summer storms in northern Australia (Parsons and Cuthbertson, 2001). Graaff (1987) suggested that low recruitment levels could minimize regeneration in lantana eradication programs though the low germination rates are offset by the very low rates of seedling mortality experienced in the field (Khoshoo and Mahal, 1967) and the high rates of seed production. Lantana is tolerant of occasional fire, occasional frost, and mechanical damage to the aerial stems, being capable of resprouting vigorously from the stem-base and of 'layering' (i.e. vegetative propagation by development of roots from stems in contact with soil).

Experimental Sites

The five sites (Boiling Pot; Maramba River, Rainforest, Palmgrove and a patch of riparian forest around the Zambia Electricity Supply Corporation (ZESCO) Power Station used for this study were in advanced stages of lantana invasion with high levels of lantana cover. The lantana thickets were mature and occupied canopy gaps in riparian and adjacent woodland. Heights collected by the line intercept method in each of the thirty plots ranged from a minimum height of 10cm to a maximum height of 4.7m. Overall, the mean heights of lantana at the five research sites were; 1.99m at the Boiling Pot site, 1.8m at Maramba, 1.7m in the Rainforest, 1.5m at Palmgrove and 1.43m at the ZESCO site. The lantana thickets in the invaded plots varied in density and diameter but in all cases covered above 75% of the demarcated $100m^2$ treatment plots.

These research sites were scattered in the southern part of the protected area, where the lantana invasion is concentrated.

The Boiling Pot, Rainforest and Maramba River sites are located in the riparian forest of the Zambezi, which is rarely more than 20-100m wide from the high water mark in this region (Fanshawe, 1975; Meynell *et al.*, 1996). The riparian woodland in the immediate area of the Victoria Falls contains larger trees like *Diospyros mespiliformis*, *Mimusops zeyheri*, *Ficus ingens*, *Ficus capensis*, *Syzygium guineense* ssp *barotsense* and *Syzygium cordatum*. Other species characteristic of this habitat are *Manilkara mochisia*, *Garcinia livingstonei*, *Hyphaene ventricosa*, *Albizia versicolor*, *Phoenix reclinata*, *Trichilia emetica* and the reeds *Phragmites mauritianus* and *Cyperus papyrus*.

The much visited narrow extension of riparian forest in front of the waterfalls is called the ‘rainforest’ because it is supported by a continuous spray from the Falls at high water (Fanshawe, 1975; Meynell *et al*., 1996), and for about four months after the main rain season. It is highly adapted to frequent moist conditions and was the site where lantana control treatments for the Rainforest site were undertaken in this study. It is dominated by the trees *Mimusops zeyheri*, *Ficus ingens*, *Phoenix reclinata* and *Diospyros mespiliformis*. The shrub layer is comprised of *Vernonia amagydlana*, *Pavetta catactaratum*, *Carissa edulis*, *Croton gratissimus* and *Euclea divinorum*. The herbs *Cyathula orthacantha*, *Blepharis mederaspatensis*, *Chlorophytum subpetiolatum*, *Asystasia gangetica*, *Commelina benghalensis* and *Justicia heterocarpa* are prevalent. The creepers *Dioscorea dumetorum*, *Vigna parkeri* and *Jasminum fluminense* occur in the area, intertwined on tree branches. The ground layer has a range of grasses and sedges.

The Boiling Pot Site is a gorge habitat immediately below the Victoria Falls. The area has a few scattered trees, dominated by *Trichillia emetica, Ficus ingens* and *Phoenix reclinata* with a dense understorey of shrubs, herbs and other forms of seasonal vegetation. There is a large amount of creepers in the Boiling Pot with species such as *Jasminum fluminense* and *Cocculus hirsutus* dominating. The invasive plants *Solanum seaforthianum* and *Opuntia ficus-indica* are also prevalent in this area.

The Maramba site lies along the banks of the Maramba River, a major tributary of the Zambezi in the Victoria Falls area. The site is mantled by the common riparian species of this region, including *Diospyros mespiliformis*, *Terminalia sericea*, *Hyphaene ventricosa*, *Ficus sycamorus and* occasional *Acacia polyacantha.* The creepers *Jasminum fluminense* and *Cocculus hirsutus* are also found. Some of the common herbs are *Bidens pilosa*, *Trichodesma zeylanicum*, *Conyza aegyptiaca* and *Oxalis corniculata* while the ground layer has a number of grasses and sedges.

The Palmgrove and ZESCO sites are located along a stream and permanently waterlogged dambo (wetland), which is on a riparian forest-mixed scrubland interface south east of the Victoria Falls. The dambo is dominated by grasses and sedges and occasional large trees such as *Ficus sycamorus*, *Acacia polyacantha* and *Vernonia amagydlana*. Mixed scrubland is one of the vegetation types that extend over most of the Victoria Falls area (Chidumayo *et al*., 2003). It is dominated by shrubs, with scattered tall trees on shallow, stony basalt soils on the south eastern boundary of the Victoria Falls World Heritage Site, and has a general distribution close to the Zambezi River and its tributaries (Meynell *et al*., 1996). Some of the notable woody species in this vegetation type are *Colophospermum mopane, Kirkia acuminata, Commiphora spp, Pterocarpus antunesii, Acacia nigrescens, Sterculia quinqueoloba, Sterculia africana, Cassia abbreviata, Burkea africana, Adansonia digitata* and *Dalbergia melanoxylon.*

All of the sites which were used in the study, except Boiling Pot and Rainforest, are frequented by elephant. Hippo and crocodile are common at the Maramba research site whereas baboons and monkey are common at all the sites. Elephants are common during the dry season but the other species are present throughout the year.

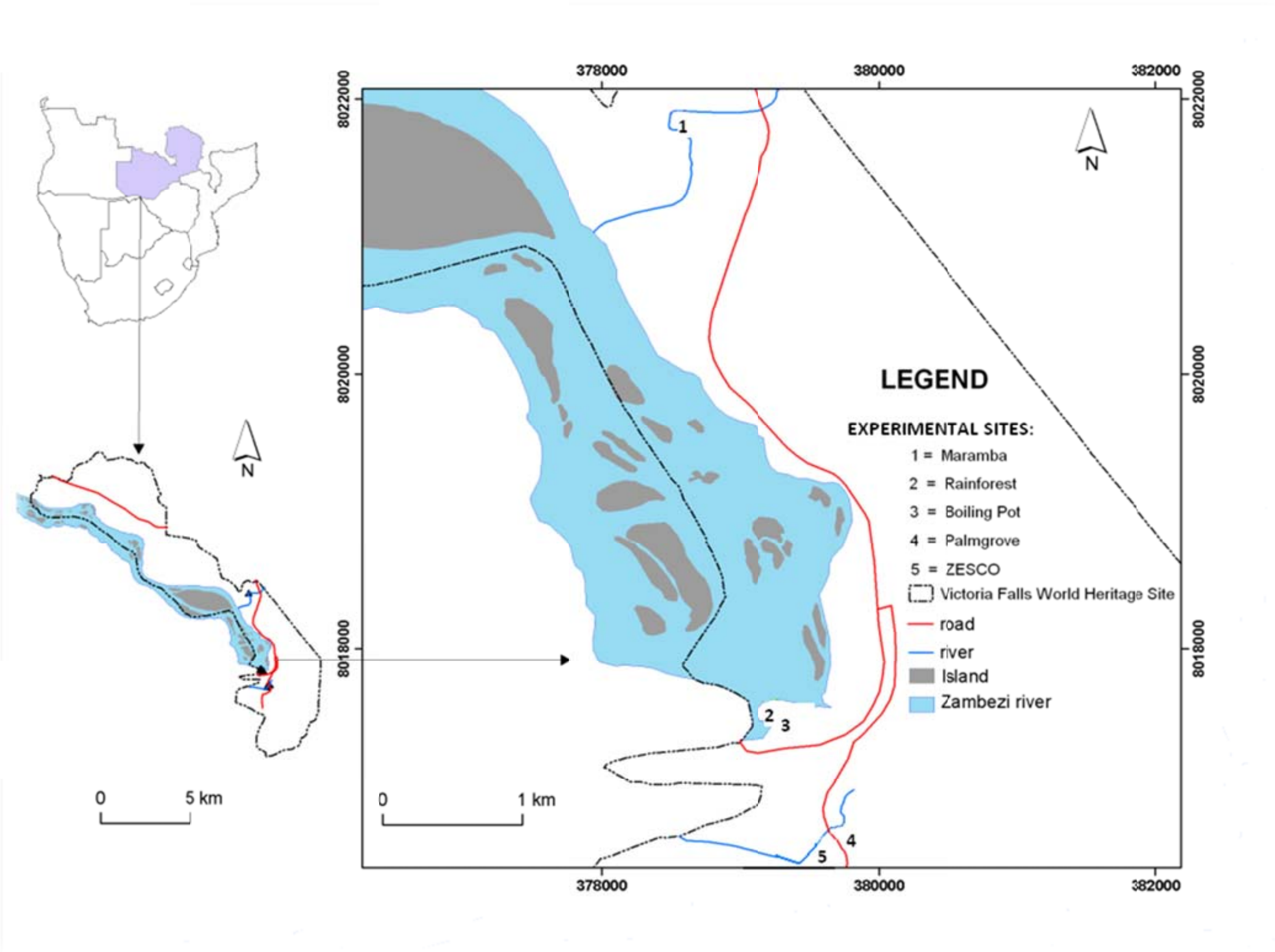

Figure 3. Map showing distribution of the five sites used for the study in the Victoria Falls World Heritage Site (Masocha and Ndaimani, 2010). River flow is north to south and the course of the Zambezi below the Victoria Falls follows the World Heritage Site boundary

Experimental Design

From previous efforts in the Victoria Falls area and elsewhere, it is apparent that mere cutting of lantana without uprooting or use of chemicals is ineffective as it leaves the plant rooted in the ground; making re-growth from the basal stems likely as long as moisture is available (Abell 1972 and 1973; Tu *et al*., 2001; National Heritage Trust, 2004; Love *et al*., 2009). Therefore, physical uprooting of lantana bushes using mattocks formed the mechanical treatment, while two of the treatments involved herbicide application on freshly cut lantana stumps using the chemicals imazapyr and metsulfron, and the fourth treatment consisted of cutting mature lantana and spraying the re-emerging lantana foliage one month later using glyphosate. The details on the concentration of chemicals are reported in Chapter 3.

The sites were of a randomized block design determined by the presence/absence and density of lantana cover. Each of the 5 sites had six 10m x 10m (100m²) plots, thus 30 plots in total. Different control treatments were applied in four of the plots at each site while two plots at each site were assigned as control plots. All the treatment plots had substantial lantana cover (lantana presence ≥75%). Out of the two control plots at each site, one was an invaded control (lantana present ≥75%) while the other was an uninvaded control (lantana absent or ≤ 25% cover) which was deemed to be largely free of lantana infestation. Since it was difficult to find areas completely free of lantana in the vicinity of invaded sites, there were some scattered lantana plants in some of the uninvaded control plots (i.e. Boiling Pot, Maramba River Lodge and ZESCO sites). Treatments for the experimental and invaded control plots were drawn at random from a hat and assigned accordingly.

In order to establish the prevailing floristic composition at the five research sites prior to treatment, a baseline assessment was undertaken in all the thirty plots in July, 2008. Five monitoring quadrats were established randomly in each of the plots in order to measure changes in species composition and lantana seedling density at subsequent sampling periods. These 1m² quadrats formed the permanent units for subsequent monitoring over the period of July 2008 to September 2009 and form the main basis for Chapter 4 and 5.

CHAPTER 3:

EFFECTS OF MECHANICAL AND CHEMICAL TREATMENTS ON *LANTANA CAMARA* L. AND THEIR RELATED COST IN THE VICTORIA FALLS WORLD HERITAGE SITE

Introduction

Invasion of biological communities by alien species is widely recognised as a major threat to ecosystem integrity of natural areas with high conservation value (Mack *et al*., 2000). Because of the resultant devastating ecological and economic impacts, significant resources are spent on the control and management of invasive alien plants worldwide (Pimentel *et al*., 2000-05). Mechanical, chemical and biological methods are the three most commonly utilized methods for control of invasive species globally (Cronk and Fuller, 1995; Wittenberg and Cox 2001; Day *et al*. 2003; National Heritage Trust, 2004), and as a result, these generally applicable methods provided options for the choice of lantana treatments in the Victoria Falls area. From the outset, it is known that each of the established lantana control methods have their merits and demerits, and it is difficult a priori to determine which method should be used in a protected natural area, without assessing their cost implications, efficacy at controlling the target species, applicability to local legal and ecological conditions, the prevailing terrain and status of the invasion.

In practice, mechanical control involves the physical removal, clearing or destruction of the target weed by cutting, digging/uprooting and hand pulling. It is deemed most suitable for invasive alien removal confined to particular localities and not extensive areas (ECZ, 2007), and when used without motorized equipment, is favoured for its limited disturbance to surrounding vegetation in natural areas. It has however been faulted as being labour intensive, and thus costly in the long run due to its continuous need for human labour, precluding control in land of low value. Further, in lantana, it is difficult to guarantee the removal of the entire root stock from the ground with mechanical control thus leaving it as a potential source for re-growth (Cronk and Fuller, 1995; NHT, 2004; Love *et al*., 2009). Mechanical control also does not address the issue of the soil stored seed bank of lantana, requiring extensive follow up after clearing. Mechanical clearing of lantana can also lead to soil erosion in steep terrain by loosening the soil, which is then readily washed off in event of rains. It is also implicated in inducing seedling germination of alien species due to soil disturbance at the time of clearing (Wittenberg and Cox, 2001; NHT, 2004).

Despite the above shortcomings, mechanical control was trialled in this study because of its perceived minimal disturbance to surrounding vegetation in natural reserves when used without motorized equipment (ECZ, 2007) and its relatively low non-target effects, though others argue to the contrary (Erasmus *et al*., 1993).Mechanical control has also shown its huge socio-economic potential in terms of employment creation as evidenced in South Africa's Working for Water Project (van Wilgen *et al*., 2001; Le Maitre *et al*, 2002). For example, the lantana control trials in the Victoria Falls World Heritage Site and the large-scale control of *Mimosa pigra* in the Lochinvar National Park at Monze, Southern Province in the years 2007-2009 resulted in the employment of a large number of workers from local communities around these two Protected Areas. Due to this reason, the initiative was praised by government and local chiefs for providing livelihood support to local communities (RBIPMA, 2008). In terms of invasive alien plants, mechanical control has also proved to be an effective tool in addressing plant invaders, as demonstrated by the use of uprooting to control the lantana invasion on the Zimbabwean side of the Victoria Falls (Chimbalanga *et al*., 2005; Pers. obs. 2008).

Uprooting, which involves cutting the plant up to a height of about 20-30m above the ground, and then digging out the rootstock with a mattock or hoe is the main mechanical method that has been used for the control of lantana in forest plantations in Zambia (Anderson, 1963) and in the Zambezi and Victoria Falls National Parks in Zimbabwe (Chimbalanga *et al*., 2005). Though the effectiveness of uprooting in species capable of re-sprouting from the root stock coupled with dense (long lived seed banks) and efficiently dispersed seed such as lantana is likely to be low without substantial follow-up, it is attractive to land managers because of its relatively low cost and acceptability in ecologically sensitive environments such as Protected Areas. In addition, follow-up of uprooted areas by uprooting seedlings and re-sprouting stumps highly enhances its effectiveness.

On the other hand, chemical control refers to the control of target invasive alien plants using herbicides (ECZ, 2007). Herbicide application can either be through foliar spray, to the basal bark or on the cut stump. Control of lantana by chemical application to cut stumps and foliar spraying has been previously undertaken in Zambia at Ndola, Copperbelt Province and Choma, Southern Province (Abel 1972; Abel 1973; Selander and Chomba, 1989). In Australia, foliar spraying is used to kill plants less than 2m in height (National Heritage Trust, 2004), whereas herbicides are applied to the lower bark of stems or immediately painted onto freshly cut stumps of mature plants in both Australia (National Heritage Trust, 2004) and South Africa (Stirton, 1977; Macdonald and Jarman, 1985; Erasmus and Clayton, 1992; Erasmus *et al*., 1993 and Wildy, 2005). The last two methods of chemical application are effective and useful for treating larger plants, and have the least impact on native species (Day *et al*., 2003; NHT, 2004) but tend to be time consuming as they require treatment of each individual stem. Lantana has also been treated with chemicals in Zimbabwe (Killilea, 1983a-b) and Hawaii in the USA (Motooka, 2000).

Similar to mechanical control, herbicides have been faulted for only reducing the numbers of established alien plants but not limiting their spread or preventing re-invasion when not applied repeatedly. In fact, though herbicides can be an effective tool for the quick control of several invasive weed species in localised areas (Rice et *al*., 1997; Motooka *et al*., 2002), they are also viewed by many as a risk to the natural environment (Wagner, 1993; Lautenschlager and Sullivan, 2002, Layton *et al*., 2003). This perception of their potential direct and indirect effects such as toxicity to wildlife and alteration of wildlife habitat has led to regulations in the use of herbicides globally (Lindsay and French, 2004). For this reason, the potential impact of herbicides on non-target species and alteration of plant communities and habitat structure is further discussed in Chapter 4. Additionally, high costs make herbicide control uneconomical for large infestations (Erasmus and Clayton, 1992; Cronk and Fuller, 1995) in land of low value and in countries with weaker currencies such as Zambia.

It has been shown that herbicides are most effective when sprayed on actively growing plants (Killilea, 1983; Motooka *et al*., 1991 and Hannan-Jones, 1998) and their efficiency is improved by spraying immediately after cutting. However to a large extent, success remains very much a function of climate, plant species involved, and application methods (Luken, 1993). In the literature, herbicides such as glyphosate, imazapyr, triclopyr, picloram, tebuithrom, 2, 4D, metsulfron have been indicated for the control of broad leaved species such as lantana in many parts of the world (Motooka, 1999; Day *et al*., 2003 NHT, 2004; Tatum, 2004; Wildy, 2005; ECZ, 2007). However, since the effectiveness of herbicide control of alien vegetation is not easily predicted, field trials of different herbicides and application methods are important before beginning a large-scale invasives control program. As in mechanical control, follow-up is essential in chemical control treatments and many years of work can be wasted if follow-up does not occur for at least two years following the last seeding (Day *et al*., 2003; Morris *et al*., 2008)

Biological control is very different from both mechanical and chemical control as it involves the suppression of weeds by insects and micro-organisms that feed on the target plant or otherwise paratisize it (Motooka *et al*., 2002). While it is extremely economical when successful, it has no guarantee of success (Motooka *et al*., 2002) and global efforts to control lantana using a number of biological agents have so far been largely unsuccessful. The low bio-control success of lantana has mainly been due to its genetic diversity and the wide range of habitats it colonizes which lead to the possibility of unfavourable climatic conditions for its natural enemies (Thomas and Ellison, 2000; Stock, 2004). Disappointingly, none of the insect agents released so far have caused significant damage to the very important common pink biotype (Thomas and Ellison, 2000) which is prevalent in the Victoria Falls area. There is also much uncertainty on the host specificity of many biocontrol agents, leading to general scepticism towards its implementation (Love *et al*., 2009). Owing to the reasons above, there is a need for clearing lantana using mechanical and/or chemical methods, at least in the short to medium term.

Consequently, this chapter concentrated on mechanical and chemical methods of lantana control which have relatively more success in many parts of the world, and were accordingly recommended by an independent EIA prior to the study (ECZ, 2007). The protected status of the study site required that adopted methods meet legal requirements for use in the area and independent consultants who undertook the EIA recommended uprooting and cut stump chemical application using imazapyr and picloram (ECZ, 2007). The chemicals which were identified in the EIA have been successful in other pan-tropical regions of the world with similar climate and ecology (Day *et al*., 2003) and the cut stump method was adopted for its perceived minimal environmental impact arising from the limited surface area to be painted with herbicide on cut stumps which reduces the risk of accidental spills and other possible negative impacts.

Since Picloram could not be readily secured from suppliers, metsulfron, a different herbicide registered for lantana control (Day *et al*., 2003; NHT, 2004; Wildy, 2005) was used. Glyphosate, applied by a motor charged 5 l applicator to regenerating lantana foliage a month after initial cutting was adopted as the fourth control method. Though metsulfron and glyphosate ware not recommended in the EIA, their use was nonetheless based on their reported use in other similar ecological zones (Killilea, 1983-84; Macdonald and Jarman, 1985; Day *et al*., 2003). All the chemicals used in this study were systemic and non selective. Systemic herbicides are herbicides that are translocated throughout the plant from the area initially treated, whereas non selective herbicides are herbicides that will kill or injure any plant they come into contact with (Motooka *et al*., 2002; Wildy, 2005). The EIA further recommended that the treatments be conducted after the rainy season; in order to lessen potential impacts of herbicides that could arise from rain induced chemical wash-off in the riparian habitats.

This section of the study therefore arises from the need to better understand issues relating to efficacy of one mechanical and three different chemical treatments of lantana and their accompanying economic implications in the Victoria Falls World Heritage Site. The effectiveness of the methods adopted for invasive alien species control is critical and the costs of control need to be properly forecast in order to facilitate execution of viable projects. Therefore in tandem with the EIA recommendations, the initial treatments were undertaken in July 2008 after the 2007 rain season had ended and the spray from the Victoria Falls had subsided in the rainforest. A follow-up operation to treat potentially re-sprouting lantana stumps and emerging seedlings in the treatment plots was undertaken 48 weeks later in June 2009, after the 2008 rain season had ended. The last monitoring activity in the research sites took place in September 2009 and focused on estimating lantana seedling density after an earlier follow-up had been undertaken in June 2009. The treatments trialled in this study were designed to resemble real-life recommended practice of lantana control, which had to inevitably include follow-up and an assessment of the related implications.

Aims

This chapter assessed the effectiveness of the physical uprooting method and three commonly employed herbicides (glyphosate, imazapyr and metsulfron) applied differently to lantana (Table 1). This was achieved by comparing adult lantana mortality and lantana seedling density in each of the treatment plots in June 2009, 48 weeks after initial clear and in September 2009 after a follow-up treatment to kill any surviving adult lantana and remove all lantana seedlings in the study plots had been undertaken. I predicted that chemical treatments would have higher adult lantana mortality than the uprooting and control plots, with high possibilities of re-sprouting from uprooted stumps. I further predicted that post clearing lantana seedling emergence in herbicide treatment plots would be higher than the control as a result of extra light availability and the effect of herbicides on the green tissues of established plants and not seeds, but would be lower than uprooting because of less soil disturbance. I also predicted that lantana seedling density in all treatment plots would be higher in the initial follow-up in June, 2009 and lower in September, 2009.

I also evaluated the cost of each treatment based on the cost of chemicals and chemical mixing materials such as adjuvants, and the labour input at initial clear and follow-up. From the ensuing labour costs, I then calculated the man hours required per treatment. Equipment costs incurred at commencement of the clearing exercise were also factored into the overall estimations and compared across treatments as start up costs. In this regard, I predicted that uprooting would comparatively have a higher labour requirement than the chemicals, but lower material costs, overall. The start up costs were expected to be higher in chemical treatments compared to mechanical treatment.

Description of herbicides used in this study

Glyphosate

Glyphosate is a broad-spectrum, non-selective, systemic herbicide that can control most annual and perennial plants (Tu *et al*., 2001). It is particularly effective against grasses in pastures, natural areas and aquatic sites and severely injures woody plants such as lantana by foliar application (Motooka *et al*, 2002). Glyphosate is easily translocated in phloem and kills plants by inhibiting the synthesis of aromatic amino acids necessary for protein formation and providing a link between primary and secondary metabolism in susceptible plants (Carlisle and Trevors, 1988; Motooka *et al*., 2002).

In the environment, glyphosate is highly water soluble, but unlike most water-soluble herbicides, it has a very high adsorption capacity and once in contact with the soil, it is rapidly bound to soil particles rendering it essentially immobile (Feng and Thompson, 1990), preventing it from being taken up from the soil by non-target plants.

Glyphosate is degraded primarily by microbial metabolism and its half-life on foliage has been estimated at 10.4-26.6 days (Newton *et al*., 1984) and about 47 days in the soil (Motooka *et al*., 2002). In water, glyphosate is rapidly dissipated through adsorption to suspended and bottom sediments, and has a half-life of 12 days to ten weeks. Glyphosate is non phytotoxic and metabolized by some, but not all plants (Carlisle and Trevors, 1988; Motooka *et al*., 2002).

Imazapyr

Imazapyr is a non-selective, systemic herbicide used for the pre-emergence and post-emergence control of a broad range of weeds including terrestrial annual and perennial grasses and broadleaved herbs, woody species, and riparian and emergent aquatic species (Tu *et al*., 2001; Motooka *et al*., 2002). Imazapyr can be used where total vegetation control is desired or in spot applications, though it is not particularly good at killing large woody species because it is relatively slow acting and does not readily break down in the plant (Tu *et al*., 2000). It is however recommended for the control of invasive broadleaved shrubby plants such as lantana (Day *et al*., 2003; NHT, 2004).

Imazapyr controls plant growth by preventing the synthesis of branched-chain amino acids (Tu *et al*., 2001). It is absorbed quickly through plant tissue and can be taken up by roots. It is then translocated into the xylem and phloem to the meristematic tissues, where it inhibits the enzymes required for protein synthesis and cell growth. The rate of plant death is usually slow (several weeks) and is likely related to the amount of stored amino acids.

Imazapyr has been found to have an average half-life of several months in soils, depending on environmental conditions (Vizantinopoulos and Lolos, 1994; El Azzouzi *et al*., 1998). El Azzouzi *et al*., (1998) reported half lives between 25 and > 58 days in two Moroccan soils. It has been reported that persistence in soils is influenced by soil moisture and that in drought conditions, imazapyr could persist for more than one year (Peoples, 1984).

Metsulfron

Metsulfron is a water dispersible granular herbicide for the control of certain broad-leaved weeds in cereals as well as invader weeds in natural pastures and conservation areas (Motooka *et al*., 2002). It is a residual sulfonylurea compound used as a selective pre-and post emergence herbicide for broadleaf weeds and some annual grasses. It is a systemic compound with foliar and soil activity and it works rapidly after it is taken up by the plant. The chemical is translocated throughout the plant, but is not persistent (Extoxnet, 1996).

Its mode of action consists of inhibiting cell division in the shoots and roots of the plant, and it is biologically active at low use rates. Due to its residual activity in soils, it is necessary to allow ample time for the chemical to break down before planting crops when used in agricultural situations (Extoxnet, 1996).

Metsulfron-methyl is relatively mobile in most soils, but will be retained longer in soils with higher percentages of organic matter. Adsorption to clays is low but it is leachable and its biodegradation rate is rapid (Motooka *et al*., 2002). Metsulfron-methyl will degrade faster under acidic conditions, and in soils with higher moisture contents and higher temperature. Half-life estimates in soil range from 14 to 180 days, with an average of 30 days. Metsulfron-methyl is stable to hydrolysis at neutral and alkaline pHs.

Adjuvants

An adjuvant is any chemically and biologically active compound that is added to a herbicide formulation or tank mix to facilitate the mixing, application, or effectiveness of that herbicide. In this study, the adjuvant SILWETT leaf cote was added to Metsulfron methyl to enhance its penetration by ensuring adequate spray coverage and keeping the herbicide in contact with plant tissues, and by increasing rates of foliar and/or stomatal penetration (TSS, 2008).

The long-term fate of SILWETT leaf cote in soils and elsewhere in the environment is unknown, partially because of the lack of long-term monitoring data in most instances where adjuvants have been used, but also because rarely are the ingredients in most adjuvants disclosed, and adjuvant labels do not include information on the compound's behaviour or fate in the environment (in plants and soil). The labels also do not describe the adjuvant's mechanism of action, rates of metabolism within plants, persistence (half-life) in the environment, potential for volatilization, or potential mobility in soil or water.

Although adjuvants are typically categorized as “inert” or “essentially non phytotoxic” compounds, many can produce wide ranging effects on physiological and metabolic processes within plants, animals, and or micro-organisms (Norris 1982; Parr and Norman, 1965), including deterred seedling germination, but the level of impact varies among plant species. Plant roots tend to be extremely sensitive to adjuvants in nutrient solutions since their fine roots have no wavy cuticle layer to prevent absorption, unlike leaves and stems. Therefore I predicted that SILWETT leaf cote would limit seed germination and seedling establishment of susceptible plants in the metsulfron treatment plots.

Methods

Four treatments (see Table 1 and Figs 4-11) were applied in $100m^2$ plots at each of the five sites (n=20), in the immediate post rain season (July 2008), and in addition a plot invaded by lantana but left uncleared was sampled as a control. All plots had a lantana cover of > 75 % at the beginning of the study. In the glyphosate treatment, lantana bushes were trimmed using slashers to a height of about 1m above ground. A month later, a gravity fed and motorized applicator was used to apply the chemical at a rate of $144g.l^{-1}$ onto re-emerging lantana foliage, thus ensuring direct application (TSS, 2008). Initial clearing was the same for the imazapyr and metsulfron treatments, where the upper brush of lantana was removed using slashers and machetes. The remaining stems were cut with bow saws to a height of about 10cm above the ground. Imazapyr was then applied to freshly cut lantana stumps in its concentrated form ($250g.l^{-1}$) using a 1 inch painting brush. In the Metsulfron treatment, the chemical was applied onto the freshly cut stem at a rate of $600gl^{-1}$ using a hand held 5l sprayer after SILWETT leaf cote (an adjuvant) was added to facilitate mixing, application and herbicide efficacy. After the cut stumps were treated with imazapyr and metsulfron, two different bright colours were used to dye the stumps in order to facilitate their identification and avoid repeated treatments (Fig 11).

In the uprooting treatment, lantana bushes were slashed to a stump height of about 20-30cm above the ground, before the stump was pulled out of the ground. In cases where the soils were too hard and the stump could not be easily pulled out by one worker, two workers were used to pull it out or digging with a mattock was undertaken at its base prior to uprooting

Table 1. Lantana treatments used in the study. All chemical data and application rates are as recommended by Technical Service Suppliers (2008)

Product	**Active ingredient**	**Treatment mode**	**Application rate/ha⁻¹**
Glyphomix	Glyphosate 144g. l^{-1}	Applied to re-emergent lantana foliage a month after initial clearing	Sprayed as premixed formulation at 15-20 l. ha^{-1} depending on size of bush
Arsenal	Imazapyr 250g. l^{-1}	Applied to freshly cut stump with 1-inch brush	Applied as paint on concentrate at 6l. ha^{-1}
Brush off	Metsulfron methyl 600g/kg with Silwett (leaf cote) added as an adjuvant	Applied to freshly cut stump using 5 lt sprayer	60-100g.ha^{-1}
-	-	Uprooting	-

Figure 4. Preliminary clearing of dense lantana thicket using slashers and machetes (July 2008)

Figure 5. A plot recently cleared of lantana prior to treatment. Note the bare ground devoid of vegetation after lantana invasion (July 2008)

Figure 6. Application of glyphosate on re-emerging lantana foliage in a treatment plot one month after cutting (August 2008)

Figure 7. Dry lantana stems six months after treatment with glyphosate (February 2009)

Figure 8. Workers preparing lantana stumps for cut stump herbicide treatments. Dense lantana stands are visible in the background (July 2008)

Figure 9. Workers applying imazapyr to lantana cut stump surface with painting brushes (July 2008)

Figure 10. Workers applying metsulfron to lantana cut stump surfaces with a hand held sprayer (July 2008)

Figure 11. A close view of a lantana stump treated with metsulfron and painted with a white dye for easy identification of treated stumps (August 2008)

Post clearing monitoring and follow up activities

Lantana mortality could not be determined immediately after the treatments were applied in July 2008, as chemicals normally have a gradual effect on weeds and the treatments were applied at a time when lantana was entering senescence. Soil moisture levels (a key requirement for lantana growth) in the treatment plots were also declining after the rain season ended, precluding any immediate possibilities of stump re-growth. Monitoring to determine the mortality of adult lantana stumps treated at the initial clearing was therefore undertaken in June 2009 accompanied by a follow-up operation in all the treatment plots, as the following growing season was coming to an end.

During the follow-up operation, all re-sprouting lantana stumps in the chemical treatments were re-treated with the same chemical used at initial clearing. In the uprooting treatments, the re-sprouting stumps were uprooted again, together with the emerging lantana seedlings. The seedlings emerging in the sampling quadrats were counted and hand pulled, regardless of the initial treatment. This was because in most cases the emerging lantana seedlings were too small to be sprayed or painted with the relevant chemicals. In addition, the non-selectivity of all the chemicals used posed an increased risk of non target effects if the lantana seedlings were to be treated with chemicals. In September, 2009, the lantana seedlings in the sampling quadrats were counted again to see how many had come up since the initial hand pulling. In practice, these follow-ups simulated what would be done in reality in a large scale invasive alien control project.

Data collection

In order to establish the costs of each treatment applied in the study, the time taken by way of labour input in each of the 20 treatment plots was recorded at both initial clearing in July 2008 and during the follow-up operations in June 2009. The costs so derived were then used to calculate the rate of man hours per treatment both at initial clearing and at follow-up. The amount of chemicals used at initial clearing and follow-up in each plot were also recorded. Lantana mortality percentage was established by counting the number of treated stumps that were still alive in June 2009 in each of the treatment plots. Lantana seedlings emerging in each of the 100m² plots were counted as well and lantana seedling densities calculated for each plot. The time taken to finish the follow up activities in each plot was also recorded, while the number of workers per treatment remained five for the entire duration of the study. The number of lantana seedlings emerging in the treatment plots after the follow-up in June 2009 was recounted in September 2009 to see how many seedlings had germinated post follow-up.

Data analysis

Adult lantana mortality and post clearing seedling densities in June 2009 were compared across the four treatments using the non parametric Friedman ANOVA in order to ascertain the most effective method for killing lantana in the short term. The Friedman ANOVA was used as the data failed to meet assumptions of normality. The Friedman's ANOVA is a non parametric test applicable to blocked designs and randomized block experiments which analyzes ranks at each site, thus comparing treatments across sites. This analysis was chosen because of the blocked design of the experiment where each replicate occurred within a block together with one replicate of each other treatment. Further the sites had a high variability and it is unlikely that normal (unblocked ANOVA) would pick up significant differences between treatments even if the rank order of the treatments was similar across the sites. Post hoc tests were undertaken using the non parametric two dependent samples Wilcoxon matched pairs test.

A second census of lantana seedlings was conducted in the treatment plots in September 2009. However no between treatment comparisons were done at this stage as all follow-up treatments for lantana seedlings in June 2009 had been by handpulling. Therefore, the interest in lantana seedling density in September 2009 was simply to determine the number of lantana seedlings which had come up in the treatment plots after follow-up.

The costs of the treatments used in this study were assessed by looking at the equipment and tools needed to undertake each treatment in an area of 1ha (start up costs. ha). However, due to issues of scale, it was recognized that the amount of tools required per ha would not remain constant as the area cleared of lantana and workers skill increased, and so the start up costs were analysed separately, based on a realistic estimation of how much equipment and tools would be required to clear the whole invaded area approximated at 524ha (Table 2). The estimated start up costs for each of the treatments must be added to the chemical and labour costs per ha (Table 3) to obtain the total estimated cost for each treatment.

The cost of undertaking initial clearing works (including application of the treatments) per ha and the cost of chemicals per ha were also quantified. The quantities of the different chemicals used at initial clearing and for treating re-sprouting stumps at follow-up were extrapolated to the total area under lantana infestation in the Victoria Falls World Heritage Site. The costs of labour for field workers were determined by the workers' hourly wage (US $ 0.75) multiplied by the number of hours spent on each treatment at each site, and up scaled to the total area under lantana invasion. The cost estimations did not account for issues such as the variations in lantana density in different parts of the World Heritage Site, nor the terrain, experience and skill of the workers, or weather. Mechanical costs were also calculated on the basis of labour required to uproot an area of 1ha.

From these data, cost estimates for the total amount of financial resources required to control the lantana invasion in the Victoria Falls area were determined. The costs are expressed in United States Dollars (US $) which is the most commonly used foreign currency in Zambia. The cost of chemicals and some of the equipment used for the calculations are based on data from Technical Services Supplies (TSS, 2008) who supplied the chemicals and most of the equipment used for the fieldwork. It is assumed that the cost ranking between the treatments derived from this study would not be affected even if a bulk purchase of chemicals for the treatment of the entire Victoria Falls World Heritage Site was initiated by the Zambian government. Similarly, while the number of worker-hours per hectare may also be reduced if bigger areas are covered (or as the experience of the workers increases) the relative costs of the treatments should not be affected.

Results

Effect of treatments on lantana

Mortality of lantana in June 2009

All the treatments caused high mortality after the initial treatment ranging from 69% (Glyphosate) to 100% (Uprooting) in different experimental plots in June 2009. Uprooting had the highest lantana mean adult mortality (89.8%) followed by imazapyr (86.2%), while metsulfron was third with a mean mortality of 79%. Glyphosate had the lowest mean mortality of 75.2%. There was no mortality in the control plots during the same period (Fig 12). The Friedman ANOVA results showed a significant difference across treatments, ANOVA Chi Sqr. (N=5, df=4)=13.85859, $p<0.05$ and a post hoc Wilcoxon matched pairs test revealed a significant difference between all treatments and the control plots (N=5; T=0.00; Z=2.22600, $p<0.05$).

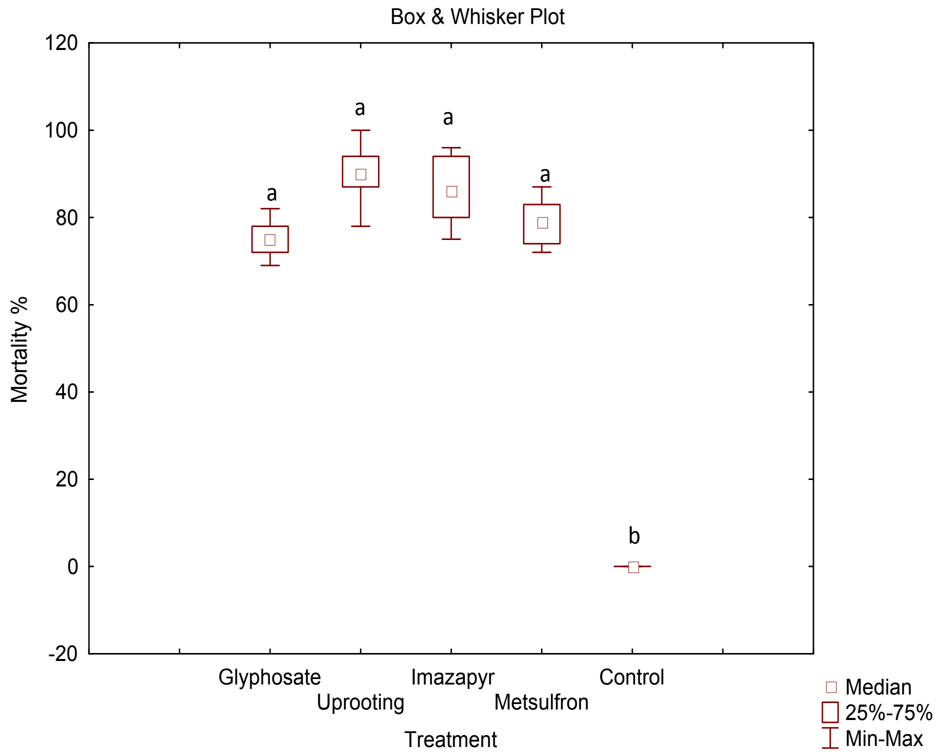

Figure 12. Box and whisker plot showing significant differences in mortality between treatments (June 2009). All the treatments are significantly different from the control but not from each other (Wilcoxon matched pairs test)

Mortality of lantana in September 2009

Three months after the follow-up, all the retreated stumps of adult lantana in the treatment plots were monitored and appeared to be dead. Subsequent monitoring in the rain season that followed, starting in October 2009 when lantana regrowth was mostly expected, confirmed that the stumps were dead.

Lantana seedling density in June 2009

There was a high number of lantana germinating from the seed bank after initial clearing in all the treatment plots, ranging from 0.1 seedlings.m^{-2} in a glyphosate plot to 8.7 seedlings.m^{-2} in a metsulfron treated plot in June 2009. The uprooting treatment had the highest mean abundance of 3.34 seedlings.m^{-2} across the sites, followed by metsulfron with 3.05 seedlings m^{-2}, glyphosate with 2.74 seedlings.m^{-2} and lastly imazapyr with 2.1

seedlings.m^{-2}. No newly germinated lantana seedlings were recorded in the control plots as at June 2009. The Friedman ANOVA test found a significant difference in lantana seedling density across the treatments, ANOVA Chi Sqr. (N=5, df=4) =11.52000, p<0.05), with the post hoc Wilcoxon matched pairs test showing all the treatments were significantly different from the control (valid N=5; T=0.00000; Z=2.22600, p<0.05) (see Fig. 13).

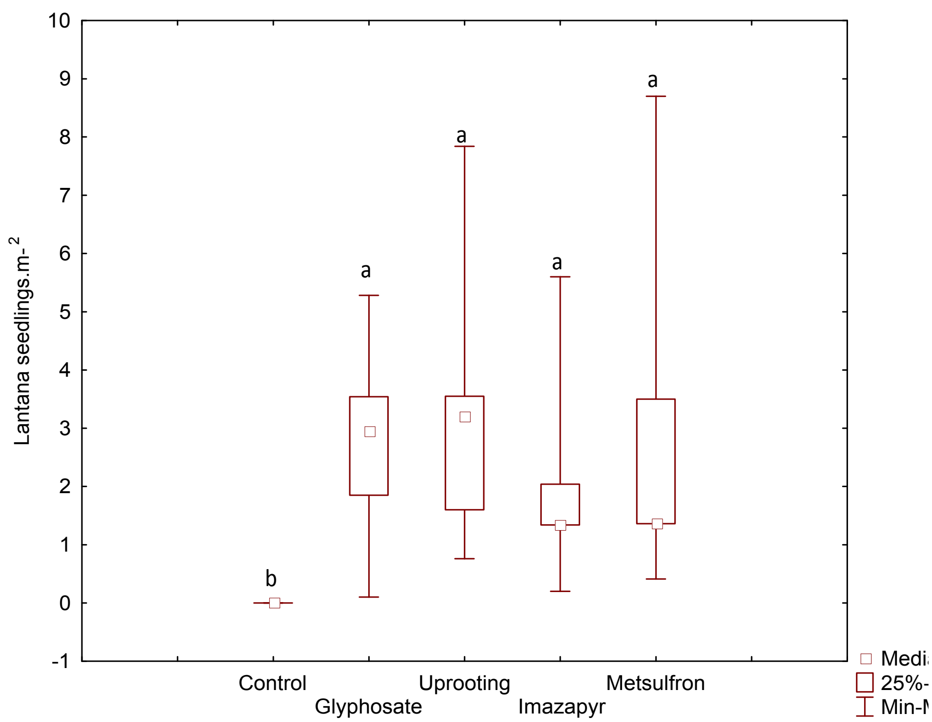

Figure 13. Box and whisker plot showing significant differences in lantana seedling after initial clearing (June 2009). All treatments are significantly different from the control (Wilcoxon Matched Pairs Test)

Lantana seedling density in September 2009

Three months after the follow-up, lantana seedlings were counted again in September 2009 in each of the 30 treatment plots. The mean seedling density across all treatment plots was 0.52. seedlings.m^{-2} which was much lower than the mean seedling density of 3.74 seedlings.m^{-2} recorded in the same sampling quadrats in June 2009. However these two values of lantana seedling density were not directly compared to each other due to the fact that September 2009 was well into the dry season and thus much drier than June 2009 which was just after the rain season and secondly, while it had taken 11 months before the follow up in June 2009, the second counting of lantana in September 2009 was only a period of three months after the follow-up.

Cost of treatments used for lantana management

Start up costs for lantana clearing

A comparison of the start-up costs required for each treatment in terms of tools and equipment (but excluding the costs of chemicals; see Table 2) established that the glyphosate treatment had by far the highest start-up costs, followed by uprooting and metsulfron methyl, while imazapyr had the lowest start-up costs. Start up costs for glyphosate were higher than the other treatments because its application equipment cost far more than the application equipment required for either imazapyr or metsulfron. Uprooting did not require any application equipment, but the mattocks and pick-axes needed for digging out lantana stumps raised its start up costs, making it more expensive than the imazapyr and metsulfron treatments. Metsulfron had higher start up costs than imazapyr due to the price of the hand held sprayers meant for its application. The slashers, machetes, bowsaws and painting brushes used for the imazapyr and metsulfron treatments were of much lower cost and did not contribute much to differences in the start up costs. However, these estimated start up costs (Table 2) do not change the overall ranking of the treatment costs.

Table 2. Start up costs for the invaded 524 ha in the Victoria Falls World Heritage Site using the four treatments in the study

Treatment	Required equipment	Quantity required	Unit cost (US $)	Total cost (US $)
Glyphosate	Machetes	100	5	500
	Slashers	100	5	500
	Motorized applicator	5	700	3500
Total				4500
Uprooting	Machetes	100	5	500
	Slashers	100	5	500
	Mattocks	100	13	1300
	Pick-axes	50	15.6	780
Total				3080
Metsulfron	Machetes	100	5	500
	Slashers	100	5	500
	Bowsaws	50	7	350
	5l pressure sprayers	50	28.5	1425
Total				2775
Imazapyr	Machetes	100	5	500
	Slashers	100	5	500
	Bowsaws	50	7	350
	1" painting brush	100	1	100
	Small containers	20	1	20
Total				1470

Cost of chemicals

There was a substantial range in the cost of the different chemicals used. The total amount of imazapyr applied on cut stumps at initial clearing of the experimental 500m² plots was 1.355 l (Table 3), translating to about 27.1l.ha^{-1}. Since the 2008 price of imazapyr was US $ 60.l^{-1} (TSS, 2008) the cost of treating the whole invaded area in the Victoria Falls World Heritage Site with imazapyr would be US $ 852,024. Considering the 0.125 ml of imazapyr used at follow up in this study, follow up for the whole invaded area would require 1310 l at a cost of US $ 106,503, leading to a total cost of US $ 958,527 for treatment of the entire Victoria Falls World Heritage Site.

For metsulfron, a total of 9.75 g was used to treat the initial $500m^2$ cleared, requiring $0.195kg.ha^{-1}$ and 102.18 kg for the whole site. At a cost of US $ 360/kg (TSS, 2008) this would amount to US $ 36,785 for treatment of the entire project site. At follow up, 2.35 g of metsulfron was used for the cleared areas, meaning $47g.ha^{-1}$and 24.628kg for the entire area. In view of this, follow up control for the whole invaded area would cost US $ 8,866. Therefore, the total cost of treating 524 ha in the Victoria Falls World Heritage Site with metsulfron followed by a single follow up activity would be US $ 45,653. Since a total of 25.5 l of adjuvant costing US $ 1,530 was added to metsulfron prior to treatment, the total treatment cost for the invaded 524 ha of the Victoria Falls World Heritage Sites would amount to US $ 47,183.

In the case of glyphosate, a total of 14 l was used during treatment of the $500m^2$ treatment plots, and 7.65 l to undertake follow up in the same areas, requiring 280 $l.\ ha^{-1}$ and 146,720 l for the whole invaded area. At a unit cost of US $ 12. l^{-1} from the supplier, the total cost of glyphosate would be US $ $3,360.ha^{-1}$ and US $ 1,760, 640 to control the invaded 524 ha in the Victoria Falls World Heritage Site. When the follow up costs of US $ 76,504 are added the total is 1,837,144. From the results discussed here, glyphosate was by far the most expensive chemical control treatment, whereas metsulfron was by far the cheapest (Table 3). Follow up costs for all the treatments, which are several times lower than the initial clearing costs, are shown in Table 3.

Labour

The costs of labour were based on the five operatives undertaking the treatments at a rate of US $ 0.75.h and the time taken to accomplish a task. The labour cost for imazapyr and metsulfron treatments was estimated at US $ 440 per ha^{-1}, based on the total time it took to clear two infested areas of $500m^2$ each and prepare the remaining lantana stumps for application of imazapyr and metsulfron. At this rate, labour costs to clear and treat the invaded 524 ha in the Victoria Falls World Heritage Site with either imazapyr or metsulfron would amount to US $ 230,560.

Labour costs for the clearing and treating of $500m^2$ with glyphosate were estimated at US $ $409.ha^{-1}$. This was derived from time taken for the initial cutting and the subsequent spraying of glyphosate on re-emergent lantana foliage a month later.

Therefore, labour to clear 524 ha of lantana and treat it with glyphosate would cost a total of US $ 214,316. Labour costs for uprooting were estimated at US $ 248.ha^{-1} and US $ 129,952 for the whole site. From the figures discussed above, imazapyr and metsulfron treatments were the most expensive control methods in terms of initial labour costs, while uprooting was by far the cheapest. In all the four treatments, the labour costs at follow-up were considerably lower than those at initial clearing as seen in Table 3 below. Uprooting had the highest labour costs per ha at follow-up followed by metsulfron and imazapyr. Interestingly, glyphosate had the lowest follow-up costs per ha. To obtain a total estimate of the cost implications of each of the treatments used in this study, a sum up of each treatment's start up costs, chemical costs and the cost of labour at both initial clear and follow-up is required.

Table 3. Cost comparison of treatments and labour per ha^{-1} including initial clear and follow-up upscaled to total invaded area of 524ha. All costs are in United States Dollars (US $).

Treatment	Total cost per ha^{-1}	Total cost invaded 524 ha
Glyphosate	3,913.37	2,053,749.88
Imazapyr	2,221.60	1,164,118.40
Metsulfron	533	279,292
Uprooting	255.5	133,882

After the labour costs for all the treatments were determined, I translated them into man hours per hectare (mh.ha^{-1}) in order to allow a more direct comparison of how labour intensive each treatment was and to facilitate estimation for other areas or future times elsewhere where labour costs would be different from my study area at the time of this study.Consistent with the labour costs, metsulfron and imazapyr had the highest mh.ha^{-1} at initial clearing of the experimental 500m^2 followed by glyphosate and lastly uprooting. The same pattern emerged when comparison of the initial clearing costs was upscaled to the whole invaded area of 524ha. However, in terms of follow up uprooting had the highest mh.ha^{-1} at both initial clearing (500m^2) and at the larger scale (524ha) followed by metsulfron and imazapyr while glyphosate had the lowest. The estimation of the man hours per ha are based on a normal 8 hour shift and a rate of US $ 0.75 hr.

Table 4 Comparisons of man hours per ha^{-1} including initial clear and follow-up for the four treatments used in the study

Treatment	Total mh.ha-^{1}	Total mh.ha^{-1} invaded 524 ha
Glyphosate	110.17	57,729.08
Imazapyr	118.49	62,088.76
Metsulfron	118.6	62,146.40
Uprooting	68.1	35,684.40

Discussion

Mortality of lantana

It was found that application of the herbicides glyphosate, imazapyr, and metsulfron effectively controlled lantana during this study, with the responses being consistent across the five experimental sites. Die-back in some of the lantana stems treated with imazapyr and metsulfron was observed in the third to fourth month after application. The glyphosate plots took a bit longer, with drying up of some of the treated stems to brittling stage observed by the fourth to sixth month. However, in most cases, complete death could not be ascertained until the subsequent rain season which is normally the period for sustained lantana regrowth.

Therefore, the resprouting stems observed in the glyphosate, imazapyr and metsulfron treatments were probably due to workers' inconsistency in the quantity of chemical application or entirely 'missing out' on treatment of individual plants at the initial clear in dense stands, rather than by chemical failure to kill lantana. Erasmus and Clayton (1992) point out that 'missing' plants during initial clear can occur when the slashing and treatment operations are separated, with one group of workers specifically slashing the brush and another group painting the cut stump surfaces. Additionally, due to the multi-stemmed nature of lantana stumps, failure to treat all the cut stems on a stump is a real possibility leading to stump resprouts.

While missing out stumps and failing to paint all stems on a multi stemmed stump are relevant to imazapyr and metsulfron treatments, different factors affected glyphosate which was applied as a post emergence treatment. As re-emerging lantana was sprayed, whole plants may have been missed out due to the density of lantana in a stand. Another particular problem related to the glyphosate used in my field experiments was that it was supplied as a pre-mixed formulation from the distributor with no dye addition to help identify which plants had been treated or not. After its application, it was not practical to apply a dye to treated foliage like in the imazapyr and metsulfron treatments where a dyeing agent was added to the stumps after treatment. Therefore there was a high possibility of workers missing out plants during treatments as the sprayed chemical did not remain on the leaf surfaces for a long period after treatment. The metsulfron mixture used to treat the $500m^2$ research plots in this study was formulated at once, ruling out chances of inconsistent mix ratios. Future work must take this into consideration in order to keep the mixing rate and quantity of chemical sprayed on the plant constant due to the use of a handheld sprayer and the necessary formulation of the chemical whenever it is to be used.

The effectiveness of chemical control and weed response to herbicides is evaluated by various methods. Motooka (2000) rates weed response on a scale of 0-100 where the score is a subjective evaluation of the severity of injury. It ranges from 0 where there are no symptoms of treatment on the target plant whatsoever, to 100% where there is complete control, resulting in mortality. Though the units of assessment used in my study are different from those of Motooka (2000), all but one of the mortality rates recorded in this study lie between 70 and 100%, representing good weed control, with very severe symptoms.

In addition, there is corroborating evidence from other studies that the chemicals used in this study have provided high adult lantana mortality in several cases elsewhere. For example, a 3% solution of glyphosate applied using a calibrated knapsack sprayer in Amatikulu Nature Reserve in Kwazulu Natal, South Africa gave lantana mortality rates higher than 95% while a 1.5% solution gave mortalities in excess of 90% (Macdonald and Jarman, 1985). Erasmus and Clayton (1992) also report >75% lantana mortality using glyphosate and imazapyr in two trials near Ngome, Northern Natal and close to Albert Falls Dam, in Kwazulu-Natal, South Africa. Though these mortality rates are higher than those recorded for glyphosate and lower than those for imazapyr in this study, they all point to the effectiveness of chemical control as predicted.

Selander and Chomba (1989) also undertook some lantana control trials in Siamambo Forest Plantation in Choma, southern Zambia using the chemicals Imazapyr, Glyphosate and Tordon 101. Tordon resulted into 96% stump mortality, whereas 91% was achieved with imazapyr. Effectiveness of glyphosate was much lower at 39 or 41% but with no chemical applied on stumps, the mortality was only 18% (Selander and Chomba, 1989). Unlike in this study, their research did not look at subsequent lantana seedling regeneration in cleared areas or evaluate the costs of the different treatments. Because their study was undertaken in a monoculture forest crop plantation, they did not investigate native species richness, diversity and composition after treatment or the seed bank potential for ecosystem recovery which Erasmus *et al.,* (1993) did in the Kruger National Park. However, (Selander and Chomba, 1989) acknowledged the need for follow-ups, and recommended the use of imazapyr at concentrations far lower than those used in this study.

Overall, uprooting caused the highest lantana mortality. The variation in mortality observed in the uprooting treatments among sites in this study was most likely due to workers' fatigue and failure to completely uproot the stump of lantana, giving it a chance to re-emerge from the rootstock. In post study discussions with the workers, they all pointed out that uprooting was the most physically demanding treatment of all perhaps justifying the possibility of incomplete removal of the rootstock in some cases.

To address such shortcomings, Love *et al*., (2009) proposed a new strategy for the removal of lantana by the cut rootstock method, which involves cutting the tap root of a lantana plant beneath the coppicing zone. Lantana's characteristic root system has a main taproot penetrating up to a depth of 1 m and lateral roots that grow horizontally, attaining a length of up to 5 m in the top 6 cm soil horizon (Love *et al*., 2009). Such root structure enables the clump to be pulled after cutting the taproot beneath the coppicing zone (3–5 cm depth of soil) without much disturbance of the soil. This reduces the number of lantana scarified seeds in the soil seed bank exposed to light and likely to germinate at the site where lantana clumps are removed (Duggin and Gentle, 1988). After cutting the main taproot and pulling out the plant, the clump is kept upside down while drying to further decrease its regeneration potential (Love *et al*., 2009).

According to Love *et al*., (2009), the rootstock method is cost effective, with lantana removal costing about US $ 90-US $113.ha^{-1} depending on the intensity of lantana and topography of the area, which is almost half the costs of uprooting found in this study (US $ 248. ha^{-1}) and much lower than the labour costs for chemical treatment (see Table 2). However, unlike in this study, Love *et al* (2009) do not report the workers' wages or the time taken to accomplish the clearing tasks in their study and so direct comparisons with my findings cannot be made. This method could not be tried in this study as it was reported in an article published after the commencement of my experiment. In addition, other than what has been reported in Love *et al*. (2009), it is unlikely that the effectiveness of this method has been tested elsewhere, compelling future assessment.

Lantana seedling density

Lantana seedlings emerged in the treatment plots at all research sites during the study, showing the seed bank abundance of lantana in invaded areas and the possibility of clearing activities accelerating reinvasion. All treatments in this study recorded a higher rate of lantana seedling regeneration compared to the control plots where no seedling germination occurred in the control plots during the same period.

Uprooting had the highest mean seedling density in comparison to the other treatments, with disturbance caused by clearing and digging activities in the treatment plots and increased light availability post clearing being the most likely reason when compared to the impenetrable lantana thickets in the invaded plots, which blocked sunlight to the understorey and suppressed germination of lantana seeds. However, the pattern did not recur after follow-up probably showing that the soil disturbance effect did not last beyond a season. The removal of the above ground biomass in the chemical treatments also increased lantana seed germination prospects compared to the control plots. As expected, lantana seedling density reduced drastically after a follow-up operation in the treatment plots and is expected to reduce further when a second follow-up is undertaken. Though it was possible that the lower number of lantana seedlings in September 2009 compared to June 2009 was a result of the short time-span since follow-up, it was more likely due to the absence of rain which resulted into lower soil moisture availability in the treatment plots.

The lantana seedling density observed in this study clearly demonstrates the need for follow-up in natural ecosystems cleared of lantana in the Victoria Falls area. Management emphasis at this stage should therefore be placed on continued removal of any re-emerging lantana seedlings in order to arrest reinvasion of cleared areas. As seen from the first follow-up in June, 2009, lantana seedling density dropped considerably in the 100 sampling quadrats uprooted at the follow-up, showing the importance of follow-up. Though there could have been an effect of stress to the lantana seedlings due to reduced moisture in the soils during the dry period, several follow-up exercises are required to suppress the alien invader and facilitate native species recovery.

This can be achieved through hand pulling of emerging seedlings, which ultimately leads to depletion of the seed bank, and re-application of chemicals on re-sprouting individuals (Holmes *et al*., 2008), for a period of about three to five years. Monitoring of the thirty 100m^2 plots used for this study should continue in order to further understand the seed bank dynamics of lantana. Since adult lantana has been successfully treated or uprooted in the treatment plots, lantana seed rain and seed bank remain the challenge and these should be addressed through ongoing management of lantana seedlings in cleared areas during the 2010 rain season and beyond if necessary. Since there is a possibility that some of the seedlings were germinating from newly introduced seed coming into the treatment plots via various means of dispersal, this is investigated in more detail in Chapter 5.

Cost of treatments

The start up costs for the treatments varied considerably, but are insignificant compared to the treatment costs at initial clearing, and so do not make a large bearing on the overall economic ranking of the treatments. Further, they are sunken costs and once incurred will not recur again for a long period. It is considered that the estimated quantity of tools and equipment should suffice for controlling lantana in the invaded 524 ha, with minor maintenance costs.

Overall the costs of chemicals used for lantana control were very high and had a wide range. Glyphosate was the most expensive chemical making it unaffordable for use at a large spatial scale. Paradoxically, it also had the lowest efficacy and the second highest labour costs. Imazapyr was the second most effective treatment, but it was far more expensive than metsulfron, which had a comparably high efficacy. These reasons are enough to render use of imazapyr at landscape scale uneconomical as the rule of thumb favours the use of a chemical that can achieve comparatively similar results at a lower cost (Motooka *et al*., 2002). While there are possibilities of inaccurate estimations of quantities used for costing chemicals, the large cost difference between glyphosate and imazapyr on the one hand and metsulfron on the other undoubtedly reflects a real and large difference in the costs between these chemicals. One reason that could have contributed to the high cost of glyphosate is its foliar application method, which has a higher likelihood of spray drift, accidental spillages and even possibilities of workers re-treating the same plants by mistake. The other possible reason for the high cost in imazapyr and glyphosate is that they were both applied as concentrates based on recommendations from the chemical suppliers.

Costs of labour

Metsulfron had the highest labour costs at initial clear followed by imazapyr and glyphosate, while contrary to expectations, uprooting had the lowest labour costs. For all the chemical treatments, labour costs were substantially lower than the cost of chemicals. Though time taken to clear a plot can be an attribute of several factors e.g. accessibility of terrain, density of invasion, skill of workers or conditions of the tools, the main reasons for the time differences in this study were the cut stump applications in metsulfron and imazapyr, which require the plant to be trimmed to a low height with a saw prior to treatment, and the repeated procedure in the glyphosate treatment, where workers had to return to slashed lantana plots to spray the re-growth after a one month period.

In terms of follow-up, the costs of the uprooting treatment were higher than all other treatments. However uprooting remained the cheapest treatment overall because it used no chemicals, which by comparison are far more expensive than labour. The longer man hours taken for uprooting at follow-up are due to the slightly higher lantana seedling density and re-sprouting stumps in uprooting plots compared to imazapyr and glyphosate. Metsulfron had the second highest costs at follow-up, but these were offset by its the relatively low cost compared to glyphosate and imazapyr, making it the second cheapest treatment after uprooting. In all cases, estimated treatment costs (and number of man hours taken) for the invaded 524 ha in the Victoria Falls with metsulfron are less than 5% of the costs of imazapyr and marginally above 10% of the glyphosate costs to clear and treat an area of same size.

Contrary to expectation at initial clearing, uprooting had lower labour costs than the chemical treatments, most probably due to the low density of lantana stumps under the impenetrable thickets that characterised the experimental sites in the Victoria Falls. As Erasmus *et al*., (1993) found in the Kruger National Park, South Africa; dense lantana invasions with high aerial cover have a surprisingly low stump density. Therefore once the workers had cleared the upper lantana brush, they only concentrated on uprooting the lantana stump with a mattock or pick axe unlike in the imazapyr and metsulfron treatments where lantana biomass had first to be cleared, followed by cutting the stump to a low height and then applying the chemical. In the case of glyphosate, time was spent slashing lantana to a low height at initial clearing, and then returning to apply the herbicide to re-emergent foliage a month later. The chemical treatments were thus more time consuming than uprooting. Though uprooting had higher labour costs per unit area at follow-up, its relative cheapness compared to the other treatments at initial clearing is a positive economic attribute.

Conclusion

This study has shown the efficacy of four treatments in controlling adult lantana at a small scale which needs to be replicated at the larger scale. This follows many unsuccessful attempts at control and management of lantana in the area. The high mortality rate from uprooting observed in this study is important for control of invasive alien species in resource constrained protected areas such as the Victoria Falls World Heritage Site because of the relatively lower costs. It is particularly suited for a majority of the invaded areas with flat topography and low erosion potential such as the rainforest, the lower reaches of the gorges, the Palmgrove, ZESCO and Maramba River sites.

Management efforts in future clearing programs should thus place emphasis on addressing post clearing seedling germination through follow-ups as it has been clearly demonstrated that adult lantana mortality arising from mechanical and chemical treatments is high. Cleared areas will require a high follow-up frequency post clearing to remove germinating seedlings in the site. To regulate the follow-up costs, hand pulling of seedlings should be undertaken within the first three months after clearing before they develop mature root systems and again a few months after commencement of the rain season. The high follow up costs related to uprooting at follow-up during this study are mainly due to the fact that follow-up in the treatment plots was undertaken 48 weeks after initial clearing, when a majority of the seedlings had grown to a large size and this should be avoided in future. The other interesting finding of this study is the relatively low cost of undertaking follow-up operations as compared to the initial clearing, meaning future costs in cleared areas will continue to drop, making the clearing progressively cheaper.

In terms of applications timing, chemical treatments are best undertaken in the season of active lantana growth, which corresponds with the rain season in the Victoria Falls area. However, the EIA assessing methods for lantana control in the Victoria Falls World Heritage Site discouraged application of chemicals in the rain season for fear of chemical wash off by rain and potential pollution of water bodies in a protected environment. It is therefore recommended, especially in the immediate 50m of the riparian zone, that chemical treatments only be undertaken after the rain season has ended (May-July) when moisture content in the soils of invaded areas is still high and lantana is still actively growing prior to going into senescence. In order to test its cost effectiveness and efficiency, I recommend that the uprooting method proposed by Love *et al* (2009) be trialled in the Victoria Falls World Heritage Site.

Finally, it has been demonstrated clearly that the four methods used in this study can ensure lantana control in the infested 524 ha of the Victoria Falls World Heritage Site provided the adopted methods are implemented on an ongoing basis. In the long term, larger scale control should consider encompassing an ongoing biological control program which will contribute to reduced lantana seed reproduction within the managed ecosystems. Though there is no proven effective biological control agent for lantana currently, some of the more successful programmes of lantana biocontrol in South Africa and Australia have been with the lantana herringbone leaf miner *Ophiomyia camarae* and the leaf mining beetle *Uroplata girardi* (Chrysomelideae). These two species are therefore recommended for further assessment, dependent on the outcome of host range trials to determine their impact and ecological safety.

Data related to the frequency of stump re-sprouts and post clearing lantana seedling density will have important economic implications as they will ultimately show whether one follow-up is enough to contain adult lantana and how many follow-ups to remove lantana seedlings are required after initial clearing. This will determine the financial implications for the control of lantana in the area, which require a long-term funding commitment to ensure successful implementation of this essential long term project.

CHAPTER 4

THE EFFECTS OF CHEMICAL AND PHYSICAL CONTROL TREATMENTS ON VEGETATION COMPOSITION AFTER CLEARING *LANTANA CAMARA* IN INVADED AREAS

Introduction

The invasion and naturalization of exotic plants in native habitats pose one of the greatest threats to natural environments worldwide (Vitousek *et al*., 1996; Crone *et al*.; 2009, Gooden *et al*., 2009). By direct competition with native plant species or through alteration of ecological conditions, weeds lead to the reduction of native species abundance in communities (Weiss and Noble, 1984; Mack and D' Antonio, 1998) resulting in the formation of monospecific stands, or depauparate assemblages of tolerant species (see Fisher, 2009a). Globally, lantana invasions and their drastic effects on native plant species through various means have been documented (Wadhawani and Bhardwaja, 1981; Achhireddy and Singh, 1984; Gentle and Duggin, 1997a; Lwando-Tembo (2008).

Owing to the recognition of the risks posed by invasive alien plants, the control of lantana in the Victoria Falls area is seen as the first important step in restoring natural vegetation structure and plant species richness and diversity. This is because the most common aim of invasive alien species control in natural ecosystems is the enhancement or maintenance of wildlife habitat and the restoration of native plant communities (Rice and Toney, 1997). However, that in itself is a complicated task as weed control methods themselves can sometimes impact negatively on native species (Matarczyk *et al*., 2002) through various effects.

As a result, there are various arguments for and against each of the methods used in the control of invasive alien plants globally, mainly relating to their cost effectiveness, efficacy and environmental acceptability. For this reason, each of these methods is implicated in the cause of some direct and indirect effects during and after its use either in a natural ecosystem or in agriculture (Wardle and Parkinson, 1990; Cronk and Fuller, 1995; Rice *et al*., 1997; Sullivan and Sullivan, 2003; Rinella *et al*., 2009). Uprooting has been reported to create soil disturbance which leads to germination of undesirable weed species by stimulating dormant seed bank in many ecosystems (D'Antonio *et al,* 1998), leading to an inevitable need for repeated follow-ups in order to prevent the target plant from re-establishing. In addition, it has also been observed that uprooting has the potential to induce soil erosion in cleared areas with steep terrain (Wildy, 2005) and can lead to the destruction of native species during clearing operations (Wildy, 2005). Despite the highlighted shortcomings (Erasmus and Clayton, 1993; Cronk and Fuller, 1995; Hobbs and Humphries, 1995; Wildy, 2005; ECZ, 2007), uprooting was included in this study in order to assess its potential post clearing effects on vegetation composition in the Victoria Falls area.

Little is known about the non-target impacts of chemicals on native species in natural and semi-natural areas (Crone *et al*., 2009). Many herbicides are non-specific and thus likely to damage non-target flora and fauna or accumulate in soils or leaf tissue due to their persistence (Tatum, 2004). The use of herbicides for conservation purposes originates from traditional agricultural use where the objective is usually to promote a single species (the crop), by removing or suppressing the growth of all other plant species (Marrs, 1984; 1985; Smith *et al*., 2006). In contrast, herbicides in natural areas are used to target suppression of one, or occasionally, a few species of invasive plants, while trying to maintain or restore the rest of the native community and or other desirable species (Hobbs and Humphries, 1995). Furthermore, whereas in most agriculture situations herbicides are often applied before the crop grows and at which time it is acceptable to kill all plants, invasive alien plants are usually surrounded by natural vegetation, making the desired results from weed control projects in native vegetation more complex (Rice and Toney, 1997) implying that methods used for assessing the impacts of herbicides should differ from agricultural crop systems, where the goals are different and target specificity is not required as long as crop production is not affected.

In an experiment for the control of the invasive *Centaurea maculosa* in western Montana, USA using the chemical picloram, a study to assess the indirect demographic effects of this chemical on a native dominant forb, arrowleaf *Balsamorhiza sagittata* was instituted. It was found that while picloram use did not affect the leaf area and density of balsamroot in the short-term (5 years), a single application considerably reduced flowering and seed set, with effects persisting for at least 4 years after spraying. Use of the herbicide reduced *B*. *sagittata* inflorescence production to 33% and densities of new recruits to 5% of that in unsprayed plots (Rice and Toney, 1997). Several other studies have also reported the residual impacts of herbicide applications for invasive plant control on native plant biomass and percentage cover (Marrs, 1985; Rice *et al*., 1997; Rice and Toney, 1998; Sheley *et al*., 2006) as herbicides may not only control the targeted weed after application, but may also leave unwanted residues in the soil, which are ecologically harmful (Grossband, 1972). This residual effect is as a result of a portion of herbicide residues in the soil that are available to plants by root uptake and may cause adverse effects to sensitive plants growing in these areas. These concerns for the potential direct and indirect effect of herbicides on non target flora and fauna have led to a number of studies (Sullivan and Sullivan, 2003; Wardle and Parkinson, 1990; Rice *et al*., 1997) and contributed to a legitimate presumption that effects of herbicides on-non target plant species are large and significant (e.g. Harris and Cranston, 1979; Cuda *et al*., 1989; Rinella *et al*., 2009).

However, some of such claims are not supported by empirical data and improved understanding of the potential effects of chemical treatments can thus lead to improved practices such as timing of herbicide applications to critical phenological windows when the foliage of sensitive native forbs or indeed any other native plants is largely absent (Hitchmough *et al*., 1994).

In an illustration of complexity, the herbicide glyphosate is widely used in controlling bitou bush (*Chrysanthemoides monilifera*) in New South Wales, Australia, because many dominant Australian species occuring in invaded habitats-notably sclerophyllous shrubs in the genera *Acacia, Banksias* and *Leptospermum* tolerate winter applications of the herbicide, while bitou bush is susceptible (Cooney *et al*., 1982; Toth *et al*., 1993;

Kohler *et al*., 1995). Increasingly, metsulfron methyl is also being used for the management of bitou bush infestations in Australia (Matarczyk *et al*., 2002; French *et al*., 2008) albeit without full understanding of the implications of its application on native species. So far, glyphosate has been implicated in the cause of severe negative effects on the rare and endangered species *Pimelea spicata* (Matarczyk *et al*., 2002; French *et al*., 2008).

Despite these assertions, most modern herbicides are more specific and affect only biochemical processes unique to plants and typically degrade quickly once they enter the environment (van Wilgen *et al*., 2001; Tatum, 2004). Therefore it has been argued from this perspective that the effect of herbicides is short-term (Miller and Witt, 1990; Miller and Miller, 2004) yet variable due to differences in ecosystem resilience, the chemical(s) applied, and prevailing site conditions (Morrison and Meslow, 1983; Miller and Miller, 2004). Consequently, it is possible to suggest that the potential effects of chemical control methods on vegetation composition vary so much from one ecosystem to another such that one generalised view may not be applicable to all situations.

Therefore in order to derive a better understanding and possibly distinguish between the immediate and residual effects of chemicals on vegetation composition in the Victoria Falls World Heritage Site, three commonly used chemicals (imazapyr, metsulfron and glyphosate) were trialled as recommended in an Environmental Impact Assessment undertaken prior to the commencement of the clearing activities (see Chapter 3). This chapter therefore focuses on the potential non-target effects and positive benefits of these treatments on the species richness, diversity, and seedling density of seedlings, herbaceous species and small woody plants in the cleared areas. Issues pertaining to the seed bank, seed rain and recruitment of mature woody vegetation post-clearing are investigated in Chapter 5.

This chapter had three main aims. Firstly, I compared species richness, diversity and density of seedlings, herbaceous species and small woody plants between invaded and uninvaded plots from baseline data collected before execution of the treatments in order to determine the effect of lantana on native plant communities. I expected the uninvaded plots to differ from the invaded ones, with higher species richness, seedling density and diversity in uninvaded sites compared to invaded sites, but with no major differences among the invaded plots.

Secondly, I assessed the immediate non-target effects of uprooting and 3 chemical treatments on native and exotic vascular plant species after lantana removal in invaded areas of the Victoria Falls World Heritage Site. This was achieved by comparing the vegetation composition at baseline in July 2008 with that of the treatment plots three months after the initial clearing of lantana (October 2008). The purpose of the comparison in October 2008 was to ascertain if there were any immediate non-target effects of chemicals on live plants. I predicted that there would be lower species richness, seedling density and species diversity in the herbicide plots compared to uprooting and the uninvaded control.

Thirdly, I examined the medium term effect of treatment by comparing the vegetation composition at baseline in July 2008 with that of September 2009. The aim of this comparison was to look for any residual effects of chemicals on emerging seedlings and the beneficial effects of clearing on seedling emergence. I predicted that the removal of lantana would positively affect native species recruitment and diversity such that species richness, seedling density and species diversity of seedlings, herbaceous plants and small woody plants would be higher in cleared sites compared to invaded control sites over time. I also expected negative effects to arise from chemical use on native species by way of immediate and perhaps residual non–target effects of chemicals compared to mechanical control

Methods

Experimental design

The experiments for this study were undertaken at five research sites with dense lantana cover namely the Boiling Pot, Maramba River, the Rainforest, Palmgrove and Zambia Electricity Supply Corporation (ZESCO) within the Victoria Falls World Heritage Site. Each site had six randomly assigned treatments which consisted of uprooting, three chemical treatments and two control plots out of which one was an invaded control and the other was an uninvaded control (For details see Chapter 2). Five permanently marked $1m^2$ quadrats for ongoing monitoring in 4 treatments and the invaded and uninvaded control plots were randomly identified in each of the thirty $100m^2$ research plots at the five research sites for the period July 2008 to September 2009.

Data collection during baseline and monitoring

All seedlings, herbaceous species and small woody plants ≤30 cm occurring in the 150 quadrats were recorded in July 2008 before clearing the plots of lantana. Thereafter, manual uprooting by mattock or application of one of the three herbicides glyphosate, metsulfron and imazapyr was undertaken. Glyphosate was applied on re-emerging lantana foliage a month after initial clearing, imazapyr applied on lantana cut stump, while metsulfron was sprayed on a cut stump. The other treatments at each site were the uninvaded (lantana absent or ≤ 25% cover) and invaded control plots (lantana present ≥75%) which are described in detail in Chapter 2.

Monitoring the response of herbaceous and small woody plant species to the various treatments commenced in October 2008, as the months after the clearing (August and September) coincided with the dry season when there was no regeneration occurring in the plots. Data were collected by laying a collapsible $1m^2$ wooden quadrat on the ground and identifying, counting and recording all individual seedlings, herbaceous and small woody plants found in each of the 150 quadrats. Specimens of all unidentified species in the field were collected from adjacent areas outside the plots for further identification at local herbaria. All individuals were identified to species level except sedges.

The two control plots at each of the sites (invaded and uninvaded) were also sampled during every monitoring event and in total the plots were monitored eight times during the study period. The data analyses in this chapter are based on the baseline data collected in July 2008 and the monitoring data for the whole eight monitoring events between July 2008 and Septemeber 2009. The trends for the treatments over time take the whole monitoring period into perspective, while the comparisons of treatment effects are based on the first monitoring event after initial clearing (October 2008) and the final monitoring in September 2009. This was in order to determine the effects of lantana in invaded areas at baseline (prior to clearing), establish the short term effects of the mechanical treatments applied as of October 2008 and to determine the positive or negative mid-term effects of the mechanical and chemical treatments in September 2009. Species richness, diversity and density for seedlings, herbaceous species and small woody plants are based on 5 $1m^2$ quadrats per treatment plot, which were pooled together into a single replicate.

Data analysis

In order to see the overall effects of time and treatment, data collected at eight monitoring intervals from baseline to September 2009 were analysed with the repeated measures analysis of variance (after species richness, species diversity and seedling density were calculated in PRIMER. Species richness, Shannon Weiner diversity index (H' log base e) and density of seedlings, herbaceous species and small woody plants recorded at baseline were calculated in PRIMER and compared between the invaded and uninvaded plots at baseline in order to determine the effect of the lantana invasion using the t-test for independent samples.

A non metric multi dimensional scaling (NMDS) ordination was done using square root transformed abundance data and Bray-Curtis similarity (Clarke, 1993; Clarke and Gorley, 2000) to determine the effect of treatments on vegetation composition in the short term using square root transformed abundance data based on the combined dates July 2008; October 2008 and September 2009. A 1-way analysis of similarities (ANOSIM) with the factor site (Clarke, 1993; Clarke and Gorley, 2000) was conducted to determine the effects of site on vegetation composition in October 2008 and September 2009.

A 2-way ANOSIM was undertaken with the factor treatment and the three dates of July 2008, October 2008 and September 2009 to determine the medium term effects of treatment on vegetation composition in the treatment plots. A similiarity percentage (SIMPER) analysis with the combined treatments but excluding the invaded and uninvaded control was run with transformed data, to determine the species contributing most to the differences in the experimental plots before and after treatment. A similiarity percentage analysis (SIMPER) was done to determine which species contributed most to the differences in the vegetation composition between baseline and the other two monitoring periods used for the comparison (October 2008 and September 2009).

Results

Understorey response to clearing in lantana invaded areas

In total 154 vascular plant species (seedlings, herbaceous species and small woody plants) were recorded in the 150 1x1m^2 quadrats over the whole monitoring period from baseline in July 2008 to September 2009. Altogether there were 63 tree species, 37 herbs, 20 shrubs, 13 grasses, 14 creepers and 7 sedges and 1 fern during the study (Appendix 1). Data collected over the eight monitoring events are used for the analyses of the effects of treatment over time (Fig 14-16).

Species richness

The treatments applied in July 2008 did not lead to any significant differences in species richness across the treatments F (5, 190.7) = 2.20, p=0.087 during the eight monitoring events (Fig 14), possibly because most of the monitoring period represented by the graph fell in the dry season. However, time effects were significantly different across the treatments F (7, 361.2) = 40.67, p< 0.05 and between treatment and time F (35, 12.9) = 1.45, p<0.05. During the dry period before December 2008, there were no differences between the plots, not even between the uninvaded plots and the rest of the treatments. After the rain season started, the response of plants in the treatment plots was very variable. The invaded control was lower than all the other plots, while the uninvaded control and the treatments had a similar pattern but with species richness being higher in the treated plots. This showed a positive effect of clearing on species richness as the treatments had higher species richness than both the invaded and uninvaded control, perhaps due to the extra light availability after clearing lantana.

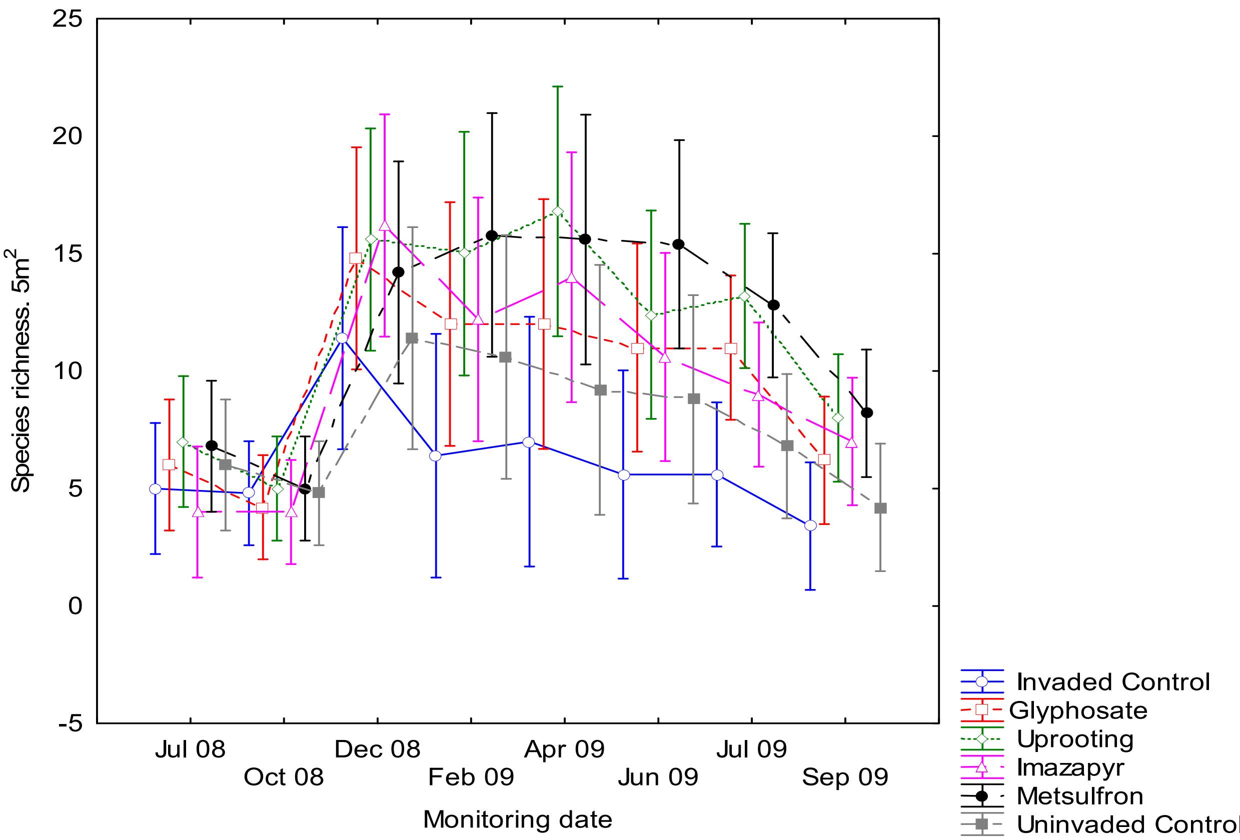

Figure 14. Trends in species richness across the six treatments and five research sites for the monitoring period July 2008 to September 2009 (Repeated measures ANOVA)

Seedling density

There were no significant differences in seedling density as a result of treatment during the monitoring period F (5, 598) = 1.44, p= 0.245; Fig 15. However there was a significant difference in seedling density over time F (7, 209) =27.52, p<0.05 and between treatment and time F (35, 127) =.1.67, p<0.05. Seedling density appears to have decreased to its lowest levels by October 2008 in all the treatment plots, three months after clearing. This was most likely an effect of reduced moisture levels due to the ending of the rain season. With the commencement of the rain season after October 2008, seedling density increased in the treatment plots reaching its peak in the uprooting and uninvaded control plots around February-April 2009 when it was very wet in the Victoria Falls area. The invaded control appeared to have a lower seedling density compared to all the other treatments. This could have most likely been due to the removal of upper lantana biomass in the cleared plots, which then allowed sunlight to penetrate to the ground, promoting germination in almost all the treatments considerably, except for metsulfron treated plots which just showed a temporary response.

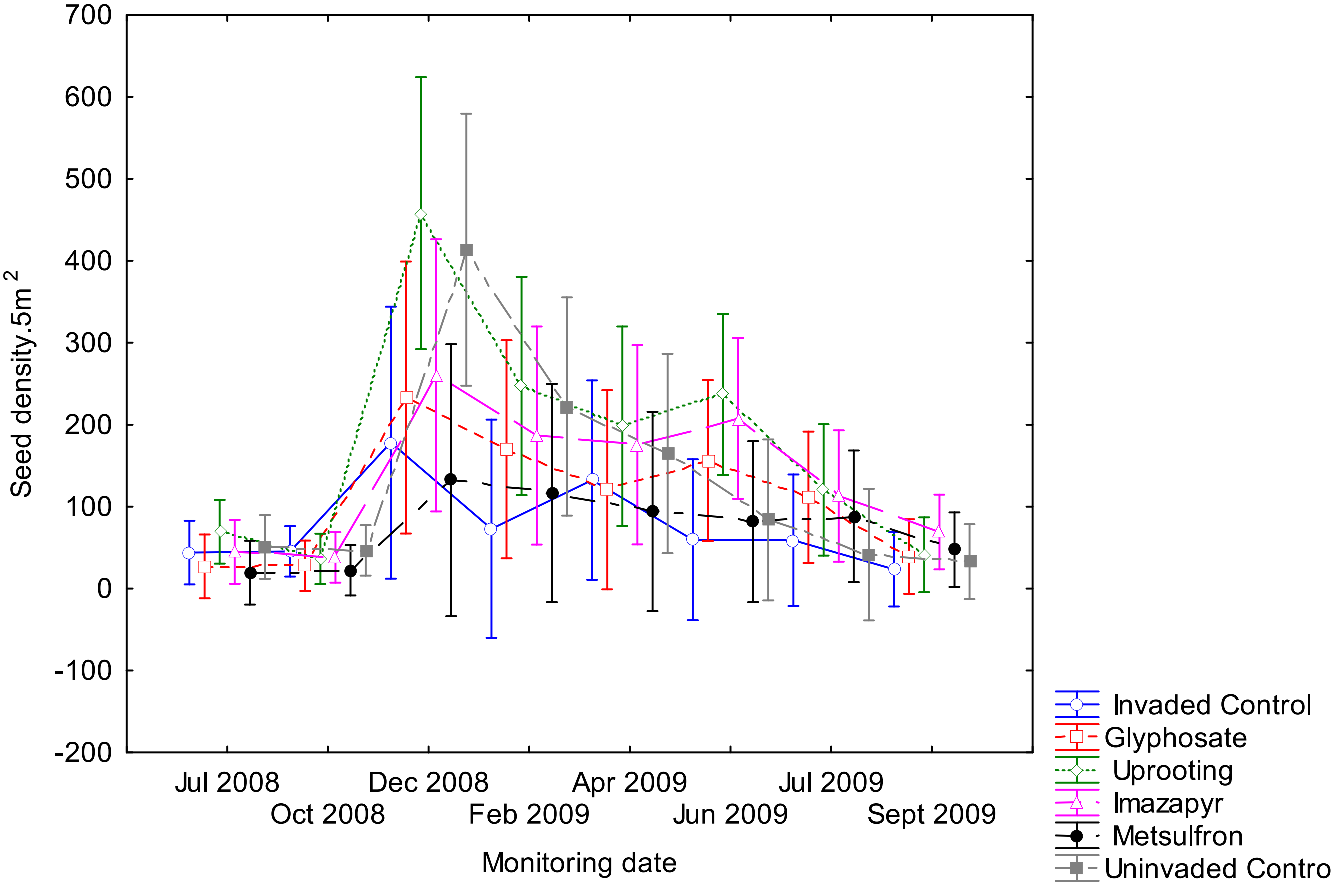

Figure 15. Trends in seedling density across six treatments and five research sites in the monitoring period July 2008 to September 2009 (Repeated measures ANOVA)

Species diversity

There were no significant differences in species diversity across the treatments F (5, 2.368) = 2.12, p = 0.097; Fig 16. However there was a significant difference between time mainly as a result of the wet and dry seasons that coincided with the monitoring F (7, 1.415) = 12.39, p<0.063. There was a significant difference of time and treatment F

(35, 0.209) = 1.83, $p<0.05$. The invaded control appears to have had the lowest species diversity around October 2008. However it progressively increased reaching a peak around December 2008 and then declining again. The uninvaded control had low species diversity for the first six monitoring events and then increased after June 2009 and declining towards September 2009. This can be related to the rainfall pattern in the Victoria Falls area and like for species richness and seedling density it is difficult to directly link it to the effects of treatment. Further no clear relationship appeared between the follow-up operation and increased species richness, density or diversity in June 2009

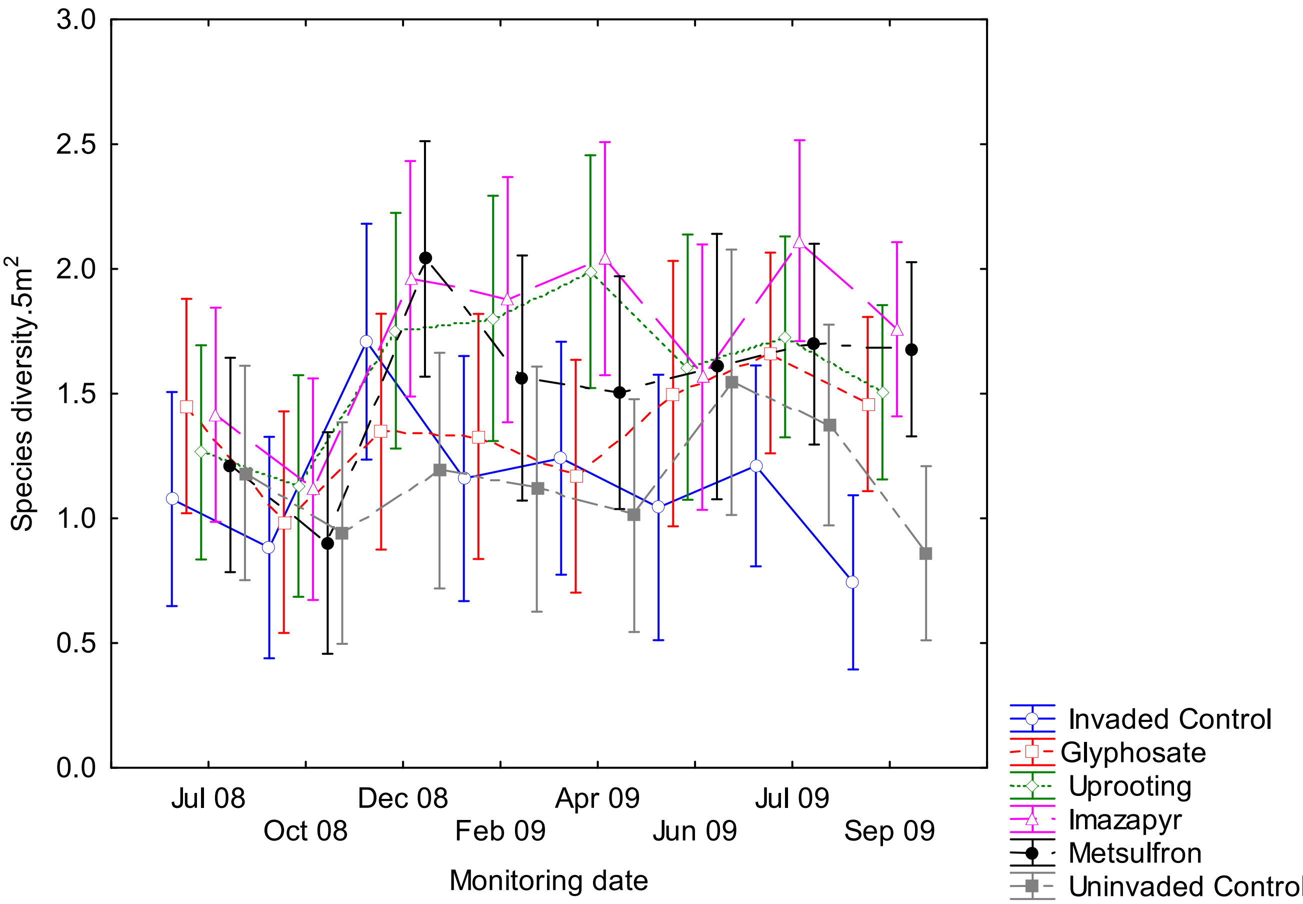

Figure 16. Trends in species diversity across six treatments in five research sites during the monitoring period July 2008 to September 2009 (Repeated Measures ANOVA)

Effects of lantana invasion on vegetation composition at baseline

Contrary to expectation, there were no significant differences in species richness, seedling density and species diversity between the invaded and uninvaded plots at baseline (t-test, data not shown). A non metric multidimensional scaling ordination showed that there was no clear pattern separating the invaded plots from the uninvaded plots at baseline (Fig 17). Additionally, a 1-way ANOSIM with the factor invaded revealed that there were no significant differences between the invaded and uninvaded plots (data not shown). This was probably because of the unbalanced sampling design where there were only 5 uninvaded sites compared to 25 invaded sites.

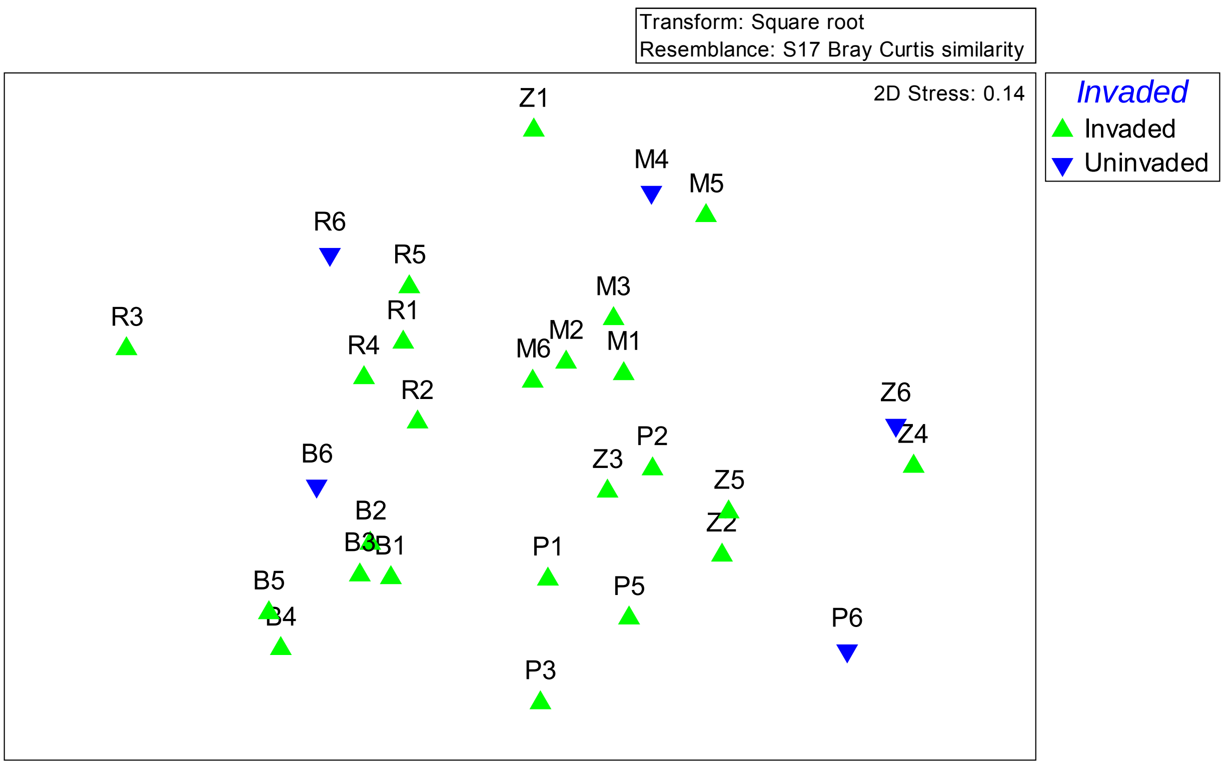

Figure 17. NMDS showing comparison between invaded and uninvaded sites at baseline (July 2008). Stress=0.14. Sites are B1-B6=Boiling Pot; M1-M6=Maramba River; R1-R6=Rainforest; P1-P6=Palmgrove and Z1-Z6=ZESCO

Effects of treatments on non-target species in the short and medium-term

A 2-way ANOSIM with the factors treatment and date revealed that there were no significant effects of treatment on vegetation composition between the three dates. An

NMDS did not show any distinct pattern in the vegetation composition resulting from the effects of treatment during the three periods (Fig 18). A 1-way ANOSIM with the factor site indicated that there was a significant influence of site (Global *R*=0.585; $p < 0.05$) and futher pairwise tests indicated that all sites were significantly different from each other.

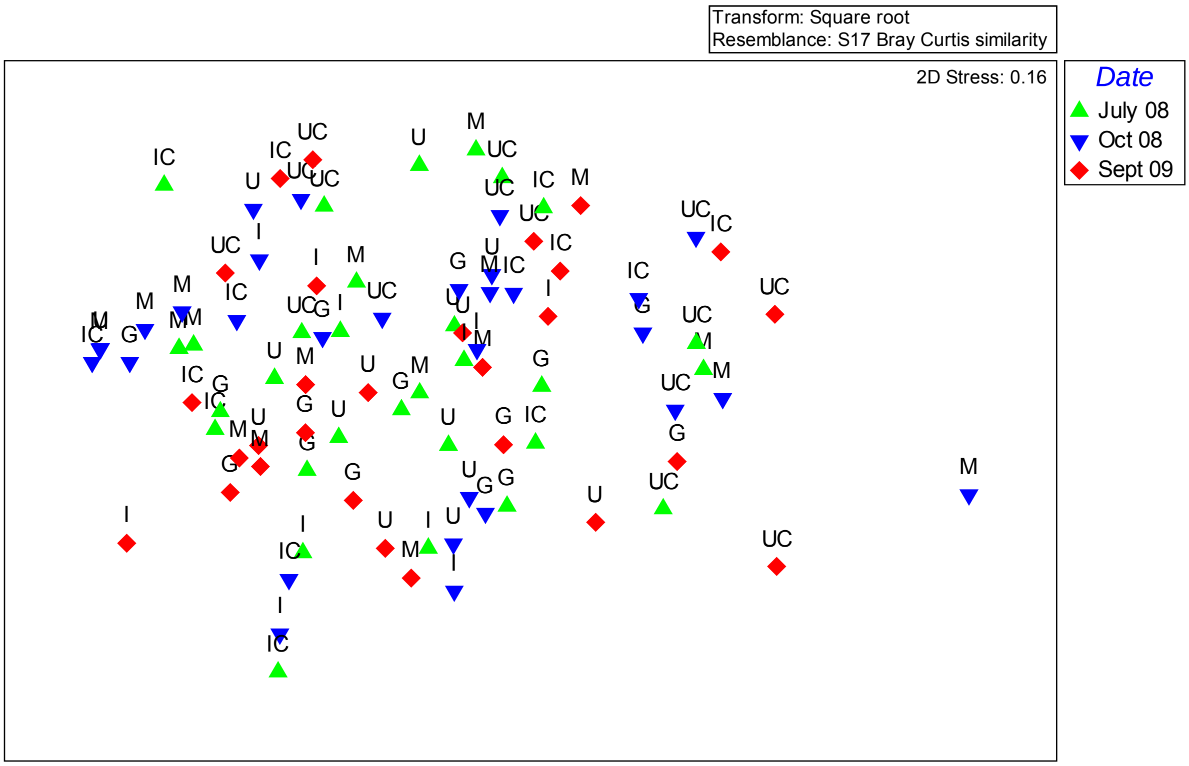

Figure 18. NMDS showing no significant effect of treatment across the research plots during the study period. Treatments are IC=Invaded Control; G=Glyphosate; U=Uprooting; I=Imazapyr; B=Metsulfron and UC=Uninvaded Control

The species contributing most to the difference between July 2008 and September 2009 was the native grass species *Oplismenus hirtellus* which appeared to have colonized most of the bare areas after clearing. However the native creepers *Jasminum fluminense* and *Hippocratea africana* decreased due to the loss of supporting plants. One of the exotic herbs *Ageratum conyzoides* increased while the other exotic herb *Achyranthes aspera* decreased post-clearing, for no clear reason. The native tree *Diospyros mespiliformis* increased perhaps due to the reduced inter-specific competition after lantana removal and the availability of suitable establishment conditions. During the same period, one of the two sedges decreased while the other increased. The density of lantana seedlings in the treated plots reduced in September 2009 after the initial clearing and a post-clearing follow-up had been undertaken (Table 5).

Table 5. Main species contributing to differences in species composition between four treatment plots between baseline, October 2008, and September 2009 excluding invaded and uninvaded controls using untransformed data (SIMPER results). Average dissimilarity =92.66. Exotic species are labelled with an asterisk.

Species	Abundance.5m^{-2}		% contribution
	July 2008	September 2009	
Oplismenus hirtellus	6.57	9.93	11.15
Jasminum fluminense	4.97	1.71	8.09
*Ageratum conyzoides**	2.50	4.39	7.54
*Lantana camara**	3.07	2.79	7.31
Hippocratea africana	2.57	2.04	6.76
Cyanthula orthacanta	5.27	2.50	4.89
*Achyranthes aspera**	2.37	1.43	4.71
Cyperus papyrus	0.00	2.14	3.25
Cyperus sp	2.10	0.39	2.72
Diospyros mespiliformis	0.70	1.00	2.61

Discussion

Effects of lantana on species richness, diversity and density at baseline

This study did not find any significant differences in species richness, seedling density and species diversity of herbaceous species and small woody plants between invaded and uninvaded areas at baseline. It is assumed that this was due to the high variability amongst the sites and the relatively lower sensitivity of the herbaceous layer which was the focus of this chapter, to disturbance compared to the woody layer. However the woody layer would take a longer time scale to investigate recovery. The dry conditions at baseline appear to have also played a role as some of the annuals had either died or gone into dormancy, with the related decrease in seedling germination during these dry periods. It was therefore concluded that the lantana infestation in the Victoria Falls World Heritage Site did not have any obvious effect on undestorey native species at baseline. However, during the rain season, species richness and seedling density were higher in uninvaded plots compared to invaded ones, pointing to the negative effect of lantana.

Effect of treatments on vegetation composition in the short and medium-term

The study did not find any significant differences in vegetation composition between baseline conditions in the short-term (July 2008) and the first monitoring in October 2008, three months after applying treatments in invaded plots. This was probably due to the absence of rainfall during the post-clearing period in the treatment plots, which hindered seedling germination and growth. The other likely reason was that most of the species in the understorey were annuals, which died off or became dormant during the dry season. Overall, it also showed that the chemical treatments had no non-target effects in the short term, as they did not significantly differ from the uprooting treatments.

In the medium-term, species richness, diversity and density of seedlings, herbs and other small woody plants did not significantly differ in treatment plots between July 2008 and September 2009. This was probably due to the high variability between the research sites. However, there was some evidence that treatment plots had higher richness, diversity and seedling density than the invaded control by the end of the study in September 2009 (Fig 14-16). In view of these findings, the conclusion that the herbicides had no non-target effects is quite likely a real finding but which is very much dependant on careful application of the chemicals.

Conclusions

It must be acknowledged that the invading habit of lantana in the Victoria Falls World Heritage Site influenced the experimental design and approach of this study as experimental sites had to be located in invaded sections with large enough area to accommodate the minimum $500m^2$ of invaded plots, and an uninvaded $100m^2$ plot in proximity. Homogeneous areas of such size were rare and far between thus affecting the spatial distribution of the research sites and ultimately the quality of data collected from heterogeneous plant communities where effects of the treatment were invariably overridden by site effects. The research aimed at representing a number of different invaded areas as it would have been inappropriate to work in a secluded section of the Victoria Falls area and extrapolate the results to the larger area. The fact that sampling at both the baseline and the end of the study was undertaken in the dry season also contributed to the failure to pick up some species.

However, it was clear that irrespective of the site where the treatments were undertaken, herbicide use appeared to have no harmful consequences when used carefully for the control of lantana, particularly at a small scale as there were no discernible non-target effects between chemical treatments compared to uprooting and untreated plots, at least in the short term. It is recommended that future studies focus on areas with larger lantana expanses, in order to shed off the possible site variability which can confound the effects of treatment. The recruitment of woody plants and their chances of recovery after lantana removal should also be further investigated. Finally, in view of the fact that the treatments appear to have a similar effect in terms of adult lantana mortality, I recommend the use of uprooting which was shown to be more effective and which has the most minimal risk of non-target effects.

Appendix 1. Species found in 1m² quadrats (n=150) at five research sites during eight month sampling period between July 2008 and September, 2009. Exotic species are labelled with an asterisk.

FAMILY	SPECIES	GROWTH FORM
Acanthaceae	*Blepharis maderaspatensis* (L.) Roth	Herb
Acanthaceae	*Justicia heterocarpa* (T.) Anderson	Herb
Acanthaceae	*Barleria matopensis* (S.) Moore	Creeper
Acanthaceae	*Ruellia cordata*	Herb
Acanthaceae	*Asystasia gangetica*	Herb
Amaranthaceae	*Achyranthes aspera* L.*	Herb
Amaranthaceae	Amaranthus spinosus	Herb
Amaranthaceae	*Amaranthus hybridus* L. subsp. Hybridus*	Herb
Amaranthaceae	*Celosia trigyna* L.	Herb
Anacardiceae	*Rhus quartiniana* A.Rich. Var. zambesiensis R.Fern	Shrub
Anacardiceae	*Sclerocarya birrea* (A.Rich.) Hochst	Tree
Annonaceae	*Friesodielsia obovata* (Benth.) Verde	Shrub
Annonaceae	*Artabotrys brachypetalus* Benth.	Shrub
Anthericaceae	*Chlorophytum subpetiolatum*	Herb
Apocynaceae	*Diplorynchus condylocarpon* (Müll.Arg.)	Tree
Apocynaceae	*Carissa edulis*	Tree
Arecaceae	*Phoenix reclinata*	Tree
Arecaceae	*Hyphaene ventricosa*	Tree
Asparagaceae	*Asparagus goetz* .L.	Shrub
Asteraceae	*Solanum nigrum*	Herb
Asteraceae	*Bidens pilosa**	Herb
Asteraceae	*Conyza bonariensis**	Herb
Asteraceae	*Conyza aegyptiaca**	Herb
Asteraceae	*Ageratum conyzoides*	Herb
Asteraceae	*Sonchus sp*	Herb
Asteraceae	*Tithonia rotundifolia*	Herb
Asteraceae	*Bidens pinnata**	Herb
Asteraceae	*Tridax procumbens**	Herb
Asteraceae	*Aspillia mossambicensis*	Herb
Asteraceae	*Bidens schimperi**	Herb
Asteraceae	*Conyza sumatrensis**	Herb
Asteraceae	*Bidens spinosus**	Herb

Balanitaceae	*Balanites maughamii* Sprague	Tree
Bignoniaceae	*Kigelia africana* (Lam.) Benth.	Tree
Bignoniaceae	*Stereospermum kunthianum* Cham.	Tree
Boraginaceae	*Cordia pilosissima* Baker	Shrub
Buddlejaceae	*Nuxia obstufolia*	Tree
Burseraceae	*Commiphora pyracathoides* Engl.	Tree
Burseraceae	*Commiphora africana* (A.Rich.) Engl. var. *africana*	Tree
Caesalpiniodeae	*Bauhinia petersiana*	Tree
Capparaceae	*Boscia angustifolia* A.Rich.var. *corymbosa*(Gilg)	Tree
Capparaceae	*Cadaba termitaria* N.E. Br.	Tree
Celastraceae	*Gymonosporia senegalensis* (Lam.) Loes.	Tree
Celastraceae	*Gymonosporia obstufolia*	Tree
Celastraceae	*Hippocratea africana* (Willd.) Loes. var. *richardiana*(Cambess)	Creeper
Celastraceae	*Gymnosporia angolensis*	Tree
Clusiaceae	*Garcinia livingstonei* T.Anderson	Tree
Combretaceae	*Combretum collinum* Fresen subsp. *elponense*(Exell) Okafor	Tree
Combretaceae	*Combretum hereroense* Schinz (*C. transvaalense* Schinz)	Tree
Combretaceae	*Terminallia stenostachya* Engl.	Tree
Combretaceae	*Combretum mossambiciensis* (Klotzsch) Engl.	Shrub
Combretaceae	*Combretum imberbe* Wawra(C. truncatumn Welw. & M.A. Lawson)	Tree
Combretaceae	*Terminalia sericea* Burch.ex DC	Tree
Combretaceae	*Combretum apiculatum* Sond. subsp. *apiculatum*	Tree
Commelinaceae	*Commelina benghalensis*	Herb
Convolvulaceae	*Ipomea mauritania**	Creeper
Convolvulaceae	*Ipomea tricolor**	Creeper
Crassulaceae	*Kalaeonche lanceolata*	Herb
Cyatheaceae	*Cyanthula oriacantha*	Herb
Cyperaceae	*Cyperus papyrus*	Sedge
Cyperaceae	*Cyperus rotundifolious*	Sedge
Cyperaceae	*Kyllinga alba*	Sedge
Cyperaceae	*Micranthus congestus*	Sedge
Cyperaceae	*Cyperus esculantum*	Sedge
Cyperaceae	*Cyperus sp*	Sedge
Cyperaceae	*Kyllinga alba*	Sedge
Dioscoreaceae	*Dioscorea dumetorum*	Creeper
Ebenaceae	*Diospyros mespiliformis* Hochst. ex A.DC	Tree
Ebenaceae	*Euclea divinorum* Hiern	Tree
Ebenaceae	*Diospyros lycoides* Desf. Subsp. Sericea (Bernh.)	Tree
Erythroxylaceae	*Erythroxyleum zambesiacum*	Tree

Euphorbiacea	*Ricinus communis**	Herb
Euphorbiacea	*Tragia okanyua*	Creeper
Euphorbiacea	*Securinega verosa*	Tree
Euphorbiacea	*Acalypha ornata* Hochst. Ex. A. Rich	Shrub
Euphorbiacea	*Bridelia carthatica* Bertol. f.	Tree
Euphorbiacea	*Antidesma venosum* E.Mey .ex. Tul.	Tree
Euphorbiacea	*Phyllanthus reticulatus* Poir. var. *reticulatus*	Shrub
Euphorbiacea	*Croton menyharthii* Pax	Tree
Euphorbiacea	*Croton gratissimus* Burch	Tree
Euphorbiacea	*Euphorbia hirta**	Herb
Euphorbiacea	*Euphorbia heterophylla**	Herb
Euphorbiacea	*Chamaesyce sp*	Herb
Fabaceae-Caesalpiniodeae	*Peltophorum africanum*	Tree
Fabaceae-Caesalpiniodeae	*Colophospermum mopane* (J.Kirk ex Benth.) J. Léonard	Tree
Fabaceae-Caesalpiniodeae	*Swartzia madagascariensis*	Tree
Fabaceae-Mimosoideae	*Faidherbia albida*	Tree
Fabaceae-Papilionideae	*Dalbergia melanoxylon*	Tree
Fabaceae-Papilionideae	*Pterocarpus antunesii*	Tree
Kirkiaceae	*Kirkia acuminata* Oliv.	Tree
Lamiaceae	*Iboza riparia* (Hochst.) N.E. Br.=tetradenia riparia	Shrub
Lamiaceae	*Ocimum canum*	Herb
Leguminosea	*Vigna parkeri*	Creeper
Leguminosea	*Chamaecrista absus*	Herb
Lythraceae	*Ammania auriculata*	Herb
Malvaceae	*Abutilon angulatum* (Guill. & Perr.) Mast.	Herb
Malvaceae	*Hibiscus* sp	Shrub
Malvaceae	*Sida alba* L.	Shrub
Malvaceae	*Hibiscus calphyllus* Cav. =*H. ovalifolius*	Shrub
Malvaceae	*Hibiscus micranthus* L.f.	Shrub
Malvaceae	*Dombeya rotundifolia* (Hochst.) Planch	Tree
Malvaceae	*Triumfetta annua**	Herb
Meliacea	*Trichilia emetica* Vahl	Tree
Menispermaceae	*Cocculus hirsutus* (L.) Diels	Creeper
Mimosoideae	*Acacia polyacantha* Willd. subsp. Camplylacantha (Hochst.ex A.Rich.) Brenan	Tree
Mimosoideae	*Dichrostachys cinerea* (L.) Wight & Arn. Subsp. *africana* Brenan & Brummitt	Shrub
Mimosoideae	*Acacia nigrescens* Oliv	Tree
Mimosoideae	*Albizia harveyi* E.Fourn.	Tree

Mimosoideae	*Mimusops zeyheri*	Tree
Mimosoideae	*Acacia nilotica* (L.) Willd.ex Delile subsp. Kraussiana (Benth.) Brenan	Tree
Mimosoideae	*Acacia sieberana* DC.	Tree
Moraceae	*Ficus sycamorus* L.	Tree
Moraceae	*Ficus capensis* Thumb. = F.sur	Tree
Myrtaceae	*Syzygium cordatum* Hochst.ex C.Krauss	Tree
Oleaceae	*Jasminum fluminense* Vell	Creeper
Oxalidaceae	*Oxalis corniculata*	Herb
Papilionoideae	*Dalbergia melanoxylon* Guill. & Perr	Tree
Papilionoideae	*Lonchocarpus capassa* Rolfe = Philenoptera violacea	Tree
Papilionoideae	*Abrus precatorius* L.	Creeper
Papilionoideae	*Pterocarpus rotundifolious*	Tree
Phyllantheceae	*Phyllanthus muerellanus*	Shrub
Poaceae	*Andropogon gayanus* Kunth	Grass
Poaceae	*Oplismenus hirtellus* (L.) P.Beauv.	Grass
Poaceae	*Andropogon contortus*	Grass
Poaceae	*Panicum maximum* Jacq	Grass
Poaceae	*Eragrostis trichloflora* Coss. & Durieu	Grass
Poaceae	*Heteropogon contortus* (L.) Roem. & Schult	Grass
Poaceae	*Digitaria eriantha*	Grass
Poaceae	*Hyparrhenia spp*	Grass
Poaceae	*Cynadon dactylon*	Grass
Poaceae	*Setaria megaphylla*	Grass
Poaceae	*Setaria homonyma*	Grass
Poaceae	*Eleusine indica*	Grass
Polygonaceae	*Oxygonum sinuatum*	Grass
Pteridaceae	*Adiantum caparis-veneris*	Fern
Ranunculaceae	*Clematis brachiata* Thumb.	Creeper
Rhamnaceae	*Ziziphus sp*	Tree
Rubiaceae	*Feretia auregenescens* Stapf	Shrub
Rubiaceae	*Gardenia resiniflua* Hiern	Shrub
Rubiaceae	*Pavetta cataractarum* S. Moore	Shrub
Rubiaceae	*Gardenia obtusifolia*	Shrub
Rubiaceae	*Canthium frangula* S.Moore = *C*. *glaucum* subsp.*frangula*	Tree
Salicaceae	*Flacourtia indica* (Burm.f.) Merr	Tree
Salicaceae	*Oncoba spinosa* Forssk.	Tree
Sapindaceae	*Paullinia pinnata* L.	Creeper
Solanaceae	*Solanum seaforthianum**	Herb
Solanaceae	*Solanum nigrum**	Herb
Sparrmanniaceae	*Grewia monticola* Sond.	Tree

Sparrmanniaceae	*Grewia pyracanthoides*	Tree
Strychnaceae	*Strychnos madagascariensis* Poir.(*s.dysophlla* subsp/*engleri*(Gilg) Bruce & Lewis	Tree
Strychnaceae	*Strychnos potatorum* L.f.	Tree
Tiliaceae	*Corchorus olitorious*	Shrub
Vitaceae	*Cyphostemma schlechteri*	Creeper
Vitaceae	*Cyphostemma congesum*	Creeper

Appendix 2. A comparison of species abundance in 1m² quadrats (n=150) at five research sites between July, 2008 and September, 2009. Exotic species are labelled with an asterisk.

FAMILY	SPECIES	GROWTH FORM	SEPT 2008	SEPT 2009
Acanthaceae	*Barleria matopensis* (S.) Moore	Creeper	27	1
Acanthaceae	*Ruellia cordata*	Herb	9	2
Acanthaceae	*Crabbea velutina*	Herb	1	0
Acanthaceae	*Blepharis maderaspatensis*	Herb	0	34
Acanthaceae	*Asystasia gangetica*	Herb	0	2
Amaranthaceae	*Amaranthus hybridus* L. subsp. hybridus	Herb	6	29
Amaranthaceae	*Achyranthes aspera* L.*	Herb	71	40
Annonaceae	*Friesodielsia obovata* (Benth.) Verde	Tree	9	7
Annonaceae	*Artabotrys brachypetalus* Benth.	Shrub	0	3
Arecaceae	*Phoenix reclinata*	Palm	2	0
Asteraceae	*Conyza aegyptiaca*	Herb	35	3
Asteraceae	*Bidens pilosa**	Herb	0	15
Asteraceae	*Ageratum conyzoides**	Herb	75	123
Asteraceae	*Tithonia rotundifolia**	Herb	0	1
Asteraceae	*Tridax procumbens**	Herb	0	6
Asteraceae	*Bidens schimperi**	Herb	0	12
Asteraceae	*Bidens spinosus**	Herb	0	23
Buddlejaceae	*Nuxia obstufolia*	Tree	1	0
Celastraceae	*Hippocratea africana* (Willd.) Loes. var. richardiana(Cambess	Creeper	77	57
Celastraceae	*Gymonosporia angolensis*	Tree	3	0
Celastraceae	*Gymonosporia senegalensis* (Lam.) Loes.	Tree	8	2
Clusiaceae	*Garcinia livingstonei* T.Anderson	Tree	8	2

Combretaceae	*Terminalia stenostachya*	Tree	1	1
Combretaceae	*Combretum collinum* Fresen subsp. elponense(Exell) Okafor	Tree	0	1
Commelinaceae	*Commelina forskaolii*	Herb	31	20
Curcubitaceae	*Momordica albassimina*	Herb	1	0
Cyatheaceae	*Cyathula orianatha*	Herb	158	70
Cyperaceae	*Kyllinga alba*	Sedge	29	0
Cyperaceae	*Cyperus papyrus*	Sedge	0	60
Cyperaceae	*Cyperus* sp	Sedge	63	11
Ebenaceae	*Diospyros mespiliformis* Hochst. ex A.DC	Tree	21	28
Ebenaceae	*Diospyros lycoides*	Tree	2	6
Ebenaceae	*Euclea divinorum* Hiern	Tree	0	1
Euphorbiaceae	*Acalypha ornata* Hochst. Ex. A. Rich	Herb	1	5
Euphorbiaceae	*Securinega verosa*	Tree	3	7
Euphorbiaceae	*Phyllanthus muerellanus*	Shrub	1	0
Euphorbiaceae	*Tragia okanyua*	Creeper	0	3
Euphorbiaceae	*Croton gratissimus* Burch	Tree	0	3
Euphorbiaceae	*Ricinus communis**	Shrub	0	2
Euphorbiaceae	*Euphorbia hirta*	Herb	0	14
Fabaceae-Mimosoideae	*Acacia polyacantha* Willd. subsp. Camplylacantha (Hochst.ex A.Rich.) Brenan	Tree	1	0
Lamiaceae	*Ocimum* sp	Herb	0	4
Leguminosae	*Vigna parkeri*	Creeper	24	0
Malvaceae	*Sida alba* L.	Shrub	11	23
Malvaceae	*Hibiscus calphyllus* Cav. =H. ovalifolius	Shrub	6	4
Malvaceae	*Abutilon angulatum* (Guill. & Perr.) Mast.	Herb	1	15
Malvaceae	*Hibiscus micranthus* L.f.	Shrub	2	30
Malvaceae	*Hibiscus filipendula*	Shrub	0	1

Malvaceae	*Triumfetta annua**	Herb	12	0
Menispermaceae	*Cocculus hirsutus* (L.) Diels	Creeper	15	9
Mimosoideae	*Acacia schweinfurthii*	Shrub	9	0
Mimosoideae	*Dichrostachys cinerea*	Shrub	0	1
Mimosoideae	*Mimusops zeyheri*	Tree	7	50
Olacaceae	*Ximenia americana*	Tree	1	5
Oleaceae	*Jasminum fluminense* Vell	Creeper	145	48
Papilionoideae	*Abrus precatorius* L.	Creeper	1	7
Papilionoideae	*Lonchocarpus capassa* Rolfe = Philenoptera violacea	Tree	17	4
Papilionoideae	*Dalbergia melanoxylon*	Tree	2	13
Papilionoideae	*Lonchocarpus nelsii*	Tree	0	6
Phyllanthaceae	*Phyllanthus reticulatus* Poir. var. reticulatus	Shrub	4	1
Poaceae	*Cynadon dactylon*	Grass	13	22
Poaceae	*Andropogon gayanus* Kunth	Grass	0	3
Poaceae	*Oplismenus hirtellus* (L.) P.Beauv.	Grass	197	278
Poaceae	*Setaria megaphylla*	Grass	1	63
Poaceae	*Hypharrenia* sp	Grass	1	0
Polygonaceae	*Oxygonum sinuatum*	Herb	2	3
Pteridaceae	*Adiantum caparis-veneris*	Fern	17	0
Rubiaceae	*Feretia auregenescens* Stapf	Tree	1	2
Saliacaceae	*Flacourtia indica* (Burm.f.) Merr	Tree	6	1
Saliacaceae	*Oncoba spinosa* Forssk.	Tree	6	0
Solanaceae	*Solanum seaforthianum**	Creeper	27	3
Solanaceae	*Solanum nigrum**	Herb	4	9
Verbenaceae	*Lantana camara**	Shrub	92	78
Vitaceae	*Cyphostemma schelecteri*	Creeper	6	0
Vitaceae	*Cyphostemma congesum*	Creeper	1	0
Rubiaceae	*Tarrena litoralis*	Shrub	1	1

CHAPTER 5

THE POTENTIAL OF NATIVE SEED BANKS AND SEED RAIN IN FACILITATING VEGETATION RECOVERY IN INVADED AREAS OF THE VICTORIA FALLS WORLD HERITAGE SITE

Introduction

Riparian ecosystems are highly vulnerable to invasion by alien plants (Hood and Naiman, 2000; Tickner *et al*., 2001; Galatowitsch and Richardson, 2005; Richardson and van Wilgen, 2004; Holmes *et al*., 2005), which negatively affect soil seed banks, seed rain and ultimately floristic composition, richness, abundance and species diversity in invaded areas (Richardson *et al*., 1997; Holmes *et al*., 2005). In response to this threat, a number of efforts have been made in several countries worldwide, including Australia, South Africa and Zambia, to clear invasive alien plants in riparian areas (Groves, 1989; Richardson *et al*., 1989; ECZ, 2004). Concerted efforts have also been made to control other invasions in riparian areas such as the invasive Salt Cedar, *Tamarix* spp in several riparian and wetland habitats of New Mexico and Texas in the USA (Brock, 1994) using mechanical and chemical methods, with varying success (Brock, 1994).

One of the most common ways of addressing invasive alien species proliferation has been mass clearing in riparian areas, with the aim of reducing and ultimately reversing the negative impacts they occasion (Richardson *et al*., 1997). Embedded in the design of such removal programmes is the assumption that indigenous ecosystems will recover naturally after removal of target invasive species (Fourie, 2008). However, in many cases vegetation resembling the pre-invasion structure and composition does not recover naturally, especially in previously heavily invaded systems, often leading to further degradation through soil erosion and/or reinvasion (Holmes, 2001).

There is need to therefore understand the processes influencing diversity levels and the pathways by which plant species colonize sites to successfully restore plant species diversity in degraded riparian areas (Richter and Stromberg, 2005). In most cases biotic manipulations alone such as the removal of invasive species may suffice for the potential restoration of riparian zones that are patchily invaded, or have only recently become densely invaded by alien plants, to their historic species composition (Holmes and Richardson, 1999). While downstream dispersal of vegetative propagules or seeds by water from intact riparian vegetation patches is one important pathway in-situ, soil-stored seed banks and seed dispersal by wind or animal vectors from adjacent terrestrial vegetation are also important potential sources of seed (Johansson *et al*., 1996; Imbert and Lefevre, 2003), though in many regions, the relative importance of seed bank and seed dispersal for recruitment in riparian ecosystems is poorly known and little attention has been paid to the subject (Richardson *et al*., 2007). In addition, there are usually gaps in the knowledge of what the initial species composition of invaded sites was and reference systems for defining restoration goals are rare throughout the world (Rosgen, 1994; Prins *et al*., 2005). In light of this, the potential role of soil-stored seed banks and seed rain in disturbed natural ecosystems is discussed further.

Seed banks

The soil seed bank refers to a reservoir of viable seeds accumulated in the soil which has the potential to germinate and contribute to local processes of vegetation regeneration (Stoner and Henry, undated). It is one of the main factors that influence the recovery of natural vegetation in riparian areas and its persistence is of great importance in facilitating recovery of ecosystems after clearance of invasive alien vegetation (Holmes and Cowling, 1997). It has been established that natural forest regeneration after a disturbance in many vegetation types depends to a large extent on the soil seed bank (Holmes and Marais, 2000; Holmes and Newton, 2004; Sakai *et al*., 2005). As a result, the soil seed bank, and the long-lived species in the seed bank in particular, provide a buffer against environmental variability by providing new seedlings to re-establish native communities after disturbances (Hyatt and Casper, 2000). Soil seed banks can provide colonizing species that will ultimately restore degraded ecosystems or accelerate forest succession (Luzuriaga *et al*., 2005).

The seed bank is dependent on seed production and composition of the seed sources, which in turn are comprised of current and previous vegetation. When riparian ecosystems are densely invaded, there is a rapid reduction of understorey cover and seed production, and the ecosystems come to rely heavily on the remaining soil seed bank for recovery. Since seed banks are reservoirs of plant propagules (Clemente *et al*., 2007) it is normally expected that they should contribute to vegetation recovery after disturbance such as plant invasion (Holmes, 2001; Goodson *et al*., 2001; Holmes and Newton, 2004; Sakai *et al*., 2005).

The seed bank in the soil of an ecosystem provides key information as to what species may have existed in the standing vegetation of the past and/or represents a pool of regenerative potential. Soil seed banks are important for maintenance of the ecological and genetic diversity of populations and communities (Thompson and Grime, 1979) and in ensuring community regeneration following disturbance (Goodson *et al*., 2001). Previous studies in rainforests have also shown that seed banks contribute to recruitment of some early successional tropical species (Cheke *et al*., 1979). Therefore the study of the relationships between seed banks and standing vegetation has become a topical issue for numerous reasons, including to establish the possible success of restoration (Leck, 2003), to ameliorate the effects of disturbances (Goodson *et al*., 2001), and for the development of management techniques for degraded areas (Kebrom and Tesfaye, 2000).

Since the main variable measured when studying seed bank-above ground vegetation relationships is floristic similarity, we can derive further insight into seed bank dynamics and its possible role in the rehabilitation of disturbed ecosystems by understanding the similarity of species composition between a seed bank and extant vegetation and the related patterns over spatial and temporal scales (Leck and Simpson, 1987; Henderson *et al*., 1988). In a review of studies pertaining to similarities between seed bank and standing vegetation across ecosystems, Hopfensperger (2007) concluded that the relationship between seed banks and vegetation provides knowledge about the resilience of a community against disturbance, the community drivers of succession, and the potential for restoration of community diversity.

It was found that most forest studies comparing above ground vegetation composition and seed banks in tropical and temperate climates found similarity below 60% (Hopfensperger, 2007). In undisturbed habitats, there is generally low correspondence between the species present in the seed bank and those in the vegetation (Warr *et al*., 1993). However, in contrast, habitats with a high frequency of disturbance such as arable land showed similar species composition of the seed bank and the vegetation (Wilson *et al*., 1985). Other studies confirm a low representation of woody species in the persistent portion of the seed bank (Leck, 1989; Thompson *et al*., 1998; Cao *et al*., 2000) while past assessments of riparian areas have confirmed a general lack of correspondence between seed banks and above ground vegetation despite variable disturbance patterns (Leck, 1989; Andersson *et al*., 2000; Goodson *et al*., 2001, Fourie, 2008; Vosse *et al*., 2008).

Some mechanisms that have been suggested for low similarity between seed banks and above ground vegetation in forest ecosystems include large seed size and seed predation of late successional species (Yorks *et al*., 2000, Decocq *et al*., 2004). As found by Bossuyt *et al*. (2002), seed size can be a major factor responsible for the scarcity of many above ground species in seed banks, because of a common negative correlation between seed size and seed longevity. Taller plants such as trees often have a tendency of storing seed in pods hanging from trees for prolonged periods, thus effectively not adding to the soil seed bank. For example, Gashaw *et al*. (2002) found several seeds of woody species attached to pods remaining in the litter layer of an Ethiopian forest, making the seed vulnerable to predators, while also keeping them from contributing to the seed bank. In any case, some have claimed that even when large seeded late successional forest species occur on the forest floor, they are prime targets for predation by small mammals (Argaw *et al*., 1999, Yorks *et al*., 2000). Early successional /short lived species tend to have dormant seeds, which are important for regeneration as adults die; whereas longer lived species tend to have seeds that germinate without dormancy, which will then produce seeds again.

Though declines in plant diversity have been recorded in seed banks from invaded areas in the fynbos region of South Africa for instance (Holmes, 2002), and a few other studies have looked at riparian seed banks in South Africa (Fourie, 2008 and Vosse *et al*., 2008), no previous studies have looked at the effect of plant invasion on soil seed banks in riparian areas of the Zambezi River. The long standing lantana invasion of habitats within the Victoria Falls World Heritage Site which dates back to the 1950's (Victoria Falls Trust, 1962) becomes of great concern as generally seed bank potential declines with increasing invasion age. Such an invasion may potentially contribute to a dearth of seeds of desirable species in the seed banks and unfavourable environmental conditions for seed germination and seedling establishment (Shono *et al*., 2006) while also substantially limiting establishment by indigenous tree species and hampering succession in the long run.

Seed rain

Seed dispersal is an essential requirement for successful recovery of degraded habitats to occur (Mendoza *et al*., 2009). This flow of seeds dispersed into a given area is what constitutes seed rain and the basic method to sample seeds that are deposited in a given site is the use of seed traps (Stoner and Henry, undated). Documenting seed rain enables a measure of how many seeds arrive in a given site though the approach is mainly efficient for small seeds that can be very abundant. For that reason, seed traps are less efficient for documenting the dispersal of large seeds as these are much less abundant and many species have supra-annual fruiting phenology.

The process of seed dispersal involves the removal and deposition of seeds in a particular area away from parent plants and arises from the fact that over time, plants have evolved various mechanisms of seed dispersal including anemochory (wind dispersal), hydrochory (water dispersal), barochory (gravity-dispersal), autochory (self-dispersal by explosion) and zoochory (animal-dispersed). Zoochory comprises of both exozoochory, where the seeds are attached to the outside of an animal's body and endozoochory, where the seeds are swallowed and finally dispersed via defecation. Dispersal of plant propagules by animals and wind is important in riparian ecosystems (Johannson *et al*., 1996; Imbert and Lefevre, 2003) and overall, endozoochory is the most important long distance dispersal mechanism in tropical ecosystems accounting for most of canopy and sub-canopy trees which are vertebrate dispersed by mammals and birds (Stoner and Henry, undated). For example, frugivorous birds, primates and small mammals were the main means of seed arrival in seed traps (through defecation and spit seeds) followed by wind dispersal and self-dispersal by explosion or gravity-dispersal (dropping) at fruit maturity during this study. The practice of hoarding seeds in caches by rodents is unlikely to have played any major role in facilitating seed dispersal into the seed traps.

Nevertheless, not all fruits removed and ingested by animals or carried by water or wind lead to effective seed dispersal as this depends on both the quantity of seeds and the quality of dispersal. Factors such as the distance moved from the parental tree and the particular microsite the seed is finally deposited in affect the quality of dispersal while the adult composition of tree species affects the quantity of seeds. In turn this depends on successful pollination, and the flower and fruiting phenology of the given species. Habitat degradation (such as in invasion of invasive alien plants) may contribute to seed limitation by lowering the density and reproductive capacity of parent trees and by altering dispersal patterns of frugivores.

For animal-dispersed species, the dispersal distance and direction from the parent plant depend upon the frugivore's or mammal's gut passage time and post feeding movements (Howe, 1982, Murray, 1988) and therefore dispersal of these species is often very patchy at small scales, with occasional long-distance dispersal occurring though most seeds are deposited locally. Bigger seed swallowed by larger animals spend more time in their gut and are generally deposited at greater distances from the mother plant, yet this varies greatly among species. However, animals that travel widely in a day will deposit seeds over a greater area than mammals that intensively exploit a smaller day range moving shorter distances and which often deposit seeds closer to the mother plant. To a large extent, the time that seed spends in the gut of an animal may enhance seed germination or actually destroy the seeds due to acids in the stomach. Defecation patterns also affect seed dispersal, in that seeds may be deposited in high-density clumps, singly or in low density clumps.

On the other hand, seed dispersal in anemochory involves the seed movement from the plant to the surface and subsequent movement of these seeds on that surface

(Bonvissuto and Busso, 2007). The relationships between wind speed and direction, height of the seed source and seed characteristics determine the position where seeds dispersed by wind shall ultimately land, whereas the suitability of the microsites where such seed arrive will determine the chances of establishment, survival and growth.

Recruitment limitation therefore has two main components which are seed/dispersal limitation (the failure of seed to arrive at all suitable sites) and establishment limitation, which arises from the reduced suitability of microsites for successful seedling establishment (Mendoza *et al*., 2009) resulting in failure of seeds and seedlings to survive and develop. For example, in intact tropical forests, dispersal or seed limitation has been reported as the primary cause of the absence of many pioneer species from most forest gaps, as well as overall constraints on species richness (Dosch, 2007). Seed limitation is usually a result of a low density of adults, reduced adult fertility and limited dispersal of seed, whereas poor germination and low survival of seed may lead to establishment limitation (Clark *et al*., 1998). In particular, large seeded plants dispersed by monkeys or terrestrial vertebrates are much more dispersal limited than small-seed ingested and dispersed by flying vertebrates (birds and bats). The latter plants produce great numbers of seeds that are defecated in a variety of sites. They may however suffer from greater establishment limitation, as the probability that small seeds germinate and develop is low compared to large seeds.

Such recognised limits to fruit dispersal contribute to the maintenance of diversity in species rich plant communities (Hubbell *et al*., 1999) which shows many species only reach few establishment sites (Dalling *et al*, 2002), and therefore less competitive species may succeed in establishing simply because superior competitors have failed to arrive at suitable microsites. This provides an opportunity for less competitive species to take their place, slowing competitive exclusion. Such a chance effect permits the possibility of poor competitors, and very rare species to be maintained in the ecosystem together with superior competitors.

Several seed addition experiments undertaken in the past have clearly shown dispersal limitation and established that seed availability may limit the population growth of many species especially in early successional natural environments. Characteristics that favour seed dispersal such as small seed size and reproductive synchrony may not favour subsequent seedling establishment, either because optimal micro-sites for the emergence or establishment of small seeded species are rare, or because seedlings are eliminated by larger seed competitors (Dalling *et al*., 2002). However, it has been proposed that the real importance of seed limitation needs to be assessed in the context of post-dispersal establishment success (Nathan and Mueller-Landau, 2000) and that natural seed rain patterns can be useful in describing spatial variations of seed dispersal during tropical secondary succession (Finegan, 1996).

In a study in the neo-tropical forests of Barro Colorado Island (BCI) in Panama, Dalling *et al*., (2002) found that seed limitation was strong for all but a few of the smallest seeded and best dispersed taxa. In most taxa, the number of seeds available was of less importance to seed limitation as compared to limited dispersal of available seeds. However, dispersal limitation was greater than source limitation (the proportion of traps that would fail to receive seeds under conditions of random dispersal) in 10 of 13 pioneer taxa. Interestingly, the highest dispersal limitation was present in animal dispersed taxa that had abundant seeds but distributed them poorly.

Aims of this study

Holmes *et al*. (2005) have suggested that the extent to which propagule supply and microsite conditions inhibit vegetation recovery is unknown. There is also very little knowledge concerning the relative importance of dispersal of vegetative propagules, dispersal of seed and soil stored seed banks in vegetation dynamics, particularly after severe disturbance such as dense invasion by invasive alien plants. Since the methods adopted for lantana control in this study did not include post clearing rehabilitation work such as replanting of native plant species in the cleared areas to expedite habitat recovery, it became apparent that an assessment of the invaded and uninvaded soil-stored seed banks and the flow of seed into the invaded and uninvaded habitats (seed rain) of the Victoria Falls World Heritage Site should be undertaken. This is in view of the possibile recruitment limitations that could arise from lantana's potential degradation of invaded habitats. The floral species composition of the invaded and uninvaded seed bank and the seed rain were thus determined with an ultimate view of establishing their potential capacity to facilitate unaided post clearing vegetation recovery.

Therefore, the first aim of this part of the study was to compare seed bank composition, species richness, diversity and seed density between invaded and uninvaded plots. I hypothesized that native seed bank species richness and diversity would be higher in soils collected from uninvaded sites compared to those from invaded areas. I expected lower species richness, altered composition and reduced number of native species (or at least non-lantana) seeds and higher densities of lantana seeds in invaded plots. I also expected that the species composition of seed banks in invaded areas would be different from that in uninvaded areas, with greater representation of herbaceous early successional, short lived and transient seeded species (seed with a survival time of up to 1 year) in the invaded seed banks, higher lantana seed density and fewer climax woody species.

The second aim was to investigate the similarity in composition between the seed banks and above ground vegetation in invaded and uninvaded areas. I expected that there would be fewer species in the invaded seed banks with a greater representation of herbaceous, short lived and early successional species as compared to the uninvaded seed banks. I also expected that the seed banks would have a higher representation of early successional and small seeded species, including lantana compared to the above ground vegetation.

Thirdly, I assessed the composition of seed rain collected from seed traps located in invaded and uninvaded areas, in order to determine its likely contribution to plant community recovery after alien clearing. I expected seed rain density to be higher in uninvaded areas under native vegetation as compared to invaded areas recently cleared of lantana because of animal dispersed seed input in natural forest areas, closer proximity of adult plants and the higher availability of bird perches in compared to cleared sites. I also expected differences in native species seed density from seed traps in invaded areas and uninvaded areas with a high abundance of lantana seed in invaded plots and lower woody species in cleared areas as a result of limited seed availability.

Methods

Sampling of seedlings, herbaceous species, small woody plants and woody vegetation

In July 2008, 30 10m x 10m (100m^2) plots were demarcated for the study at five research sites across the study area (i.e. Boiling Pot, Maramba River, Rainforest, Palmgrove and ZESCO; see Chapter 2 for details). Out of these plots, 25 were invaded and 5 were uninvaded leading to 4 treatment plots, 1 invaded and 1 uninvaded control plot at each site. Vegetation sampling for seedlings, herbaceous species and small woody plants ≥30cm was undertaken in the 5 1m^2 quadrats while woody plants were sampled in the entire 100m^2 area of each of the 30 plots. Most of the seedlings, herbaceous plants, small woody plants, sedges, grasses, shrubs and trees in the plots were identified to species or genus level and recorded as the above ground vegetation. Pressed samples of any unidentified species were collected for later identification at local herbaria. This was the vegetation data used to compare the similarity of invaded and uninvaded seed banks to above ground vegetation at a later stage.

Sampling methods for seed bank

Soil samples were thereafter collected from two randomly selected 1m^2 quadrats in each of the 30 experimental plots. In total 50 soil samples were collected from invaded plots and 10 from uninvaded control plots. These 60 soil samples measuring 15cm x 15cm to a depth of 8cm (1800cm^3) were collected using a specially fabricated metal square for the purpose of investigating soil seed bank composition. The collected soil was placed into plastic bags and transported to a nursery where samples were air dried and sieved using 2mm and 4mm wire gauzes.

All seeds found in the soil were photographed and a preliminary identification of seed was attempted at this stage. Since most of the seeds could not be identified, they were all returned to the soil and introduced into plastic trays in the nursery for germination monitoring using the seedling emergence method (Roberts, 1981). The soils in the trays were spread to a thin layer measuring 2-4cm above a sterile sand medium and placed randomly under a shade cloth erected on the top and sides of wooden poles. Ten trays with sterilized sand only were introduced into the same shed at the same time to act as controls for seed contamination. The soils were watered as often as necessary to keep soil moist at all times and seedling germination observed over a period of six months (Fig 19). Species identification and counting of individuals in the trays ensued as young plants emerged. Seedlings that could not be identified immediately were transplanted into polythene pots in order to allow them to grow further and flower for identification. Seeds that were readily identifiable were counted and removed from the germination trays at the nursery. Monitoring continued until March 2009, when germination of any new species in the seed banks had ceased. Nomenclature follows Phiri (2005).

Figure 19. Herbaceous plants and a grass growing in a seed tray from a soil sample collected in the Boiling Pot (BP2/1)

Sampling methods for seed rain

Six seed-traps were established at each of the five research sites (n=30) in March 2009 to investigate seed rain. They were made of wooden poles about 1m above the ground, covered by 1m² sack material at the top. The poles were treated with wood preservative to protect them against termite attack. Three of the seed-traps were randomly placed in uninvaded areas such as the uninvaded control plot and other similarly wooded areas in the vicinity. The other three seed-traps were randomly placed in areas cleared of dense lantana invasion at each site. Seed was collected fortnightly from the seed traps for the first four weeks and once monthly thereafter. Difficulties were experienced in sustaining this sampling as troops of chacma baboon continuosly damaged the traps. Termite attacks were also rife leading to the repeated collapse of the seed traps. During the hot and dry season, the sacks would shrivel and tear due to excessive heat. This sampling was therefore discontinued after three months because it became impractical to continue servicing the seed traps each time they were damaged. After field sampling, seeds that were readily identifiable were counted and removed, while those that were not identified were counted and introduced into seed trays with sterilized soils for post germination identification at the nursery.

Data Analysis

To determine floristic composition of the soil seed banks, plants emerging from the seed bank in the nursery were identified and classified according to family, genus and species level. Seed density, species richness and Shannon diversity for the seed banks in invaded and univaded areas were calculated in PRIMER 6. I then compared the seed banks from invaded and uninvaded plots in the study area for differences in species richness, seed density and Shannon index using the Mann Whitney U test (STATISTICA 9) since my data was not normally distributed. The Mann Whitney U test is a non parametric alternative to the t-test for independent samples and assumes that the variable under consideration is measured on at least an ordinal scale. Multivariate analyses were undertaken using the community analysis package PRIMER (Clarke and Warwick, 2001). Square root transformed abundance data were used for the comparison of seed bank species composition between invaded and uninvaded plots by means of non metric multi-dimensional scaling (NMDS) and Bray Curtis similarity as a measure of how different they are, while presence/absence data was used for the comparison of similarity between invaded and uninvaded seed banks to above ground vegetation. A 2-way mantel-type Monte Carlo analysis of similarities (ANOSIM) was done with the factors invaded/uninvaded and above/below to assess the compositional differences between the seed banks of invaded and uninvaded plots and between invaded and uninvaded seed bank and above ground vegetation using a non metric multidimensional scaling ordination based on the species composition and abundance data of woody plants, herbaceous plants and grasses recorded at baseline (Appendix 1 in Chapter 4) and the species that emerged from the 60 soil seedbank samples in the nursery (Appendix 2). Main species contributing to the within group similarities as well as differences amongst the invaded and uninvaded seed banks and between the seed banks and the above ground vegetation were determined from presence-absence data using the similarity percentage analysis (SIMPER).

Estimation of seed rain

Due to the repeated destruction of the seed traps by baboons, the data collected from the seed traps was too patchy to be analyzed statistically. Therefore, I restricted the analysis to a comparison of the species composition and seed densities of captured seed between seed traps in invaded and uninvaded areas over the three months sampling period.

Results

Comparison of invaded and uninvaded seed banks

A total of 1,919 seedlings comprised of 66 species representing 27 families (see Appendix 2) emerged in the trays during the period of the study, including the invasive alien species *L. camara* (Verbenaceae), *Solanum seaforthianum* (Solanaceae), *Tithonia rotundifolia* (Astereceae) and *Ricinus communis* (Euphorbiaceae). The species were classified as trees, shrubs, creepers, herbs, grasses and sedges. In total 7 tree species germinated from the seed bank, representing about 10.6% of the species which germinated. Of these tree species, 4 were from the genus *Ficus*, while *Mimusops zeyheri, Securinega verosa* and *Carissa edulis* were the other tree species from different genera. Herbs dominated the seed bank (36.4%), followed by creepers and grasses (18.2% each). Shrubs had 13.6% representation and lastly sedges with 3% in terms of taxonomic composition. Grasses (Poaceae) dominated the seed banks with 12 species reflecting 17.9% of the total number of species, followed by the families Euphorbiaceae and Asteraceae with 7 species each (10.4% each). The third most represented families were Cyperaceae and Amaranthaceae which contributed three species each.

Sedges (Cyperaceae) exhibited the highest density in the germinating trials with 794 individuals (almost 42%) out of the total 1,919 individuals that germinated. Mainly, the sedges were only identified to family Cyperaceae level and so the counts included a whole suite of very similar species found in the study area whose seedlings are very difficult to distinguish. Other than *Cyperus papyrus* and *Cyperus rotundus*, other sedges in different genera such as *Mariscus congestus* and *Kyllinga alba* could only be identified after further growth. It was impossible to grow all 794 sedge seedlings to a sufficient size to distinguish species. The 4 other most abundant species in the seed banks after sedges were *Ageratum conyzoides* (322 seedlings), *Lantana camara* (127 seedlings), *Andropogon gayanus* (126 seedlings), and *Triumfetta annua* (95 seedlings). Out of these five species, three species including lantana are exotic to the Victoria Falls area.

All the tree species that germinated from the seed banks had very low densities in comparison to herbs and invasive plants. *Ficus capensis* and *Securinega verosa* were the most common indigenous tree species in the seed bank with four individuals, followed by *Carissa edulis* (3 individuals), while *Ficus sycamorus*, *Ficus ingens*, *Mimusops zeyheri* and *Ficus* sp were each represented by one individual. Amongst the indigenous shrub species, the most abundant were *Hibiscus callyphylus* (24 seedlings), *Acalypha ornata* (13) and *Phyllanthus reticulatus* (11).

Table 6. The ten most abundant taxa. m^{-2} emerging from the soil seed bank germination trials in seed trays (n=60) compared between seed banks from invaded and uninvaded plots. Exotic species are labelled with an asterisk.

Species	Abundance		Life form
	Invaded	Uninvaded	

*Ageratum conyzoides**	4.6	0.77	Annual herb
*Lantana camara**	2	0.12	Shrub
Cyperaceae	12.96	0.27	Sedges
Triumfetta annua	1.4	0.18	Annual herb
*Achyranthes aspera**	0.68	0.23	Perrenial herb
Andropogon gayanus	0.23	0	Grass
*Bidens pilosa**	0.28	0.02	Herb
Oplismenus hirtellus	0.05	0.6	Grass
Conyza aegyptiaca	0.62	0.07	Herb
Hibiscus callyphylus	0.38	0.02	Shrub

Effects of lantana invasion on seed banks in invaded areas

No significant differences were found in species richness, diversity and density between invaded and uninvaded seed banks using the Mann Whitney U Test. A two dimensional non metric multi dimensional scaling ordination (NMDS) showed no separation of invaded plots from the uninvaded plots (Fig. 20). The uninvaded control plot at Palmgrove research site was an outlier as it had no seed germination in the nursery and was thus removed from the analysis. An ANOSIM did not reveal a significant difference in seed bank composition between invaded and uninvaded plots. However an ANOSIM using the factor site showed a significant difference between sites (Global R=0.35, p<0.05). The ANOSIM further revealed that all the sites were significantly different from each other except Maramba River and ZESCO. An NMDS ordination showed the separation of invaded and uninvaded sites due to site influence (Fig 21).

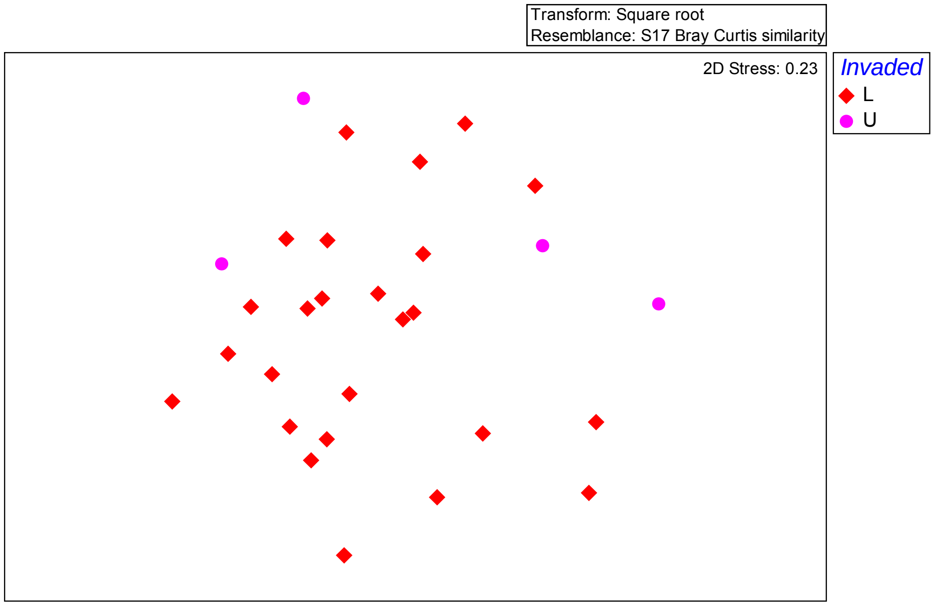

Figure 20. NMDS showing species composition in seed banks of invaded and uninvaded areas (Stress=0.23). L=Lantana Invaded Plots; U=Uninvaded Plots..

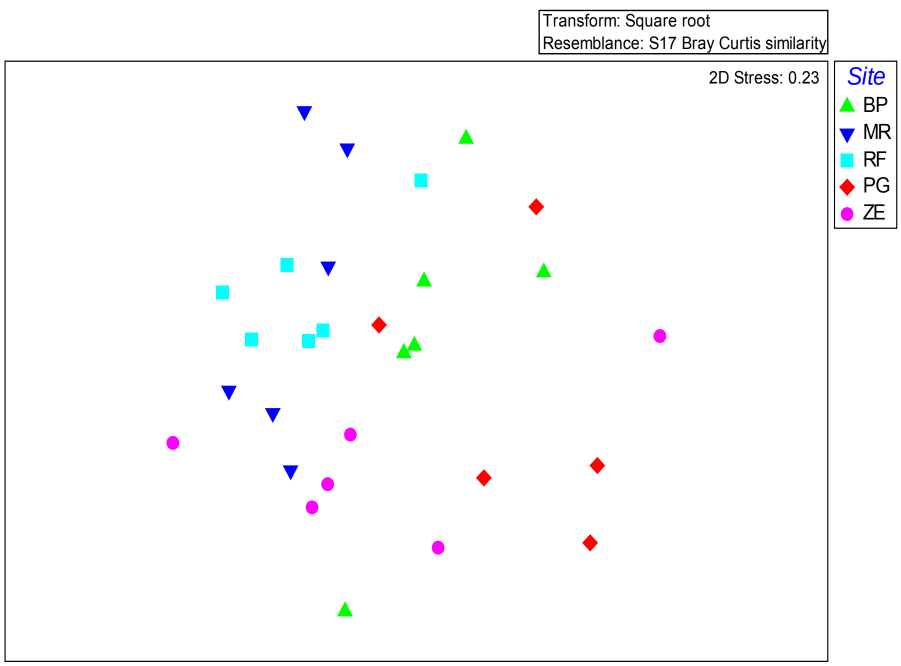

Figure 21. NMDS showing species compositional differences in seed banks from five research sites. Sites are BP=Boiling Pot, MR=Maramba River; RF=Rainforest; PG=Palmgrove and ZE=ZESCO

Comparison of invaded and uninvaded seed bank species composition to above ground vegetation

An NMDS showed differences in species composition between the invaded and uninvaded seed banks and above ground vegetation (Fig 22). A one-way ANOSIM with the factor above/below revealed that there was a significant difference between above ground vegetation and the seed bank (Global R=0.19, p<0.05).

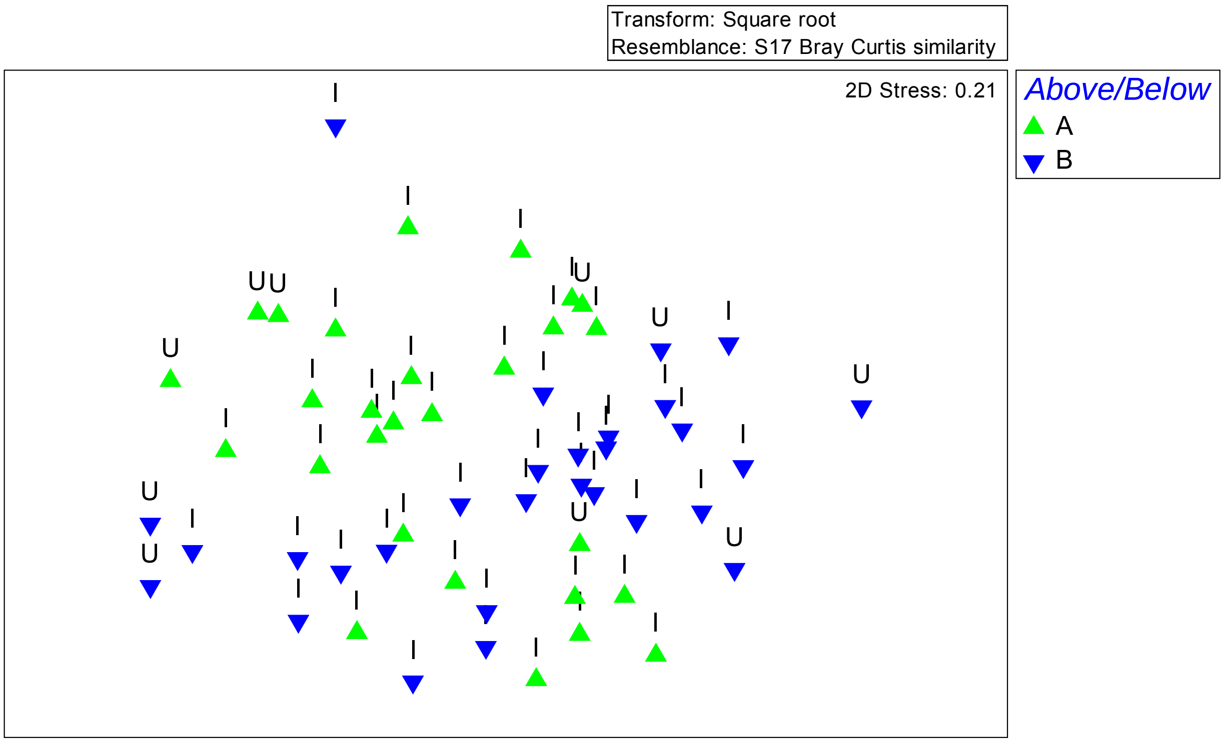

Figure 22. NMDS (Stress=0.21) showing differences in composition between invaded and uninvaded seed banks above ground vegetation. I=Invaded and U=Uninvaded.

SIMPER results showed that out of the ten species contributing most to the differences between the seed banks and above ground vegetation; five were more abundant in the seed bank in comparison to above ground. As expected, exotic species were more abundant in the seed bank in comparison to above ground, except in the case of *Achyranthes aspera* which was more abundant above ground. Two of the recorded exotic species in the seed banks were herbaceous while the third was a shrub. On the other hand, above ground vegetation had a higher abundance of native species such as the creepers *Jasminum fluminense* and *Hippocratea africana*, and the trees *Diospyros* *mespiliformis* and *Lonchocarpus capassa*. This was completely different form the seed banks which had no tree species at all. One exotic species *Achyranthes aspera* was more abundant above ground compared to the seed bank (Table 5).

Table 7. Ten species contributing most to dissimilarity between above and below ground vegetation based on presence-absence data (SIMPER results). Exotic species are labelled with an asterisk

Taxa	% Contribution	More abundant	
		Above ground	Below ground
*Ageratum conyzoides**	5.26		x
*Lantana camara**	4.51		x
Jasminum fluminense	4.49	x	
Cyperus sp	4.49		x
*Achyranthes aspera**	3.56	x	
Hippocratea africana	3.35	x	
Diospyros mespiliformis	3.14	x	
Conyza aegyptiaca	2.51		x
Lonchocarpus capassa	2.16	x	
Andropogon gayanus	2.13		x

Composition of seed rain in cleared and uncleared areas

A total of 27 species numbering 623 individual seeds were collected from the seed traps in invaded and uninvaded areas over an intermittent period of three months. Among the ten most abundant species in the seed rain, lantana had the highest arrival rate of 19.2. seeds.m^{-2} mo^{-1} from the thirty seed traps in invaded and uninvaded areas, followed by *Phoenix reclinata* with 16.5. seeds.m^{-2} mo^{-1}, *Ricinus communis* (12.2 seeds.m^{-2} mo^{-1}), *Flacourtia indica* with 10.2 seeds.m^{-2} mo^{-1}, and *Terminalia stenostachya* with 9.5 seeds.m^{-2} mo^{-1}. The other abundant species were *Clematis brachiata*, *Terminalia sericea, Frielsodiesia obovata, Mimusops zeyheri* and *Panicum maximum*.

Among these ten most abundant species in the seed rain were six tree species characteristic of the riparian zones of the Zambezi around the Victoria Falls area and four of these tree species were more abundant in uninvaded areas compared to invaded areas. The two exotic weed species in the seed rain (Lantana and *Ricinus* *communis*) were by far more abundant in seed traps located in invaded areas as compared to those in uninvaded areas. The remaining seeds of other species collected in the seed traps were too patchy for analysis (See Table 4 and Appendix 3).

Figure 23. Seed collected from seed traps in uninvaded areas in the rainforest (top left) showing fruit of *Mimusops zeyheri*, *Frielsodiesia obovata*, *Clematis brachiata* and others compared to seed collected from seed traps in the invaded areas (top right). Clumped lantana seed from a seed trap in an invaded area of the Boiling Pot (bottom left) compared to another seed trap without lantana seed in an invaded plot at the same monitoring period. May 2009.

Table 8. Ten most abundant species in the seed traps (n=30) in invaded and uninvaded areas in the Victoria Falls World Heritage Site over a period of three months. Exotic species are labelled with an asterisk.

Species	Family	No.seeds	Seeds.$m^{-2}.mo^{-1}$	Abundance in Invaded	Abundance in Uninvaded	Dispersal agent
Lantana camara *	Verbanaceae	113	19.2	103	13	Bird
Phoenix reclinata	Arecaceae	99	16.5	9	90	Bird,Mammals
*Ricinus communis**	Euphorbiaceae	73	12.2	73	0	Explosive
Flacourtia indica	Salicaceae	61	10.2	34	27	Bird, Mammals
Terminalia stenostachya	Combretaceae	57	9.5	0	57	Wind
Clematis brachiata	Ranunculaceae	43	7.2	0	43	Wind
Terminalia sericea	Combretaceae	37	6.2	37	0	Wind
Frielsodiesia obovata	Annonaceae	29	4.8	0	57	Bird, Mammals
Mimusops zeyheri	Sapotaceae	18	3	1	17	Bird, Mammals
Panicum maximum	Poaceae	15	2.5	15	0	Birds

Discussion

Effect of lantana on species richness, diversity and abundance in invaded and uninvaded seedbanks.

Results from this study found that there were no significant differences in species richness, diversity and density between invaded and uninvaded seed banks, contrary to my initial predictions. However, the main taxa in the invaded seed banks were mainly weedy exotic species of herbaceous growth forms, lantana, native sedges and a few native creeper species emerging from the seed bank. Among other things, these dominant herbaceous species were more abundant in comparison to the woody plants as a result of their persistent seed banks in the soil, which tend to be small and compactly shaped, while the transient seeds of native woody species are comparatively larger, flattened or elongated and thus more susceptible to predation (Thompson, 1987; Fenner, 1993; Thompson *et al*., 1993). The success of the smaller seeds of herbaceous species could have further been enhanced by their relative ease of burial, large numbers and wider dispersal in the seed banks (Venable and Brown, 1988). Sedges (Cyperaceae) which had high abundance in the seed bank have also been implicated in the rapid colonization of disturbed habitats as they produce persistent and dormant seed which is highly adapted to exploitation of infrequent occurrence of gaps (Leck and Schutz, 2005).

The other possible reason for the lower abundance of native woody plants could be due to the fact that seed bank density and species richness decreases with successional maturity of the vegetation (Thompson, 1978; Nakagoshi 1984-85) and thus late successional communities, such as climax forests, often have relatively few viable buried seeds (Donelan and Thompson, 1980; Galatowitsch and Richardson, 2005).

This finding confirmed the prediction that invaded seed banks would be dominated by early successional, short lived species tolerant of lantana (and lantana itself), which tend to have high seed reproduction and higher seed density of typically seed bank forming species. Overall, the findings clearly showed that very few of the characteristic riparian or forest species of the area were represented in the invaded and uninvaded seed bank, consistent with what was found in riparian areas of the South African fynbos (Fourie, 2008; Vosse *et al*., 2008). It is also evident that the invaded seed banks in the riparian areas of the Victoria Falls World Heritage Site are dominated by several weedy herbs and native sedges, and lesser abundances of native creepers and grasses with trees having much lower germination densities.

Similarity of seed bank species composition to above ground vegetation

While no significant differences were found in species richness, diversity and seed density in invaded and uninvaded areas, there was a significant difference in species composition between the invaded and uninvaded seed banks and the above ground vegetation at all of the five sites from where soil samples were collected. The seed banks had more seedlings of the exotic *Ageratum conyzoides*, lantana, the grass *Andropogon gayanus*, sedges and the weedy *Conyza aegyptiaca* germinating while the above ground vegetation had one exotic herb species, two native creepers and the two trees *Diospyros mespiliformis* and *Lonchorcapus capassa* in comparison. However, interestingly, it appeared that these exotic species were not easily able to colonize adjacent uninvaded areas, which had dense upper forest cover and native grasses as undergrowth. Other than *Achyranthes aspera*, no other exotic species were found among the main species in above ground vegetation. Two native creepers, *Jasminum fluminense* and *Hippocratea africana* were more prevalent in the seed banks compared to the above ground vegetation. Most likely this was due to the fact that prior to the clearing of lantana, these two species were found in dense lantana infestations growing on lantana thickets for support. It is therefore assumed that seed deposits took place during that period, giving rise to their germination from invaded seed banks. On the other hand, native species with high seed production and persistent seed banks such as *Triumfetta annua*, *Conyza aegyptiaca* and the sedges (Cyperaceae) were present in the invaded seed banks, mainly due to efficient seed dispersal by wind and or other vectors.

The higher percentage of herbaceous species, exotic species and the dearth of woody plants in the seed bank compared to the above ground vegetation found in this study was expected. Other studies confirm a low representation of woody species in the persistent portion of the seed bank (Leck, 1989; Thompson *et al*., 1998; Cao *et al*., 2000) while past assessments of riparian areas have confirmed a general lack of correspondence between seed banks and above ground vegetation despite variable disturbance patterns (Leck, 1989; Andersson *et al*., 2000; Goodson *et al*., 2001, Fourie, 2008; Vosse *et al.*, 2008). Overall, the differences between invaded and uninvaded seed banks and above ground vegetation may also be a factor of the reproductive of strategies, as most of the herbaceous species recorded here are known to produce many short lived seeds, while the woody species produce very few.

Some other mechanisms that have been isolated for the cause of low similarity between seed banks and above ground vegetation in forest ecosystems include large seed size and seed predation of late successional species (Yorks *et al*., 2000, Decocq *et al*., 2004). It has been suggested that seed size can be a major factor responsible for the scarcity of many above ground species in seed banks, because of a common negative correlation between seed size and seed longevity (Bossuyt *et al*. 2002).

Seed rain

The findings of this study show that lantana had the highest rate of seed rain in invaded areas (Fig 23). However, this was recorded only at the Boiling Pot and was not the case at all the other sites. As expected, the other invasive species in the seed rain *Ricinus communis* was also more abundant in seed traps located in invaded areas as compared to those in uninvaded areas, suggesting a clumped dispersal pattern. While lantana is mainly dispersed by birds and to a lesser degree by primates, *Ricinus communis* is mainly dispersed by autochory. Therefore the use of the seed traps as perch by frugivorous birds and the proximity of seed sources for both species could have contributed to their high arrival rate in seed traps in invaded areas. While these two species also contributed to the seed rain in uninvaded areas, they were comparatively less abundant.

As expected, the six tree species found among the ten most abundant species (Table 4) in seed traps from invaded and uninvaded areas mostly occurred in seed traps from uninvaded areas, with the exotic invasives being more common in the invaded areas. Two of the native species found in the seed traps in uninvaded areas (*Clematis brachiata* and *Terminalia stenostachya*) are wind dispersed while another species in the same genus, *Terminalia sericea* was found to be more abundant in seed traps from invaded areas, suggesting no clear pattern in the distribution of wind dispersed seed between seed traps located in invaded and uninvaded areas.

However, five of the native species found in seed traps in this study were animal dispersed species under forest cover, indicating the importance of animals as dispersal agents in areas with canopy cover, where wind dispersal may be limited by altered wind speed due to the vegetation structure and density of surrounding forest patches (Greene and Johnson, 1996). Overall, while there appeared to be no clear evidence of seed/dispersal limitation, it was not possible to predict if there would be no establishment limitation considering the degraded nature of the forest gaps recently cleared of lantana. Since species establishment incorporates germination, seedling establishment, and growth to maturity, it is essential that specific microsites with optimal soil moisture levels, light conditions, temperature fluctuations, or other environmental conditions (e.g fire) are available for the seeds of a particular species to germinate, failure to which these requirements can limit the distribution of a species in the landscape (Holmes *et al*, 2005).

From the above findings, it appears seed immigration and deposition to the seed bank from nearby forest patches has a high potential in the natural forest ecosystems. Despite the continuous disruption from primates and the relatively few, small seed traps representing a very low proportion of the plot area, the amount of seed captured over an intermittent period of three months in the 30 seed traps has shown that seed rain has the potential to effectively enrich the seed bank in the Victoria Falls World Heritage Site, with a continued input of woody species into both invaded and uninvaded areas.

The other interesting fact is that other than lantana and *Ricinus communis*, the other eight of the ten most abundant species in the seed rain were indigenous species, including six trees. This is a complete contrast to the seed banks, which were dominated by exotic weedy herbaceous and woody shrubs. The high numbers of lantana seed arriving in the sampled habitats show that if lantana is not cleared at a larger scale, constant reinvasion will occur. Since the invaded patches in the Victoria Falls area are relatively localised, seed dispersal from nearby sources can be of more benefit compared to habitats where the patches of plant invaders are extensive therefore reducing seed rain as seeds have to travel longer distances to the cleared areas. Therefore, seed rain can be an important driver in ecosystem recovery of cleared areas in the Victoria Falls as in almost all cases; lantana invades open forest gaps surrounded by mature forest, which has potential for long-term propagule supply into cleared areas.

Conclusions

This section of the study found that there were no significant differences in species richness, diversity and density between the invaded and uninvaded seed banks. This could be due to the fact that uninvaded plots used for the comparison were too few compared to the invaded plots. The high number of exotic seeds in the seed bank especially that of lantana, suggest that the potential of lantana reinvasion is very high. While it was found that the seed bank was mainly a source of early successional species as expected, seed rain looks like a promising source of later successional species as long as the lantana infestation is not too extensive.

Appendix 3. A list of species found in the seed bank using the seedling emergence method in seed trays (n=60) during the period October 2008-March 2009. Exotic species are labelled by an asterisk.

FAMILY	SPECIES	LIFE FORM
Acanthaceae	*Ruellia cordata*	Herb
Acanthaceae	*Asystasia* sp	Herb
Amaranthaceae	*Achyranthes aspera*	Herb
Amaranthaceae	*Cyathula orthacantha (Hochst. ex Asch.) Schinz*	Herb
Amaranthaceae	*Amaranthus hybridus L. subsp. Hybridus*	Herb
Anacardiceae	*Pupalia lappacea (L.) Juss.*	Herb
Annonaceae	*Artabotrys brachypetalus Benth*	Shrub
Anthericaceae	*Chlorophytum subpetiolatum (Baker) kativu*	Herb
Apocynaceae	*Carissa edulis Vahl*	Tree
Apocynaceae	*Riocreuxia profusa N.E.Br*	Creeper
Asparagaceae	*Asparagus spp*	Shrub
Asteraceae	*Bidens pilosa**	Herb
Asteraceae	*Ageratum conyzoides* L.*	Herb
Asteraceae	*Tithonia rotundifolia* (Mill.) S.F. Blake**	Herb
Asteraceae	*Conyza aegyptiaca (L.) Aiton*	Herb
Asteraceae	*Conyza bonariensis* (L.) Crong*	Herb
Asteraceae	*Aspilia mossambicensis (Oliv.) Wild*	Herb
Asteraceae	*Bidens schimperi**	Herb
Commelinaceae	*Commelina forskaolii Vahl*	Herb
Convolvulaceae	*Ipomoea mauritiana Jacq*	Creeper
Convolvulaceae	*Ipomoea tricolor**	Creeper
Cyperaceae	*Cyperus sp*	Sedge
Cyperaceae	*Mariscus congestus*	Grass
Cyperaceae	*Cyperus rotundus*	Sedge
Euphorbiaceae	*Euphorbia hirta*	Herb
Euphorbiaceae	*Phyllanthus reticulatus Poir.var. reticulatus*	Shrub
Euphorbiaceae	*Euphorbia heterophylla*	Herb

Euphorbiaceae	*Securinega virosa (Roxb. Ex Wild.)*	Tree
Euphorbiaceae	*Chamaesyce sp*	Herb
Euphorbiaceae	*Ricinus communis* L.*	Shrub
Euphorbiaceae	*Acalypha fimbriata Schumach. and Thonn.*	Herb
Fabaceae-Papilionoideae	*Vigna parkeri baker subsp. Maranguensis*	Creeper
Lamiaceae	*Ocimum sp*	Herb
Malvaceae	*Triumfetta annua L*	Herb
Malvaceae	*Hibiscus ovalifolius (Forssk.) Vahl*	Shrub
Malvaceae	*Sida alba L.*	Shrub
Malvaceae	*Corchorus olitorious L.*	Shrub
Malvaceae	*Hibiscus micranthus L.f.*	Shrub
Malvaceae	*Abutilon angulatum (Guill. & Perr.)Koehne*	Herb
Moraceae	*Ficus capensis Thunb = F. sur*	Tree
Moraceae	*Ficus sp*	Tree
Moraceae	*Ficus ingens (Mig.)Mig*	Tree
Moraceae	*Ficus sycamorus L*	Tree
Oleaceae	*Jasminum fluminense Vell*	Creeper
Oxalidaceae	*Biophytum abbysinicum Steud. Ex A. Rich*	Herb
Papilionoideae (Faboideae)	*Abrus precatorious L.*	Creeper
Passifloraceae	*Adenia gummifera (Harv.) Harms*	Creeper
Poaceae	*Andropogon gayanus Kunth*	Grass
Poaceae	*Heteropogom contortus*	Grass
Poaceae	*Oplismenus hirtellus L.P.Beauv*	Grass
Poaceae (Graminae)	*Eleusine indica(L.) Gaertn*	Grass
Poaceae (Graminae)	*Chloris gayana Kunth*	Grass
Poaceae (Graminae)	*Chlorix pycnothrix*	Grass
Poaceae (Graminae)	*Setaria megaphylla*	Grass
Poaceae (Graminae)	*Sporobolus panicoides*	Grass
Poaceae (Graminae)	*Panicum maximum*	Grass
Poaceae (Graminae)	*Eragrotis aspera*	Grass
Poaceae (Graminae)	*Digitaria eriantha*	Grass
Ranunculaceae	*Clematis brachiata Thunb*	Creeper

Sapotaceae	*Mimusops zeyheri Sond*	Tree
Solanaceae	*Solanum seaforthianum**	Creeper
Solanaceae	*Solanum nigrum*	Herb
Turneraceae	*Tricliceras longepedunculatum (Mast.) R. Fern*	Creeper
Verbaneceae	*Lantana camara L*	Shrub
Vitaceae	*Cyphosterma schlechteri Gilg & Brandt Desc.ex Wild and R.B. Drumm*	Creeper
Vitaceae	*Cyphosterma congestum (Baker) Desc.ex Wild and R.B. Drumm*	Creeper

Appendix 4. Seed rain species composition and abundance as collected from seed traps (n=30) found in invaded and uninvaded areas in the study site. Exotic species are labelled by an asterisk.

Family	Species	Abundance
Acanthaceae	*Ruellia cordata* Thunb	3
Annonaceae	*Friesodielsia obovata* (Benth.) Verdc	29
Apocynaceae	*Carrisa edulis* Vahl	2
Arecaceae	*Phoenix reclinata* Jacq	99
Asteraceae	*Conyza aegyptiaca* (L) Aiton.	1
Asteraceae	*Bidens pilosa** L.	2
Celastraceae	*Gymnosporia senegalensis* (Lam.) Loes	4
Combretaceae	*Combretum hereroense* Schinz	9
Combretaceae	*Terminallia stenostachya* Engl.	57
Combretaceae	*Terminallia sericea Burch. Ex DC*	37
Convolvulaceae	*Ipomoea tricolor**	1
Ebeneceae	*Diospyros quiloensis* (Hiern.) F. White	2
Ebeneceae	*Diospyros mespiliformis*	6
Euphorbiaceae	*Securinega virosa* (Roxb. Ex Wild.)	1
Euphorbiaceae	*Ricinus communis** L.	73
Fabaceae-Mimosoideae	*Acacia nigrescens* Oliv.	1
Fabaceae-Mimosoideae	*Peltophorum africanum* Sond.	2
Fabaceae-Mimosoideae	*Albizia harveyi* E. Fourn.	1
Fabaceae-Papilionoidea	*Lonchocarpus capassa*	6
Malvaceae	*Triumfetta annua* L.	1
Malvaceae	*Grewia* sp	4
Meliaceae	*Trichilia emetica* Vahl.	5
Oxalidaceae	*Oxalis corniculata* L.	2
Passifloraceae	*Adenia gummifera* (Harv.) Harms	2
Poaceae	*Panicum maximum* Jacq.	15

Poaceae	*Eleusine indica* (L.) Gaertn	1
Poaceae	*Eragrostis* spp	1
Ranunculaceae	*Clematis brachiata* Thunb.	43
Salicaceae	*Oncoba spinosa* Forssk	7
Salicaceae	*Flacourtia indica (Burm.f). Merr*	61
Sapotaceae	*Mimusops zeyheri* Sond.	18
Solanaceae	*Solanum seaforthianum**	2
Strychnaceae	*Strychnos potatorum* (S. stuhlmannii Gilg)	3
Verbaneceae	*Lantana camara* L	113
Vitaceae	*Cyphostemma schlechteri* Gilg & Brandt Desc. Ex Wild and R.B. Drumm	9

CHAPTER 6
DISCUSSION

Introduction

This study was necessitated by the long standing lantana invasion of the riparian areas in the Victoria Falls World Heritage Site which has been a concern to management authorities for well over 5 decades. It is the first study to assess the cost and effectiveness of lantana control methods and their subsequent effects on native species and natural habitats in the Victoria Falls area. It is also the first study to investigate the seed bank and seed rain potential of invaded and uninvaded areas in terms of unaided post-clearing recovery of invaded ecosystems in Zambia. Though studies assessing the effectiveness of physical, chemical and even biological control methods of lantana have been undertaken before in Zambia (Anderson, 1963; Abell, 1972-73; Lottyniemi, 1982; Selander and Chomba, 1989; NHCC, 1993) and most recently Lwando-Tembo (2008) who investigated the impact of lantana groves on species diversity in adjacent areas; none of these other studies assessed the cost efficiency of the adopted control methods, nor the potential effects of lantana control on vegetation composition in invaded areas. Because most of these studies were undertaken in forest plantations on the Copperbelt and Southern Province, except Lwando-Tembo (2008) who worked at a private game ranch in Lusaka, potential non-target effects of the chemicals used and the accompanying response of native species were not investigated.

Elsewhere in the world, several studies on the treatment and impacts of lantana have been undertaken using various methods (Killilea, 1983 a-b; Acchireddy and Singh, 1984; Macdonald and Jarman, 1985; Graff, 1986-87; Motooka *et al*.; 2000; Gooden *et al*., 2008; Gooden *et al*., 2009; Love *et al*., 2009). However, none of them have investigated all the parameters explored in this study at once, though Erasmus and Clayton (1992) and Erasmus *et al*. (1993) did review the costs and efficiency of lantana control in Kwazulu-Natal and in the Kruger National Park, South Africa. This study therefore presents a multi faceted perspective of lantana control and management, which can be used in protected areas under lantana invasion in other parts of the world. This study had three main aims which are discussed in this chapter, reporting the key findings and recommendations arising from the study.

Effectiveness and cost of mechanical and chemical treatments in the control of lantana

This study showed that lantana can be adequately controlled using mechanical and chemical treatments. This is because proper application of phytotoxic and non specific chemicals should inevitably kill any target weed. The level of active ingredient in the formulation as well as the timing of the application can contribute to herbicide efficacy. In mechanical treatments, careful uprooting of lantana with complete removal of its rootstock, all lateral roots and stems should equally result into mortality, as was evidenced in this study. However there is a chance of re-sprouting if any part of the plant is left in the ground and Love *et al*., (2009) has proposed a method to ensure complete removal of lantana rootstock and thus ensure its death. Therefore, both mechanical and chemical methods provided good control of lantana without exception, with uprooting recording the highest mean adult mortality. High lantana mortality has been demonstrated elsewhere in various trials undertaken with a range of herbicides (and herbicide formulations) as well as mechanical control (Macdonald and Jarman, 1985; Selander and Chomba, 1989; Erasmus and Clayton, 1992; Erasmus *et al*., 1993; Motooka *et al*., 2000; Love *et al*., 2009) using different units for the assessment of success.

There was a high regeneration of lantana seedlings across all experimental plots irrespective of the treatments. The high seedling density post-clearing appeared to be a result of clearing the dense lantana biomass that characterised the invaded areas. For example, uprooting with mattocks and pick-axes loosens the soil and scarifies the seed around lantana clumps and readily exposes buried seed to light and moisture. Since light and moisture are a pre-requisite for successful lantana seed germination, seedling emergence is promoted in this way.

The differences in the cost of treatments were mainly due to the use or non use of chemicals and the type of application equipment needed which tended to raise the start up costs. Uprooting was therefore primarily cheaper than all the other treatments because no chemicals were used in this treatment and also because lantana was uprooted at an appropriate time of the year when there was minimal labour input required because of the soil conditions. The low start up costs and the ready availability of the tools and equipment needed for its execution made it cheap. Despite this, it still produced the highest mean adult lantana mortality, making it the most viable option. However, initial follow-up costs were higher in uprooting, presumably due to the lantana seedlings and re-sprouting stumps that needed uprooting compared to the chemical treatments. This implies that the soil seed banks in the invaded areas have high lantana seedling density and follow-up should be taken as an integral part of the overall clearing program of lantana in the Victoria Falls World Heritage Site. Since uprooting has been recommended as the main method of lantana control in the Victoria Falls area, accompanied by uprooting follow-up, management authorities should ensure that follow-up operations after initial clearing are undertaken timeously in order to avoid regeneration and growth of lantana seedlings to a point where the effort required for uprooting them is equivalent to that of initial clear.

It is clear from the cost of the chemical treatments that lantana control using herbicides is expensive, and that in most cases the cost of treating 1ha of land, would be well above the economic value of that land, particularly where such land is of marginal value (Erasmus and Clayton, 1992; NHT, 2004). However the Victoria Falls World Heritage Site is a prime conservation area of great aesthetic beauty, biodiversity and tourism value such that any treatments of lantana are justified in order to enhance its ecosystem integrity.

Management should thus focus on implementing the two recommended methods, guided by their demonstrated suitability and efficacy, while recognising their specific limitations. Since most invasive alien control projects are resource constrained, they will favour cost effective methods that can achieve comparable results to those that are more expensive. It is expected that when uprooting and metsulfron are applied together in the Victoria Falls World Heritage Site, lantana control costs will be reasonably low, while the effectiveness of the treatments will be high. Follow-up and management activities should be sustained for as long as practically possible in order to ensure successive depletion of the seed bank, and reduced density and spread of lantana in the Victoria Falls World Heritage Site. In future, there is need for further research to determine the optimal time frame, frequency and timing of the follow-ups in cleared areas.

Effects of mechanical and chemical treatments on vegetation composition in cleared areas

The fact that the control of invasive alien plants has potential to significantly disturb natural communities if clearing activities have residual effects that lead to non-target effects on vegetation composition is widely acknowledged (Adair and Groves, 1998). However, this study found that there were no effects from the mechanical and chemical treatments on vegetation composition both at the short and medium-term scale. This was probably because of the high variability amongst the research sites where the experiments were conducted and also because the composition of the seedlings, herbaceous species and small woody plants used for the assessment did not really seem to be affected by either lantana or the treatments.

This is most likely because after invasion of an ecosystem, its vegetation composition is altered and a number of uncharacteristic species are established, diverting away from the original vegetation. When such areas are cleared, several other opportunistic species that are disturbance and stress adapted easily colonize the sites, in essence returning them to their invasion status or simply allowing some of the available understorey vegetation in the immediate vicinity into the cleared plots, particularly at the level of the herbaceous layer.

The results therefore confirmed that when appropriately utilised, chemical and mechanical control methods can be used in protected areas without undue concern for the potential of non-target effects even when they are not selective. The critical requirement is to ensure that the methods of chemical application are appropriate, accidental spillages are minimised and operatives are enlightened about the sensitive environment in which they are working in order to enhance best practice and environmental responsibility. Thus it would appear that the recommended practice of manual uprooting and use of the herbicide metsulfron for future control of lantana in the Victoria Falls area are suitable with appropriate use. Future research focusing on the phenology of native species and their response to herbicide use should be undertaken, as such effects are not easily detectable, but their good understanding can be an asset to invasive species managament in a protected ecosystem.

The potential of native seed banks and seed rain to facilitate vegetation recovery in cleared areas

There were no significant differences between invaded and uninvaded seedbanks in terms of species richness, diversity and seed density, and no significant differences in vegetation composition between invaded and uninvaded seed banks. This was most likely due to the variability amongst the sites and the relatively smaller number of uninvaded plots compared to that of invaded plots. On the other hand, the low similarity between the seed banks and above ground vegetation was largely as a result of the absence of seed of woody plant species in the seed bank, and its domination by herbaceous and exotic weeds with persistent seed bank as found in other studies elsewhere (Vosse, 2006; Fourie, 2008). The presence of exotic species in the seed banks, particularly that of lantana should be of prime concern to management authorities in the Victoria Falls World Heritage Site as it implies that lantana and other exotic weeds have substantial seed banks in the area which require further management.

The uninvaded seedbanks were largely free of exotic weeds and other invasive and alien plants except *Achyranthes aspera*. This improves the management prospects of the invasive alien plants, as efforts for control only have to focus in the cleared areas where conditions for re-infestation by lantana are highest and establishment of other ruderal species is most likely. Ongoing lantana control should therefore be the norm, accompanied by the removal of other incidental weeds such as *Ageratum conyzoides*, *Ricinus communis*, and *Solanum seaforthianum*.

In terms of the likelihood of seed dispersal aiding recovery of the degraded habitats in the Victoria Falls area, a fair amount of seed rain representing a diverse suite of life forms and species which could be important in long-term recovery of the ecosystem was observed, especially considering the limited sampling density, short temporal scale and the possible seasonal variations in propagule availability and supply which limited this study. The majority of the seeds arriving in the seed traps were either those dispersed by wind (anemochory) or those dispersed by mammals and birds through defecation, spitting or dropping (endozoochory) into the seed traps, with the future prospects of the dispersed species depending on availability of favourable microsites for establishment.

This was most likely because the areas cleared of lantana are surrounded by well developed forests which have a range of perching sites and species favoured by frugivores, primates and other small mammals, while the effect of clearing lantana patches rendered them free of mature vegetation thus allowing wind effect to transport seed. The rates of native woody species dispersed into the seed traps were high, giving these species a fair chance of establishing if they are distributed to favourable micro-sites. However the seed rain of lantana was very high and points to an urgent need for large scale lantana control. Overall, seed rain can make a substantial contribution to ecosystem recovery, as long as the fecundity of the forest patches which host dispersers and trap wind borne seeds around the lantana thickets are maintained. However, a realistic estimation of the amount of seed rain would require better data and comparisons with rates in other studies. It would also be important to develop a better understanding of the relationships between seed dispersal and different seasons in the Victoria Falls area.

Conclusion

The control of invasive alien species is a complex process which begins with recognition of the impacts of the invading species and the need for its containment. This must be guided by clear objectives for future management of the area under invasion. The methods to be used for control of invasive alien plants must be carefully selected, based on effectiveness, cost, and environmental acceptability. Control of invasive alien species is a costly enterprise calling for prudent and realistic decisions at the inception of clearing projects as this will ultimately determine their success or failure. The potential effect of the methods selected for use, particularly in protected areas, should not be in conflict with the overall objectives of the sites in which they are implemented. Accordingly, the methods recommended for use in the Victoria Falls area in this study have been assessed and found suitable when applied appropriately.

Following initial clearing, follow-up treatments using the recommended method of uprooting or use of the chemical metsulfron are required, particularly since lantana is a re-sprouting species which also has dense soil stored seed banks requiring several follow-ups. Correct utilization of follow-up treatments could allow the alien infestations to be brought under control, as this reduces the amount of seed input by new recruits and reduces the amount of seed available in the soil seed bank.

The failing of most of the previous attempts at lantana control in the Victoria Falls World Heritage Site was due to lack of clear lantana control objectives resulting into the lack of follow-up and localised clearing efforts which left several other thickets of lantana which continued to serve as seed sources for further re-inavsion. This study has established that some of the pathways for vegetation recovery in cleared riparian areas are the seed bank if the lantana infestation is brought under control, augmented by seed rain into degraded riparian forest habitats. When seed has arrived into these areas, availability of suitable micro-sites will influence its establishment and survival. To develop a better understanding of the recruitment dynamics however, more data is required on succession in cleared areas.

Restoring plant species diversity to degraded riparian areas depends on a good understanding of the processes influencing diversity levels and the pathways by which plant species colonize sites (Richter and Stromberg, 2005) and a better understanding of dispersal, seed bank dynamics and recruitment in riparian species would greatly facilitate the planning and execution of restoration activities (Holmes *et al*, 2005).The short duration of this study does not meet the temporal scale at which realistic predictions for the long-term trajectory cleared areas will take in the process of reverting to desired reference conditions can be made.

However in the short-term, this study found that even after heavy lantana invasion, the seed bank and seed rain were diverse enough to initiate community restoration, but that some key riparian species were absent in invaded seed banks entailing need for further intervention to expedite the restoration process by monitoring lantana re-invasion in the cleared areas. The future management strategy of the Victoria Falls ecosystem should depend on recruitment properties of remaining native plants and propagules, as recovery mainly results from bird and mammal species dispersal of seed from surviving plants in the area, soil-stored seed banks, and medium distance wind dispersal (Holmes and Richardson, 1999).

Finally, my work shows the magnitude of the lantana control problem in the Victoria Falls area, including on the steep and inaccessible terrain of the gorges downstream of the waterfalls and the need for sustained follow-up because of the high density of lantana seed in the seed bank and also arriving by seed rain. An effective bio-control strategy would really be the best answer in combination with continued clearing using mechanical and chemical methods as necessary, contributing towards a long-lasting solution to the lantana invasion in the Victoria Falls World Heritage Site.

REFERENCES

Abell, T. 1972. The eradication/control of *Lantana camara* in plantations. Division of Forest Research Final Report No 2P/6/3 Mimeo. 16pp

Abell, T. 1973. The value of herbicides to Forestry in Zambia: a survey of work to date by the Research Division. Zambia Forest Department. Newsletter 128:43-45

Achhireddy, N. R. and Singh, M. 1984. Allelopathic effects of lantana (*Lantana camara*) on milkweed vine (*Morrenia odorata*). Weed Science 32: 757-761

Adair, R., and Groves, R. 1998. Impact of Environmental Weeds on Biodiversity: A Review and Development of a Methodology. Environment Australia, Canberra

Alcova, P. A. 1987. The effects of the presence of *Lantana camara* on local bird populations in Brisbane Forest Park. Project Report No T (AS) 99. Queensland University of Technology, Brisbane.

Anderson, P. E. 1963. Lantana eradication by manual means. Rhodesian Agricultural Journal. 60:95-96

Andersson, E., Nilsson, C and Johansson, M. E. 2000. Plant dispersal in boreal rivers and its relation to the diversity of riparian flora. Journal of Biogeography 27:1095-1106

Anon, 2007. Working for Water Programme Strategic Plan 2008 – 2012. The Working for Water Programme, Department of Water Affairs and Forestry, 15 pp.

Arevalo, J. R and Fernandez-Palacios, J. M. 2000. Seed bank analysis of trees in two stands of the Tenerife Laurel Forest (Canary Islands). Journal of Vegetation Science 9: 297-306

Argaw, M., Teketay, D. and Olsson, M. 1999. Soil seed flora, germination and regeneration pattern of woody species in an Acacia woodland of the Rift Valley in Ethiopia. Journal of Arid Environments 43:411-435

Baker, H. G. 1989. Some aspects of the natural history of seed banks. In: Ecology of Soil Seed Banks. Leck, M. A. A., Parker, V. A., and Simpson, R. L (Eds.). Academic Press, San Diego.

Beater, M. M. T., Garner, R. D., and Witkowski, E. T. F. 2008. Impacts of clearing invasive alien plants from 1995 to 2005 on vegetation structure, invasion intensity and ground cover in a temperate to subtropical riparian ecosystem. South African Journal of Botany 74: 495 – 507

Bellingham, P. J., Peltzer, D. A., and Walker, L, R. 2005. Contrasting impacts of a native and an invasive exotic shrub on flood-plain succession. Journal of Vegetation Science 16: 135 – 142.

Bisht, R. S. and Bhatnagar. 1979. Some insects, mammals and birds feeding on *Lantana camara* Linn. in Kumaon. Indian Journal of Entomology 41:196-197

Bjerknes, A., Totland, O., Hegland, S. J., Nielsen, A. 2007. Do alien plant invasions really affect pollination success in native plant species? Biological Conservation 138: 1-12

Bonvissuto, G. L. and Busso, C. A. 2007. Seed rain in and between vegetation patches in arid Patagonia, Argentina. International Journal of Experimental Botany 76: 47-59

Bossuyt, B and Hermy, M. 2004. Seed bank assembly follows vegetation succession in dune slacks. Journal of Vegetation Science 15: 449-456

Bossuyt, B., Heyn, M., and Hermy, M. 2002. Seed bank and vegetation composition of forest stands of varying age in central Belgium: consequences for regeneration of ancient forest vegetation. Plant Ecology 162: 33-48

Brock, J. H. 1994. *Tamarix* spp. (Salt Cedar), an Invasive Exotic Woody Plant in Arid and Semi-arid Riparian Habitats of Western USA. In: de Waal, L. C., Child, L. E., Wade, P. M. and Brock, J. H (Eds) Ecology and Management of Invasive Riverside Plants, pp 27-45. International Centre of Landscape Ecology, John Wiley & Sons, England

Cao, M., Tang, Y., Sheng, C. Y. and Zhang, J. H. 2000. Viable seeds buried in the tropical forest soils of Xishuangbanna, South west China. Seed Science Research 10: 235-264.

Carlisle, S. M. and Trevors, J. T. 1988. Glyphosate in the environment. Water Air Soil Pollution 39:409-420

Chidumayo. E.N., Lumbwe. F., Mbata. K.J., and Munyandarero*,* J. 2003. Review of baseline status of critical species habitats in the Mosi-oa-tunya National Park and Kafue National Parks, Department of Biological Sciences, UNZA, Lusaka.

Chimbalanga, J., Ndaimani, H., Mudzingwa, R., and Chirinda, G (2005). Alien Invader Plant Species Monitoring and Eradication in the rainforest and Environs-A summer Monitoring Report, Environment Africa, Victoria Falls, Zimbabwe

Cilliers, C. J. 1983. The weed *Lantana camara* L. and the insect natural enemies imported for its biological control into South Africa. Journal of the Entomological Society of Southern Africa 46: 131-136

Clark, J. S., Macklin, E., and Wood. L. 1998. Stages and spatial scales of recruitment limitation in southern Appalachain forests. Ecological Monographs 68:213-235.

Clarke, K. R. 1993. Non parametric multivariate analysis of changes in community structure. Australian Journal of Ecology 18: 117-143

Clarke, K. R., Gorley, R. N. 2000. PRIMERv6: User Manual/Tutorial. PRIMER-E Ltd., Plymouth

Clarke, K. R., Warwick, R. M. 2001. Primer-E Ltd, 6th Edition. Plymouth Marine Laboratory, Prospect Place, Plymouth.

Clemente, A. S., Rego, F. C., Correia, O. A. 2007. Seed bank dynamics of two obligate seeders, *Cistus monspeliensis* and *Rosmarinus oficinalis,* in relation to time since fire. Plant Ecology 190: 175-188.

Clifford, H. T. and Drake, W. E. 1985. Seed dispersal by kangaroos and their relatives. Journal of Tropical Ecology 1: 373-374

Cooney, P. A., Gibbs, D. G., Golinski, K. D. 1982. Evaluation of 'Round up' for control of Bitou bush (*Chrysanthemoides monilifera*). Journal of Soil Conservation Service of New South Wales 38: 6-12

Crone, E., Marler, M and Pearson, D. E. 2009. Non-target effects of broadleaf herbicide on a native perennial forb: a demographic framework for assessing and minimizing impacts. Journal of Applied Ecology 46-673-682

Cronk, Q. C. B and Fuller, J. L. 1995. Plant Invaders; A People and Plants Conservation Manual. Chapman and Hall

Cuda, J. P., Sindelar, B. W. and Cardellina II, J. H. 1989. Proposal for an integrated management system for spotted knapweed (*Centaurea maculosa* lam.). Knapweed Symposium Proceedings EB45. Fay, P. K. and Lacey, J. R. (Eds), pp 197-203. Plant Soil Department and Extension Service, Montana State University, Bozeman

Cummings, J., Reid, N., Davies, J., Grant, C. 2007. Experimental manipulation of restoration barriers in abandoned Eucalypt plantations. Restoration Ecology 15: 156–167.

Daehler, C. C. and Strong, D. R. 1994. Native plant biodiversity versus the introduced invaders; state of the conflict and future management options. In Majumdar, S. K., D' Antonio, C. M. and Vitousek, P. M (Eds). Biological invasions by exotic grasses, the grass/fire cycle, and global change, Annual Review of Ecology, Evolution and Systematics 23: 63-87

D' Antonio, C. M., Hughes, R. F., Mack, M., Hitchcock, D and Vitousek, P. M. 1998. The response of native species to removal of invasive exotic grasses in a seasonally dry Hawaiian woodland, Journal of Vegetation Science 9: 699-712

D' Antonio, C. M and Vitousek, P. M. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annual Review of Ecology and Systematics, Vol 23: 63-87

Dalling, J. W., Muller-Landau, H. C., Wright, S. J. and Hubbell, S. P. 2002. Role of dispersal in the recruitment limitation of neotropical pioneer species. Journal of Ecology 90: 714-727.

Danvind, M. and Nilsson, C. 1997. Seed floating ability and distribution of alpine plants along a northern Swedish river. Journal of Vegetation Science 8 (2): 271-276

Davis, M. A., Grime, J. P., and Thompson, K. 2000. Fluctuating resources in plant communities: a general theory of invasibility, Journal of Ecology 88: 528-534

Day, M.D., Wiley, C. J., Playford, J. and Zalucki, M. P. 2003. Lantana: Current Management, Status and Future Prospects. Australian Centre for International Research: Canberra 2003

Duggin, J. A. and Gentle, C. B. 1988. Experimental evidence on the importance of disturbance intensity for invasion of Lantana camara L. in dry rainforest-open ecotones in north eastern NSW, Australia. Forest Ecology and Management 109: 279-292

Decocq, G., Valentin, B., Toussaint, B., Hendoux, F., Saguez, R. and Bardat, J. 2004. Soil seed bank composition and diversity in a managed temperate deciduous forest. Biodiversity Conservation 13: 2485-2509

De Ferrari, C. M., and Naiman, R. J. 1994. A multi-scale assessment of the occurrence of exotic plants on the Olympic peninsula, Washington. Journal of Vegetation Science 5: 247-258

Dessaint, F., Chadeouf, R. and Barralis, G. 1997. Nine years' soil seed bank and weed vegetation relationships in an arable field without weed control. Journal of Applied Ecology 34: 123-130

Donelan, M., Thompson, K. 1980. Distribution of buried viable seeds along a successional series. Biological Conservation 17: 297-311

Dosch, J. J., Peterson, C. J. and Haines, B. L. 2007. Seed rain during initial colonization of abandoned pastures in the premontane wet forest zone of southern Costa Rica. Journal of Tropical Ecology 23:151-159

Du, X., Qinfeng, G., Xianming, G. and Keping, M. 2007. Seed rain, soil seed bank, seed loss and regeneration of *Castanopsis fargesii* (Fagaceae) in a subtropical evergreen broadleaf forest, Forest Ecology and Management 238: 212-219

ECZ. 2004. Implementation of invasive plant prevention and control programmes in Zambia. Report submitted to the CAB International Africa Regional Centre under the PDF-B phase of the UNEP/GEF Project: Removing Barriers to Invasive Plant Management in Africa (RBIPMA), ECZ, Lusaka, Zambia

ECZ.2007. Environmental Impact Assessment on proposed biological, chemical and mechanical control interventions on invasive alien plant species at the Victoria Falls Pilot Site and other locations in Livingstone

El Azzouzi, M. A., Dahcour, A., Bouhaouss, and Ferhat, M. 1998. Study on the behaviour of imazapyr in two Morrocan soils. Weed Research 38: 217-220

Ellenberg, H. 1988. Vegetation Ecology of Central Europe, Cambridge University Press.

Erasmus, D. J. and Clayton, J. N. G. 1992. Towards costing chemical control of *Lantana camara* L. South African Journal of Plant Soil 9: 206-210

Erasmus, D. J., Maggs, K. A. R., Biggs, H. C. and Zeller, D. A. 1993. Control of *Lantana camara* in the Kruger National Park, South Africa and subsequent vegetation dynamics, Brighton Crop Protection Conference-Weeds-1993

Extoxnet. 1996. Glyphosate. Pesticide information profiles. Extension Technology Network. http://ace.orst.edu/info/extoxnet. Accessed 12.09.2010

Fanshawe, D.B. 1975. The Flora. In: Philipson, D.W (Ed) Mosi-oa-Tunya: A Handbook to the Victoria Falls Region, Longman Publishers, Zimbabwe.

Feng, J. C and Thompson, D. G. 1990. Fate of glyphosate in a Canadian forest watershed: 2. Persistence in fliage and soils. Journal of Agricultural Food Chemistry 38: 1118-1125.

Fenner, M. 1985. Seed Ecology. Chapman and Hall, New York

Fenner, M. 1993. Seed Ecology. Reprinted. Chapman and Hall, London. pp 57-71

Fenner, M and Thompson, K. 2005. The Ecology of Seeds. Cambridge University Press, 260 pp

Fensham, R. J., Fairfax, R. J., Carnell, R. J. 1994. The invasion of *Lantana camara* L. in Forty Mile Scrub National Park, north Queensland. Australian Journal of Ecology 19: 237-305

Finegan, B. 1996. Pattern and process in neotropical secondary rain forests: the first 100 years of succession. Trends in Ecology and Evolution 11:119-124

Fisher, J. L., Lonegran, W. A., Dixon, K., Delaney and Veneklaas, E. J. 2009. Altered vegetation structure and composition linked to fire frequency and plant invasion in a biodiverse woodland. Biological Conservation 142: 2270-228

Fourie, S. 2008. Composition of the soil seed bank in alien invaded grassy fynbos: potential for recovery after clearing. South African Journal of Botany 74: 445-553

French, K and Buckley, S. 1998. The effects of the herbicide metsulfron methyl on litter invertebrate communities in a coastal dune invaded by *Chrysanthemoides monilifera* ssp Rotundata. Weed Research 48: 266-272

Galatowitsch, S. M., Richardson, D. M. 2005. Riparian scrub recovery after clearing of invasive alien trees in headwater streams of the Western Cape. Biological Conservation 122: 509-521

Gashaw, M., Michelsen, A., Jensen, A., and Friis, I. 2002. Soil seed bank dynamics of fire prone wooded grassland, woodland and dry forest ecosystems in Ethiopia. Nordic Journal of Botany. 22:5-17

Gentle, C. B and Duggin, J. A. 1997a. Allelopathy as a competitive strategy in persistent thickets of *Lantana camara* L. in three Australian forest communities. Plant Ecology 132: 85-95.

Gentle, C. B. and J. A. Duggin. 1997b. *Lantana camara* L invasions in dry rainforest-open forest ecotones: The role of disturbances associated with fire and cattle grazing. Australian Journal of Ecology 22: 298-306.

Gentle, C. B. and Duggin, J. C. 1998. Interference of *Choricarpia leptopetala* by *Lantana camara* with nutrient enrichment in mesic forests of the Central Coast of New South Wales, Plant Ecology 136: 205-211

Gooden, B., French, K. and Turner, P. J. 2009. Invasion and management of a woody plant, *Lantana camara* L., alters vegetation diversity within wet sclerophyll forest in southeastern Australia, Forest Ecology and Management 257: 960-967

Goodson, J.M., Gurnell, A.M., Angold, P.G., Morrisey, I.P. 2001. Riparian seed banks: Structure, process and implications for riparian management. Progress in Physical Geography 25: 301-325

Graaff, J. L. 1986. *Lantana camara*, the plant and some methods for its control, South African Forestry Journal 136: 26-30

Graaff, J. L. 1987. The seedfly *Ophiomyia lantanae* and other factors responsible for reducing germination in *Lantana camara* forms found in Natal. South African Journal of Botany 53: 104-107

Greene, D. F. and Johnson, E. A. 1996. Wind dispersal of seeds from a forest into a clearing. Ecology 77: 595-609

Grossbard, E. 1972. Do herbicides affect the micro-organisms in soil? Weed Research Organisation 45: 1-63

Groves, R. H. 1989. Ecological control of invasive terrestrial plants. In: Drake, J., Mooney, H. A., di Castri, F, Groves, R., Kruger, F., Rejmanek, M., Williamson, M. (Eds). Biological Invasions: A Global Perspective. John Wiley and Sons, Chichester, pp 215-255

Gurevitch, J. and Padilla, D. K. 2004. Are invasive species a major cause of extinctions? Trends in Ecology and Evolution 19: 470-474.

Gurnell, A. M. 1995. Vegetation along river corridors: hydrogeomorphological interactions. In: Gurnell, A. M. and Petts, G. E. (Eds) Changing river channels. Chichester: John Wiley and Sons: 237-260

Hannan-Jones, M.A. 1998. The seasonal response of *Lantana camara* to selected herbicides. Weed Research 38: 413–423

Harper, J. L. 1977. Population Biology of Plants. Academic Press, New York.

Harris, P. and Cranston, R. 1979. An economic evaluation of control methods for diffuse and spotted knapweed in Western Canada. Canadian Journal of Plant Science 59: 375-382

Henderson, C. B., Petersen, K. E. and Redak, R. A. 1988. Spatial and temporal patterns in the seed bank and vegetation of a desert grassland community. Journal of Ecology 76: 717-728

Henderson, M., Fourie D.M.C., Wells, M. I. and Henderson, L. 1987. Declared Weeds and Alien Plants in South Africa.

Hitchmough, J. D., Kilgour, R. A., Morgan, J. W. and Shears, L. G. 1994. Efficacy of some grass specific herbicides in controlling exotic grass seedlings in native grassy vegetation. Plant Protection Quarterly 9:28-34

Hobbs, R. J. and Humphries, S. E. 1995. An integrated approach to the ecology and management of plant invasions. Conservation Biology 9: 761-770

Holmes, P. M. 1990. Vertical movement of soil stored seeds at a sand plain fynbos site. South African Journal of Ecology 1: 8-11

Holmes, P. M. 2001. Shrubland Restoration Following Woody Alien Infestation and Mining: Effects of Topsoil depth, Seed Source, and Fertilizer Addition. Restoration Ecology 9: 71-84

Holmes, P. M. 2002. Depth distribution and composition of seed-banks in alien invaded and uninvaded fynbos vegetation. Austral Ecology 27: 110-120

Holmes, P. M. and Cowling, R. M. 1997. Diversity, composition and guild structure relationships between soil-stored seed banks and mature vegetation in alien plant invaded South African fynbos shrublands. Plant Ecology 133: 107-122

Holmes, P. M., and Marais, C. 2000. Impacts of alien plant control on vegetation in the mountain catchments of the Western Cape. Southern African Forestry Journal 189: 113-117

Holmes, P. M and Moll, E. J. 1990. Effect of depth and duration of burial on alien *Acacia saligna* and *Acacia cyclops* seeds. South African Journal of Ecology 1: 12-17

Holmes, P. M., and Newton, R. J. 2004. Patterns of seed persistence in South African fynbos. Plant Ecology 172: 143-158

Holmes, P. M. and Richardson, D. M. 1999. Protocols for restoration based on recruitment dynamics, community structure and ecosystem function: Perspectives from South African fynbos. Restoration Ecology 7: 215-230

Holmes, P. M., Richardson, D. M., Esler K. J., Witowski, E. T. F., Fourie, S. 2005. A decision-making framework for restoring riparian zones degraded by invasive alien plants in South Africa. South Africa Journal of Science 101: 553-564.

Holmes, P. M., Richardson, D. M., Esler, K. J., and Witkowski, E. T. F. 2008. Guidelines for improved management of riparian zones invaded by alien plants in South Africa. South African Journal of Science 101:553 – 564.

Hopfensperger, K.N. 2007. A review of similarity between seed bank and standing vegetation across ecosystems. Oikos 116: 1438-1448

Hood, W. G., Naiman, R. J. 2000. Vulnerability of riparian zones to invasion by exotic vascular plants. Plant Ecology 148: 105-114.

Howard, R. A. 1969. A checklist of cultivar names used in the genus lantana. Arnoldia 29: 73-109

Howe, H. F. and Smallwood, J. 1982. Ecology of seed dispersal. Annual Review of Ecology and Systematics 13: 201-228

Hubbell, S. P., Foster, R. B., O'Brien, S. T., Harms, K. E., Condit, R., Wechsler, B., Wright, S. J. and Loo de Lao, S. 1999. Light-gap disturbances, recruitment limitation, and tree diversity in a neo-tropical forest. Science 283: 554-557

Hyatt, L. A. and Casper, B. B. 2000. Seed bank formation during early secondary succession in a temperate deciduous forest. Journal of Ecology 88: 516-527

Imbert, E. and Lefevre, F. 2003. Dispersal and gene flow of *Populus nigra* (Salicacea) along a dynamic river system. Journal of Ecology 91: 447-456

Johansson, M. E, Nilsson, C and Nilsson, E. 1996. Do rivers function as corridors for plant dispersal? Journal of Vegetation Science 7: 593-598

Kebrom, T and Tesfaye, B. 2000. The Role of Soil Seed banks in the Rehabilitation of Degraded Hillslopes in Southern Wello, Ethiopia. BIOTROPICA 32 (1): 23-32

Khoshoo, T. N. and C. Mahal. 1967. Versatile reproduction in *Lantana camara*. Current Science 8: 200-203.

Killilea, D.M. 1983a. Chemical control of *Lantana camara* L. 1. Application of Chemicals to cut stem. Zimbabwe Journal of Agricultural Research 21: 51–57.

Killilea, D.M. 1983b. Chemical control of *Lantana camara* L. 2. Foliar spray applications of various arboricides. Zimbabwe Journal of Agricultural Research 21: 59–67.

Kobe, R. K. and Vriesendorp, C. F. 2009. Size of sampling unit strongly influences detection of seedling limitation in a wet tropical forest. Ecology Letters 12: 220-228

Kohler, G. E., Tets, I. V. and Whelan, R. J. 1995. Effects of herbicide spraying on native flora and fauna: Bitou bush control study-Hawks Nest, New South Wales. Report prepared for the Biological and Chemical Research Institute, New South Wales

Kolb, S. R. 1993. Islands of secondary vegetation in degraded pasture of Brazil: their role in re-establishing Atlantic coastal forest. Ph.D. dissertation. University of Georgia, Athens.

Lake, J. C. and Leishman, M. R. 2004. Invasion success of exotic plants in natural ecosystems: the role of disturbance, plant attributes and freedom from herbivores. Biological Conservation 117: 215-226

Lamb, D. 1991. Forest regeneration research for reserve management: some questions deserving answers. In: Tropical Rainforest Research in Australia: Present Status and Future directions for the Institute for Tropical Rainforest Studies. Goudberg, N., Bonell, M. and D. Benzaken (Eds.). Institute for Tropical Rainforest Studies, Townsville, Australia, pp 177-181

Lautenschlager, R. A and Sullivan, T. P. 2002. Effects of herbicide treatments on biotic components in regenerating northern forests. The Forestry Chronicle 78: 695-731

Layton, P. A., Guynn, S. T. and Guynn, D. C. Jr. 2003. Wildlife and biodiversity metrics in forest certification systems. National Council for Air and Stream Improvement Technical Bulletin No. 857, Research Triangle Park, North Carolina, USA.

Leck, M. A. 1989. Wetland seed banks. In: Leck, M. A., Parker, V. T. and Simpson R. L., (Eds.), Ecology of soil seed banks. San Diego, California. Academic Press, pp. 283-305

Leck, M. A. and Schutz, W. 2005. Regeneration of Cyperaceae, with particular reference to seed ecology and seed banks. Perspectives in Plant Ecology, Evolution and Systematics 7: 95-133

Leck, M. A. and Simpson, R. L. 1987. Seed bank of a freshwater tidal wetland-turnover and relationship to vegetation change. American Journal of Botany. 74: 360-370

Leishman, M. R. and Westoby, M. 1994. The role of large seed size in shaded conditions: experimental evidence. Functional Ecology 8: 205-214

Leishman, M. R. and Westoby, M. 1998. Seed size and shape are not related to persistence in soil in Australia in the same way as in Britain. Functional Ecology 12: 480-485.

Le Maitre, D. C., Van Wilgen, B. W., Gelderblom, C. M., Bailey, C., Chapman, R. A., Nel, J. A. 2002. Invasive alien species trees and water resources in South Africa. South African Journal of Botany 74:526-537.

Lindsay, E. A. and French, K. 2004. *Chrysanthemoides monilifera* ssp *rotundata* alters decomposition rates in coastal areas of south-eastern Australia. Forest Ecology and Management 198: 387-399

Lonsdale, W. M. 1999. Global patterns of plant invasion and the concept of invasibility. Ecology 80 (5): 1522-1536

Lottyniemi, K. 1982. Evaluation of the use of insects for biological control of *Lantana camara* (Verbenaceae) in Zambia. Tropical Pest Management, 28: 14-19

Love, A., Babu, S., and Babu, C. R. 2009. Management of Lantana, an invasive alien weed, in forest ecosystems of India. Current Science 97:10

Luken, J. O., Beiting, S. W., and Kumler, R. L. 1993. Target/Non Target effects of herbicides in power-line corridor vegetation, Journal of Aboriculture 19 (5)

Luzuriaga, A. L., Escudero, Olano, J. M. and Loidi, J. 2005. Regenerative role of seed banks following an intense soil disturbance. Acta Oecolgica 27: 57-66

Lwando-Tembo, C. 2008. An investigation into the role of allelopathy in influencing plant diversity around *Lantana camara* groves. MSc thesis, University of Zambia, Lusaka.

Macdonald, I. A. W. and Frame, G. W. The invasion of introduced species into nature reserves in tropical savannas and dry woodlands. Biological Conservation 44: 67-93.

Macdonald, I. A. W. and Jarman, M. L. 1985. Invasive alien plants in the terrestrial ecosystems of Natal, South Africa. South African National Scientific Programmes Report No 118

Macdonald, I., Loope, L., Usher, M and Hamann, O. 1989. Wildlife conservation and the invasion of nature reserves by introduced species: a global perspective. In: Drake, J., Mooney, H. A., di Castri, F, Groves, R., Kruger, F., Rejmanek, M., Williamson, M. (Eds). 1989. Biological Invasions: A Global Perspective. John Wiley and Sons, Chichester, pp 215-255

Mack, M. C. and D' Antonio, C. M. 1998. Impacts of biological invasions on disturbance regimes. Trends in Ecology and Evolution 13: 195-198

Mack, R., Landsdale, W. M., Evans, H., Clout, M., and Bazzaz, F. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. Ecological Applications 10: 689-710

Marrs, R. H. 1984. The use of herbicides for nature conservation. Aspects of Applied Biology 5: 265-274

Marrs, R. H. 1985. The effects of potential bracken and scrub control herbicides on lowland *Calluna* and grass heath communities in East Anglia, UK. Biological Conservation. 32: 13-32

Masocha, M. and Ndaimani, H. 2010. Mapping of the priority Invasive Alien Plant Species in the Victoria Falls/Mosi-oa-Tunya Pilot Site, Harare, Zimbabwe

Mason, T. J. and French, K. 2007. Management regimes for a plant invader differentially impact resident communities. Biological Conservation 136: 246-259

Matarczyk, J. A., Willis, A. J., Vranjic, J. A. and Ash, E. 2002. Herbicides, weeds and endangered species: management of bitou bush (*Chrysanthemoides monilifera* ssp. Rotundata) with glyphosate and impacts of the endangered shrub, Pimelea spicata. Biological Conservation 108: 133-141

Mendoza, I., Gomez-Aparicio, L., Zamoa, R. and Matias, L. 2009. Recruitment limitation of forest communities in a degraded Mediterraneaen landscape. Journal of Vegetation Science 20: 367-376.

Meynell, P. J., N. Nalumino and L. Sola (Eds). 1996. Strategic Environmental Assessment of Developments around Victoria Falls, IUCN-ROSA, Harare, Zimbabwe. 3 Volumes.

Miller, K. V. and Miller, J. H. 2004. Forestry herbicide influences on biodiversity and wildlife habitat in southern forests. Wildlife Society Bulletin 32: 1049-1060

Miller, K. V. and Witt, J. S. 1990. Impacts of forestry herbicides on wildlife. Pages 795-800. In: Coleman, S. S. and Neary, D. G (eds). Proceedings of the sixth biennial southern silvicultural research conference. United States Department of Agriculture Forest Service General Technical Report SE-70, Washington, D. C., USA

Milton, S. J., and Hall, A. V. 1981. Reproductive biology of Australian acacias in the southwestern Cape Province, South Africa. Transactions of the Royal Society of South Africa 44: 465-487.

Mohan Ram, H. Y. and Mathur, G. 1984. Flower colour changes in *Lantana camara*. Journal of Experimental Botany 35: 1656-1662.

Morris, T. L., Witkowski, E. T. F., and Coetzee, A. J. 2008. Initial response of riparian plant community structure to clearing of invasive alien plants in Kruger National Park, South Africa. South African Journal of Botany 74: 485-494

Morrison, M. L. and Meslow, E. C. 1983. Impacts of forest herbicides on wildlife; toxicity and habitat alteration. Transactions of the North American Wildlife and Natural Resources Conference 48: 17

Morton, J. F. 1994. Lantana, or red sage (*Lantana camara* L. [Verbanaceae]), Noxious Weed and Popular Garden Flower; Some Cases of Poisoning in Florida. Economic Botany 48(3): 259–270.

Motooka, P. 2000. Summaries of Herbicide Trials for Pasture, Range and Non Cropland Weed Control, College of Tropical Agriculture and Human Resources, University of Hawaiʻi at Manoā.

Motooka, P., Ching, L., and Nagai, G. 2002. Herbicidal Weed Control Methods for Pastures and Natural Areas of Hawaii, Cooperative Extension Sevice, College of Tropical Agriculture and Human Resources, University of Hawaiʻi at Manoā

Motooka, P., Ching, L. and Nagai, G. 1991. Mesulfuron efficacy on *Lantana camara* with different surfactants. *In*: Proceedings of the Combined 14th Asian-Pacific and 10th Australian Weed Science Society Conference, Brisbane, Australia: 303–307

Murray, K. K. 1988. Avian seed dispersal of three neotropical gap dependant plants. Ecological Monographs 58: 271-298

Naiman, R. J and Decamps, H (1997). The ecology of interfaces: Riparian zones. Annual Review of Ecology and Systematics 28: 621-658.

Naiman, R. J., Decamps H and Pollok, M. 1993. The role of riparian corridors in maintaining regional biodiversity. Ecological Applications 3: 209-212

Nakagoshi, N. 1984. Buried viable seed populations in forest communities of the Hiba Mountains, southwestern Japan. Journal of Science, Hiroshima University Series B, Division 2, 19: 1-56.

Nakagoshi, N. 1985. Buried viable seed in temperate forests. In White, J., (Ed.). The population structure of vegetation, Dordrecht, Junk, pp. 551-570

Nalumino, N. (1997). Physical Resources and Landscapes of the Musi-oa-Tunya National Park, Livingstone. 44 pp

Nathan, R. and Muller-Landau, H. C. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. TREE 15:7

Natural Heritage Trust (NHT). 2003. Lantana-*Lantana camara*. CRC Weed Management Guide. Australia

Natural Heritage Trust. 2004. Current management and control options for lantana (*Lantana camara* in Australia. NHT, Australia

Nepstad, D. C., Uhl, C., Pereira, C. A., and Cardoso da Silva. 1996. A comparative study of tree establishment in abandoned pasture and mature forest of eastern Amazonia. Oikos 76: 25-39

Newton, M. et al. 1984. Fate of glyphosate in an Oregon forest ecosystem. 32:1144-1151

NHCC (1992). Rehabilitation of the Victoria Falls: Annual Report 1992. Livingstone, Zambia.

NHCC (1993). Rehabilitation of the Victoria Falls: Natural Heritage Management Bulletin. Issue No. 1.

NHCC. 2008. Conservation Status Report for the Victoria Falls World Heritage Site, Livingstone, Zambia.

Norris, R. F. 1982. Action and fate of adjuvants in plants. In Adjuvants for Herbicides, WSSA, Champaign, Illinois, pp 68-83

Parr, J. F and Norman, A. G. 1965. Considerations in the use of surfactants in plant systems: A review. Botanical Gazette 126(2): 86-96

Parsons, W. T. and Cuthbertson E. G. 2001. Common lantana. In: Noxious Weeds of Australia, CSIRO Publishing, Melbourne: 627-632

Peoples, T. R. 1984. Arsenal herbicide (AC 253, 925): a development overview. Proceedings of the Southern Weed Science Society. 37: 378-387

Phiri, P. S. M. 2005. A checklist of Zambian vascular plants, SABONET Report No. 32, SABONET, Pretoria

Pimentel, D., Lach, L., Zuniga, R., and Morrison, D. (2000). Environmental and economic costs of non-indigenous species in the United States. BioScience 50: 53-65

Pimentel, D., R. Zuniga, and D. Morrison. 2005. Update on the environmental and economic costs associated with alien invasive species in the United States. Ecological Economics 52:273–288.

Planty-Tabacchi, A. M., Tabacchi, E., Naiman, R. J.,De Ferrari, C., Decamps, H., 1996. Invasibility of species rich communities in riparian zones. Conservation Biology 10: 598-607

Poiani, K. A. and Johnson, W. C. 1989. Effect of hydroperiod on seed bank composition in semi permanent Praire wetlands. Canadian Journal of Botany 67: 856-864.

Prins, N., Holmes, P. M., and Richardson, D. M. 2005. A reference framework for the restoration of riparian vegetation in the Western Cape, South Africa, degraded by invasive Australian Acacias. South African Journal of Botany 70: 767-776

Prinsloo, F. W., and Scott, D. F. 1999. Streamflow responses to the clearing of alien invasive trees from riparian zones at three sites in the Western Cape Province. South African Forestry Journal 185: 1-7.

Pysek, P and Prach, K. How important are rivers for supporting plant invasions? Pp. 23-31. In: de Waal, L., Child, L. E., Wade, P. M., and Brock, J. H. (Eds). Ecology and Management of invasive riverside plants. John Wiley and Sons, Chichester

RBIPMA. 2008. Semi Annual Report for 2008. Environmental Council of Zambia, Lusaka.

Rice, P. M., Toney, C. J., Bedunah, D. J., and Carlson, C. E. 1997. Plant community diversity and growth form responses to herbicide applications for control of *Centaurea maculosa*. Journal of Applied Ecology 34: 1397-1412

Richardson, D. M., Holmes, P. M., Esler, K. J., Galatowitsch, S. M., Stromberg, J. C., Kirkman, S. P., Pysek, P. and Hobbs, R. J. 2007. Riparian vegetation: degradation, alien plant invasions and restoration prospects. Diversity and Distributions 13:126-139

Richardson, D. M., Macdonald, I. A. W., Hoffman, J. H. and I. Henderson. 1989. Alien Plant Invasions. In: Biological Invasions: a Global Perspective, J. Drake (Ed), John Wiley and Sons Ltd

Richardson, D. M., van Wilgen, B. W. 2004. Invasive alien plants in South Africa: how well do we understand the ecological impacts? South African Journal of Science 100: 45-52

Richter, R., Stromberg, J. C. 2005. Soil seed bank of two montane riparian areas: Implications for restoration. Biodiversity and conservation 14: 993-1016

Rico-Gray, V., and Garcia-Franco, J. G. 1992. Vegetation and soil seed bank of successional stages in tropical lowland deciduous forest. Journal of Vegetation Science 3: 617-624.

Rinella, M. J., Maxwell, B. D., Fay, P. K., Weaver, T., and Sheley, R. L. 2009. Control effort exacerbates invasive-species problem. Ecological Applications 19 (1) pp 155-162

Roberts, H. A. 1981. Seed banks in soils. Advances in Applied Biology 6: 1-56

Rosgen, D. I. 1994. A classification of natural rivers. Catena. 22: 169-199

Sahu, A. K. and Panda, S. 1998. Population dynamics of a few dominant plant species around industrial complexes, in West Bengal, India. Bombay Natural History Society Journal 95: 15-18.

Sakai, A., Sato, S., Sakai, T., Kuramoto, S., Tabuchi, R. 2005. A soil seed bank in a mature conifer plantantion and establishment of seedlings after clear-cutting in southwest Japan. Journal of Forest Research 10: 295-304

Selander, J. and Chomba, B. M. 1989. Control of *Lantana camara* in Forest Plantations. Forest Department, Division of Forest Research, Kitwe, Zambia.

Shalwindi, F.K.M. (2000). Vegetation of the Victoria Falls Area-A Brief for the Victoria Falls Field Museum, NHCC, Livingstone.

Sharma, O. P., Makkar, H. P. S. and R. K. Dawra. 1988. A review of the noxious plant *Lantana camara*. Toxicon 26: 975-987

Sharma, G.P., Singh, J. S and Raghubanshi, A. S. (2005). Plant Invasions: emerging trends and future implications. Current Science 88:5.

Sheley, R. L., Mangold, J. M. and Anderson, J. L. 2006. Potential for successional theory to guide restoration of invasive plant dominated rangeland. Ecological Monographs 76: 365-379

Shono, K., Davies, S. J. and Kheng, C. Y. 2006. Regeneration of native plant species in restored forests on degraded lands in Singapore. Forest Ecology and Management 237: 574-582

Smith, R. G., Maxwell, B. D., Menalled, F. D. and Rew, L. J. 2006. Lessons from agriculture may improve the management of invasive plants in wildland systems. Frontiers in Ecology and the Environment. 4: 428-434

Smith, L. S. and Smith, D. A. 1982. The naturalised *Lantana camara* complex in Eastern Australia. Queensland Botany Bulletin 1: 1-26

Spies, J. J. 1983-84. Hybridization potential of *Lantana camara* (Verbeneceae) from South Africa. South African Journal of Botany 3: 231-250

State of Conservation Report, 2010. Periodic Report to UNESCO and the World Heritage Committee on the conservation status of the Victoria Falls World Heritage Site produced by Zambia and Zimbabwe.

Stirton, C. H. 1977. Some thoughts on the polyploidy complex *Lantana camara* L. Verbanaceae. In: Proceedings of the Second National Weeds Conference of South Africa, Stellenbosch, South Africa: 321 - 340

Stock, D. H., Wild, C. H. 2002. The capacity of Lantana (*Lantana camara* L.) to displace native vegetation. In: 13th Australian Weeds Conference-papers and proceedings: (Eds Spafford-Jacob, E., Dodd, J., and Moore, J. H) pp 104-107. Plant Protection Society of WA Inc. (Perth, WA).

Stock, D. 2005. The dynamics of *Lantana camara* (L.) invasion of subtropical rainforest in southeast Queensland. Ph. D. Thesis, School of Environmental and Applied Sciences, Griffith University, Australia

Stoner, K. E. and Henry, M. undated. Seed dispersal and frugivory in tropical ecosytems. International Commission on Tropical Biology and Natural Resources. http://www.eolss.net/ebooks . Accessed 04.12.10

Sullivan, T. P and Sullivan, D. S. 2003. Vegetation managament and ecosystem disturbance: impact of glyphosate herbicide on plant and animal diversity in terrestrial systems. Environmental Review 11: 37-59

Swarbick, J. T., Wilson, B.W., Hannan-Jones, M. A. 1995. The biology of Australian Weeds 25. *Lantana camara* L. Plant Protection Quarterly 10: 82-95.

Swarbick, J. T., Willson, B.W., Hannan-Jones, M. A. 1998. *Lantana camara* L. In: Panetta, F. D., Groves, R. H., and Shepherd, R. C. H. (Eds). The Biology of Australian Weeds, Melbourne, pp. 119-140

Tatum, V. L. 2004. Toxicity, transport, and fate of forest herbicides. Wildlife Society Bulletin 32: 1042-1048.

Technical Service Suppliers. 2008. Cost of chemicals for lantana control. Lusaka, Zambia.

Thomas, S. E. and Ellison, C. A. 1999. A Century of Classical Biological Control of *Lantana camara*: Can Pathogens Make a Significant Difference? In: Spencer, N. R. (Ed) Proceedings of the X International Symposium on Biological Control of Weeds, Montana State University, Bozeman, Montana USA, pp 97-104

Thompson, K. 1978. The occurrence of buried viable seeds in relation to environmental gradients. Journal of Biogeography 5: 424-430.

Thompson, K. 1987. Seed and seed banks. New Phytologist. 106:1, Frontiers of Comparative Plant Ecology, pp 23-24.

Thompson, K. 1992. The functional ecology of seed banks. In Fenner, M., (Ed). Seeds, the ecology of regeneration in plant communities, Wallingford, CAB International, pp. 231-258.

Thompson, K. 1993. Seed persistence in soil. In: Hendry, G. A. F., Grime, J. P., (Eds.) Methods in comparative plant ecology. London, Chapman and Hall, pp. 199-202.

Thompson, K., Band, S. R. and Hodgson, J. G. 1993. Seed size and shape predict persistence in soil. Functional Ecology 7: 236-241

Thompson, K., Bakker, J. P., Bekker, R. M. and Hodgson, J. G. 1998. Ecological correlates of seed persistence in soil in north-west European flora. Journal of Ecology 86: 163-169

Thompson, K., and Grime, J. P. 1979. Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. Journal of Ecology 67: 893-921

Tickner, D. P., Angold, P. G., Gurnell, M. A., and Owen Mountford J. 2001. Riparian plant invasions: Hydrogeomorphological control and ecological impacts, Progress in Physical Geography 25 (1): 22-52

Tilman, D. 1987. On the meaning of competition and the mechanisms of competitive superiority. Functional Ecology 1: 304-315.

Toth, J. M., Milham, P. J., and Meszaros, I. 1993. Herbicide control of bitou bush In: Proceedings of a National Workshop on *Chrysanthemoides monilifera*, Port Maquarie, pp 39-42

Tu, M., Hurd, C and Randall, J. M. 2001. Weed Control Methods Handbook, The Nature Conservancy, USA.

Turner, P. J., Virtue, J. G. 2006. An eight year removal experiment measuring the impact of bridal creeper (*Asparagus asparagoides* (L.) Druce) and the potential benefit from its control. Plant Protection Quarterly 21: 79-84.

United Nations Environmental Programme (2004). Project on Removing Barriers to Invasive Plant Management in Africa. Environmental Council of Zambia, Lusaka

van der Valk, A. G., Pederson, R. L. 1989. Seed Banks and the Management and Restoration of Natural Vegetation. In Leck, M. A., Parker, T. V., Simpson, R. L. (Eds.) Ecology of Soil Seed Banks. Academic Press Inc. San Diego. pp 329-363.

Van Wilgen, B.W., Richardson, D and Higgins, S. 2001. Land Use and Water Resources Research 1(5): 1-6

Van Wilgen, B. W., Richardson, D. M., Le Maitre, D. C., Marais, C., and Magadlela, D. 2001. The economic consequences of alien plant invasions: examples of impacts and approaches to sustainable management in South Africa. Environment, Development and Sustainability 3: 145-168

Vernable, L. D and Brown, J. S. 1988. The selective interactions of dispersal, dormancy and seed size as adaptations for for reducing risk in variable environments. The American Naturalist 131:3

Victoria Falls Trust (1962). Annual Report for the Management of the Victoria Falls Area, Livingstone, Northern Rhodesia.

Vila, M and Weiner, J. 2004. Are invasive plant species better competitors than native plant species? – evidence from pair-wise experiments. Oikos 105:229-238

Vitousek, P. M. 1990. Biological invasions and ecosystem processes: towards an integration of population biology and ecosystem studies. Oikos 57:7-13.

Vitousek, P. M., D' Antonio, C. M., Loope, L. L., Westbrooks, R. 1996. Biological invasions as global environmental change. American Scientist 84: 468-478.

Vosse, S. 2006. The restoration potential of fynbos riparian seed banks following alien clearing. MSc Thesis. Stellenbosch University.

Vosse, S, Richardson, K. J., and Holmes, P. M. 2008. Can riparian seed banks initiate restoration after alien plant invasion? Evidence from the Western Cape, South Africa

Vizantinopoulos, S., and Lolos, P. 1994. Persistence and leaching of the herbicide imazapyr in soil. Bulletin of Environmental Contamination and Toxicology 52: 404-410

Vranjic, J. A., Woods, M. J. and Barnard, J. 2000. Soil mediated effects on germination and seedling growth of coastal wattle (Acacia sophorae) by the environmental weed, bitou brush (*Chrysanthemoides monilifera* ssp *rotundata*). Australian Ecology 25: 445-453

Wadhawani, C. and Bhardwaja, T. N. 1981. Effect of *Lantana camara* L. extract on fern spore germination. Experentia 37 245-246

Wagner, R. G. 1993. Research directions to advance forest vegetation management in North America. Canadian Journal of Forest Research 23: 2317-2327

Walck, J. L., Baskin, J. M. and Baskin, C. C. 1999. Effects of competition from introduced plants on establishment, survival, growth and reproduction of the rare plant *Solidago shortii* (Asteraceae). Biological Conservation 88: 213-219

Wardle, D. A. and Parkinson, D. 1990. Effects of three herbicides on soil microbial biomass and activity. Plant and Soil 122:21-28

Warr, S. J., Thompson, K. and Kent, M. 1993. Seed banks as a neglected area of biogeographic research, a review of literature and sampling techniques. Progress in Physical Geography 17 (3):329-347

Waterhouse, D. F. (Chairman). 1970. Biological control of lantana review. CSIRO, Division of Entomology, Brisbane.

Weiss, P. W., and Noble, I. R. 1984. Status of coastal dune communities invaded by *Chrysanthemoides monilifera*. Australian Journal of Ecology 60: 675-695.

Welling, C. H., Pederson, R. L., van der Valk, A. G. 1988. Recruitment from the seed bank and the development of emergent zonation during drawdown in a praire wetland. Journal of Ecology 76: 483-496.

Wells, M. J. and Stirton, C. H. 1988. *Lantana camara* a poisonous declared weed. Farming in South Africa Weeds. A. 27: 1-4

White, P. S., and Pickett, S. T. A. 1995. Natural disturbance and patch dynamics: an introduction. In White, P. S (Ed). The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, New York, pp 3-13

Whisenant, S, G. 1999. Repairing Damaged Wildlands. Cambridge University Press, Cambridge.

Wildy, E. 2005. Management and Control of Invasive Alien Plants in Kwa-Zulu Natal, Alien Invaders Project, Wildlife and Environmental Society of South Africa, Kwa Zulu Natal, South Africa.

Wilson, R. G., Kerr, E. D., and Nelson, L. A. 1985. Potential for using seed weed content in the soil to predict future weed problems. Weed Science 33: 171-175

Wittenberg, R. and Cock, M. J. W. (eds). 2001. Invasive Alien Species: A Toolkit of Best Prevention and Management Practices. CAB International, Wallingford, Oxon, UK, xii-228

Witkowski, E. T. F. and Garner, R. D. 2000. Seed production, seed bank dynamics, resprouting and long term response to clearing of the alien invasive *Solanum mauritianum* in a temperate to subtropical riparian ecosystem. SA Journal of Botany Vol 74:3: 476-484

Witkowski, E. T. F., and O' Connor, T. G. 1996. Topo-edaphic, floristic and physiognomic gradients of woody plants in a semi-arid African savanna woodland. Vegetatio 124: 9-23.

Witkowski, E. T. F., and Mitchell, D. T. 1987. Variations in soil phosphorous in the fynbos biome, South Africa. Journal of Ecology 75: 1159-1171.

Witkowski, E. T. F. and Wilson, M. 2001. Changes in density, biomass, seed production and soil seed banks of the non native invasive plant, *Chromolaena odorata*, along a 15 year chronosequence. Plant Ecology, 152: 13-27

Yelenik, S., Stock., W. D., and Richardson, D. M. 2004. Ecosystem and community-level impacts of invasive alien *Acacia saligna* in the fynbos vegetation of South Africa. Restoration Ecology 12: 44-51.

Yorks, T. E., Leopold, D. J. and Raynal, D. J. 2000. Vascular plant propagule banks of six eastern hemlock stands in the Catskill mountains of New York. Journal of the Torrey Botanical Society 127:87-93.

Young, K. R. 1985. Deeply buried seeds in a tropical wet forest in Costa Rica. Biotropica 17: 338-386

Young, R. 2007. The Role of Maramba River Lodge in Pilot Site Project (Pers. Comm), Livingstone.

Yurkonis, K. A., Meiners, S. J. and Wachholder, B. E. 2005. Invasion impacts diversity through altered community dynamics. Journal of Ecology 93: 1053-1061.

Zavaleta, E. S. Hobbs, R. J. and Mooney, H. A. 2001. Viewing invasive species removal in a whole ecosystem context. TRENDS in Ecology and Evolution 16:8

Zimmerman, J., Pascarella, J and Aide, M. 2000. Barriers to forest regeneration in an abandoned pasture in Puerto Rico. Restoration Ecology 8: 328 – 338.